Theropoda

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--ORNITHISCHIA
`--+--Herrerasauridae
   |--SAUROPODOMORPHA
   |
   THEROPODA
   |--Eoraptor
   `==Podokesauridae
      `--+--Ceratosauria
         `--Tetanurae
            |==Megalosauroidea
            `--Avetheropoda
               |--Allosauroidea
               |  |--Neovenatoridae
               |  `--Carcharodontosauridae
               `==COELUROSAURIA
                   `--AVES
```

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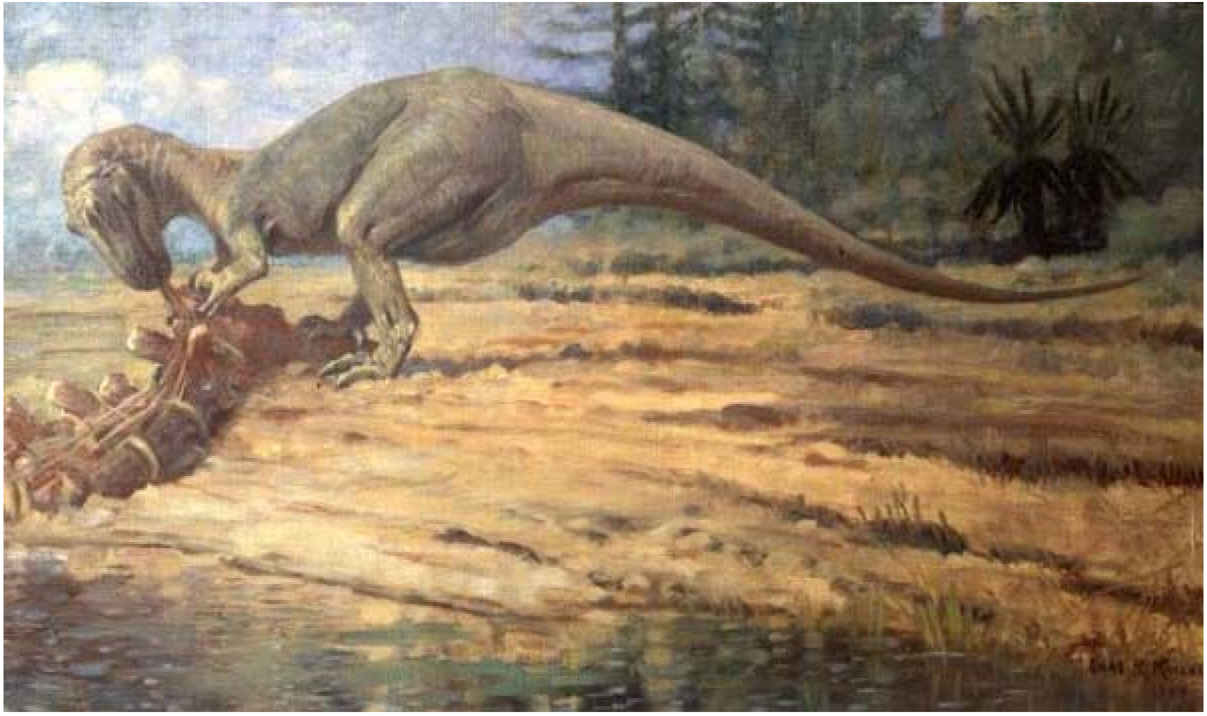

The Jurassic apex predator *Allosaurus*, painting by Charles R Knight
From Copyright Expired, via Wikipedia

Of all the dinosaur types, the theropods are the ones that seem to exert the greatest fascination, perhaps because of their beauty and grace, and the coolness factor inherent in being the largest and most formidable terrestrial preditors the Earth has seen, perhaps due to the fact that even some "smaller" (by dinosaurian standards, by mammalian standards these were still large preditors) ones like *Deinonychus* seemed to be equipped with weaponry out of all proportion to their size, perhaps because more than any other group of prehistoric animals they constuitute a splendid illustration of evolution and transitional forms, constituting a series that began with dinosaurs and culminated in birds, and that, therefore, they are, phylogenetically speaking, the only "dinosaurs" to have survived the end Cretaceous extinction, and not only survived but flourished.

There are books, websites, and blogs devoted solely to theropods (among books, none has been able to top Greg Paul's now sadly out of date *Predatory Dinosaurs of the World*, a book that inspired a generation of paleo geeks with its combination of great readability and beautiful illustrations). It is only proper therefore that we at Palaeos likewise devote a number of pages to these spectacular creatures.

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Theropoda: Overview

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   `--THEROPODA
      |--Herrerasauridae
      `--+--Eoraptor
         `--+--Daemonosaurus
            `--+--Tawa
                `--+--Podokesauridae
                   `--+--Ceratosauria
                       `--Tetanurae
                          `--Avetheropoda
                             |--Carnosauria
                             ==COELUROSAURIA
                               `--AVES
```

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1. Theropoda

The Origin of the Theropods

Saurischia is split into two large lineages, the giant, plant-eating sauropodomorphs and the medium to small-sized theropods. Theropods are the line of mainly carnivorous, bipedal dinosaurs from which birds evolved. They may be defined as all saurischians whose last common ancestor with birds is closer than their last common ancestor with *Apatosaurus*. Or, to use the usual shorthand, birds > brontosaurs. This unit covers only the non-avian theropods. Birds are taken up in later units.

Like the prosauropods and the ornithischians, theropods evolved from lagosuchid ornithodires, perhaps some time in the early or middle Carnian. The most primitive type are the herrerasaurs. From some similar ancestral form, theropods diverged into ceratosaurs and carnosaurs during the later Triassic, allosaurians during the Early Jurassic, and finally more advanced types during the earliest Cretaceous, following the Tithonian mass-extinction. The direct ancestorsof these advanced Cretaceous meat-eating dinosaurs presumably appeared during the Jurassic, but the Jurassic remains attributed to them are mostly isolated teeth, and their actual forms are largely unknown

Most theropods retained the basic bipedal carnivorore form, but still they evolved into a huge diversity of different types, in different shapes and sizes, the most spectacular of all being the birds and bird-dinosaurs. However, as Dr. Tom Holtz points out, "Theropod dinosaurs (bipedal, primarily carnivorous forms) have received widespread attention in recent years owing to their importance in understanding the origin of birds. However, the evolution of theropods was more than a 'bird factory'. Indeed, these dinosaurs represent one of the most successful radiations of terrestrial predators in Earth history." (Holtz 1998, p.1276)

Phylogeny: Two Types Of Theropod Dinosaurs?

Until the 1980's, the theropods were divided according to size. The small, agile forms were called Coelurosaurs ("hollow- tailed saurians"), ancestral to the birds. The large to gigantic predators, such as *Allosaurus*, and *Tyrannosaurus*, were called Carnosaurs ("flesh(-eating) saurians"), which group evolved from early Coelurosaurs.

This clear-cut distinction was upset in the 1960s and 70s by the discovery of unusual medium-sized theropod dinosaurs such as *Deinonychus*. A growing number of paleontologists rediscovered the observation of vonHuene in the 1920's that some carnosaurs, notably *Tyrannosaurus*, were more similar in structure, and hence more closely related to, certain coelurosaurs than they were to other carnosaurs. The term "Carnosaur" is now somewhat disfavored, although it is retained here as meaning the stem group consisting of everything more closely related to *Allosaurus* than to birds. Another, and deeper split in the theropod dinosaurs is the division between primitive forms (Ceratosauria), and more advanced and bird-like forms (Tetanurae). This clasification may also be simplistic, for there are a number of forms, sometimes referred to as "Megalosaurs", which do not fit easily into one or the other of these camps.

The coelurosaurs can still not be arranged with much confidence. The tyrannosauroids and *Compsognathus* are undoubtedly more basal than the other forms, but the exact relationships are not clear. Bear in mind that the Late Jurassic *Archaeopteryx* is a bird. Therefore, the origin of all of the other coelurosaurian groups must have occurred earlier. However, they are little known until the middle of the Cretaceous, so we are dealing with some fairly long "ghost lineages" -- groups of dinosaurs which must have existed, but which have little or no known fossil record.

Giant Theropods

Big is beautiful, at least in the dinosaur world. Time and again, little ancestors evolve into great big descendants. Every line of theropods has its giants; in the late Jurassic period (the time of the great sauropods) no less than four groups - the Ceratosauridae, Megalosauridae, Eustreptospondylidae, and Allosauridae - all included great predators; 10 to 14 metres in length and 3 to 6 tonnes or so in weight (the size of a fully-grown elephant) Packs of these giant meat-eaters were the only creatures big enough and fierce enough to bring down a full-grown sauropod.

During the early to mid Cretaceous there were other similarly sized giant types - the slender Spinosaurs - and several parallel lines of allosauroids - acrocanthosaurs, chilantosaurs, cacharodontosaurs, and bahariasaurs.

And during the late Cretaceous there appeared the bigger tyrannosaurs, the last, among the largest, and certainly most formidable of all the theropods. Yet these evolved not from the giant allosaurs but from small coelurosaur-sized forms. So it seems that the small ancestor evolves into small and large descendants; the large forms rule the Earth for a while and then die out, while the small ones give rise in turn to large and small descendants.

Issues

Since dinosaurs are popular -- almost as popular with scientists as with the public -- they have generated a good many questions. Just a few of the current issues in the literature include:

1. A good deal of attention is being given to the large bird-like forms such as therizinosaurs and oviraptorosaurs because they are hard to fit into the typical cladograms. Are they early birds which have lost the ability to fly? Aberrant dromeosaurs? Something else?

2. When did feathers get started among dinosaurs? Why? But mostly, how?

3. How about flight? Did it evolve from the ground up? From the trees down? How was this related to feathers, and in what order did the adaptations for flight occur?

4. The great cold-blooded vs. warm-blooded debate is still unresolved. Less has been published on the issue in the last few years, but the problem of dinosaur metabolism is still very controversial.

5. Despite the popularity of *Tyrannosaurus*, the evolution of the Tyrannosauridae is just beginning to make sense. A number of other theropod groups are also still rather mysterious, and the theropod cladogram still gets significantly rearranged every year or so. It looks (as of 2002) as though things are beginning to settle down a bit, but many of the Gondwanan dinosaur lineages, particularly torvosauroids, are still rather poorly understood.

6. Although the family tree is beginning to make sense, the biogeography is still confused. Less than ten years ago, most paleontologists believed there was a fairly strict separation between Laurasian and Gondwanan theropods after the Early Cretaceous. The picture now is rather more disorganized. It seems that at least some interchanges occurred between Europe and Africa, and between the Americas.

7. The cause of the end-Cretaceous extinction still unclear. All dinosaurs except birds disappeared in a space of time which may have been practically overnight -- or at least very short compared to the 100 million year history of the dinosaurs as a whole. Almost everyone now admits that a significant factor was a an extraterrestrial object, at least several km in diameter, which hit the Yucatan Penninsula in Mexico about 65 million years ago. However, the selectivity with which the extinctions occurred is puzzling, and other factors may have played a major role.

8. Much attention is being given to theropod biomechanics, particularly walking and jaw movements.

-- ATW & MAK 020308

Descriptions

Theropoda: *Eoraptor*. Neornithes > *Cetiosaurus*. Padian *et al.* (1999).

Range: From Late Triassic.

Phylogeny: Saurischia: Sauropodomorpha + * : Herrerasauridae + (*Eoraptor* + (*Daemonosaurus* + (*Tawa* + (Podokesauridae + (Ceratosauria + Tetanurae)))))

Characters: **$** skull pneumatized; nares formed by premaxilla & nasals, excluding maxilla [CC00]; nasal cavities communicate laterally to large diverticula at antorbital fossa; promaxillary fenestra usually present at anteroventral apex of the antorbital fossa [CC00]; **$** lacrimal extends to top of skull; horns & crests (display?) common; nasals usually unsutured at midline [CC00]; other diverticula invade palate & peri-orbital bones (antorbital diverticula increase in advanced species.); trend to more anterior-facing orbits and increased brain size; opisthotic and exoccipitals always fused; **$** intramandibular joint present; external mandibular fenestra present [CC00]; posterior end of angular usually anterior to articular; long palatine-maxilla suture; some have diverticula from throat through middle ear to

braincase; **$** angular with anterior hook; teeth usually laterally compressed, curved, with 2 serrated edges; normally 23 pre-sacral vertebrae; **$** prominent prong-shaped cervical vertebral epipophyses (lost in some advanced species.); long caudal prezygapophyses; limb bones extensively pneumatized, as are ribs & vertebrae; diverticula may communicate with lungs; **$** strap-like scapula; humerus <50% of femur; **$** metacarpals I-III dorsally pitted (ligament attachments); phalanges of hand elongate; loss or reduction of manus 4 & 5; **$** claws, especially on manus, long curved & sharp; ilia large and blade-like; expanded distal end of pubes ("pubic boot"); astragalus tends to enlarge, calcaneum to be reduced lost; astragalus with pronounced ascending process; metatarsals tend to increase in size relative to femur; pes 1 tends to develop large "raptor" claw; metatarsals II & IV come in contact & metatarsal III reduced (shock-absorbing *arctometatarsalia*); note several adaptations for increased speed. Diversity markedly higher than herbivorous dinosaurs in any given location, but species less localized.

Image: *Eoraptor*: upper sketch by Rob Gray, reproduced by permission. Lower photo from the **Wittmer Lab.**

Links: DinoData: Theropoda; Theropod Dinosaurs; Lectures 19-20: Late Cretaceous; Lecture 19 - Late Jurassic: Solnhofen; GEO212 HOMEPAGE. Dinosaur Paleontology (cranial anatomy); UTCT Image folio: Birds and their Dinosaur Relatives; Theropoda (German); Theropoda (Tree of Life); Theropod - Paleontology and Geology Glossary; FPDM - Theropoda (Index to the excellent Fukui Prefectural Museum pages); Theropoda; Discovery and Classification | Theropoda; THEROPODA (German); ??:????? Theropoda (Japanese); Witmer's Lab Dinosaur Skull Collection- Theropoda (of many good sites, **Best on the Web**); Theropoda List (another Japanese model site); Literature - Theropoda; GEOL 104 Lecture 22- Theropoda I- Dinosaurs red in tooth and claw; National Dinosaur Museum - Theropoda; GEOL 104 Lecture 24- Theropoda III- Raptors, Archaeopteryx, and ...; Nathis Fauna Dinosauria Sauirschia Theropoda (Dutch); Theropoda - families after Paul, 1988; Theropoda (selected synapomorphies).

References: Currie & Zhao (1993); Currie & Carpenter (2000) [CC00]. ATW060214.

Comments: The Theropoda are best known as the clade of carnivorous dinosaurs. They also, through the birds, include the only dinosaurs to survive to the present day. However, outside the Neotheropoda, the status of basal taxa such as the Herrerasauridae and *Eoraptor* as theropods remains contentious. Some analyses place them outside the clade formed by the Theropoda and the Sauropodomorpha, while a few have placed them outside the dinosaurs entirely. These basal taxa are known from the Upper Triassic of North and South America. - CKT110614 Variety of Life - Theropoda

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Theropoda: Basal Theropods

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   `--THEROPODA
      |--Herrerasauridae
      `--+--Eoraptor
         `--+--Daemonosaurus
            `--+--Tawa
                `==Podokesauridae
                     `--+--Ceratosauria
                         `--Tetanurae
                            `--Avetheropoda
                               |--Carnosauria
                               `==COELUROSAURIA
                                   `--AVES
```

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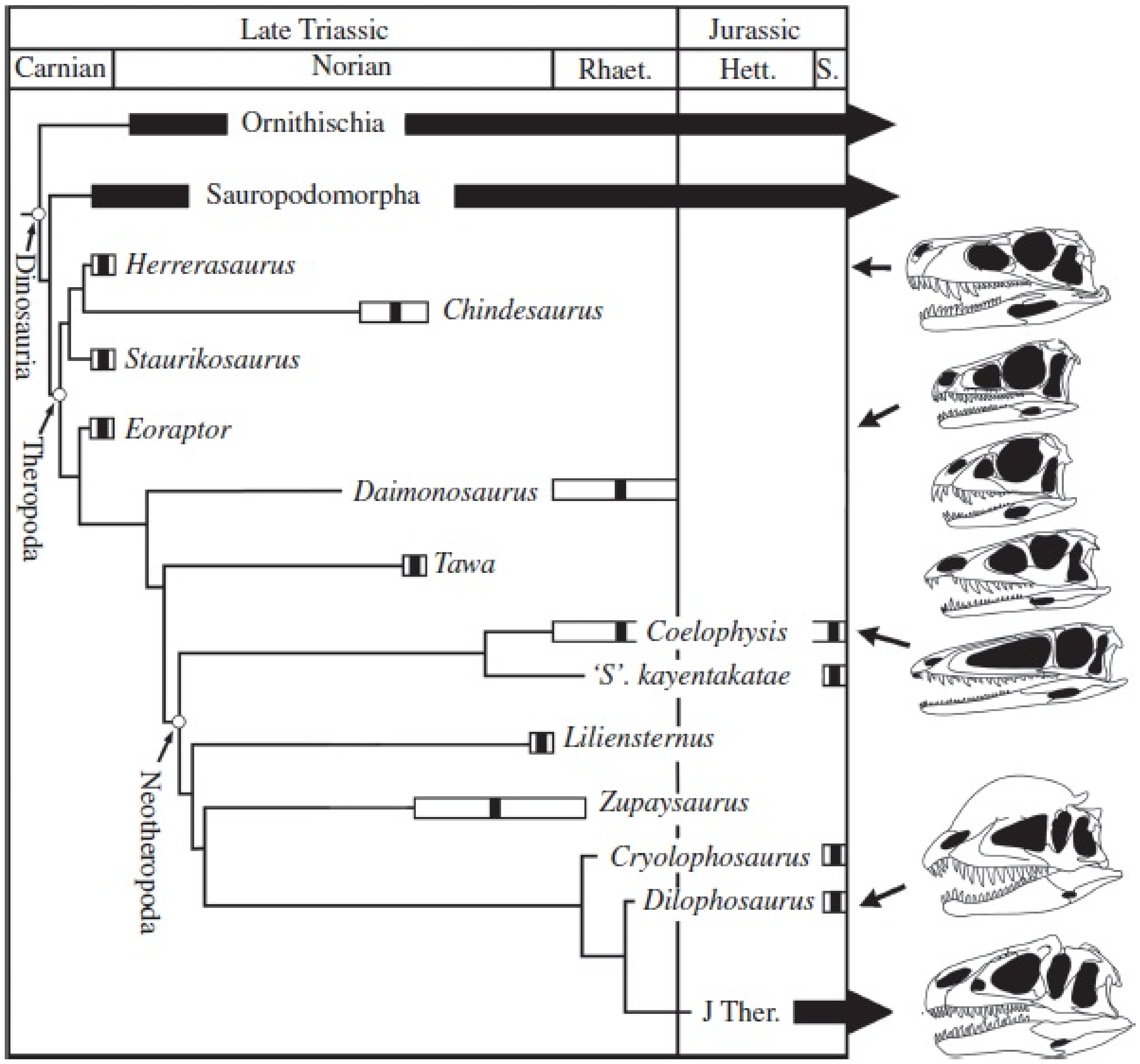
1. *Daemonosaurus* X
2. *Eoraptor* X
3. *Tawa* X

The Earliest Theropods

The general theropod condition - a medium sized, lightly built, fast-running bipedal predator - seem to represent the plesiomorphic condition not only for saurischia but



Early theropod evolution, from Sues et al 2011. Ages of fossils are denoted by black bars. This topology presents Herrerasaurs and *Eoraptor* as basal theropods
copied from Smithsonian Com

even for dinosaurs as a whole, as indicated by the ambiguous status of taxa such as late Carnian and early Norian taxa such as *Eoraptor*, *Herrerasaurus*, *Staurikosaurus*, *Chindesaurus*, *Guaibasaurus*, and *Eodromaeus*, which stand at the dawn of theropod and indeed dinosaurian evolution. It is not hard to see how bipedal protodinosaurs could have given rise to these animals. In this way, other lines of dinosaurs may have successively arisen from prototheropod ancestors, through reversals and loss of early theropod attributes, and acquiring of new ones. It is interesting also that with the classic proto-theropod *Eoraptor* we find a move to omnivory, also characterises the earliest sauropodomorphs (prosauropods).

By the time we get to the middle Norian to Rhaetian, the theropod condition is unambigiously established. Here the newly discovered and described transitional genera *Daemonosaurus* and *Tawa* bridge the morphological gap between these earlier forms and bird-like theropods (neotheropoda or avepoda). They constitute the intermediate links between the first pulse or wave of theropod evolution, consisting of primitive types like *Eoraptor* and the Herrerasaurs, and the second, represented by the earliest three-toed neotheropods, the podokesaurs. It was these latter animals, beginning with little *Coelophysis* and its cousins (representing a third stage of theropod evolution), that would set the standard that would define theropod dinosaurs for the rest of the Mesozoic, and which would in the late Jurassic give rise to the most succesful of all the dinosaurian clades, the birds.

As shown by the chronogram at the right, even Triassic theropods and prototheropods were a diverse assemblage, with a number of lineages evolving in parallel during the Norian, although only the neotheropods would continue through to the early Jurassic and beyond. MAK120207

Descriptions

Eoraptor lunensis Sereno et al., 1993

Range: Carnian of SAm

Phylogeny: basal Theropoda or basal Saurischia; we are using Theropoda **:** Herrerasauridae + ((*Daemonosaurus* + (*Tawa* + Neotheropoda)) + *) but alternative hypotheses would be just as valid, although it is agreed that *Eoraptor* is more basal than *Daemonosaurus* or *Tawa*.

Comments: one of the earliest and most primitive dinosaurs. Although most commonly interpreted as a basal theropod more primitive than herrarasaurs (Sereno et al 1993, Novas 1997) or more derived than them (Nesbitt et al 2009, Ezcurra 2010, Nesbitt 2011, Sues et al 2011), it has also been interpreted as a stem saurischian more basal than (, Upchurch et al 2007) or more advanced than herrerasaurs (Langer 2004, Yates 2005, Yates 2007, Apaldetti et al 2011), and even a basal sauropodomorph (Martinezetal2011, substituting *Eodromaeus* in *Eoraptor*'s old station as basal theropod). Strangely for such an early theropod, and unlike most of its contemporaries, *Eoraptor* is thought to have been omnivorous; if true this would support either an omnivorous ancestry for the dinosaurs, or a proto-sauropodomorph phylogeny (i,.e. either it is in the process of evolving away from, or towards, omnivory), or both. The name, which means 'dawn plunderer from the Valley of the Moon', denotes where it was originally discovered (the badlands where the Ischigualasto formation outcrops, known as *Valle de la Luna* ("Valley of the Moon") due to their arid, otherworldly appearance - Wikipedia). Emphasising the arbitrary line between theropod and basal sauruischian, we have retained *Eoraptor* as the most primitive known theropod here, although it could just as easily be placed among the basal dinosauria. MAK120207

Daemonosaurus chauliodus Sues et al., 2011

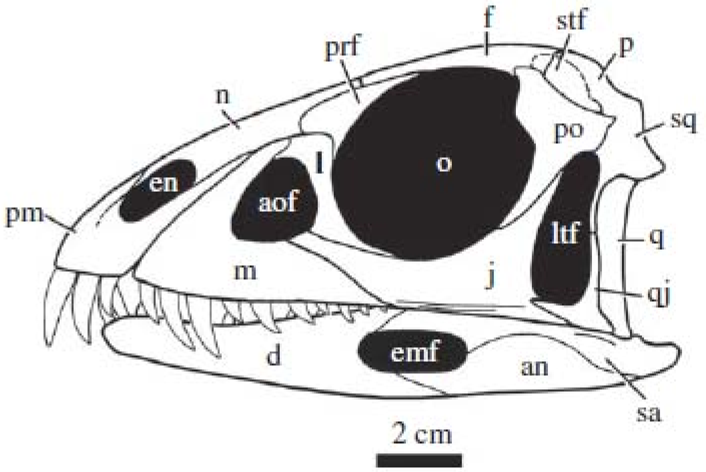


Figure 2. *Daemonosaurus chauliodus* gen. et sp. nov., outline reconstruction of the skull in left lateral view (based on CM 76821). Abbreviations: an, angular; aof, antorbital fenestra; d, dentary; emf, external mandibular fenestra; en, external narial fenestra; f, frontal; l, lacrimal; ltf, lower temporal (infratemporal) fenestra; m, maxilla; n, nasal; o, orbit; p, parietal; po, postorbital; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; stf, supratemporal fossa.

The holotype skull of *Daemonosaurus*, from Sues et al 2011
copied from Dino Paradise (in Japanese)

Horizon: latest Triassic siltstone member of the Chinle Formation of the Coelophysis Quarry at Ghost Ranch, New Mexico - Rhaetian

Phylogeny: Theropoda **:** Herrerasauridae + (*Eoraptor* + ((*Tawa* + Neotheropoda) + *))

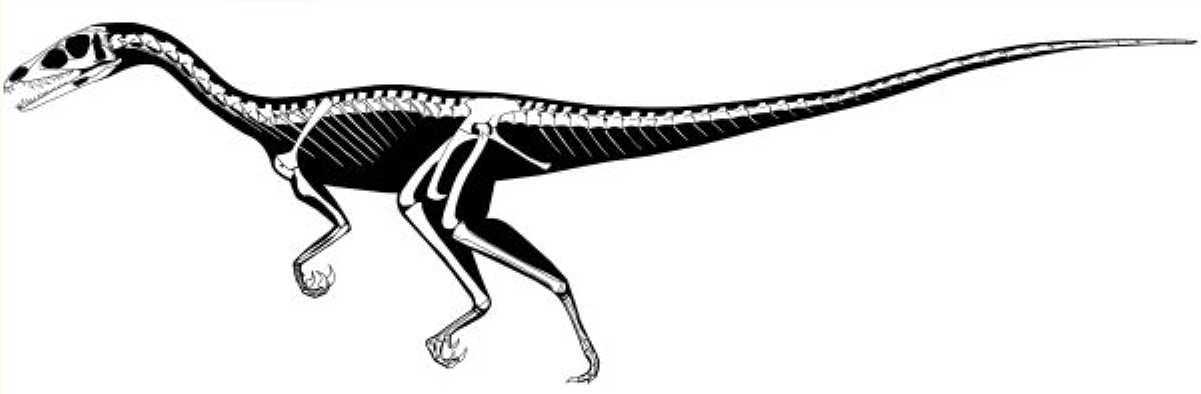
Size: length about 1.5 m long.

Comments: Known from a skull, some vertebrae, and ribs collected from the Ghost Ranch quarry in the 1980s. Fossils of *Coelophysis* were present on the same block that contained the skull of *Daemonosaurus*. The skull is remarkable for its short snout and large premaxillary and maxillary teeth in the upper jaw. Teeth projecting forward from the tips of the upper and lower jaws give it a buck-toothed appearance (which is what the species name *chauliodis* roughly means). May or may not be a juvenile. Phylogenetic analysis reveals Daemonosaurus to be more closely related to coeval neotheropods (e.g. Coelophysis bauri) than to Herrerasauridae and *Eoraptor*. Closely related to, but apparently even more primitive, than *Tawa*, the two bridging the morphological gap between Herrerasaurs and neotheropods (Sues et al 2011). This animal is remarkable for its unusually short (by Triassic theropod standards) snout (reminiscent of early prosauropod and ornithschian herbivores); all other early theropods had long heads and jaws. David Peters suggests that it is actually the most basal member of the Phytodinosauria, a clade proposed by

Robert T. Bakker his *Dinosaur Heresies* in the 1980s. Bakker rejected the Saurischia-Ornithschia divide and instead placed the theropods in their own group and the sauropodomorphs and ornithischians in another, with the segnosaurs intermediate between the two. As it is now known that the segnosaurs are actually theriznosaur theropods closely related to birds, and most phytosaur characteristics can be explained in terms of convergences the hypothesis has long fallen out of favour (See a 2001 discussion re Phytodinosauria on the Dinosaur Mailing List).

Links: Paleoexhibit - Nobu Tamura, Wikipedia, Smithsonian Com, Theropods blog MAK120206

Tawa hallae, Nesbitt et al 2009



Horizon: Hayden Quarry, Ghost Ranch, Rio Arriba County, New Mexico, in the lower portion of the Petrified Forest Member Ghost Ranch in New Mexico (~215 to 213 mya) - Middle Norian

Phylogeny: Theropoda **:** Herrerasauridae + (*Eoraptor* + (*Daemonosaurus* + (Neotheropoda + *)))

Comments: named after the Hopi sun god, this newly discovered theropod dinosaur described by Sterling Nesbitt and co-workers is known from several remarkably well preserved and nearly complete skeletons, which reveal a mosaic of plesiomorphic and derived features. Cladistic analysis reveals it to be more basal than *Coelophysis* and the sister taxon of Neotheropoda. . It also shows that "Coelophysoidea" is probably an artificial grouping because *Tawa* combines classic coelophysoid (podokesaur) with basal theropod characteristics. Shares with coelophysoids a kink between the maxilla and the premaxilla, and a longer-necked, slender build which distinguishes it from earlier forms such as Herrerasaurs and *Eoraptor*. *Tawa*'s intermediate characteristics between Herrerasaurs and *Coelophysis* also argues for the formers' inclusion under the theropoda (Nesbitt et al 2009). The animal was about 2 m long, average for Triassic theropods and proto-theropods. The specific name honours Ruth Hall, founder of the Ghost Ranch Museum of Paleontology.

Links: Tawa hallae - National Science Foundation coverage **best on the web**; Paleoblog; Wikipedia MAK120207

Image: *Tawa hallae* skeleton. Sterling Nesbitt, National Science Foundation

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Theropoda: Basal Theropods: Herrerasauridae

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   `--THEROPODA
      |--Herrerasauridae
      `--+--Eoraptor
         `--+--Daemonosaurus
            `--+--Tawa
                 `--+--Podokesauridae
                    `--+--Ceratosauria
                        `--Tetanurae
                           `--Avetheropoda
                              |--Carnosauria
                              `==COELUROSAURIA
                                  `--AVES
```

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1. Herrerasauridae X

Herrerasaurus feeding on a small cynodont
Artwork by Dmitry Bogdanov, Wikipedia

Introduction

These medium-sized hunters are among the earliest known and most primitive dinosaurian lineage. They died out before the Triassic period ended. There is some disagreement whether Herrerasaurs should be considered primitive theropod (Sereno 1999, Nesbitt et al 2009, Nesbitt 2011, Sues et al 2011), basal saurischian (Langer & Benton 2006; Ezcurra 2010, Novas et al 2011) or pre-Saurischian dinosaur ancestors. If herrerasaurs are theropods, that indicates that the three main dinosaurian groups diverged very early on, and that all three lineages independently evolved several dinosaurian features, such as a more advanced ankle joint or, say, an open acetabulum (where the hind limb attaches to the pelvis). Indeed, the discovery of the extremely primitive prosauropod *Saturnalia* seems to confirm this. (adapted from MAK, revised MAK120207)

Phylogeny

The first two of the following dendrograms are adapted from Wikipedia The first follows one proposed analysis by Novas et al (2011). In this review, Herrerasaurus is a primitive saurischian, but not a theropod. The second is based on an analysis by Sues et al 2011, according to which Herrerasaurus is a basal theropod. -

```
Dinosauria
|--Ornithischia
`--Saurischia
   |--Herrerasauridae
   |  |--Herrerasaurus
   |  |--Staurikosaurus
   |  `--Unnamed herrerasaurid
   `--Eusaurischia
      |--Theropoda
      |  |--Chindesaurus
      |  `--+--Tawa
      |     `--+--Eoraptor
      |        `--Neotheropoda
      `--Sauropodomorpha
```

After Novas et al (2011)

```
Dinosauria
|--Ornithischia
`--Saurischia
   |--Sauropodomorpha
   `--Theropoda
      |--Herrerasauridae
      |  |--Staurikosaurus
      |  `--+--Herrerasaurus
      |     `--Chindesaurus
      `--+--Eoraptor
         `--+--Daemonosaurus
            `--+--Tawa
               `--Neotheropoda
```

After Sues et al 2011 (Nesbitt et al 2009 fig.3 is similar)

```
Dinosauria
|--Ornithischia
`--Saurischia
   |--Sauropodomorpha
   `--Theropoda
      |--Herrerasaurus
      `--+--Staurikosaurus
         `--+--Eoraptor
             `--+--Tawa
               `--Neotheropoda
```

Modified from Nesbitt 2011 (part of a larger cladogram)

The implication of these very different results may be that Herrerasaurs in the broad sense constitute a paraphyletic assemblage of ancestral or stem group theropods, saurischians, or even dinosaurs, at first prior to, and then evolving alongside more specialised and typical dinosaur groups, in a similar manner to the relation of various dinosauromorph lineage sto dinosaurs as a whole. During the late Triassic, early dinosaur and proto-dinosaur evolution constituted a rich tapestry of diverse lineages. Of these many early lineages, only the three crown groups - the neotheropods, sauropodomorphs, and ornithischians, survived the end Triassic extinction, and dominated mnedium and large herbivore, ominover and carnivore niches for the next 150 million years. MAK1201204

Descriptions

Herrerasauridae: *Herrerasaurus, Staurikosaurus*.

Range: Late Triassic of South America & North America.

Phylogeny: Either basal/ancestral dinosauria, basal saurischia or basal theropoda, if the latter then Theropoda **:** (*Eoraptor* + (*Daemonosaurus* + (*Tawa* + (Podokesauridae + (Ceratosauria + Tetanurae))))) + * MAK020206

Characters: 2-5m bipedal predators; large teeth; intramandibular joint; vertebrae: 15+9+2+~50 (note primitive 2 sacrals); dorsal vertebrae and processes axially compressed; accessory dorsal intervertebral

articulations present; axial skeleton pneumatized; distal caudal prezygapophyses overlap next vertebra; scapula narrow & unexpanded; well developed acromial process of scapula (deltoid muscle); elongated manus; manus IV&V greatly reduced, I, II, and II elongate w large claws; but acetabulum bony and only slightly perforate; brevis fossa insignificant; great distal enlargement of pubis; leg primitive; pes with 5 digits; pes I-IV with uncurved claws. ATW031204.

Links: Introduction to Herrerasaurus; Herrerasaurus « Dave Hone's Archosaur Musings; Paleo DataBase - Herrerasauridae; Herrerasaurus - Wikipedia and Herrerasauridae - Wikipedia (follow links for other taxa); Herrerasaurus - Jurassic Times; Herrerasaurus dinosaur fact net; Dino Family Spotlight: Herrerasauridae - Super Raptor Paleoblog; Re: Herrerasauridae - Dinosaur Mailing list archives 2002; DINOBASE, John Sibbick's drawing; van Dijk's Dinosaurus Sted - Herrerasaurus. Referencer; Herrerasaurus Fact Sheet - EnchantedLearning.com; Herrerasaurus and Sanjuansaurus - David Peters MAK120206

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this page MAK1201206

Theropoda: Neotheropoda

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Herrerasauridae
   |--Eoraptor
   `--Neotheropoda
      |--Podokesaurinae
      |   |--Coelophysis kayentakatae
      |   `--+--Coelophysis bauri
      |       `--Coelophysis rhodesiensis
      |--Segisaurus
      |--Liliensternus
      `--+--Zupaysaurus
          `--+--Dilophosaurus
             `--Averostra
                |--Ceratosauria
                `--Tetanurae
                   `--Avetheropoda
                      |--Carnosauria
                      `==COELUROSAURIA
                         `--AVES
```

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The basal neotheropod *Coelophysis bauri*, latest Triassic of central western Pangea.
From Rare Resource - Dinosaur Gallery

What is a (Neo)Theropod?

The clade Neotheropoda was first coined by Bob Bakker (1986), and further defined by Sereno, 1998 and Nesbitt 2011. Basically this group includes all theropods other than a few very early primnitive ones, and also other than the Herrerasaurs (which are so close to the ancestral stem of dinosaurs that they may or may not even be theropods; alternatively, proto-theropods might be considered the original line from which all other dinosaur types evolved). Coelophysids, dilophosaurs, ceratosaurs, allosaurs, tetanurines, allosaurs, coelurosaurs, tyrannosaurs, maniraptors, and birds, are all, technica;lly speaking, neotheropods. Indeed, such is the taxonomic uncertainty around the stem of the dinosaur family tree that the demarcation between neotheropods and theropods may not be clear. However, we have followed Nesbitt 2011 in recognising the Neotheropoda as the clade including *Coelophysis*, modern birds, their common ancestor, and all its descendents. In other words, all theropods above the herrerasaur, *Eodromaeus*, *Eoraptor*, *Daemonosaurus*, and *Tawa* grade. Admittedly it seems pretty silly to refer to 99.999% of theropods and about 95% of their evolutionary history as "-neo" (new), but cladistic nomenclature often comes up with irritating jargon (e.g. Pseudosuchia (false crocodiles) a sthe calde that includes true crocodiles), and rather than use little known alternatives like Eutheropoda or the splendidly appropriate but unfortunately junior synonym Avepoda ("bird feet") (Paul 2002, Paul 2010), we have decided the easiest course of action is just to go with the consensus.

As Justin Tweet (Thescelosaurus website) puts it "the main difference between Theropoda and Neotheropoda is that neotheropods show the first big digital reduction: they have lost the fifth finger entirely, shrunk the fourth finger and metacarpal (if present) to very little or do away with it altogether, and the feet show only three truly functional digits, the fifth reduced to a splint of metatarsal and the first drawn high up the metatarsals." The result in other words was the bird-like three-toed foot, hence Greg Paul's very descriptive term. Very likely there were other differences as well, including soft-body physiology, metabolic and ecological ones, since the neotheropods survived the end-Triassic extinction event, whereas the ancestral theropods didn't, (a more dramatic analogy can be made with neornithes surviing the K-T extinction relatively unscathed

The rise and fall of Ceratosaur and Coelophysoid

monophyly

The earliest and most primitive of the neotheropods are a broad assemblage referred to as ceratosaurs. Ceratosaurs were one of the first clades (as opposed to linnaean ranks) of dinosaurs to be named (Gauthier 1984), along with its sister taxon the Tetanurae (Gauthier 1986). They often feature unusual crests on their head, perhaps a device for intraspecific rivalry or mating. They seem to have become extinct during the end Jurassic in Laurasia, although if abelisaurs are Ceratosaurs (and this is generally stated but still not certain), than these animals survived in Gondwanaland right up to the end of the age of dinosaurs.

Only a decade or two ago the Ceratosauria were accepted in mainstream dinosaurology to be a monophyletic group (e.g. Rowe & Gauthier 1990). A 1994 analysis by Holtz follows Gauthier in having the coelophysoids and neoceratosaurs forming a clade (Ceratosauria), and *together* forming the outgroup to Tetanurae. Very soon though, cracks began to appear, and it was suggested that these two taxa may not form a clade exclusive of other known theropods (e.g. Rauhut 2000). There are also some derived features found in neoceratosaurs (*Ceratosaurus* and Abelisaurs) which are not found in coelophysoids. This would be evidence that neoceratosaurs are closer to tetanurines than to coelophysoids. In this case, the neoceratosaur/coelophysoid characters would have to be convergences and/or primitive neotheropod features lost in Tetanurae, and the Ceratosauria are paraphyletic or even polyphyletic.

It is now looking increasingly likely that all the Ceratosauria as originally defined, and for that matter its included subclade Coelophysoidea (which includes the (families Podokesauridae (better known as Coelophysidae) and Dilophosauridae), are a series of smaller clades (Yates 2006, Smith et al 2007), or even a paraphyletic assemblage or an evolutionary grade, rather than monolithic clade (Nesbitt et al 2009, Nesbitt 2011). This also makes sense from a stratigraphic context, as otherwise we are burdened with innumerable ghost lineages and non-existent ancestors, when the ancestors (or at least their close cousins) and transitional foms were before us all the time.

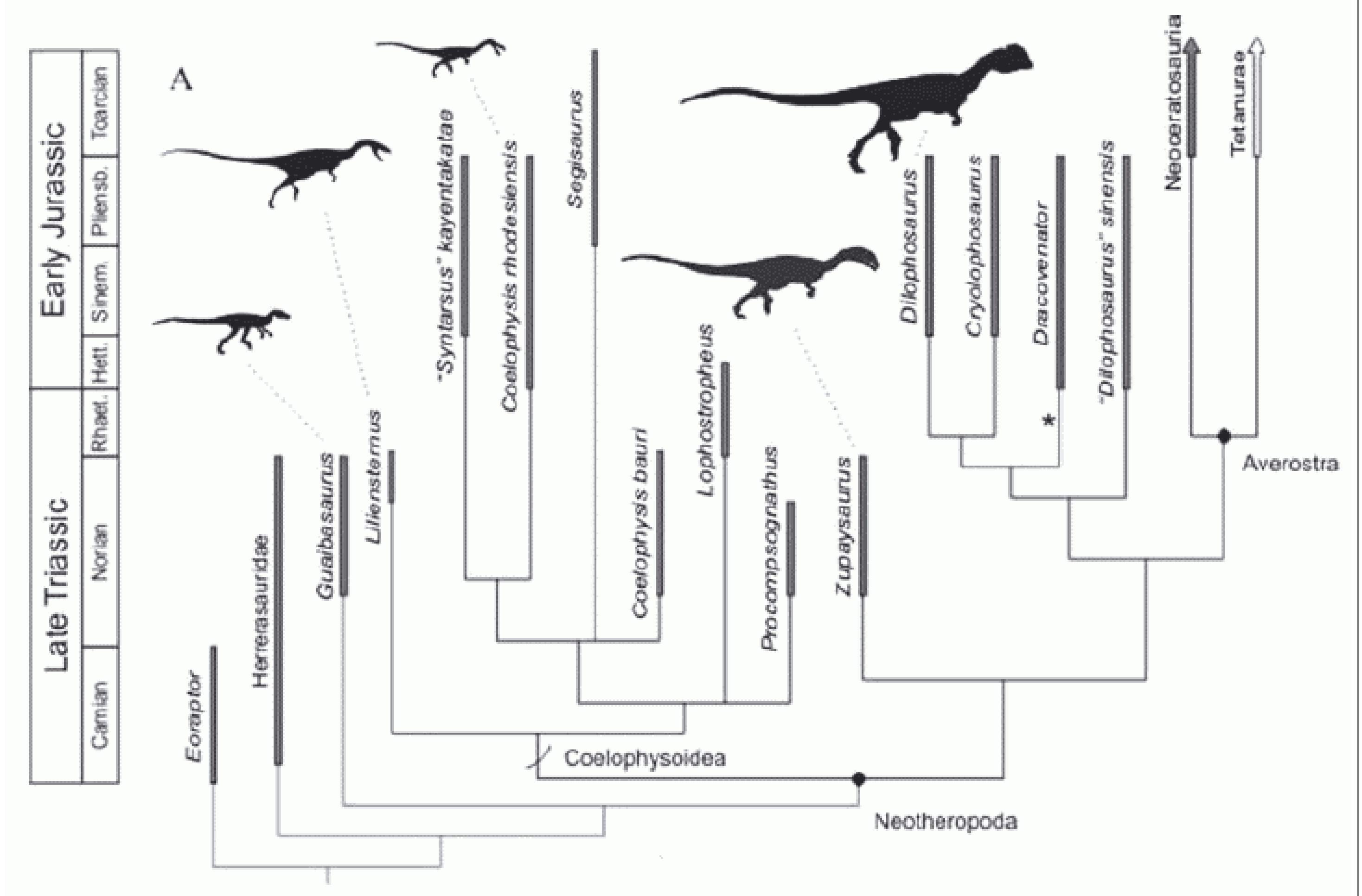
On the other hand, the monophyletic status of the Tetanurae has never been challenged, so we can confident that birds and various higher theropods (*Allosaurus*, *Velociraptor*, *T. rex*, and other less famous representatives) all share a single common ancestor. Moreover, a more restricted Ceratosauria, including both the Jurassic *Ceratosaurus* and the Cretaceous Gondwanan Abelisaurs, and equivalent to the old Neoceratosauria, likewise constitute a natural group (e.g. Carrano & Sampson 2008). Both of these groups are described in the following pages. The present page however is concerned with the earliest and most primitive of the neotheropods, a broad assemblage of light-built carnivores that in the past were included under the postulated clades Coelophysoidea and Ceratosauria, and the family Podokesauridae. MAK011128 updated 120206

Neotheropod phylogeny

The following dendrogram shows early neotheropod relationships; based on Ezcurra & Cuny 2007 and Smith et al 2007

```
Neotheropoda
      |--Coelophysoidea
      | |--Liliensternus
      | `--+--Lophostropheus
      |    |--Procompsognathus
      |    |--Segisaurus
      |    `--+--Coelophysis kayentakatae
      |       `--+--Coelophysis bauri
      |          `--Coelophysis rhodesiensis
      `--+--Zupaysaurus
         `--+--Dilophosauridae
            |    |--"Dilophosaurus" sinensis
            |    `--+--Dracovenator
            |         `--+--Cryolophosaurus
            |              `--Dilophosaurus
            `--Averostra
               |--Ceratosauria
               `--Tetanurae
```

When this basic phylogeny is plotted against time, the result is as follows:



Time calibrated phylogenetic relationships of basal theropods. "Coelophysoids" are here shown to be a paraphyletic group. The asterisk indicates an alternative placement of *Zupaysaurus* as sister taxon to *Dracovenator*, according to Yates (2005); dotted lines indicate uncertain position of herrerasaurids and *Eoraptor* according to Sereno (1999) and *Guaibasaurus* according to Langer & Benton (2006). Diagram and caption from Langer et al 2010 fig 17.

A similar but low resolution cladogram is provided by Xu et al 2009; the following is adapted from a larger cladogram (fig S4 uin the supplementary material), names for supra-generic taxa are added for the sake of comparison

```
Neotheropoda
      |--Coelophysoidea
      | |--Liliensternus
      | `--Coelophysidae
      |     |--Coelophysis kayentakatae
      |     |--Segisaurus
      |     |--Coelophysis rhodesiensis
      |     `--Coelophysis bauri
      `--+--Zupaysaurus
         `--+--Dilophosauridae
            |    |--Dracovenator
            |    |--Dilophosaurus wetherilli
            |    |--"Dilophosaurus" sinensis
            |    |--Cryolophosaurus
            |    `--Berberosaurus
            `--Averostra
               |--Ceratosauria
               `--Tetanurae
```

The above phylogenies all assume a monophyletic Coelophysoidea (Coelophysidae + *Liliensternus*) within a paraphyletic Coelophysoidea (sensu Gauthier). A different picture is presented in Nesbitt et al 2009's (and following them Sues et al 2011)'s cladogram for example has *Liliensternus* more derived than *Coelophysis*, and *Zupaysaurus* more derived than *Liliensternus*, giving the following: *Coelophysis* (*Liliensternus* (*Zupaysaurus* (*Cryolophosaurus* (*Dilophosaurus* (Averostra)))). Or in dendrogram form

```
Neotheropoda
      |--Coelophysis
      `--+--Liliensternus
         `--+--Zupaysaurus
            `--+--Cryolophosaurus
                `--+--Dilophosaurus
```

```
                     `-- Jurassic Theropods (=Averostra)
```

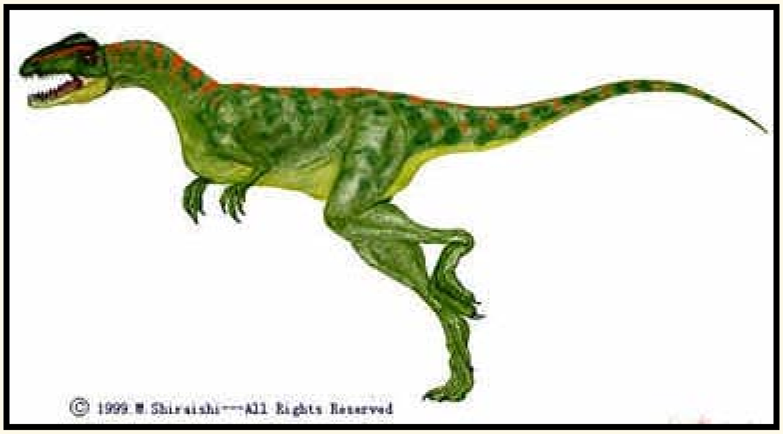
Rather than being a basal taxon, *Liliensternus* is now intermediate between the small *Coelophysis* and the transitional Rhaetian taxon *Zupaysaurus*. In this pectinate arrangement these early theropods also form a general evolutionary gradation that broadly fits with the stratigraphy (the dilophosaurs come after the earlier Coelophysines, *Procompsognathus* etc) and the clades Coelophys-inae/idae/oidea collapse into a small cluster of species around *Coelophysis*. The following "low resolution" phylogeny is from Tom Holtz who in turn has incorporated a number of sources

```
Neotheropoda
       |--Liliensternus
       |--Coelophysidae
       |--Zupaysaurus
       `--+--Cryolophosaurus
          |--Dilophosaurus
          `--Averostra
             |--Ceratosauria
             `--Tetanurae
```

Regardless of the specific phylogeny, the general agreement is that in terms of theropod "evolutionary pulses", there are first the Herrerasaurs and co, then the Triassic and Early Jurassic coelophysids, then the larger types such as *Dilophosaurus* and *Cryolophosaurus* in the early Jurassic (*Zupaysaurus* being transitional here both morphologically and straigraphically), and finally the higher (Ceratosauria and Tetanurae) theropods that first appear in the middle Jurassic, representing highly successful types that continue to the end of the Mesozoic (and in the case Tetanurae, evolve into birds). MAK120217

Descriptions

Neotheropoda:(=Coelophysoidea?): *Coelophysis*, *Dilophosaurus*, and more derived theropods. Pigeons > Prototheropods.



Definition: *Coelophysis*, Neornithes, their most recent common ancestor and all descendants (Sereno, 1998). The least inclusive clade containing *Coelophysis bauri* (sensu Colbert et al., 1992), and *Passer domesticus* (Nesbitt 2011.)

Synonyms: Avepoda, Eutheropoda

Range: Late Triassic to Late Cretaceous.

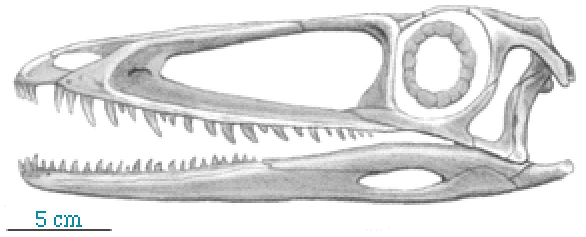
Phylogeny: Theropoda **:::** *Tawa* + * **:** Podokesauridae + *Liliensternus* + (*Zupaysaurus* + (*Dilophosaurus* + ((Neo)Ceratosauria + Tetanurae))).

Characters: clavicles are fused into a single mid-line bone (furcula or "wishbone") that functioned as a spring/shock absorber, perhaps to deal with stresses on the forelimbs and shoulders from struggling prey. (It is not known whether or not Tawa, Eodromaeus, and even the herrerasaurs had furculae.); Manual digit V lost (so only four fingers or fewer); Five or more sacral vertebrae; Increased pelvic muscles, revealed by increase in size of attachment surfaces on ilium; Pedal digits I and V reduced (making the foot functionally tridactyl ("three toed"): metatarsal V lacks a toe, while metatarsal I is reduced with a small digit I (Tom Holtz).

Image: *Liliensternus liliensterni*, artwork © M. Shiraishi, reproduced with permission

Links: (the following is for Ceratosauria - these links haven't been checked and in any case need to be sorted taxonimically updating MAKDinoData: Ceratosauria; DinoData: Coelophysis; Coelophysis; Staab Studios -

Coelophysis Model; The Fernleaf: Karen Carr; Ceratosaurian Theropods; Ceratosauria (Mikko's Phylogeny); Ceratosauria (Dutch -- brief introduction & chart); A BASAL ABELISAURIA NOVAS, 1992 (THEROPODA-CERATOSAURIA) FROM ... (full text paper on relationships); Megalosaurus = Torvosaurus in Europe (and following); ceratosauria.htm (Justin Tweet); Dinosaurier Interesse.de - Stanley- Ceratosaurier (German); GEOL 104 Lecture 22- Theropoda I- Dinosaurs red in tooth and claw (lecture notes from Tom Holtz); Ceratosauria. ATW030313.



Drawing of *Coelophysis* skull courtesy of Professor Paul Olsen

Podokesauridae von Huene 1914 **:** *Coelophysis, Segisaurus*

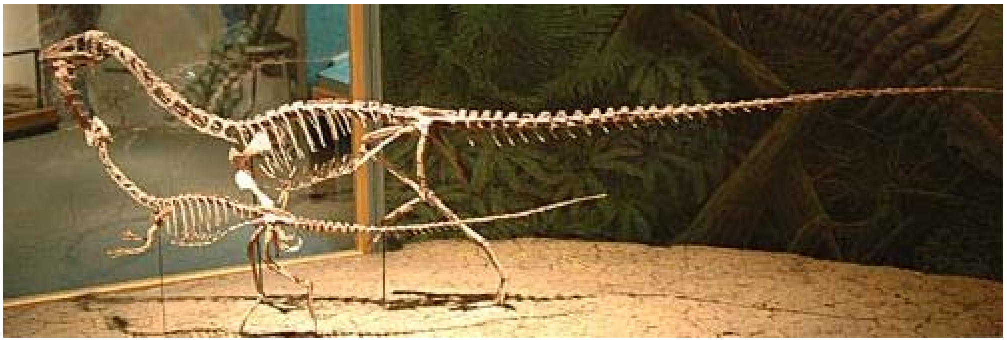
Definition: As originally defined, Podokesauridae was an evolutionary Linnaean taxon (and can still be used in that context). Sereno proposes a number of nested clades here, using Coelophysidae rather than Podokesauridae (see also comments section for reason for name changes), as follows: *Coelophysoidea*: The most inclusive clade containing *Coelophysis bauri* (Cope 1889) but not *Carnotaurus sastrei* Bonaparte 1985, *Ceratosaurus nasicornis* Marsh 1884, or *Passer domesticus* (Linnaeus 1758). taxon search. *Coelophysidae*: The least inclusive clade containing *Coelophysis bauri* and *Procompsognathus triassicus* Fraas 1913. taxon search. *Coelophysinae*: The most inclusive clade containing *Coelophysis bauri* but not *Procompsognathus triassicus*. taxon search. Unfortunately *Procompsognathus* is not a good choice of anchor taxon; it is a poorly preserved form that, depending on who you ask, might be a chimera (in this case a sphenosuchian skull and podokesaur skeleton), a non-Dinosaurian ornithodiran, or an unspecified ceolophysid (Wikipedia, see elso refs cited there), so the last two definitions are not of much use. *Segisaurus halli* Camp, 1936 may be a better choicxe, but even there the skull is missing, so detreming the precise relationship is difficult. How many species are included in the stem-based definition of Coelophysoidea depends on whether this assemblage of early theropods turns out to be a monophyletic or a paraphyletic group.

Synonyms and included taxa: Coelophysidae, Coelophysinae, Coelophysoidea, Halticosauridae, Procompsognathidae, Segisauridae

Range: Middle Norian to Early Jurassic

Phylogeny: Neotheropoda **:** *Liliensternus* + (*Zupaysaurus* + (*Dilophosaurus* + Averostra)) + * (paraphyletic?) **:** *Coelophysis arizonensis* + *Coelophysis bauri* + *Coelophysis kayentakatae* + *Coelophysis rhodesiensis* + *Segisaurus* (see Podokesaur phylogeny for various hypotheses)

Characters: The following are characteristics of the "Ceratosauria": Maxilla & premaxilla weakly attached; large tooth from lower jaw fits into marked diastema; no maxillary fenestrae; **$** 2 pairs of pleurocoels in cervical vertebrae; **$** fusion of sacral vertebrae & ribs (adults); retain 4 digits in hand; **$** 2 fenestrae in pubic plate; **$** flange at distal end of fibula overlaps ascending process of astragalus anteriorly. ATW (no date).



Coelophysis bauri, Denver Museum of Nature and Science.
Photo by Firsfron, Wikipedia Creative Commons Attribution

Comments: Coelophysoidea was known as Podokesauridae until as recently as Carroll 1988. Paul 1988 points out that the original fossil remains of *Podokesaurus*, whose phylogenetic status was debatable to begin with, was lost in a fire, and all that remain are some poor quality casts. On those grounds he proposed renaming the taxon to reflect the better known *Coelophysis*. Holtz (1994) and Sereno (1998) formalised the terminology (although the family rank taxon Coelophysidae apparently goes back to Nopcsa 1928. Unfortunately, Baron von Nopsca was only familiar with Cope's *Coelophysis*, which was a Silesaur proto-dinosaur, and not Colbert's small Ghost Ranch theropod, which was a totally different animal, despite being assigned to the same genus. What's more, there is no requirement for the type species or type genus of supra-specific taxa to be based on good material for it to be valid - consider Phytosauridae for example! We have therefore followed Olshevsky 1991 in restoring von Huene's original taxon name (Matthew Martyniuk has also recently argued in favour of restoring Podokesauridae). Actually this is in keeping with a general trend in dinosaurology, in which over the past two decades or so taxa based on poor material are first renamed and then have their original moniker restored. So Megalosauridae changed into Torvosauridae and even Spinosauroidea before becoming once again Megalosaur-idae/oidea, and Titanosauridae spent several years as Saltosauridae before again returning to Titanosauridae. Hence Podokesauridae is used here in preference to Coelophys-idae/oidea.

Life reconstruction of *Coelophysis bauri*, by John Conway.
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The Podokesaurs are the most primitive of the neotheropods, and this linnaean/evolutionary taxon is certainly paraphyletic (i.e. it is the ancestral grade of all higher theropods - if one were to draw a romerogram it would be the bubble at the bottom from which the bubbles or balloons derive. Greg Paul divided these early theropod dinosaurs into two groups, the smaller Coelophysines and the larger Halticosaurines (the Dilophosaurs). (Paul 1988). A recent cladistic analysis reveals that the Halticosaurines are an artificial grouping, with some (*Liliensternus* and *Lophostropheus*) more primitive than both the smaller coelophysines and the Jurassic dilophosaurs (Smith et al 2007). A revision of Triassic stratigraphy by S. G. Lucas (1998) shows *Coelophysis bauri* to be late Norian or Rhaetic (latest Triassic) in age, rather than late Carnian as originally stated, so that it lived after both the large *Liliensternus* and small *Procompsognathus*. Of course, it may be that large size was a primitive feature of the neotheropods, with *Coelophysis* and co as later minaturised forms which continued through to the early Jurassic.

Although the position of *Liliensternus* is uncertain, current phylogenetic analyses agree on a monophyletic *Coelophysoidea* (sensu Sereno), even if they disagree on details. Because -*oidea* is the suffix for superfamily, and this does not seem to be a very diverse group, we have taken the liberty of replacing this with a subfamily ranking of Podokesaurinae (although Cladistics is rank free, in this way the name can do double duty as a linnaean taxon). Podokesaurinae is here considered to include a number of species, all of which can be placed in the genus *Coelophysis* (the present writer (MAK) rejects the move to monospecific genera, as this results in a disjunction between paleoherpetology and the rest of biological nomenclature (botany, zoology, invertebrate paleontology e.g. brachiopods, molluscs, trilobites, etc)).

There seems to be little agreement regarding the phylogenetic details here.

So for example Carrano et al 2005 give the following (below left) whereas Ezcurra & Cuny 2007 (amended in Ezcurra & Brusatte 2011, adding *C. arizonensis*) offer the cladogram on the right

```
|--Procompsognathus
|--Segisaurus
`--+--Coelophysis bauri
   `--+--Coelophysis kayentakatae
      `--Coelophysis rhodesiensis
```

```
|--Coelophysis kayentakatae
`--+--Coelophysis bauri
   `--+--Coelophysis rhodesiensis
      `--Coelophysis arizonensis
```

The podokesaurs seem to have radiated quickly during the Norian and Rhaetian. The smaller forms - represented by the genus *Coelophysis* - survived into the Early Jurassic, where they flourished as small/medium-sized carnivores. Throughout the early Jurassic, Coelophysids and Dilophosaurids existed alongside each other for some 20 million years or so, indicating that these animals were very successful in their environment. Both large and small species show a tendency for head ornamentation in the form of crests, almost certainly for intraspecific display. The of all these large and small forms seem to have developed independently in different lineages, rather than all podokesaurs being descended from a single crested ancestor. It is not even known whether some taxa, such as *Liliensternus*, even had head crests at all. MAK120217

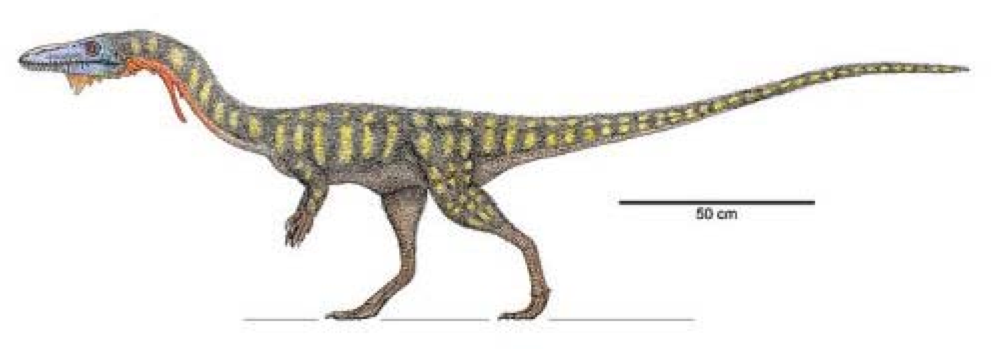
Coelophysis arizonensis (Hunt, Lucas, Heckert, and Lockely, 1998)

Synonym/Monotypic name: *Camposaurus arizonensis* Hunt, Lucas, Heckert, and Lockely, 1998

Range: Early/Mid Norian of Arizona

Phylogeny: Podokesauridae **:** * (see Podokesaur phylogeny for differing hypotheses)

Comments: The oldest known neotheropod, based on partial lower leg bones. Originally considered a synonym of *C. bauri*. Cladistic analysis (Ezcurra & Brusatte 2011) places it as sister taxon to the early Jurassic *C. rhodesiensis*. Unfortunately this creates an aweful lot of ghost lineages, an alternative stratigraphic phylogeny might have *C. arizonensis*, *C. bauri*, and *C. rhodesiensis* as part of a single ancestor-descendant series, or perhaps the real picture is between these two extremes. MAK120216



Coelophysis bauri (Cope, 1887)

Synonyms: *Coelurus bauri* Cope 1887; *Rioarribasaurus colberti* Hunt & Lucas 1991

Horizon: Chinle Formation, Arizona, New Mexico, and Utah (late Norian or Rhaetian (Lucas 1998), p.374)

Phylogeny: Podokesauridae **:** * (see Podokesaur phylogeny for differing hypotheses)

Size: length 2.5 to 3 meters, weight 15 to 30 kg (Paul 1988)

Comments: Very lightly built, long bodied, head long, weak bite, numerous small teeth, crests absent (Paul 2010 p.72). There are two morphs, indicating sexual differences.

This little animal is best known from the hundreds of specimens from the Ghost Ranch quarry in New Mexico, discovered, studied, described in detail, and popularised by Edward Colbert, who made it the archetypal primitive theropod. There's not much that can be said here that isn't already stated in the description of the group as a whole, see for example Podokesauridae characters (or see Wikipedia for a detailed non-technical coverage)

It was at one time believed that this animal practiced cannibalism (not uncommon among crocodilians), because some Ghost Ranch skeletons have juvenile-sized skeletons in the area of their stomachs, but thesewere later shown to to be misinterpreted (several specimens were actually small sphenosuchids such as *Hesperosuchus*, while in some cases it was simply that the remains of bigger individuals lay on top of smaller ones).

Cope's original type specimen of *Coelurus bauri* (= *Coelophysis bauri*) has turned out to be different species (now known to a Silesaurid protodinosaur) quite distinct from the Ghost Ranch species. This means that technically *Coelophysis bauri* could no longer be used for the latter. Paleontolgists Adrian Hunt and Spencer Lucas, who made this discovery, therefore coined a different name, *Rioarribasaurus*, for the Ghost Ranch quarry specimens. But because the name *Coelophysis* was so well known and had been used in most of the scientific literature, Co;lbert and coworkers petitioned the International Commission on Zoological Nomenclature (ICZN) to have the type specimen of *Coelophysis* transferred from the poorly-preserved original specimen to one of the well-preserved Ghost Ranch specimens. The unpronouncable *Rioarribasaurus* became a *nomen rejectum*, or "rejected name", and *Coelophysis* a *nomen conservandum* ("conserved name"). Cope's original specimen became *Eucoelophysis baldwini* Sullivan and Lucas, 1999. MAK120216

Image: *Coelophysis* by Jeff Martz, via Wikipedia

Coelophysis rhodesiensis (Raath, 1969)

Synonyms: *Syntarsus rhodesiensis* Raath, 1969, *Megapnosaurus rhodesiensis* (Raath, 1969)

Horizon: Upper Elliot Formation, Cape Province, South Africa; and Forest Sandstone of Matabeleland, Zimbabwe, (Hettangian/Sinemurian)

Phylogeny: Podokesauridae **:** * (see Podokesaur phylogeny for differing hypotheses)

Size: length 2 to 3 metres; weight 10 to 25 kg

Comments: A descendent of the Triassic *Coelophysis bauri*, this active little animal shows a number of more advanced features, such as a much larger "window" (the antorbital fenestra) in the front side of the snout, possibly for housing a gland of some kind, and teeth that are entirely forward of the eye. There is also the fusion of some of the upper foot-bones (metatarsals), a bird-like characteristic that would increase the strength of the leg. The behaviour appears to be the same as *C. bauri*, for the remains of large numbers of this species, in various ages, are found concentrated together in a single small quarry area. Like present-day birds, *Syntarsus* seems to have lived in large groups or flocks of individuals (the species is known from at least 30 partially articulated skeletons, juvenile to adult, found in one locality). (Paul 1988 p.262f.). Leg longer relative to the body than *C. bauri* (Paul 2010 p.73). A related form, known from fragmentary remains, has been found in the Early Jurassic Lufeng Formation (Yunnan Province, China) (Irmis2004), showing that these animals had a global distribution. As with *C. bauri*, head crests are absent.

Podokesaurs seem to have a particular problem with the names they are given. This particular animal's name has been much more of a controversy than *Coelophysis*/*Rioarribasaurus* (see above) ever was. The original name *Syntarsus* ("fused ankle", referring to the common podokesaurid condition of fused tibio-tarsal and fibula-tarsal bones) turned out to already have been given to a Colydiine beetle (in nomenclatural jargon we say the name was "preoccupied"). The entomologists who made this discovery instead coined the substitute generic name *Megapnosaurus* Ivie, Slipinski, and Wegrzynowicz, 2001. This was considered very bad form in the paleontological community, mostly because because taxonomists are expected to allow original authors of a name to correct any mistakes in their work, and the meaning of the new name ("big dead lizard") didn't help. Raath himself was aware of the homonymy and was planning to emend it, but the group who coined the new name had been unable to contact him, and came to the conclusion that he was deceased (see discussion on dinosaur mailing list archives beginning here and here). Raath later argued that the genus is a junior synonym of *Coelophysis* (a suggestion originally proposed by Greg Paul (1988)), as did Adam Yates (Yates 2005), and as a result, few palaeontologists accept the new name, although *Megapnosaurus* remains a valid name which must be used if a monotypic (one genus, one species) nomenclature is used. MAK120216

Coelophysis kayentakatae (Rowe, 1989)

Synonyms: *Syntarsus kayentakatae* Rowe, 1989, *Megapnosaurus kayentakatae* (Rowe, 1989)

Horizon: Kayenta Formation, Arizona (late Sinemurian or early Pliensbachian)

Phylogeny: Podokesauridae **:** * (see Podokesaur phylogeny for differing hypotheses)

Size: 2.5 meters, weigth about 30kg (Paul 2010 p.74)

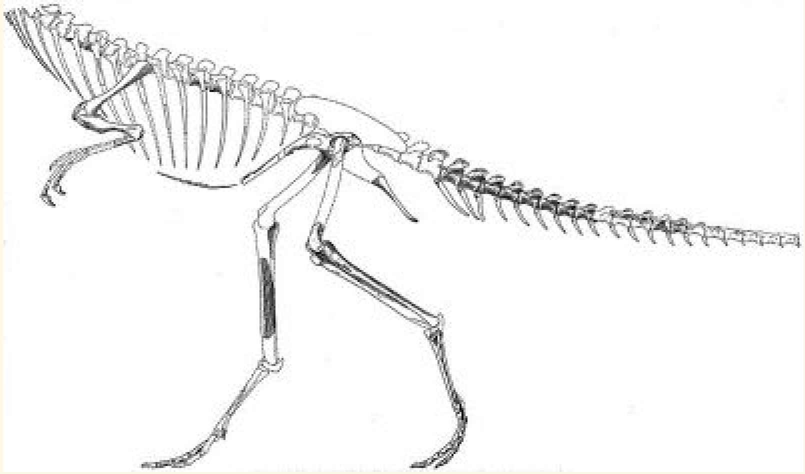
Comments: Head fairly deep, more robust and teeth larger and less numerous than in other species, (Paul 2010 p.74). two small crests, similar to those of its larger cousin *Dilophosaurus*. As with other species of *Coelophysis*, it is represented by a number of specimens, indicative of social behaviour, in this case 16 individuals, juvenile to adult. MAK120217

Segisaurus halli Camp, 1936

Horizon: Navajo Sandstone of Arizona (Toarcian)

Phylogeny: Neotheropoda **:** *

Size: length about 1.3 meters, weight 5 kg? (Paul 1988)



Comments: known only from a partial, headless skeleton, and previously placed in its own family, the Segisauridae, this is a small, very slender animal. It was originally thught that some of its limb bones were solid rather than hollow as they are in all other small theropods, but solid, but this turned out not to be the case, and Segisaurus is pretty typical in this regard. Also, for a long time it was unusual for being one of the few theropods for which a good clavicle was known. Its hip bones have unusual holes and flattening. According to Gregory Paul, it also possesses some advanced features. (Paul 1988). It is now considered a primitive podokesaur ((basal coelophysoid), perhaps related to *Procompsognathus* Carrano et al 2005. If that is the case then there were at least two lineages of small early theropods, podokesaurines and segisaurines (subfamily (new rank) Segisaurinae) MAK120216

Image: Restoration of *Segisaurus halli* holotype skeleton, from Camp 1936, via Wikipedia, public domain

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Liliensternus liliensterni (von Huene, 1934)

Horizon: upper Keuper of Thuringia, Germany (late Norian)

Phylogeny: Neotheropoda **:** Podokesauridae + (*Zupaysaurus* + (*Dilophosaurus* + Averostra)) + *

Size: length 5.15 meters, weight 127 kg (Paul 1988)

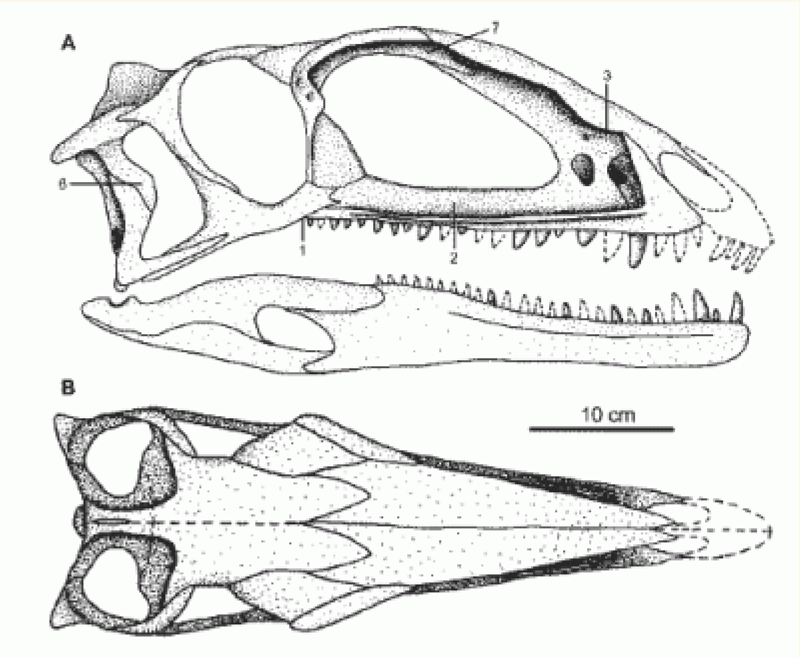
Comments: Originally known as *Halticosaurus*; the specific and later generic name honours the German amateur paleontologist, Dr. Hugo Rühle von Lilienstern, who discovered the original fossils in the eraly 1920s. a poorly known form, consisting of disarticulated remains of at least two individuals, and fragmentary skull material. This was a lightly built animal, more like an oversized *Coelophysis* than a dilophosaur Greg Paul 2010) p.74) . Depending on who you ask, *Liliensternus* is either as a basal taxon of a monophyletic Coelophysidae (Ezcurra & Cuny 2007, Smith et al 2007, Xu et al 2009), or a derived/advanced taxon intermediate between coelophysids and dilophosaurs (Paul 1988 pp.267-8, Nesbitt et al 2009). Following Greg Paul (1988), this species is uniformly drawn with head crests, although it is not known if it actually had them. *Lophostropheus* (originally *Lilensternus*) *airelensis*, from the Rhaetian of France , known from partial remains, may be related, although it is different enough to deserve its own genus. About all that can be said of these poorly known animals is that they show that respectable sized theropods were around in the late Triassic. These animals were about the same length, but much lighter, then contemporary rauisuchian thecodonts; the two types of creature obviously filled very different ecological roles.

Links: material online is as scanty as knowledge of these species in general: Wikipedia, here as often elsewhere, the best coverage; *Thescelosaurus!* - short entry on this species and every other dinosaur taxon; Dinosaur mailing list - a few comments by Mickey Mortimer, the page is good overview of Triassic European theropods (and shows how scrappy this material is; in contrast to contemporary plateosaurs, known from excellent material)

Zupaysaurus rougieri Arcucci and Coria, 2003

Horizon: Los Colorados of Argentina (?Rhaetian)

Phylogeny: Neotheropoda **:** Podokesauridae + Liliensternus ((*Cryolophosaurus* + *Dilophosaurus* + Dracovenator + Averostra) + *)



Size: Sull: 45 cm, Length: up to 4 meters (Wikipedia)

Comments: known from an almost complete skull and partial postcrania. Originally considered the earliest known and most basal tetanuran, supporting the original (now no longer supported) cladistic division of Ceratosauria and Tetanurae (which would have required Triassic tetanurans). Later studies placed it as a basal coelophysoidean (Carrano et al 2005), a member of a monophyletic Dilophosauridae Yates 2006, a non-coelophysid coelophysoid (Ezcurra & Novas 2007), or intermediate between coelophysids and dilophosaurs (Smith et al 2007; Nesbitt et al 2009, Xu et al 2009); the latter interpretation being the one we have followed here. The apparent Tetanurae synapomorphies (maxillary fenestra, caudally forked ascending ramus of the maxilla) are therefore better interpreted as homoplasies (convergence). (Ezcurra & Novas 2007). *Zupaysaurus* is distinguished by a moderately deep skull, large snout, and well developed paired crests (Paul 2010 p.75)

Links: Palaeocritti; Wikipedia, *Thescelosaurus!* (short entry) MAK120216

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Theropoda: "Dilophosaurs"

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Herrerasauridae
   |--Eoraptor
   `--Neotheropoda
      |==Podokesauridae
      `--+--Zupaysaurus
          `--+--"Dilophosaurus"  sinensis
             |--Dracovenator
             |--Cryolophosaurus
             |--Dilophosaurus
             `--Averostra
                |--Ceratosauria
                `--Tetanurae
                   `--Avetheropoda
                      |--Carnosauria
                      `==COELUROSAURIA
                         `--AVES
```

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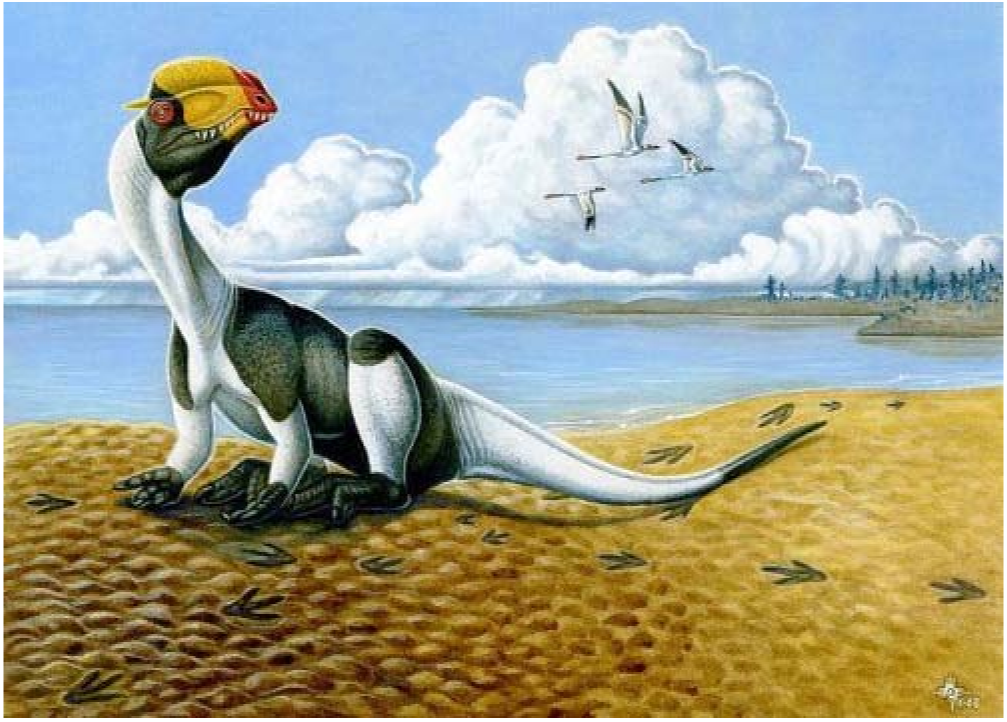
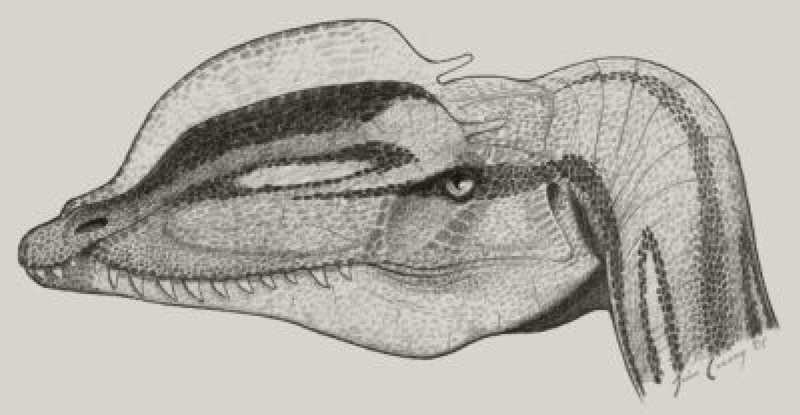


Restoration of Early Jurassic environment preserved at the SGDS, with the theropod Dilophosaurus wetherilli in bird-like resting pose, demonstrating the manufacture of SGDS.18.T1 resting trace.
Artwork by Heather Kyoht Luterman, via Wikipedia, Creative Commons Attribution



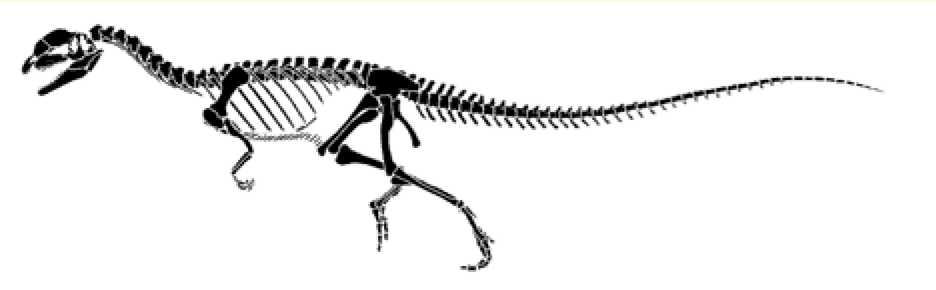
Dilophosaurus wethrelli, artwork © John Conway 2012.
Creative Commons Attribution Non Commercial Non Derivative

The Dilophosaurs are a cosmopolitan assemblage of early Jurassic theropod dinosaurs. These were large graceful bipedal preditors with lengths of 4 to 6 to 7 metres and estimated adult weights of 300 to 500 kg.. Originally included with *Coelophysis* and co in the Podokesauridae, they are generally now considered more closely related to more advanced theropods, so that the "Coelophysoidea" as conventionally defined constitute a paraphyletic and gradational stepwise series transitional between primitive and more advanced theropods (Smith et al 2007, Nesbitt 2011). There is still no agreement though as to whether the dilophosaurs themselves constitute a monophyletic clade (Yates 2006, Smith et al 2007, Xu et al 2009) or a paraphyletic grade between the Triassic ceolophysids and the middle Jurassic and later Averostra (Nesbitt et al 2009, Tom Holtz dendrogram). We have tentatively gone for the latter option as it fits the stratigraphic sequence better, although the former could also be true, in which case the averostrans would have been rare theropods alongside the successful dklophosaurs

At upto 6 or 7 meters in length, and 300 to 450 kg in weight, Dilophosaurs were both larger and more heavily built than even the biggest Triassic podokesaurs; it is likely that with the extinction of the large Rauisuchian thecodonts at the end of the Triassic, there were no large natural predators, so podokesaurs quickly grew to fill the role. Dinosaurs were to dominate the terrtrial top predator role for almost 150 million more years.

Not only were they larger, but they were also more evolved, aquiring characteristics absent in Triassic and early Jurassic Podokesaurs. According to Tom Holtz, dilophosaurs share several derived features (synapomorphies) with later theropods (averostrans), including: a lacrimal fenestra (airsac opening into the upper corner of the lacrimal), reduced total number of maxillary teeth, and modified jaw joint. This is just the hard skeletal characteristics, obviously there would have bene physiological and other changes as well. As yet there is no official name for the dilophosaur + averostra clade.

At one time it was thought that the large late Triassic carnivores such as



Liliensternus, *Lophostropheus* and *Gojirasaurus* were included here, but the first two are now considered standard podokesaurs (coelophysids), and the last named has, unfortunately (because it has the coolest name - "Godzilla lizard") turned out to be a chimera, a mixture of rauisuchian thecodont, *Coelophysis*, and other elements (Nesbitt et al 2007). It may be that the large primitive coelophysids were killed off by the end Triassic mass extinction, to be replaced by more specialised types like the early Jurassic *Dilophosaurus wetherilli*, although, if *Liliensternus* is a transitional form (Nesbitt et al 2009) they may also constitute the ancestors of the dilophosaurs. MAK120208

Graphic: drawing of *Dilophosaurus* from Professor Paul Olsen's course notes

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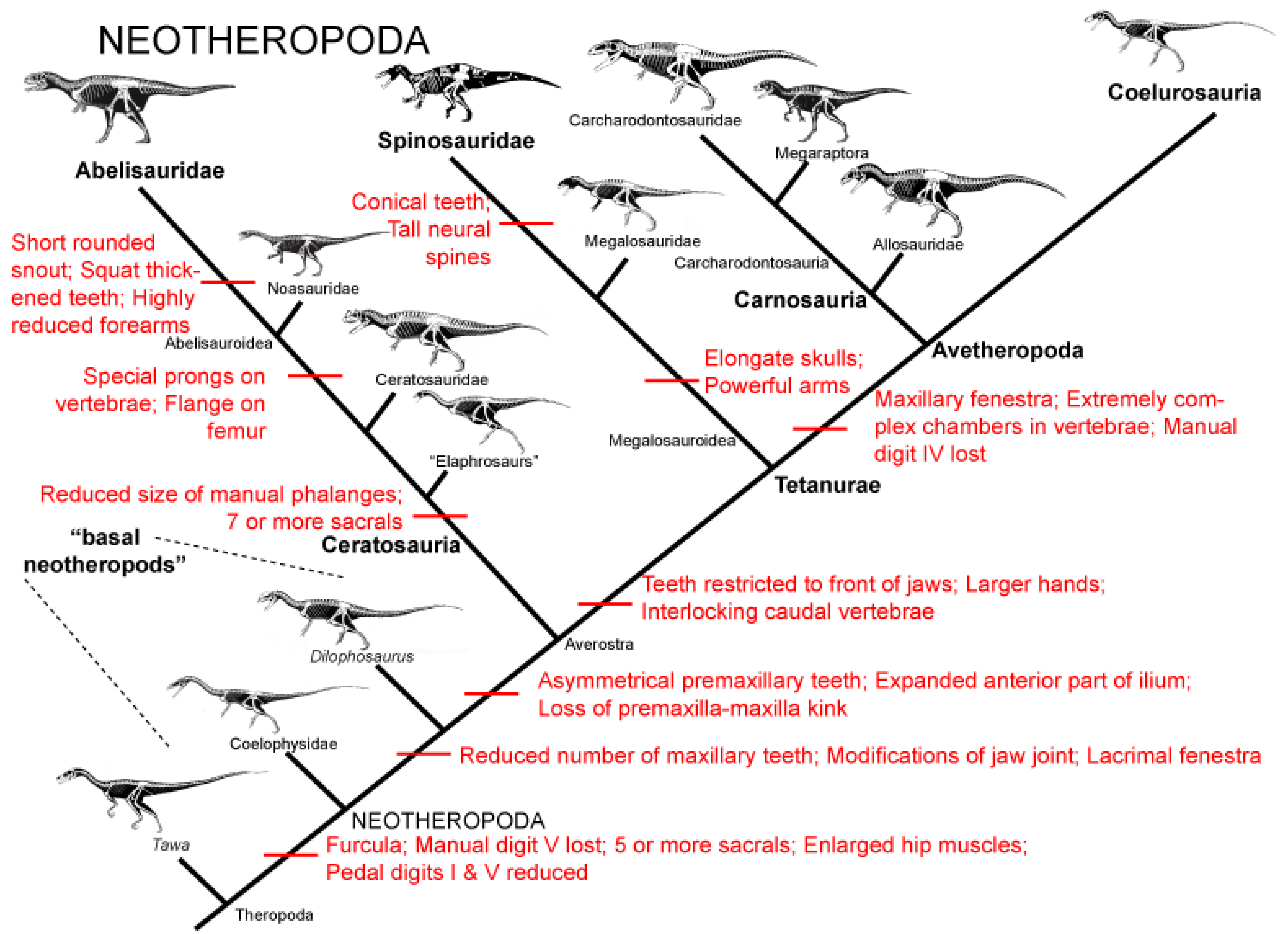


Simplified cladogram by Tom Holtz (Geology 104) showing the phylogenetic relationships and main synapomorphies of the Neotheropoda. Following a linear progressive development through basal theropods, coelophysids and dilophosaurs, the theropds diverged into two main lineages, the ceratosaurs and tetanurae, the latter of which further branched out into spinosaurs, allosaurs (here called carnosurs) and coelurosaurs. Each evolutionary stage is characterised by the loss or acquiring of various specialised characteristics (apomorphies). Determining the branching pattern (topology) of the cladogram is made more difficult by the independent acquiring of traits by different groups (convergences) as well as the loss of earlier traits (reversals). Recently, the discovery of the ostrich mimic *Limusaurus* (which would be located alongside *Elaphrosaurus* on this tree) has provided new insights regarding the loss of digits in the transition from theropod hand to bird wing. It was previously thought that digit IV was lost and the three inner ones retained, it is now known that theropods, in keeping with bird embryological development, lost the two outer digits I and V (the thumb and "pinkie"). Hence for example the avetheropoda (upper right of cladogram) are defined, among other things, by the loss of digit V (not IV)

Descriptions

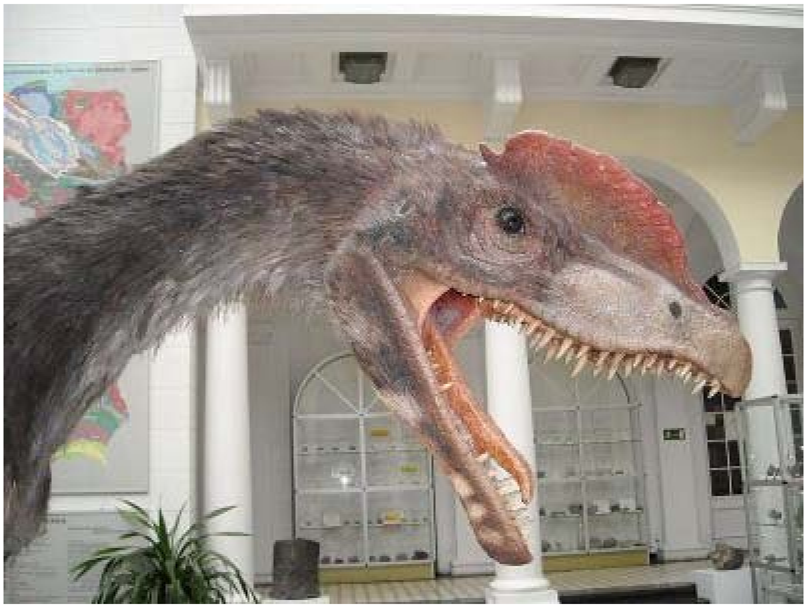
Dilophosaurus wetherilli (Welles, 1954)


Dilophosaurus wetherilli, Royal Tyrrell Museum.
Photo by Sebastian Bergmann, Flikr, Wikipedia, Creative Commons Attribution

Horizon: Kayenta Formation, Arizona (late Sinemurian / early Pliensbachian)

Phylogeny: Neotheropoda : Podokesauridae + *Zupaysaurus* + (*Cryolophosaurus* + "Dilophosaurus" *sinensis* + *Dracovenator* + Averostra + *)

Size: length 6 to 7 metres, weight: weight 300 to 450 kg (Paul 1988)

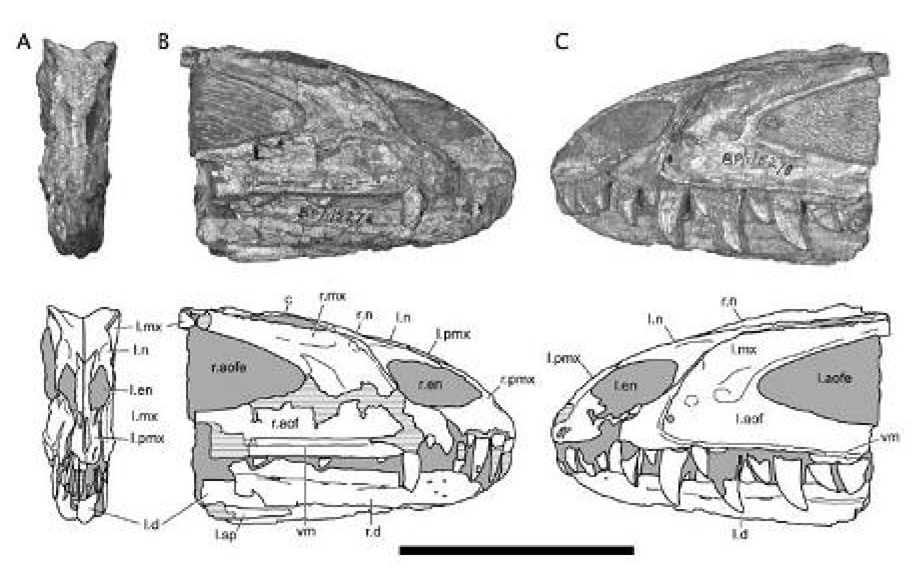

Head of a model of *Dilophosaurus wetherilli* nicknamed "Dyzio" in the Geological Museum of the Polish Geological Institute in Warsaw.
Photography by Wikipek, via Wikipedia, Creative Commons Attribution

Comments: The dominant preditor of the early Jurassic, more heavily built than earlier podokesaurs, this animal is distinguished by its large low build, large deep skull, unusually long teeth, and distinctive twin crests (left). Known from two possibly subadult skeletons, two skulls, additional partial skeleton and fragmentary remains .

This handsome animal has had the misfortune of being represented in the movie *Jurassic Park* as a sort ofdiminutive cross between a gremlin and a frill-necked lizard. Not only is the size in the movie version wrong, but the lower jaw is the wrong shape as well. The fallacy that the delicate head crests and "weak" snout (actually now known to be reinforced) only capable of made it unable to tackle live prey may also have led to the most unkely assumption (which first appears in Michael Chrichton's novel) that it spat poison (no archosaur is known to).

D. breedorum Welles vide Welles and Pickering, 1999 is probably a synonym. It has been suggested on basis ofan imprint of a similarly-sized theropod sitting down that these animals may have been feathered.

Dracovenator regenti Yates, 2006



Horizon: Upper Elliot Formation (Hettangian or Sinemurian)

Phylogeny: Neotheropoda : Podokesauridae + *Zupaysaurus* + (*Cryolophosaurus* + *Dilophosaurus wetherilli* + "Dilophosaurus" *sinensis* + Averostra + *)

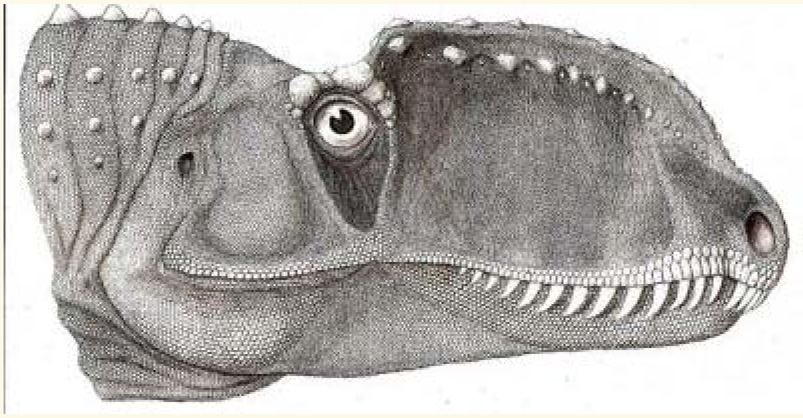
Size: estimated 5.5 to 6.5 meters long

Comments: known from a partial skull, which displays a mosaic of podokesaur and advanced theropod characteristics. Cladistic analysis finds this taxon is closely related to Dilophosaurus and Zupaysaurus, although the clade formed by these three taxa is not robustly supported (Yates 2006)

Links Adam Yates blog - The Story of Dracovenator - Part 1, part 1; Dinosaur mailing list (abstract); Wikipedia

Image copied from Gigadino

"Dilophosaurus" _sinensis_ Hu, 1993



Horizon: Lower Lufeng Series, Yunnan, China - Early Jurassic (Hettangian/Sinemurian/Pliensbachian)

Phylogeny: Neotheropoda : Podokesauridae + *Zupaysaurus* + (*Cryolophosaurus* + *Dilophosaurus wetherilli* + *Dracovenator* + Averostra + *)

Size: about 5 or 6 meters long

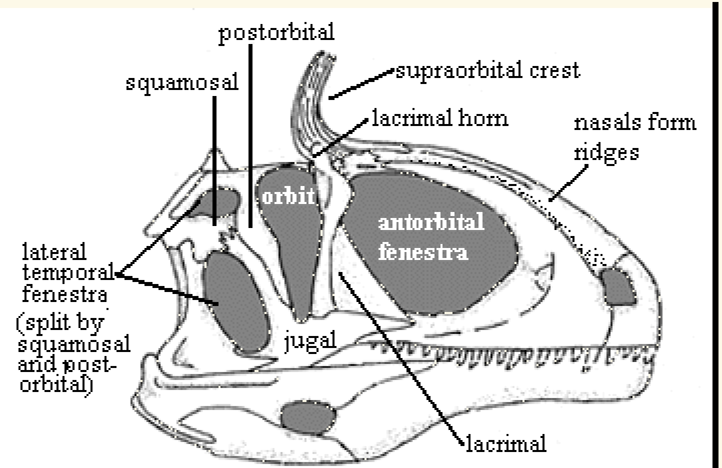
Comments: known from a skull and almost complete skeleton recovered from the Yunnan Province of China in 1987 (Hu1993), this animal was more heavily built than *D. wetherilli*, with an expanded scapula (shoulder blade) and taller, more robust pair of crests that are further forward on the skull. The kink in the upper jaw was not as noticable as in *D. wetherilli*, and the skull is somewhat similar to that of *Ceratosaurus*. It has been variously proposed that it is close to the tetaneura as it shares a number of synapomorphies (Irmis2004) a transitional form between Dilophosaurs and later theropods, or the most basal member of a monophyletic Dilophosauridae (Yates 2006). It may be closely reated to *Cryolophosaurus* (Wikipedia).

Image: *Dilophosaurus sinensis*, by Deviant Paleoart at en.wikipedia; Creative Commons Attribution-Share Alike license.

Cryolophosaurus ellioti Hammer and Hickerson, 1994; (informal senior synonym: *Elvisaurus*)

Horizon: Hanson Formation (Falla Formation), Central Transantarctic Mountains (Pliensbachian)

Phylogeny: Neotheropoda : Podokesauridae + *Zupaysaurus* + (*Dilophosaurus wetherilli* + "Dilophosaurus" *sinensis* + *Dracovenator* + Averostra + *)



Cryolophosaurus skull in right lateral view. Modified from Rich et al. (1997).

Characters: Large (6-7 m) theropod. Skull 65 cm long; skull tall & narrow; large antorbital fenestra; nasals form ridges which merge with supraorbital crest; crest extends whole distance between orbits; crest mainly composed of lacrimal; 2 small lacrimal horns posterolateral to crest; lacrimal pneumatized; lateral temporal fenestra divided by processes of postorbital and squamosal; quadrate short; hindlimbs primitive. ATW010511

Comments: As the name implies, *Cryolophosaurus* is a crested theropod from a cold land. This in fact is misleading, because during the early Jurassic Antarctica was part of the vast temperate landmass of Gondwana. The first Antarctic dinosaur to be officially named, it was recovered from Mt. Kirkpatrick, a site at a *paleo*latitude of 61-70° S (presently 84° S). This animal was found in association with prosauropods (Smith et al 2007b). This advanced (for its time) animal was a contemporary of the big Dilophosaurs, but is more heavily built and provably had different feeding strategies. *Cryolophosaurus* was originally considered the oldest known Tetanuran, but later interpreted as a dilophosaur, either a derived member of monophyletic clade (Yates 2006, Smith et al 2007 or the sister taxon of a clade composed of *Dilophosaurus* and averostrans (Nesbitt et al 2009); in both hypotheses it is placed adjacent to *Dilophosaurus*. The skull is high and narrow, with a peculiar nasal crest runs just over the eyes, where it rises up perpendicular to the skull and fans out transversely (from side to side; unlike most Allosauroid and dilophosaur crests, seems to have been structured for anteroposterior, not lateral, display.). It is furrowed, giving it a comb-like appearance. No other theropod has this feature (either the crests run from front to rear, or they form small hornlets, or both), which raises the possibility that there might be some sort of post-mortem deformation, although the consensus is universally that this animal really did look like this. Owing to the resemblance of this structure to Elvis Presley's pompadour hairstyle in the 1950s, this dinosaur was at one point informally known as "Elvisaurus". MAK010506 120220

Links: Cryolophosaurus - DinoData; Cryolophosaurus; Cryolophosaurus by Keith Strasser; Cryolophosaurus (Dutch); Polar dinosaurs in Australia; Augustana Geology Department In Antarctica. ATW050619

References: Rich *et al.* (1997).

Image: Cast of a *Cryolophosaurus ellioti* skull at the Australian Museum, Sydney. Photo by Matt Martyniuk; Wikipedia, GNU Free Documentation/Creative Commons Attribution-Share Alike license. This cast and the above drawing may be quite speculative as only parts of the skull are known, it portays Cryolophosaurus as having Allosaurian proportions, something that would be very unlikely given our current understanding of the placement of this species. Greg Paul (2010) gives a more realistic dilophosaurian reconstruction, witha long low skull and kinked snout. MAK120220

Averostra Paul, 2002 **:** Ceratosauria + Tetanurae

Definition: *Ceratosaurus nasicornis*, *Allosaurus fragilis* and all the descendants of their most recent common ancestor; node-based (Ezcurra & Cuny 2007, Langer et al 2010)

Synonyms: Neotheropoda (sometimes)

Range: Middle Jurassic to Recent

Phylogeny: Neotheropoda **:** Podokesauridae + *Zupaysaurus* + (*Cryolophosaurus* + *Dilophosaurus wetherilli* + "Dilophosaurus" *sinensis* + *Dracovenator* + * **:** (Neo)Ceratosauria + Tetanurae)

Characters: Asymmetrical premaxillary teeth (not simple cones); Exapanded anterior end of the ilium, with a hook-like blade (Tom Holtz).

Comments: neotheropoda (avepoda) above the level of stem taxa (paraphyletic Podokesauridse / Coelophysoidea). Paul Sereno has criticised Greg Paul's apomorphy-based definition, but we are following the node-based definition of Ezcurra & Cuny 2007 and later workers. The name Averostra means "bird snouts", aesthetically this would be a nice complement to Greg Paul's Avepoda (so the feet evolve first for increased locomation, then the snouts for grasping prey). Quoting Tom Holtz: "The basal members of Ceratosauria and Tetanurae typically have mediolaterally narrow, dorsoventrally deep skulls: sometimes nicknamed "hatchet heads". This skull patterns is good for striking hard against a victim and slicing it up. However, it is not particulary strong if shaken back-and-forth, and so these dinosaurs probably did not hold onto their prey for very long with their jaws. This made primitive averostrans "bite-and-slice" feeders: they could carve chunks out of victims, or wound them, but could not hold onto them with their jaws." Generally more heavily built, and hence able to tackle larger prey, than their dilophosaur ancestors and predecessors. There do not seem to be any known stem Averostrans (averostrans that have not yet become Ceratosaurs or Tetanurae, although this is not surprising given the poor fossil record from this time. Future analyses, discoveries, and reinterpretations of already known taxa may fill out this group. Perhaps poorly known ambiguous taxa like *Sarcosaurus* may belong here. Tom Holtz (see previous link) suggests that the more powerful build of averostrans may be a co-evolutionary "arms race" with larger and more advanced herbivorous dinosaurs such as thyreophorans, iguanodontians, and eusauropods. In any case, ancestral Averostrans quickly evolved into two clades, the persitantly primitive true Ceratosaurs and the highly succesful and more bird-like Tetanurae. The former would dominate southern continents, the latter, norththern. MAK120207

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Theropoda: Ceratosauria

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Herrerasauridae
   `--+--Podokesauridae
      `--+--Dilophosaurus
         |--Ceratosauria
         |   |--Spinostropheus
         |   |--"Limusauridae"
         |   |   |--Elaphrosaurus
         |   |   `--Limusaurus
         |   `--+--Ceratosauridae
         |      |   |--Ceratosaurus nasicornis
         |      |   `--Ceratosaurus 
dentisulcatus
         |      |?--Bahariasaurus/Deltadromeus
         |      `--Abelisauroidea
         |         |--Noasauridae
         |         `--Abelisauridae
         `--Tetanurae
            `--Avetheropoda
               |--Allosauroidea
               `==COELUROSAURIA
                   `--AVES
```

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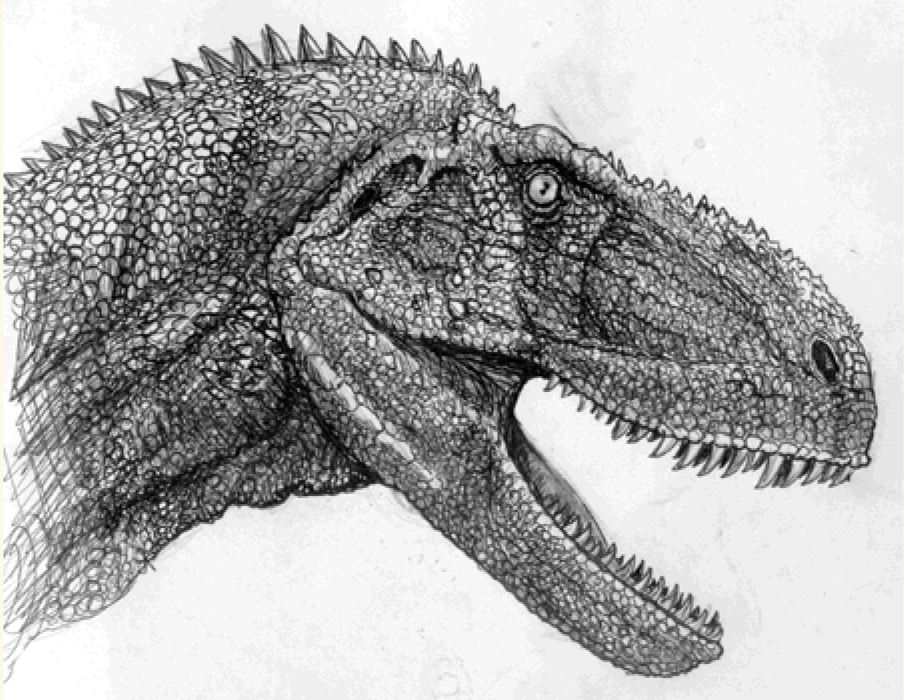
7. *Elaphrosaurus* X
8. "Limusauridae" X
9. *Limusaurus* X
10. *Spinostropheus* X



Abelisaurus, artwork courtesy of Frank DeNota

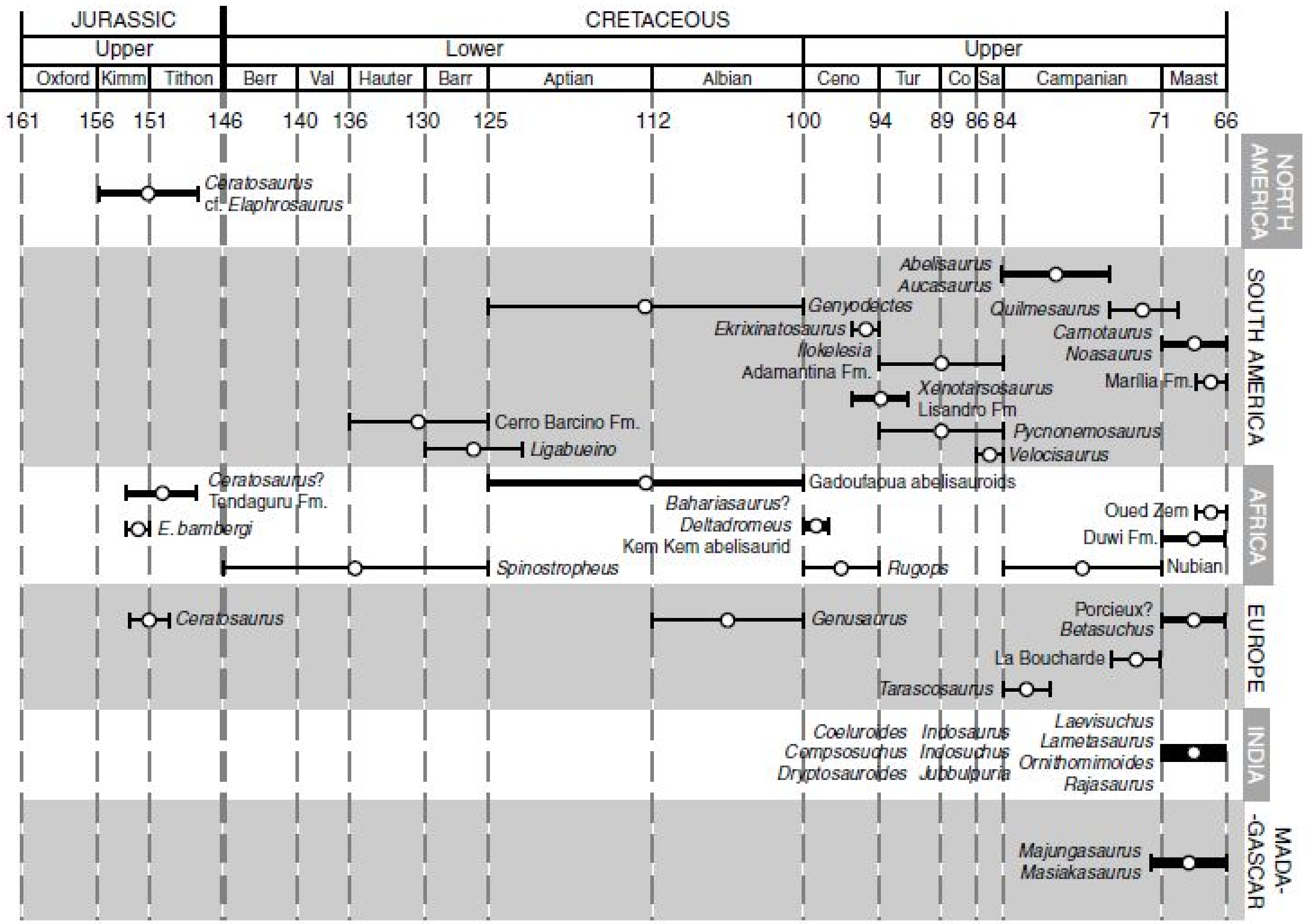
Ceratosauria - the other theropods

For more than one and a half centuries, dinosaur discoveries were characterised by predominantly northern (Laurasian) faunas, reflecting the fact that science (including paleontology) was centered in countries like Britian, France, Germany, and the United States, and that fossils from these countries (and their expeditions) would feature strongly and determine the way we thought about the evolution of life on Earth. So in the case of the Mesozoic, we think of the Late Triassic Keuper (Germany) and Chinle (SW USA) formations, and animals like *Plateosaurus* and *Ceolophysis*, the Early Jurassic the Liassic *Scelidosaurus* of England and Middle Jurassic *Megalosaurus* and *Cetiosaurus* of the same country and *Poekilopleuron* and *Omosaurus/Lexovisaurus* of France, late Jurassic the Morrison (central West USA) and Tendaguru (East Africa - German expedition) with their spectacular megafauna, the Early Createceous Wealden of England (with its classic trio of *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*), and the abundant latest Certaceous dinosaurs of Alberta, Montana, and Wyoming, the rich fauna of tyrannosaurs, ostrich dinosaurs, horned dinosaurs, duckbills, and the rest. When fossils from other parts of the world were discovered, they were slotted into northern taxa, so in the case of theropods, *Elaphrosaurus* was a coelurosaur (then an ornithomimosaur), *Genyodectes* a megalosaur, *Indosuchus* a megalosaur or an allosaur

In the late 20th century, dinosaurology underwent multiple shifts of focus. John Ostrom and his student Bob Bakker initiated the dinosaur renaissance and the realisation that dinosaurs were active animals closely related to birds, in China spectacular discoveries were made of feathered dinosaurs, supporting Ostrom and Bakker's hypothesis, and in South America (mostly Argentina) spectacular discovceries wer made not only of the earliest dinosaurs at the base of the family tree, but Cretaceous faunas very different to those of the ornithischian dominated north, including meat-eating dinosaurs that did not fit in to the normal model of theropod evolution.

When beginning in the mid 90s these Southern (Gondwanan) theropods were analysed via cladistic methods, it was realised that they constituted a large group totally disntinct from the familiar northern faunas. These are the Ceratosauria - the other theropods.

The Ceratosauria are a lineage of persistantly primitive theropods that suddenly appear in the fossil record around the later Middle/earlier Late Jurassic mark and continue right through to the end of the Cretaceous, co-existing with the standard theropods (or tetaneura). Phylogenetically, they are defined as including all species more closely related to *Ceratosaurus* than to birds. As well as larger forms such as *Ceratosaurus* and the Abelisauridae, the ceratosaurs also included smaller forms such as the primitive Limusaurs and the advanced Noasaurids. Although *Ceratosaurus* itself came from the Jurassic of North America, these animals had dissapeared from the northern continents by the early Cretaceous. By the Middle to Late Cretaceous this formerly minor lineage had come to dominated the medium to large carnivore niche not only throughout in Gondwana (with representatives known from South America, Africa, India, and possibly Australia), but in Europe as well. It is not known why these more primitive animals were able to supplant their more advanced, birdlike, and successful tetaneuran cousins (equivalent to the if Cretaceous marsupials had to supplant Cenozoic mammals); indeed, this is a good example of how misleading terms like "primitive" and advanced" can be, in terms of evolutionary success. MAK120210



Ceratosaur stratigraphic and geographical distribution, arranged by continent. Error bars reflect uncertainty in age, not time range. The line thickness is based on the number of taxa. No phylogenetic relationships are implied here. Diagram from Carrano & Sampson 2008, timescale from Gradstein et al. (2004). According to Greg Paul (2010), Spinostropheus might actually be Middle Jurassic in age, rather than Early Cretaceous, which would make it the earliest known Ceratosaur Abbreviations: Barr, Barremian; Berr, Berriasian; Ceno, Cenomanian; Co, Coniacian; Fm., Formation; Hauter, Hauterivian; Kimm, Kimmeridgian; Maast, Maastrichtian; Oxford, Oxfordian; Sa, Santonian; Tithon, Tithonian; Tur, Turonian; Val, Valanginian.The following , shows stratigraphic range, illustrating how primitive ceratosaurs conrtinued to co-exuist alongside more advanced forms.

Ceratosauria phylogeny - a study in phylogenetic controversy

Although the broad brush-strokes of Ceratosaur phylogeny are agreed upon, there is some disagrement when it comes to details of relationships between individual taxa, especially Abelisaurs. This is in part due to the incomplete nature of many species, known only from scrappy remains, and in part due to different cladistic methodologies and approaches. Holtz (1994) was the first to provide a formal cladistic analysis that included both podokesaurs and abelisaurs. He resolved the Ceratosauria into two clades: Coelophysoidea and Abelisauroidea, including *Ceratosaurus*, *Elaphrosaurus* and Abelisauridae.

```
==Theropoda
```

```
   |--Tetanurae
    `--Ceratosauria
       |--Coelophysoidea
       |   |--Coelophysidae
       |   `--Dilophosaurus
       `--Abelisauroidea
         |--Ceratosaurus
         `--+--Elaphrosaurus
             `--Abelisauridae
```

We now know that the Coelophysoidea (i.e., Podokesauridae) as originally defined were a paraphyletic assemblage, but the Abelisauroidea remain valid, and eventually became the redefined Ceratosauria

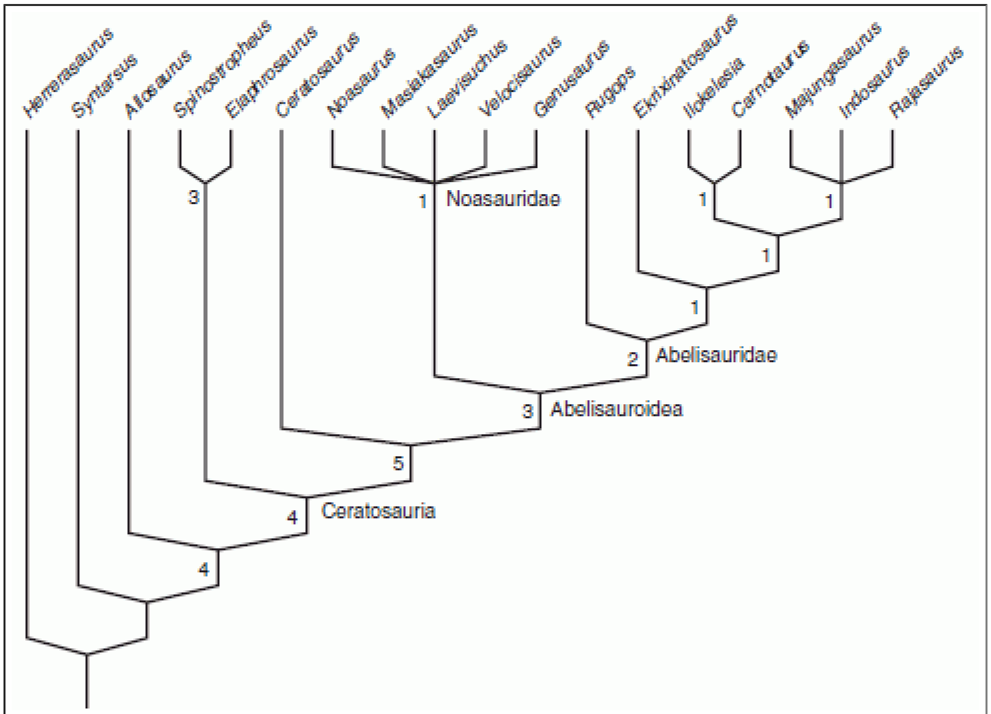
In any case, there followed a number of other papers. The most notable was Sereno et al 2004 which also described two new species, *Spinostropheus gautieri* and *Rugops primus*. These constitute intermediate forms, both morphologically and stratigraphically, between the more basal late Jurassic ceratosaurs *Ceratosaurus* and *Elaphrosaurus*, and the more advanced Cretaceous abelisaurs. In this way they arrived at the following cladogram:

```
==Ceratosauria
    |--Elaphrosaurus
    `--+--Ceratosaurus
         `--+--Spinostropheus
              |--Noasauridae
              |    |--Deltadromeus
              |    |--Noasaurus
              |    `--Masiakasaurus
              `--Abelisauridae
                   |--Rugops
                   |?-Ilokelesia
                   `--+--Abelisaurus
                      `--Carnotaurinae
                        |--Rajasaurus
                        `--+--Majungatholus
                           `--Carnotaurus
```

The most famous of the abelisaurs, the two-horned *Carnotaurus*, is here placed as a highly derived form at the summit of a scalloped Abelisauridae, whilst the Noasauridae constitute an unresolved polytomy (i.e. it is not clear which species in the group are related to which). Excluding the poorly resolved *Ilokelesia* (which seems to jump about almost at random, perhaps due to both its incomplete and its primitive or ancestral nature), the topology (tree shape) is *Rugops* + (*Abelisaurus* + (*Rajasaurus* + (*Majungatholus* + *Carnotaurus*))). The last three constitute the Carnotaurinae, the most specialised forms, whereas the eponymous Abelisaurus, which lacks the more dramatic crests and horns characteristic of most other members of the family, belongs with *Rugops* in a basal position. Indeed, most studiessupport a a close relationship between *Carnotaurus* and *Majungatholus* (more properly called *Majungasaurus*), with *Abelisaurus* as the outgroup (Sereno 1999; Sampson et al. 2001, Wilson et al 2003; Sereno et al 2004; Tykoski & Rowe 2004; Figs 2, 3).

A radically revised abelisaur phylogeny, based on strict consensus cladogram, was provided by Carrano & Sampson 2008, as follows:

```
==Theropoda
    |--Herrerasaurus
    `--+--Coelophysis rhodesiensis
         `--+--Allosaurus
            `--Ceratosauria
                |--+--Spinostropheus
                |   `--Elaphrosaurus
                `--+--Ceratosaurus
                   `--Abelisauroidea
                      |--Noasauridae
                      |   |--Laevisuchus
                      |   |--Masiakasaurus
                      |   |--Noasaurus
                      |   |--Velocisaurus
                      |   `--Genusaurus
                      `--Abelisauridae
                         |--Rugops
                         `--+--Ekrixinatosaurus
                            `--+--+--Ilokelesia
                                |    `--Carnotaurus
                                `--+--Majungasaurus
                                   |--Indosaurus
                                   `--Rajasaurus
```



Ceratosaur Cladogram, from Carrano & Sampson 2008 fig 4, the numbers are decay indices. The higher the number, the more robust the cladogram. This doesn't mean that the clades with the highest numbers are more likely to be true, only that they come up most strongly in this particular analysis

Rather than begining with a single new species, or a few well-known taxa, they incorporated a much larger number of taxa, and this diffent methodology not surprisingly resulte din a different tree topology. Their tree supports a monophyletic Abelisauroidea, Abelisauridae and Noasauridae, but Abelisaurus is no longer a primitive basal form, and the Carnotaurinae dissappear in an unresolved polytomy. *Ceratosaurus* is intermediate between the three basal African taxa (*Elaphrosaurus*, *Deltadromeus* and *Spinostropheus*) and the Abelisauroidea. There is no internal resolution in the Noasauridae, but within Abelisauridae, *Rugops* remains the most basal taxon in the latter family. It and *Ekrixinatosaurus* are successive outgroups to the more derived species (including *Abelisaurus*, here equal with *Carnotaurus* and co). Also in contrast to Sereno et al 2004, the three Madagascan and Indian taxa, *Majungasaurus*, *Rajasaurus* and *Indosaurus*, now form a single unnamed clade, supporting the idea of evolution (or more precisely adaptive radiation) through geographic isolation. This makes a lot of sense, as too often cladistics is based on specimens abstracted from geography and stratigraphy, a sif they were idealised platonic forms. Interestingly, early placental mammal evolution similarly appears to have been geographically determined, if molecular phylogeny is anything to go by.

In this particular analysis, Adams consensus revealed that *Deltadromeus*, *Abelisaurus* and *Aucasaurus* acted as 'wildcard' taxa, and so they were pruned to give a more stable cladogram in which *Elaphrosaurus*, and *Spinostropheus* are sister taxa (Limusauridae?). The primitive *Ilokelesia* is also paired with the highly derived *Carnotaurus* in a rather unlikely clade. The low decay indices (the numbers 1) show how weakly supported some of these results are, although that in itself does not mean they are necessarily incorrect.

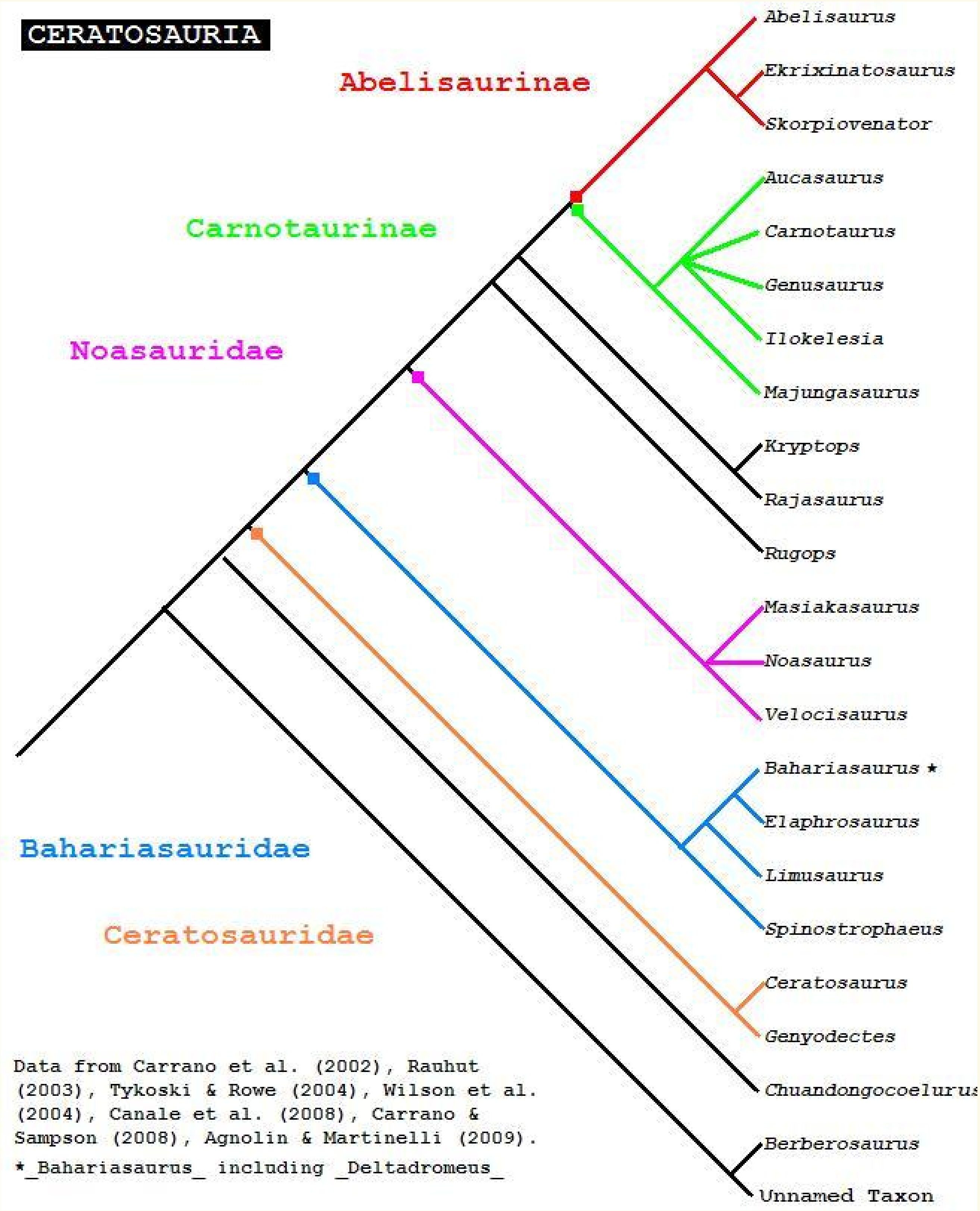
Canale et al 2008 return to a more conventional topology (along the lines of Sereno et al 2004), at least as far as abelisaurs go. Their analysis is similarly based on the discovery of a new species, in this case,*Skorpiovenator bustingorryi*, the most complete abelisaur discovered so far. The Carnotaurines are revived, along with a new clade, Brachyrostra. *Rugops* remains the most primitive abelisaurid, but *Ekrixinatosaurus* is now a highly specialised form, paired with *Skorpiovenator* and *Ilokelesia*, which is no longer closely related to *Carnotaurus*. *Elaphrosaurus* has become a stem-Noasaurid, reflecting the ambiguity among these basal forms.

```
==Theropoda
    |--Coelophysoidea
    `--+--Spinosauroidea
       |   |--Allosaurus
       |   `--Carcharodontosauridae
       `--Ceratosauria
           |--Ceratosaurus
           `--Abelisauroidea
               |--+--Ligabueino
               |  `--+--Elaphrosaurus
               |     `--+--Noasaurus
               |        `--Masiakasaurus
               `--Abelisauridae
                   |--Rugops
                   `--+--Abelisaurus
                      `--Carnotaurinae
                          |--Majungasaurus
                          `--Brachyrostra
                              |--+--Carnotaurus
                              |  `--Aucasaurus
                              `--+--Ilokelesia
                                 `--+--Skorpiovenator
                                    `--Ekrixinatosaurus
```

Finally, a detailed cladistic statistical analysis by Xu et al (2009) using a data matrix incorporating 65 taxa (from *Marasuchus* to *Confusciornis*) and 413 morphological characters and the newly described Jurassic ceratosaur *Limusaurus inextricabilis*, provided the following hypothesis of ceratosaur phylogeny:

```
==Ceratosauria
    |--Spinostropheus
    |--Deltadromeus
    |--+--Elaphrosaurus
    |  `--Limusaurus
    `--+--Ceratosaurus
        `--+--Noasauridae
            |    |--Noasaurus
            |    `--Masiakasaurus
            `--Abelisauridae
               |--Rugops
               |--Majungatholus
               |--Ilokelesia
               |--Ekrixinatosaurus
               |--Carnotaurus
               |--Aucasaurus
               `--Abelisaurus
```

The webpage Basal Ceratosauria (in Polish) includes these and many more cladograms, which have been cmbined in the following:



Data from Carrano et al. (2002), Rauhut (2003), Tykoski & Rowe (2004), Wilson et al. (2004), Canale et al. (2008), Carrano & Sampson (2008), Agnolin & Martinelli (2009).

*_Bahariasaurus_ including _Deltadromeus_

The following Ceratosaur supertree is modified from a dendrogram by Christopher Taylor, 111206, and incorporates the above phylogenies (some *incertae sedis* taxa removed)

```
==Ceratosauria [Neoceratosauria]
    |--Spinostropheus Xu et al 2009
    |--+--Elaphrosaurus bambergi Janensch 1920 Xu et al 2009, Holtz 2000
    |  `--Limusaurus inextricabilis Xu, Clark et al. 2009 Xu et al 2009
    `--Ceratosauroidea WS03
         |--Ceratosaurus nasicornis Marsh 1884 Xu et al 2009, Holtz 2000
         |?-Deltadromeus agilis Sereno, Dutheil et al. 1996 Xu et al 2009, Holtz 2000
         `--Abelisauroidea Xu et al 2009
              |--Noasauridae Xu et al 2009
              |    |--Noasaurus leali Bonaparte & Powell 1980 Xu et al 2009, N85, WS03
              |    `--Masiakasaurus knopfleri Sampson, Carrano & Forster 2001 Xu et al 2009,
SCF01
```

```
          `--Abelisauridae [Abelisauria] Xu et al 2009
             |--Rugops Xu et al 2009
             `--+--Abelisaurus comahuensis Bonaparte & Novas 1985 Holtz 2000
[Abelisaurinae] WS03
               |--+--Majungasaurus crenatissimus WS03 (= Majungatholus atopus Sues &
Taquet 1979 WS03, S03)
               |  `--Rajasaurus narmadensis Wilson, Sereno et al. 2003 WS03 (? =
Indosaurus matleyi Huene & Matley 1933 WS03)
               `--Brachyrostra Canale et al 2008 (we have made this a revised
Carnotaurinae WS03)
                 |--+--Ekrixinatosaurus Xu et al 2009
                 |  `--+--Ilokelesia Xu et al 2009
                 |     `--Skorpiovenator
                 `--+--Aucasaurus Xu et al 2009
                    `--Carnotaurus sastrei Bonaparte 1985 WS03, Holtz 2000
```

Descriptions

Ceratosauria Marsh 1884 **:** *Ceratosaurus*, Abelisaurs.

Definition: *Ceratosaurus* > birds. Padian *et al.* (1999)

Synonyms: Neoceratosauria

Range: Late Jurassic to Late Cretaceous.

Phylogeny: Averostra **:** Tetanurae + * **:** "Limusauridae" + (*Ceratosaurus* + Abelisauroidea)

Characters: Reduced size of manual phalanges, resulting in relatively weak, or even functionless, hands. This pattern seems to have been reversed in at least a few fingers on the hands of noasaurids) 7 or more sacral vertebrae (Tom Holtz).

Comments: Originally included a number of Triassic and early Jurassic taxa now considered to be basal neotheropoda. The status of the poorly known early Jurassic *Sarcosaurus* is uncertain, as it has been variously assigned to either the Ceratosauria or the Coelophysoidea, perhaps it is an intermediate form betwene the two. MAK120206

"Limusauridae" (informal taxon name) **:** *Elaphrosaurus*, *Limusaurus*, ?*Spinostropheus*

Range: Middle? to Late Jurassic of Afr, Asia, NAm, Eur.

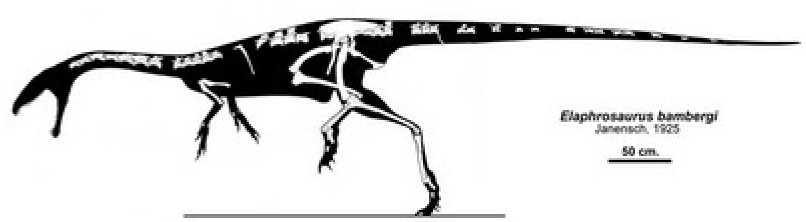
Phylogeny: Ceratosauria **:** (*Ceratosaurus* + Abelisauroidea) + * **:** *Elaphrosaurus* + *Limusaurus*

Comments: It seems that several smaller basal ceratosaurs formed an evolutionary lineage (or several) distinct from the large Ceratosaurids. This seems to be a group of medium-sized, diminutive-armed forms, at least some being toothless omnivores or herbivores. According to Carrano & Sampson 2008, *Elaphrosaurus* clusters with *Spinostropheus*; according to Xu et al 2009 with *Limusaurus*. We might informerly given this new taxon the name "Limusauridae" rather than "Elaphrosauridae" because *Limusaurus*is known from better material. If *Bahariasaurus/Deltadromeus* also belongs here (perhaps rather unlikely given the very different forearm proportions and modes of life, although this is not to deny that they might not still be related) then Bahariasauridae von Huene 1948 is an already avaliable name. MAK120217

Elaphrosaurus bambergi Janensch, 1920

Phylogeny: "Limusauridae" **:** *Limusaurus* + *

Horizon: Tendaguru beds of Tanzania (Kimmeridgian/Tithonian) (Late Jurassic of Afr)



Silhouetted skeletal reconstruction of *Elaphrosaurus bambergi* by Jaime Headden.

Size: length 6.2 meters, weight 210 kg

Comments: Known from a partial skeleton lacking skull, In build it is one of the slenderest and longest (in proprtion to height) of the theropods. *Elaphrosaurus* was originally considered a typical coelurosaur (using the trem in the the old non-cladistic sense of a wastebasket taxon for any small Jurassic theropod). It was then interpreted as an ancestral Ornithomimid (unlikely in view of the difference in hip structure) and a late surviving coelophysid (Greg Paul). In the absense of a skull, more cannot be determined. The current consensus, confirmed by independent cladistic studies, is that it is a primitive ceratosaur. This has bene further supported with the discovery of a more complete *Limusaurus*. Isolated remains indicate contemporary French and North American species which may or may not be assigned to this genus MAK010202 120224

Reference: Paul 1988, Xu et al 2009

Limusaurus inextricabilis Xu et al 2009

Horizon: Upper Shishugou Formation in the Junggar Basin of western China. (Oxfordian)

Phylogeny: "Limusauridae" **:** *Elaphrosaurus* + *

Comments: the first ceratosaur known from Asia, and the most completely known basal ceratosaur. Cladistic analysis places it as a sister taxon to *Elaphrosaurus* (Xu et al 2009), so we have united the two in the unofficial family "Limusauridae" (hence the inverted commas). The toothless beak and herbivorous diet make it convergent with Triassic Shuvosaurs, Cretaceous Ornithomimids, and Cenozoic ratites; all being similar in size and general appearance, a remarkable example of convergent evolution among three distinct archosaur lineages. MAK120206

The most extraordinary thing about *Limusaurus* is what it reveals of the development of the theropod hand and bird wing. To quote Wikipedia:

Limusaurus was a very basal ceratosaur characterized by hands retaining four digits (I-IV), digit I being strongly reduced. It was traditionally thought that the hands of dinosaurs evolved into the wings of birds by the disappearance of the two outward digits (IV and V), in contradiction to embryological studies on birds that showed that the retained digits are the three middle ones (II-III-IV). The hand structure of *Limusaurus* with its reduced digit I adds more weight to the digit II-III-IV identities for Tetanurae, among which are birds. Previous to the discovery of *Limusaurus*, theropods were assumed to have progressively evolved reduced digits on the ulnar side of the manus. This concept, known as Lateral Digit Reduction (LDR) is in contrast to Bilateral Digit Reduction (BDR), the reduction on digits on both sides of the hand commonly seen in all other tetrapod groups excluding dinosaurs. However, in *Limusaurus*, the first digit (Digit I) is strongly reduced, along with other ceratosaurs, suggesting that BDR occurred in their sister group the Tetanurae as well. (Xu et al 2009)

Previously, it was thought that digits I-III were retained in tetanurans as a homology with basal theropods, giving credence to the LDR hypothesis. However, the evidence of BDR in *Limusaurus* suggests that other non-avian theropods may also have exhibited BDR and the apparent digits I-III in tetanurans may actually be digits II-IV, a previous idea considered by Thulborn and Hamley, but largely ignored in the paleontological community. (Thulborn & Hamley 1982)

Despite the interesting possibilities brought up by *Limusaurus*, paleontologists are unlikely to stop calling tetanuran digits I, II, and III and switch to calling them II, III, IV. This is because most of their morphological traits resemble those of digits I, II and III of other theropods. It remains possible that bilateral digit reduction occurred in Ceratosauria but not in Tetanurae. The embryology of the bird wing could be explained by a homeotic frameshift of digital identity, as suggested by recent gene expression and experimental data. (Vargas et al 2009)

Links Darren Naish - Limusaurus: awesome and wonderful, with or without the hands

Reference: Xu et al 2009

Images: Theropod Hand Evolution from The Theropod Blog

Spinostropheus gautieri Sereno, Wilson, and Conrad, 2004

Horizon: Tiouraren of Niger - Middle Jurassic of Nth Afr

Phylogeny: Ceratosauria **:::** *.

Size: Estimated length: about 4 meters

Comments: Originally *Elaphrosaurus gautieri* Lapparent, 1960, there seems to be little relation between this species and *E. bambergi*, apart from the fact that they are both basal ceratosaurs of approximately the same size. Despite the fact that all that is known of this animal is a series of presacral vertebrae, it has been coded in various ceratosaur cladistic analsyses and not surprisingly tends to jump around a lot, although there is agreement on aplacement stemward of (more primitive than) the Abelisauroidea. The Tiouraren formation, from which highly distinct dinosaurs such as Jobaria and Afrovenator have been recovered has bene reinterpreted as Middle Jurassic in age (Rauhut & Lopez-Arbarello 2009), although the dating still remains uncertain. MAK120206

Ceratosauridae: ;

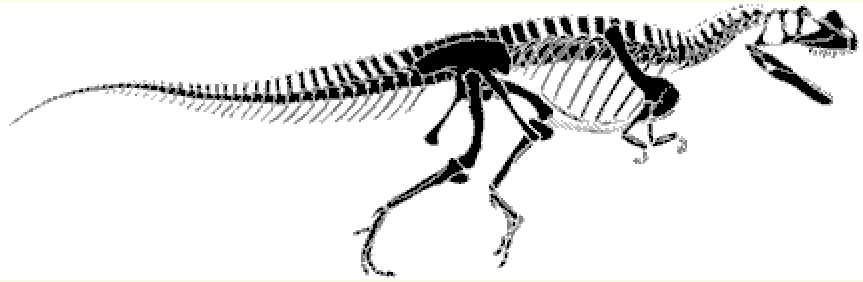
Range: Late Jurassic of NAm, Eur, ?Afr

Phylogeny: Ceratosauria **:** "Limusauridae" + (Abelisauroidea + * **:** *Ceratosaurus nasicornis* + *Ceratosaurus dentisulcatus*)

Comments: Monotypal family of large late Jurassic ceratosaurs, consisting so far only of several species of the single genus *Ceratosaurus*. These animals existed alongside the better known and more successful Allosaurids. A huge theropod known only from teeth from the Tendaguru of Africa is usually attributed to this group as *Ceratosaurus ingens*, but could pertain to any large theropod.

Image: *Ceratosaurus nasicornis*, sketch of skull, from Steele, 1970

Ceratosaurus nasicornis Marsh, 1884



Horizon: Lower and Middle Morrison formation (Kimmeridgian to Early Tithonian) of NAm

Phylogeny: Ceratosauridae **:** *Ceratosaurus dentisulcatus* + *.

Size: length about 5.7 meters, weight 500 kg

Comments: For a long time the only well-known ceratosaur, distinguished by its nasal horn/crest. Smaller and less common than it's contemporary *Allosaurus*. These were ambush predators with large bladed teeth. The deep and heavy tail may have been used for swimming (Paul 2010 p.85). Often (Carrano & Sampson 2008, Xu et al (2009)) considered morphologically intermediate between basal ceratosaurs and abelisaurs. Interesting because it is structurally so much more primitive than its allosaur contemporaries, this medium-sized theropod is characterised by its tall nose horn and smaller preorbital horns in front of the eyes. It also possesses a row of bony nodules down the spine, similiar to those of pseudosuchian thecodonts and the earliest dinosaurs. The skull lightly-constructed skull is armed with quite proportionally large teeth. It is unlikely this animal could bring down large game (in contrast to the *Allosaurs*); it probably preyed on smaller animals like ornithopods. *C. nasicornis* is the type species of the genus. *C. magnicornis* appears to be a synonym (growth stage or intra-specific variation), although it may be a related species or descendant (Paul 1988, Paul 2010) MAK001213 120224

Image: *Ceratosaurus nasicornis* skeletal reconstruction, redrawn from Greg Paul, from The Real Jurassic Park - Professor Paul Olsen

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Ceratosaurus dentisulcatus Madsen and Welles, 2000

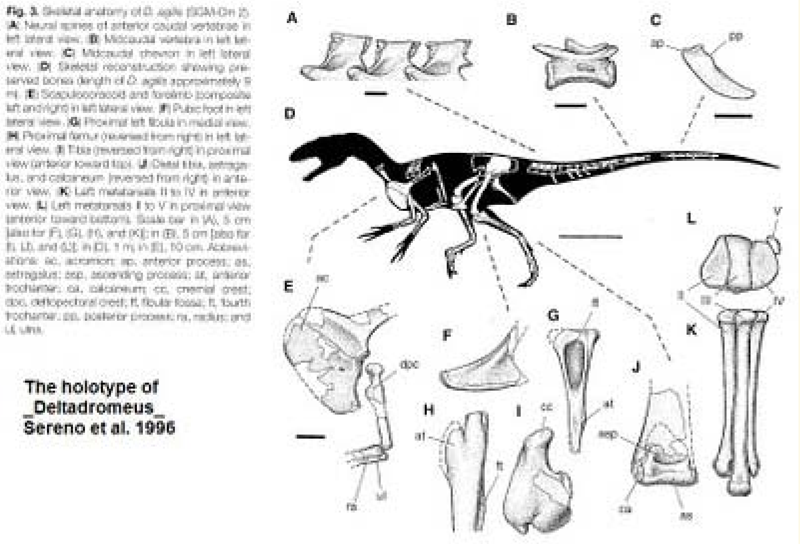
Horizon: Upper Morrison formation of Utah (Middle Tithonian)

Phylogeny: Ceratosauridae **:** *Ceratosaurus nasicornis* + *.

Size: length 7 meters, weight about 1 tonne

Comments: A large ceratosaur. Quoting Tim Williams (Dinosaur Mailing List): "*C. dentisulcatus* is the second new Ceratosaurus species named by Madsen and Welles. It appears to be more distinct from *C. nasicornis* than *C. magnicornis* is, and so can more reliably be considered a new species. It gets its species name by the distinct grooves (sulci) running down the length of the anterior teeth of the upper jaw. C. dentisulcatus also has fewer maxillary and dentary teeth, and the front of the dentary is strongly curved and upturned. There are also proportional differences in the elements of the skull (such as a lower snout) and postcranium compared to the two other North American *Ceratosaurus* species. The nasals and lacrimals are not preserved in *C. dentisulcatus* so its "horns" (assuming it had them) cannot be compared with the other two species." MAK001213 A very similar (Mateus et al 2006), somewhat smaller form is known from Lourinha in Portugal, at the time a large, seasonally dry island with open woodlands, may represent a new species Paul 2010 p.85

Bahariasaurus ingens Stromer, 1934,



The holotype of
Deltadromeus
Sereno et al. 1996

Synonym: or closely related species: *Deltadromeus agilis* Sereno et al 1996

Range: Mid Cret (Early Cenomanian) of Nth Afr

Phylogeny: Ceratosauria **:::** *

Size: 11 to 13.3 meters long, 2.5 to over 4 tonnes in weight (Mortimer 2003, Paul, 2010).

Comments: *Bahariasaurus ingens* Stromer, 1934, was a gigantic (estimated length 11 meters or more) theropod known from partial postcrania. It was one of several enormous species of dinosaurs unearthed in the Sahara by the German paleontologist Ernst Stromer in the early part of the 20th century; others included Aegyptosaurus, Carcharodontosaurus, and Spinosaurus, as well as the giant crocodilian Stomatosuchus. In 1944, Stromer's entire fossil collection - housed in a Munich museum - was destroyed by an Allied Royal Air Force bombing raid. (Wikipedia). All taht remained were drawings of the spectacular specimens. Forward almost a century and modern paleontologist Paul Sereno andd co-workers undertook their own expeditions to the Sahara, where they found many secimens of what were apparently the same taxa, or at least similar species. For example, the somewhat smaller (8 meters) *Deltadromeus agilis* Sereno, Dutheil, Iarochene, Larrson, Lyon, Magwene, Sidor, Varricchio, and Wilson, 1996 (certainly author part of a scientific name has grown a lot longer since Stromer's day) appears to be the same animal as *Bahariasaurus*, probably a juvenile or sub-adult. This was a long-legged, gracile (lightly built) animal, which seems to have been built for speed, but also with unusually large coracoids (part of the shoulder girdle), suggesting long and strong forearms (see illustration of holotype). Originally described as a giant coelurosaur, it was then reinterpreted as a giant Noasaurid (Sereno et al 2004), although most more recent cladistic studies suggest it was actually a basal ceratosaurian (Carrano & Sampson 2008, Carrano et al 2011), with a few dissenters (Cau, et al 2011for example places *Deltadromeus* in a new clade with -*Limusaurus* and *Masiakasaurus*). No skull or complete skeleton is known, and the exact phylogenetic relationship of this animal remains controversial. As to why this part of

North Gondwana during the middle Cretaceous featured no less than *three* quite different gigantic predators is not clear. MAK120210

We have followed Sereno et al 2004 in placing *Deltadromeus/Bahariasaurus* as a more advanced taxon (above the Ceratosaurid grade), owing to its late appearance. No other basal (primitive) ceratosaur is known from the Cretaceous, and its important not to let ghost lineages multiply out of all proportion. Whether *Bahariasaurus* is a gigantic noasaur is another matte. it is likely that there were many lines of intermediate-level ceratosaurs in Gondwana at this time. MAK120226

Images: *Deltadromeus* holotype, from The Theropod Blog

Abelisauroidea Bonaparte 1991 **:** *Abelisaurus*, *Carnotaurus*, *Noasaurus*, etc

Phylogenetic definition: The least inclusive clade containing *Carnotaurus sastrei* Bonaparte 1985 and *Noasaurus leali* Bonaparte and Powell 1980 (node-based) (Wilson et al 2003) (Paul Sereno - Taxon Search)

Synonyms: Abelisauria

Range: Middle to Late Cretaceous (Aptian/Albian-Maastrichtian) of SAm, India, Madagascar, Europe, Aus

Phylogeny: Ceratosauria **:::** *Ceratosaurus* + (*Bahariasaurus* + * **:** Abelisauridae + Noasauridae)

Characters: anterolateral articulation for nasal process, intramandibular socket (Sereno et al 2004), vertebrae with prongs, flange on their femur (Tom Holtz).

Comments: The "crown group" of Createcous ceratosaurs. They are divided into the small noasaurids and the large abelisaurids This recalls the old and outmoded distinction of theropods in general into large (carnosaurs) and small (coelurosaurs), and one may question how accurate such interpretations are. The noasaurs have few if any defining synapomorphies, and may simply represent a primitive assemblage (paraphyletic grade), one particcular lineage of which became the large and specialsed abelisaurids. MAK120217

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Theropoda: Ceratosauria: Abelisauridae

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Herrerasauridae
   `--+--Podokesauridae
      `--+--Dilophosaurus
         |--Ceratosauria
         |   |--"Limusauridae"
         |   `--+--Ceratosaurus
         |      `--Abelisauroidea
         |         |--Noasauridae
         |         `--Abelisauridae
         |            |--Kryptops
         |            `--+--Rugops
         |               `--+--Abelisaurus
         |                  |--"Majungasaurinae"
         |                  |   |--Majungasaurus
         |                  |   `--Rajasaurus
         |                  `--Brachyrostra  (= monophyletic
Carnotaurinae?)
         |                     |--Ekrixinatosaurus
         |                     `--+--Ilokelesia
         |                         `--+--Skorpiovenator
         |                             `--Carnotaurini
         |                                |--Aucasaurus
         |                                `--Carnotaurus
         `--Tetanurae
            `--Avetheropoda
               |--Carnosauria
               `==COELUROSAURIA
                  `--AVES
```

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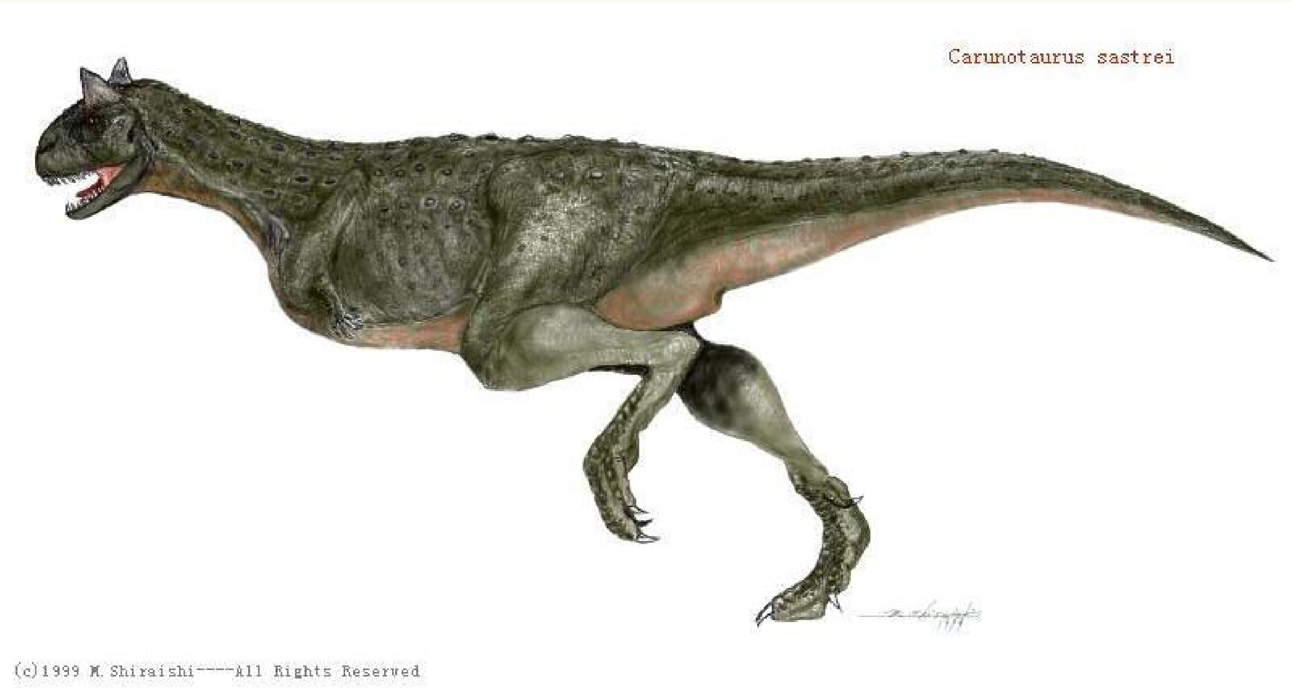
8. *Kryptops* X
9. *Ilokelesia* X
10. "Majungasaurinae" X
11. *Majungasaurus* X
12. *Rajasaurus* X
13. *Rugops* X
14. *Skorpiovenator* X



Carnotaurus sastrei, artwork courtesy of M. Shiraishi

The Abelisauridae are an important Cretaceous group known mainly from Gondwana. They are also among the more recent dinosaur groups to be discovered, only being unearthed in the 1980s, from rocks of the Latest Cretaceous (Maastrichtian) age in Argentina. In the following decades, other representative oif the group have come to light, whether new discoveries or reinterpretations of older ones, not only in South America but also Madagascar, India, north Africa, and France.

The group includes a number of strange-looking, large to very large, theropods, characterised by a tendency to horns or crests above the eyes (best represented by the iconic horned dinosaur *Carnotaurus sastrei*), thickening of the skull roof, deep skulls, very lightly built lower jaws, and vestigal, apparently useless arms and hands, reduced so they became even smaller than the tiny forelimbs of the Tyrannosaurs. The abelisaur phylogenetic placement was at one time very questionable. As they combine tyrannosaurid as well as ceratosaur and carcharodontosaur characters, their evolutionary relationship in the past has been difficult to determine. Cladistic analysis however has since unanimously agreed that they are late surviving ceratosaurs. Along with spinosaurs and carcharodontosaurs, abelisaurs make up a unique assemblage of Cretaceous Gondwanan theropods, whose co-existence woudl have been due to niche partitioning. In the later Cretaceous however, abelisaurids were the only large preditors in the southern continents. MAK990512 120211

The following material is copied from the Wikipedia pages on Abelisauridae and *Majungasaurus*

The abelisaurid skull

Although skull proportions varied, abelisaurid skulls were generally very tall and often very short. In Carnotaurus, for example, the skull was nearly as tall as it was long. The premaxilla in abelisaurids was very tall, so the front of the snout was blunt, not tapered as seen in many other theropods.

Two skull bones, the lacrimal and postorbital bones, projected into the eye socket from the front and back, nearly dividing it into two compartments. The eye would have been located in the upper compartment, which was tilted slightly outwards in *Carnotaurus*, perhaps providing some degree of binocular vision. The lacrimal and postorbital also met above the eye socket, to form a ridge or brow above the eye.

Sculpturing is seen on many of the skull bones, in the form of long grooves, pits and protrusions. Like other ceratosaurs, the frontal bones of the skull roof were fused together. Carnotaurines commonly had bony projections from the skull. Carnotaurus had two pronounced horns, projecting outward above the eyes, while its close relative

Reconstructed *Abelisaurus* skull, "Dinosaurs of Patagonia" exhibit. Note the rough bone surfaces and projections from the lacrimal and postorbital bones into the eye socket.
Photo by , Wikipedia Creative Commons Attribution

Aucasaurus had smaller projections in the same area. *Majungasaurus* and *Rajasaurus* had a single bony horn or dome, projecting upwards from the skull. These projections, like the horns of many modern animals, might have been displayed for species recognition or intimidation (Bonaparte et al 1990, Wilson et al 2003, Tykoski&Rowe 2004)

Forelimbs and hands

The forelimbs are known only in the advanced abelisaurids *Aucasaurus*, *Carnotaurus*, and *Majungasaurus*. All had forelimbs which were vestigial. The bones of the forearm (radius and ulna) were extremely short, only 25% of the length of the upper arm (humerus) in *Carnotaurus* and 33% in *Aucasaurus*. The entire arm was held straight, and the elbow joint was immobile.Senter 2010

As is typical for ceratosaurs, the carnotaurine hand contained four basic digits. However, it is there that any similarity ends. No wrist bones existed, with the four palm bones (metacarpals) attaching directly to the forearm. There were no finger bones on the first or fourth digits, only one on the second digit and two on the third digit. These two external fingers were extremely short and immobile, and lacked claws Senter 2010

It is unknown if this peculiar forelimb structure applies to more basal abelisaurids, as their forelimbs have not been discovered (Coria et al 2002). More primitive relatives such as *Noasaurus* and *Ceratosaurus* had longer, mobile arms with fingers and claws (Agnolin & Chiarelli 2010).

Hind limbs

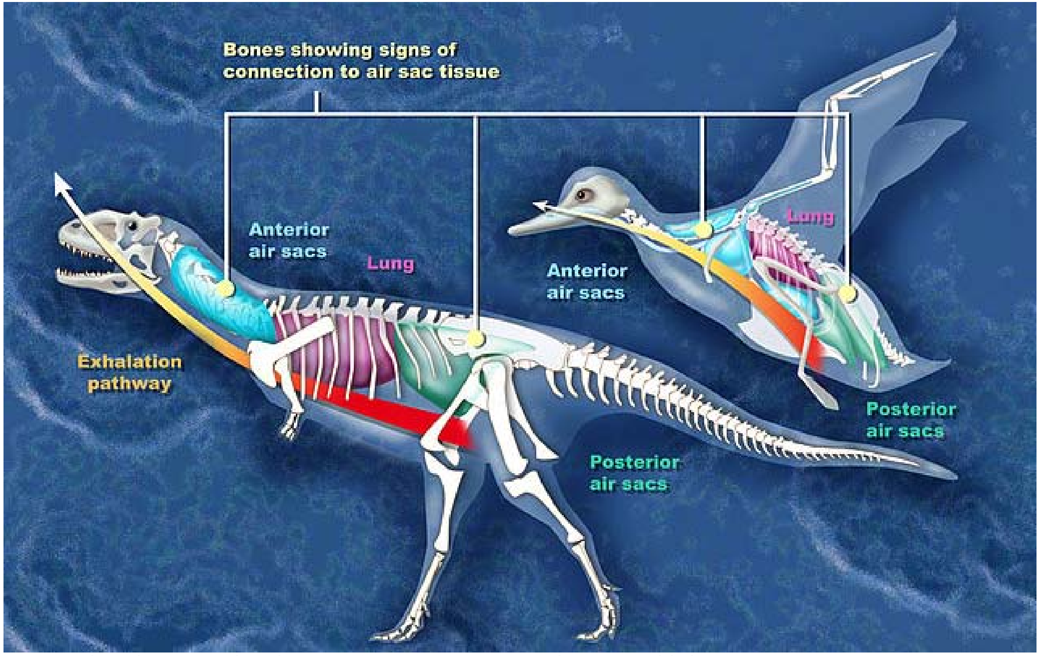
Abelisaurid hindlimbs were more typical of ceratosaurs, with the astragalus and calcaneum (upper ankle bones) fused to each other and to the tibia, forming a tibiotarsus. The tibia was shorter than the femur, giving the hindlimb stocky proportions. There were three functional digits on the foot (the second, third, and fourth), while the first digit, or hallux, did not contact the ground.Tykoski & Rowe 2004. The astragalus and calcaneum (ankle bones) were fused together, and the feet bore three functional digits, with a smaller first digit that did not contact the ground. (Carrano 2007).

Feeding

Scientists have suggested that the unique skull shape of abelisaurids indicate different predatory habits than other theropods. Whereas most theropods were characterized by long, low skulls of narrow width, abelisaurid skulls were taller and wider, and often shorter in length as well.(Sampson & Witmer 2007) The narrow skulls of other theropods were well-equipped to withstand the vertical stress of a powerful bite, but not as good at withstanding torsion (twisting) (Rayfield et al 2001). In comparison to modern mammalian predators, most theropods may have used a strategy similar in some ways to that of long- and narrow-snouted canids, with the delivery of many bites weakening the prey animal. (Van Valkenburgh & Molnar 2002)

Respiratory system

Scientists have reconstructed the respiratory system of the advanced abelisaurid *Majungasaurus* based on a superbly preserved series of vertebrae (UA 8678) recovered from the Maevarano Formation. Most of these vertebrae and some of the ribs contained cavities (pneumatic foramina) that may have resulted from the infiltration of



Comparison between the air sacs of *Majungasaurus* and a recent bird.
Graphic by Zina Deretsky, National Science Foundation, via Wikipedia Public Domain

avian-style lungs and air sacs. In birds, the neck vertebrae and ribs are hollowed out by the cervical air sac, the upper back vertebrae by the lung, and the lower back and sacral (hip) vertebrae by the abdominal air sac. Similar features in *Majungasaurus* vertebrae imply the presence of these air sacs. These air sacs may have allowed for a basic form of avian-style 'flow-through ventilation,' where air flow through the lungs is one-way, so that oxygen-rich air inhaled from outside the body is never mixed with exhaled air laden with carbon dioxide. This method of respiration, while complicated, is highly efficient.

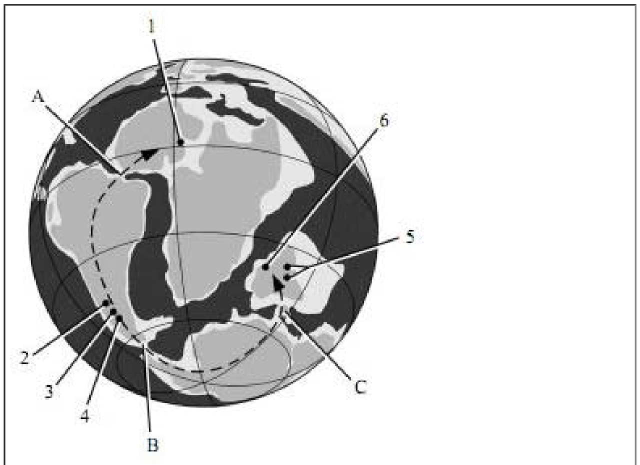
The recognition of pneumatic foramina in *Majungasaurus*, besides providing an understanding of its respiratory biology, also has larger-scale implications for evolutionary biology. The split between the ceratosaur line, which led to *Majungasaurus*, and the tetanuran line, to which birds belong, occurred very early in the history of theropods. The avian respiratory system, present in both lines, must therefore have evolved before the split, and well before the evolution of birds themselves. This provides further evidence of the dinosaurian origin of birds. (O'Connor & Claessens 2006)

Brain and inner ear structure

Computed tomography, also known as CT scanning, of a complete *Majungasaurus* skull (FMNH PR 2100) allowed a rough reconstruction of its brain and inner ear structure. Overall, the brain was very small relative to body size, but otherwise similar to many other non-coelurosaurian theropods, with a very conservative form closer to modern crocodilians than to birds. One difference between *Majungasaurus* and other theropods was its smaller flocculus, a region of the cerebellum that helps to coordinate movements of the eye with movements of the head. This suggests that *Majungasaurus* and other abelisaurids like *Indosaurus*, which also had a small flocculus, did not rely on quick head movements to sight and capture prey.

Inferences about behavior can also be drawn from examination of the inner ear. The semicircular canals within the inner ear aid in balance, and the lateral semicircular canal is usually parallel to the ground when the animal holds its head in an alert posture. When the skull of *Majungasaurus* is rotated so that its lateral canal is parallel to the ground, the entire skull is nearly horizontal. This contrasts with many other theropods, where the head was more strongly downturned when in the alert position. The lateral canal is also significantly longer in *Majungasaurus* than in its more basal relative *Ceratosaurus*, indicating a greater sensitivity to side-to-side motions of the head. (Sampson & Witmer 2007)

Abelisaurs and Paleogeography



Early Late Cretaceous (Early Cenomanian, palaeogeographic map (Scotese 2001) showing all known Late Cretaceous abelisaurid localities (numbers) and key land bridges (letters). The arrow shows the southern high-latitude dispersal route of the 'Africa-first' and 'panGondwana' models of Cretaceous biogeography. The 'Africa-first' model argues that land bridge A was broken in the Early Cretaceous, 30-50 Myr earlier than land bridges B and C; the 'pan-Gondwana' model argues for

The discovery of Abelisaurids in India and Madagascar as well as Argentina inspired theories of paleogeographical migration similar to those postulated for the early evolution of mammals. The most popular is the "Africa-first" model, which supposes that Africa split away from the rest of Gondwana first, the remainder of the supercontinent being unified by two land bridges until the Late Cretaceous (figure 1, land bridges B, C). This is contradicted both by palaeogeographic reconstructions (which have several landmasses separated by intervening seaways early in the Cretaceous (Smith et al. 1994; Roeser et al. 1996), as well as paleontological evidence such as notosuchian crocodylomorphs that show a close connection between of mid-Cretaceous African and South American crocodylomorphs, carcharodontosaur dinosaurs, and so on. An alternative model is the "pan-Gondwana" hypothesis, where three narrow and probably intermittent, passages connected major Gondwanan landmasses during the Early Cretaceous (figure 1, land bridges A-C). These were severed during a relatively brief interval during the middle Cretaceous. This differs from the "Africa-first" model in the presence of a trans-Atlantic passage (land bridge A). Similarity of faunas across continets during this time (including Abelisaurs such as *Rugops* even in continental Africa) supports a narrow time interval for their permanent separation (Sereno et al 2004)

Significantly however, recent research (Carrano & Sampson 2008) supports the existence of an endemic central Gondwanan (India and Madagascar) clade distinct final separation at land bridge A at the end of the Early Cretaceous. Land bridges: A, Walvis Ridge, Rio Grande Rise; B, Palmer Land Block, South Georgia Island Terrane; C, Kerguelan Plateau, Gunnerus Ridge. Abelisaurid localities: 1, *Rugops primus*; 2, *Aucasaurus garridoi*; 3, *Abelisaurus comahuensis* and *Ilokelesia aguadagrandensis*; 4, *Carnotaurus sastrei*; 5, *Rajasaurus narmadensis*; 6, *Majungatholus (= Majungasaurus) atopus*. Diagram and caption from Sereno et al 2004).

from the West Godwnana (South American) forms. It is likely that this group evolved in the late Cretaceous following separation of the continents, although the West Gondwanan clade (Brachyrostra) is known even from the middle Cretaceous

Descriptions

Abelisauridae Bonaparte and Novas 1985 **:** *Abelisaurus*, *Carnotarus*

Phylogenetic definition: The most inclusive clade containing *Carnotaurus sastrei* Bonaparte 1985 but not *Noasaurus leali* Bonaparte and Powell 1980, *Coelophysis bauri* (Cope 1889), or *Passer domesticus* (Linnaeus 1758). (stem-based) (Paul Sereno - Taxon Search)

Range: Middle to Late Cretaceous (Aptian/Albian-Maastrichtian) of SAm, India, Madagascar, Europe

Phylogeny: Abelisauroidea **:** Noasauridae + * **:** *Rugops* + (*Abelisaurus* + Carnotaurinae)

Characters: Very rugose (horny) texture of the bones of the face: this would have supported some sort of softer tissue, but whether keratin (horn-like structures) or some thickened skin is not ceratin; Short rounded snouts; Thickened skull roof; Squat thickened teeth; Forearms highly reduced: the ulnae and radii are practically no more than carpals; Relatively short and stocky hindlimbs. (Tom Holtz), groove-and-pit ornamentation, basic abelisaurid skull design (Sereno et al 2004).

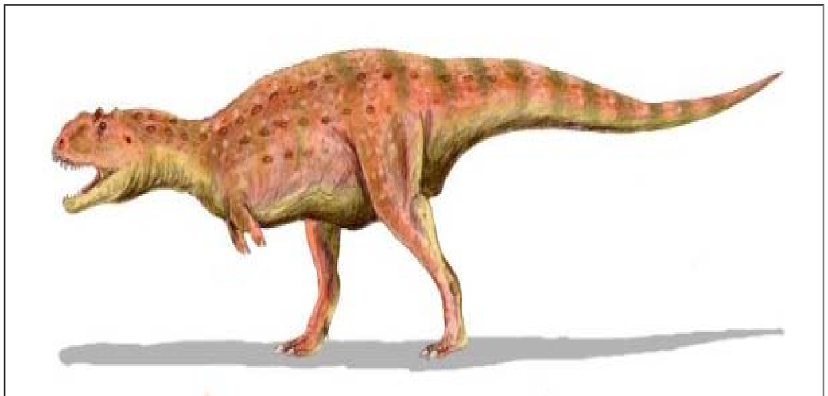
Comments: A remarkably succesful clade of large theropods, known from South America, India, Madagascar, and Northern Africa. No doubt future discoveries will reveal and even greater distribution. During the Middle Cretaceous they not only co-existed with giant charcharodontosaur and spinosaur theropods, but actually outlived them, becoming the apex predators of every continet except Asia-America. These were large preditors that filled the same ecological role in middle and late Cretaceous Gondwana as Allosaurs and Tyrannosaurs did during the Cretaceous of the northern supercontinent (Laurasia). An original division of abelisaurids into abelisaurines, with rather long, flat skulls that resemble in some ways the skulls of tyrannosaurids, and carnotaurines, with short, deep, ornamented skulls, has not been confoirmed by cladistic analysis and so is rejected here. It seems instead that the development of horn-like structures and differential cranial thickening appear to be convergently acquired within Abelisauridae. These short thin crests or horns are very different to the dilophosaur crests. All abelisaurs appear to have had side-to-side expanded "cheeks," like those of tyrannosaurids. Whilst *Abelisaurus* and *Carnotaurus* are the two best known genera, there are a number of other forms that have recently been placed here, and more are being discovered all the time. Abelisaurids had the greatest reduction in forelimbs among the theropods, even tyrannosaurs had proprtionally larger arms. The vestigal arms (reminiscent of the tiny hind limbs of early whales) would have been useless in grappling or any other purpose. As with tyrannosaurs, the powerful skulls and jaws were used to subdue prey. MAK990512 120210

Kryptops palaios Sereno & Brusatte, 2008

Horizon: Gadoufaoua, on the western edge of the Ténéré Desert, Elrhaz Formation (Aptian–Albian)

Phylogeny: Abelisauridae **:** (*Rugops* + (*Abelisaurus* + "Majungasaurinae" + Brachyrostra/Carnotaurinae)) + *

Characters: secondary wall on the maxilla that obscures the antorbital fenestra in lateral view, articular trough for the nasal on the maxilla is narrower and less developed, which is a primitive condition. Texturing of the external surface of the maxilla composed of shorter grooves than on other abelisaurids. The sacrum and ilium are also more primitive than in Majungasaurus and Carnotaurus, sacrum with only five vertebrae, and ilium with a relatively deeper preacetabular process. (Sereno & Brusatte 2008 p.18)



Kryptops palaios, known fossil elements, after Sereno & Brusatte 2008.
Artwork by Nobu Tamura, Wikipedia, GNU Free Documentation/Creative Commons Attribution

Comments: Known from a maxilla (part of upper jaw) and postcranial elements, this is the oldest known and most primitive Abelisaurid. Features of the maxilla such as vascular grooves and a narrow antorbital fossa place *Kryptops* among the abelisaurids (Sereno & Brusatte 2008). This is one of those instances, useful in vertebrate paleontology when dealing with incomplete specimens, where a sintgle bone can identify a species. As many distinct lineages of abelisaurids co-existing in this area is perhaps not likely, it is possible that *Kryptops* ("hidden face") was the ancestor, or at least a very close cousin, of *Rugops* ("rugged face"). Both lived in the same geographic region, and the latter only ten million or so years later. This animal was a contemporary of theprimitive carcharodontosaur *Eocarcharia dinops*, both abelisaurids and carcharodontosaurs appeared at the same time and would evolve in parallel in Gondwana during the middle Cretaceous MAK120226

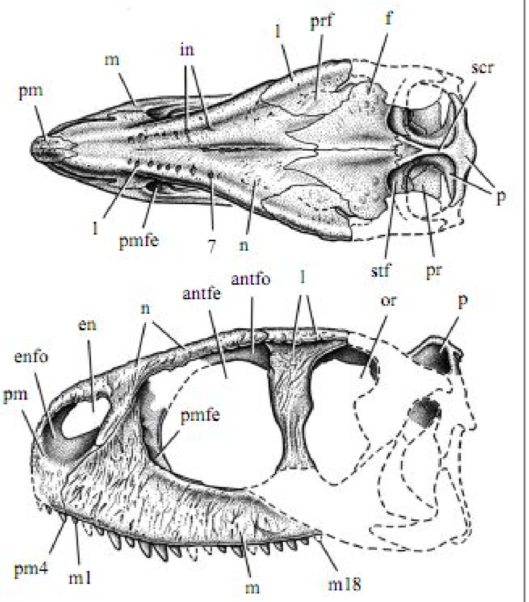
Rugops primus Sereno, Wilson, and Conrad, 2004

Horizon: In Abangharit, Niger Republic; Echkar Formation (Cenomanian)

Phylogeny: Abelisauridae : *Kryptops* + (*Abelisaurus* + "Majungasaurinae" + Brachyrostra/Carnotaurinae) + *)

Characters: small fenestra (opening) in the skull roof between the prefrontal, frontal, post-orbital and lacrimal, and a row of seven small invaginated depressions on the dorsal surface of each nasal. Sereno et al 2004

Comments: Known from a partial skull lacking the palate and most of the bones along the side of the face behind the eyes, this is one of the earliest abelisaurids with textured external skull surfaces. It consistently resolves as a basal form in cladistic analyses



Rugops primus. skull length 31.5 cm Already in this basal form the characteristic short high morphology has developed, but not yet the thickening of the skull roof and the ridges and crests found in some highly derived species. Drawing from Sereno et al 2004 fig. 3. *1-18*, tooth positions or number of nasal invagination; *antfe*, antorbital fenestra; *antfo*, antorbital fossa; *en*, external naris; *enfo*, external narial fossa; *f*, frontal; *fo*, foramen; *in*, invagination; *l*, lacrimal; *m*, maxilla; *n*, nasal; *or*, orbit; *p*, parietal; *pm*, premaxilla; *pmfe*, promaxillary fenestra; *pr*, prootic; *prf*, prefrontal; *scr*, sagittal crest; *se*, septum; *stf*, supratemporal fossa

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Unnamed Node: Higher Abelisaurids

Range: Cenomanian-Maastrichtian of SAm, India, Madagascar

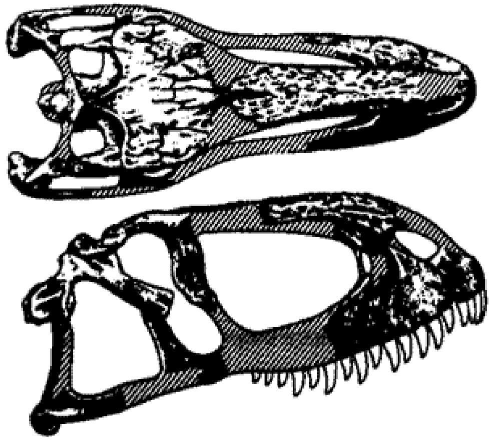
Phylogeny: Abelisauridae ::: (*Abelisaurus* + "Majungasaurinae" + Brachyrostra/Carnotaurinae) + *

Characters: thickened skull roof Sereno et al 2004

Comment: All analyses agree that *Abelisaurus* and Carnotaurines share a common ancestor above the level of *Rugops*, regardles sof whether or not Carnotaurinae are a natural group. The Cenomanian appears to have been an important time in abelisaurid evolution. MAK120210

Abelisaurus comahuensis

Bonaparte and Novas, 1985 (monospecific Abelisaurinae)



Abelisaurus comahuensis, type specimen, MC 11098 . Drawing by Greg Paul, *Predatory Dinosaurs of the World*, p.284

Synonyms: Abelisaurinae (Paul 1988), *Genyodectes*?

Horizon: Allen Formation, Rio Negro, Argentina; early or mid Campanian

Phylogeny: Abelisauridae : *Kryptops* + (*Rugops* + ("Majungasaurinae" + Brachyrostra/Carnotaurinae + *))

Comments: Known only from a large, nearly complete skull, *Abelisaurus* was unusual when first discovered in view of its late occurance and primitive megalosaur-like features. The eye socket's orbital bar and simple lower cheek bones indicate it is closely related to *Carnotaurus*. *Genyodectes serus* Woodward, 1901, also from the latest Cretaceous of Argentina, and based on part of the front end of some theropod jaws, may be closely related, if not synonymous. MAK990512

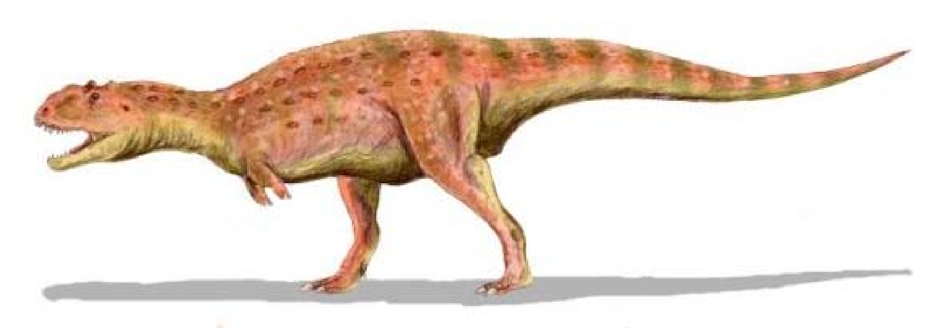
The basal position of *Abelisaurus* assumes that the rugged horned and crested form only evolved once (Carnotaurinae) (Sereno et al 2004, see also cladogram in Wilson et al 2003), Current cladistic analaysis indicates there was a lot of parallelism in abelisaurid evolution (Carrano & Sampson 2008, Canale et al 2008), since both horned and hornless forms evolved among higher taxa, there is no reason why *Abelisaurus* should be discriminated against. Therefore we have moved this taxon to the crown group Abelisaurids MAK120211

Majungasaurinae: *Indosaurus*, *Majungasaurus*, *Rajasaurus*

Range: Maastrichtian of India & Madagascar

Phylogeny: Abelisauridae : *Kryptops* + (*Rugops* + (*Abelisaurus* + Brachyrostra/Carnotaurinae + * : *Majungasaurus* + *Rajasaurus*))

Comments: analysis by Carrano & Sampson 2008 recovered a clade of large, powerfully-built abelisaurids, that populated Central Gondwana (India and Madagascar). As it doesn't seem to have a name we here informally refer to this lineage as Majungasaurinae, after the best known species, *Majungasaurus crenatissimus*



Majungasaurus crenatissimus, life reconstruction.
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The Majungasaurines represent a distinct lineage to the short-headed, highly derived West Gondwanan forms. The total tibia-femur length is notably short compared to other similarly sized theropods, indicating a relatively slow moving animal. They also lack the unique caudal morphology and powerful leg muscles of the advanced West Gondwanan forms (Persons & Currie 2011 pp.1-2). These differences may reflect different faunal compositions. For example, ornithopods are unknown from Central Gondwana. These powerfully built abelisaurs therefore would have preyed on large and slow titanosaurs (sauropods) rather than smaller and faster ornithopods, All members of this unnamed clade are currently known only from the Maastrichtian, implying a ghost lineage of thirty or forty million years.

Majungasaurus crenatissimus, Field Museum, Chicago.
Photo by Ed Bierman, Wikipedia Creative Commons Attribution

Majungasaurus crenatissimus (Depéret, 1896)

Synonyms: *Megalosaurus crenatissimus* Depéret, 1896, *Dryptosaurus crenatissimus* (Depéret, 1896) , *Majungatholus atopus* Sues and Taquet, 1979

Horizon: Maevarano Formation, Mahajanga Basin, northwestern Madagascar (Maastrichtian)

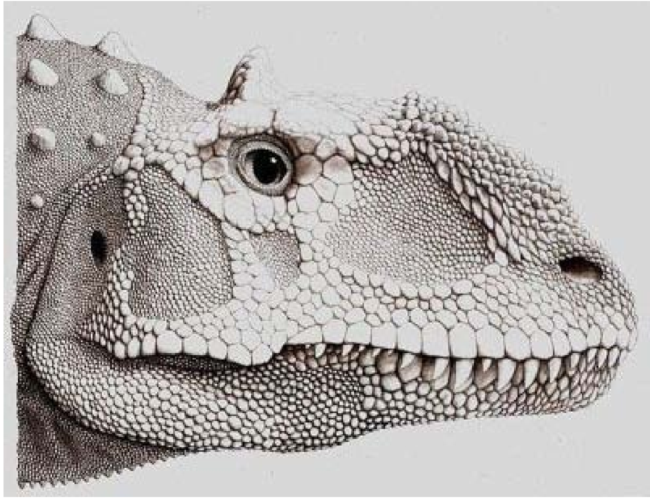
Phylogeny: "Majungasaurinae" **:** *Rajasaurus* + *

Characters: thickened nasals, a horn on the frontal, a parietal prominence, and pneumatic chambers.

Size: average 6-7 meters in length (Krause et al 2007), reached lengths of more than 8 meters, average weight 750 (Paul 2010) to 1100 kilograms, although large specimens heavier ((Sampson & Witmer 2007)

Comments: This theropod was for a long time considered to be a large pachycephalosaurid, called *Majungatholus atopus*. It is distinguished by thickened nasal bones, a horn on the frontal bone, and a parietal (skull bone near the rear) prominence. The earlier named *Majungasaurus crenatissimus*, originally based on an incomplete dentary from the same time and place, has a curved mandible is very like that of *Carnotaurus*. Recent excavations undertaken by the Mahajanga Basin Project resulted in abundant and spectacular remains of this theropod, including multiple specimens of various size and presumably age ranges, and covering the great majority of the skull and skeleton, make *Majungasaurus* among the best known of Gondwanan theropods, and conclusively placing it within Abelisauridae . The confused taxonomy is also resolved, with *Majungasaurus crenatissimus* as the valid name for this theropod (Krause et al 2007). Previously considered closely related to Carnotaurus (Wilson et al 2003), new analysis places it separate from the South American forms (Carrano & Sampson 2008, Canale et al 2008)

Matching tooth marks on bones show that this species sometimes fed on its own kind (Rogers et al 2007) (Cannibalistic behaviour had previously been attributed to *Coelophysis bauri*, but this is now known not to have been the case)



The face of *Majungasaurus crenatissimus*
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The following material is copied or adapted from the Wikipedia page on *Majungasaurus*:

The skull of Majungasaurus is exceptionally well-known compared to most theropods. Like other abelisaurid skulls, its length was proportionally short for its height, although not as short as in Carnotaurus. The skulls of large individuals measured 60-70 centimeters (24-28 in) long. The tall premaxilla (frontmost upper jaw bone), which made the tip of the snout very blunt, was also typical of the family. The nasal bones were extremely thick and fused together, with a low central ridge running along the half of the bone closest to the nostrils. A distinctive dome-like horn protruded from the fused frontal bones on top of the skull as well. In life, these structures would have been covered with some sort of integument, possibly made of keratin. Computed tomography (CT scanning) of the skull shows that both the nasal structure and the frontal horn contained hollow sinus cavities, perhaps to reduce weight (Sampson & Witmer 2007). The hollow cavity inside the frontal horn of Majungasaurus would have weakened the structure and probably precluded its use in direct physical combat, although the horn may have served a display purpose (Tykoski & Rowe 2004). While there is variation in the ornamentation of Majungasaurus individuals, there is no evidence for sexual dimorphism.(Sampson & Witmer 2007). The teeth were typical of abelisaurids in having short crowns, although Majungasaurus bore 17 teeth in both the maxilla of the upper jaw and the dentary of the lower jaw, more than in any other abelisaurid except *Rugops* (Smith2007).

Abelisaurids may instead have been adapted for a feeding strategy more similar to modern felids, with short and broad snouts, that bite once and hold on until the prey is subdued. *Majungasaurus* had an even broader snout than other abelisaurids, and other aspects of its anatomy may also support the bite-and-hold hypothesis. The neck was strengthened, with robust vertebrae, interlocking ribs and ossified tendons, as well as reinforced muscle attachment sites on the vertebrae and the back of the skull. These muscles would have been able to hold the head steady despite the struggles of its prey. Abelisaurid skulls were also strengthened in many areas by bone mineralized out of the skin, creating the characteristic rough texture of the bones. This is particularly true of Majungasaurus, where the nasal bones were fused and thickened for strength. On the other hand, the lower jaw of *Majungasaurus* sported a large fenestra (opening) on each side, as seen in other ceratosaurs, as well as synovial joints between certain bones that allowed a high degree of flexibility in the lower jaw, although not to the extent seen in snakes. This may have been an adaptation to prevent the fracture of the lower jaw when holding onto a struggling prey animal. The front teeth of the upper jaw were more robust than the rest, to provide an anchor point for the bite, while the low crown height of *Majungasaurus* teeth prevented them from breaking off during a struggle. Finally, unlike the teeth of Allosaurus and most other theropods, which were curved on both the front and back, abelisaurids like *Majungasaurus* had teeth curved on the front edge but straighter on the back (cutting) edge. This structure may have served to prevent slicing, and instead holding the teeth in place when biting.(Sampson & Witmer 2007)

Majungasaurus was the largest predator in its environment, while the only known large herbivores at the time were sauropods like Rapetosaurus. Scientists have suggested that Majungasaurus, and perhaps other abelisaurids, specialized on hunting sauropods. Adaptations to strengthen the head and neck for a bite-and-hold type of attack might have been very useful against sauropods, which would have been tremendously powerful animals. This hypothesis may also be supported by the hindlegs of Majungasaurus, which were short and stocky, as opposed to the longer and more slender legs of most other theropods. While *Majungasaurus* would not have moved as fast as other similar-sized theropods, it would have had no trouble keeping up with slow-moving sauropods. The robust hindlimb bones suggest very powerful legs, and their shorter length would have lowered the animal's center of gravity. The tibia (lower leg bone) of *Majungasaurus* was even stockier than that of its relative, the sprinter *Carnotaurus*, with a prominent crest on the knee (Carrano 2007). Thus *Majungasaurus* may have sacrificed speed for power (Sampson & Witmer 2007) Majungasaurus tooth marks on Rapetosaurus bones confirm that it at least fed on these sauropods, whether or not it actually killed them. (Rogers et al 2007) - Wikipedia

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Rajasaurus narmadensis Wilson, Sereno, Srivastava, Bhatt, Khosla, and Sahni, 2003

Synonyms: *Lametasaurus*, *Indosaurus*?

Horizon: Narmada Valley, Rajasthan, India; Infratrappean Beds of the Lameta Formation; Maastrichtian

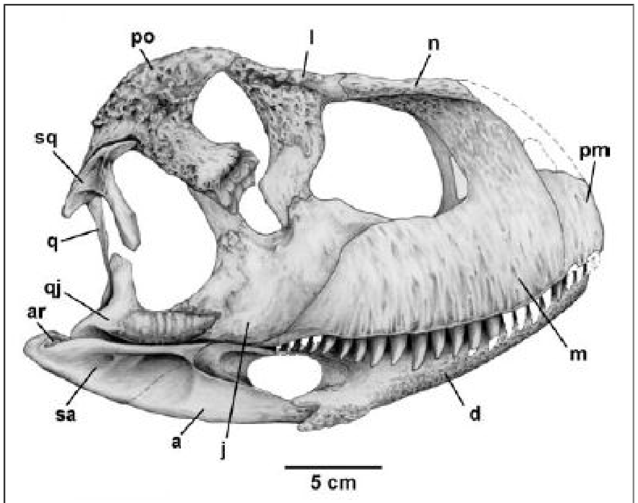
Phylogeny: "Majungasaurinae" **:** *Majungasaurus* + *

Characters: single nasal-frontal horn, the elongated proportions of its supratemporal fenestrae (holes in the upper rear of the skull), and the form of the ilia (principle bones of the hip) which feature a transverse ridge separating the brevis shelf from the hip joint. (Wilson et al 2003)

Size: 7.6-9 m long, 2.4 m high, weight about 3 to 4 tons (Wikipedia); presumably the weight estimate is for the larger end of the size range). This was a very large animal, although Greg Paul's (2010) length estimate of 11 meters would seem to be excessive

Comments: the first Indian theropod preserving associated cranial and postcranial remains; known from an almost complete skull and partial skeleton . The skull was short, measuring 60 cm (23.6 in) in length, and bore a distinctive low rounded horn or crest, made of outgrowths from the nasal and frontal bones. The configuration of its nasal bones and possession of a growth ("excrescence") on its frontal bone places it among the carnotaurine abelisaurids (Wikipedia), although the presence of these features developed independently among the abelisauruids (hence *Abelisaurus* itslef may not be as basal as usually portrayed (Carrano & Sampson 2008)). *Rajasaurus* seems to have been a fairly heavily built animal. *Indosaurus matleyi* from the Lower Lameta Group, Madhya Pradesh, India (mid-late Maastrichtian) may be a synonym or at least a very closely related species (which would mean renaming *Rajasaurus*), although the type material is lost. It was known from a skull roof and other cranial and post-cranial elements, with frontal bones massively thickened into what appear to be the bases of horn cores above the eyes. In any case, proper identification of these Indian forms is hampered by poor preservation Carrano & Sampson 2008. The contemporary *Indosuchus*, known from very scrappy remains, was a smaller, longer-legged animal (Paul 2010).

Brachyrostra: *Carnotarus*, *Skorpiovenator*



Skull of *Skorpiovenator bustingorryi*, showing the short high shape typical of advanced abelisaurids. Compare with the more familiar, but probably distorted, shape of Carnotaurus, below. *d* Dentary, *a* angular, *sa* surangular, *ar* articular, *pm* premaxilla, *m* maxilla, *n* nasal, *j* jugal, *l* lachrymal, *po* postorbital, *qj* quadratojugal, *q* quadrate, *sq* squamosal. From Canale et al 2008 fig.2.

Phylogenetic definition: *Carnotaurinae*: The most inclusive clade containing *Carnotaurus sastrei* Bonaparte 1985 but not *Abelisaurus comahuensis* Bonaparte and Novas 1985. (stem-based) (Paul Sereno - Taxon Search). However Carrano & Sampson 2008's findings collapse traditional abelisaurid phylogeny and present the Carnotaurinae as paraphyletic; the relationship between *Carnotaurus*, *Abelisaurus*, and other higher taxa dissapears in an unresolved polytomy. A sim8ilar but not synonymous stem-based clade would be *Brachyrostra*: all abelisaurids more closely related to *Carnotaurus sastrei* than to *Majungasaurus crenatissimus* (Canale et al 2008). For now, we have chosen to present *Abelisaurus*, *Carnotaurus*, and *Majungasaurus* as representing three equally distinct clades.The position of *Ekrixinatosaurus* is uncertain; it may represent a more basal form than all three, or a stem member of the *Carnotaurus* clade (Brachyrostra/Carnotaurinae)

Range: Late Cretaceous (Late Cenomanian/Early Turonian-Maastrichtian) of SAm

Phylogeny: Abelisauridae **:** *Kryptops* + *Rugops* + (*Abelisaurus* + "Majungasaurinae" + * **:** *Ekrixinatosaurus* + (*Ilokelesia* + (*Skorpiovenator* + Carnotaurini)))

Comments: The Brachyrostra ("short snouts") are a postulated clade of abelisaurs geographically limited to South America, showing that abelisaurids divided early on along geographical lines, which fits with the timing of the break up of Gondwana. Distinct from both the Abelisaurines and the Majungasaurines, these advanced abelisaurs were characterised by a shortening of the skull and hyperossification (thickening of the bone) of the skull roof seem to be correlated with a progressive enclosure of the orbit. This may be related to shock-absorbing, implying head-butting intra-specific behaviour. Canale et al 2008. Phylogenetic analysis of Canale et al 2008, recovered three species ina stratigraphic sequence, the newly discovered *Skorpiovenator*, the Carnotaurus-like *Ekrixinatosaurus*, and the poorly known *Ilokelesia* as part of a newly discovered clade that is the sister group to the Carnotaurini (*Aucasaurus* + *Carnotaurus*). This contradicts Sereno et al 2004, for whom *Ilokelesia* is a basal form, and Carrano & Sampson 2008, who place *Ekrixinatosaurus* intermediate between *Rugops* and higher Abelisaurs, although the latter authors did recover a connection between *Ilokelesia* and *Carnotaurus*. Persons & Currie 2011 in their study of abelisaurid tail morphology note that these five taxa form both a morphological and a stratigraphic series, especially in view of their close geographic proximity, and we have followed this hypothesis here. Although Canale et al 2008 find that in *Skorpiovenator* and *Ekrixinatosaurus* horns consist of dorsally inflated postorbital bones, distinct from the frontal horns of *Carnotaurus*, such reversals would not be unusual in any evolutionary (anagenetic) sequence. Advanced members of this clade became progressively more cursorial, culminating in *Carnotaurus*, the fastest known large theropod (Persons & Currie 2011)

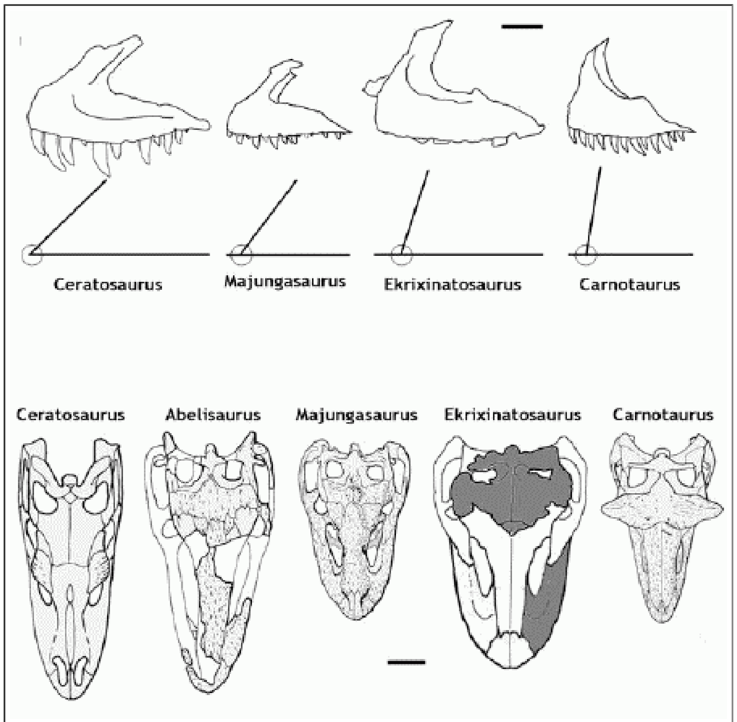
Ekrixinatosaurus novasi Calvo et al. 2004

Horizon: Upper Candeleros Formation of Patagonia, Argentina (Early Cenomanian)

Phylogeny: Brachyrostra **:** (*Ilokelesia* + (*Skorpiovenator* + Carnotaurini)) + *

Size: Originally described as 7 - 8 meters in total length (Calvo et al. 2004), revised estimates put this at 10 to 11 meters, making this the largest known abelisaur (Juarez Valieri et al 2011)

Comments: *Ekrixinatosaurus* (the name means "explosion-born lizard," as it was discovered during a blasting operation (ref Thescelosaurus)) is based on a partial skeleton and skull elements. It shares a mixture of characters with several other abelisaurids, highlighting the homoplastic, probably ontogenetic, nature of many of these traits (Carrano & Sampson 2008). Either a fairly large abelisaur with an oversized head, or the postcrania from one indivdual along with skull fragments of a much lartger one. A particularly robust animal, a contemporary of the even larger carcharodontosaurid Giganotosaurus. As a result of the post-Cenomanian Carcharodontosaurs, both animals being the largest known representatives of their respective clades. (Juarez Valieri et al 2011). Stratigraphically this is earliest of the Brachyrostra, and as its stocky build and lacks of advanced cursorial adaptations means it was not a fast moving animal (Persons & Currie 2011 p.2). Variously considered a derived (Canale et al 2008) or a primitive (Carrano & Sampson 2008, Persons & Currie 2011) species, the combination of brachyrostran head and "Majungasaurine" body and locomotary traits, along with early stratigraphic position (the earliest well known abelisaurid) support its more basal position.



Determining phylogentic placement from oinly a few partial elements. The maxilla of *Ekrixinatosaurus* possesses a dorsally projected ascending ramus and a short rostral ramus, suggesting a relatively high skull, most similar to that of *Skorpiovenator* and *Carnotaurus* rather than the longer-headed *Majungasaurus* or *Rugops*. The relationship between the length of the maxilla and the width of the skull roof also implies a short skull, intermediate in length between those of *Majungasaurus* and *Carnotaurus*, and similar to *Skorpiovenator*. All these taxa belong to the Brachyrostra or short-headed clade. Diagram and some of text from Juarez Valieri et al 2011

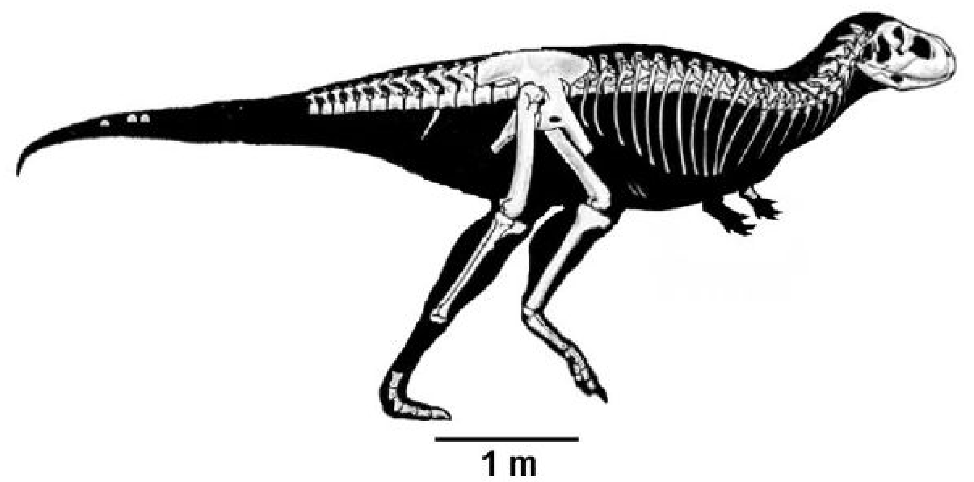
Ilokelesia aguadagrandensi Coria and Salgado, 2000

Horizon: Río Limay Formation, Neuquén Group, Neuquén Province, Argentina. Late Cenomanian

Phylogeny: Brachyrostra **:** *Ekrixinatosaurus* + ((*Skorpiovenator* + Carnotaurini) + *)

Size: length 4 meters; weight 200 kilograms (Paul 2010)

Comments: Known from fragmentary material, and initially thought to be a basal abelisauroid due to the retention of basal characteristics, it now seems to a more advanced animal, representing an early stage in the brachyrostral lineage Canale et al 2008 and/or related to *Carnotaurus* (Carrano & Sampson 2008) or may be an intermediate form between *Ekrixinatosaurus* and *Skorpiovenator* (Persons & Currie 2011) The base of the tail is exceptionally broad (Paul 2010)



Skorpiovenator bustingorryi, reconstruction skeleton, from Canale et al 2008 fig.1.

Skorpiovenator bustingorryi

Horizon: lower Huincul Formation of Patagonia (Late Cenomanian/Early Turonian)

Phylogeny: Brachyrostra **:** *Ekrixinatosaurus* + (*Ilokelesia* + (Carnotaurini + *))

Size: length 7.5 meters; weight 1670 kilograms (Paul 2010)

Comments: Known from a complete skull and most of the skeleton, an dnamed after the large number of scorpions at the fossil locality, this long legged form represents the beginning of the tendency towards advanced cursorial ability rapid sprinting and - by implication, as these were the largest predators of their environment - pursuit that reached its culmination in the avanced carnotaurini (Persons & Currie 2011)

Based on similarities between *Skorpiovenator* and carcharodontosaurid tooth morphology, it is quite likely that stratigraphically younger isolated teeth originally referred as Carcharodontosauridae belong to abelisaurids Canale et al 2008. Since no post-Cenomanian Carcharodontosaurs are otherwise known, this implies that that group became extinct at the end of the Cenomanian, their ecological role being replaced by large abelisaurs, although their smaller (average 6 meters) cousins or descendents the neovenatorids continued to flourish in the medium megapredator role.

Links: Smithsonian - Dinosaur tracker

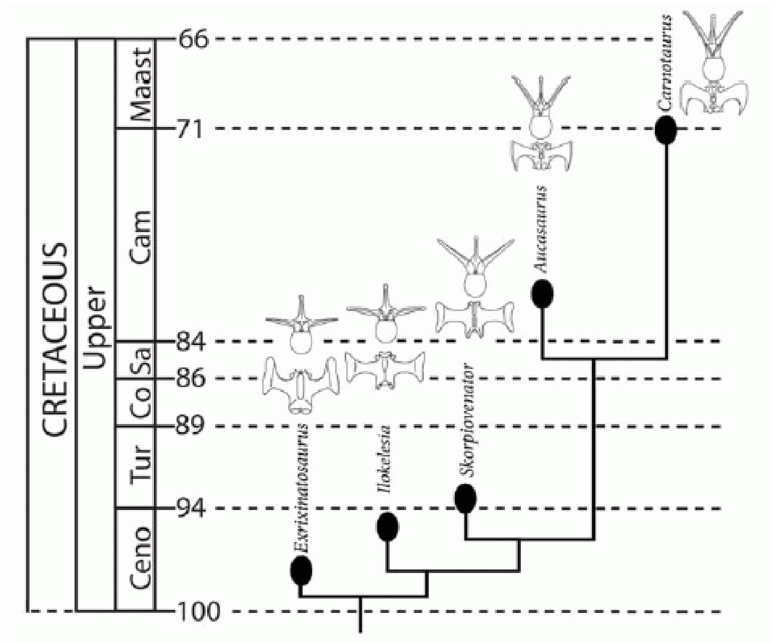
Carnotaurini: *Aucasaurus, Carnotaurus*

Range: Late Cretaceous (Campanian-Maastrichtian) of SAm

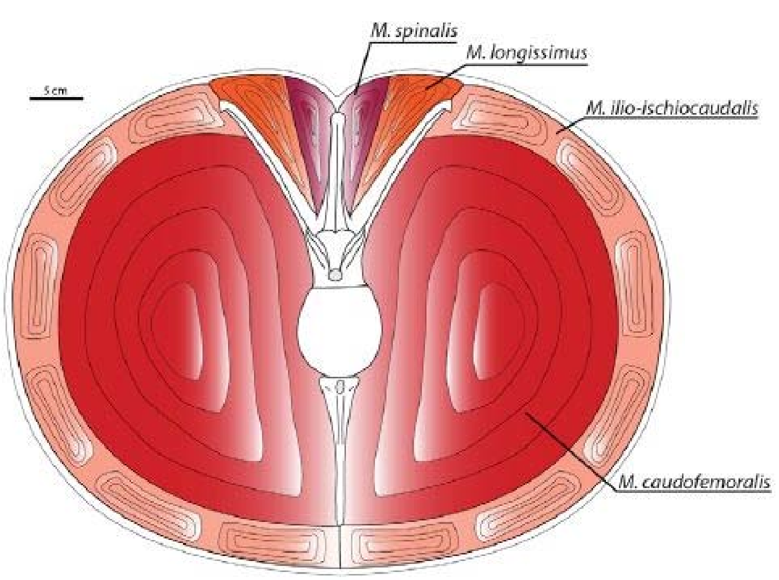
Phylogeny: Brachyrostra : *Ekrixinatosaurus* + (*Ilokelesia* + (*Skorpiovenator* + * : *Aucasaurus* + *Carnotaurus*))

Carnotaurus sastrei, cast of skeleton, Canadian Museum of Nature, Ottawa. Photo by D. Gordon E. Robertson, Wikipedia GNU Free Documentation/Creative Commons Attribution

Comments: Canale et al 2008 place Carnotaurus and Aucasaurus as sister taxa in the tribe Carnotaurini. This was the only West Gondwanan abelisaurid lineage to survive to the end of the Cretaceous. In comparison to other Abelisaurids, the legs are long and gracile. This lineage of large theropods specialise din fast pursuit, unlike the more heavily built central Gondwanan clade. As Persons & Currie 2011 explain "In the South American abelisaurids *Carnotaurus sastrei*, *Aucasaurus garridoi*, and, to a lesser extent *Skorpiovenator bustingorryi*, the anterior caudal ribs project at a high dorsolateral inclination and have interlocking lateral tips. This unique morphology facilitated the expansion of the caudal hypaxial musculature at the expense of the epaxial musculature. Distinct ridges on the ventrolateral surfaces of the caudal ribs of Aucasaurus garridoi are interpreted as attachment scars from the intra caudofemoralis/ilio-ischiocaudalis septa, and confirm that the M. caudofemoralis of advanced South American abelisaurids originated from a portion of the caudal ribs Digital muscle models indicate that, relative to its overall body size, *Carnotaurus sastrei* had a substantially larger M. caudofemoralis than any other theropod yet studied. In most non-avian theropods, as in many extant sauropsids, the M. caudofemoralis served as the primary femoral retractor muscle during the locomotive power stroke. This large investment in the M. caudofemoralis suggests that *Carnotaurus sastrei* had the potential for great cursorial abilities, particularly short-burst sprinting. However, the tightly interlocking morphology of the anterior caudal vertebrae implies a reduced ability to make tight turns." (from the abstract)



Chronostratigraphy and hypothesized phylogeny of South American Abelisauridae with representative caudal vertebrae for each in anterior and dorsal views. Note: although each taxon is demarked by a separate branching event, given the close geographic and temporal proximities of these taxa, combined with the unlikelihood that multiple other as-yet-unknown large-bodied carnivorous abelisaurids were coexistent, it is probable that some of these taxa have a direct anagenetic relationship with others. Caption and figure from Persons & Currie 2011 fig.6 Creative Commons Attribution



Cross-section through the tail of *Carnotaurus sastrei* showing caudal vertebra 6 and accompanying musculature. Note: the cross-section is an anatomical abstraction and depicts the neural arch and chevron in the same vertical plane. Caption and figure from Persons & Currie 2011 fig.5

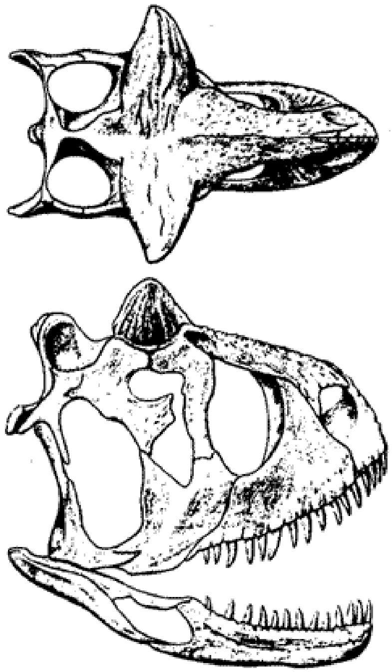
Aucasaurus garridoi Coria, Chiappe, and Dingus, 2002

Horizon: Anacleto Formation of Argentina (Early Campanian)

Phylogeny: Carnotaurini **:** *Carnotaurus* + *

Comments: Related to but smaller than *Carnotaurus*, and lacking the head crests, with a longer, lower skull with bumps instead of horns. The arms were also somewhat longer. Based on an almost complete skeleton, including soft tissue impressions about the hips. (Ref - *Thescelosaurus*). Despite the complete fossil, this animal remains poorly known.

Aucasaurus garridoi - Mounted skeleton reconstruction
Photo by Kabacchi, Wikipedia, Creative Commons Attribution



Carnotaurus sastrei, type specimen, CH894. Drawing by Greg Paul, *Predatory Dinosaurs of the World*, p.284. The exceptionally short proportions of the skull, even by abelisaur standards, may be the result of post-moortem deformation.

Carnotaurus sastrei

Horizon: Gorro Frigio Formation, Chubut, Argentina (Maastrichtian of SAm)

Phylogeny: Carnotaurini **:** *Aucasaurus* + *

Remains: skull and almost complete skeleton, skin impressions.

Size: length 7.5 to 9 meters; weight 1500 to 2000 kilograms .(Mazzetta et al 1998, Paul 2010

Comments: This theropod is known from a virtually complete skeleton (lacking only the hind feet and end of the tail), a skull with extensive skin impressions. The skull is very high and short with two stout horn-cores, which in life were the basis of extended horns. this has inspired the strange name "flesh-eating bull". The horns were probably quite blunt and used for intraspecific combat (head butting etc). The eyes are quite small (much of the orbit cut off by a bar of bone) although Greg Paul raises the possibility the deep snout may have contained nasal organs. Perhaps unlike most other theropods this dinosaur hunted by smell rather than sight. The skin empressions show this animal to have had widely-spaced rows of nonbony scutes. The hands and arms are so small as to be practically useless.

Carnotaurus seems to have had a highly kinetic skull and could gape widely to swallow large objects. A prokinetic hinge rostral to the orbits would have allowed (as in birds) elevation of the rostrum while the eyes could remain fixed on prey. The vaulted skull gave a fast, rather than a strong, bite. Carnotaurus was envisioned as an active predator of fast, small prey.. These large speialised animals were among the last of the South American abelisaurids

It is possible the distinctive shape of the type skull of*Carnotaurus* is due to distortion. Mark Goodwin et al., in their initial presentation on *Majungatholus* (=*Majungasaurus*), suggested that the deep and narrow skull shape of Carnotaurus owed itself to compaction and might not have been natural. (SVPCA - Darren Naish)

This was the fastest large theropod, with the largest M. caudofemoralis in proportion to its size (Persons & Currie 2011). It represented the culmination of the West Gondwanan brachyrostran lineage.

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Theropoda: Ceratosauria: Noasauridae

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Herrerasauridae
   `--+--Podokesauridae
      `--+--Dilophosaurus
         |--Ceratosauria
         |   |--"Limusauridae"
         |   `--+--Ceratosaurus
         |      `--Abelisauroidea
         |         |--Noasauridae
         |         |   |--Laevisuchus
         |         |   |--Masiakasaurus
         |         |   |--Noasaurus
         |         |   `--Velocisaurus
         |         `--Abelisauridae
         `--Tetanurae
            `--Avetheropoda
               |--Carnosauria
               `==COELUROSAURIA
                  `--AVES
```

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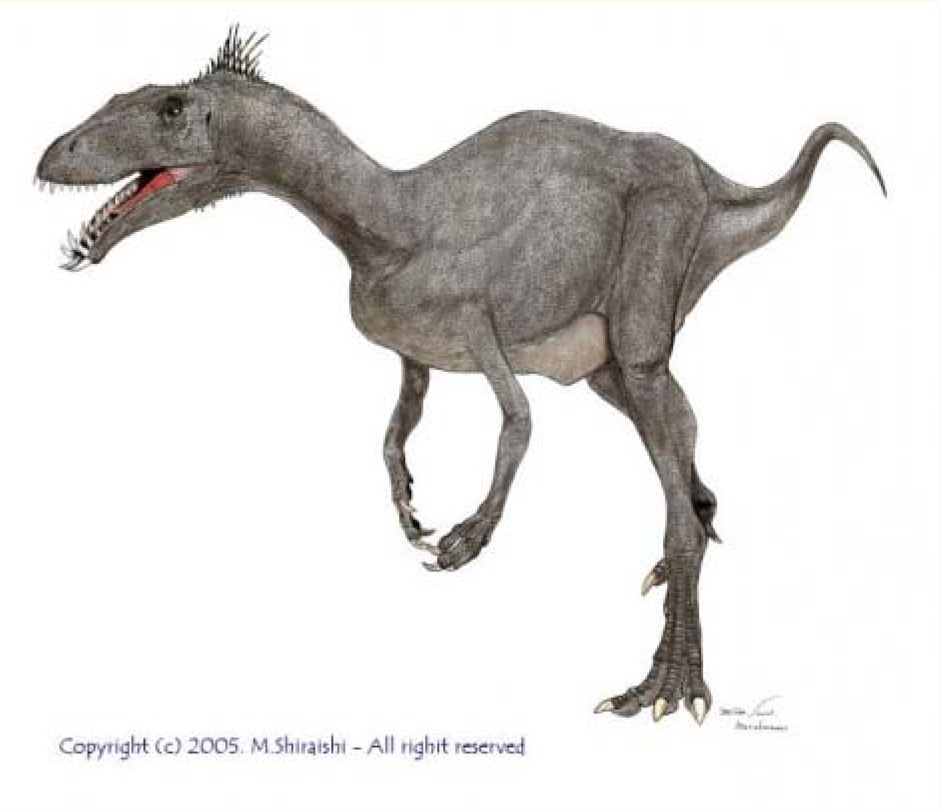
2. *Masiakasaurus* X
3. Noasauridae X
4. *Noasaurus* X
5. *Velocisaurus* X



Masiakasaurus, artwork courtesy of M. Shiraishi

The Noasaurs were the Coelurosaurs of the south. These highly successful animals ranged across Gondwana, and even reached Europe. They are actually derived ceratosaurs, and although cladistically they always appear as the sisiter taxon to the Abelisauridae (given the current data sets), morphologically they are intermediate between more primitive forms such as Ceratosaurus and Elaphrosaurus, and the Abelisaurids proper. It is quite likely that with further discoveries and better material the group may turn out to be a paraphyletic or evolutionary grade. They include both small animals such as *Velocisaurus* of South America, and medium sized (1.5 to 32m) long *Noasaurus* of Late Cretaceous South America and *Masiakasaurus* of Late Cretaceous Madagascar. Perhaps because of the scrappy material of most taxa (apart from *Masiakasaurus*), phylogenetic relationships are uncertain. MAK120208

Descriptions

Skull of *Masiakosaurus* at the Field Museum of Chicago
Photo by DinoGuy2, Wikipedia, /Creative Commons Attribution Share Alike

Noasauridae Bonaparte & Powell, 1980 : *Noasaurus*, *Masiakasaurus*

Phylogenetic definition: The most inclusive clade containing *Noasaurus leali* Bonaparte and Powell 1980 but not *Carnotaurus sastrei* Bonaparte 1985, *Coelophysis bauri* (Cope 1889), or *Passer domesticus* (Linnaeus 1758). (stem-based) (Paul Sereno - Taxon Search)

Range: Middle to Late Cretaceous (Albian to Maastrichtian) of Europe (France), South America (Argentina), India, Madagascar, and Africa (Niger). (Carrano et al 2011)

Phylogeny: Abelisauroidea **:** Abelisauridae + * **:** *Laevisuchus* + *Masiakasaurus* + *Noasaurus* +

Velocisaurus

Characters: metatarsal IV distal end reduced (Sereno et al 2004).

Comments: Noasaurids differ from Abelisauridae in retaining plesiomorphic long forelimbs with well developed claws, as occurs plesiomorphically in most basal theropods (e.g., Coelophysis). (Agnolin & Chiarelli 2010). the noasaurid skull was not especially modified relative to those of other ceratosaurs except with regard to the anterior portions of the jaws. In some external element sculpturing and lacrimal morphology, they exhibit an intermediate condition between more basal ceratosaurs and abelisaurids. Ddiffers from abelisaurids in feeding specializations, as well as body-size reduction, but the many derived characters shared between noasaurids and abelisaurids indicate a great deal of functional similarity in the lower jaw, axial column, shoulder girdle, and hind limb between these groups. Carrano et al 2011 (MAK120211)

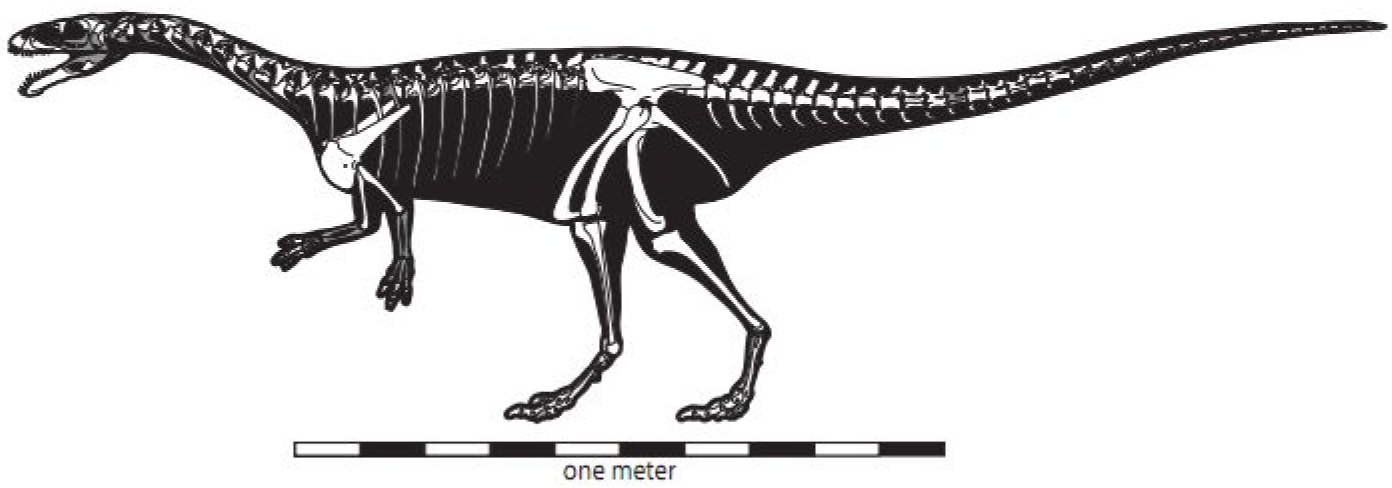
Noasaurus leali Bonaparte and Powell, 1980

Horizon: Lecho Formation, El Brete, Salta, Argentina (early Maastrichtian)

Phylogeny: Noasauridae ::: *

Characters: maxillary tooth count reduced to no more than 10; cervical neural arch with anterior epipophyseal prong (Bonaparte & Powell, 1980)

Comments: known from skull elements, vertebrae, pedal (foot) elements, and a large claw, it was originally thought that *Noasaurus* was a Gondwanan equivalent of the sickle-clawed maniraptors of the northern continents, perhaps by analogy with the parallel sabre toothed cats and the South American sabre-toothed marsupials that lived during the same time but in isolation. But restudy of the dissarticulated non-ungueal phalanges of the Argentinean *Noasaurus leali* and *Ligabueino andesi* revealed that the supposed raptorial claw of the second pedal digit of *N. leali* actually belongs to the first or second finger of the manus (hand), and the non-ungual phalanges previously attributed to the feet of both genera also pertain to the hand. This also blurs the distinctions between Noasauridae and Velocisauridae. (Agnolin & Chiarelli 2010) MAK120211



Composite skeletal reconstruction of Masiakasaurus knopfleri in left lateral view, showing recovered (white) and missing (gray) elements. Illustration and caption from Carrano et al 2011 fig.1

Masiakasaurus knopfleri Sampson et al., 2001

Horizon: Maevarano Formation of northwestern Madagascar. (Middle Maastrichtian)

Phylogeny: Noasauridae ::: *

Size: about 2 meters long

Comments: By far the most completely known noasaurid, *Masiakasaurus* was first described from disassociated elements representing nearly 40% of the skeleton, and now known from abundant new materials that help further resolve its phylogenetic status, including most of the skull and about 65% of the skeletal elements, permitting a much more accurate reconstruction, and greater insight into the specializations of noasaurids in general. Carrano et al 2011. AUnfortunately the incompleteness of other noasaurid taxa means there are few opportunities for detailed comparisons.

Masiakasaurus was highly unusual by its forward-jutting teeth, indicating a specialized diet, probably piscivous. The forelimbs, although much shorter than the hindlimbs, were not vestigal in the way they are in abelisaurids. The type species, Masiakasaurus knopfleri, was named after the musician Mark Knopfler, the guitarist and singer/songwriter of the band *Dire Straits*, whose music inspired expedition crews.

Laevisuchus indicus Huene and Matley, 1933

Horizon: Lower Lameta Group, Madhya Pradesh, India Age: mid-late Maastrichtian

Phylogeny: Noasauridae **:::** *

Length: estimated about 2 meters

Comments: known only from a few vertebrae, this theropod has previously been considered a coelurid, but has more recently been shown to probably be a small abelisaurian. Th vertebrae share some synapomorphies with *Masiakasaurus* and *Noasaurus*, so all three can be placed in the Noasauridae (Carrano et al. 2002; Carrano & Sampson 2008). This is only one of a large number of small, poorly known forms are known from the Lameta Beds (*Coeluroides*, *Compsosuchus*, *Dryptosauroides*, *Jubbulpuria*, *Laevisuchus*, *Lametasaurus*, and *Ornithomimoides*). Whilst most likely Ceratosaurian, their relation to the abelisaurids is not clear, although at least some if not all are probably synonyms, and belong to the Noasauridae (Carrano & Sampson 2008, Carrano et al 2011) MAK120211

Velocisaurus unicus Bonaparte, 1991

Horizon: Neuquen, Argentina (Coniacian/Santonian)

Phylogeny: Noasauridae **:::** *

Length: estimated about 1.2 meters

Comments: known only from a partial hindlimb, this was a small swift-running animal. Originally placed in its own family, Velocisauridae, it now appears to be a Noasaurid. The middle metatarsal bone in the foot is greatly enlargened, while the outer ones were reduced. the reduction of metatarsal II, the same as with *Masiakasaurus* and *Noasaurus*. Although probably an adaptation for running, it is the opposite to that of many running coelurosaurs (whose outer metatarsals became stronger, greatly reducing the inner one). The toe proportions suggest it fed like a chicken, through scratching at the ground. MAK990512 120211

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page MAK120219

Theropoda: Basal Tetanurae : The Megalosaurs

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Herrerasauridae
   `==Podokesauridae
        `--+--Ceratosauria
           `--Tetanurae
              |--Xuanhanosaurus
              `--+--Megalosaurinae
                  |   |--Duriavenator
                  |   `--+--+--Megalosaurus
                  |       |    `?-Poekilopleuron
(may be a Sinraptorid)
                  |       `--Torvosaurus
                  |--+--Eustreptospondylus
                  |   `--Spinosauridae
                  `--+--+--Piatnitzkysaurus
                      |   `--Marshosaurus
                      |--+--Afrovenator
                      |   `--Dubreuillosaurus
                      `--Avetheropoda
                         |--Carnosauria
                         `==COELUROSAURIA
                             `--AVES
```

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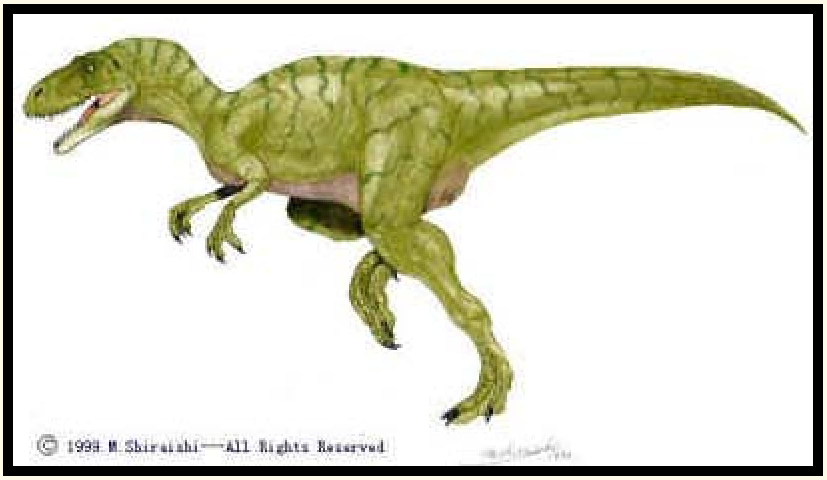
2. *Dubreuillosaurus* X
3. *Duriavenator* X
4. *Eustreptospondylus* X
5. *Marshosaurus* X
6. Megalosaurinae X
7. *Megalosaurus* X
8. *Piatnitzkysaurus* X
9. *Poekilopleuron* X
10. Tetanurae
11. *Torvosaurus* X

12. *Xuanhanosaurus* X

Basal Tetanurae, aka the Megalosaurs

As with Pelycosauria and Synapsida, Thecodontia and Archosauria, and Podokesauridae and Neotheropoda, we are once again at one of those phylogenetic and evolutionary nodes where evolutionary systematics gives one term to refer to a stem group consisting of similar forms from which many other evolutionary lineages diverge, while cladistics gives a totally different name to refer to that exact same evolutionary node and the exact same taxa, but also including all the descendents, regardless of how distinct they are. In this instance, the *Megalosauridae* are a family (and grade) of large but otherwise unexceptional Jurassic theropods that replaced the large podokesaurs (dilophosaurs) and were in turn replaced by their descendents the allosaurs in the late Jurassic. The Tetanurae are a clade of theropods that include not only all the megalosaurs but everything that evolved from them, or from their descendents or their descendents descemndents, including tyrannosaurs, ostrich dinosaurs, segnosaurs, proto-birds, modern birds of every sort, and many other wondrous creatures, many of which bare not the slightest resemblance to their big bodied, short but stocky fore-armed, ancestors. What they do have in common though are certain shared traits (or synapomorphies) by which the clade is defined.

The situation is complicated however by the fact that - *unlike* the Pelycosauria vis a vis the Synapsida, or the Thecodonts re the Archosaurs - not everyone agrees that megalosaurs are an ancestral group; some argue that they are a sister clade of the more bird-like avetheropods. This depends on the type of cladogram that results from a phylogenetic analysis; some analyses show the megalosaurs are an artifical (in cladistic, not evolutionary, terms) group, others as a monophyletic clade. We have followed occam's razor in arguing the former, the reason being that megalosaurs are both morphologically and stratigraphically intermediate between Early Jurassic dilophosaurs (advanced podokesaurs) and Mid to Late Jurassic avetheropods; if they aren't the ancestors then where are they? In other words, the apparent monophyly of the megalosaurs is - as with the ceratosaurs - an artifact of cladistic analysis, due to the problems such as reversals, homoplasies, and so on MAK120222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The Megalosaurs presumably evolved from a dilophosaur- like ancestor during the earlier Jurassic, becoming the dominant large preditor by the middle Jurassic, before being in turn supplanted by the Allosaurs. Cretaceous forms were specialised semi-aquatic fish-eaters, mostly confined to Gondwanaland, and sometimes attaining very large size and a *Dimetrodon*-like sail on the back. They seem to have died out some time during the earlier late Cretaceous, along with their contemporaries the giant carcharodontosaurs. The terms Megalosaur, Megalosauridae, etc were unbtil recently rarely used, as firstly the original or type species of *Megalosaurus* is known from only very fragmentary material, and secondly Megalosaurs are a paraphyletic group, defined mostly by shared primitive features, and hence not considered valid in the current, cladistic, paradigm, although a phylogenetic analysis is emerging that sheds new light on this fascinating but little known period of theropod history.

The *Tetanurae* ("stiff tails") consist of a number of parallel lineages of theropods, all of which seemed to have evolved increasingly bird-like features. For example, their rib-cages indicate they had a sophisticated air-sac-ventilated lung system, which exists today only in birds. Such an advanced respiratory system would have been accompanied by an advanced circulatory system (even the ectothermic crocodiles (the nearest living dinosaur-ancestors after birds) have an efficient four-chambered heart, like mammals and birds, rather than the inefficient three-chambered reptile heart). All this indicates a high metabolic rate; like birds, advanced theropods were certainly endothermic (warm-blooded).

The clade Tetanurae includes both birds and the most famous of classic theropods. All Tetanurans lack the fourth digit of the hand, have all their maxilliary (upper jaw) teeth in front of their eyes, have a strap-like scapula (shoulder blade), and various other anatomical characteristics, which indicate that all tetanurans evolved from a single common ancestor. Tetanurans are generally subdivided into two clades, the Carnosauria and the Coelurosauria.

Megalosaurs represent a sort of intermediate group that does not fit in neatly with either the Ceratosauria or the Tetanurae, although nowadays the tendency is to consider at least some megalosaurs (or Torvosauroidea or Spinosauroidea, to give alternative names) as the most primitive (basal or underived) members of the Tetanurae ("stiff tails"), a clade that includes both birds and the advanced theropods. Megalosaurs were previously included with the Allosaurs and Tyrannosaurs in the polyphyletic (artificial) taxon "Carnosauria." The old-style definition of Carnosaurs is actually an ecotype rather than a true evolutionary group, designating any large (around 200 kg or more in weight) carnivorous theropods, posessing large skulls, short necks, and small forearms. MAK010506 revised 120221

Descriptions

Tetanurae: Definition: birds > *Ceratosaurus*. Padian *et al.* (1999)

Range: From Early Jurassic.

Phylogeny: Averostra : Ceratosauria + * : *Xuanhanosaurus* + (Megalosaurinae + (*Eustreptospondylus* + Spinosauridae) + ((*Piatnitzkysaurus* + *Marshosaurus*) + (*Afrovenator* + *Dubreuillosaurus*) + Avetheropoda))

Characters: **$** Increased pneumaticity of skull; nasals narrow & elongate [H+01]; **$** maxillary fenestrae present; **$** maxillary teeth only anterior to orbit(?) or to antorbital fenestrae(?); procoelous dorsal vertebrae [H+01]; stiffened tails (reduced importance of tail in walking?); scapula straplike [H+01]; coracoid tapers posteriorly [H+01]; **$**(?) metacarpals 1&2 broadly in contact [H+01]; **$**(?) manus with 3 digits; manus elongate [H+01]; **$**(?) obturator notch on ilium; **$** fibula reduced and "clasped" by tibia; **$** anterior horizontal groove on astragalar condyles. ATW

Comments: As indicated, the name of the clade refers to the development of a stiffened tail; members of the clade are also characterised by the loss of an external fourth digit on the hand, though some basal members did retain the fourth metacarpal (Holtz 1998). Most basal members of the Tetanurae are large species, the 'carnosaurs' of older authors. Within the Tetanurae, a well supported clade, variously called Avetheropoda and Neotetanurae, unites the Coelurosauria with the Allosauroidea. (adopted from CKT)

Note: Sereno's (1999) diagnosis of the Tetanurae seems to include features more appropriate to Avetheropoda and Maniraptora.

Links: The Tetanuran Theropods: Diverse carnivorous dinosaurs - UCMP; Tetanurae - Wikipedia; Tetanurae - Thescelosaurus!, includes listing of every species; Mikko's Phylogeny a dendrogram and references; Variety of Life: Tetanurae - another dendrogram and references; Tetanury (Tetanurae) bazalne detailed description in Polish, with oodles of cladograms at the end; Megalosauroidea part of Mickey Mortimer's theropod pages, not just every every taxon but every museum specimen listed down to the smallest detail; the most comprehensive (if rather technical) coverage you will find anywhere. Checked MAK120223

References: Hutt *et al*. (2001) [H+01].

Comments on Torvosauroidea = Spinosauroidea = Megalosauroidea:

Synonyms: Torvosauridae Jensen, 1985, Eustreptospondylidae Paul, 1988, Streptospondylidae Kurzanov, 1989

Phylogenetic definitions: assuming a monophyletic Megalosauridae: (1) any dinosaur that shares a common ancestor with *Poekilopleuron valesdunensis* (= *Dubreuillosaurus*), *Torvosaurus*, and *Afrovenator* (Allain 2002) (2) all dinosaurs more closely related to *Megalosaurus* than to *Spinosaurus*, *Allosaurus*, or modern birds (represented by Passer domesticus). Holtz et al 2004 (3) (as Torvosauridae) same definition as Holtz but replacing *Megalosaurus* with *Torvosaurus* (Sereno 2005, Taxon Search) (via Wikipedia).

Range: Middle to Late Jurassic of Eur, NthAm, & Afr

Characters: In essence, all Tetanurae other than Avetheropods. May be para- or polyphyletic. Known material is scrappy and includes both highly derived Spinosaurs as well as relatively general *Allosaur*-like Torvosaurids. Elongated rostral ramus of maxilla; pinched rostral ramus of lacrimal; **$** large sickle claw on manus 1.

Comments: A distinction should be made between a monophyletic, cladistic Megalosauridae and a paraphyletic, similarity-based, Megalosauridae; the one being far more restrictive than the other (corresponding perhaps to only a single linnaean subfamily or tribe). The former can be defined on gross morphology alone, and represnts one of those stem bubbles at the base of a romerogram. the latter is very hard to determine, and, as with Ceratosauria and Coelophysoidea (= Podokesauridae), there is the problem of homoplasies and reversals which hide the original morphology-based phylogenetic signal. So, cladistically, this taxon is monophyletic according to Allain 2002, Holtz et al. 2004 and Benson, 2010, but paraphyletic according to Smith et al 2007, Smith et al 2008, Sadlier et al 2008 and Xu et al 2009. Of course in either definition there would still be a monophyletic Megalosauridae, assuming *Megalosaurus bucklandii* isn't the literal ancestor of later theropods (and here remember that unlike evolutionary systematics, cladistics does not accept actual ancestors, only hypothetical ones), but the monophyletic clade would be greatly restricted, perhaps to only a few species. A paraphyletic definition makes sense not only morphologically (by allowing a continuous sequence of evolution forms) but also stratigraphically by eliminating the annoying ghost lineage regarding the absense of Jurassic spinosaurs.

This group includes *Megalosaurus, Torvosaurus, Poikilopleuron*, and possibly also *Edmarka, Erectopus,* and *Xuanhanosaurus*. These were large animals (upto 9 or more meters long), with short, stout arms. Paul Sereno rejected the use of the name Megalosauridae, due to the fragmentary nature of *Megalosaurus*, and used the name Torvosauridae (based on the well known late Jurassic form *Torvosaurus*. Hence Torvosauroidea and so on. This was a shame I feel, because *Megalosaurus* has a nice historical heritage. The English species *Megalosaurus bucklandii* was the very first dinosaur to be described, some years before Richard Owen coined the term Dinosauria in 1842. Unfortunately, the name *Megalosaurus*, like *Plesiosaurus*, became something of a taxonomic waste basket, and there is some doubt now among paleontologists whether it even is a valid genus. That is, although the remains are of a large primitive theropod dinosaur of "megalosaur" (or torvosaur) relationships, it is not possible to identify them more closely. At present there are three species still included. At times Megalosauroidea and Torvosauroidea were replaced by Spinosauroidea. More recently Megalosaurus, Megalosaridae, and Megalosauroidea have made a comeback, and the old historical trem now seems to be the accepted term for this clade of large early primitive theropods (e.g. Benson et al, 2010). At the same time, some of these taxa, su ch as *Eustreptospondylus* and *Piatnitzkysaurus*, are sometimes considered to have allosaurian or basal avetheropodan attributes (Paul 1988, With all of these basal tetanerans, the precise phylogenetic placement, and even whether they are related to each other in the first place, is not clear MAK010506, revised 120222

Xuanhanosaurus qilixiaensis Dong, 1984

Horizon: Lower Shaximiao Formation of China (Bathonian-Callovian)

Phylogeny: Tetanurae/Megalosauroidea/Megalosauridae **:** (Megalosaurinae + (*Eustreptospondylus* + Spinosauridae) + ((*Piatnitzkysaurus* + *Marshosaurus*) + (*Afrovenator* + *Dubreuillosaurus*) + Avetheropoda)) + *

Size: length about 4.5 meters, weight 250 kg (Paul 2010)

Comments: Known from a partial skeleton, this robust, moderately sized theropod is remarkable in that it has a large heavily-built forelimb, which led to the idea it was quadrupedal, although it is more likely that it used its arms to grab prey. It is rarely include din cladograms, but when it is it tends to appear near or at the bottom of the tree, as a stem tetaneuran, as in Holtz et al 2004. Benson et al, 2010 places it near *Marshosaurus* and *Piatnitzkysaurus*, although in vuiew of the highly endemic nature of Chinese Jurassic dinosaur faunas this may not be likely. Cau & Maganacu's cladogram (unpublished data, online) place it beneath the megalosaurs. MAK120222

Megalosaurinae Huxley, 1869 **:** *Megalosaurus, Torvosaurus*, ?*Poekilopleuron*.

Definition: same as Megalosauridae sensu Holtz et al., 2004; *Megalosaurus bucklandii* > *Spinosaurus aegyptiacus, Allosaurus fragilis, Passer domesticus*

Synonyms: Torvosauridae Jensen, 1985

Range: Middle to Late Jurassic of Eur & NthAm

Highly speculative Phylogeny: Tetanurae/Megalosauroidea/Megalosauridae **:** *Xuanhanosaurus* + ((*Eustreptospondylus* + Spinosauridae) + ((*Piatnitzkysaurus* + *Marshosaurus*) + (*Afrovenator* + *Dubreuillosaurus*) + Avetheropoda) + * **:** *Duriavenator* + (*Megalosaurus* + *Torvosaurus*)))

Comments: Considered monophyletic by Sereno et al. (1998), Allain 2002, Holtz et al. 2004 and Benson, 2010, paraphyletic taxon or evolutionary grade by Holtz 2000, Smith et al 2007, Sadlier et al 2008, Xu et al 2009. Status of *Poekilopleuron* is uncertain, it may be a sinraptorid (Benson et al, 2010). Other taxa like *Afrovenator* and *Eustreptospondylus* may be associated with Avetheropoda and Spinosaurids MAK120224

Duriavenator hesperis

Synonyms: *Megalosaurus hesperis* Waldman, 1974

Horizon: Upper Inferior Oolite of Dorset, England (late Bajocian)

Phylogeny: Megalosaurinae **:** (*Megalosaurus* + *Poekilopleuron*?) + *Torvosaurus*) + *

Size: about 5 meters? weight about 300 kg (Paul 1988)

Comments: Known only from teeth and snout fragments, this is another of those scrappy Jurassic theropods. From the little that is known of it this early, medium-sized animal seems to be quite similar to *M. bucklandii*. (Paul 1988). It was recently redescribed by Roger Benson, who found that several features show it to be distinct from the lectotype dentary of *Megalosaurus* (Benson, 2008a); He therefore erected a new genus, *Duriavenator* (combining the Latin name of Dorset, Duria, with Latin for "hunter", venator) Wikipedia. Cladistic analysis places it at the base of the Megalosaurine (Torvosaurine) line (Benson, 2010, Benson et al, 2010). With *Magnosaurus*, it is one of the oldest-known tetanurans. MAK120221

Megalosaurus bucklandii Meyer, 1832

Horizon: Stonesfield Slate, Inferior Oolite, Great Oolite, Forest Marble, and Coralline Oolite of England, unamed unit of Indr, France (Bathonian-?early Oxfordian)

Phylogeny: Megalosaurinae **:** *Duriavenator* + (*Torvosaurus* + (*Poekilopleuron*? + *))

Size: length about 7 to 7.3 meters, weight about 1.1 tonnes (Paul 1988)

Comments: The first dinosaur to be named, this specimen is known from fragmentary remains. The original specimen was a dentary, but many other elements have been referred to it, including teeth and postcrania . Few dinosaurs have gone through so many changes in intrepretation, from being considered the thigh bone of a biblical giant, to being likened to a set of testicles (*Scrotum humanum*, a name that technically has priority of *Megalosaurus bucklandii*, although fortunately for theropod nomenclature it has never been applied), to a crocodile-headed Victorian antedilevian quadraped, to the familiar bipedal theropod, as shown below.

From Wikipedia: *Megalosaurus* may have been the first dinosaur to be described in the scientific literature. Part of a bone was recovered from a limestone quarry at Cornwell near Chipping Norton, Oxfordshire, England in 1676. The fragment was sent to Robert Plot, Professor of Chemistry at the University of Oxford and first curator of the Ashmolean Museum, who published a description in his Natural History of Oxfordshire in 1676. He correctly identified the bone as the lower extremity of the femur of a large animal and he recognized that it

NATURAL HISTORY

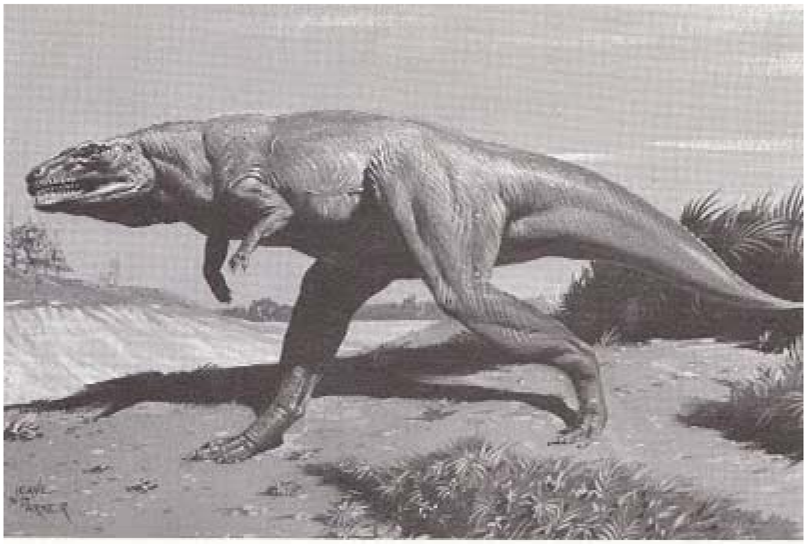
OXFORD-SHIRE,

ENGLAND.

By R.P. LL.D.

was too large to belong to any known species. He therefore concluded it to be the thigh bone of a biblical giant, such as those mentioned in the Bible. The bone has since been lost but the illustration is detailed enough that some have since identified it as that of *Megalosaurus*. The Cornwell bone was described again by Richard Brookes in 1763. He jokingly named it *Scrotum humanum*. **Image:** Cover of Robert Plot's *Natural History of Oxfordshire*, 1677 (right), and illustration of a fossilized lower extremity of a *Megalosaurus* femur (left) taken from that book. Public domain, via Wikipedia.

Modified from Wikipedia: In 1852, Benjamin Waterhouse Hawkins was commissioned to build a model of *Megalosaurus* for the exhibition of dinosaurs at the Crystal Palace in Sydenham, where it remains to this day. Huge and visually impressive even by today's standards, *Megalosaurus* became one of the park's three 'mascot dinosaurs' along with the *Iguanodon* and (less so) *Ichthyosaurus*. Yet it is arguably the most inaccurate of all of Hawkins's models, with a huge crocodile-like head and walking on all fours. The hump on the back of the sculpture in Crystal Palace and other restorations from the 1800s was based on the material now referred to as *Becklespinax*. **Image:** *Megalosaurus* at the Crystal Palace, London. Photo by C. G. P. Grey; Creative Commons Attribution, via Wikipedia.



MEGALOSAURUS

It was not until the middle of the nineteenth century, when more complete remains of theropod dinosaurs began to be discovered in North America, that a more accurate picture of these animals as long tailed bipeds developed. *Megalosaurus* was soon supplanted by its better known American counterparts, *Allosaurus* and *Tyrannosaurus*. The iconic image of *Megalosaurus* however, and one that exerted a strong influence on the present author (MAK) during his childhood dinosaur studies, is the representation by the now sadly little known paleo artist Neave Parker. Considering his work predates the dinosaur renaissance of the 70s and 80s, his *Megalosaurus*, shown taking long strides with a horizontal back and elevated tail, is remarkably modern in posture, the only criticism being the head should be held above the body with the neck in the classic archosaurian S-shaped posture. **Image:** Love in the Time of Chasmosaurus - Vintage Dinosaur Art: Dinosaurs - British Museum (Natural History) MAK120224

For a long time the genus *Megalosaurus* was something of waste basket or taxon for poorly known mostly Jurassic theropods; it is currently associated only with the type species, *M. bucklandii*. This was a rather big animal, clearly the top preditor of its day. Cladistic analysis sometimes (Holtz et al. 2004, Benson et al, 2010) places it close to *Torvosaurus*, although it has also been placed separately (Sadlier et al 2008, Mortimer) MAK010506

Poekilopleuron bucklandii Eudes-Deslongchamps, 1838

Synonyms: Poecilopleuron (l. c.) AC02, Poecilopleurum (l. c.) AC02, Poicilopleuron (l. c.) AC02, Poikilopleuron (l. c.) AC02]; Poekilopleuron bucklandii Eudes-Deslongchamps 1838 [=Megalosaurus poikilopleuron Huene 1926, Poecilopleuron bucklandi (l. c.), Poecilopleurum bucklandi (l. c.), Poekilopleuron bucklandi (l. c.), Poicilopleuron bucklandi (l. c.), Poikilopleuron bucklandi (l. c.)] AC02 - CKT110613

Horizon: Calcaire de Caen, Calvados, France (early Bathonian)

Phylogeny: Megalosaurinae **:** *Duriavenator* + (*Megalosaurus* + (*Poekilopleuron*? + *))

Size: length about 7 meters, weight about 1 tonne (Paul 1988)

Comments: *Poekilopleuron* is to French paleontology what Megalosaurus is to English, and quickly became a similar taxonomic wastebasket. Add to that the fact that it is almost impossible to spell, leading to innumerable synonyms. The fate of the original specimen was rather unfortunate. Apparently fairly complete when found, a lot of the material was destroyed before collection, and the rest during WWII. The taxon has since had to be studied on the basis of cast replicas. Subsequent discoveries of theropod remains from France may belong to this species (Paul 1988). The most distinctive part of this animal are its forelimbs. Quoting Wikipedia: "Their length, about 60 cm, was a sign of this theropod's more original build. Unlike later Theropoda, whose forelimbs tended toward reduction in length in proportion to the animals' size, Poekilopleuron's were long and, by implication, potent. The length mostly resided in the elongated but powerfully muscled humerus. The antebrachia (forearms) were markedly short and robust, a characteristic shared with Poekilopleuron's slightly later and considerably larger American cousin Torvosaurus." Its phylogenetic position is uncertain. It may be related to or identical to *M. bucklandii*, or some material assigned to the latter may belong to this species. (Paul 2010). Considered part of a monophyletic Megalosauridae close to *Eustreptospondylus* and *Dubreuillosaurus* by Allain 2002, and sister taxon of *Megalosaurus* + *Torvosaurus* by Holtz et al. 2004; conversely placed in the Sinraptoridae by Benson et al, 2010 this may be yet another exmple of mosaic evolution, an intermediate form between megalosaurids and sinraptorids MAK010506, revised 120224

References: APS03, AC02 CKT110613

Torvosaurus tanneri Galton and Jensen 1979

Synonyms: *Edmarka rex* Bakker, Kralis, Siegwarth, and Filla, 1992

Horizon: Middle Morrison Formation of Colorado, Wyoming, & Utah (early Tithonian)

Phylogeny: Megalosaurinae **:** *Duriavenator* + (*Megalosaurus* + *Poekilopleuron*?) + *)

Size: length about 9 meters weight about 2 tonnes (Paul 1988, 2010)

Comments: Known from a partial forelimb, pelvis, and skull, this was among the largest of the Morrison preditors. This animal was larger and more heavily built than *Allosaurus*. Yet it has a number of primitive features that indicate relationships with typical Middle Jurassic theropods like *Gasosaurus* and *Poekilopleuron*. The absense of a calcaneal notch, already present in the much earlier *Eustreptospondylus*, indicates that, like

Mounted cast of *Torvosaurus tanneri* in the North American Museum of Ancient Life. The smaller skeletons at the bottom left are the small hypsilophodonts *Othnielia rex*
Photographed by Ninjatacoshell, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

Ceratosaurus, this animal was a sort of "living fossil", continuing to survive and flourish alongside much more specialised and advanced theropods MAK010506. This species has also been reported from Portugal (Mateus et al 2006

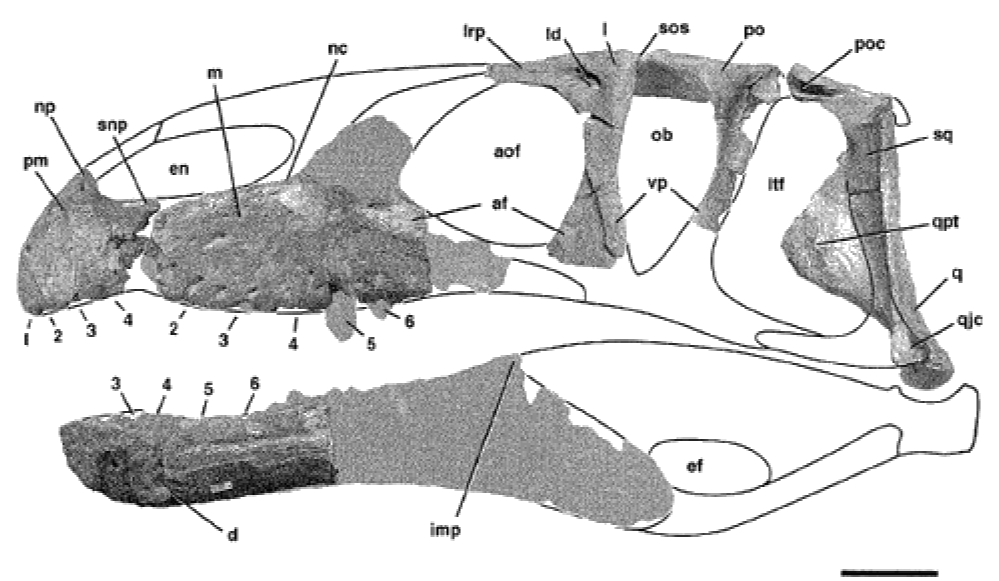
Reference: Paul 1988

Links: Torvosauroidea; Re- Torvosauroidea was [R- Torvosaurus & Giganotosaurus];

Eustreptospondylus oxoniensis
Walker, 1964

Synonyms: *Megalosaurus cuvieri*, *Streptospondylus cuvieri* ; Monotypal rank: Eustreptospondylidae Paul, 1988, Streptospondylidae Kurzanov, 1989

Horizon: Middle Oxford Clay, England (late Callovian), also NW France - Late Callovian/Early Oxfordian (for *Streptospondylus altdorfensis*)



Eustreptospondylus oxoniensis skull in left lateral view. Scale = 5 cm. from Sadlier et al 2008, (copied from Origin and Evolution of Spinosauridae)

Phylogeny: Tetanurae/Megalosauroidea/Megalosauridae : *Xuanhanosaurus* + (Megalosaurinae + ((*Piatnitzkysaurus* + *Marshosaurus*) + (*Afrovenator* + *Dubreuillosaurus*) + Avetheropoda) + (Spinosauridae + *))

Size: length 4.63 meters (adult would be larger), weight 218 kg (juvenile) (Paul 1988)

Comments: known from a partial skull and skeleton of juvenile/subadult, this is among the better known of the middle Jurassic theropods, and until the discovery of *Baronyx* the most complete theropod skeleton from England. According to Greg Paul (1988), this animal is more or less intermediate between Megalosaurus and more advanced forms like Allosaurus, Cladistic analysis hawever found *Eustreptospondylus* to be a fairly typical megalosaur (Sereno et al. (1998), Allain 2002), albeit in a different clade to *Megalosaurus* and/or *Torvosaurus* (Holtz et al. 2004, Benson, 2010) , a basal megalosaurid (Ortega et al 2010), or in a paraphyletic Megalosauria (Holtz 2000).

Similarily, the family Eustreptospondylidae was coined by Gregory Paul to include a number of advanced megalosaur and primitive allosaur like animals. All have the allosaur-like flexible ball-and-socket neck articulation, but in other respects they are too primitive to be considered allosaurs. More recent cladistic analysis shows the family as Paul defined it (which included *Eustreptospondylus*, *Piatnitzkysaurus*, *Gasosaurus*, and *Marshosaurus* to be an artificial assemblage, and it would seem that their allosaur-like chracteristics are either convergences or shared primitive features. One analysis still finds a clade centered on *Eustreptospondylus*, which could be call Eustreptospondylinae, as a subset of the Megalosauridae Benson, 2010.

Others find *Eustreptospondylus* to be a sister taxon/stem spinosaur or place it with the spinosaurs (Smith et al 2007, Sadlier et al 2008, Smith et al 2008, Xu et al 2009, Cau, et al 2011), so perhaps it's a megalosaurid evolving towards the spinosaurid condition. As no Jurassic spinosaurids are known (apart from a few referred teeth, which could be anything), this would make *Eustreptospondylus* a nice non-missing link. In view of the gradational nature of evolution, it would not be surprising if clades like Megalosauroidea and Megalosauridae go the way of the old clades Ceratosauria and Coelophysoidea, to be replaced by a stepwise series of smaller lineages. In any case, this shows that there is no sharp dividing line between megalosaurids, spinosaurids, and allosaurs, but rather evolutionary gradations.

The very poorly known *Streptospondylus* is often placed near *Eustreptospondylus* (Allain 2001, Smith et al 2007, Smith et al 2008) alone or, in addition to that taxon, the even more poorly known *Magnosaurus* (Benson et al, 2010) .

Streptospondylus altdorfensis Meyer, 1832 is a contemporary French species known from assorted postcrania (Allain & Pereda Suberbiola 2003). Even more than most 19th century Jurassic European theropods known from scrappy material, this animal is a taxonomic nightmare, see the Wikipedia page for more. This may be the same species as *E. oxoniensis* in which case the earlier name has priority Greg Paul (2010)). Or it may be the same genus but a slightly different species. For now we have decided to retain *Eustreptospondylus* MAK010506 revised 120222

Piatnitzkysaurus floresi Bonaparte, 1979

Horizon: Cerro Condor Formation of Argentina (Callovian/Oxfordian)

Phylogeny: Tetanurae/Megalosauroidea/Megalosauridae : *Xuanhanosaurus* + (Megalosaurinae + (*Eustreptospondylus* + Spinosauridae) + ((*Afrovenator* + *Dubreuillosaurus*) + Avetheropoda + (*Marshosaurus* + *)))

Size: length about 4.5 meters, weight 275 kg (Paul 1988)

Comments: Known from two partial skulls and a partial skeleton this moderately sized theropod and originally described as a primitive allosaur (Bonaparte, 1979, Bonaparte, 1986). It was a lightly built medium-sized bipedal carnivore with robust forearms. The discovery of *Piatnitzkysaurus* was important in that it was the first South American theropod known from fairly complete remains and still remains the only well-known Jurassic South American theropod Despite its fairly complete status, it shares with most other middle Jurassic theropods a problematic phylogentic placement. In other words, there is little agreement as to where it belongs on the theropod evolutionary tree. It has has variously been considered a basal tetaneuran (Rauhut 2003, Smith et al 2007, Xu et al 2009, Rauhut et al 2010), united with other medium-sized taxa such as *Piatnitzkysaurus* and *Marshosaurus* in a distinct lineage of basal tetanurans or basal megalosauroidea (Benson, 2010, Benson et al, 2010), as a basal monophyletic megalosaur (Holtz et al 2004, as a primitive (Sadlier et al 2008) or an advanced (Holtz 2000) taxon of a paraphyletic megalosaur sequence, an allosaur-like (transitional) "eustreptospondyline" megalosaur (Paul 1988), a basal avetheropod (Paul 2010, Cau, et al 2011), or a primitive allosaur (Chure, 2000). Since this pretty much covers every lineage of early Mid Jurassic theropod other than proto-tyrannosaur, we can sum up by saying that no one seems to know what it is. Of course, that is nothing unusual as far as megalosaurs go. The problem with placement of "transitional" mid Jureassic theropods like *Piatnitzkysaurus* and *Monolophosaurus* (which in very similar fashion has likewise been located everywhere from basal tetaneuran to stem allosaur, depending on tree topology) is that in parsimony analysis of atomistic character traits, it is not possible to determine if a taxon is very primitive and has not yet acquired apomorphies (unique traits) of more derived clades, or is very advanced and has lost those same synapamorphies (shared traits) through reversal. If either or both *Piatnitzkysaurus* and *Monolophosaurus* are stem tetaneura or stem-megalosauroidea, this means that allosaurian traits have evolved repeatedly by convergence. if they are stem-avetheropods it means that some very primitive traits are retained even in advanced intermediary forms, a common phenomenon known as mosaic evolution. Either explanation is equally plausible. For now, we have placed these taxa as stem avetheropods, although future studies may well result in revising this phylogeny.

Assuming a stem-avetheropod interepretation, Greg Paul's observation (Paul 1988) that this Jurassic South American animal is more advanced than the South American abelisaurs that lived later, in the Cretaceous period is pertinant, although we now know that highly derived allosaurs (megaraptorans) continued alongside abelisaurs even to the end of the Createcous.

Condorraptor currumili Rauhut 2005 seems to be a closely related form (Xu et al 2009, Benson et al, 2010). MAK010506 revised 120227

Marshosaurus bicentesimus Madsen, 1976

Horizon: Morrison formation of Utah and ?Colorado (Late Kimmeridgian)

Phylogeny: Tetanurae/Megalosauroidea/Megalosauridae : *Xuanhanosaurus* + (Megalosaurinae + (*Eustreptospondylus* + Spinosauridae) + ((*Afrovenator* + *Dubreuillosaurus*) + Avetheropoda + (*Piatnitzkysaurus* + *)))

Size: length about 4.5 meters , weight about 225 kg (Paul 1988)

Comments: Known from a partial skeleton, this is a poorly known animal of uncertain relationships, it may be a primitive allosaur, or alternatively a megalosaur. It is intermediate in both size and evolutionary development between the contemporary small but advanced coelurosaurs and large but primitive ceratosaurs, but also the same size as the earlier *Gasosaurus* and *Piatnitzkysaurus*. The pelvis alone contains features reminiscent of coelophysoids, coelurids, sinraptorids, and allosaurids. The forearms seem to have been quite short (a megalosaurid feature). Benson et al, 2010 places it as a basal tetaneuran close to *Piatnitzkysaurus* MAK010506

Afrovenator abakensis Sereno, Wilson, Larsson, Dutheil, and Sues, 1994

Horizon: Tiouraren Formation (Bathonian-Oxfordian) of Niger

Phylogeny: Tetanurae/Megalosauroidea/Megalosauridae : *Xuanhanosaurus* + (Megalosaurinae + (*Eustreptospondylus* + Spinosauridae) + ((*Piatnitzkysaurus* + *Marshosaurus*) + Avetheropoda + (*Dubreuillosaurus* + *)))

Size: length 8 to 9 meters, weight 1 or 2 tonnes (Paul 2010)

Comments: Known from the majority of the skull and a partial skeleton, this is one of of the better known types of dinosaur, and in fact the most complete skeleton of a Mesozoic large theropod ever found in Africa (most dinosaurs are only known from a few scraps of bone). This was a lightly built animal, with long legs implying a pursuit predator. the head is long and low, with proportionally large teeth (Paul 2010) this respectable-sized animal seems similiar to *Eustreptospondylus* (Allain 2002, Holtz et al. 2004), although it has also been placed as basal avetheropod (Holtz 2000). A recent cladistic analysis place it in a more basal position in the Megalosaurine (Torvosaurine) line (Xu et al 2009. Benson, 2010, Benson et al, 2010). It has also been placed near the avetheropoda (Smith et al 2007, Sadlier et al 2008), and these two latter findings may be complementary; i,e, *Afrovenator* may reprsent a transitional form between megalosaurids/ines and avetheropods. In any case there seems to be little difference between all the species at the base of the tetanuran family tree. Originally believed to be of Hauterivian (Early Cretaceous) age (Sereno et al., 1994), a sort of "living fossil" alongside its more advanced cousins, the Tiouraren Formation in which *Afrovenator* has been found is now considered Mid Jurassic in age (Rauhut and Lopez-Arbarello, 2009). Closley related to *Dubreuillosaurus*, indicating that these animals ranged widely MAK010506 021221

Dubreuillosaurus valesdunensis (Allain, 2002) (or *Afrovenator valesdunensis*

Range: Mid Bathonian of France

Phylogeny: Tetanurae/Megalosauroidea/Megalosauridae : *Xuanhanosaurus* + (Megalosaurinae + (*Eustreptospondylus* + Spinosauridae) + (Avetheropoda + (*Piatnitzkysaurus* + *Marshosaurus*) + (Afrovenator + *)))

Comments: Known from an excellent skull and fragmentary postcrania (the result of the skeleton being blown to pieces when the quarry where the fossil was found was reopened). Originally assigned to the genus *Poekilopleuron* (Allain & Pereda Suberbiola 2003), this megalosaur had an unusually low and long skull, with the length of the skull being three times the height. Cladistic analysis consistently places it close to the contemporary genus *Afrovenator* (Holtz et al. 2004, Smith et al 2007, Xu et al 2009, Benson, 2010, Benson et al, 2010), perhaps it should be placed in the same genus, although it would make the name *Afrovenator* a seem bit incongruous for a European species. MAK120221

Links: Thescelosaurus, Wikipedia, Theropod Database (Mickey Mortimer - places this taxon in a monophyletic Eustreptospondylinae) MAK120224

Image Artwork by Nobu Tamura - Wikipedia Gnu/3.0 - by-

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Theropoda: Spinosauridae

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Herrerasauridae
   |--Herrerasauridae
   `--+--Ceratosauria
       `--Tetanurae
           |--Megalosaurinae
           |--+--Eustreptospondylus
           |   `--Spinosauridae
           |      |--Baryonychinae
           |      |  |--Baryonyx walkeri
           |      |  `--Baryonyx tenerensis
(=Suchomimus)
           |      `--Spinosaurinae
           |          |--Irritator
           |          `--Spinosaurus
           `--Avetheropoda
              |--Carnosauria
              `==COELUROSAURIA
                  `--AVES
```

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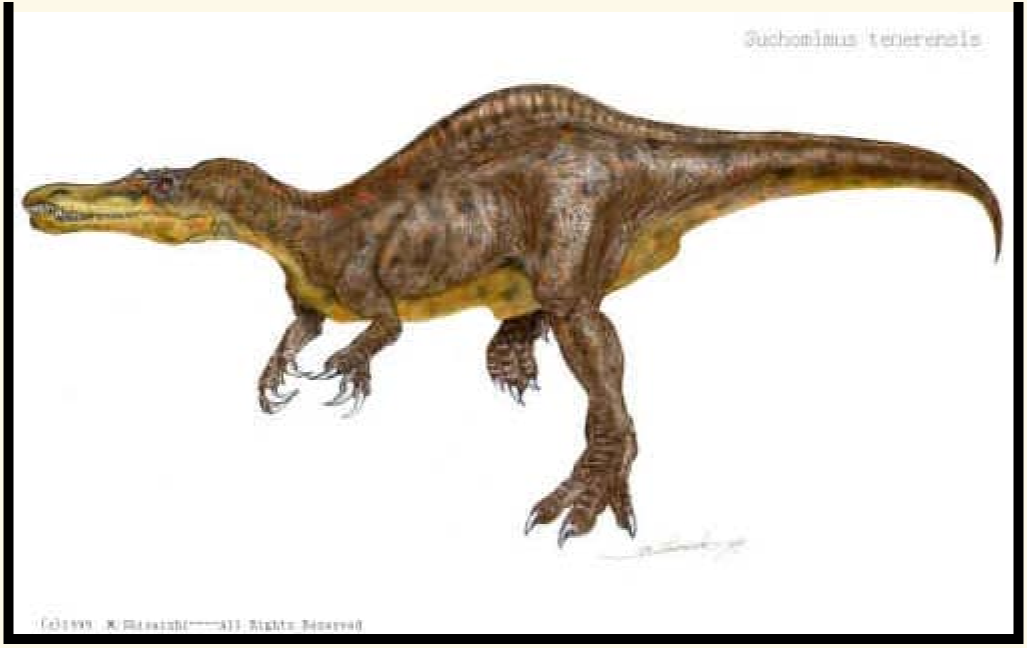
Spinosaurs - semiaquatic theropods

Spinosauridae. Among the more unusual of the theropod dinosaurs, spinosaurids were lightly built



predators with elongated vertebral spines and crocodile-like jaws with specialized teeth. Fish probably formed most of their diet. Two main groups exist: the baryonychids, who are most famous for their elongated, many-toothed skulls and large hand claws; and the spinosaurids, which had more cranial ornamentation and generally a larger sail (reminiscent of *Dimetrodon*). Spinosaurids, like *Baryonyx tenerensis* (also known as *Suchomimus*), have very short and stocky arms, thumb claws which are dramatically larger than the other unguals, unguals with greater angles of curvature, a tapering shaft, and more oval slender cross-section (like that of a carnosaur or *Torvosaurus* claw). Spinosaurid teeth are much more oval in cross-section than in typical theropods. There are a number of crocodilian like features in the skulls of spinosaurids: including the elongate snout, conical teeth, secondary palate (so it could breath through it's nostrils, even while the mouth is closed, a mamamlian feature not shared by most reptiles), and more. These features have been associated with the adoption of a piscivorous diet in crocodylomorph evolution. As with modern crocodiles, spinosaurs were not obliged to only eat fish. They could eat land animals as well. Remnants of *Iguanodon* bones as well as *Lepidotes* fish scales are found among the fossil stomach contents of *Baryonyx walkeri*. The paleoenvironments from which known spinosaurids come all support diverse communities of fish, some of which were very large. There is currently no evidence that these were seasonal communities, and would seem likely to be permanent residents. Thus, we have very large packages of fish meat not otherwise easily exploitable by theropods, although they would have been in competition with contemporary giant crocodiles. The relationship of the spinosaurids is not completely clear, although the most likely option is that the spinosaurs are cousins to the megalosaurids. Greg Paul in his **Predatory Dinosaurs of the World** however suggests that they might actually be late surviving (and giant) coelophysoids (podokesaurs). An interesting piece of evidence here is the presence of a "subnarial gap" or kink in the jaw, under the nostrils, that is found only in the Podokesauridae (Coelophysoidea) and Spinosauridae. There is no evidence of a ' subnarial gap ' in any other theropods groups outside of those two. It is however a feature that is common in archosaurs in general. *Eoraptor* apparently has a subnarial gap, but *Herrerasaurus* does not. There are differing views over whether either is a true theropod. However in an scientific paper Paul Sereno *et al.* affirm Megalosaur (Torvosaur) relationships. There may be only a superficial resemblence between spinosaurids and coelophysids in respects to the premaxillary/maxillary portion of the skull in profile. In addition, the anatomical arrangement in coelophysoids differs from the condition in spinosaurids (although the latter could be derived from the former). But now that the postcranial anatomy of spinosaurids are a lot better known than back in the mid-1980s, it seems that there is not much in the rest of the skeleton to link spinosaurids and coelophysoids. Some restorations of spinosaurians made recently show them as quadrupedal, a mistake based on early descriptions of the arms of *Baryonyx walkeri*. MAK120304

Habits

The following is taken verbatum from Wikipedia:

A 2010 publication by Romain Amiot and

colleagues found that oxygen isotope ratios of spinosaurid bones indicates semiaquatic lifestyles. Isotope ratios from teeth from the spinosaurids *Baryonyx*, *Irritator*, *Siamosaurus*, and *Spinosaurus* were compared with isotopic compositions from contemporaneous theropods, turtles, and crocodilians. The study found that, among theropods, spinosaurid isotope ratios were closer to those of turtles and crocodilians. *Siamosaurus* specimens tended to have the largest difference from the ratios of other theropods, and *Spinosaurus* tended to be have the least difference. The authors concluded that spinosaurids, like modern crocodilians and hippopotamuses, spent much of their daily lives in water. The authors also suggested that semiaquatic habits and piscivory in spinosaurids can explain how spinosaurids coexisted with other large theropods: by feeding on different prey items and living in different habitats, the different types of theropods would have been out of direct competition. (Amiot et al 2010)

Descriptions

Spinosauridae

Range: Barremian to Cenomanian of Eur., Afr, SAm, & ?Aus

Phylogeny: Tetanurae/Megalosauroidea/Megalosauridae **:** *Xuanhanosaurus* + (Megalosaurinae + ((*Piatnitzkysaurus* + *Marshosaurus*) + (*Afrovenator* + *Dubreuillosaurus*) + Avetheropoda) + (*Eustreptospondylus* + * **:** Baryonychinae + Spinosaurinae))

Comments: MAK010506

Links Thesceosaurus (short but useful description of each species); Wikipedia; Mikko's phylogeny (dendrogram only); Origin and evolution of Spinosauridae in French, argues for *Eustreptospondylus* as a basal spinosaur

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Baryonychinae

Range:

Phylogeny: Spinosauridae **:** + Spinosaurinae + *

Comments: Baryonychines are characterized by (among other traits) the increased number and decreased size of dentary (jawbone) teeth (about 30) and a blade-shaped ventral keel to the anterior dorsal centra of the vertebrae. MAK010506

Baryonyx walkeri Charig and Milner, 1986

Synonyms: *Suchosaurus cultridens*, *Suchosaurus girardi*

Horizon: Wealden formation of Surrey, England and Spain (Barremian)

Phylogeny: Spinosauridae **:**

Size: Length 9.5 meters estimated, weight about 1.7 tonnes (Paul 1988)

Comments: Known from most of a skull and skeleton, this is the most complete theropod dinosaur unearthed to date in Britian. Originally referred to as the "Surrey dinosaur", and nicknamed "Claws" on account of its huge claws, which conjured images of a gigantic dromaeosaurid, this animal is now known to be a close relative of *Spinosaurus*. It was probably a fish-eater. *Suchomimus* is a close relative, and probably belongs in the same genus. MAK010506

Baryonyx tenerensis (Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sider, Varricchio, G. Wilson, and J. Wilson, 1998)

Synonym: *Suchomimus tenerensis*

Horizon: Elrhaz Formation, Tenere Desert region, Niger (Late Aptian)

Phylogeny: Spinosauridae **:**

Size: length over 11 meters, weight several tonnes

Boring but (un)necessary nomenclatural note: As there is little to distinguish *Suchomimus* from *Baryonyx*, or for that matter from the more poorly known *Cristatusaurus lapparenti* Taquet and Russell, 1998, it is likely that the three are congeneric. This is a rare instance where sufficient material shows how similar two species can be, invalidating the usual need for monotypal fossil genera. *Baryonyx* having taxonomic priority (being named in the 1980s) would be the default genus name, so *Suchomimus tenerensis* becomes *Baryonyx tenerensis*. It is possible also that *C. lapparenti* is a senior synonym of *S. tenerensis* and so has priority over the latter, see comments by Mickey Mortimer, which would give *Baryonyx lapparenti* as the correct name for *Suchomimus tenerensis*. Of course these cdould also be different but closely related species, so at least "tenerensis" is probably safe. In any case, the name *Suchomimus* is so familar among dinophiles, and this is such a distinctive animal, that it will doubtless be known as *Suchomimus* for a very long time MAK120304

Comments: *Baryonyx tenerensis* ("Suchomimus") had an elongate snout and piscivorous adaptations that make the skull resemble a fish-eating crocodilian such as the gavial. It differs from Baryonyx in that the snout is even more crocodilian like. The skull is estimated at about 1.2 m (4 ft) in length, the overall creature was 11 meters or more. The robust forelimbs armed with very large curving claws, including a sickle-like thumb, that could be used like gaffing hooks on fish or other prey. Tall blade-like neural spines ran along its back, rising into a low (60cm tall) "sail" over the hip region (sacral vertebrae) and base of the tail.

Nearly 3.5 m (12 ft) high at the hips, *B. tenerensis* may have waded into rivers and lakes like to catch fish, but probably could swim in deeper water as well, using its back legs and possibly its tail for propulsion. Suchomimus may have swept its mouth back and forth through the water, much like a pelican, and snapped when it encountered prey. This would allow it to keeps its eyes above the waterline and still reach down into the muddy waters for large lungfish.

Fish-eating habits are indicated by structural parallels with modern crocodiles. Crocodiles species such as the Nile, Salt-Water, Muggers have jaws on par with *Baryonyx walker*. Although thinner than most animals but still wide enough and strong enough to take down large animals like water buffalo. The piscivorous crocodylians like the gharial and false gharial and the African slender snouted croc all have jaws suitable for fishing and small animal catching. If they were to attempt to tackle a large animal their jaws would snap under the stress. *B. tenerensis* had jaws like the latter, so the same rules seem to apply.

Unlike conventional fish-eaters *B. tenerensis* had relatively high skull. Piscivores need a long low skull so they can swip the skull through the water to catch fish. Onviously Suchomimus 's methods of catching food were different to crocodiles.

B. tenerensis is likely to have eaten land animals as well as fish. It had a relatively long, thin neck, plus very strong forearms and massive (by theropod standards) shoulders. It shared the local environment with a massive (10-15 meter) crocodile, built on a rather modern design, which occupied the lurk-in-the-water carnivore niche. The long jaw was better able to withstand twisting than the wider skull of Carcharodontosaurus, so it would have attacked different, probably smaller, prey on land. The thin jaws could not have tackled animals like iguanodonts. MAK010506

Spinosaurinae

Range: Albian to Cenomanian of Afr & S Am

Phylogeny: Spinosauridae **:** Baryonychinae + *

Size: (Paul 1988)

Comments: Spinosaurines are characterized by very straight teeth lacking serrations, and lack the derived increase in dentary tooth number. The difference between baryonychine and spinosaurine teeth is that spinosaurine teeth seem to be less curved, whereas baryonychines retain something closer to the original theropod curvature in lateral view. They remain, however, much rounder in cross-section than allosaur or ceratosaur teeth of the same height. MAK010506

Irritator challengeri Martill, Cruickshank, Frey, Small, and Clarke, 1996

Synonym: possibly *Angaturama limai* Kellner and Campos, 1996

Horizon: Romualdo Member of the Santana formation, Albian of Brazil

Phylogeny: Spinosaurinae **:**

Size: Length about 5.5 to 6 meters, weight about 500 or 600 kg

Comments: This animal's name comes from the fact that the skull was both damaged and artificially lengthened by amateur fossil hunters before it was described. *Angaturama limai* Kellner & Campos, 1996, another unusual theropod from the same formation, consisting of the front part of the jaws, is probably from the same species. MAK010506

Spinosaurus aegyptiacus

Horizon: Baharija Beds of Egypt, also Morocco (Albian-Cenomanian)

Phylogeny: Spinosaurinae **:**

Size: about 15 meters estimated, weight about 4.5 tonnes (Paul 1988)

Comments: A huge but lightly built animal, with vertebral spines taller than a man (the tallest part of the large bony sail is over the thorax - the mid-dorsal vertebrae), Spinosaurus did not seem to compete with the contemporary Cacharodontosaurs. Perhaps, like the Baryonchines, it was semi-aquatic; probably a fish-eater. Early illustrations wrongly showed *Spinosaurus* to resemble a conventional carnosaur (like Allosaurus) with a Dimetrodon-style sail or fin on the back (there are still some illustrations that show Spinosaurus as a chunky animal with long thick forearms, sometimes in a quadrapedal pose). The remains were lost in WWII. Spinosaurus marrocanus Russell, 1996, from the ? Albian of Morocco may or may not be the same species. Material referred to as "Spinosaurus B" seems to belong to two theropods: the vertebrae to *Sigilmassasaurus* (a large theropod of uncertain relationships - Wikipedia), and the limb material to the allosaur *Carcharodontosaurus* (Thescelosaurus). MAK010506

Image: Skeletal reconstruction of *Spinosaurus aegyptiacus*, photo by Kabacchi, via Wikipedia, Creative Commons Attribution

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Theropoda: Avetheropoda

Cryolophosaurus, Monolophosaurus, & Sinraptor

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Ceratosauria
   `--Tetanurae
      |==Megalosauroidea
      `--Avetheropoda
         |--Carnosauria)
         |   |--Monolophosaurus
         |   `--Allosauroidea
         |       |--Lourinhanosaurus
         |       |--+--Metriacanthosaurus
         |       |  `--Sinraptoridae
         |       |     |--Yangchuanosaurus 
shangyouensis
         |       |     `-
-Yangchuanosaurus/Sinraptor dongi
         |       `--+--Allosaurus
         |          `--+--Neovenator
         |             |--Carcharodontosauridae
         |             `--Megaptora
         `==COELUROSAURIA
             `--AVES
```

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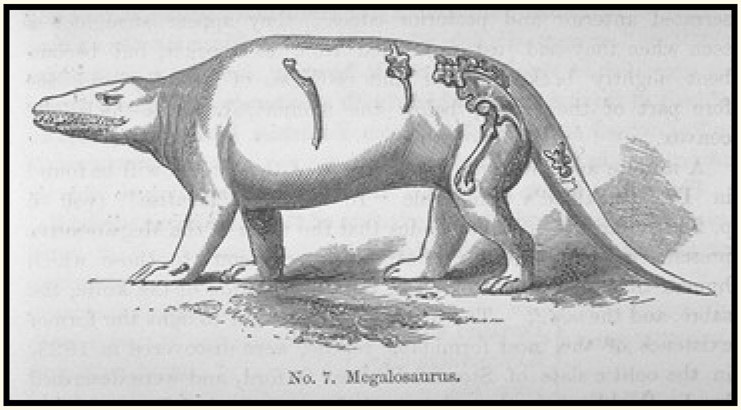
5. *Metriacanthosaurus* X
6. *Monolophosaurus* X
7. *Sinraptor/Yangchuanosaurus dongi* X
8. Sinraptoridae X
9. *Yangchuanosaurus shangyouensis* X

Carnosauria


No. 7. Megalosaurus.

Carnosauria was originally used as a general term for all of the big theropods, including the elusive and quite possibly non-existent, *Megalosaurus*, the Snark of dinosaurs. In the 1920's Huene suggested that, despite its position as the biggest and baddest theropod, *Tyrannosaurus* looked a lot more as if it belonged with the "small" theropods, the Coelurosauria. However, this was the Jurassic of paleontology, and most dinosaur paleontologists were lumbering, slow-moving, low-metabolism forms. With the advent of cladistic adaptations in the 1980's, dinosaur paleontologists became faster, hungrier and more predatory. The more derived forms began dismembering virtually defenseless nineteenth century taxa with lightning-fast computers, developing, in the process, enlarged manual phalanges from entering data. Others began hunting in packs, with alpha professors leading viscious gangs of slavering, pencil-wielding graduate students through the Mesozoic halls of their museums in search of prey.

Just in this manner was Carnosauria decimated. At first, only the oldest and weakest members, like *Megalosaurus*, were picked off. But the blood lust of the new paleontology knew no bounds. In just a few short years, all that was left of Carnosauria were *Allosaurus* and a few meager, nondescript bones at the bottom of the largest and rustiest drawers of the most obscure museums.

Recently, however, intensive conservation efforts by Tom Holtz and others have resulted in a remarkable worldwide resurgence. With the discovery of *Giganotosaurus* and related forms, Carnosauria is once again the home of the world's largest terrestrial predators. *Cryolophosaurus* and other, as yet undescribed, species from Gondwanaland could lead to a renaissance of the Carnosauria. Even so, the threat of extinction remains very real. Paul Sereno, backed by the awesome commercial might of the National Geographic Society, has sworn to exterminate the Carnosauria and crush its quivering remains into Allosauroidea, leaving nothing but coelurosaurs and a random miscellany of basal "neotetanurines" (i.e. avetheropods).

Citizens! This is the taxon that made Victorian Englishmen gasp in horror at the Crystal Gardens in 1854. This is the clade that made movie critics shudder at "Carnosaur." This is the group that even made paleontologists scream at the publication in a kids' book of "*Elvisaurus*." Save the Carnosaurs!

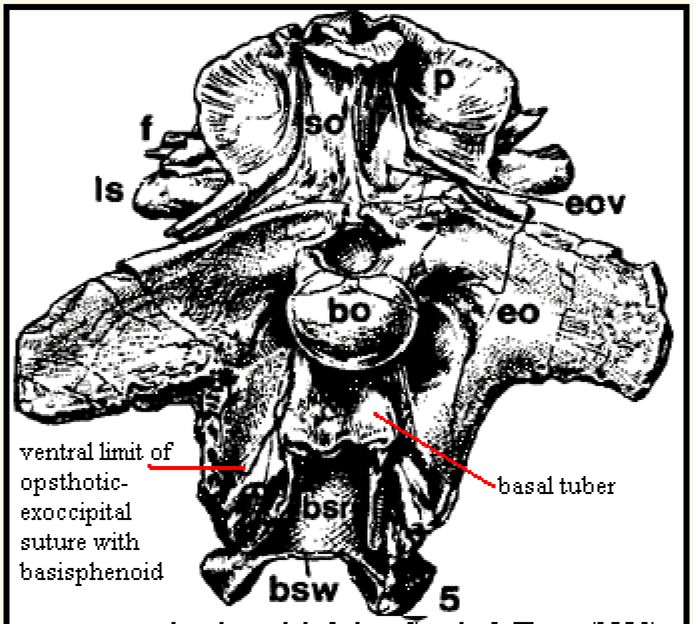
Sinraptoridae

Something about carnosaurs seems to draw the best from people. Some of the most extraordinary monographs in paleontology were inspired by the giant Jurassic killers, and Currie & Zhao (1993) is one of them. It is well-written, copiously illustrated, reflects careful comparison with related forms, and contains some useful reflections on the functional significance of some of the more important morphological findings. It is everything a monograph should be.

It is important to be clear on the many strong points of this article, because I am going to take issue with its one weak point. Many readers will of the article will not have the several hours it takes to work through the entire piece. In fact, perhaps the majority will only read the family and species diagnosis at the beginning, and one or two anatomical points of special interest to them.

The problem is that there appear to be some significant errors or ambiguities in the family diagnosis. These are contained in a long list of characters which unite sinraptorids with allosaurids as follows:

(a) "**upper qudratojugal prong of jugal shorter than jugal prong**." *Sinraptor* has *three* prongs on the quadratojugal process of the jugal. the external (i.e. lateral) prongs are roughly the same size. It is the medial prong that is long. Dorsoventrally, this is neither the upper or lower prong, but falls between the lateral prongs. The medial prong is likely homologous to the lower prong of two in, e.g., *Allosaurus*, but the description as given is either confusing or erroneous.



Sinraptor: occiput in occipital view. Currie & Zhong (1993), figure 7A.

(b) "**braincase box has opened up posteriorly between tubera, which are no longer pedunculate**." The actual conformation of the occiput is shown in Currie & Zhao's Figure 7A, which is reproduced at right. The braincase box, as I understand the term (which is not used elsewhere in the text), does not open up posteriorly, and there is nothing between the basal tubera which are, in fact, at least slightly pedunculate. Perhaps the authors are referring to some other tubera. Perhaps "posterior" was not the correct indication. Perhaps I have misunderstood the text. However, at a minimum, the diagnosis is unclear.

(c) "**oval muscular attachment on basioccipital**." Nothing at all is said about this in the text.

(d) "**posteroventral limit of the exoccipital-opisthotic contacts the basisphenoid but is separated from the basal tubera by a notch.**" This may be correct, but it is not clear from the actual description, which reads: "*Sinraptor* is unusual in that the exoccipitals extend significantly more ventrally than the basal tubera. In most theropods, including ... allosaurids ... the ventral limit of the exoccipital-opisthotic along the basioccipital and basisphenoid suture is either at the same level or is dorsal to the level of the basal tubera. A notch separates the basal tuber from the more anteroventral extension of the exoccipital-basisphenoid suture as in allosaurids." (*Id.* at 2049, citations omitted). So, the notch is common to sinraptorids and allosaurids. However, the entire morphology of the occiput here is quite distinct. The similarity exists but is not likely to be an indication of common ancestry.

(e) "**Tenth presacral vertebra in process of incorporation into dorsal, rather than cervical region**." What could "in process of incorporation" mean? What the text actually indicates is that the 10th presacral vertebra is a *cervical* vertebra, although it bears some similarities with the tenth presacral in *Allosaurus*, which is a dorsal vertebra. (*Id.* at 2057 & 2065).

(f) "**triangular neurapophysis**." What is meant here is apparently "triangular neurapophysis on the axis-atlas complex." (see *id.* at 2055).

The really interesting and peculiar thing about sinraptorids may be the way in which the head was held. As Currie & Zhong note: "The shapes and alignment of the axial intercentrum and centrum served to bring the neck underneath the occipital condyle to support the skull in a manner that is unique amongst Jurassic theropods, with only *Monolophosaurus*, *Y[angchuanensis] magnus* and an undescribed theropod showing a tendency towards doing the same thing." (*Id.* at 2057, citations omitted.)

This posture is reflected in life restorations of *Sinraptor* and *Allosaurus* by Shiraishi Mineo. The head of *Sinraptor* is held higher. The anterior part of the back is arched to compensate (as also noted by Currie & Zhao). The difference in carriage may well be responsible for a number of differences between *Allosaurus* and *Sinraptor*, such as the anteroventral extension of the opisthotic-exoccipital, the use of the 10th presacral vertebra as a cervical, rotation of the atlas intercentrum, and apparently greater emphasis on stiffening the back with hyposphenehypantrum articulations.

To speculate further on function, one might envision *Sinraptor* as a slower, but more maneuverable, version of *Allosaurus*. *Sinraptor* was more anteroposteriorly compact and laterally rigid. It might well have been able to shift its weight rapidly from side to side, as suggested by Currie & Zhao's notes on locomotion discussed in the main entry. The raised position of the head combined with rapid shifts in its center of gravity would also allow *Sinraptor* to attack over a wider angle compared to the antero-posterior axis of its body when the attack began. Running in this position would be awkward, but *Sinraptor* would have the advantage in an ambush attack. Perhaps this is also the reason for the fact that *Sinraptor* has an even more completely pneumatized skull than *Allosaurus*. *Allosaurus* would rely on the lightness and speed of its entire body. *Sinraptor* would rely more on the speed of its head. This is, perhaps, a parallel development to the changes in posture which led to the upright carriage of birds.

Descriptions

Avetheropoda: (= Neotetanurae = Allosauria = Allosauroidea of some authors) Birds + *Allosaurus* (Padian *et al.* (1999))

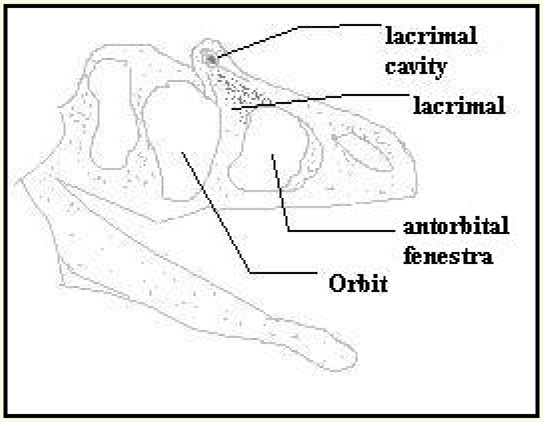
Range: Early Jurassic-Late Cretaceous.

Phylogeny: Tetanurae/Megalosauroidea/Megalosauridae : *Xuanhanosaurus* + (Megalosaurinae + (*Eustreptospondylus* + Spinosauridae) + ((*Piatnitzkysaurus* + *Marshosaurus*) + (*Afrovenator* + *Dubreuillosaurus*) + * : Carnosauria + Coelurosauria)))

Characters: U-shaped premaxillary symphysis; tapering posterior of coracoid; proximal half of metacarpal I closely appressed to metacarpal II; pubic boot; loss of obturator foramen; cnemial process originates on lateral surface (of tibia). ATW

DinoData: Avetheropoda

Carnosauria (= Allosauroidea *sensu* Sereno (1999)) *Allosaurus* > birds (Padian *et al.* (1999)). **:** *Monolophosaurus, Allosaurus,*, etc.



Range: Mid Jurassic to Late Cretaceous.

Phylogeny: Avetheropoda **:** *Monolophosaurus* + ((Coelurosauria + ?*Gasosaurus*) + * **:** Sinraptoridae + (Allosauridae + (Carcharodontosauridae + Neovenatoridae)))

Characters: Large, long, narrow skull; **$** enlarged nares; **$** nasal participates in antorbital fossa; pre-orbital horns, commonly based in lacrimal; antorbital fenestra is expanded upwards; **$** large cavity in lacrimal at antero-dorsal margin of orbit (possible gland of unknown function); skull commonly crested; large orbits; cheek flat, vertical, at sharp angle to skull roof [CC00]; quadrate with broad quadratojugal flange; quadrate short, with head at mid-orbit level; basioccipital excluded from basal tubera (but *Sinraptor*?); **$** *basipterygoid process* very short; basi- parasphenoid formed by delicate-looking thin webs of bone; opisthocoelous vertebrae; pubic boot longer anteriorly than posteriorly; pubic boot triangular with apex posterior in ventral view; femur larger than tibia.

References: Currie & Carpenter (2000) [CC00]; Currie & Zhao (1993); Sereno (1997). ATW021222.

Comments: With the exclusion of Tyrannosauroidea (now considered a giant Coelurosaur lineage), only the Allosaurids and their relatives make up the Carnosauria. The name "Allosauria" was coined by Greg Paul in his superb book *Predatory Dinosaurs of the World* and seems to have caught on, although "Carnosauria" is still sometimes used. In any case, these were big to enormous bipedal terrestrial preditors, that for some one hundred million years or so were the dominant form of life on land. MAK010506

Note: the stem-based definition of Carnosauria is more inclusive than the node-based definition of Allosauroidea:

- *Carnosauria* (Huene, 1920): the largest clade that includes *Allosaurus fragilis* but not *Passer domesticus* (modified from Padian and Hutchinson, 1997)
- *Allosauroidea* (Marsh, 1878 vide Currie and Zhao, 1994) the smallest clade that includes both *Allosaurus fragilis* & *Sinraptor dongi* (Holtz, Molnar and Currie, 2004; modified from Padian and Hutchinson, 1997)

(Definitions from Carnosauria (in Polish)

With new phylogenies reshufling basal tetaneuran and avetheropodan taxa, some of which were only recently described to begin with, it has become hard to know if a primitive theropod is a basal Allosauroid, a non-Allosauroid (i.e. stem-taxon) Carnosaur, a basal Megalosauroid, or a basal Tetanuran! *Monolophosaurus* for example has been considered all of these at some point or another. With the main debates in early theropod evolution being now about whether a taxon belongs in a monophyletic Megalosauroidea or paraphyletic basal Tetanura, or either of the latter or Avetheropoda, or vs Avetheropoda, most cladograms now have a simple node that is not distinguished further for re Allosauroidea/Carnosauria. MAK120227

Links: DinoData: Carnosauria; The Brutal Carnosaurs; carnosauria; VPTHEROPOD; Lecture 14 - Late Jurassic: Morrison, Tendaguru; MEA592D Dinosaur Osteology: Lecture 4; Carnosauria; Carnosaurs: ZoomDinosaurs.com; What groups of dinosaurs existed?; Allosauria (Dutch); theropods; CARNOSAURS; Untitled Document (Japanese); Carnosauria; ???????(Carnosauria) (Korean);

Monolophosaurus jiangi Zhao and Currie, 1995

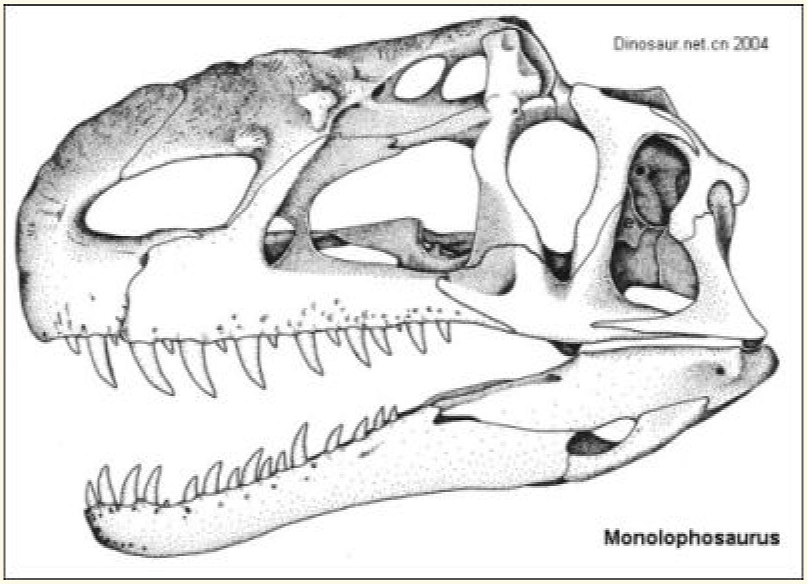
Horizon: Wucaiwan Formation of Junggar Basin, Xinjiang, China (Oxfordian)

Phylogeny: Carnosauria **:** Allosauroidea + *

Characters: Dorsal surface of nasal convex and rugose; facial horns present [CC00]; dorsal surface of frontals convex [CC00]; some caudal vertebrae with hyposphenes; supraacetabular shelf continuous with lateral margin of pubic peduncle.

References: Currie & Carpenter (2000) [CC00]; Currie & Zhao (1993). ATW060206.

Size: about 5.5 meters long, estimated weight 475 kg (Paul 2010)



Comments: Known from a partial skeleton and compressed skull, *Monolophosaurus* is a medium-sized early theropod distinguished by a single very large midline ridge-like head crest running from its nose to the rear of the skull. Beyond that, there is nothing particularily distinctive about it, and, as with its megalosaur cousins, exactly where it belongs on the theropod evolutionary tree is a matter of some controversy. The situation here seems to be very similar to that of *Piatnitzkysaurus*, another mid Jurassic theropod that has had the misfortunate of being bounced all aroudn the theropod family tree by rival phylogenetic analyses.

Originally, things were pretty straightforward. Holtz 2000,Holtz et al 2004, Novas et al 2005, and Corria & Currie 2006 are among the references that considered it an early allosauroid, which places it here among the avetheropods. Pretty soon however things started to go stemward. Smith et al. (2007), in a radical study using *Cryolophosaurus* (until then considered an allosaur) reinterpreted the positions of many taxa, and demolished the old clades Ceratosauria and Coelophysoidea, and found *Monolophosaurus* to be as a basal avetheropod. Similarily, Rauhut 2003 had previously found this species to be part of a paraphyletic megalosauria leading to allosaurs. Worse was to come with Benson, 2008b, in a paper on European megalosaurs, noting various primitive features of the skull and skeleton suggest that *Monolophosaurus* is actually a basal megalosauroid. This position was also recovered in a cladogram by Cau, et al 2011 in a paper on carcharodontosaurs. The implication here would be that characters previously considered apomorphies of the Allosauroidea are plesiomorphic (shared primitive traits, not unique to allosaurs) (Zhao et al. 2010 and Brusatte et al. 2010). Mickey Mortimor mega-matrix analysis finds it to be either a sister to Avetheropoda or a basal megalosauroid. As against placement as a basal tetaneuran, a cladogram in the recent a paper on on the megalosaur *Eustreptospondylus* (Sadlier et al 2008) and another of the advanced allosaur *Acrocanthosaurus atokensis* (Eddy & Clarke (2011)) both recover *Monolophosaurus* as a basal allosauroid. This brings us full circle, and we are back where we started after oceans of ink and reams of computer print-outs. It is pretty clear here as elsewhere that the choice of taxa and traits keyed into to the analysis would determine the outcome of the cladogram. It may be that a monophyletic Allosauroidea has to be replaced by any number of parallel megalosaurian lineages. Or this may simply be an example of mosaic evolution, a common feature in transitional taxa, so that early allosaurs or avetheropods were megalosaur-like, primitive basal megalosaur-like, in many ways. Or that Mid Jurassic theropod evolution is such a jumble that a lot more material is required before any even half complete phylogeny can emerge. For now, we've gone with the mosaic evolution option and retained Monolophosaurus as a basla carnosaur, although Smith et al. (2007)'s similar interpertation of this species as a basal avetheropod may be equally valid

Incidentally, *Monolophosaurus* wasn't the only theropod with a mono loph. A similar but even more exaggerated feature is found in the contemporary basal tyrannosaur *Guanlong wucaii*. If *Monolophosaurus* is a basal tetanuran then the two are not related and such characters would arise through convergence (Brusatte et al. 2010). If *Monolophosaurus* is a primitive avetheropod (whether stem-avetheropod or stem-carnosaur) then the two would only have fairly recently diverged, and these sort of crests may well be a common shared characteristic among basal avetheropods. The appareance of paired crests among ancestral neotheropods (podokesaurs) and horns and ridges among ceratosaurs and abelisaurs illustrates the repeated occurance of exotic head structures among theropods, doubtless for intra-specific display.

Monolophosaurus has been related to another taxon, *Chuandongocoelurus* (Benson, 2008b), known only from a single medium-sized partial skeleton, although the association isn't very strong (see Theropod database for comments), and was later considered a more basal form (Ortega et al 2010). If they are related they would constitute an endemic theropod clade (to which we could give the informal name Monolophosauridae (Bakker 1997), so far known from the Middle Jurassic of Asia (Zhao et al. 2010). But this may however be yet another example of convergence. Also, because no skull is known for *Chuandongocoelurus*, comparisons with *Monolophosaurus* and other taxa are made more problematic. MAK120223

Image: Dinosaur.net.cn - Monolophosaurus (in Chinese)

Allosauroidea . *Lourinhanosaurus*, Allosaurus + Sinraptor. (Padian *et al.* (1999)).

Range: Mid Jurassic to Late Cretaceous.

Phylogeny: Carnosauria : *Monolophosaurus* + * : *Lourinhanosaurus* + Sinraptoridae + (Allosauridae + (Carcharodontosauridae + Megaraptora))

Characters: Usually 7-10m long, laterally compressed. Long, narrow skull; flange-shaped lacrimal process on palatine; **$** articular with pendant(?) medial process; **$** participation of nasal in antorbital fossa; antorbital fenestra expanded dorsally; maxillary fenestra expanded dorsally to form hole in lacrimal (probably plesiomorphic for carnosaurs); pneumatic excavation of ascending ramus of maxilla (same character, described differently); lacrimal recess, single opening present (another aspect of the same character state); narial prominences comprised of paired ridges along lateral edges of nasals; postorbital prominences present; orbits large; lacrimal horns and crests common; quadrate articultion projects well ventral of ventral surface of maxilla; horizontal shelf on lateral surface of surangular, rostroventral to mandibule condyle, prominent and pendant; caudal dorsal neural spines oriented cranially; three fingers per hand; manus digits 2 & 3 roughly equal with 2 slightly longer; pubic boot triangular (apex caudal) in ventral view, acute angle between shaft and caudal portion of boot; **$** femur usually larger than tibia; 2 distal tarsals (III & IV).

References: Currie & Zhao (1993). ATW031029.

Comments: Allosauroidea proper is now considered a monophyletic clade divided into three similiarily monophyletic families: the Sinraptoridae, the Allosauridae, and the Carcharodontosauridae.

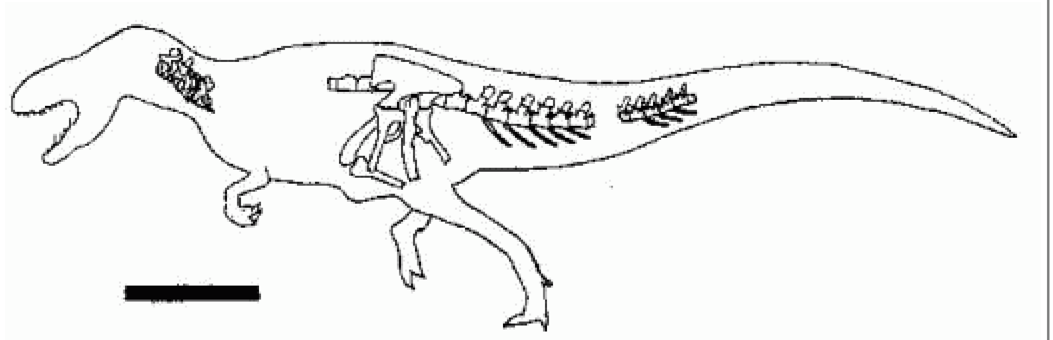
Greg Paul considers the small late Jurassic *Ornitholestes* and the earlier and larger *Proceratosaurus* to be also Allosaurs. This has not caught on, and current understanding classifies *Ornitholestes* as a basal (i.e. primitive/ancestral) coelurosaur, while *Proceratosaurus* has recently been identified as a basal tyrannosaur. MAK010506 revised 120225

Links: (Allosauroidea) DD: Allosauroidea; theropods; carnosauria; Dann's Dinosaur Info: Allosauroid; MEA592D Dinosaur Osteology: Lecture 4; Currie & Carpenter (full text article); PhyloCode Discussion - Message 2003-07-0007- Allosaurus whitei ...; Redescription de Streptospondylus altdorfensis , le dinosaure ...; Click Here!.

Lourinhanosaurus antunesi
Mateus, 1998

Horizon: Amoreira-Porto Novo of Lourinha, Portugal (late Kimmeridgian/early Tithonian)

Phylogeny: Allosauroidea : (*Metriacanthosaurus* + Sinraptoridae) + (Allosauridae + (Carcharodontosauridae + Megaraptora)) + *



Type of *Lourinhanosaurus antunesi*. Scale bar 0.5 m.. Caption and illustration from Mateus (1998)

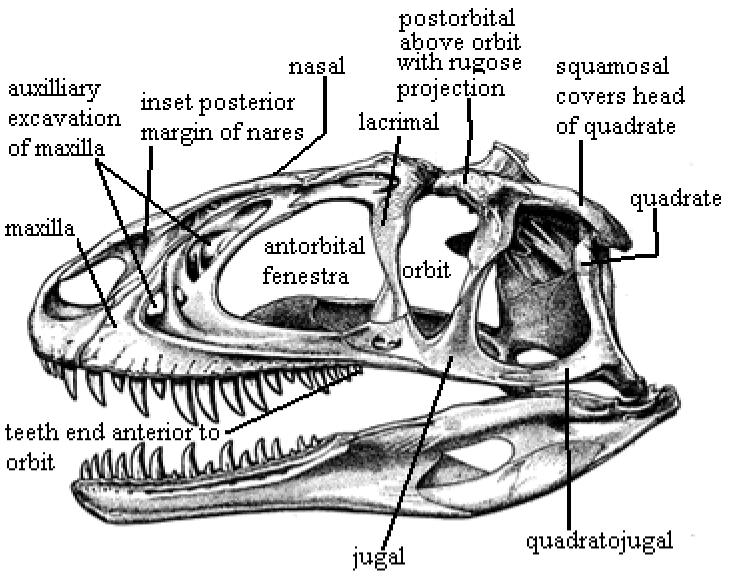
Size: length about 4.5 meters, weight about 200kg (Paul 2010)

Comments: Known from a fragmentary skeleton, this medium-sized theropod may be a sinraptorid (Mateus (1998), Benson, 2008, 2010) an unspecified carnosaur (Holtz et al 2004), an allosaur (Paul 2010), , or a distinct non-avetheropod tetaneran clade that also includes *Streptospondylus* (Mickey Mortimer). In any case, it represents a more primitive form than *Allosaurus* and *Acrocanthosaurus* (Mateus (1998)). If it is a sinraptorid it shows the lineage was established in Europe as wlel as China. Of course, Sinraptorid attributes may simply be common primtive characteristics, as well as some specialised traits that were lost in more advanced forms. This means that whilst Lourinhanosaurus may be a sinraptorid grade theropod, it still may or may not be necessarily a sinraptorid in the strict sense MAK120225

Sinraptoridae: *Sinraptor*, *Yangchuanosaurus*, *Metriacanthosaurus*?, *Poekilopleuron*?; *Sinraptor* > *Allosaurus*. Padian *et al.* (1999).

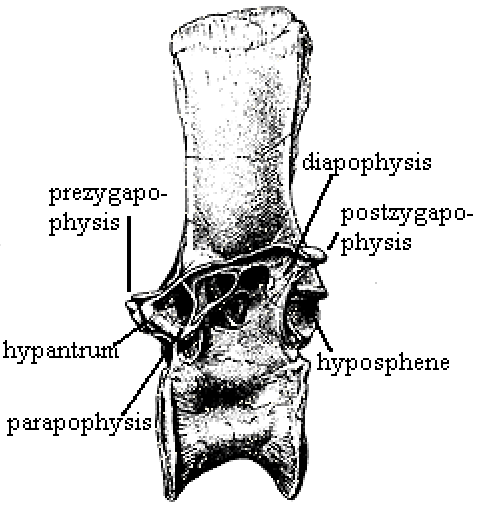
Range: Late Jurassic of China.

Phylogeny: Allosauroidea : *Lourinhanosaurus* + (Allosauridae + (Carcharodontosauridae + Megaptora)) + (*Metriacanthosaurus* + * : *Yangchuanosaurus shangyouensis* + *Sinraptor/Yangchuanosaurus dongi*)



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

Characters: **$** at least 2 accessory pneumatic excavations of maxilla; complex, variable network of pnumatic fossa associated with maxilla and nasals; maxilla rugose only above tooth row; maxilla longer than tall [CC00]; external nares with marked inset of posterior margin; antorbital sinus extends into lacrimal, nasal & jugal; ventral process of lacrimal with 2 convexities and process for suborbital ligament (marking ventral extent of eyeball); lacrimal does not contact maxilla; dorsolateral horn of lacrimal low; nasal very long, flat, and smooth; smooth internasal articulation (nasals may have been able to move upward and away from each other); nasal with pneumatic openings; nasal provides groove for ridge on internal process of maxilla (may allow some outward rotation of maxilla); tight sutures of nasal with lacrimal and frontal; small triangular prefrontal; frontal flat dorsally; no sagittal crest; strong nuchal crest; ventral end of postorbital above ventral margin of orbit; bulbous, rugose anterior projection on post-orbital; complex, layered jugal-maxilla articulation; **$** posterior (quadratojugal) process of jugal has 3 prongs with medial prong much longer (2 equal prongs in other carnosaurs; note that only the two lateral prongs can be seen in the figure); jugal & quadratojugal do not invade lateral temporal fenestra [CC00]; **$** squamosal flange covers head of quadrate in lateral view; parietal forms obtuse angle with occiput [CC00]; paroccipital process broad & shallow, turning ventrally at lateral ends, with distal posterior projection [CC00]; large crista prootica on prootic; downturned paroccipital process; basioccipital participates in small basal tubera (*but see* Sereno,1997); paroccipital process turns downwards slightly; slight or "incipient" separation of exit for opthalmic



Sinraptor: 9th dorsal vertebra in left lateral view. Modified from Currie & Zhao (1993).

branch of Vth cranial nerve; vomers fused anteriorly only; vomers contact pterygoids; symphysis of lower jaw probably flexible; dentary makes sliding contact with surangular and angular; elongate articular with retroarticular process; 4 pairs of premaxillary teeth; 15 maxillary teeth [CC00]; last maxillary tooth anterior to orbit; teeth with "tooth plates (modified cingula?) on lingual side; tooth plates not fused; triangular neurapophysis on atlas-axis complex; 10 opisthocoelous cervical vertebrae, but 10th is similar to allosaurid dorsal; neck held below skull in unique fashion; dorsal vertebrae amphiplatyan; back arched in thoracic region; hyposphene - hypantrum articulation on all dorsal vertebrae; 5 sacral vertebrae; some caudal vertebrae with hyposphenes; pectoral girdle largely unknown; sternum smaller than in *Allosaurus*; manus digit 1 relatively slight; vestigial manus 4 present; wide supraacetabular shelf continuous with lateral margin of pubic peduncle (see *figure*); brevis shelf narrow; pubes meet in symphysis along distal half of length; moderately expanded pubic boot; well-developed obturator process; strongly developed lesser & 4th trochanters; leg swung out (*abducted*) when swung forward (*protracted*) & hips shifted over opposite leg; lower leg generally same as in *Allosaurus*; astrgalus tightly linked to tibia; astragalus has extensive contact with fibula; ascending process of astragalus low.

Note: (1) Holotype of *Sinraptor dongi* is not fully mature. The holotype bears unhealed bite marks (possibly related to its death), as well as healed broken ribs. ATW

Comments: These are the most primitive allosauroids, although even at this early stage they were equipped with elaborate crests. While several European theropods have been placed here, it is not sure if they belong here, as many known only from quite inadequate material. Sinraptorids proper are known from China (hence sinraptorids), but that is more likely because Chinese dinosaur fossils are the best representatives of the middle Jurassic, rather than the group itself being limited to that region. However, it is still possible that Eastern China was cut off from the rest of Laurasia, as a distinctive fauna (Shunosaurine sauropods, *Beinotheroides* tritylodontids, and brachyopoid labyrinthodonts, seem to be indiginous to that region. MAK010506 revised 120225

Images: modified from Currie & Zhao (1993).

Links: DinoData: Sinraptoridae; Dinosaur Images; carnosauria cladogram; carnosauria; The Natural History Museum's Dino Directory; sinoyang.jpg; FPDM : Sinraptor dongi; SINRAPTOR (brief notes & references); Currie & Carpenter (pdf file of article which touches on phylogeny); Sinraptor (Dinosaurus site); Bibliography Project - About the Fighting Dinosaurs (discussion of dysfunctional family); EXPO 2002 (Japanese: nice image of fossil with brief note on relationships).

References: Currie & Carpenter (2000) [CC00]; Currie & Zhao (1993); Sereno,1997. ATW060206.

Sinraptor dongi Currie and Zhao, 1993 (= *Yangchuanosaurus dongi*)

Horizon: Wucaiwan Formation of Junggar Basin, Xinjiang, China (Oxfordian)

Phylogeny: Sinraptoridae **:** *Yangchuanosaurus shangyouensis* + *

Size: 8 meters long, 1.3 tonnes (Paul 2010)

Comments: Known from complete skulls and the majority of a skeleton, this was a typical large theropod. It's cranial ornamentation is rather modest. *S. hepingensis* is a closely reated species, or perhaps a synonym (see *Thescelosaurus!* website). If Yangchuanosaurus and Sinraptor are co-generic, than the former name has priority, and this species becomes *Yangchuanosaurus dongi* (Paul 2010) MAK010506 revised 120223

Yangchuanosaurus shangyouensis Dong, Chang, Li and Zhou, 1978

Synonym: *Y. magnus* Dong, Zhou, and Zhang, 1983

Horizon: Shangshaximiao Formation of Sichuan, China (Oxfordian)

Phylogeny: Sinraptoridae **:** *Sinraptor/Yangchuanosaurus dongi* + *

Size: length 11 meters, weight 3.5 tonnes (Paul 1988)

Comments: The largest carnivore of its time, this three and a half tonne preditor dominated its enviroment. The cranial ornamentation involves dual ridges above the snout and eyes. It also has a low fin fin, down its back, again, possibly for display purposes. Greg Paul (1988) considered this species similiar enough to go under *Metriacanthosaurus*. It is very similar to *S. dongi* MAK010506

Metriacanthosaurus parkeri Walker, 1964

Synonym: *Megalosaurus parkeri* Huene, 1926

Horizon: Upper Oxford Clay of England (early or middle Oxfordian)

Phylogeny: Allosauroidea **:** *Lourinhanosaurus* + (Allosauridae + (Carcharodontosauridae + Megaptora)) + (Sinraptoridae + *)

Size: length about 7.5 meters, weight about 1 tonne (Paul 1988)

Comments: From the little that is known of this animal (a few postcranial elements: some vertebrae, a femur) it appears similar to the Sinraptorids, where it is usually placed (Paul 1988, Benson, 2010). The two also lived at more or less the same time. The presence of fin-like ridge along back (as indicated by the tall-spined vertebrae) meant that for a long time this animal was considered an ancestral spinosaurid (Steele, 1970). As Justin Tweet (*Thescelosaurus!* website) notes, following a brief fifteen minutes of fame in the 1980s (thanks to Greg Paul's *Predatory Dinos of the World*, associating it with *Yangchuanosaurus*, or rather vice-versa) and 1990s (because of Paul's influence the name showed up in the movie version of *Jurassic Park)*, this taxon sank back into obscurity.

Because the more recent name Sinraptoridae (Currie & Zhao 1994), is used instead of the first published name, Metriacanthosauridae (Paul 1988), it has been suggested the latter should take precedence. But because it was not accompanied by a formal description, it cannot be considered a scientific valid under formal rules of nomenclature. In any case it is no longer used, not even by Greg Paul himself, we have not tried to revive it. Perhaps this is understandable given the scrappy nature of the eponymous genus. We've placed*Metriacanthosaurus* next to the sinraptorids, but it may well turn out to be a totally different lineage of early avetheropod. If neither *Metriacanthosaurus* or *Lourinhanosaurus* are sinraptorids, then the latter taxon is endemic to China, home of many unique Jurassic dinosaurs MAK010506 revised 120223

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Theropoda: Avetheropoda: Allosauridae

Acrocanthosaurus & Carcharodontosaurus

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DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Ceratosauria
   `--Tetanurae
      |==Megalosauroidea
      `--Avetheropoda
          |--Allosauroidea
          |   |--Sinraptoridae
          |   `--Allosauridae
          |       |--Allosaurus fragilis
          |       |--Allosaurus atrox
          |       |--Allosaurus amplexus
          |       |--Allosaurus europaeus
          |       |?--Allosaurus tendagurensis
          |       `--+--Neovenator
          |          |--Carcharodontosauridae
          |          `--Megaptora
          `==COELUROSAURIA
              `--AVES
```

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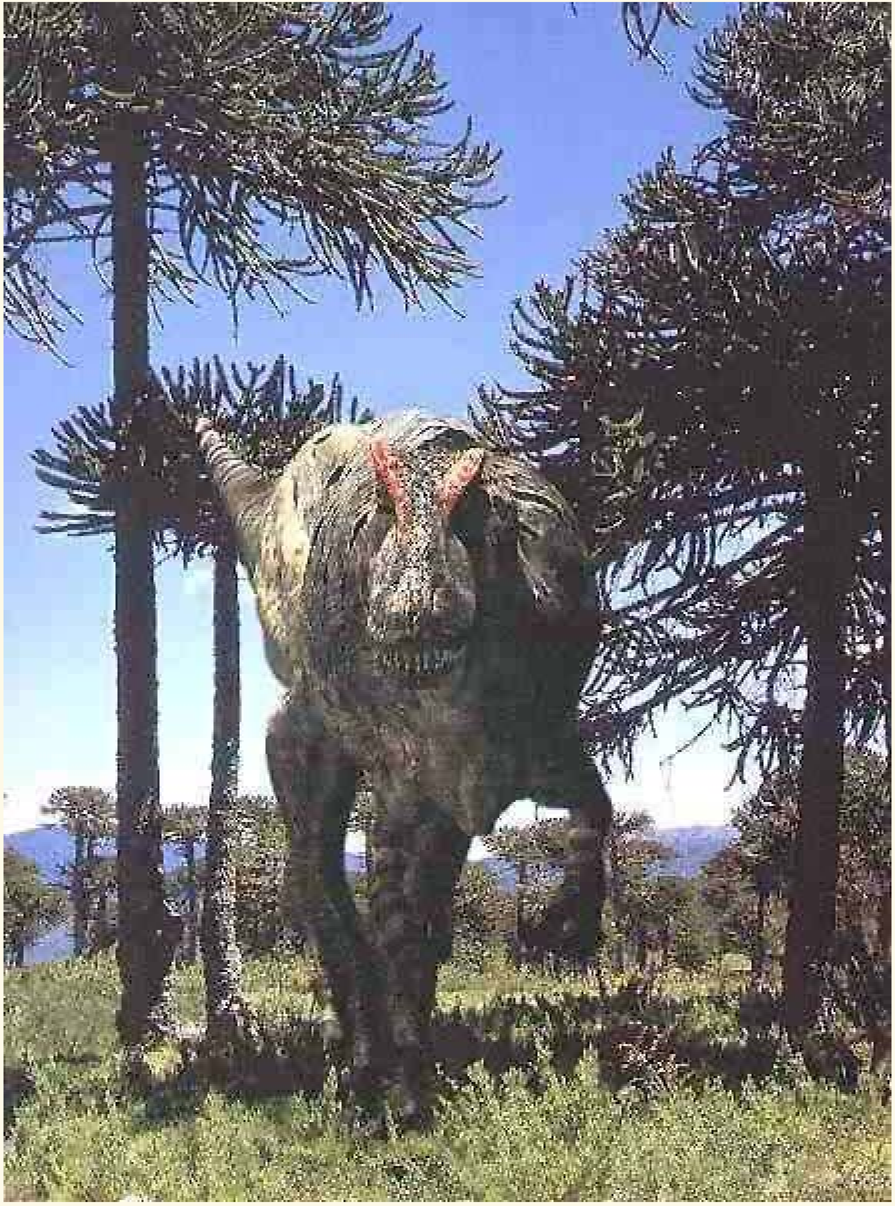


Face to face with Big Al. Image from Walking with Dinosaurs © 1999 ABC, BBC

While usually - apart that is from the little known giant species like *A. amplexus* - not in the same size range as *T. rex*, *Allosaurus* was an iconic member of the late Jurasisc megafuana, a huge and powerful predator, and clearly a very ecologically successful animal, as it easily outnumbered contemporary megapredators such as *Ceratosaurs* and *Torvosaurus*. An adult allosaur combined a flightless bird-like body, physiology, and agility with the brain of a crocodile and the mass of a medium-sized rhino; which means that it would basically lunge at anything that moved and looked like lunch(which basically was any other animal large enough to notice). Camptosaurs, stegosaurs, medium-sized sauropods, even other theropods, there was probably nothing short of a thirty-tonne apatosaur it wouldn't take on. With its powerful jaws and hind limbs, strong grasping forelimbs, and long counterbalancing tail, this impressive yet graceful animal very much typified the large preditor ecotype of the mid-Mesozoic. MAK120229

Allosaurus - master of the Jurassic, descendant of sinraptorids, ancestor of carcharodontosaurs

The above rather melodramatic title is intended as a sedgeway into a discussion on *Allosaurus* and phylogenetic methodology. For rthose who don't know, *Allosaurus* was the dominant megapredator of the late Jurassic (see also above paragraph). Phylogenetic methodology is how we work the evolutionary tree of life on Earth.[1]

Over the last two decades, a number of different phylogenetic hypotheses (a fancy way of saying "family trees" or "evolutionary relationships") regarding the evolution of the allosaurs have been proposed. One option for example has Sinraptoridae and Carcharodontosauridae as sister groups (sharing a common ancestor), with *Allosaurus* and *Acrocanthosaurus* as a side branch (Smith et al 2007). The current tendency however is to have something like Sinraptoridae + (*Allosaurus* + (*Acrocanthosaurus* + (higher Carcharodontosaurs)) (e.g. Benson et al, 2010, Eddy & Clarke 2011). This is the phylogeny we have followed here.

We can be pretty sure that *Allosaurus* evolved from something like *Sinraptor* or one of his cousins, and replaced them as the top carnivores of the Kimmeridgian and Tithonian ages (the latest Jurassic period). The two are pretty similiar in size and appearance and no doubt lifestyle, and differ only in detail, however Allosaurus has some advanced minor features not found in early or more primitive texa, as revealed in details of the skeleton (doubtless there were physiological and soft tissue details as well).

Morphologically (in terms of the evolution of form) as well as stratigraphically (the sequence in deep time revealed by fossil remains), *Allosaurus* represents the non-missing link between the Middle Jurassic Sinraptorids and the Cretaceous Carcharodontosaurs. If sinraptorids and equivalent taxa, such as *Lourinhanosaurus*, constituted the first pulse of allosauroidean evolution, then *Allosaurus* (or Allosaurines) were the second, and the dual Cretaceous adaptive radiations of giant carcharodontosaurs and medium-sized megaraptorans the third and culminating one. Here as elsewhere, the fossil record reveals the evolutionary history of life on Earth as beautiful sequence of transformation of form, with one type evolving into or being replaced by another through the course of deep time.

While some more fastidious phylogenetists might not want to state hypotheses too literally, citing the incompleteness of the fossil record as a reason to avoid statements about transitional forms or identification of any known taxa as actual objective (rather than hypothetical and abstract) ancestors, or rejecting the premise that cladograms provide insight into evolution in deep time, we would rather avoid such phylopessimism and adopt a more concrete and optimistic approach. We affirm that stratigraphy and the fossil record provide a strong phylogenetic signal which helps reveal details ofthe evolutionary tree of life.

This raises the problem of how such dendrograms should be drawn. Dendrograms such as the ones we employ here are not as strict or rigorous as cladograms, but they do provide popular representations of them (and are often confused with them). Cladistic methodology is - unlike evoluitionary systematics - not concerned with describing actual common ancestors; cladograms are simply abstract diagrams for conveying phylogenetic hypotheses, generally arrived at through statistical parsimony analysis. In such a diagram, *Allosaurus* might be shown on one terminal node, *Sinraptor* on another, and so on, without any comment as to whether one is the actual ancestor of the other. We say that *Sinraptor* is placed in a more basal position (as we have done here), but that doesn't make it an ancestor in cladistic formalism.

Formalism can lead to problems though. When popular adaptions of such cladograms are drawn online (i.e. dendrograms), it may seem that all the species assigned to a clade appear as a distinct and quite dramatic evolutionary radiation, as in Mikko's Phylogeny, Wikipedia dendrograms, or the Theropod Database, when all that is being done is representing sister-group relationships in simple diagramatic format. (scroll down for*Allosaurus* on the Theropod Database link). This is where Pattern Cladists get it right; such hypotheses should not be intended as literal geneologies. The problem is, at this poor level of resolution, it is often very difficult to know which species gave rise to which. So they tend to bunch into artificially monophyletic clusters (we saw this with groups like Ceratosauria and Ceolophysoidea). And even if (using here the linnaean genus and species hierarchy) a genus (a group of species) is ancestral to a later group (i.e. one of the species, known or unknown, in that genus directly evolved by Darwinian means into subsequent species, genera, and/or clades) traditional cladistics does not allow this to be represented (because it is only concerned with sister relationships, not ancestors and descendents).

Now, since *Allosaurus* is the only large advanced avetheropod known from the latest Jurassic, and assuming the phylogenetic hypothesis Sinraptoridae + (*Allosaurus* + (*Neovenator* + (Carcharodontosauridae + Megaptora)) or similar (e.g. (Carcharodontosauridae + (*Neovenator* + Megaptora))), it would be a paraphyletic taxon (grade). Even if we don't know which species of *Allosaurus* gave rise (via speciation) to the lineage culminating in early Cretaceous forms, it would still have been one of the species (or more than one, if they forma series), even if it is not one currently known to science, or even one that never fossilised.

So do we put, giving as examples the taxa on the current and adjacent pages

this or *this?*

```
Allosauroidea
  |--Sinraptoridae
  `--+--Allosauridae/Allosaurus
     |    |--Allosaurus fragilis
     |    |--Allosaurus atrox
     |    |--Allosaurus amplexus
     |    |--Allosaurus europaeus
     |    `?--Allosaurus tendagurensis
```

```
Allosauroidea
  |--Sinraptoridae
  `--Allosauridae/Allosaurus
      |--Allosaurus fragilis
      |--Allosaurus atrox
      |--Allosaurus amplexus
      |--Allosaurus europaeus
      |?--Allosaurus tendagurensis
```

```
  `--+--Neovenator
     |--Carcharodontosauridae
      `--Megaptora
```

```
  `--+--Neovenator
     |--Carcharodontosauridae
      `--Megaptora
```

The one on the left is a version of the type found everywhere online, which is based on a sort of cladistic literalism; as common ancestors are not referenced, we have instead a ghost lineage alongside a brief-flowering but ultimately sterile *Allosaurus* clade. The one on the right however is based on the premise that *Allosaurus* is a paraphyletic taxon, i.e. that it is the actual ancestor of Cretaceous allosauroidea. Of course, this still could be refuted if another advanced and intermediate late Jurassic taxon is found (in which case that taxon becomes the new transitional, paraphyletic grade), but on the basis of current knowledge. For this reason, we're introducinga new method of drawing dendrograms. At least that goes for the present author, some of the time. Other*Palaeos* contributers will differ according to whether they are phylogenticists, evolutionary suystematists, evolutionary phylogenetists, stratocladists, or some other methodology or combination of methodologies. Hence there is unlikely to be andy rigorous attempt at consistency in these webpages for quite some time, if at all MAK120225

Note

[1] Technically speaking, "phylogeny" is used by specialists to refer to cladistics and molecular phylogeny, either alone or in combination, whereas "evolutionary systematics" is applied to the pre-cladistic methodology. Since these two methodologies are complementary rather than contradictory, we tend to use these terms synonymously, or even combine them to refer to the need (very rarely acknowledged) for an all-methodology approach MAK120225

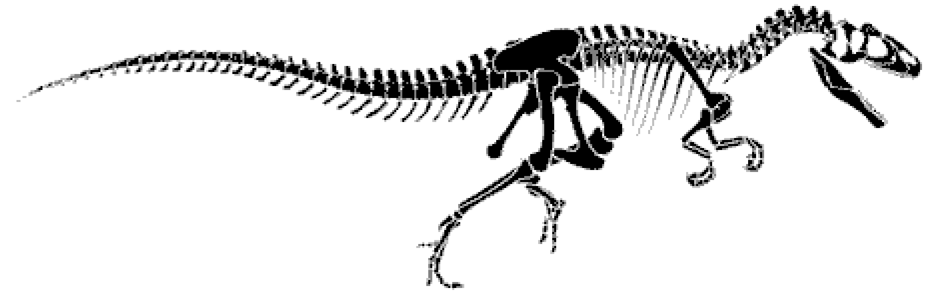
Descriptions

Allosauridae: *Allosaurus*. *Allosaurus* > *Sinraptor*. Padian *et al.* (1999).

Range: Late Jurassic of NAm, Eur, Afr

Phylogeny: Allosauroidea : Sinraptoridae + (Carcharodontosauridae + Neovenatoridae) + * : *Allosaurus atrox* + *Allosaurus fragilis* + *Allosaurus europaeus* + *Allosaurus amplexus* + *Allosaurus tendagurensis*

Characters: Most of the following applies to *Allosaurus*, the only certain member of the taxon. Up to 12 m for *Allosaurus*, but * may also include the larger *Giganotosaurus* (more probably a Carcharodontosaur); skull large but very narrow (indeed the entire animal is extraordinarily narrow in anterior view); skull is largely composed of buttressed arches, rather than plates, except for the nasal-lacrimal shield along the dorsal midline; skull apparently had ability to expand laterally; in *Allosaurus*, the lacrimal seems remarkably fragile above the orbits and may have been protected by a crest or horn-like structure attached to rugose flanges of the lacrimals on the postero-dorsal margin of the pre-orbital fenestrae. Premaxilla with 5 pairs of teeth; "tooth plates" (modified cingula?) at base of teeth; all tooth plates fused together; posterior end of angular *not* anterior to articular; unique, neomorphic anarticular bone present; vomers do not contact pterygoid; **$** single mandibular fenestra small externally; upper jaw with about 20 teeth, lower jaw with 13; **$** deep anterior ramus of surangular; nasal with 1-3 pneumatic openings; dorsolateral horn of lacrimal high; ventral process of lacrimal uniformly convex; lacrimal may contact maxilla externally; small, triangular prefrontal; small rugose anterior projection on post-orbital; **$** short quadrate, with head at the level of middle of orbit; separate exit from braincase for opthalmic branch of trigeminal (Vth) nerve; large basal tubera below occiput; paroccipital process turns strongly downward; hyposphene hypantrum articulation present only from 6th dorsal vertebra; caudal vertebrae without hyposphenes; furcula present; sacrum massive; manus bears 3 strongly recurved unguals, although arm is short and slender; brevis shelf narrow; pubic boot is very prominent; **$** pubic boot longer anteriorly than posteriorly & triangular in ventral view; ribs and distal elements of hind limb are oddly delicate and slender; tall ascending process of astragalus; astragalus lacks extensive contact with fibula.



Links: Dinodata: Allosauridae.

References: Currie & Carpenter (2000); Currie & Zhao (1993) . ATW010426.

Comments: An important and highly successful group of species, known so far from North America, Europe, and probably also Africa. Doubtless the only reason they aren't found more widely would be absense of knowledge of other latest Jurassic faunas. They were the classic large dinosaurian predators, generally about 7 to 8 meters long and over a tonne in weight, and retained the strong forearms of their megalosaurian ancestors. Apart from a few holdovers like *Ceratosaurus* and *Torvosaurus*, which occured with Allosaurus in Europe as well as America (Mateus et al 2006), allosaurs dominated the large theropod niche for some ten million or so years. All these animals, and many otehrs, were a victim of the end Jurassic extinction event, which brought about the end of the familiar Jurassic ecosystem with its allosaurs, coelurids, stegosaurs, diplodocids, and camarasaurs (the brachiosaurs however were among the few groups unaffected).

At one time the family Allosauridae included such diverse taxa as *Allosaurus, Neovenator,* and *Acrocanthosaurus*, and even all of the Carcharodontosaurs, as well as the poorly known *Valdoraptor*, *Wakinosaurus* and "*Chilantaisaurus maortuensis.*" Nowadays everything apart from *Allosaurus* (and probably synonyms such as *Saurophaganax*) are placed in other families, specifically the Carcharodontosauridae. Unless giant forms such as *Epanterias* et al are given their own generic name, *Allosaurus* would have to revert to its senior synonym of *Antrodemus*, because there would then only be one genus of large Morrison carnosaur, and *Antrodemus* would no longer be indeterminate (such are the rules of scientific nomenclature). This would be the same situation as *Triceratops* and *Torosaurus* being renamed *Agathaumas* should they all turn out to be part of a single growth series. MAK120307

Image: Above right: *Allosaurus* skeleton mounted in the lobby of the San Diego Natural History Museum. Wikipedia, public domain.; bottom left: *Allosaurus* sp., skeletal reconstruction, redrawn from Greg Paul, from The Real Jurassic Park - Professor Paul Olsen

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Allosaurus fragilis Marsh, 1877

Horizon: Lower Morrison formation of western North America (Rocky Mountain states) (Early / Middle Kimmeridgian)

Phylogeny: Allosauridae **:** *

Size: length about 7.4 meters, weight about 1 tonne (Paul 1988, the size of the type specimen, however Paul 2010 gives the same dimensions as A. atrox, 8.5 meters and 1.7 tonnes, which would be the larger specimen (AMNH 600) mentioned in his earlier book))

Comments: the type species of *Allosaurus*. The number of species assigned to this genus is controversial (Wikipedia, but in view of great temporal range of the Morrison formation, it is quite possible that the remains assigned to *A.*

fragilis don't all pertain to one species. We have however followed Gregory Paul in distinguishing this second species. As defined here, *A. fragilis* is known from one good skeleton, various skull and postcrania. It is therefore much rarer than *A. atrox* (making it unlikely the differences are due to sexual dimorphism), has taller, more pointed horns just above the eyes, and seems to have a more slender build, especially in the neck and forelimbs. In relation to *A. atrox* the head is shorter, deeper, and subtriangular. According to Robert Bakker it also occurs in earlier strata (the Garden Park and other quarries of the lower Morrison formation), so it may be an ancestor of *A. atrox*. "A. jimmadseni" may be a juvenile of this species or a distinct, primitive form. It is based on a nearly complete skeleton and skull. MAK010506 revised 120225

Allosaurus atrox (Marsh, 1878)

Synonyms: *Creosaurus atrox* Marsh, 1878a, "Poekilopleuron" *valens* Leidy, 1870, *Antrodemus valens* (Leidy)

Horizon: Middle Morrison formation of western North America (Rocky Mountain states) - Late Kimmeridgian to Early-Middle Tithonian

Phylogeny: Allosauridae **:** *

Size: length 8 to 8.5 meters, weight 1.3 to 1.7 tonnes

Allosaurus atrox in dynamic pose - cast from a Cleveland-Lloyd Quarry specimen. South Australian Museum public display (Adelaide, South Australia). Photo and caption by James St. John, original url

Comments: Usually considered a synonym of *A. fragilis*, *A. atrox* has been suggested by Bob Bakker and Gregory Paul as a second valid species, but its status remains unclear. It is distinguished by a longer, shallower, and more subrectangular skull. A specimen from the the late Kimmeridgian-early Tithonian of Portugal may also belong here, or it may be a closley related species or subspecies. This was a common animal - complete and many partial skulls, many partial and complete skeletons - and seems to have replaced the earlier *A.fragilis*. The Cleveland-Lloyd quarry contains the disarticulated remains of over sixty individuals; peresumably this was a preditor trap, like the Pleistocene La Brea tar pits. MAK010506. Referred to as "*Allosaurus* unnamed species" by Paul 2010 because of the inadequate nature of the type specimen

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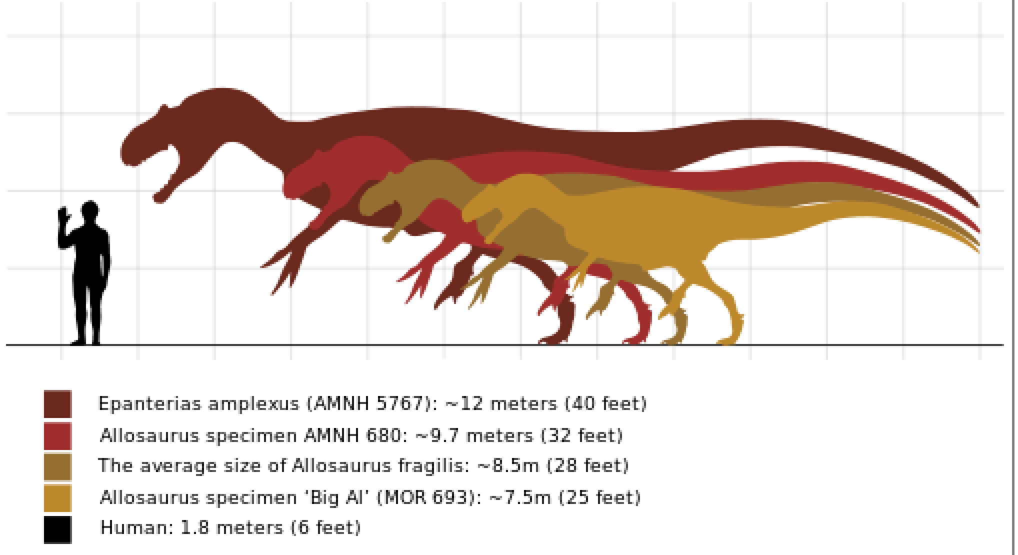
Allosaurus amplexus (Cope, 1878) / ***A. rex*** (Bakker, Kralis, Siegwarth and Filla 1992) / ***A. maximus*** (Chure, 1995)

Synonyms and related species: *Epanterias amplexus* Cope, 1878, *Edmarka rex* Bakker, Kralis, Siegwarth and Filla 1992, *Saurophaganax maximus* Chure, 1995,



Comparitive estimated sizes of *Allosaurus* specimens, - graphic by steveoc 86, silhouettes by Scott Hartman. Silhouettes are based on an Allosuaurs skeletal reconstructions by Scott Hartman. Allosaururs lengths have been measured along the vertebral column. MOR 693 scaled using the scale bar in Hartman's Reconstruction. Average size 8.5m based on Glut 1997. Allosaurus AMNH 680 and *Epanterias* estimates based on Mortimer 2003. Madsen (1976) estimated *Epanterias* at 13m. (Madsen1976/1993).
From Wikipedia, Creative Commons Attribution Share Alike

Horizon: uppermost Morrison Formation of Oklahoma and possibly Colorado (Middle Tithonian)

Phylogeny: Allosauridae **:** *

Size: length 10.5 to 13 meters, weight about 3 to 5 tonnes

Comments: These *Tyrannosaurus*-sized giants were the last and largest of the Morrison Allosaurs. The climate was growing more arid, and the animals, interestingly, were becoming bigger (perhaps to be able to manage the long journeys between water holes). Unfortuantely little is known about them because they are only known from fragmentary remains. It is also not clear whether the 3 tonne *Saurophaganax maximus* and the even larger (5 tonne) *Epanterias amplexus* and *Edmarka rex* are the same, or two or three different giant species. If they are the same than the older name has priority. This giant allosaur preyed on the enormous sauropods with which it shared its environment MAK010506

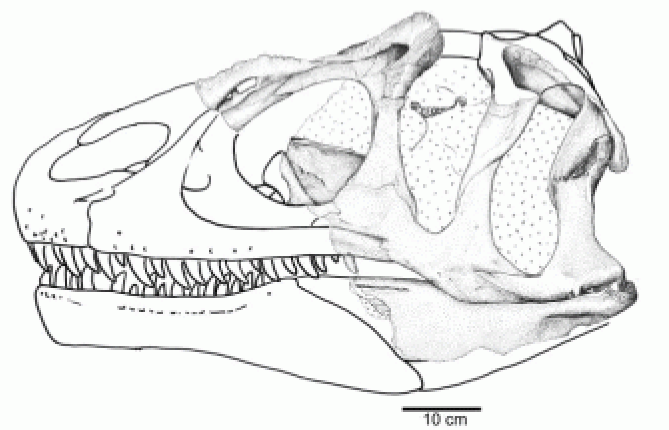
Allosaurus europaeus Mateus, Walen and Antunes, 2006

Horizon: Porto Novo Member of Lourinha Formation, Portugal (Kimmeridgian-Tithonian)

Phylogeny: Allosauridae **:** *

Size: length about 7 meters, weight 1 tonne

Comments: known from a partial skull and a few postcranial elements, this species would have been closely related to the Morrison forms, especially since at the time the European archipelego was very close to North America (Mateus et al 2006 Paul (2010)). Not enough of this species is known to determine its exact relationships, but if it was an island form it would quite likely be an endemic species MAK120225



Skull of *Allosaurus europaeus* in left lateral view, from Vale Frades, Porto Novo Member of the Lourinhã Formation, Portugal. The illustration is based on the two sides of the skull. Caption and illustration from Mateus et al 2006

"Allosaurus" tendagurensis Janensch, 1925

Horizon: Tendaguru of Tanzania (Kimmeridgian)

Phylogeny: Allosauridae **:** *

Size: around 10 meters long and 2.5 metric tons in weight (Mortimer 2003).

Comments: Known only from a single limb bone, this huge theropod is too fragmentary to be classified with certainty. From Wikipedia *A. tendagurensis* was named in 1925 by Werner Janensch for a partial shin (HM 67) found in the Kimmeridgian-age rocks of Tendaguru, in Mtwara, Tanzania. This species has not had strong support in recent years, with opinions on its identity ranging from a tentatively valid species of Allosaurus, to a basal tetanuran, to simply a dubious theropod. One recent analysis has placed it in carcharodontosauridae. - Wikipedia. If this species is a carcharodontosaur it would be the only Jurassic member of the group, and show a Gondwanan origin, similar to the titanosaur sauropods. But similarities could also be convergences due to large size (especially as early carcharodontosaurs like *Neovenator* were only modestly proportioned). For now we have tentatively retained it in *Allosaurus* (*Barosaurus*, *Dryosaurus*, and *Elaphrosaurus* are other genera known from both continents, although the African brachiosaurs beloings to a distinct genus (*Giraffatitan*) from the North American form). Of course, the genus Allosaurus itslef could be a paraphyletic/ancestral taxon, from which all Cretaceous carnosaurs evolved. MAK120225

Image: *Allosaurus tendagurensis* tibia, Naturkunde Museum Berlin. from Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

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checked ATW050619, page MAK120225

Theropoda: Avetheropoda: Carcharodontosauridae

Acrocanthosaurus & Carcharodontosaurus

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Ceratosauria
   `--Tetanurae
      |==Megalosauroidea
      `--Avetheropoda
         |--Carnosauria
         |   |--Monolophosaurus
         |   `--Allosauroidea
         |      |--Sinraptoridae
         |      `--+--Allosauridae
         |           `--Carcharodontosauria
         |              |--Neovenatoridae
         |              |   |--Neovenator
         |              |   `--Megaptora
         |              `--Carcharodontosauridae
         |                  |--Kelmayisaurus
         |                  |--+--Concavenator
         |                  |     `--Becklespinax
         |                  |--Eocarcharia
         |                  `--+-
-Acrocanthosaurus
         |                        `--+-
-Shaochilong
         |                            `-
-Carcharodontosaurinae
         `==COELUROSAURIA
             `--AVES
```

Contents

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2. *Becklespinax* X
3. Carcharodontosauria X
4. Carcharodontosauridae X
5. *Concavenator* X
6. *Eocarcharia* X
7. *Kelmayisaurus* X

8. *Neovenator* X
9. Neovenatoridae X
10. *Shaochilong* X

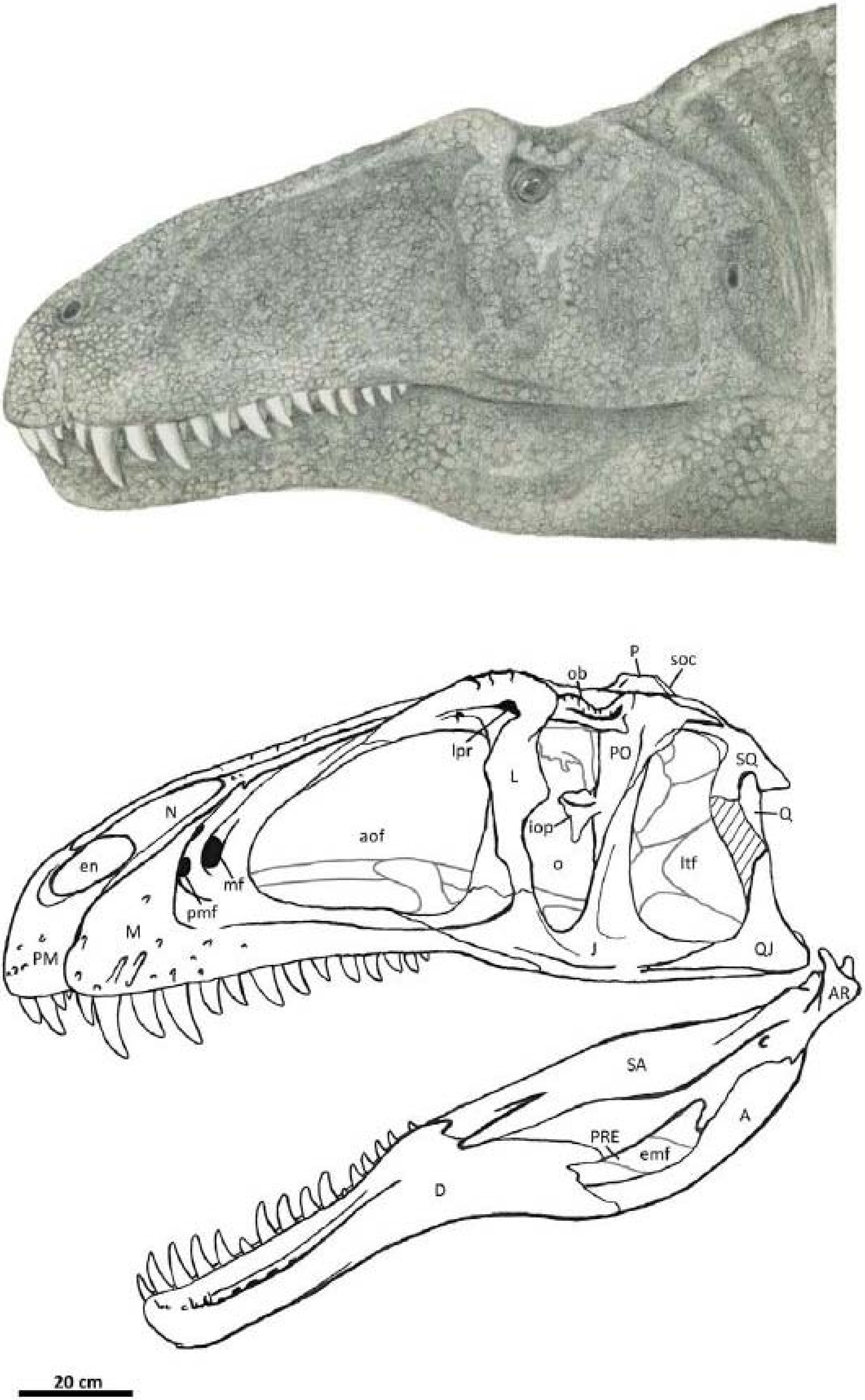
The Carcharodontosaurs constitute a major evolutionary radiation of allosaurs during the Cretaceous period. For the first two thirds of the Cretaceous they had a cosmopolitan duistribution, dominating the large preditor niche and overshadowing the ceratosaurs. During this time, tyrannosaurs were common but limited to the middle preditor niche.

Carcharodontosaurs were a diverse group that included a number of distinct but related lineages - neovenators, acrocanthosaurs, concaventors, carcharodontosaurines, shilantaisaurs, and megaraptors. In a nukmber of thes elines there was a tendency towards gigantism, with lengths in excess of 10 meters being standard. Clearly, like their allosaurine ancestors, these were apex predators that dominated their environments. Of these, the endemic gondwanan carcharodontosaurines were the most impressive.

With the end-Cenomanian extinction event, carcharodontosaur diversity was greatly reduced, and only a single lineage of medium-sized forms, the megaraptors, continued to flourish, mostly in Gondwana, until the end of the Cretaceous. There they co-existed with the uniquely specialised Abelisaurids, which now filled the large predator role in the south, just as tyrannosaurs did in the north.

The recent discovery of this advanced and varied clade of large theropods, previously known only from a few species distributed among the Megalosauridea and Allosauridae, shows once again how paleontology is always making exciting new discoveries about our planet's evolutionary past MAK120304

Descriptions



Flesh reconstruction and line drawing of the skull of Acrocanthosaurus atokensis (NCSM 14345) in left lateral view. Hatched lines represent missing bone. **A**, angular; **aof**, antorbital fenestra; **AR**, articular; **D**, dentary; **emf**, external mandibular fenestra; **iop**, intraorbital process of postorbital; **J**, jugal; **L**, lacrimal; **lpr**, lacrimal pneumatic recess; **ltf**, lateral temporal fenestra; **M**, maxilla; **mf**, maxillary fenestra; **N**, nasal; **o**, orbit; **ob**, orbital boss of postorbital; **P**, parietal; **PM**, premaxilla; **pmf**, promaxillary fenestra; **PO**, postorbital; **PRE**, prearticular; **Q**, quadrate; **QJ**, quadratojugal; **SA**, surangular; **soc**, supraoccipital; **SQ**, squamosal. Image and caption by Eddy & Clarke 2011 fig.2 (doi:10.1371/journal.pone.0017932.g002), Creative Commons Attribution

Carcharodontosauria Benson et al 2010

Phylogenetic definition: The most inclusive clade comprising *Carcharodontosaurus saharicus* and *Neovenator salerii* but not *Allosaurus fragilis* or *Sinraptor dongi* (rank free, stem-based) (Benson et al 2010).

Range: Cretaceous of SAm, Afr, Eur, Asia, Aus, N AM

Phylogeny: Allosauroidea **:** Sinraptoridae + (Allosauridae * **:** Carcharodontosauridae + Neovenatoridae)

Comments: Characterised by by numerous synapomorphies, for which see the supplementary material by Benson et al 2010. Equivalent to the Carcharodontosauridae of Holtz et al. 2004. All known Cretaceous Carnosaurs and Allosauroids belong here. MAK120226

Neovenatoridae Benson et al 2010 **:** *Neovenator*, *Chilantaisaurus*, *Megaraptor*

Phylogenetic definition: The most inclusive clade comprising *Neovenator salerii* but not *Carcharodontosaurus saharicus*, *Allosaurus fragilis* or *Sinraptor dongi* (family rank, stem-based) (Benson et al 2010).

Range: Cretaceous of SAm, Afr, Eur, Asia, Aus, N AM

Phylogeny: Carcharodontosauria **:** Carcharodontosauridae + * **:** *Neovenator* + Megaptora

Comments: Characterised by by numerous synapomorphies, for which see the supplementary material by Benson et al 2010. Equivalent to the Carcharodontosauridae of Holtz et al. 2004. All known Cretaceous Carnosaurs and Allosauroids belong here. MAK120226

Neovenator salerii Hutt, Martill, and Barker, 1996

Horizon: Wealden Clay of Isle of Wight, (Barremian)

Phylogeny: Neovenatoridae **:** (*Chilantaisaurus* + Megaptora) + *

Size: length 6 (subadult) to 7.5 meters, weight 0.6 to 1.5 tonnes

Comments: partial skeleton and skull, originally considered an Allosaurid. Later study showed this large animal to be very primitive carcharodontosaurid. It has a very distinctive puffin-like snout. Its discovery, and that of another very primitive contemporary carcharodontosaurian, *Concavenator*, from the Las Hoyas in Cuenca, Spain, relates the early evolutionary history of this Gondwanan group to the Early Cretaceous of Europe (Ortega et al 2010). *Neovenator* appears to be a good example of an animal at the evolutionary cross-roads, intermediate or transitional between *Allosaurus*, primitive Carcharodontosaurs, and Megaptora. This powerful animal would have played an *allosaurus*-like role in the Early Cretaceous of central Laurasia. MAK010506 revised MAK120302

Image: *Neovenator salerii*, reconstructed skull, Dinosaur Isle Museum, Isle of Wight, photo by Mo Hassan

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Carcharodontosauridae Stromer 1931 **:** *Giganotosaurus*, *Carcharodontosaurus* > *Allosaurus*

Phylogenetic definition: The most inclusive clade comprising *Carcharodontosaurus saharicus* but not *Neovenator salerii Allosaurus fragilis* or *Sinraptor dongi* (family rank, stem-based) (Benson et al 2010).

Range: Early Cretaceous-Late Cretaceous of Eur., Afr., NAm, SAm, & Asia

Phylogeny: Carcharodontosauria **:** Neovenatoridae + * **:** (*Becklespinax* + *Concavenator*) + *Kelmayisaurus* + *Eocarcharia* + (*Acrocanthosaurus* + (*Shaochilong* + Carcharodontosaurinae))

Characters: promaxillary foramen of maxilla enlarged to form a fenestra (independently derived in sinraptorids); pneumatic fenestra in maxillary ascending process forming a distinct, open fenestra, unlike in sinraptorids and *Ceratosaurus* this postorbital contacts lacrimal; postorbital process developed as a small spur (transformed to a large, curving flange in *Acrocanthosaurus* and more derived carcharodontosaurids); anteroventral end of maxillary paradental groove (defining the dorsal margin of the interdental plates) slants anteroventrally; tall dorsal neural spines more than 1.9 times centrum height. - Benson et al 2010

Kelmayisaurus petrolicus Dong, 1973

Horizon: Lianmugin Formation, of Sichuan, China (Valanginian- Albian)

Phylogeny: Carcharodontosauridae **:** (*Becklespinax* + *Concavenator*) + *Eocarcharia* + (*Acrocanthosaurus* + (*Shaochilong* + Carcharodontosaurinae)) + *

Comments: *Kelmayisaurus* is one of those fossils where a supposedly anomalous form known only from very fragmentary remains later turns pout to be part of an ordinary lineage of that time. It is based on parts of the upper and lower jaws (maxilla and dentary), both of which have resemblances to both *Ceratosaurus* and *Megalosaurus bucklandii*. Originally it seemmd as if, as with Ceratosaurus and Megalosaurs, this was a "living fossil" a persistantly primitive form existing alongside more advanced theropods for millions of years. Restudy shows that this species is more likely a basal carchrodontosaur. . A second species, K. giganticus, based on a vertebral column, will probably turn out to be a sauropod. MAK010506 120302

Becklespinax altispinax (Paul,1988)

synonyms: Altispinax dunkeri, Acrocanthosaurus altispinax Paul,1988, Becklespinax altispinax Olshevsky, 1991

Horizon: Wealden Clay of Battle, England (Hauterivian or Barremian)

Phylogeny: Carcharodontosauridae **:** *Kelmayisaurus* + *Eocarcharia* + (*Acrocanthosaurus* + (*Shaochilong* + Carcharodontosaurinae)) + (*Concavenator* + *)

Size: Length 5 to ?8 meters, weight about 1 tonne?

Comments: Known from a set of three tall-spined vertebrae is a genus of large theropod dinosaur based on a type specimen of three tall-spined vertebrae found in 1884 in Sussex, England by the fossil collector Samuel H. Beckles. The *Megalosaurus* in Crystal Palace, London gets its hump from these vertebrae (Dinosaur Mailing List). (Wikipedia) A partial metatarsus and teeth were also attributed.

The nomenclature of this species is rather convoluted. *Becklespinax* is based on the high-spined vertebrae that were at one time combined with


Becklespinax holotype BMNH R1828, as illustrated by Richard Owen (*A History of British Fossil Reptiles* -- Dinosauria Pl. 24) in the 1850s. Owen comments "The extraordinary size and strength of the spines of these anterior dorsal vertebræ, indicate the great force with which the head and jaws of the Megalosaurus must have been used."
Via Wikipedia, Public Doamin

a Megalosaur tooth species to produce *Altispinax dunkeri*, which was placed in the family Spinosauridae (on the basis of the vertebrae), being assumed to be a more primitive species in which the vertebrae had not yet extended into a "sail". It was then found that the teeth could not confidently be assigned to the same animal as the postcrania, which were reassigned to a new species of *Acrocanthosaurus*, another high-spined theropod with similar vertebrae. The species was thus called *Acrocanthosaurus altispinax*. But further study showed it could not confidently be placed with the genus *Acrocanthosaurus* either. So it was placed in a new genus and is now known as *Becklespinax altispinax*. for a while is was placed among the Sinraptoridae, as a smaller version of *Yangchuanosaurus*, a much earlier animal that likewise had a low fin along the back. The discovery of *Concavenator* shed new light on this species, both lived around the same time and place, *Concavenator* lived only slightly (i.e. several millions of years) later), and both have the same set of elongate vertebrae. See also brief comments on Thescelosaurus, and more complete comments at the Theropod Database. At the time of writing, the two have not been described in a peer reviewed paper. MAK010506 revised 120226

Concavenator corcovatus Ortega, Escaso and Sanz 2010 (possibly = *Becklespinax corcovatus* (Ortega, Escaso and Sanz) ?)

Horizon: Calizas de La Hue´rguina Formation, Late Barremian (Early Cretaceous); Las Hoyas, Cuenca, Spain

Phylogeny: Carcharodontosauridae : *Kelmayisaurus* + *Eocarcharia* + (*Acrocanthosaurus* + (*Shaochilong* + Carcharodontosaurinae)) + (*Becklespinax* + *)

Size: about 6 meters long

Comments: *Concavenator corcovatus*, the "hump backed hunter from Cuenca",

Concavenator corcovatus using its hump as a thermoregulatory device, absorbing sunlight in the warmth of a morning sunrise. Artwork by Emily Willoughby, via Wikipedia, Creative Commons Attribution

is a recently discovered dinosaur from the Las Hoyas lagerstatte, discovered by José Luis Sanz, Francisco Ortega and Fernando Escaso from the Autonomous University of Madrid and the National University of Distance Learning.

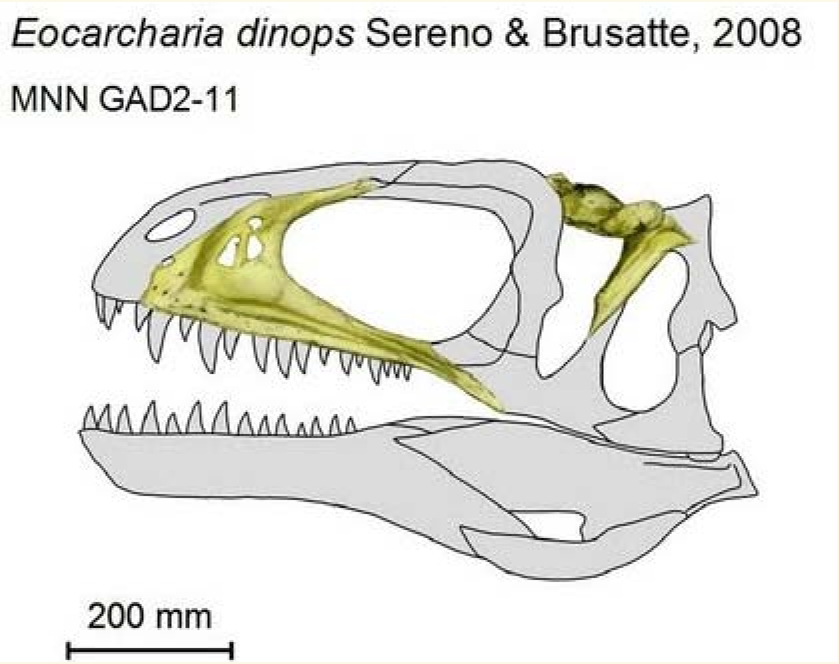
Apart from *Neovenator*, *Concavenator* is the most primitive known carcharodontosaurid. It is the most complete individual of a carcharodontosaurian theropod, and the first one in which direct and indirect evidence of integumentary structures is reported. This animal is remarkable for the presence of two extremely tall vertebrae in front of the hips formed a tall but narrow and pointed crest on its back. The function of such a crest is not clear; it could be like the head-crests used in intra-species visual displays, or it could also be a thermal regulator (see illustratuion at right), rather the fin or sail on the back of edaphosaur and sphenacodontid pelycosaurs. Similar elongate vertebrae are found in spinosaurs (although they have a longer "sail")

Another curious feature is that the forelimb (ulna) shows evidence of what may be quill knobs or homologous structures, an anatomical feature so far known only in animals with large, quilled feathers on the forelimb. If this is the correct explanation, it shows that feathers appared much earlier in theropod evolution than previously thought (at the avetheropod rather than the maniraptoran grade). Although it is less surprising in view of the presence of tubular quill-like structures in ornithischian dinosaurs such as the heterodontosaurid *Tianyulong* and the basal ceratopsian *Psittacosaurus* (Ortega et al 2010, p.205). Darren Naish of tetrapod zoology is sceptical of this interpretation, pointing out that the bumps were unusually far up the arm and irregularly spaced for quill knobs. His alternative explanation is that such structures are found along intermuscular lines, acting as tendon attachment points for example. (Naish 2010b) modified from Wikipedia MAK120302

Eocarcharia dinops Sereno & Brusatte, 2008 (possibly = *Acrocanthosaurus dinops* (Sereno & Brusatte) ?)

Horizon: "Gadoufaoua" on the western edge of the Ténéré Desert, Niger; Elrhaz Formation (Aptian-Albian).

Phylogeny: Carcharodontosauridae : (*Becklespinax* + *Concavenator*) + *Kelmayisaurus* + ((*Shaochilong* + Carcharodontosaurinae) + *Acrocanthosaurus*) + *



Comments: *Eocarcharia* (meaning "dawn shark", in reference to its basal status in the "shark toothed" dinosaurs) is a carcharodontosaurid from the early part of the Middle Cretaceous. its fossil remains were discovered in the Sahara desert (where in places dinosaur bones are just appearing out of the sand dunes) in 2000 on an expedition led by University of Chicago paleontologist Paul Sereno (Wikipedia). It is represented by several cranial bones (fragments of skull & jaws) and isolated teeth. The species name *dinops* is from the Greek "fierce-eyed", in reference to the massive ornamented brow above the orbit.

This basal carcharodontosaurid is similar to and contemporary with *Acrocanthosaurus*. (Sereno & Brusatte 2008). The two are sometimes grouped in a single clade, so it is possible they are congeneric, although Paul 2010, who is (like the present author (MAK) a lumper when it comes to species and genera, does not do so here. in any case, the known remains of *Eocarcharia* are so fragmentary that is difficult to be sure of its exact phylogenetic plaxcement, beyond basal carcharodontosaurid. The presence of a close relative of the North American *Acrocanthosaurus* on Africa suggests that carcharodontosaurids had already achieved a trans-Tethyan distribution by the mid Cretaceous. (Sereno & Brusatte 2008). This animal was a contemporary of the abelisaurid, *Kryptops*. The co-exstence of several totally different lineages of large theropods was a common occurance from the Late Jurassic through to the Middle Cretaceous. MAK120226

Image: type specimen of *Eocarcharia dinops*; illustration by Norbu Tamura, following Sereno & Brusatte 2008; from Palaeocritti

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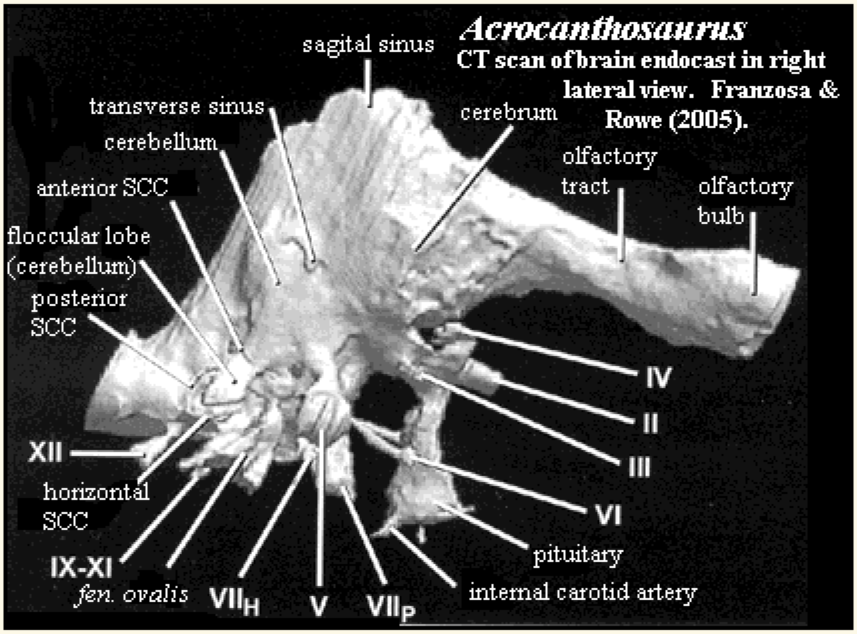
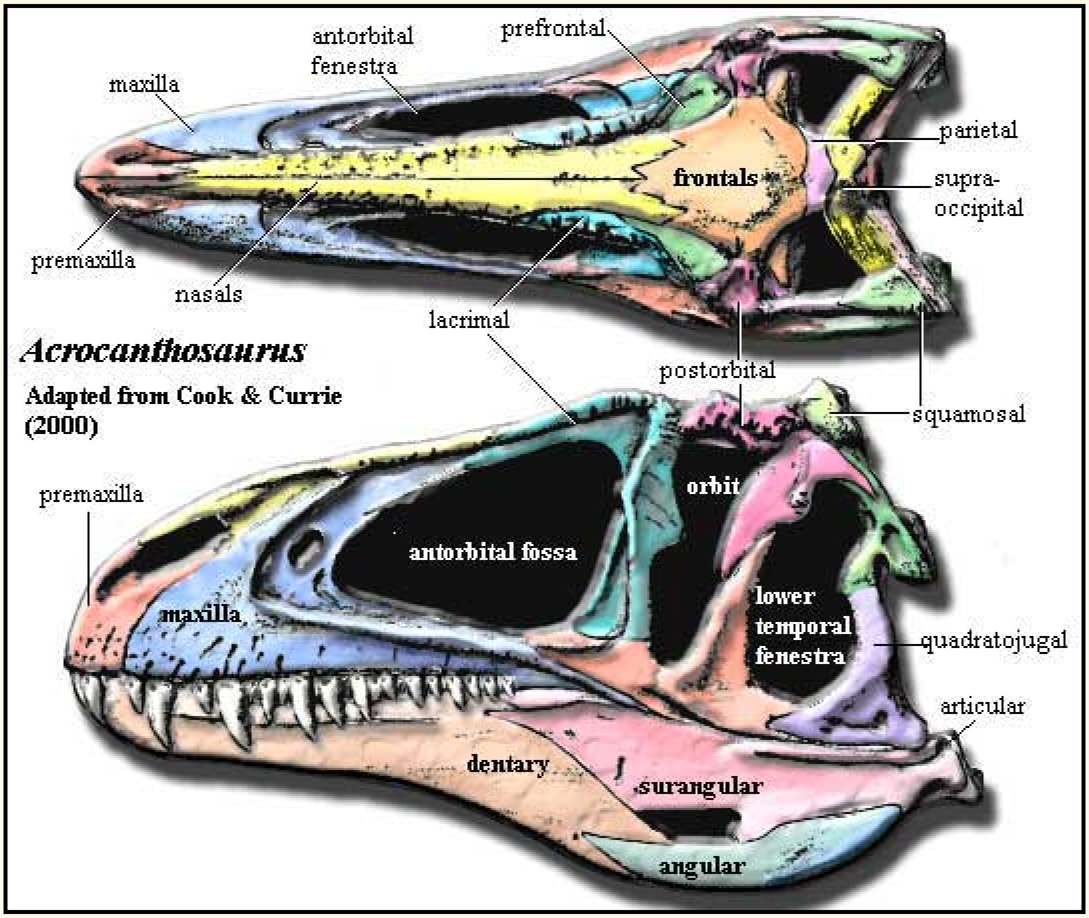
Acrocanthosaurus: Stovall & Langston, 1950.
A. atokensis Stovall & Langston, 1950.

Range: Early Cretaceous (Aptian-Albian) of North America (Oklahoma)

Phylogeny: Carcharodontosauridae : (*Becklespinax* + *Concavenator*) + *Kelmayisaurus* + *Eocarcharia* + (*Shaochilong* + Carcharodontosaurinae) + *)



Characters: 6+m [CC00]; ***Dermal skull:*** skull 129cm long [CC00]; facial horns absent [CC00]; premaxillae meet at acute angle, forming sharp, narrow anterior margin [CC00]; subnarial foramen between premaxilla & maxilla [CC00]; antorbital fenestra very large & triangular [CC00]; antorbital fenestra with overhanging anterioventral rim, covering small promaxillary fenestra [CC00]; nares small & elongate [CC00]; naris formed by premaxilla & nasal, excluding maxilla [CC00]; maxilla with 2 accessory fenestra [CC00]; maxilla taller than long [CC00]; maxilla, anterior margin slopes posterodorsally [CC00]; maxilla forms most of anterior margin of *antorbital fenestra* [CC00]; maxilla *rugose* only anteriorly & near tooth row [CC00]; maxilla posterodorsal process passes between nasal and antorbital fenestra, bifurcating distally to embrace anteroventral process of lacrimal.[CC00]; maxillary fenestra between naris & antorbital fenestra [CC00]; nasal flat, narrow, 4x length of frontal [CC00]; nasal with groove for maxilla articulation, allowing some lateral rotation of maxilla [CC00]; nasal overlaps lacrimal & frontal [CC00]; lacrimal forming low ridge anterior to orbit (but not horn as in *Sinraptor*) [CC00]; lacrimal contacts postorbital under *lappet* of prefrontal [CC00]; "the posterior margin of the ventral (preorbital) process of the lacrimal has a double concavity separated by a short process (for attachment of the *ligamentum suborbitale*) that marks the anteroventral extent of the eyeball itself (diameter was about 11 cm)" [CC00]; nasal & lacrimal with straight, slightly rugose ridge separating dorsal & lateral exposures [CC00]; prefrontal large & triangular [CC00]; prefrontal contacts postorbital & may participate in orbit, excluding frontal [CC00]; frontals "more or less" fused, as is frontal-parietal suture [CC00]; skull roof narrow [CC00]; parietals perpendicular to vertical occiput [CC00]; *sagittal crest* absent [CC00]; jugal participates in antorbital fenestra [CC00]; jugal overlaps lacrimal so that lacrimal-maxilla contact absent [CC00]; jugal form posteroventral margin of orbit [CC00]; jugal, postorbital process huge & triangular [CC00]; orbit key-hole shaped & narrow [CC00]; cheek flat, vertical, at sharp angle to skull roof [CC00]; postorbital with thick, rugose rim [CC00]; postorbital, intertemporal ramus short and almost vertical [CC00]; postorbital forming wide *postorbital bar* [CC00]; lower *temporal fenestra piriform* & bordered dorsally by short *intertemporal bar* [CC00]; jugal & quadratojugal moderately invade lateral temporal fenestra [CC00]; quadratojugal overlaps quadrate, curving onto occipital surface [CC00]; squamosal with deep quadrate *cotylus*, probably exposing head of quadrate in lateral view [CC00]; "Posteroventrally, the squamosal extended along the dorsal surface of the *paroccipital process*, covering up the ventrolateral process of the parietal and wrapping around onto the anterodorsal surface of the distal end of the paroccipital process. The squamosal was inclined in such a manner that it would have roofed over the posterior temporal musculature" [CC00: 217]; ***Occiput:*** supraoccipital forms double *boss* behind low *nuchal crest* [CC00]; supraoccipital with strong midline ridge [CC00]; paroccipital process broad & shallow, turning ventrally at lateral ends, without distal posterior projection [CC00]; *occipital condyle* circular, not flattened [CC00]; ***Mandible:*** jaw with large external mandibular fenestra [CC00]; dentary long and low, laterally smooth with large *mental foramina* [CC00]; dentary with ventral process under *symphysis* [CC00]; angular with thickened ventral rim [CC00]; angular having sliding contact with dentary [CC00]; *retroarticular process* oriented posteromedially [CC00]; *supradentary* present, unknown if fused to coronoid [CC00]; ***Dentition:*** premaxilla with 4 teeth, maxilla with 15 teeth (dentary count unknown) [CC00]; teeth without wrinkled enamel [CC00]; premaxillary teeth blade-like, not D-shaped [CC00]; ***Axial:*** body high and narrow [CC00]; neural spines >2.5x length of centra [CC00]; precaudal centra strongly excavated with complex *pleurocoels* [CC00]; cervical neural spines with triangular anterior processes inserting into depressions under overhanging processes on preceding neural spines [CC00]; mid- and distal caudals with posteriorly placed neural spines [CC00]; mid-caudal vertebrae with accessory transverse processes [CC00]; ***Appendicular:*** arm short (81% femur length) [CC00]; scapula long slender, gently curved [CC00]; *deltopectoral crest* large, quadralateral [C00].



Acrocanthosaurus

Adapted from Cook & Currie (2000)

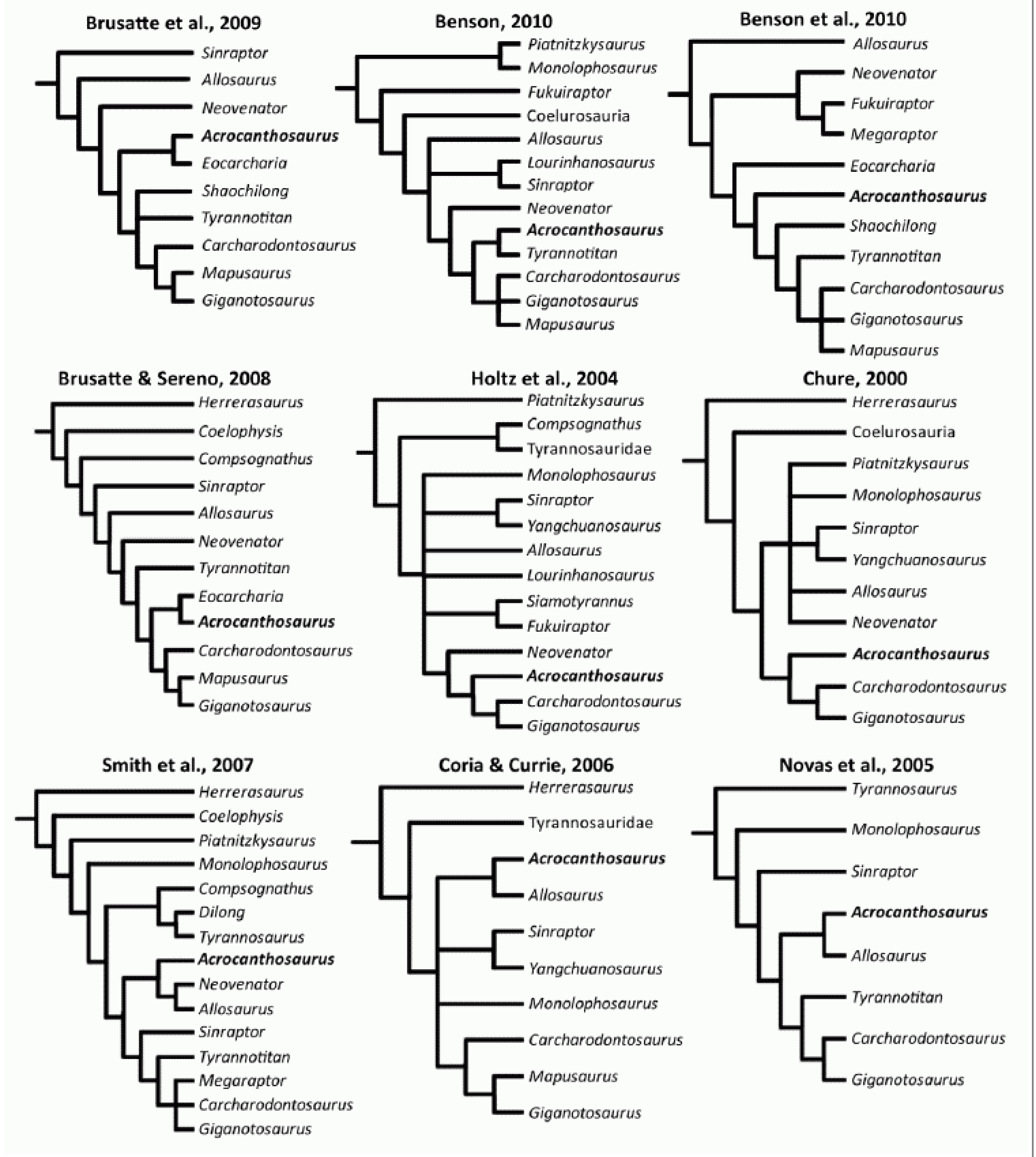
References: Currie & Carpenter (2000) [CC00]; Franzosa & Rowe (2005) [FR05]. ATW060217.

Size: length 8 to 12 meters, weight upto 3 to 4.4 tonnes

Comments: A huge preditor, filling the same ecological role in the north as the Carcharodontosaurines did in the south, Acrocanthosaurus is distinguished by tall vertebral spines giving it a metricanthosaur-like appearance. The basal carcharodontosaurid Becklespinax has a similar but taller fin. *Acrocanthosaurus*, or an animal very much like it, made some of the famous Paluxy River dinosaur tracks in Texas, including a sequence where an individual appears to pursue a large brachiosaurid (probably *Pleurocoelus*), which also left its geeat basin-sized prints in the mud. (silly trivia note: creationists argue that some of the *Pleurocoelus* fore-foot prints are actually "man tracks" made by giant humans). This indicates that this Tyrannosaurid-sized carnivore was not afraid to take on even the biggest sauropods in its environment. Represents a transitional form between allosaurids and primitive charcharodontosaurids and carcharodontosaurines proper. This was the last-known large Allosaurian in North America (Western Laurasia), apart from a relict lineage (*Labocania*) in the very South-West of the continent. The Acrocanthosaurs disappear at the end of the mid Cretaceous, perhaps victims of the Cenomanian mass-extinction. The Tyrannosaurids take their place in the north. In the south, the Carcharodontosaurines are replaced by Abelisaurs. MAK010506 revised MAK120226

Use of the forelimb in handling prey: Unlike other highly specialised large theropods like Abelisaurs and Tyrannosaurs, *Acrocanthosaurus* would have used its small but functional forearms to secure prey. The range of motion in the forelimb of *Acrocanthosaurus* is similar to that of *Herrerasaurus* and *Dilophosaurus*, and greater than that of *Tyrannosaurus*. The limited forward range of motion of the forelimb indicates that *Acrocanthosaurus* captured prey with its jaws. The forelimb could grasp prey that had been moved by the jaws to beneath the chest. Struggling prey would have been impaled upon the strongly flexed first ungual. *Acrocanthosaurus* exhibits a greater manual range of motion than ornithomimid and deinonychosaurian coelurosaurs, but less at the shoulder and elbow. Coelurosaurian theropods exhibit reduced digital flexion and hyper-extension, which suggests a change in the use of the hand. Senter & Robins 2005) MAK120307

Note: usually placed in the Carcharodontosauridae, less often in the Allosauridae. *But see*, Currie & Carpenter (2000).



Brusatte et al., 2009

Benson, 2010

Benson et al., 2010

Brusatte & Sereno, 2008

Holtz et al., 2004

Chure, 2000

Smith et al., 2007

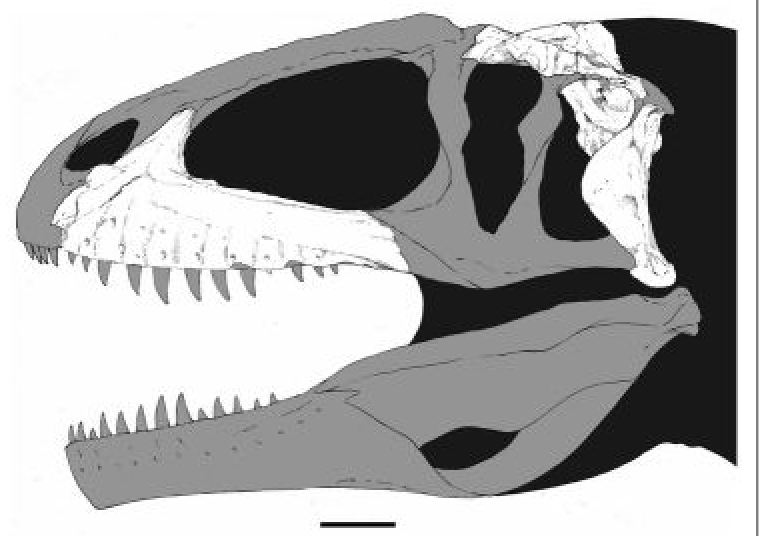
Coria & Currie, 2006

Novas et al., 2005

Nine phylogenetic hypotheses, showing various interpretations of *Acrocanthosaurus* in the Allosauroidea. Analyses along the top two rows recover Acrocanthosaurus atokensis as a member of Carcharodontosauridae, whereas the bottom row represents those that place *Acrocanthosaurus atokensis* as close relative and/or sister taxon to *Allosaurus*. Image and some of caption by Eddy & Clarke 2011 fig.33 (doi:10.1371/journal.pone.0017932.g033), Creative Commons Attribution

Shaochilong maortuensis Brusatte, Benson, Chure, X. Xu, Sullivan, and Hone, 2009

Synonym: *Chilantaisaurus maortuensis* Hu, 1964, *Alashansaurus*



Reconstruction of the skull of *Shaochilong maortuensis*, from Brusatte et al 2010b, based on IVPP V2885. Known parts in white. Scale = 5 cm. Illustration by Brett Booth Original url

Horizon: Ulansuhai Formation of Outer Mongolia (Turonian)

Phylogeny: Carcharodontosauridae **:** (*Becklespinax* + *Concavenator*) + *Kelmayisaurus* + *Eocarcharia* + (*Acrocanthosaurus* + (Carcharodontosaurinae + *))

Size: based on the length of the maxillary tooth row, estimated length of 5 to 6 metres (16 to 20 ft). Based on partial femur, weight approximately 500 kilograms

Comments: Known from skull fragments and some vertebrae, and it seems some limb bones, *Shaochilong* (meaning "shark toothed dragon") is unusual both in its northern distribution and late straigraphic range. Originally identified as a carnosaur of the genus *Chilantaisaurus* and then a primitive coelurosaur (Wikipedia), a re-description by Brusatte and coworkers in 2009 found that it was in fact a carcharodontosaurid, the first recognized from Asia. Phylogenetic analysis performed by indicate that *Shaochilong* is deeply nested within the carchorodontosaurids, and appears to be more closely related to the classic Gondwanan carcharodontosaurids (Tyrannotitan, Carcharodontosaurus, Mapusaurus, Giganotosaurus) than the Laurasian ones (such as Neovenator and Acrocanthosaurus). It shows that allosaurs rather than tyrannosaurs were still the dominant group of large-bodied theropods in Laurasian as late as the early Late Cretaceous. Compared to other taxa however it was a small bodied and short-snouted representative of the group. The dominance of the tyrannosaurids in Asiamerica was therefore confined to the very end of the Cretaceous. (Brusatte et al 2009, Brusatte et al 2010b)

Shaochilong maortuensis may or may not be related to *Labocania anomala* Molnar, 1974 of the Late Campanian El Gallo Formation, Baja California, Mexico, this large but very poorly known animal (estimated length about 7.5 m; weight about 1.2 tons) has been variously interpreted as a tyrannosaur-like allosaurid (Paul 1988) a possible tyrannosauroid (Holtz2004), and an avemetatarsalian, it has also been related to *Shaochilong* Chure (2000) . Mickey Mortimer suggests carcharodontosaurid related to *Shaochilong*. As East Asia and Western North America were closely connected during the late Cretaceous, this makes sense from a paleogeographic as well as stratigraphic perspective. If so, two distinct lineages of carcharodontosaurs survived till the end of the Cretaceous, showing that late Cretaceous large theropod diversity was a lot greater than previously realised. This also means that allosaurs were independently evolving tyrannosaur characteristics. Alternatively, and rather more likely given the stratographic and geographic location and morphological characteristics, this could simply be another basal tyrannosaur. In this case, no carcharodontosaurids survived to end of the Mesozoic. MAK120302

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checked ATW050619, page MAK120302

Theropoda: Avetheropoda: Carcharodontosaurinae

Carcharodontosaurus & *Giganotosaurus*

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Ceratosauria
   `--Tetanurae
      |==Megalosauroidea
      `--Avetheropoda
         |--Carnosauria
         |   |--Monolophosaurus
         |    `--Allosauroidea
         |        |--Sinraptoridae
         |        `--+--Allosauridae
         |           `--Carcharodontosauria
         |              |--Neovenatoridae
         |              `--Carcharodontosauridae
         |                  |--Acrocanthosaurus
         |                  `-
-Carcharodontosaurinae
         |                          |--Tyrannotitan
         |                          `--+-
-Carcharodontosaurus
         |                              `-
-Giganotosaurini
         |                                 |-
-Mapusaurus
         |                                 `-
-Giganotosaurus
         `==COELUROSAURIA
             `--AVES
```

Contents

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2. *Carcharodontosaurus* X
3. Giganotosaurini X
4. *Giganotosaurus* X
5. *Mapusaurus* X
6. *Tyrannotitan* X

Carcharodontosaurids are huge Allosaurid cousins that flourished in Gondwanaland (but with a few exceptions not, strangely enough, in the north). They include the largest ever land carnivores, and some even exceeded *Tyrannosaurus rex* in size (although not by much). The skull of carcharodontosaurids is long and narrow. Unlike the tyrannosaurs, these animals could not have possessed binocular vision *if* they normally looked down the length of the snout. This assumption about the direction of theropod vision may itself be flawed. Many theropods have *frontated* orbits, eyes which were separated only by a narrow strip of frontal. They may, therefore have looked at the world over the bridge of the nose (like humans) with the mouth directed downwards. (ATW & MAK)

Descriptions

Carcharodontosaurinae Stromer 1931 **:** *Giganotosaurus*, *Carcharodontosaurus* > *Allosaurus*

Range: Mid Cretaceous of Afr & SAm

Phylogeny: Carcharodontosauridae **:** (*Becklespinax* + *Concavenator*) + *Kelmayisaurus* + (*Acrocanthosaurus* + *Eocarcharia* + (*Shaochilong* + * **:** *Tyrannotitan* + (*Carcharodontosaurus* + Giganotosaurini)))

Characters: Very large allosauroids; maxilla with strongly rugose lateral face [CC00]; lacrimal forming low ridge anterior to orbit [CC00]; horizontal shelf of bone covering each eye; parietal forms obtuse angle with occiput [CC00]; paroccipital process with distal posterior projection [CC00]; eustachian system tripartite as in crocodiles; teeth with wrinkled enamel [CC00]; teeth not curved; horizontal undulations on compressed, blade-like teeth; undulations curved toward the tip of tooth near its cutting edges; lowest tibia / femur ratio of non-avian theropods;

Links: DD: Carcharodontosauridae; Carcharodontosaurids; Giganotosaurus - Enchanted Learning Software; Discussion of Deltadromeus and Carcharodontosaurus; g00n2a3.pdf; MEA592D Dinosaur Osteology: Lecture 4.

References: Currie & Carpenter (2000) [CC00]. ATW060214.

Comments: here used in an informal manner to refer to advanced Carcharodontosaurs, Brusatte and Sereno, 2008 us e the more limited node-based definition of *Carcharodontosaurus saharicus* + *Giganotosaurus carolinii* which unfortunately would exclude *Tyrannotitan chubutensis*. Since the latter is also an enormous, highly specialsed carcharodontosaur, we decided to expand the definition somewhat, perhaps this could be *Carcharodontosaurus* > *Shaochilong* or similar. MAK120303

Tyrannotitan chubutensis Novas et al., 2005

Range: Aptian of Argentina

Phylogeny: Carcharodontosaurinae **:** (*Carcharodontosaurus* + Giganotosaurini) + *

Size: length 13 meters. weight 7 tonnes

Comments: huge carcharodontosaur, closely related to but somewhat more primitive that *Giganotosaurus* and *Carcharodontosaurus*. Rather tall vertebral spines over the tail MAK120302

Carcharodontosaurus saharicus Stromer, 1931

Synonyms: *Megalosaurus saharicus* Deperet and Savornin, 1927, *Cacharodontosaurus saharicus* (Deperet & Savornin, 1927), *Megalosaurus africanus* Huene, 1956,

Horizon: Baharije Formation of Egypt, also known from Morocco, Algeria, Tunisia, Libya, and Niger (Early Cenomanian according to Paul 2010)

Phylogeny: Carcharodontosaurinae **:** *Tyrannotitan* + (Giganotosaurini + *)

Size: length upto 13.5 meters. weight upto 7 tonnes

Comments: As the name indicates, this animal was originally based on some shark-like teeth. Later, better material has been discovered, including, recently, a very large, nearly complete skull MAK010506 revised 1202266

Carcharodontosaurus shows some unusual convergences with the abelisaurids, another group of Gondwana theropods, specifically regarding certain features in the nature of the skull (Novas 1997b). However other features unite it with *Giganotosaurus*, while further cranial and postcranial character states are shared in common with *Acrocanthosaurus* (Holtz 2000), showing without doubt the allosaurian affinities of this species, which has only been confirmed by later cladistic analysis the unquestioned tetanurine It seems therefore that the two lineages had to evolve in similiar ways to similiar unique environmental conditions. (MAK1202266)

Giganotosaurini Coria & Currie 2006; originally Giganotosaurinae

Range: Cenomanian of Sth Am

Phylogeny: Carcharodontosaurinae **:** *Tyrannotitan* + (*Carcharodontosaurus* + * **:** *Mapusaurus* + *Giganotosaurus*)

Characters: femur with weak fourth trochanter, and a shallow, broad extensor groove on the distal end - Coria & Currie 2006

Comments: With the discovery of Mapusaurus in 2006, Rodolfo Coria and Phil Currie erected a subfamily of Carcharodontosauridae, the Giganotosaurinae, to contain the most advanced South American species, which they found to be more closely related to each other than to the African and European forms. Coria and Currie did not formally refer *Tyrannotitan* to this subfamily, pending a more detailed description of that genus, but noted that based on characteristics of the femur, it may be a giganotosaurine as well. (Coria & Currie 2006) - Wikipedia Other phylogenies however place *Tyrannotitan* as more basal to *Carcharodontosaurus*. We have therefore modified the rank to rank, so Giganotosaurinae becomes Giganotosaurini, and in this way can be nested in the subfamily Carcharodontosaurinae MAK120303

Mapusaurus roseae Coria & Currie 2006 (= *Giganotosaurus roseae* (Coria & Currie 2006)

Horizon: Huincul Formation, Río Limay Group (Middle Cenomanian according to Paul 2010), Neuquén Province, Argentina

Phylogeny: Giganotosaurini **:** *Giganotosaurus* + *

Characters: Differs from *G. carolinii* in that the skull is deeper and narrower, as the maxilla is not elongate, and the nasals thick, rugose unfused and narrower (Coria & Currie 2006)

Size: 10.2 metres, 3 tonnes (Wikipedia)

Comments: Known from the remains of at least seven individuals at various growth stages discovered in a bone bed, this was a large carcharodontosaur very similar to *Giganotosaurus carolinii*, which lived only a few million years earlier. The tendency in dinosaur taxonomy is to make every new species a monotyal genus (although this is standard in vertebrate paleontology in general). Greg Paul is one of the very few who resists this trend (Paul 1988), although he is unsystematic in applying a multi-species approach (see Paul 2010). As it is unlikely that there would be multiple independent lineages of giant allosaurians in a single geographic region, it makes more sense that *Mapusaurus* is a descendent of at most a close relative of *Giganotosaurus*. In this case it would be better interpreted as another species of *Giganotosaurus*, which most likely would be the case if this was a beetle or brachiopod rather than a carcharodontosaur, although this would make the subfamily Giganotosaurinae synomous with the (non monotypal) genus *Giganotosaurus*. MAK120226

Giganotosaurus carolinii Coria and Salgado, 1995

Horizon: Rio Limay Formation, Neuquen, Argentina (Early Cenomanian according to Paul 2010)

Phylogeny: Giganotosaurini **:** *Mapusaurus* + *

Size: 14 meters, weight 7 tonnes

Comments: Frequently mispelled Gigantosaurus. This is an enormous theropod, known from a partial skeleton and skull. With Carcharodontosaurus, this is the largest known land carnivore; longer and heavier than the famous *Tyrannosaurus rex*. It probably preyed on the huge titanosaurid sauropods with which it shared its envoronment MAK010506 revised 120226

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Theropoda: Avetheropoda: Megaptora

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Ceratosauria
   `--Tetanurae
      |==Megalosauroidea
      `--Avetheropoda
         |--Carnosauria
         |   |--Monolophosaurus
         |    `--Allosauroidea
         |       |--Sinraptoridae
         |       `--+--Allosauridae
         |          `--Carcharodontosauria
         |             |--Neovenatoridae
         |             |    |--Neovenator
         |             |    `--+-
-Chiliantaisaurus
         |             |       `--Megaptora
         |             |          |--Fukuiraptor
         |             |          |-
-Siamotyrannus
         |             |          `--+-
-Australovenator
         |             |             `--+-
-Megaraptor
         |             |                 |-
-Aerosteon
         |             |                 `-
-Orkoraptor
         |             `--Carcharodontosauridae
         |                  |--Acrocanthosaurus
         |                  `-
-Carcharodontosaurinae
         `==COELUROSAURIA
             `--AVES
```

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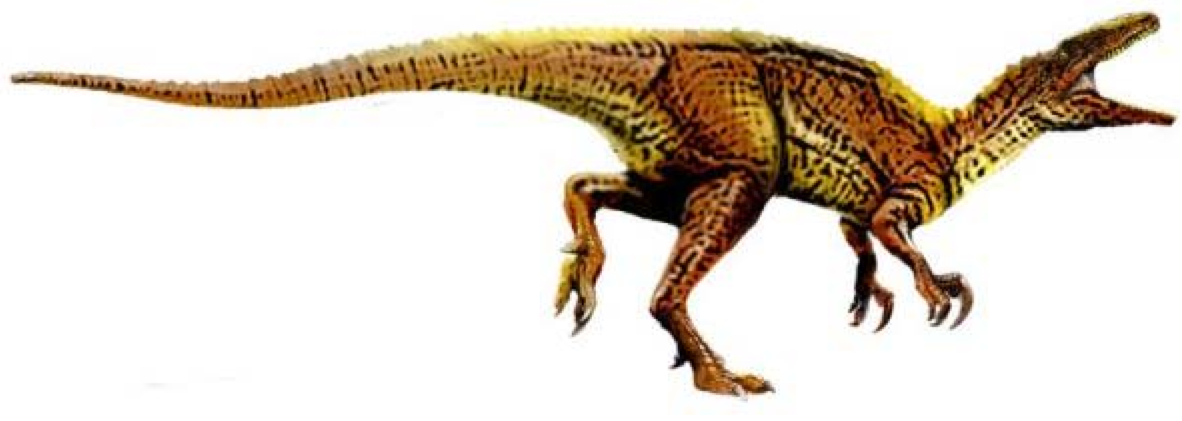
2. *Australovenator* X
3. *Chiliantaisaurus* X
4. *Fukuiraptor* X
5. *Megaraptor* X
6. Megaptora X
7. *Orkoraptor* X
8. *Siamotyrannus* X



Australovenator wintonensis, Middle Cretaceous (Late Aptian), South-East Gondwana. Length 6 meters
Artwork by T. Tischler, Australian Age of Dinosaurs Museum of Natural History, from Hocknull et al 2009; Creative Commons Attribution; also on Wikipedia

Despite the name, the megaraptors are not giant speilbergian scaly dinosaurs, but a newly recognised (Benson et al 2010) group of lightly built, long legged, fast running, highly specialised Cretaceous mostly gondwanan allosaurs with long grasping forelimbs, small to medium size, bird-like physiology, and other coelurosaur-like qualities. They averaged around 5 to 6 meters in length (Paul 2010) although the largest reached 9 to 10 meters. Although variously placed with Carcharodontosaurines (in the case of *Megaraptor* - Smith et al 2007), as a paraphyletic assemblage intermediate between allosaurids and carcharodontosaurids (Hocknull et al 2009) or as basal coelurosaurs (Mortimer - Theropod Database), we have followed Benson et al 2010, who provide the most complete study of the group, and retrieve the Megaptora as a monophyletic clade alongside the Carcharodontosaurids. It is not clear how megaraptors interacted with abelisaurs, although clearly there was some sort of niche partitioning that would allow the co-existence of two groups of large theropods over some tens of millions of years. MAK120304

Descriptions

Chilantaisaurus tashuikouensis Hu, 1964

Horizon: Ulanhushi Formation of the Dashigou Group, Nei Mongol, China (Aptian-Albian according to Mortimer, Turonian, making this species contemporary with *Shaochilong maortuensis*, according to Paul 2010

Phylogeny: Neovenatoridae **:** *Neovenator* + (Megaptora + *)

Size: length 11 meters. weight 2.5 to 4 tonnes

Comments: known from various postcrania, this giant theropod was originally placed in the Megalosauridae, then the Allosauridae-Tyrannosauridae spectrum (in the days when these were still both placed in a monophyletic Carnosauria, e.g. Paul 1988) and finally in the Neovenatoridae by Benson et al 2010. It therefore constitutes an independent lineage of giant mid Cretaceous theropods. A heavily built species, with well-developed arms and huge claws and hands (Paul 2010; Thescelosaurus) it appears to be an early off-shoot of the megaraptors that attained large size MAK120303

Megaraptora Benson et al 2010

Phylogenetic definition: The most inclusive clade comprising *Megarator namunhuaiquii* but not *Chilantaisaurus tashuikouensis*, *Neovenator salerii*, *Carcharodontosauus. saharicus* or *Allosaurus fragilis* (rank-free, stem-based). (Benson et al 2010).

Range: Barremian or Aptian to Maastrichtian of S Am, Aus, & E Asia

Phylogeny: Neovenatoridae **:** *Neovenator* + (*Chiliantaisaurus* + * **:** *Fukuiraptor* + ?*Siamotyrannus* + (*Australovenator* + (*Megaraptor* + *Aerosteon* + *Orkoraptor*)))

Characters: long, gracile metatarsals (Benson et al 2010).

Comments: Unites a number of problematic taxa into a distinct but previously unrecognised clade; essentially, "crown group" (using the trem in a non-neontological context) neovenatorids. We have provided a very speculative phylogeny for this group, combining the dendrograms at Hocknull et al 2009, Mikko's phylogeny, and the Theropod Database MAK120304

Fukuiraptor kitadaniensis

Horizon: Kitadani Formation of the Akaiwa Subgroup of the Tetori Group, Japan (either Barremian or Albian)

Phylogeny: Megaptora **:** *Siamotyrannus* + (*Australovenator* + (*Megaraptor* + *Aerosteon* + *Orkoraptor*)) + *

Size: Length about 4.2 meters (Mortimer n.d.), weight 175 kg (Benson et al 2010)

Comments: Known from the partial remains of individuals from several growth stages, this species was originally considered a large dromaeasaur, its hand claw its hand claw mistaken for the maniraptoran foot claw. (Wikipedia) Similar to *Australovenator* in that both share a prominent posterolateral extension of the astragalus (Benson et al 2010), although *Fukuiraptor* might be a more basal form (Hocknull et al 2009). If the Barremian date is correct, this is the oldest known megaraptoran. MAK120304

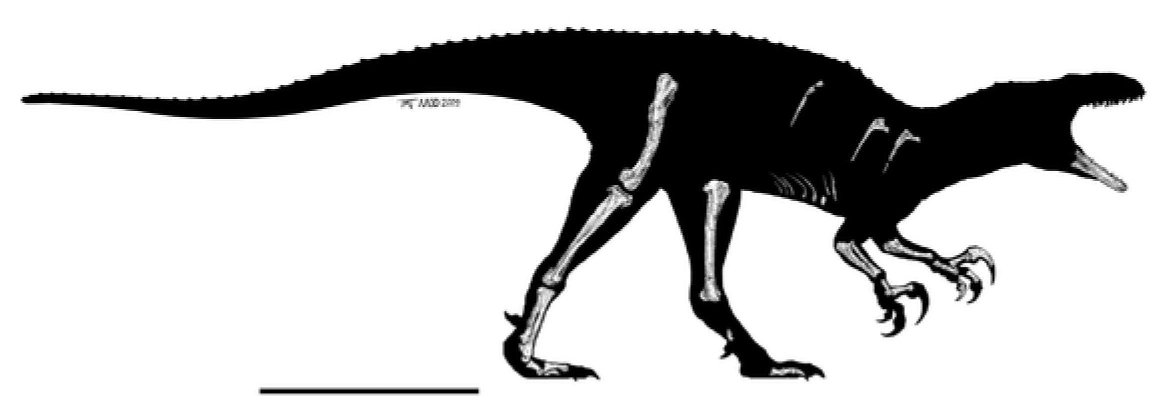
Siamotyrannus isanensis Buffetaut, Suteethorn, and Tong, 1996

Horizon: Sao Khua Formation, Isan region of Thailand, (Early Cretaceous but not more precisely dated)

Phylogeny: Megaptora **:** *Fukuiraptor* + (*Australovenator* + (*Megaraptor* + *Aerosteon* + *Orkoraptor*)) + *

Size: length about 6.5 meters

Comments: Known from a fragmentary skeleton (partial hip, some vertebrae), this medium-sized theropod was originally described as the oldest known tyrannosaurid (Buffetaut et al., 1996), but is now considered a carnosaur of uncertain relationships, although Holtz et al 2004 placed *Siamotyrannus* with *Fukuiraptor* . Mickey Mortimer tentatively suggests allosaurid associations, although also noting some similarities to basal coelurosaurs, but resolves the taxon as intermediate between sinraptorids and *Allosaurus*. Because neither sinraptorids nor allosaurines are known from the Early Cretaceous, it would be unlikely that this taxon belongs there. We have placed it in the Megaraptora, pending new discoveries. MAK120304



Australovenator wintonensis Hocknull, White, Tischler, Cook, Calleja, Sloan, and Elliott, 2009

Horizon: Winton Formation, latest Albian, near Winton, central Queensland

Phylogeny: Megaptora **:** *Fukuiraptor* + *Siamotyrannus* + ((*Megaraptor* + *Aerosteon* + *Orkoraptor*) + *)

Size: length 4.8 meters (Mortimer, n.d.); or 6 meters and weight about 500 kg (Paul 2010)

Comments: a small to medium-sized allosauroid, known from teeth, dentry (lower jaw), and postcrania (Hocknull et al 2009).. The flat geography of Australia does not provide many geological outcrops, and so there are no impressive dinosaur skeletons such as have been found on other continents. The partially known Australovenator is therefore the most complete Australian theropod, and the only one known to date from more than a single bone. This animal was very similar to both *Fukuiraptor* and to "Allosaurus sp." known from an astragalus (ankle bone) from Victoria. it is also similar to NMVP186076, a Megaraptor-like form from the Early Cretaceous of Antarctica. *Rapator ornitholestoides* (known only from a single opalised bone), from the Aptian Griman Creek Formation of New South Wales, previously considered a coleurosaur, may also belong to this species or a very similar one. Phylogenetic analysis by Hocknull et al 2009 places *Australovenator* more basal than *Neovenator*, and *Fukuiraptor* more basal again, making the Megaptora a paraphyletic assemblage of Cretacous allosaurs. We have however followed the more complete anlaysis of Benson et al 2010 who retrieve the Megaptora as a monophyletic clade. MAK120304

Image: Australovenator wintonensis gen. et sp. nov. (QMF 7292), showing the material of the holotype. Artwork: T. Tischler, Australian Age of Dinosaurs Museum of Natural History. From Hocknull et al 2009; Creative Commons Attribution; also on Wikipedia

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Megaraptor namunhuaiquii Novas, 1998

Horizon: Late Turonian/Early Coniacian of the Portezuelo Formation of Rio Neuquen Subgroup, Argentina

Phylogeny: Megaptora **:** *Fukuiraptor* + ?*Siamotyrannus* + (*Australovenator* + (*Aerosteon* + *Orkoraptor* + *))

Comments: Originally based on a single huge claw, about 30 cm long, that resembled a larger version of the "switchblade" giant toe claw of dromaeosaurs, *Megaptor* was at first considered an enormous dromaeasau. Later, the discovery of a complete forelimb, showed that the claw actually came from the first finger of the hand, and *Megaptor* was transferred to the spinosaurs. However the claws and hands are a different shape to that of spinosaurs (see also Wikipedia). Finally, Smith et al 2007 placed it with the Carcharodontosaurinae, while Benson et al 2010locate it in a new clade of carcharodontosaur cousins, the megarptora MAK120304

Image: *Megaraptor namunhuaiquii*, hand claw, photo by Haplochromis, Gno Free document license, Creative Commons Attribution-Share Alike, via Wikipedia

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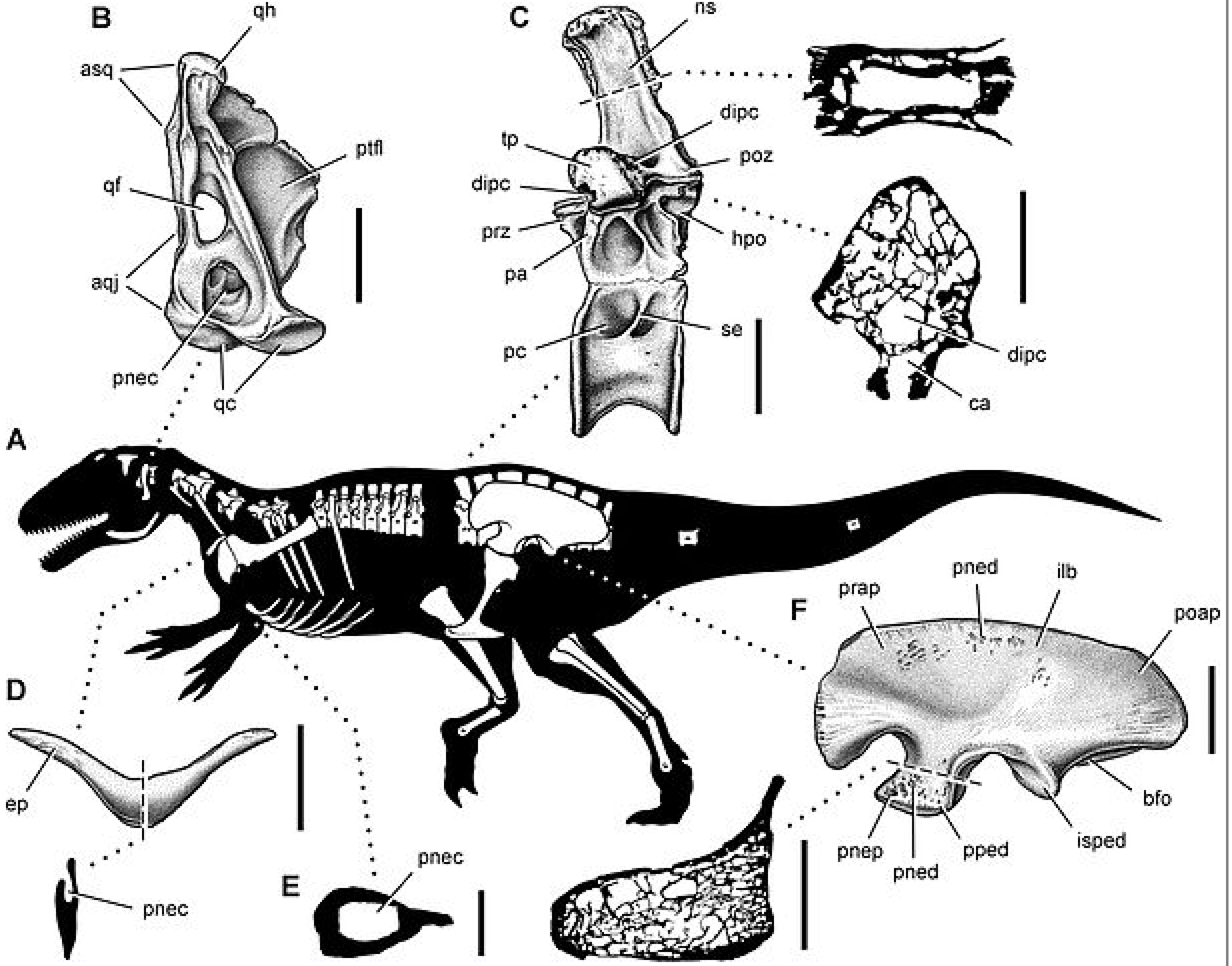
Aerosteon riocoloradensis

Horizon: Anacleto Formation, Río Colorado, Mendoza, Argentina. (Late Santonian / Early Campanian)

Phylogeny: Megaptora **:** *Fukuiraptor* + ?*Siamotyrannus* +



Summary of pneumatic features of the theropod *Aerosteon riocoloradensis*. (A)-Silhouette reconstruction in left lateral view showing preserved bones of the holotype and referred specimens (MCNA-PV-3137-3139); body length approximately 9-10 m. (B)-Left quadrate in posterior view. (C)-Dorsal 14 in left lateral view with enlarged cross-sections of the neural spine and transverse process. (D)-Furcula in anterior view with sagittal cross-section. (E)-Cross-section of medial gastral element from the anterior end of the cuirass showing pneumatocoel. (F)-Left ilium in lateral view with enlarged cross-section of pubic peduncle. Scale bars equal 5 cm in B, 10 cm (3 cm for cross-sections) in C, 10 cm (same for cross-section) in D, 2 cm in E, and 20 cm (6 cm for cross-section) in F. Abbreviations: aqj, articular surface for the quadratojugal; asq, articular surface for the squamosal; bfo, brevis fossa; ca, canal; dipc, diapophyseal canal; ep, epicleideum; hpo, hyposphene; ilb, iliac blade; isped, ischial peduncle; ns, neural spine; pa, parapophysis; pc, pleurocoel; pnec, pneumatocoel; pned, pneumatic depression; pnep, pneumatopore; poap, postacetabular process; poz, postzygapophysis; pped, pubic peduncle; prap, preacetabular process; prz, prezygapophysis; ptfl, pterygoid flange; qc, quadrate condyles; qf, quadrate foramen; qh, quadrate head; se, septum; tp, transverse process.. Caption and illustration from Sereno et al 2008, Creative Commons Attribution; also on Wikipedia

(*Australovenator* + (*Megaraptor* + *Orkoraptor* + *))

Size: 9 to 10 meters

Comments: probably similar to *Megaraptor* (Benson et al 2010), although somewhat later in time. At 9 to 10 meters in length, this was the largest known Megaptoran. The fossils are remarkable for the way they reveal a bird-like respiratory system; the bones contain air-filled spaces, including hollowing of the furcula and ilium, and pneumatisation of several gastralia (belly ribs), all of which suggests a respiratory air-sac system similar to that of modern birds. The air sacs would have acted like bellows, moving air into and out of the animal's relatively inflexible lungs, instead of the lungs being expanded and contracted as occurs with mammals. Hence *Aerosteon* - "air + bone" (Sereno et al 2008, via Wikipedia). All theropods would have had a similar physiology, but this is rarely preserved in fossil bones. MAK120304

Orkoraptor burkei Novas, Ezcurra, and Lecuona, 2008

Horizon: Pari Aike formation, Early Maastrichtian of southern Argentina (Paul 2010)

Phylogeny: Megaptora **:** *Fukuiraptor* + ?*Siamotyrannus* + (*Australovenator* + (*Megaraptor* + *Aerosteon* + *))

Size: 6 or 7 meters (Thescelosaurus)

Comments: Known only from fragmentary remains, this is the last known member of the Neovenatoridae, it shows that allosaurs continued to flourish until the very end of the Mesozoic. Its affinities with other Megaraptora are currently unclear Benson et al 2010; although Mickey Mortimer (Theropod Database) places it with *Megaraptor* and *Aerosteon*. if this interpretation is correct it would group all the Late Cretaceous west gondwanan megaraptors in a single clade,. MAK120304

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Dinosaurs, Birds, and Cladistics

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--ORNITHISCHIA
`--+--Herrerasauridae
   |--SAUROPODOMORPHA
   |
   THEROPODA
   |--Eoraptor
   `==Podokesauridae
      `--+--Ceratosauria
         `--Tetanurae
            |==Megalosauroidea
            `--Avetheropoda
               |--Allosauroidea
               |  |--Neovenatoridae
               |  `--Carcharodontosauridae
               `==COELUROSAURIA
                   `--AVES
```

Contents

Dinosaurs, Birds, and Cladistics

The evolution from theropod to bird, like all such evolutionary sequences (e.g. ungulate to whale) is a fascinating object of study. Yet perhaps one of the hardest things for the layperson to grasp in phylogenetic thinking is the statement "birds are dinosaurs". This is because such a statement requires not one but *two* cognitive shifts, from old style scaly dinosaurs to updated dinosaurs, and from evolutionary linnaean ancestor-descendant to cladistic sister group relationships. Yet the premise that "birds are dinosaurs" stands at the foundation of the modern revolution in evolutionary thinking as regards dinosaurs and prehistoric reptiles in general, including online popularisations. It is the result of us not only thinking in a different way about birds, but also about dinosaurs (and vice versa).

A big part of the problem is that if you say "dinosaur", people think of this.

This evocative painting by Charles R Knight, perhaps the greatest and most influential of all paleo artists, dates from 1897. For its time it was a totally accurate representation of what science knew of the animal called *Brontosaurus*. Generations of budding paleontologists, paleo artists, and lay enthusiasts (including the presnet writer) had their imagination captured by this awesomke image. The massive bulk and tiny head (and by implication brain) of this massive swamp dweller, its enormous weight bouyed up by water, its slow movements suggested by the image, the hippo like skin with just a hint of scales reflectings its semi-aquatic lifestyle, the short stumpy legs, great arch of the torso and back, long neck, long dragging tail, the small rounded head on the lookout for its main enemy *Allosaurus*, from whom refuge can be sought by retreating into deeper water (for some reason, during the golden age of dinosaur art and discovery, theropods were considered to be frightened of water), the lush swampy vegetation and steamy primordial forest, all this screams "dinosaur".

Whereas if you say "bird", they think of this:

The usual response, not surprisinglty, is how could anything like the huge Brontosaurus, bigger than a house, evolve into a tiny little bird? (The author recalls many years arguing with a creationist who asked just such a thing.)

Even worse, how can anyone in their right mind call a duck or a sparrow a dinosaur? It looks nothing like the animal in the above painting! Even accepting evolution, it doesn't feel right.

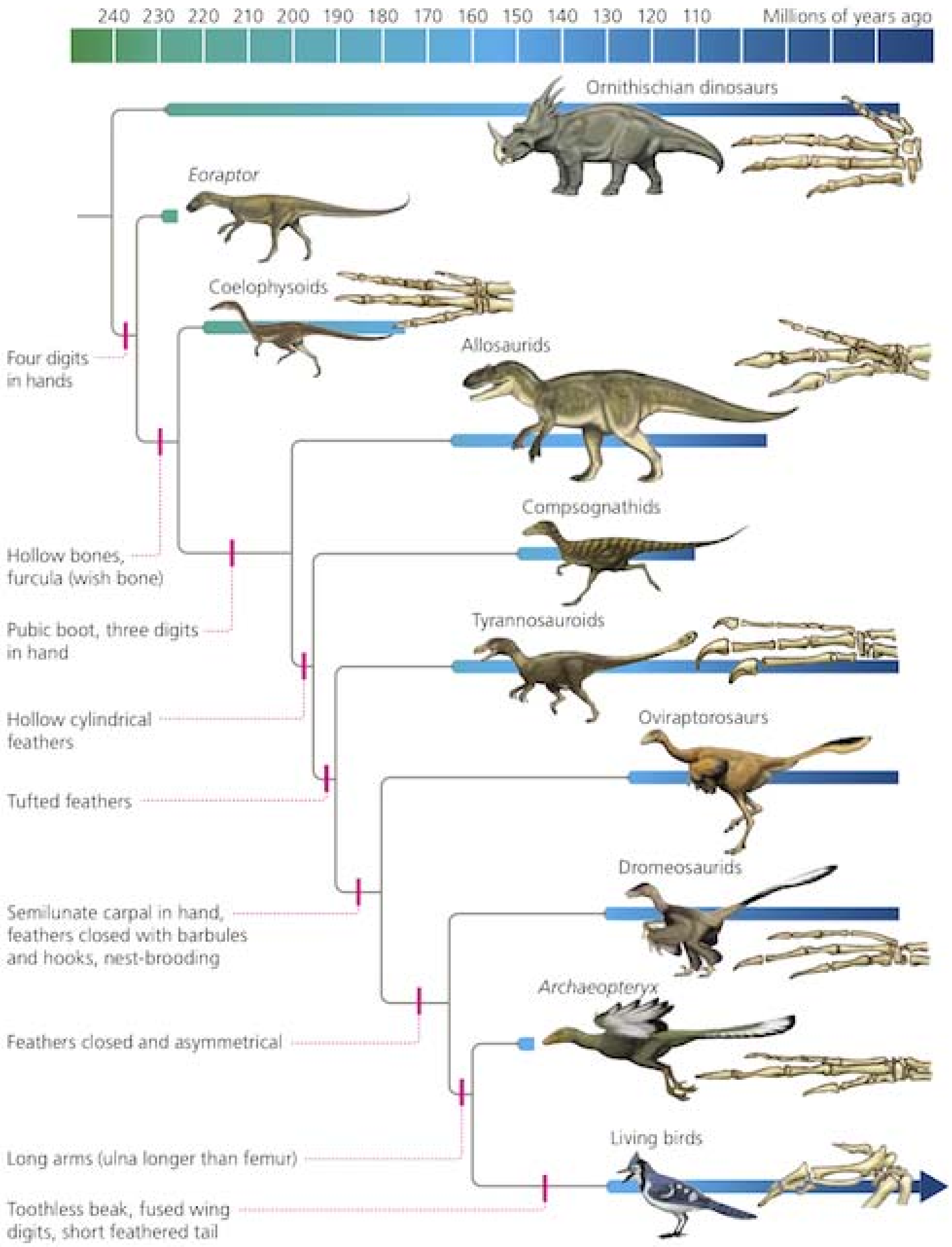
Here we have the problem of what one roleplaying game blogger has very perceptively reffered to as the Dinosaur Lag Effect. Science has moved on, but the general populace still is stuck in images from decades or even a century or more past. From this point of view it can be the [anything] Lag Effect; it's just that dinosaurs make a pretty good case study.

Let's get back to the early to mid 20th century. At this time, dinosaurs were thought to have evolved from small bipedal reptiles called thecodonts (Heilmann 1926), which looked something like this (*right*). These small Triassic bipedal reptiles, called pseudosuchians ("false crocodiles", although some have since turned out to be actual stem- and proto-crocodiles after all, and many were neither small nor bipedal) were considered the stem group from which all other archosaurs evolved, as well as birds (which at this time were not referred to as archosaurs, since the latter were still included in the Class Reptilia). But if we look at reconstructions of peudosuchian thecodonts, such as the one on the right, or this one, it is clear that they look much more like birds than Brontosaurus, Triceratops or Tyrannosaurus rex

Then, during the 60s, 70s and 80s, three things happened that changed everything we knew and thought we knew about these prehistoric saurians.

First was the Dinosaur renaissance of the mid 70s onwards. John Ostrom of Yale University, who had, just a few years before, described the newly discovered coelurosaur *Deinonychus* Ostrom 1969), came to realise that it was actually very similar to early birds such as *Archaeopteryx* (Ostrom 1973, 1975, 1976). Ostrom's charismatic student Bob Bakker popularised and further developed the dinosaur bird link, emphasising dinosaurs as intelligent, active, warm-b;looded animals (Bakker 1975, 1986). And Bakker's student Greg Paul not only further popularise these new discoveries and insights with beautiful artwork and field guides (Paul 1988, 2002 and 2010). This is the second cognitive shift referred to at the start of this essay, dinosaurs are not dim-witted behemoths (nor were they necessarily scaly, but we'll come back to that in a minute). Incidentally, Greg Paul is also the author of the radical suggestion (of enormous appeal to the lay paleo enthusiast, but mostly frowned upon by serious researchers) that advanced coelurosaurs, including Ostrom's *Deinonychus* were actually neo-flightless birds descended from *Archaeopteryx*, rather than the other way around. But that's a whole other story.

The second great revolution, simultaneous with the dinosaur renaissance, was the development of cladistics, as a means of empirically testing hypotheses regarding evolutionary relationships (called phylogeny), shown in branching tree-like diagrams called cladograms (the Palaeos and other interent (e.g. Wikipedia) dendrograms are popularised and informal versions therof). Cladistics began in the 1960s with the work of German entomologist Willi Hennig (1966). About two decades later it was applied to the evolution of reptiles and birds by vertebrate paleontologist Jacques Gauthier (Gauthier 1984, 1986). Using cladistics, Gauthier demonstrated that birds were a derived (i.e. an advanced or specialised) group of theropod dinosaurs, with the dinosaurs themselves representing a series of progressively more birdlike groups - called clades - (Theropoda, Tetanurae, Maniraptora...) with the dromaeosaurids (*Deinonychus* and co) as birds' nearest relatives. During this early period of cladistics, phylogeny was determined on the basis of a few obvious shared characteristics (called synapomorphies) organised in the most parsimonious manner. The following diagram by Carl Zimmer (from Zimmer 2009), maps out these various evolutionary stages, from ancestral theropod dinosaur to modern bird, including the main synapomorphies and timescale (note that actual cladograms, which are concerned with unique characteristics only, do not use timescales), and illustrating the changing structure of the bones of the hand, as the hand changes from locomotory organ (in quadrapedal walking), to grasping organ, to part of the wing (the blog page the diagram link points to includes useful discussion on definitions of dinosaurs, birds, etc, cladistics and so on).



Cladistics marked a radical change from the earlier evolutionarily systematics in one important way. It is no longer about which species or group *evolves into* which (ancestor-descendent relationship), but rather which species *shares a common ancestor with* which other species (sibling, or sister-group, relationship; this is the second cognitive shift referred to earlier). All species that share the same ancestor belong to the same clade, the same family group. Because birds share a common ancestor with different types of dinosaurs, they are included in the dinosaur clade. Therefore, cladistically speaking, birds *are* dinosaurs. This is illustrated in the above diagram where theropod dinosaurs are divided into various subgroups (clades), *including* birds. From this perspective of hierarchical categories we say that birds (bottom two clades) are maniraptors (includes the next two up - dromaeasaurs and oviraptorosaurs), maniraptors are coelurosaurs (includes the next two up - tyrannosaurs and compsognathids), coelurosaurs are theropods (includes the next three up - allosaurs, coelophysids (= podokesaurs) and *Eoraptor*), and theropods are dinosaurs.

By the 1990s, cheaper computing meant that cladistics was able to move from focusing only on a few personally chosen synapomorphies to statistical analysis of hundreds of anatomical traits, some quite minor and even arbitrary from dozens of species. As computer power increased further, more character traits could be keyed in and more species analysed in huge supermatrixes. Now we are finding that the previous parsimony-based algorithms are giving way to the more reliable but also more computationally intensive, maximum-likelihood statistical technique. But all of these analyses confirmed the dinosaurian origin of birds, and therefore retained birds as a subgroup of theropod dinosaurs (Senter 2007, Lee & Worthy 2011)

The third great discovery are fossilised feathers found in beautifully preserved dinosaurs found in China. The development of feathers, from simple filamentous structure sto proper flight feathers, matches both the cladistic series of increasingly more birdlike dinosaurs, and the evolutionary developmental biology of how feathers form in birds (contray to earlier theories, feathers are not modifoied scales) (Prum & Brush 2002, Prum & Brush 2003)

As a result, we no longer interpret dinosaurs as lumbering reptiles, but rather as agile proto-birds.

Even iconic Brontosaurus has changed in every way. It's now called *Apatosaurus* (due to a quirk of nomenclature), it's fully terrestrial like elephants, its legs are long and strong, its body lighter, because of avian-type air sacs distributed through the bones and soft tissue, and while still massive it is now more graceful in appearance, and its tail no longer dragged like the tail of a big lizard, but was held erect, waving in the air and snapping its tip at supersonic speeds. It had a complex social behaviour and lived in herds, and once it reached adult size and strength no theropod would be foolish enough to attack (so it didn't need to retreat to water, and anway, theropods could swim, and some were semi-aquatic). Even its head is different (for a long time, *Brontosaurus/Apatosaurus* had a *Camarasaurus* skull in place of its own, more pointed, *Diplodocus*-like head)

Brief mention should be made here of paleornithologist Alan Feduccia, one of the very few scientists who rejects a dinosaur origin for birds, as does fellow paleoornithologist Larry Martin, and argues instead that birds originate from small arboreal archosaurs in the Triassic (essentially, a modified version of the old thecodont origin theory). Cladistic evidence does not support the neo-flightless hypothesis (see e.g. Dinosaurs and Birds - an Update by Kevin Padian), nor have any plausible alternatives to the theropod origin been found. Feduccia cites *Protoavis texensis*, described by Sankar Chatterjee of Texas Tech University, allegedly an animal more advanced than *Archaeopteryx*, although it existed during the Norian (Chaterjee himself argues for the theropod origin of birds). Current consensus is that *Protoavis* is a chimera, a jumble of several different species. Exactly which types of animals is unclear, because of the poor preservation, but podokesaur ("ceratosaur") limbs and drepanosaur head and neck have been suggested (Wikipedia).

Nevertheless, while the theropod ancestry of birds is as solid as any scientific hypothesis could be, the semantic problem of saying "birds are dinosaurs" remains, even allowing for the new model *Apatosaurus*, *Deinonychus*, and co. Although cladistics has so swept the field that it is not possible to find a current reference to an ancestor descendant phylogeny that shows dinosaurs evolving into birds (i.e. because birds are dinosaurs, dinosaurs cannot evolve into birds, any more than mammals can evolve into bats [1], this doesn't mean that rival paradigms such as evolutionary systematics are incorrect. Simply that they have not been found as easily verifiable as cladistics. At the same time, a hierarchy of clades of sister-group relationships is not itself a phylogeny. It is a means of building hypothesis that can be applie dto phylogeny. Phylogeny itself involves the dynamic (*sensu* Heraclitus, flux and flow) transformation of species in deep time with one evolutionary stage being replaced by the next (Cladistics of course is also all about evolution, but it doesn't map evolution in this particular way). It is this difference between gradism and cladism that results in so much confusion, because gradism uses a stratigraphic (sequence according to the fossil record) deep time evolutionary ancestor-descendant (anagenetic) approach (birds evolved from dinosaurs), and cladism a hypothesis-testing sister group (cladogenetic) approach (birds are dinosaurs). For the present author (MAK), cladism and gradism, hypothesis building and phylogeny, are complementary. It is not that one is wrong and one is right, when actually they are both correct. And doubtless phylogenetic insights and hypothesis building will continue to develop and incorporat enew insighst and methodologies (for example cladism considers stratigraphy irrelevant, the exception being stratocladistics, which strangely very few standrad cladists seem to be interested in).

Summing up, we can confidentally state that the hypothesis that birds evolved as (cladism) and from (gradism) theropod dinosaurs, through a number of transitional stages such as those described in the above diagram, is the only hypothesis that fits all the evidence: paleontological, stratigraphic, morphological, physiological, embryological, molecular, and more. Through discoveries such as these, we painstakingly yet confidentally map out the evolutionary tre eof life on Earth. MAK120310 120315

Notes

[1] The present author (MAK) however finds the birds are to dinosaurs as bats are to mammals analogy used on that link useful but not entirely correct. Whereas bats are indeed specialised flying mammals, just as birds are indeed

specialised flying dinosaurs, birds are more distinct from their ancestors in at least three important ways: miniaturisation (interestingly, this was also a factor in the evolution of reptiles (amniotes) from amphibians), retaining their infant endothermic metabolism throughout adulthood (whereas dinosaurs tend to gigantothermy), and development of a brain to bodyweight ratio and behaviour equivalent to mammals (in contrast to dinos with their crocodile-like brains and typically reptilian brain to bodyweight). Significantly, the feathered dinosaurs known as maniraptors bridge this divide in all three areas, thus once again refuting creationism and showing how fossils reveal non-missing links between major taxa)

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Theropod Classification

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--ORNITHISCHIA
`--+--Herrerasauridae
   |--SAUROPODOMORPHA
   |
   THEROPODA
   |--Eoraptor
   `==Podokesauridae
      `--+--Ceratosauria
         `--Tetanurae
            |==Megalosauroidea
            `--Avetheropoda
               |--Allosauroidea
               |  |--Neovenatoridae
               |  `--Carcharodontosauridae
               `==COELUROSAURIA
                    `--AVES
```

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Order Theropoda

Traditional classification

The current page is the first (in order of writing it, 20 Feb 2012, not in topic sequence) of a new page type for Palaeos, the taxonomic classification page. These pages have been written to fill the need for a traditional rank-based (rather than phylogeny based) taxonomic list of various organisms and groups covered in each unit. The following therefore is not a cladistic or phylogenetic classification of the sort pioneered by Gauthier (1986) or Holtz (2000), but , which was purely Linnaean, a la Carroll 1988). As we have often stated, the Linnaean and Cladistic methodologies of organising the nartural world are only contradictory when it is assumed that there can only be one. Since we believe that these (and any number of other possible) methodologies are non-exclusive, there is no reason why both cannot equally be used in their respective contexts.

We have not attempted to equate Linnaean ranks with clades, because the result would be the need for a near-infinite series of ranks, and a confusing of similarity-based categories with phylogenetic branching points. As we have often stated, the Linnaean and Cladistic methodologies of organising the nartural world are only contradictory when it is assumed that there can only be one. Since we believe that these (and any number of other possible) methodologies are non-exclusive, there is no reason why both cannot equally be used in their respective contexts.

The following taxonomy is based mainly on Carroll (1988), as the most recent comprehensive linnaean classification of the Vertebrates, and an update of Romer 1966 *Vertebrate Paleontology*. This has in turn been updated in a few places, but we have tried to limit the number of new taxa, as it is so easy to go overboard with this sort of thing.

Newly coined taxa are indicated by inverted commas. Each taxon is listed by rank, name, and original author, and followed by a short description. For the phylogenetic arrangement see the dendrogram page. For a rather unweildly attempt at a linnaean-cladistic synthesis, see below. The remainder of the theropoda can be found listed in the Coelurosauria classification page MAK120220 120312 120506

Infraclass Archosauromorpha Huene, 1946 (*cont.*)

Order[1] Theropoda Marsh, 1881 bipedal, mostly carnivorous, dinosaurs.

Suborder[2] Herrerasauria Galton 1985 small to medium-sized ancestral theropods, limited to the late Trias.

Family Staurikosauridae Colbert, 1970 Typal family for *Staurikosaurus pricei*, a primitive herrerasaur

Family Herrerasauridae Reig, 1963 Typical herrerasaurs, medium-sized very primitive theropods

Suborder unspecified

Eodromaeus, *Eoraptor*, *Daemonosaurus*, and *Tawa* small, primitive/ancestral late Trias types

Suborder Ceratosauria Marsh, 1884 diverse group of small to very large, primitive theropods with three-toed feet, four-fingered hands, and a tendency to deveop crests and horns for intraspecific display. [3].

Family Podokesauridae Huene, 1914 small to large, lightly built, ancestral theropods, frequently with paired head crests. The head is long, the front of the snout with a distinctive kink. Late Trias to early Jur, cosmopolitan

Subfamily Podokesaurinae small ancestral types, LTr to EJu, previously included under "Coelurosauria".

Subfamily Dilophosaurinae Charig & Milner, 1990 large ancestral types, essentially overgrown podokesaurs with a few more advanced features, EJu, Cosmopolitan, intermediate between Podokesaurinae and both Carnosauria and higher Ceratosaurs.

Family Ceratosauridae Marsh, 1884 large, persistantly primitive, late Jur theropods, mostly in the shadow of their more successful and advanced Allosaurid contemporaries, monotypal (*Ceratosaurus*)

Family "Limusauridae" Nov. medium-sized, lightly built, highy specialised late Jur theropods, include toothless ostrich mimics

Family Bahariasauridae Huene, 1948 huge, lightly built, long-legged, ceratosaurs; so far known only from the MidCret of north-central Gondw (nth Afr)

Family Noasauridae Bonaparte & Powell, 1980 small, lightly built ceratosaurs, intermediate between more primitive types and abelisaurids, and closely related to the latter. Mid to Late Cret of Gondw

Family Abelisauridae Bonaparte & Novas, 1985 large to very large, advanced and highly specialised ceratosaurs, frequently with horns or crests. Forearms extremely diminutive. Advanced forms were the fastest large theropods. Mid to Late Cret of Gondw & Eur

Suborder Carnosauria Huene, 1920 originally the term for all large to huge theropods. Here used to refer to the evolutionary range of large types intermediate between ceratosaurs and coelurians

Superfamily Megalosauroidea Huxley, 1889 ancestral and persistantly primitive Carnosaurs

Family Megalosauridae Huxley, 1889 unspecialised Jurassic forms

Subfamily Megalosaurinae Huxley, 1889 the most common primitive carnosaurs, flourished during the mid and late Jur

Subfamily: Eustreptospondylinae Paul, 1988 similar to and contemporary with the Megalosaurinae, ancedtral to the spinosaurids

Family Spinosauridae Stromer, 1915 large to gigantic fish-eating megalosaurs with elongated vertebral spines and crocodile-like jaws with specialized teeth, have a long kinked snout reminscient of podokesaurs Early to Mid Cret of Eur & Gondw

Subfamily Baryonychinae Charig & Milner, 1986 large to very large, little or no sail on back

Subfamily Spinosaurinae medium-sized to gigantic spinosaurs

Tribe Spinosaurini gigantic fin-backed theropods, Mid Cret of North Africa, monotypal (*Spinosaurus*)

Tribe Irritatorini Martill, Cruickshank, Frey, Small & Clarke, 1996 smallish west Gondwanan spinosaurines, monotypal (originally family Irritatoridae)

Superfamily Allosauroidea Marsh, 1878 advanced Carnosaurs

Family "Monolophosauridae" Bakker, 1997 ancestral crested forms, perhaps intermediate between megalosaurs and allosaurs, known so far only from a single species from the Mid Jur of China

Family Sinraptoridae Currie & Zhao, 1994 [4] large to gigantic Mid to Late Jur allosaurs known from Asia & Europe, intermediate between megalosaurs and higher allosaurs. Alternatively, could be a subfamily of the Allosauridae

Family Allosauridae Marsh, 1878 large to gigantic, advanced carnosaurs, late Jur to Late Cret

Subfamily Allosaurinae the classic large Late Jur theropod, strong three-fingered forearm, monotypal (*Allosaurus*), usually ranked as a family

Subfamily Carcharodontosaurinae Stromer, 1931 gigantic early to Mid Cret allosaurs, including the largest terrestrial predators. Usually given family ranking

Subfamily Neovenatorinae Benson, Carrano & Brusatte, 2010 here used as a monotypic taxon for the large but slender *Neovenator saleri* Hutt, Martill & Barker, 1996, Neoventoridae is a monophyletic taxon that includes *Neovenator* and the megaraptors

Family Megaraptoridae Benson, Carrano & Brusatte, 2010 medium-sized lightly built allosaurs, same as Clade Megaraptora, convergent with coelurosaurs, Mid to Late Cret of Gondwanan, We believe this group is distinct enough to deserve family ranking

Suborder Coeluria Marsh, 1881 (= Coelurosauria Huene, 1914) (see next unit)

Hybrid classification

While for the most part we have following a conventional linnaean approach in these taxonomic pages, we have also been inspired by Olshevsky 1991. In his important amateur (non-peer reviewed) paper, Olshevsky distinguished between paraphyletic and monophyletic taxa (grades and clades). But whereas he only used one prefix, para- in front of the rank of paraphyletic taxa (e.g. parafamily, monophyletic taxa being unmodified), by adopting the following key:

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

When no prefix is used, we haven't gotten around to assessing the taxon (or the current page is still under construction). *Cont.* for Continued means that the taxon begins in a previous unit.

Linnaean names may not match their cladistic equivalents. For example, that a linnaean and evolutionary/gradist taxon, in excluding certain descendent groups from a taxon, can be a Paraorder or Parainfraclass in this schema. By including those descendents the same taxon would be an unranked monophyletic clade according to a strictly cladistic scheme. Hence Theropoda can be both a para(sub)order of dinosaurs and an unranked clade.

The following hybrid taxonomy It is also so experimental and unweidly that we at first thought of deleting it, but in the end decided to subordinate it to a more conventional page. Other attempts at cladistic/linnaean synthesis include Paul (1988) (the obvious inspiration for Olshevsky (1991)), and Benton (2005). MAK120220 120312 120506

Parainfraclass Archosauromorpha Huene, 1946 (*cont.*)
 Paraorder Theropoda Marsh, 1881 bipedal, mostly carnivorous, dinosaurs.
  Parasuborder Herrerasauria Galton 1985 small to medium-sized ancestral theropods, limited to the late Trias.
   Monofamily Staurikosauridae Colbert, 1970 Monotypal family for *Staurikosaurus pricei*, a primitive herrerasaur
   Ambifamily Herrerasauridae Reig, 1963 Typical herrerasaurs, medium-sized very primitive theropods
  Parasuborder unspecified
   Eodromaeus, *Eoraptor*, *Daemonosaurus*, and *Tawa* small, primitive/ancestral late Trias types
  Parasuborder Ceratosauria Marsh, 1884 diverse group of small to very large, primitive theropods with three-toed feet, four-fingered hands, and a tendency to deveop crests and horns for intraspecific display.
   Parafamily Podokesauridae Huene, 1914 small to large, lightly built, ancestral theropods, frequently with paired head crests. The head is long, the front of the snout with a distinctive kink. Late Trias to early Jur, cosmopolitan
    Evosubfamily Podokesaurinae small ancestral types, LTr to EJu, previously included under "Coelurosauria".
    Ambisubfamily Dilophosaurinae Charig & Milner, 1990 large ancestral types, essentially overgrown podokesaurs with a few more advanced features, EJu, Cosmopolitan, intermediate between Podokesaurinae and both Carnosauria and higher Ceratosaurs.
   Monofamily Ceratosauridae Marsh, 1884 large, persistantly primitive, late Jur theropods, mostly in the shadow of their more successful and advanced Allosaurid contemporaries, monotypal (*Ceratosaurus*)
   Evofamily "Limusauridae" Nov. medium-sized, lightly built, highy specialised late Jur theropods, include toothless ostrich mimics
   Monofamily Bahariasauridae Huene, 1948 huge, lightly built, long-legged, ceratosaurs; so far known only from the MidCret of north-central Gondw (nth Afr)
   Ambifamily Noasauridae Bonaparte & Powell, 1980 small, lightly built ceratosaurs, intermediate between more primitive types and abelisaurids, and closely related to the latter. Mid to Late Cret of Gondw
   Holofamily Abelisauridae Bonaparte & Novas, 1985 large to very large, advanced and highly specialised ceratosaurs, frequently with horns or crests. Forearms extremely diminutive. Advanced forms were the fastest large theropods. Mid to Late Cret of Gondw & Eur

Parasuborder Carnosauria Huene, 1920 originally the term for all large to huge theropods. Here used to refer to the evolutionary range of large types intermediate between ceratosaurs and coelurians

Parasuperfamily Megalosauroidea Huxley, 1889 ancestral and persistantly primitive Carnosaurs

Evofamily Megalosauridae Huxley, 1889 unspecialised Jurassic forms

Evosubfamily Megalosaurinae Huxley, 1889 the most common primitive carnosaurs, flourished during the mid and late Jur

Evosubfamily: Eustreptospondylinae Paul, 1988similar to and contemporary with the Megalosaurinae, ancedtral to the spinosaurids

Holofamily Spinosauridae Stromer, 1915 large to gigantic fish-eating megalosaurs with elongated vertebral spines and crocodile-like jaws with specialized teeth, have a long kinked snout reminscient of podokesaurs Early to Mid Cret of Eur & Gondw

Holosubfamily Baryonychinae Charig & Milner, 1986 large to very large, little or no sail on back

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Monotribe Spinosaurini gigantic fin-backed theropods, Mid Cret of North Africa, monotypal (*Spinosaurus*)

Monotribe Irritatorini Martill, Cruickshank, Frey, Small & Clarke, 1996 smallish west Gondwanan spinosaurines, monotypal (originally family Irritatoridae)

Evosuperfamily Allosauroidea Marsh, 1878 advanced Carnosaurs

Monofamily "Monolophosauridae" Bakker, 1997 ancestral crested forms, perhaps intermediate between megalosaurs and allosaurs, known so far only from a single species from the Mid Jur of China

Evofamily Sinraptoridae Currie & Zhao, 1994 large to gigantic Mid to Late Jur allosaurs known from Asia & Europe, intermediate between megalosaurs and higher allosaurs. Alternatively, could be a subfamily of the Allosauridae

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Monosubfamily Neovenatorinae Benson, Carrano & Brusatte, 2010 here used as a monotypic taxon for the large but slender *Neovenator saleri* Hutt, Martill & Barker, 1996, Neoventoridae is a monophyletic taxon that includes *Neovenator* and the megaraptors

Holosubfamily Megaraptorinae Benson, Carrano & Brusatte, 2010 medium-sized lightly built allosaurs, same as Clade Megaraptora, convergent with coelurosaurs, Mid to Late Cret of Gondwanan, If ranked as Holofamily Megaraptoridae, then Allosauridae and Carcharodontosaurinae become a Parafamily and Parasubfamily respectively

Parasuborder Coeluria Marsh, 1881 (= Coelurosauria Huene, 1914) (see next unit)

Notes

[1] Theropoda is conventially paced as a suborder of Order Saurischia Seeley, 1887. But since the three dinosaurian groups (Theropoda, Sauropodomorpha, and Ornithischia) all diverged at the same time and remained consistently distinct and diverse lineages, we felt that Theropoda should be promoted to Ordinal status, and Saurischia become an unranked taxon. Similarily, although Superorder Dinosauria Owen, 1842 is a totally valid taxon, this has not been listed because it would require creating artificial monotypic superorders for other archosauromorph orders (e.g. Thecodonts, Pterosauria, Crocodylia). In keeping with our classification system, Theropoda is here ranked as a paraphyletic order, because under the gradist evolutionary paradigm theropods evolve into birds, but are not themselves birds. In a cladistic classification system that uses Linnaean ranks, Birds would be a suborder of Theropoda. In these classification pages however we follow Carroll 1988 and traditional linnaeanism in giving birds their own class rank. Transitional forms such as *Archaeopteryx* could equally correctly be clasisfied under birds or dinosaurs.

[2] With Theropoda becoming an order, previous infraorders (such as Herrerasauria) now become suborders.

[3] The changing cladistic definition of the Ceratosauria is discussed here. At one time considered a monophyletic clade, this latter usage has now been redefined for more advanced forms only. To avoid excessive multiplication of suborders (such as a new suborder Ceolophysoidea or similar), Ceratosauria is here used in the context of Suborder Ceratosauria *sensu* Paul (1988) (but with abelisaurs added), or Parasuborder Ceratosauria *sensu* Olshevsky 1991 (but minus Megalosaurids); i.e. as a paraphyletic group including both ancestral (podokesaurid) and specialised (= monophyletic Ceratosauria) forms.

[4] Metriacanthosauridae Paul, 1988 was coined earlier but was not associated with a formal description, and so cannot be used as an official name

Links: The major dinosaur families at Enchanted Learning; Taxon tree; Linnean Theropoda, dinosaur mailing list, draws strongly on Greg Paul 1988 but with inflated ranks (subfamilies become families etc)

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Theropod Dendrogram

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Eoraptor
   `==Podokesauridae
      `--+--Ceratosauria
         `--Tetanurae
            |==Megalosauroidea
            `--Avetheropoda
               |--Allosauroidea
               |  |--Neovenatoridae
               |  `--Carcharodontosauridae
               `==COELUROSAURIA
                   `--AVES
```

Contents

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA ToL, MH
   |--Herrerasauridae
   `--+--Eoraptor
      `--+--Daemonosaurus
         `--+--Tawa
            `--Neotheropoda
               |?--Procompsognathus
               |--Podokesaurinae
               |   |--Coelophysis kayentakatae
               |   `--+--Coelophysis bauri
               |       `--Coelophysis rhodesiensis
               |--Segisaurus
               |--Liliensternus
               `--+--Zupaysaurus
                   `--+--"Dilophosaurus" sinensis
                      |--Dracovenator
                      |--Cryolophosaurus
                      |--Dilophosaurus
                      `--Averostra
                         |--Ceratosauria Th, MH
                         |   |--Spinostropheus
                         |   |--+--Elaphrosaurus
                         |   |  `--Limusaurus
                         |   `--+--Ceratosaurus
                         |      |--Bahariasaurus/Deltadromeus
                         |      `--Abelisauroidea
                         |         |--Noasauridae
                         |         |   |--Laevisuchus
                         |         |   |--Masiakasaurus
                         |         |   |--Noasaurus
                         |         |   `--Velocisaurus
                         |         `--Abelisauridae
```

```
|            |--Kryptops
|            `--+--Rugops
|               `--+--Abelisaurus
|                  |--"Majungasaurinae"
|                  |   |--Majungasaurus
|                  |   `--Rajasaurus
|                  `--Brachyrostra  (= monophyletic Carnotaurinae?)
|                     |--Ekrixinatosaurus
|                     `--+--Ilokelesia
|                         `--+--Skorpiovenator
|                             `--Carnotaurini
|                                |--Aucasaurus
|                                `--Carnotaurus
`--Tetanurae  Th, MH
   |--Xuanhanosaurus
   `--+--Megalosaurinae
      |  |--Duriavenator
      |  `--+--+--Megalosaurus
      |     |  `--Poekilopleuron
      |     `--Torvosaurus
      |--+--Eustreptospondylus
      |  `--Spinosauridae
      |     |--Baryonychinae
      |     |  |--Baryonyx walkeri
      |     |  `--Baryonyx tenerensis (=Suchomimus)
      |     `--Spinosaurinae
      |         |--Irritator
      |         `--Spinosaurus
      `--+--+--Piatnitzkysaurus
         |  `--Marshosaurus
         |--+--Afrovenator
         |  `--Dubreuillosaurus
         `--Avetheropoda
            |--Carnosauria Th, MH
            |  |--Monolophosaurus
            |  `--Allosauroidea
            |      |--Lourinhanosaurus
            |      |--+--Metriacanthosaurus
            |      |   `--Sinraptoridae
            |      |       |--Yangchuanosaurus shangyouensis
            |      |       `--Yangchuanosaurus/Sinraptor dongi
            |      `--+--Allosaurus
            |         `--Carcharodontosauria
            |            |--Neovenatoridae
            |            |   |--Neovenator
            |            |   `--+--Chiliantaisaurus
            |            |      `--Megaptora
            |            |         |--Fukuiraptor
            |            |         |--Siamotyrannus
            |            |         `--+--Australovenator
            |            |            `--+--Megaraptor
            |            |               |--Aerosteon
            |            |               `--Orkoraptor
            |            `--Carcharodontosauridae
            |               |--Kelmayisaurus
            |               |--+--Concavenator
            |               |   `--Becklespinax
            |               |--Eocarcharia
            |               `--+--Acrocanthosaurus
            |                  `--+--Shaochilong
            |                     `--Carcharodontosaurinae
            |                        |--Tyrannotitan
            |                        `--+--Carcharodontosaurus
            |                           `--Giganotosaurini
            |                              |--Mapusaurus
            |                              `--Giganotosaurus
            `--COELUROSAURIA MH
                `--AVES
```

Note on update: *Because of limitations of time (specifically, the need to get the revised site completed as soon as possible), the theropoda have so far only been completely revised as far as the Carcharodontosaurs. Also, some taxon pages, like the Herrerasauridae and Carcharodontosaurinae, are very incomplete, essentially just holding pages. As Palaeos moves from a single authored to a community authored project, these various matters can be addressed. MAK120310*

Theropod References

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   |
   THEROPODA
   |--Herrerasauridae
   `==Podokesauridae
      `--+--Ceratosauria
         `--Tetanurae
            |==Megalosauroidea
            `--Avetheropoda
               |--Allosauroidea
               |  |--Neovenatoridae
               |  `--Carcharodontosauridae
               `==COELUROSAURIA
                   `--AVES
```

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Abelisauridae

Vargas AO, Wagner GP, and Gauthier JA. (2009) *Limusaurus* and bird digit identity. Available from Nature Precedings
Limusaurus

Wilson, J.A., Sereno, P.C., Srivastava, S., Bhatt, D.K., Khosla, A. and Sahni, A. (2003). "A new abelisaurid (Dinosauria, Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India." (PDF) Contributions from the Museum of Paleontology [University of Michigan], 31(1): 1-42. **pdf**
Ceratosauria, *Majungasaurus*, *Rajasaurus*, Tetanurae

Xu, X., J. M. Clark, J. Mo, J. Choiniere, C. A. Forster, G. M. Erickson, D. W. E. Hone, C. Sullivan, D. A. Eberth, S. Nesbitt, Q. Zhao, R. Hernandez, C.-K. Jia, F.-L. Han & Y. Guo. 2009. A Jurassic ceratosaur from China helps clarify avian digital homologies. Nature 459: 940-944. PDF Supplemetary
Ceratosauria, *Monolophosaurus*. Ornithomimosauria, Tetanurae

Yates, A. M. (2005). A new theropod dinosaur from the Early Jurassic of South Africa and its implication for the early evolution of theropods. *Palaeontologia Africana* 41, 105-122.
Eoraptor, Neotheropod phylogeny

Yates, A. M. (2007). Solving a dinosaurian puzzle: the identity of *Aliwalia rex* Galton. *Historical Biology* 19, 93-123.
Eoraptor

Zhao, Xijin; Benson, Roger B. J.; Brusatte, Stephen L.; Currie, Philip J. (2010). "The postcranial skeleton of Monolophosaurus jiangi (Dinosauria: Theropoda) from the Middle Jurassic of Xinjiang, China, and a review of Middle Jurassic Chinese theropods". Geological Magazine 147 (1): 13–27. doi:10.1017/S0016756809990240. **pdf**

Monolophosaurus

Zimmer, C. 2009 *The Tangled Bank: An Introduction to Evolution*, Roberts and Company Publishers
Dinosaurs to birds

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checked ATW021022, modified MAK120207, 120315

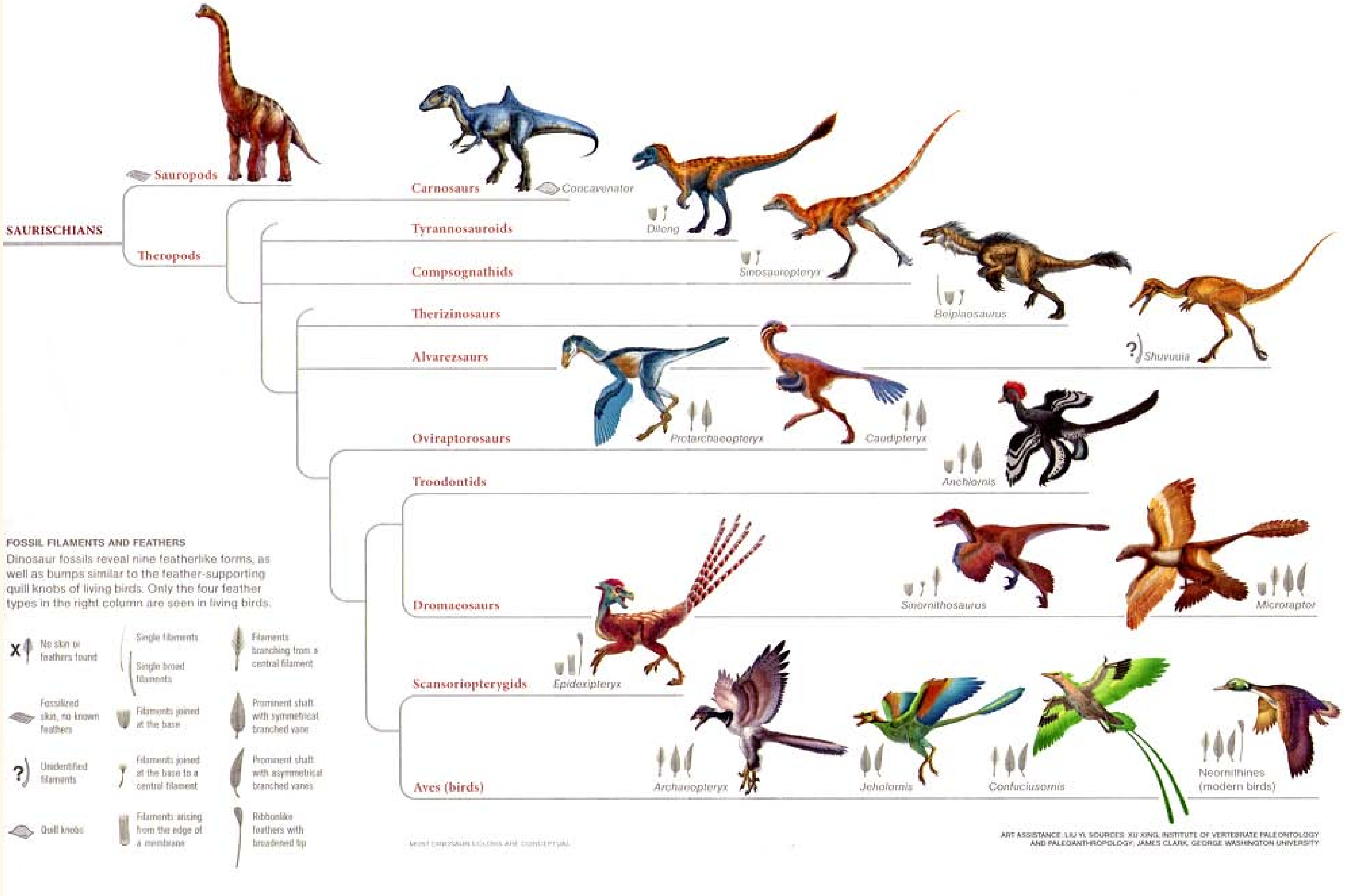
Coelurosauria

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--Metornithes
                  |--Alvarezsauridae
                  `--+--Oviraptorosauria
                     `--Paraves
                        |--Deinonychosauria
                        |   |--Troodontidae
                        |   `--Dromaeosauridae
                        `--Avialae
                           |--Scansoriopterygidae
                           `--AVES
```

Contents

Neither dinosaurs (using the colloquial, paraphyletic, definition) nor true birds[1], but perfectly intermediate and transitional between the two, the coelurosaurs or feathered dinosaurs, appeared during the late Jurassic, becoming a major part of terrestrial faunas in the Middle and Late Cretaceous, when they co-existed with both conventional dinosaurs and the first representatives of true birds. They constitute a highly diverse group of theropods that include everything from giant tyrannosaurs to swift-running ornithomimids and even and even ground sloth mimics. They include carnivores, omnivores, and herbivores, tree dwellers, gliders, powered flyers, and all manner of terrestrial forms. But the most extraordinary thing about them, only revealed in the last two decades through beautifully preserved Chinese specimens, is the presence of feathers. In life these creatures would have looked nothing like the scaly monsters of fantasy, and everuything like extraordinary, long-tailed, flightless (and sometimes even flying) birds. The following dendrogram by Carl Zimmer maps out the origin and evolution of feathers as revealed through fossils and cladistic analysis, and gives a good overview of the Coelurosauria, not as dry bones but as living animals.



Family Tree of Coelurosaurs (feathered dinosaurs). Artwork by Xing Lida, from Zimmer, 2011), via Fantasy Game Book, Feathered Dinosaurs and the Dinosaur Lag Effect. *Anchiornis* (above) can be seen at the middle right

In this unit we will consider these various groups (some more comprehensively than others, at the current time of writing) before moving on to orther dinosaurs. Although this may not be the most logical approach, the problem with a linear review is that it is not always possible to follow the branching path of evolution. The latter in this case involves the nested clades of Dinosauria --> Theropoda --> Maniraptora --> Aves (True Birds). But we still haven't considered the spectacular sauropods and the diverse and specialised ornithischians; in the following two units they are reviewed, before the narrative returns to avian evolution MAK120310

Notes

[1] We are aware of course that cladistically speaking, birds *are* a specialised sub-set of dinosaurs, in which case the opening sentence of this page would be misleading. On the other hand, evolutionarily speaking, birds are the *descendents* of the dinosaurs;in which case the opening sentence makes total sense. Cladistically, if dinosaurs are to be a natural (monophyletic) taxon, birds need to be included, otherwise dinos would go the way of the reptiles, a 19th century taxonomic anachronism of no more than colloquial usage. For the evolutionary gradist in contrast, ancestral taxa are not a problem. Hence dinosaurs evolve into birds. Ultimately though, it doesn't matter which taxonomic, systematic, or phylogenetic paradigm or classification system one prefers; it's the same evolutionary family tree of Life on Earth. Because all these different perspectives contribute to the big picture, there is no need to be rogorous about obnly one. For this reason, the narrative on *Palaeos* tends to jump rather haphazardly from one paradigm to another, depending on who the writer is, or even the mood of the same writer; we are less concerned with phylogenetic or taxonomic rigour than with conveying the wonderful and awesome story of the history and evolution of life.

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Coelurosauria: Coelurosauria

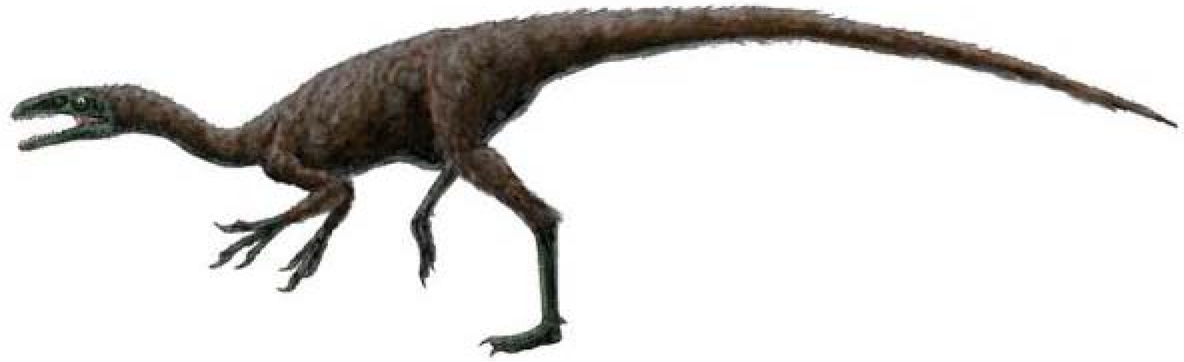
Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |?--Gasosaurus
         `--+--Tyrannosauroidea
            |--Compsognathidae
            `--+--Coelurus
               `--Maniraptoriformes
                  |--Ornithomimosauria
                  `--+--Ornitholestes
                     `--Maniraptora
                        |--Therizinosauroidea
                        `--+--Alvarezsauridae
                           `--+-
-Oviraptorosauria
                              `--+--+-
-Troodontidae
                                 |     `-
-Dromaeosauridae
                                 `--AVES
```

Contents

Taxa on this Page

1. Coelurosauria
2. *Coelurus* X
3. Compsognathidae X
4. Maniraptoriformes
5. *Ornitholestes* X



Life reconstruction of the mid Cretaceous Compsognathid *Mirischia asymmetrica*, Albian of Brazil; length about 2 meters. Most small coelurosaurs would have been very similar in size and appearance. These animals were covered in fine hair-like protofeathers (known to be present in the related *Sinosauropteryx*), and exceptional preservation reveals what appear to be bird-like air sacs (Wikipedia)
Artwork by FunkMonk (Michael B. H.), via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

Introduction: "Coelurosauria" has meant a number of different things. Originally it referred to small as opposed to large theropods - everything from *Coelophysis* to *Ornithomimus* - but this is now known to be an artificial, polyphyletic grouping group. The popular cladistic meaning is the monophyletic taxon that encompasses all advanced theropods, as well as their descendants the birds (beginning with *Archaeopteryx*). The terms Maniraptoria and Maniraptoriformes (refering to the grasping hands of many of these small advanced theropods) are approximately equivalent, but refer to slightly more specialised forms). (adapted from MAK)

Descriptions

Coelurosauria: *Nqwebasaurus*, *Piveteausaurus*, *Proceratosaurus*, *Timimus*. Avetheropods closer to birds than to Carnosaurs. Padian *et al.* (1999). Traditionally, the smaller bipedal carnivores.

Range: from Middle Jurassic

Phylogeny: Avetheropoda: Carnosauria + * **:** ?*Gasosaurus* + (Tyrannosauroidea + Compsognathidae + (*Coelurus* + Maniraptoriformes)). MAK120307

Characters: nasals do not participate in antorbital fossa [H+01]; **$** expanded, circular orbit; jugals reach antorbital fenestrae; Fenestra in roof of mouth; **$** <16 caudals have transverse processes; "boat-shaped" chevrons; fused sternal plates; "cranial notch" between scapula & coracoid absent [H+01]; coracoid with well-developed posterior projection [H+01]; elongated forelimbs, especially manus [H+01]; semilunate carpal in wrist; metacarpal I reduced; long, thin metacarpal III ; **$** ischium reduced to <2/3 length of pubis; **$** loss of ischial foot; **$** triangular obturator process on ischium; generally femur substantially shorter than epipodialia; **$** ascending process of astragalus >25% length of tibia; knee and ankle hinge-like; fibula reduced and immobile in relation to tibia; tarsal bones elongated; metatarsal III pinched between II & IV (arctometatarsalian condition or similar); feathers?.

Notes: [1] "Coelurosauria" is a name which has been used to describe a number of different groups in this general phylogenetic area at different times. Thus, the dates are uncertain because the definitions used by different authors vary, and also because some of the earlier material is not conclusively identifiable. In these Notes, Coelurosauria is the stem group birds > *Allosaurus*. **[2]** Note the many adaptations which may limit maneuverability as they increase speed and stability to impact. ATW

Comments: Comprehensive phylogenetic analysis by Senter 2007 gives the following topology: Tyrannosauroidea + (Compsognathidae + (Arctometatarsalia + (Ornitholestes + (Therizinosauroidea + (Alvarezsauridae + (Oviraptorosauria + (Avialae + (Troodontidae + Dromaeosauridae)))))))). This has mostly been accepted by later workers in the field. MAK120307

Image: Representation of *Coelurus fragilis* as a feathered dinosaur, artwork by Nobu Tamura , via Wikipedia, GNU Free Documentation/Creative Commons Attribution. Compare with the old-style (pre Dinosaur renaissance) illustration below

Links: DD: Coelurosauria; Coelurosaurs!; Coelurosauria; theropods; Coelurosauria; DGF, Geological Society of Denmark, Geologisk Tidsskrift Nr. 4, 1996; Basal Coelurosauria; Oudst bekende coelurosaurier (Dutch); Coelurosauria.

References: Hutt *et al*. (2001) [H+01]. ATW010517.

Gasosaurus constructus Dong & Tang, 1985

Synonym: ?Kaijiangosaurus lini He, 1984

Horizon: Dashanpu formation of Sichuan, China (Bathonian-Callovian)

Phylogeny: Coelurosauria **:** (Tyrannosauroidea + Compsognathidae + (*Coelurus* + Maniraptoriformes)) + *

Size: length about 4 meters, weight about 160 kg (Paul 1988)

Comments: a poorly known, medium-sized theropod, known from humerus, pelvis, femur, other postcranial elements, but no skull, Gasosaurus has features characteristic of an ancestral coelurosaurian or ancestral avetheropod, such as a primitive pelvis. Paul 1988 considers it closer to *Piatnitzkysaurus* (which he considered an advanced form) than *Eustreptospondylus* (later (2010) he places it under carnosauria (=allosauria) miscellania), whereas Holtz 2000 places it as a basal colurosaur, while Cau & Maganacu's cladogram (unpublished data, online) has it at the absolute bottom of the teanuran tree. Apart from that, no one seems to say anything about it. The Wikipedia page features rather optimistically complete skeltal rconstructions, complete with non-existant skull. Since we have no idea where to put this taxon, we've placed it at the base of the avetheropoda, with *Monolophosaurus* which, no doubt, is a totally unrealted form. For now we've place dit near the base of the Coelurosaurs. MAK120223

Compsognathidae: *Compsognathus, Sinosauropteryx(?)*.

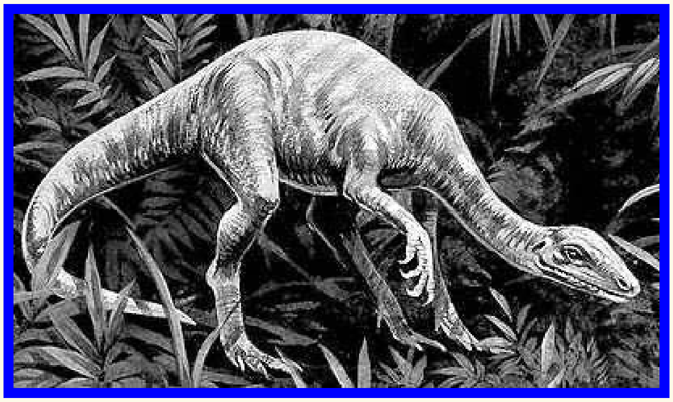
Range: Late Jurassic-Early Cretaceous. of Eur.

Phylogeny: Coelurosauria **:** ?*Gasosaurus* + (Tyrannosauroidea + (*Coelurus* + Maniraptoriformes) + *)

Characters: The following description relates to *Compsognathus*, as it is not clear what other forms may be contained in the group. About 1m; skull long and low, with sharply tapering snout; lower jaw slender, no coronoid process or external mandibular fenestrae (unusual); very lightly constructed skull , with large openings; paired skull elements not fused; orbit large; pleurocoels only in cervical vertebrae; centra spool-shaped and amphiplatyan; fan-shaped neural spines; no transverse processes on caudals; cervical zygapophyses not flexed; proximal caudal vertebrae long, slender, and somewhat spool-shaped; small curved chevrons; ribs continue to sacrum; cervical ribs double-headed, not fused to vertebrae, taper distally; fine bony gastrula; forelimb about 1/3 length of hind limb; lacks bowed ulna and extended metacarpal III; prominent obturator process on ischium; pes digit I reduced; some forms feathered (if *Sinosauropteryx* is *); lizard found as stomach contents; presence in Solnhofen indicates * may have been sympatric with *Archaeopteryx*.

Comments: now generally placed near Tyrannosaurs (Zanno et al 2009, Zanno 2010), or intermediate between Tyrannosaurs and ornithomimids (Senter 2007, Zhang et al 2008, Zhang et al 2007, Xu et al 2011, Lee & Worthy 2011). May be a paraphyletic assemblage of coelurosaurs (Chiappe & Göhlich(2010), some may be even juvenile forms of larger animals

Links: Compsognathus sp.; Compsognathus Skeleton; Compsognathus Skull; Sino-Dino.jpg.



Coelurus: *C. fragilis* Marsh 1879.

Range: Late Jurassic (Kimmeridgean) of North America.

Phylogeny: Coelurosauria : ?*Gasosaurus* + (Tyrannosauroidea + Compsognathidae + (Maniraptoriformes + *)).

Characters: ~2m long (all specimens may be subadult); skull shorter & taller than *Ornitholestes* [M+98]; neck very long [C87]; vertebrae slender, especially cervicals & caudals [C87]; vertebrae and long bones strongly pneumatic [M84]; vertebrae hollow, with large central cavity and thin walls [C87]; cervicals that possess diapophyseal shelves that are broad and curved; anterior cervicals "convexo-concave" (opisthocoelous?), other "bicoelous" (?!) [M84]; cervicals lack hypapophyses (so not maniraptoran?); cervicals coosified with ribs [M84]; dorsal centra are elongate [S88] and spool-shaped; dorsal centra and neural arches laterally compressed [S88]; neural spines much reduced [S88]; relatively low neural arches [S88]; pleurocoel in neural arch divided by vertical septum [S88]; dorsal ribs have undivided heads [S88]; 4 sacral vertebrae [C87]; elongated prezygapophyses in distal caudals & cervicals [M+98]; scapula strap-like [M+98]; humerus much shorter than femur [C87]; ulna bowed [M+98]; manus long & slender [M+98]; semilunate carpal [M+98]; manus I short; manus II & III long, with sharp claws; phalanges elongate [C87]; digits capable of "great flexion and extension" [C87]; laterally compressed unguals [C87]; theropod pelvis (?) [C87]; femur with major trochanter anterior [C87]; below major trochanter is "low, longitudinal ridge-like angle" [C87] (probably lesser trochanter, described as "low & square" in [M+98]); relatively little flexion at knee based on limited antero-posterior extension of femoral condyles [C87]; tibia longer than femur [M+98]; metatarsals very long & slender [M84], with very thin walls [M88].

Note: [1] Phylogenetic position follows Holtz (2001). **[2]** Seeley (1888) is describing a rather different animal, but repeatedly uses *Coelurus* as a point of comparison.

Comment: Senter 2007 finds *Coelurus* and its sister taxon *Tanycolagreus* to be basal Tyrannosauroidea. Zanno et al 2009 (see cladogram in supplementary material) find *Coelurus* to be a stem maniraptoram more derived than *Ornitholestes*. Since there is no agreement here, we have left this genus in its previous position as a stem Maniraptoriforme, MAK120307

Links: DinoData: Coelurus; COELURUS; Coelurus (Dutch); Coelurus; Coelurus The Natural History Museum's Dino Directory; Paleontology and Geology Glossary: Co; Saurischian dinosaurs: Coelophysid: Coelurus; MEA592D Dinosaur Osteology: Lecture 6; Coelurus; COELURUS (Spanish); Coeluro (Spanish); Exotenwelt-Coelurus (German); ????? (Japanese models).

References: Cope (1887) [C87]; Holtz (2001); Marsh (1884) [M84]; Marsh (1888) [M88]; Miles *et al*. (1988) [M+98]; Seeley (1888) [S88]. ATW030420.

Maniraptoriformes: *Scipionyx*? Could be basal coelurosaur. Defined as *Ornithomimus* + birds. Holtz (1996a).

Synonym: Arctometatarsalia *sensu* Senter 2007

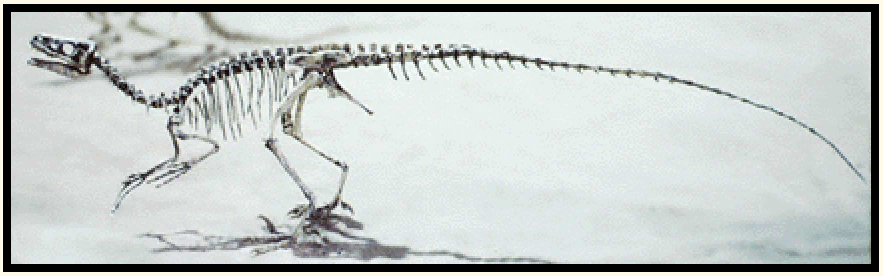
Range: From the Late Jurassic.

Phylogeny: Coelurosauria : ?*Gasosaurus* + (Tyrannosauroidea + Compsognathidae + (*Coelurus* + * : Ornithomimosauria + (*Ornitholestes* + Maniraptora)))

Description: $** 3rd antorbital fenestra; brain enlarged; bony secondary palate; **$ elongated ant cervical zygapophyses; **$** obturator process on ischium is distal; ischium ends in point; length of forelimb 75%+ of presacral spine; ulna bowed posteriorly; **$** semilunate carpal (fusion of distal carpals I&II) which permits hand to flex both laterally and dorso-ventrally (grasping and avian flight stroke); **$** thin, bowed metacarpal III.

Links: DD: Maniraptoriformes; Cladograms: The Groups of Dinosaurs; GEOL 104 Lecture 20: Theropoda II; Maniraptoriformes (German); GEOL 104 Lecture 20- Theropoda II- Tyrants, raptors, ostrich ... (Holtz lecture notes). ATW030829

Ornitholestes:



Range: Late Jurassic of NAm (Bone Cabin & ComoBluff).

Phylogeny: Maniraptoriformes : Ornithomimosauria + (Maniraptora + *)

Characters: Lightly-built, small (2m, 15kg?) carnivore. Small head, but with robust lower jaw; upper & lower jaws curved apart distally; ornamental crest on rostrum; very long (1m) tail, cervical zygapophyses are not elongated; relatively long arms with strong manual unguals; femur length about equal to tibia.

Image: *Ornitholestes* from Lectures 17 and 18 - Late Jurassic: Morisson, Tendaguru.

Links: DD: Ornitholestes; BBC Online - Walking with Dinosaurs - Fact Files; jurassic images; Lecture 18 - Late Jurassic: Morisson, Tendaguru; Ornitholestes Printout- ZoomDinosaurs.com; Saurischian dinosaurs: Coelurosaur: Ornitholestes; REFERENCES for ORNITHOLESTES; Ornitholestes (Dutch); Looking at Ornitholestes; An Agile Ornitholestes, 1914; Osborn's Ornitholestes, 1903; Ornitholestes hermanni; Ornitholestes Image Layout 1. ATW030910.

Comments: Previously considered a fairly basic coelurosaur, more recent analyses place *Ornitholestes* as a stem or basal maniraptoran (Senter 2007, Zhang et al 2008, Zhang et al 2007, Xu et al 2011, Lee & Worthy 2011. However Zanno et al 2009's cladogram places *Coelurus* in that position, slightly above *Ornitholestes*). MAK120307

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checked ATW050619, revised MAK120307

The Evolution of Feathers

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--Metornithes
                  |--Alvarezsauridae
                  `--+--Oviraptorosauria
                     `--Paraves
                        |--Deinonychosauria
                        |   |--Troodontidae
                        |   `--Dromaeosauridae
                        `--Avialae
                           |-
-Scansoriopterygidae
                           `--AVES
```

Contents

Editor's note: the following page has been downloaded directly from EvoWiki, Evolution of Feathers. MAK120315

The Quintessence of Birdness--The Origin, Evolution, and Debate, on Feathers

Contents

Introduction

As long as scientists have studied birds, they have puzzled over and marvelled at that most intricate and perplexing of avian traits--the feather. It is an amazing feat of biological engineering, functional and aesthetic (though birds care little of this, one might argue). Long has the feather delighted creationists and the proponents of so-called "intelligent design" with its fantastically complex structure. AIG has labelled the feather as quite simply something which cannot have evolved. Ornithologists, too, have been guilty of imputing to the feather, by virtue of its amazing properties, almost divine origin (e.g., Feduccia 1996). And yet the question has been and still is, "How did feathers originate and how have they evolved since then?"

We know a great deal about feathers, their function, the molecular and developmental pathways by which they are derived, their gross morphology, and so on. The great mystery is how they came about. It is a debate which, arguably, is at the very heart of avian phylogenetics, whether this is warranted, or not. Ostrom (1976) argued that if you solved the ancestry of *Archaeopteryx* you had solved the ancestry of birds. Many, whether of ornithological or paleontological inclination, would argue that once you have solved the origin of feathers (which includes isolating those taxa that display their most basal precursors), the debate on avian origins is effectively over.

While such a precise degree of resolution is perhaps not possible, the past quarter century has seen vast advances in this field of ornithological research, and today we stand on the brink of putting to rest these age-old questions.

Seeking Resolution Within the Context of the Intuitively Facile

Historically, two major schools of thought have dominated research into feather evolution. One has attempted to use ancestral feather function to generate hypotheses about early feather morphology. According to the other, ancestral morphologies of more derived feathers are hypothesized according to integument found in modern bird lineages; that is, the integument found in more basal lineages were assumed to be themselves more basal (Dyck 1985). In both, there has been a great deal of "common sense" involved in such explanations (Regal 1985), perhaps to their detriment.

The latter is seriously deficient, and is easily dispelled. The obvious problem is that the earliest known (chronologically speaking) feathers are already modern (Prum & Brush 2002), and the "basal" feathers of derived birds display derived characters that rule them out as ancestral; for example, the differentiated barbs of down feathers are clearly derived from pennacous feathers (Prum 1999, Dyck 1985).

If these feathers truly represented a basal morphology, then given that modern birds share common ancestry with *Archaeopteryx*, we would have to assume that the asymmetrical remiges in both Neornithes and *Archaeopteryx* are convergent, a possibility so remote as to be effectively rejected. Rather, the feathers of the most basal extant neornithine lineages should be seen as "secondarily simplified" (Prum & Brush 2002). Complicating the matter are potentially confused neornithine phylogenies. Proponents of “ratite” (e.g. Cracraft & Clarke 2002) holophyly and the concomitant assumption that ratites are primitive neornithes, have argued that their feathers are the most primitive (Lowe 1935). But the holophyly of "Ratitae" has been called into question, and perhaps is not a basal stem. The same is much clearer for various other Neornithes that were under consideration, including penguins.

While a full review of all the various early theories of feather origin that subsume the former methodology is beyond the scope of a primer such as this, which seeks to discuss the principal theories for feather origin as the debate now stands, a brief catalogue of prior models is nonetheless in order. Historically, functional hypotheses have essentially been polarized into two prevailing schools of thought. Feduccia (1985, 1996) has incorrectly expressed this dichotomy as one between adherents of the arboreal origin of flight and terrestrial origin of flight, but it is more accruately considered in terms of adaptation and exaptation. Those who hold to the adaptive school (e.g., Savile 1962, Bock 1965, Parkes 1966, Feduccia 1980, 1996) have argued that feathers arose in an aerodynamic context, either before or during the advent of homeothermy. In contrast to this view is that first elucidated by Ostrom in a series of publications in the 1970s in which it was postulated that feathers originally appeared to insulate endothermic proavians and were only later exaptated for flight. This idea found popular support in the work of Robert Bakker (Bakker 1975, 1986), and has since become the leading explanation for the original context in which feathers or feather precursors appeared, whether this is merited or not.

The principal argument of the so called adaptive school is the known relationship between even the smallest increase in integumentary surface area and the ability to sustain a glide or parachuting effect in an arboreal form. While this much is undeniably correct, perhaps the most glaring flaw in this hypothesis is the reliance it places upon a classical view of feather evolution in which feathers can be derived via simple (relatively speaking) distal ramification and segmentation of elongate scales. Yet the combined molecular and embroygenic data suggest that feathers are much more than "scales gone frayed", which has been assumed implicitly or explicitly by most researchers until recently. Feathers are composed of a sub-class of beta-keratin called feather (phi) keratins. Beta-keratins as a whole are remarkably distinct from alpha-keratins, which are present in the epidermis of every amniote, being much smaller and occuring as tandem repeats throughout the genome. Within beta-keratins, different classes of phi-keratin are themselves rather distinct. The sub-class that forms avian scutate scales, claws and beaks are larger than those present in feathers. The only keratins that *are* similar to those of other reptiles are the nonfeather type beta-keratins that make up the avian reticulate scales.

Morphogenesis is also wildly different. Feathers and scutate scales begin development as a visibly distinct placode. However, this is not present in reticulate scales and all reptilian scales, whose placode remains indistinguishable from the epidermis (Maderson & Alibardi 2000). Subsequent stages of development are unknown outside of feathers, from the branching of barbs, the tubular invagination that forms of the follicle, to the barb ridges. Even the planar surface, so loved by functionalist advocates of an aerodynamic origin, is not homologous. Scales are inherently planar; their surfaces are derived directly from the placode. Planar feathers (pennaceous) , by contrast, obtain their shape *only* after its growth from the cylindrical sheath, making them primarily cylindrical, and only secondarily flat (Prum & Brush 2002, Prum 2003). Any theory of feather evolution, then, must account for this.

For these reasons, various hypotheses, arising from speculation about function or the phylogenies of exant birds, and riding on the mistaken notion of "scales gone frayed", have fallen by the wayside. For the most part. Although ostensibly suitable "structurally homologous scales" are still sometimes advanced (Jones et al 2000, Zhang & Zhou 2002) there is a considerable amount of equivocation in their presentation (compare, for example, Feduccia in Jones et al 2000 with Feduccia 1999). Old habits, it seems, die hard.

The alternative hypothesis, in which basal feather precursors or even the general remigial architecture observed in flying birds arose in a strictly thermoregulatory context, has generally observed that feathers serve a demonstrable role in biothermal energetics and serve as insulatory mechanisms. The principal data in support of this hypothesis is phylogenetic, as opposed to the aerodynamic scenario; i.e., the thermoregulatory model most closely matches the best supported phylogeny of Aves. The greatest strength of the thermoregulatory model is that is closely congruent with the most current data on the embryogenesis of feathers. Nevertheless there are numerous objections, the simplest and most emphasized (e.g., Parkes 1966, Feduccia 1996) being: "why feathers?" Further objections raised and best summarized by Feduccia (1996) include:

a) Down feathers are secondarily derived in birds and thus cannot represent an ancestral feather morphology

b) Hairlike integumentary derivatives would do just as well as feathers for thermoregulation, as is seen in mammals.

c) Flight feathers degenerate in cursorial flightless birds

d) Pterylae contradict an initially thermoregulatory role

e) Feathers are fundamentally designed to be aerodynamic structures

The first of these objections is entirely irrelevant, as no one postulates that down feathers seen in extant birds represent the original feather morphology in any context, whether thermoregulatory or aerodynamic. The second objection *is* valid but the preponderance of evidence argues that the earliest feathers *were* simple, filamentous derivatives. The third objection, heavily stressed by Feduccia (1985, 1996, 1999a, b) is also irrelevant in that it merely demonstrates that aerodynamic pressures constrain the morphology of remiges in extant birds. The same can be said for the presence of pterylae, whose existence and conformation in extinct archaic birds cannot be known. Indeed, in some ratites, (e.g., *Struthio* and *Rhea*) pterylosis is not known, at least in the conformation of the secondary feathers. And lastly, the aerodynamic properties of feathers merely indicate that aerodynamic pressures govern the morphological features we observe in feathers amongst today's birds.

A logical objection to the hypothesis that feathers arose in an endothermic form is to argue that endothermy and feathers as insulatory mechanisms arose simultaneously in a reciprocal feedback loop, perhaps correlated with the initial ecological shift towards an arboreal lifestyle (e.g., Bock 1985).

Although the thermoregulatory and aerodynamic functional hypotheses have been at the center of the debate, they are by no means the only ones to have been advanced. Ostrom (1974, 1976) proposed that feathers arose primarily to aid in the capture of prey in a highly cursorial insectivorous (loosely defined) form, a form he argued was typified by *Archaeopteryx*. Distal ramification to increase the effectiveness of the "fly swatter" would have led to the derivation of advanced feathers later coopted for aerodynamic function. Ostrom later abandoned this model entirely after it received extensive criticism (e.g., Martin 1983) and revision by Caple et al. (1983).

Hypotheses in which the origin of feathers has been tied to sexual selection, have been proposed in one form or another (e.g., Stephen 1974, Cowen & Lipps 1982). While they do logically invoke the known influence of sexual selection upon evolutionary trajectories, they lack the ability to explain why such advanced integumentary derivatives as feathers would appear in lieu of some simpler and embryogenically and morphogenically more conservative structure, or any ability to predict the morphology of basal precursors. While these hypotheses cannot be entirely ruled out, it does not seem probable that they alone can account for the origin of feathers and their subsequent evolution.

More generally, there are problems with these explanations above and beyond what has already been mentioned. Obviously, generating hypotheses about morphology based on hypotheses of adaptive (or exaptive) function are probably not the strongest inferences. There is, in addition, a tendency for advocates of these views to reject homologous structures because of their functional preconceptions; that is, to attempt to establish homology according to function rather than form. There is no better example than Feduccia and his cohorts strenuously arguing that coelurosaurian integument is little more than frayed collagen fibers. Consequently, they also have a tendency to accept analogous structures that seem to fit; for example, the appendages of *Longisquama* (if they are appendages at all). Further still, this is part of a deeper tendency to conflate ones favorite avian phylogeny with feather function. For example, Feduccia insists birds are clearly derived from a "thecodont" stock and were arboreal. Therefore feathers must have functioned in an aerodynamic context.

The Feather: From Placode to Pterylae

In the past ten years or so, the field of evolutionary developmental biology has largely revolutionized our understanding of feather embryogenesis and ontogeny, which has in turn clarified our view of how feathers first appeared, regardless of the reason for which they appeared.

Placode - graphic to be added0

The feather placode above a condensation of dermal cells

Previous attempts, as mentioned above, did not take the complex heirarchical nature of feather development into account when hypothesizing basal feather morphs, and were therefore led down untenable paths. To understand feather evolution, one must first understand how they come into being.

Feather development begins with an epidermal placode situated above a condensation of dermal cells which specifies the particular feather's location.

From below, dermal cells work themselves upwards, forcing the epidermis into a finger-like projection called the papilla, or feather bud. Signaled by the dermis, the epidermal cells around the base of the papilla then sink down, creating an invagination called the lumen, or follicle cavity. Subsequent morphogenesis proceeds from the epidermal collar. Along its length, keratinoctyes proliferate and form barb ridges.

Papilla - graphic to be added

The papilla, or feather bud

These barb ridges are helically displaced as they grow, eventually making their way to the anterior midline and fusing to form the rachis ridge, which later becomes the feather rachis. Opposite the rachis ridge, new barb ridges spring out of the collar, these fusing with the rachis ridge anteriorly. On the barb ridges themselves, peripheral cells organize themselves into horizontal layers. Following the death of cells in the middle, those on either side become the paired barbules, with those more central fusing to become the ramus.

Finally, the whole structure, which until this point has remained essentially tubular, opens up. The outer surface becomes the dorsal surface of the fully developed feather, and the interior becomes the ventral. It should now be clear precisely why the planar surfaces of scales and feathers are not homologous; scales develop from the anterior and posterior surfaces of the placode directly, feathers round-aboutly develop their surface from the inner and outer surfaces of the cylindrical collar.

Also of great importance is the hierarchically contingent nature of the developmental processes. Barbs can only form on a collar, and a rachis can only be formed after the growth and displacement of the barbs. Distal and proximal barbules cannot close a vane unless they have barbules of some sort to grow from, which themselves originate from barbs. One step necessarily precedes the other.

The Evo-Devo of Feathers

Guided by the hierarchically contingent developmental process described above, Prum (1999) proposed a theory that seamlessly harmonizes the morphogenetic, biochemical and paleontological data in a way previous theories have failed to do. It involves essentially five stages, one built on top of another, broadly mimicking feather development while explicitly not being based on the discredited Haeckelian "law" of recapitulation.

The first stage is hypothesized to have originated with the first feather follicle. As above, the dermis would have pushed the epidermis into a collar, with the epidermis sinking around its base. This would have yielded a hollow, tubular structure much like the calamus of modern feathers. Stage II involves the origin of barbs. Derived from the collar, these would have opened up into a simple "tuft" extending from a calamus. Stage III has two stages which the theory cannot distinguish between in terms of temporal origination; either could have occurred first. What Prum labels IIIa involves the helical displacement of the stage II barbs and their fusion to form the rachis on the midline. The fully developed feather would have been pinnate, and superficially quite similar to modern feathers. With the evolution of stage IIIb, stage II barbs would have evolved barbules and ramus. Together, both stages would yield an open pennaceous feather complete with a rachis, ramus, barbs, and barbules. The following stage, stage IV, sees the evolution of distal and proximal barbules, built off IIIb, which would have hooked together and closed the vane. Fully developed, these are essentially modern, but symmetrical, feathers. All subsequent morphologic variety is subsumed under stage V, including asymmetrical flight feathers, and down.

How these changes are accomplished is a rather complicated matter, and all the intricacies have not yet come to light. What is known, however, is that plesiomorphic developmental pathways were co-opted and changed in such a way that novel feather structures were developed. An illustrative examples comes by way of Harris et al (2002), who looked at patterns of Shh and Bmp2 expression in a chicken (*Gallus*), duck (*Anas*), and alligator (*Alligator*). What they found was that at the placode stage, when both feathers and scales are just condensations of dermal cells, there is a conserved expression of Shh in the posterior domain, and of Bmp2 along the anterior border -- in both timing and polarity -- in each. Subsequent to this stage, we see derived coexpression of Shh and Bmp2 in the distal epithelim at which point the papilla is growing. Subsequent patterns of expression are also unique to feathers.

What all of this shows it that the placode and placode development are plesiomorphic in archosaurs, and that the Shh-Bmp2 module was probably co-opted during development multiple times, leading to a novel feather morphology after each. That is, in the primitive scaled precursor to feathered theropods in which Shh was expressed posteriorly and Bmp2 anteriorly, mutation altered this such that Shh and Bmp2 now additionally expressed themselves in the distal epithelium. Although this is my no means the entire story, the role of Shh and Bmp2 are illustrative of the molecular pathways Prum and his colleagues envision.

The Evolution of Feather Keratins

As noted above, phi-keratins are remarkably different from both alpha-keratins and other beta-keratins. Those of various feathers and their parts are a heterogeneous bunch, all with a mass of roughly 10.6 Kd. Those of scutate scales, claws and beaks yeild a similar electrophoretic array, but are larger, with a mass of 14.5 Kd (Brush 1996). This size difference, according to Walker & Bridgen (1976), is due to a repeating tripeptide sequence (Gly-Gly-X, where X is either Phr, Leu or Tyr) of 3 Kd. Other differences exist in the precise specifications for the beta-pleated sheath, and shorter/longer globular portions.

Because feather specific phi-keratins are clearly similar enough to establish homology, and non-feather classes broadly so, Brush proposed that an ancestral non-feather type phi-keratin gene (recently discovered in alligator claws by Sawyer et al. 2000, making it plesimorphic in archosaurs) underwent duplication and subsequent deletion of the Gly-Gly-X region, resulting in the two distinct sizes. Subsequent duplication and modification explain the similarity of all the smaller feather phi-keratins (Brush 1993, 1996, Prum & Brush 2002).

It is unknown if feather specific phi-keratins were present in the most basal feathers. Brush (1996, 2001) suggested they were, but Prum (1999) has argued that the morphological novelty of the feather itself probably preceded it.

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Coelurosauria: Tyrannosauroidea

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
                |--Tyrannosauroidea
                |  |--Eotyrannus
                |  `--Tyrannosauridae
                `--Maniraptora
                    |--Therizinosauroidea
                    `--+--Alvarezsauridae
                       `--+--Oviraptorosauria
                          `--+--+--Troodontidae
                             |  `--Dromaeosauridae
                             `--AVES
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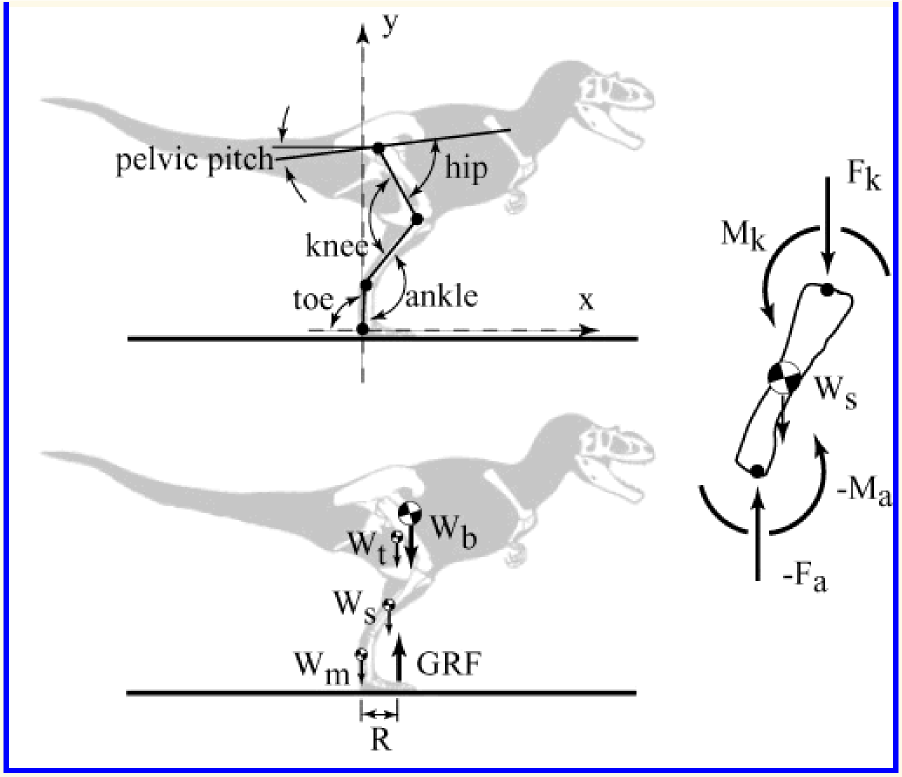
2. Tyrannosauroidea X

Tyrannosauroidea: Superpredator, Scavenger or Soprano?

Tyrannosaurs have generated a remarkable number of interesting disputes over the years. It would be impossible for us to add anything of merit to the various debates -- which, of course, will not discourage us from dispensing opinionated drivel as we see fit. Most of the issues are spin-offs from the hunter-scavenger debate: were the tyrannosaurs superpredators, gigantic garbage disposals, or something else? Saying anything about the behavior of long-extinct animals is chancey. Hypotheses in this area tend to be inherently unscientific because they are difficult to test rigorously. We are forced to measure the unknowable indirectly, using criteria that are themselves uncertain. So, were the tyrannosaurs "superpredators"? Fortunately, when it comes to "superness," there are certain widely accepted tests which we may apply.

Faster then a speeding bullet?

One of the more astounding claims made for *Tyrannosaurus* is that it was able to run at 20m/sec (72 kph) or more. See, *e.g.*, Bakker (1986) and

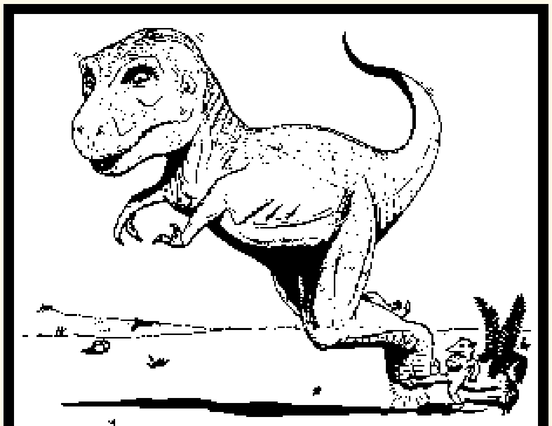


several papers by Gregory Paul. **[1]**. However, the supposition is not as unreasonable as it may seem at first. *Tyrannosaurus* was very lightly built for its size, with long legs and enormous potential for muscle development in the right places. Its legs seem at least arguably capable of standing the shock of repeated impacts, and its excellent vision might allow it to navigate at speed. We cannot dismiss the possibility that it was capable of near-highway speeds for at least short sprints.

Nevertheless, we tend to doubt that tyrannosaurs were capable of quite such athleticism. Two critical studies on the subject have taken different approaches, but have arrived at similar negative conclusions. The first is by one of the masters of Mesozoic mechanics, John Hutchinson. Hutchinson & Garcia (2002). Hutchinson probably knows as much as anyone about theropod hindlimb muscles and locomotion. See Hutchinson (2001), Hutchinson (2001a) and Hutchinson & Gatesy (2000). He has not only rewritten the book on theropod myology, but has spent a good many years applying it to locomotion studies. Hutchinson & Garcia take advantage of this detailed knowledge of musculature to calculate the minimum percentage of body mass which must be devoted to leg extensors in order to keep a running tyrannosaur moving.

Hutchinson & Garcia apply the simplifying assumptions available at mid-*stance phase* (shown in the figure). This is the point during the running cycle when the body's center of gravity is lowest. At this stage of the running cycle, one foot is squarely on the ground, the vertical velocity is zero, and all of the force is directed straight up ($d^2x/dt^2 = dy/dt = 0$). Now, forget about running for the moment and assume that the dinosaur is just standing on one leg. Yes, he's off balance, but we're only interested in forces for the moment, and all the forces are vertical at this point in the running cycle. Since, for this fraction of a second, the body is not moving vertically, we know that the force of the animal against the ground is equal to its weight (W), and that the equal and opposite ground reaction force (GRF) will be the same. Newton's First Law, right? Now look at the diagram of the lower leg over on the right of the image. -Fa is the force at the ankle and Fk is the weight of the animal above the knee. These numbers aren't quite the same as W and GRF because we have to adjust for the weight of the foot below the lower leg and the weight of the shank itself. However, those are easy to estimate. The point is that two vertical forces, both of which we can calculate, are acting at opposite ends of the shank. Since the lower leg is not vertical, these forces tend to rotate it as shown. We can make good, conservative estimates of the angles involved. **[2]** Thus, we can calculate the *torque* as a function of the animal's weight. If the tyrannosaur has zero vertical velocity, we can then calculate the force needed to keep the leg from collapsing. Since we know, generally, where the muscles are, how strong vertebrate muscle is, where the muscles attach, and the angles these attachments make to the bone, we can estimate the amount of muscle needed to generate this force – again as a function of the weight of the tyrannosaur. Finally, because this *is* a running dinosaur, we apply a "fudge factor" to allow for the fact that the beast has to be accelerating vertically to make his next step. This turns out to be a fairly constant number (2.5) in all vertebrates. Obviously, the number gets higher for faster running speeds, but 2.5 does it for the basic running cycle. (Actually, H&G's calculation is much more complex, since they used a model with at least 2 segments which could rotate independently. However, the basic approach is as described.)

Because we have calculated everything as a function of weight, we don't have to know how heavy our tyrannosaur is. The answer is expressed in terms of muscle mass as a percentage of total mass of the dinosaur. Hutchinson & Garcia tested their model on a number of systems: people, chickens and alligators. These gave good results and indicated that bipedal runners usually have about twice the muscle mass they theoretically "need" as a safety factor. (In fact, safety factors of 2-3 seem to be an evolutionary constant). However, *even without a safety factor*, a running *Tyrannosaurus* would need to devote about 83% of its mass to leg extensors, which is plainly impossible.



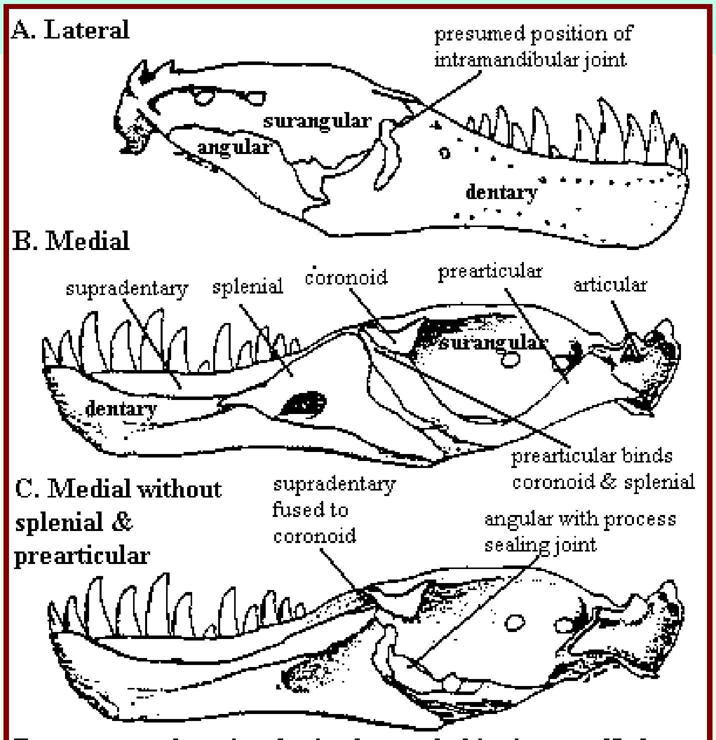
"How to kill a Tyrannosaurus rex" from Farlow et al. (1995).

As Hutchinson & Garcia point out, this doesn't really relate to the scavenger/predator issue because the same general parameters would apply to tyrannosaur prey animals. However, a similar result was reached by Farlow *et al*. (1995), using a completely different approach which is somewhat more specific to large, obligate bipeds like the tyrannosauroids. In discussing this paper, we will make the assumption that the reader has had about all the math she wants to deal with in the preceding paragraphs. Accordingly, we will deal only in qualitative terms. In essence, Farlow & Co. ask what would happen if a roughly 6000 kg *Tyrannosaurus*, moving at 20 m/sec, stepped on the Mesozoic equivalent of a banana peel. This is a fair question. As one might expect, the results of a 6 ton object, moving at 70 kph, hitting the ground from a height of a couple of meters are not pretty and would very likely be lethal for the object involved. Farlow *et al.* make the calculations based several different assumptions about substrate and come up with a train wreck each time. These results are not due to pessimistic assumptions. In fact the authors ignore effects which would make the injuries considerably more serious. **[3]**. Such accidents go to the heart of the evolutionary process. Species which engage in risky behaviors do not survive to reproduce unless the rewards are at least high enough to justify the risk.

It's a Bird?

Definitely not. The teeth of tyrannosauroids, particularly *Tyrannosaurus*, are unusual among theropods because they are individually large and heavy. There is little question that these teeth are capable of crushing bone. See image under Tyrannosaurinae. The question is whether tyrannosauroids regularly did so and under what circumstances. The assumption in the literature seems to be that bone-crushing is correlated with a scavenging life-style. Thus, those who view tyrannosaurs as cowardly scavengers tend to treat this feature as a point in their favor. Those who view tyrannosauroids as noble hunters tend to minimize the significance of this behavior.

One factor which seems to favor bone-crushing as a significant behavior is the design of the tyrannosauroid jaw. Older reconstruction of tyrannosaurs usually incorporated the typical theropod jaw, which includes an intramandibular joint. This joint connects the anterior dentary, splenial and (if present) supradentary with the posterior surangular, angular, coronoid, prearticular and articular. Since this connection is hinged, the lower jaw bends outward in the middle when it is stressed -- as, for example, when the teeth hit something rather hard. Accordingly, most bone would not be crushed. Rather the teeth would slide over it as the jaw deformed, causing the bone to be swallowed whole or rejected.



Tyrannosaurus: lower jaw showing features locking intramandibular joint. Adapted from Hurum & Currie (2000).

This arrangement is certainly operative in carnosaurs, and perhaps even basal tyrannosauroids. However, Hurum & Currie (2000) have shown that tyrannosaurinids block the joint. The supradentary overgrows the joint and fuses with the coronoid. This connection is reinforced by a long process of the prearticular which articulates with both the coronoid and the splenial. An anterior process of the angular also bridges the gap ventrally. In addition, the supradentary sends ridges between the teeth, further immobilizing the lower tooth row.

Farlow & Holtz (2002) state that "there is no indication that tyrannosaurids deliberately crushed bones, in the manner of some mammalian carnivores, even though their teeth and jaws were strong enough to handle bone-breaking ... bone-biting seems to have been incidental to feeding on meat." The problem here is the "deliberate" part. Unlike first degree murder, bone-crushing requires no legal *scientur*. *Mens rea*, or an evil state of mind, is not an element of the offense to be proven. Tyrannosaurs seem to have evolved in a direction from which we may infer selective pressure to treat bone as edible.

Buchholtz (1997) notes that broken teeth are extremely common among tyrannosauroids. However this is not a universal trait. Lambe (1917) remarks, with some surprise, that the teeth of his *Gorgosaurus* showed no signs of wear at all. Fortunately we have at least two direct indications of tyrannosauroid diets: one enormous *coprolite* and some fossilized stomach contents. Varricchio (2001). Both seem to contain an unreasonable amount of juvenile hadrosaur bone. On the basis of this completely inadequate sample, we may speculate that, for the type of prey normally consumed by tyrannosaurs, their dentition and jaw mechanics simply allowed them to treat bone as irrelevant.

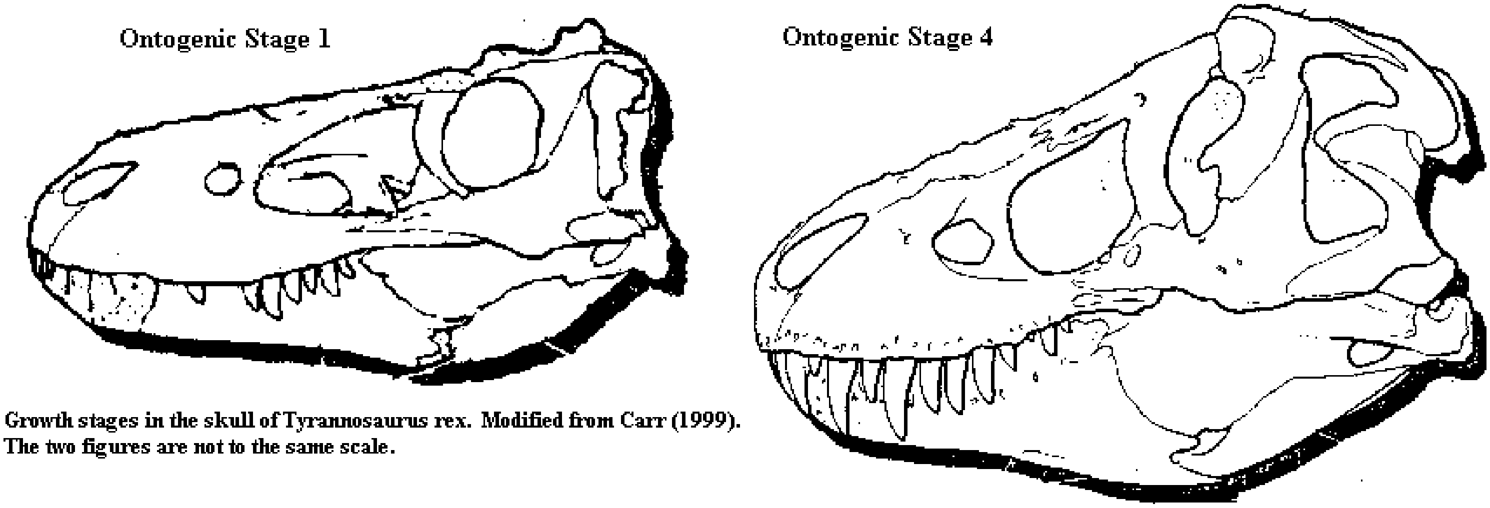
It's a Plane?

Farlow & Holtz (2002) discuss the work of Farlow on range sizes for large predators. Range sizes for living predators are closely correlated with body mass. If that relationship applies to Mesozoic predators, the home range size of the 2500 kg *Acrocanthosaurus* would have extended for hundreds or thousands of square kilometers. The home range of a 5000 kg tyrannosaur might be proportionately higher. At some point, the size of the range needed to support the predator becomes too large for comfort. A territory of several thousand square kilometers cannot be effectively kept free of competitors, because patrolling and marking become impossible. When individuals are so far apart, locating a mate also becomes a major concern. Farlow & Holtz speculate that metabolic requirements for tyrannosaurs might be unexpectedly low, or prey productivity unexpectedly high. However, there are other solutions. Tyrannosaurs may have followed herds, for example, or taken advantage of some other behavior which ensured locally high prey densities and allowed boy to meet girl -- the Late Mesozoic equivalent of a freshman mixer.

Strange Visitor from a Distant Planet?

... Well, perhaps not. But the actual provenance of tyrannosauroids remains at least a bit mysterious. Proposed closest relatives include Allosauridae, *Acrocanthosaurus*, Ornithomimosauria, and Therizinosauroidea. One of the best bets is Lambe's (1917) original intuition that tyrannosauroids were sisters of the Ornithomimosauria. Lambe should know, since he was the first to describe both *Ornithomimus* and *Gorgosaurus*. This is also the relationship most frequently recovered from cladograms. Holtz (2000) (reviewing previous work). Holtz ultimately concludes that ornithomimosaurs and tyrannosaurs probably form a monophyletic group, although his calculations do not yield a clean separation. In any case, that's the position we have taken here.

Much more recently, Carr (1999) has described a new, and disturbing, problem area in tyrannosaurid phylogenetics. It appears that many of the characters used to distinguish species and develop phylogenies are subject to considerable ontogenetic variation. That is, they change significantly over the life cycle of individuals. So, for example, a young *Tyrannosaurus* has a nasal with a smooth dorsal surface, while an old individual has a more rugose nasal. The first maxillary tooth changes from incisiform to conical, the postorbital shortens and develops a process running under the orbit, and the parietal develops a much larger nuchal crest. A review of the various characters, even synapomorphies, assigned to individual tyrannosaur species reveals that species differentiations are made on just such characters. So then, are we looking at artifacts of ontogeny or examples of paedomorphism and/or precociality? How do we score these age-related characters to calculate a cladogram? Some of the conceptual problems associated with ontogenic changes are discussed in connection with the work of Steyer (2000) on temnospondyl phylogeny. Carr's extensive list of character state changes suggests that this is a common and serious problem which needs to be addressed more carefully.



Growth stages in the skull of Tyrannosaurus rex. Modified from Carr (1999). The two figures are not to the same scale.

Powers and Abilities Far Beyond Those of Mortal Men?

One of the relatively few undisputed ecological facts about the tyrannosauroids is that, whatever they did, they were the only ones who could do it. In most dinosaur-dominated faunas, a number of large predatory dinosaurs co-existed, and predator sizes graded down to successively smaller types. In the Late Cretaceous of North America and East Asia, the tyrannosauroids -- usually only one species at a time -- held the large predator job alone. The next largest carnivores were usually dromaeosaurs or other, much smaller theropods. Farlow & Holtz (2002). Thus, if tyrannosaurs were primarily scavengers, we must be willing to accept that these ecosystems had *no* large predators. That seems unlikely, to say the least.

Bend Steel in His Bare Hands?

One argument made by the proponents of scavenging is that the arms of tyrannosaurs were so useless as to preclude prey capture as a way of life. In response, Carpenter & Smith (2001) have built a good case that these diminutive arms were perhaps not so useless as they might appear. Carpenter & Smith map out the muscles on the pectoral girdle of *Tyrannosaurus*. While it is not necessary to get into the myological detail, C&S do effectively make the point that the girdles were large and well-muscled. The implication -- that the arms must have been useful for *something* -- is clearly brought home. Their discussion of the biomechanics of the arms is a little less convincing only because it is limited to the *m. biceps*. C&S attempt to work backward from the size of the tendon scar on the forearm to calculate the power and mechanical advantage of this muscle, the argument being that a strong biceps indicates an ability to hold struggling prey. The chain of reasoning -- all from the size of 70 million year old tendon marks on two individuals -- seems a bit attenuated. However, they mention two additional points which are better substantiated.

First, the arms are so constructed that adduction of the forearm (by the biceps) brings the hands toward each other. This tends to also to flex the digits, so that the most natural motion looks like clutching something close to the body. So far, so good. But, second, the range of motion is extremely limited. Its hard to say what this implies, but the restricted range of motion weighs strongly against the forearms being a prey-capturing device. It may also be worth noting that the area of origin for the *m triceps* is extensive, and the olecranon process of the ulna is notably large. Yet one of the specimens shows signs of an avulsion injury to the triceps origin. The triceps is a forearm *extensor*, the opposite of the biceps. Why should this muscle be particularly enlarged but, apparently, not yet large enough to withstand some severe strain placed on it? There are no obvious answers. We can only note that this is not what we might expect if the arms primarily served to immobilize prey.

Mighty Hunter, Sniveling Scavenger, or ... ?

So where does this leave the hunter-scavenger debate? Nowhere really. We have tentatively concluded that tyrannosaurs were slow. That conclusion is drawn from studies on flat ground, where tyrannosaurs and prospective tyranno-groceries were, so to speak, on a level playing field. But life, and terrain, are not so simple. One can only imagine tyrannosaur locomotion on broken slopes, terrain that would have given adult hadrosaurs (facultative quadrupeds, beautifuly designed for scampering uphill) an overwhelming advantage in mobility. Tyrannosaurs may have preferred juveniles and possessed dentition allowing them to make quick and highly efficient use of this resource. But juveniles are not always available. Large size and huge teeth *always* allow a carnivore to intimidate smaller killers, get a couple of quick bites in (ignoring bones), and amble off before the owners get organized. The arms could conceivably be used to subdue struggling prey, but don't they seem a whole lot *better* designed to contain and confine non-struggling, dead prey and keep it out of reach of smaller hunters while the tyrannosaur runs off with it? How about the range sizes? If tyrannosaurs needed a behavioral trick to concentrate food sources, how about following small groups of more efficient killers? The relationship need not have been purely parasitic. Four or five dromaeosaurs could probably harass and immobilize all but the largest herbivores of the Cretaceous, but even a mortally wounded hadrosaur would be unreasonably dangerous for the bird-boned predators. But, just about then, the local tyrannosaur would finally catch up and assume the minimal (to a tyrannosaur) risk of the final kill in exchange for first dibs on body parts. This kind of antagonistic commensalism requires no cooperation at all, but would naturally result in a predatory system of very high efficiency -- perhaps high enough to eliminate competition from traditional large predators. So, our provisional speculation is that tyrannosaurs were neither superpredators nor scavengers. They may have been more like thugs, living by a combination of smash-and-grab, extortion, gang violence and contract executions: not superpredators, and not scavengers -- but Sopranos. ATW030308

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[1] I regret that I was unable to lay hands on a copy of Paul (2000). I understand that the argument for a swift, cursorial *Tyrannosaurus* is very well made in this piece. Interested readers should consult Paul, G (2000), *Limb design, function and running performance in ostrich-mimics and tyrannosaurs*. **Gaia** 15: 257-270.

[2] Could we fiddle with the angles to improve the results? Yes. However, the bottom line is that the angle is a function of speed. The faster Dino moves, the more bent over he is. The angles increase and the mechanical problem gets much worse. This, and some other questions are answered at *Tyrannosaurus* Was Not A Fast Runner

[3] Farlow and co-workers treat the head and body as rigid objects. They aren't. When the head and torso of the critter hit the ground, these portions decelerate very rapidly. But the tail and hindquarters are still moving at 20 m/sec. The combined torque, shear and compression effects are unpleasant to consider. They would almost certainly result in catastrophic spinal injuries. Tyrannosaurs are not well designed to perform somersaults.

Descriptions

Tyrannosauroidea: Definition: *Tyrannosaurus* > Tinamous. Includes: *Itemirus, Labocania, Siamotyrannus, Stokesosaurus,*

Range: Early Cretaceous to Late Cretaceous of North America, Europe, Mongolia, Central Asia & Southeast Asia.

Phylogeny: Coelurosauria **:** Compsognathidae + (*Coelurus* + Maniraptoriformes) + * **:** *Eotyrannus* + Tyrannosauridae.

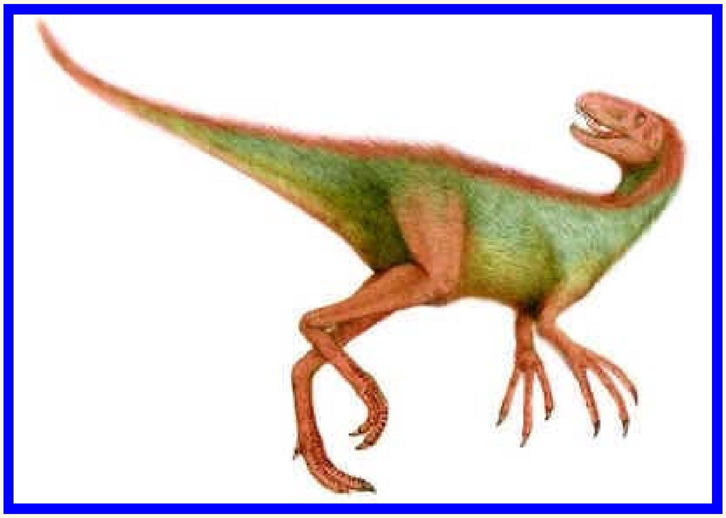
Characters: skull large; jaw & neck muscle attachment areas expanded; prefrontal reduced or absent [S97]; upper temporal fenestrae separated only by sagittal crest [S97]; squamosal with pneumatic recess [H00*]; jaw articulation anterior to occipital condyle [H00]; palatines do not meet medially [H00]; palatal fenestra between palatine & pterygoid [S97]; premaxillary teeth U-shaped in cross-section [H00]; premaxillary teeth incisor-like with both carinae of each tooth being placed along the same plane perpendicular to the main axis of the skull [H00*]; semilunate carpal block reduced or absent [H00*]; ischial foot absent [S97]; semicircular scar on posterior face of ischium {H00*]; long tibia & metatarsi; primitively, medium-sized predators.

Notes: **[1]** according to Holtz, *Stokesasaurus* and *Itemirus* are a separate clade, which shares very deep pockets on the lateral surface of the *basipterygoid process*. **[2]** the characters ascribed to [S97] are those which unite tyrannosaurs and Maniraptora. The characters ascribed to [H00*] are those which unite tyrannosaurs and ornithomimosaurs.

Links: Tyrannosauroidea (Tree of Life); Tyrannosauroidea (Mikko); tyrannosauroidea.htm; GEOL 104 Lecture 23- Theropoda II- Tyrants, ostrich mimics, and ...; Thomas R. Holtz, Jr..

References: Holtz (2000) [H00], Sereno (1997) [S97]. ATW021210.

Eotyrannus: *E. lengi* Hutt *et al.* 2001.



Range: Early Cretaceous (?Barremian) of Europe (England).

Phylogeny: Tyrannosauroidea: Tyrannosauridae + *.

Characters: ~5m (subadult); premaxilla small [H+01]; premaxilla anterior border almost vertical [H+01]; premaxilla taller than long [H+01]; maxillae with anterior portion laterally flattened [H+01]; maxilla having sharp lateral border with antorbital fossa [H+01]; maxilla ventral edge straight [H+01]; nasals fused [H+01]; nasals dorsally concave [H+01] **[1]**; quadrate robust [H+01]; dentary thin, internally flat, with parallel dorsal & ventral borders having a slightly convex outline in lateral view [H+01]; teeth with denticulations continuing across the crown [H+01]; premaxillary tooth row oriented more or less transversely [H+01]; premaxillary teeth smaller than lateral teeth & D-shaped in cross-section [H+01]; premaxillary teeth with serrated carinae [H+01]; premaxillary teeth with straight, conical roots [H+01]; maxillary teeth carinate, with anterior denticles smaller than posterior [H+01]; lateral teeth not laterally expanded [H+01]; neural spines low, transversely thin & extend entire length of centrum [H+01]; postzygapophyses directed posteriorly & flaring laterally to twice width of prezygapophyses [H+01]; anterior dorsal vertebrae with elongate centra, constricted at midlength and flared at ends [H+01]; dorsal centra shorten towards sacrum {H+01]; sacrals with pleurocoels; scapula strap-like, with distal expansion (if present) not preserved [H+01]; acromion and glenoid much wider than scapular shaft [H+01]; coracoid with circular glenoid facing posteriorly (??) [H+01]; boss-like coracoid tubercle present on ventral part of lateral surface [H+01]; arms fairly long; humerus 2/3ds length of scapula (23 cm) [H+01]; humeral head well-separated from shaft [H+01]; humerus with very large deltopectoral crest terminated abruptly at ~40% shaft length [H+01]; humerus with large internal cavity dorsally & smaller cavities ventrally just distal to deltopectoral crest [H+01]; carpals not reduced [H+01]; tridactyl hand [H+01]; Mc I very long (other Mcs incomplete) [H+01]; hands elongate (manus II is 95% of humerus length) and slender [H+01]; unguals also elongate, curved and laterally compressed [H+01]; hindlimbs gracile {H+01]; cnemial crest poorly developed [H+01] fibula with proximal crest & large foramen just distal to crest [H+01]; Mt II slender with expanded proximal head & medial facet for Mt III; Mt IV similar, with convex dorsal surface

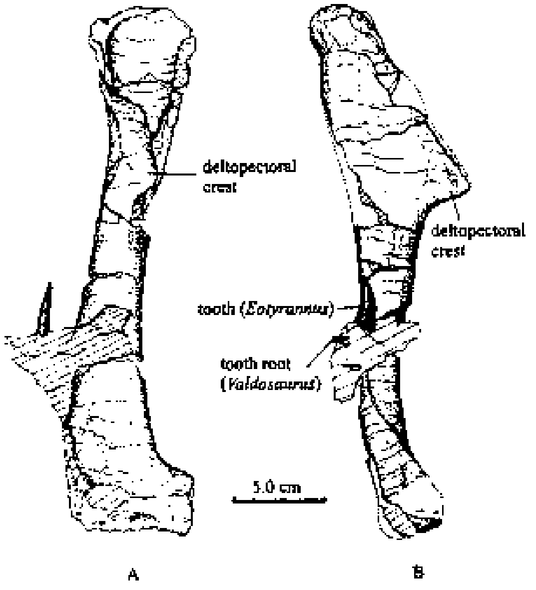


Figure 5. *Eotyrannus lengi* (MIWG 1997.550). Right humerus of *Eotyrannus lengi* in A, cranial, and B, lateral views. A single maxillary tooth of *E. lengi* and a tooth root of cf. *Valdosaurus* are attached to the matrix.

Notes: **[1]** it appears that the medial branch of the usual three-pronged posterior end of the nasal is longer than the lateral branches.

Image: Right: from Site-No-Di, by Mituse Komiyagi (I think). Left: from [H+01].

Links: DinoData Dinosaurs E079 EOTYRANNUS lengi; Eotyrannus Fact Sheet - EnchantedLearning.com; DinoWight- Eotyrannus, an Isle of Wight Tyrannosaurid; Eotyrannus lengi (Dutch); Eotyrannus attacking Hypsilophodon; Eotyrannus (Dutch); ???????-eotyrannus (Japanese); USATODAY.com - Ancestor of T-rex discovered in Britain; Isle of Wight & Natural History Museum Dinosaur Displays.

References: Hutt *et al*. (2001) [H+01]. ATW021210.

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checked ATW0**50619**

Coelurosauria: Tyrannosauroidea: Tyrannosauridae

Alectrosaurus

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
               |--Tyrannosauroidea
               |  |--Eotyrannus
               |  `--Tyrannosauridae
               |     |--Alectrosaurus
               |     `--Tyrannosaurinae
               `--Maniraptora
                   |--Therizinosauroidea
                   `--+--Alvarezsauridae
                      `--+--Oviraptorosauria
                         `--+--+--Troodontidae
                            |  `-
-Dromaeosauridae
                            `--AVES
```

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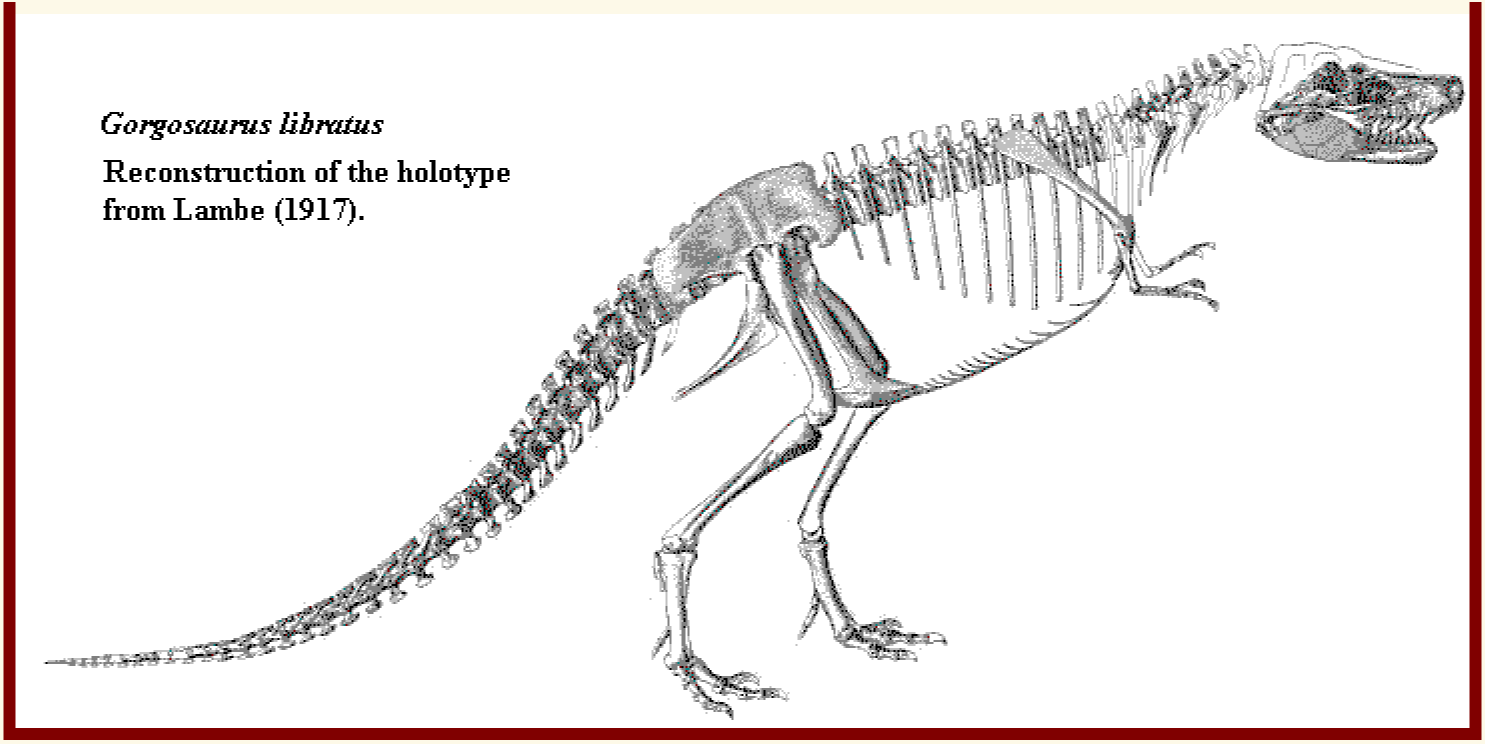
The Tyrannosauridae



Gorgosaurus libratus

Reconstruction of the holotype from Lambe (1917).

Considering the various lines of theropods, it is interesting that the most primitive forms have very long tails, long bodies, relatively small heads, short hind legs, and relatively large forelimbs. The later and more advanced types had relatively shorter bodies and tails, larger heads, larger hind legs, and (in the case of the giant forms) smaller and smaller forelimbs. This evolutionary trend reaches its culmination in the Tyrannosauridae of the late Cretaceous of the Asiamerican landmass.

At this time a narrow north-south seaway divided what is now North America into two large islands; the same thing happened in Asia. But a land-bridge linked east Asia (Mongolia, China, etc) with western North America. Apart from one very primitive form from India (then an island), it was only on this Cretaceous continent, called "Asiamerica", that the more derived tyrannosaurs are found .

Although old drawings of *Tyrannosaurus rex* give the beast an almost erect stance and a long reptilian tail, which dragged on the ground. This is now thought to be incorrect. Lambe's (1917) illustration at right was actually somewhat ahead of its time. In fact, in his description of *Gorgosaurus* he speculates that the animal dragged its tail little, if at all. It is now believed that back was held horizontally, as in other theropods (although the animal could likely rear up when the situation required); and the tyrannosaur tail was, as a proportion of overall length, the shortest of any large theropod. The fearsome eagle-taloned feet of the tyrannosaurs are also a myth; the claws on the hind feet were short, rounded, and hoof-like. All the killing was done by the huge jaws with their array of 15-centimetre steak-knife- like teeth. The power of these jaws has been the subject of a great deal of research, and was almost incredible. Think of a huge terrestrial Great White shark. The animal could bite out a wound a metre long and well over thirty centimeters deep and wide. Yet only with such ferocity could it possibly take on prey like the elephant-sized horned dinosaur *Triceratops* -- if it did. Jack Horner (and very few others) has strongly argues that the big tyrannosaurs were almost exclusively scavengers, using their obvious power to intimidate smaller killers, rather than hunting themselves. Recent work by John Hutchinson and others have suggested that *Tyrannosaurus* was a relatively slow animal. If correct, this would be consistent with a role as a Mesozoic extortionist, rather than a hunter.

One thing that is quite bizarre about the tyrannosaurs are their tiny little forelegs [1]. Despite their diminutive status, they clearly served some purpose, indicated by the the relative robustness of the arms and repeated stress fractures [2]. But generally, like ground-living large running birds, the big theropods would have acted more like huge flightless birds of prey than the overgrown bipedal lizards of popular imagination. Interestingly, after the extinction of the dinosaurs, a number of real flightless birds -*Diatryma*, *Phorusrhacos*, etc - took over the ecological niche of the theropods, becoming huge-headed, fast-running predators, 1.5 to 2 metres or more in height.

Although the derived tyrannosaurids have sometimes been divided into two subfamilies: the small primitive aublysodontines and the large tyrannosaurines, but the fragmentary material of the former means they might not constitute a valid taxon. In fact *Aubylson* is believed to be a misinterpretation of juvenile tyrannosaurine material. All are known only from fragmentary remains. They are based almost entirely on distinctive nose and ridged premaxilla teeth (in the front of the jaw). It has been plausibly argued that the teeth are just typical teeth of young tyrannosaurids.

Further, whilst *Aublysodon*-like teeth are fairly common and found in practically all horizons where tyrannosaurid body fossils are found, not one adult theropod skull is known from North America with such a tooth actually in place in a premaxilla. The best-known aubylsodont, the so-called "Jordan theropod" (*Aublysodon molnari* [Paul (1988)], = *Stygivenator molnari* [Olshevsky (1995)]), actually just a snout with some teeth, has been variously interpreted as Aublysodontine (Paul, Holtz), dromaeosaurid, and tyrannosaurid, but is most likely a juvenile (length about 3.8 meters, weight around 200 kg) specimen of *T. rex*. MAK990512 revised 121205

Tyrannosauridae or Deinodontidae?

When is Tyrannosauridae not Tyrannosauridae? Answer: when its Deinodontidae

Earlier, mention was made of Podokesauridae, the more correct senior synonym of Coelophysidae/Coelophysoidea.

Now it seems that the more correct term for Tyrannosauridae is Deinodontidae. To quote Matthew Martyniuk

> Deinodontidae (Cope 1866)...was in clear, widespread use through the mid 20th Century (as in Maleev 1955) and almost always treated as the senior synonym of Tyrannosauridae (Osborn 1905). However, Russel (1970) argued that Deinodontidae be abandoned, because he considered the type specimens of *Deinodon* (isolated teeth) not diagnostic, rendering the name a *nomen dubium*. However, the teeth are clearly diagnostic at the family level and possibly even genus and species, as they must have come from either *Daspletosaurus* or (more likely) *Gorgosaurus*, and the rocks those dinosaurs come from are well enough sampled to rule out the presence of a third large tyrannosaur species unless such compelling evidence is found. Similarly, it is questionable whether or not the pertinant ICZN rules allow for abandoning a name due to a dubious type genus. Even if this is the case, it is only followed sporadically in the literature, and many family names remain in use that are based on dubious type material, including Hadrosauridae, Ceratopsidae, and Troodontidae (the latter is also based exclusively on teeth of questionable diagnosability at the genus and species levels). Olshevsky (1991) recognized this, but argued that the name is still invalid because Cope initially spelled it Dinodontidae, and the name Deinodontidae was an emended spelling not published until 1914, after Tyrannosauridae. He concluded that therefore Deinodontidae (with an e) is a junior synonym and Dinodontidae (no e) is a *nomen oblitum*. However, Olshevsky's argument is incorrect because the ICZN clearly mandates that any family names based on misspellings or unjustified spelling changes of their type genus (Cope spelled the name Dinodon) can and must be emended by any subsequent revisor, and that this does not change the original authorship or date of the name (ICZN Article 35.4.1). Also, note that even if Deinodontidae and Deinodontoidea are ignored, several studies have found *Coelurus fragilis* to be a "tyrannosauroid", and so the next available name for that group after Deinodontoidea is Coeluroidea (Marsh 1881).

Were we to be totally consistent and rigorous, we would have to stop using Tyrannosauridae and replace it instead with Deinodontidae, (and Deinodontinae and Deinodontoidea. Or even, for that last, Coeluroidea). The present author for one (and I know I am not alone here) has never gotten over the loss of the marvellously imaginative *Brontosaurus* ("thunder lizard") in favour of that insipid *Apatosaurus* ("deceptive lizard"). And while "terrible tooth" is a cool name, it is still no substitute for "tyrant lizard". For this reason -, and while acknowledging it is not *technically* correct - we have opted to retain Tyrannosaur-inae/idae/oidea as the names for those Linnaean and Cladistic taxa, of which the great king of the tyrant lizards is both the nomenclatural and evolutionary culmination. - MAK120209

Notes

[1] The present author (MAK) had originally suggested that tyrannosaur forelimbs became smaller as the creatures evolved, and would have dissappeared entirely had their evolution not been cut short by the terminal Mesozoic catastrophe. Two inspirations for this claim were Greg Paul (1988) and Dougal Dixon (1988). However, a correspondent points out in an email (121202) that this hypothesis is not supported by more recent research. As he explains, "Of the genera ascribed to the family tyrannosauridae, Currie points out that the different genera have forelimbs of the same size (the exception of the rule is Tarbosaurus, which have forelimbs smaller than the "standard" size), (Currie 2003) although there can be some differences in hand bone proportions in different genera, as pointed out by Holtz 2004. One should also remember the morphological variation seen in animals of closely related, and even within the same genera....Gregory Paul also seems to have changed his view on the subject. He have told me (email November 2012) that larger sample size currently seems to speak for a forelimb size stable over geological time (rather than the idea of gradual forelimb reduction) and believe there are new unpublished data which might could settle the issue. "

[2] More on forelimb function comes from Lipkin and Carpenter 2008 who compared the forelimbs of different tyrannosaurids (*Gorgosaurus, Albertosaurus, Daspletosaurus* and *Tyrannosaurus*).

Descriptions

Tyrannosauridae: Definition: *Tyrannosaurus* + *Aublysodon*. Includes: *Alioramus, Aublysodon, Daspletosaurus, Tarbosaurus, Tyrannosaurus*.

Range: Early Cretaceous to Late Cretaceous of North America, Europe, Mongolia, North China and Japan [M99]

Phylogeny: Tyrannosauroidea: *Eotyrannus* + * **:** *Alectrosaurus* + Tyrannosaurinae.

Characters: Large head [C97]; skull akinetic, laterally compressed, boxy in lateral view [C97]; curved jaws (brings all teeth to bear at same time, as opposed to slicing -- compare Prosauropoda or *Coelophysis*); mandibular symphysis cartilaginous; ventral ramus of premaxilla taller dorsoventrally than long rostrocaudally [**$**H01a]; marked ventral curvature of maxilla [**$**H01a]; snout deep [C97]; nasals fused [C00] [**$** H01a]; nasals narrow caudally behind external nares; orbits large [C97]; possibly stereoscopic vision, at least in some [C97]; snout surface rugose [C00]; rugose dorsal, preorbital surface of lacrimals with bone "horn" in some species; prefrontals reduced [**$?**H01a]; lacrimal-frontal contact present; supratemporal fossa occupies at least the posterolateral third of frontal [**$**H01a]; well-developed sagittal crest on dorsal surface of parietals [**$**H01a]; lateral nuchal crest formed by parietals [**$?**H01a], jugal & quadratojugal deeply invade lateral temporal fenestra [CC00]; at least twice as tall as foramen magnum vertical height [C00]; quadrate height 40-50% of skull height at mid-orbit; quadrate and/or articular invaded by air sacs connected to middle ear [W97]; squamosal- quadratojugal flange intruding anteriorly into infratemporal fenestra, nearly contacting rostral margin [**$**H01a] [**$**MB89]; squamosal with large pneumatic space [W97]; pair of tab-like processes on supraoccipital wedge [**$?**H01a]; optic & olfactory nerve tracts enlarged [C97]; rostral portion of fused vomers expanded to greater than twice shaft width; in some, palatine dorsal surface without prominent muscular fossae [**$?**H01a]; air sinus in ectopterygoids is complex & reticulated [W97]; basisphenoidal sphenoidal sinus deep, with large foramina [**$?**H01a]; supradentary fused to coronoid, restricting lateral motion of intramandibular joint; caudal surangular foramen very large [**$**H01a] [**$**MB89]; retroarticular process of articular absent [**$**H01a]; premaxillary tooth row arcade more mediolaterally than rostrocaudally oriented [**$?**H01a]; premaxillary teeth incisiform, D- or U-shaped in cross-section with median ridge on caudal surface [C00] (or with two carinae "in same plane perpendicular to the skull axis" [**$?**H01a]); dentition heterodont; premaxillary teeth smaller than lateral teeth [**$**H01a]; incisiform premaxillary teeth; large, curved, serrated teeth; lateral teeth incrassate and capable of crushing bite [C00]; probable large wattle on neck [C97]; short, heavily-built neck [C97]; cervicals short & wide (shorter, stronger neck related to large head) [C97]; cervical air sacs pneumatize vertebrae at least as far anteriorly as 2nd cervical [W97]; neural spines short & robust (muscle & ligament attachments to support large head) [C97]; presacral centra axially short [C00]; body deep & short [C97]; gastralia from coracoids to pubis [C97]; distal caudal neural spines axially elongate (what does this mean?) [**$?**H01a]; forelimb reduced [**$**MB89]; scapula contributes more than half of the glenoid [**$?**H01a]; acromion expansion well-developed, more than twice scapula midshaft width [**$?**H01a]; scapular-humerus ratio between 2.2 and 2.5 [**$?**H01a]; humerus greatly reduced; femur-humerus ratio between 2.8 and 3.5 [**$**H01a]; radius, distal end flattened anteroposteriorly; fibular cranial tubercle distal to cranial expansion composed of two longitudinal ridges [**$**H01a]; distal carpals of adults poorly formed and lack trochlear surfaces [**$?**H01a]; metacarpal III very reduced and bears no digit [**$?**H01a]; manus with 2 digits [**$**MB89]; manus I curves away from II [C97]; pollex (I) ungual roughly equal to ungual of digit II in size; horizontal medial shelf from preacetabular blade to sacral ribs [**$?**H01a]; preacetabular notch on ilium [**$?**H01a]; broad ventral hook-like projection from preacetabular blade of ilium [**$?**H01a]; supraacetabular crest on ilium reduced [**$?**H01a]; dorsal surfaces of iliac blades very close to the midline [**$?**H01a]; ilium long, slight shorter than femur [**$?**H01a]; distal end of iliac pubic peduncle oriented horizontally; pubes with large "boot", about half as long as pubic shaft [**$?**H01a];

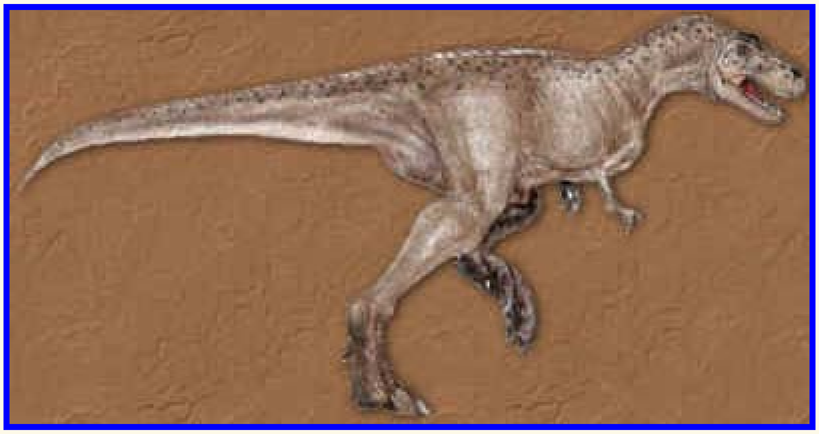
ischium shaft long but more slender and shorter than pubis [$?H01a]; pronounced semicircular scar on the anterolateral surface of the ischium, just distal to iliac process [$?H01a]; ischial foot absent (pointed tip) [$?H01a] [$MB89]; femoral anterior trochanter as tall as greater trochanter; lesser trochanter at least as tall as femoral head [$?H01a] (probably same as previous character); anterior and greater trochanter junction at distal end of anterior trochanter; long ascending process of astragalus [C97]; tibiae and metatarsi elongate relative to other theropods of same femoral length [$?H01a]; fibula with large, bipartite protuberance on anterior face, near proximal end [$MB89]; presence of an arctometatarsus (proximal end of metatarsal III reduced to a solid splint) [C00] [$?H01a]; dorsal surface of metatarsal III crescentic and restricted to distal portion of the metatarsal dorsal surface [$?H01a]; metatarsals II and IV contact at mid-shaft on plantar surface; 3 substantial forward pointing pedal digits with large claws; small round or hexagonal scales on tail.

Notes: [1] tooth fractures very common in this group, with distal crowns snapped off sometimes in the majority of teeth. The root was apparently retained in the mouth for considerable periods of time. This may be related to bone-crushing as a common practice [B97]. Particularly high degree of cranial bone pneumaticity may also be associated with crushing, as this allowed strong, but light bones having a considerable degree of flex in response to mechanical stress. [W97]. This differs from the construction of, for example, carnosaurs, which tended to solid bones but with considerable cranial kinesis. Thus, in carnosaurs, flexibility was achieved by permitting the bones to move relative to each other. In tyrannosaurids, the bones were fixed in position, but were designed to bend. [C97].

Links: Welcome to the UCMP T. rex Expo!; The Story and Contest of Dinosaur Stan the Tyrannosaurus rex; Discovery of a furcula ...; Tyranosaurids; Review of the Tyrannosauridae; Tyrannosauridae; Tyrannosaurids; What's the difference between Tyrannosauridae, Tyrannosaurinae, etc.?; Tyrannosauroidea; Tyrannosaurids.

References: Buchholtz (1997) [B97]; Carpenter (1997c) [C97]; Currie (2000) [C00]; Currie & Carpenter (2000) [CC00]; Holtz (2001), Mader & Bradley (1989) [MB89], Manabe (1999) [M99], Witmer (1997) [W97]. ATW060214.

Alectrosaurus: *A. olseni* Gilmore 1933.



Introduction: *Alectrosaurus* is a stand-in here for a poorly known clade frequently referred to as Aublysodontinae. *Alectrosaurus* itself was founded on a partial leg and some forelimb material, leftover gleanings from the Third Mongolian Expedition. The long arms are now believed to be unrelated portions of a therizinosaur [MB89]. However, these same forelimbs look a bit like the arms of *Eotyrannus* [H+01]. Perhaps this issue is worth a second look. There is not much phylogenetic distance between a basal tyrannosaurid and a basal therizinosaur. Perle referred additional material to this taxon in 1977. Thisreference has been accepted by some [e.g. H01a], but questioned by others [MB89].

Range: Late Cretaceous of China, Mongolia & Central Asia?

Phylogeny: Tyrannosauridae: Tyrannosaurinae + *.

Characters: ~5m? 8-9m?; long, low, sloping head [C00] [H01a]; nasals smooth [C00]; $ premaxillary teeth lacking serrations [C00] [H01a]; $ premaxillary teeth with prominent vertical ridges on lingual surface [H01a]; first 2-3 maxillary teeth incisiform [$H01a] [C00]; 17 maxillary & 19 dentary teeth (more than Tyrannosaurines) [C00] [H01a]; lateral teeth narrower & more blade-like than in Tyrannosaurinae [C00]; femur & tibia of about equal length [MB89]; femur, medial distal condyle with spike-like dorsal process [CT05]; tibia with stout, laterally curved cnemial crest [MB89]; distal tibia expanded laterally & flattened anteroposteriorly [MB89]; distal tibia with ridge articulating with groove on astragalus (as in all Tyrannosauridae) [CT05]; fibula with proximal end much expanded anteroposteriorly, with large concavity on medial surface [MB89]; fibula very thin below proximal expansion [MB89]; fibula anterior surface below proximal expansion with protuberance formed from 2 lateral ridges [MB89]; astragalus with strong ventrolateral buttress just proximal to trochlea [MB89] [CT05]; calcaneum taller than wide, narrow in anterior view [MB89] [CT05]; distal articular surfaces of metatarsals II & IV, and of most phalanges, elevated on pedicles [CT05]; Mt I much reduced (13% of Mt IV length) [MB89]; Mt II & IV unusually thin for length [MB89];

MtII with seep fossa for medial collateral ligament [MB89]; Mt III strongly compressed proximally (arctometatarsus) [MB89]; distal condyle of Mt III surrounded by a marked lip [MB89]; Mt V vestigial, laterally compressed & curves anteriorly at distal end [MB89]; phalangeal formula 23450 [MB89]; phalangeal collateral ligament fossae well-developed [MB89]; all phalangeal articulations hinge-like [MB89]; flexor tubules on pedal phalanges large and posteriorly extensive [MB89] pes III shorter relative to Mt III than in other tyrannosaurids [MB89].

Image: from Alectrosaurus.

Links: Alectrosaurus olseni; Paleontology and Geology Glossary; Alectrosaurus (Korean); Nanotyrannus; Gigadispute; Alectrosaurus Specimens.

References: Carr *et al*. (2005) [CT05]; Currie (2000) [C00]; Holtz (2001a) [H01a]; Hutt *et al*. (2001) [H+01]; Mader & Bradley (1989) [MB89]. ATW031029, revised ATW080117.

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Coelurosauria: Tyrannosauroidea: Tyrannosaurinae

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         |  |--Eotyrannus
         |  `--Tyrannosauridae
         |     |--Alectrosaurus
         |     `--Tyrannosaurinae
         |        |--+--Albertosaurus
         |        |  `--Gorgosaurus
         |        `--Tyrannosaurini
         `--Maniraptora
            |--Therizinosauroidea
            `--+--Alvarezsauridae
               `--+--Oviraptorosauria
                  `--+--+--Troodontidae
                     |  `--Dromaeosauridae
                     `--AVES
```

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Descriptions

Tyrannosaurinae: *Alioramus, Shanshanosaurus*

Range: Late Cretaceous (Campanian to Maastrichtian) of East Asia & North America

Phylogeny: Tyrannosauridae: *Alectrosaurus* + * **:** (*Albertosaurus* + *Gorgosaurus*) + Tyrannosaurini.

Characters: nasals rugose [$H01a]; frontals with posterior end laterally expanded [$H01a]; supratemporal fossa occupies posterolateral half of frontal [$H01a]; lateral nuchal crest formed by parietals present, at least twice as tall as foramen magnum vertical height; pair of tab-like processes on supraoccipital wedge; basisphenoidal sphenoidal sinus deep, with large foramina; vomers fused, with anterior portion expanded to greater than twice shaft width; palatine dorsal surface without prominent muscular fossae; supradentary fused to coronoid, restricting lateral motion of intramandibular joint; premaxillary teeth serrated [C00]; premaxillary tooth row more mediolaterally than anteroposteriorly oriented; maxillary tooth count <17 [C00]; maxillary & dentary teeth wide & tall [C00]; distal caudal neural spines axially elongate; acromial expansion well-developed, more than twice scapula midshaft width ("acromial expansion"?); scapula contributes more than half of the glenoid; scapular-humerus ratio between 2.2 and 2.5; metacarpal III very reduced and bears no digit; ilium long, slight shorter than femur; ilium with horizontal medial shelf from preacetabular blade to sacral ribs; ilium preacetabular blade with broad ventral hook-like projection; ilium with pronounced midline crest; supraacetabular crest on ilium reduced; pubic boot enlarged, approximately one-half pubis length; Ischium shaft long but more slender and shorter than pubis.

Notes: what appear to be group death assemblages are known for both *Albertosaurus* and *Tyrannosaurus*, particularly the former. This suggests that tyrannosaurines were at least sometimes gregarious. [C97].

Image: typical laterally expanded incisiform premaxillary tooth from a Japanese site.

Links: DinoData Classification Tyrannosaurinae; Further review of the tyrannosaurids; Tyrannosaurid Systematics; Untitled Document (Japanese); TYRANNOSAURIDAE (German).

References: Currie (1997a) [C97]; Currie (2000) [C00]; Holtz (2001a) [H01a]. ATW021212.

Albertosaurus: *A. sarcophagus* Osborn 1905.

Range: Late Cretaceous (Early Maastrichtian) of North America (Alberta) [H01a].

Phylogeny: Tyrannosaurinae:: *Gorgosaurus* + *.

Characters: 7.5-9.0m; premaxilla very broad & short; pro-maxillary fenestra well in front of the maxillary fenestra; maxillary fenestra higher than long; maxillary fenestra separated from antorbital fenestra by a thin bar of maxilla; moderate lacrimal horn; lacrimal horn oriented dorsally [**$?**H01a]; lacrimal horn anterior to descending ramus of lacrimal [**$?**H01a]; suborbital prong of postorbital prominent [**$?**H01a]; suborbital prong of postorbital anterior margin jagged [**$**H01a]; "orientation of occipital region caudoventral" [**$**H01a]; basal tubera reduced [**$**H01a]; basisphenoid foramina in sphenoidal sinus each lie in separate fossa [**$**H01a]; 2+ foramina on ventral surface of palatine [**$?**H01a]; ventral pocket of ectopterygoid chamber strongly reduced [**$?**H01a]; small surangular foramen; strong, forwardly inflected scapular blade; distal end of scapula expanded to more than twice midshaft width [**$**H01a] [CS01]; deltopectoral crest relatively large (reversal) [**$**H01a]; gracile tibia; femur to tibia length ratio over 1.0.

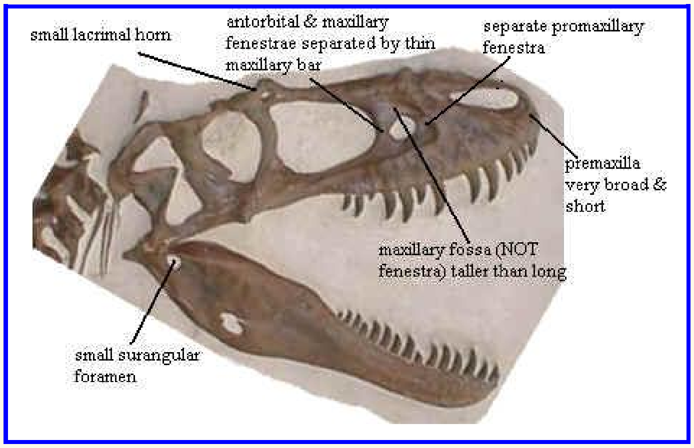


Image: (right) from CM Studio (left) adapted from Michael Corriss.

Links: **DinoData Dinosaurs A050 ALBERTOSAURUS;** Albertosaurus1 (carefully watch the quicktime movie & ask yourself whether you buy this sequence for a 2500 kg animal); Albertosaurus- Enchanted Learning Software (good discussion of the running problem); Albertosaurus; Albertosaurus ?????????; Dino Land Travels Database Field Museum- Albertosaurus; ALBERTOSAURUS; Morales Albertosaurus; Albertosaurus sarcophagus; Spotlight on Albertosaurus; Albertosaurus; Dinosaurios- Albertosaurio; Albertosaurus; Albertosaurus & Therapods; Wanted- Albertosaurus @ nationalgeographic.com; Albertosaurus; DinoNews.net - Le dinosaure Albertosaurus.

References: Carpenter & Smith (2001) [CS01]; Holtz (2001a) [H01a]. ATW030302.

Gorgosaurus: *G. libratus* Lambe 1914. May be a junior synonym of *Albertosaurus*, but the weight of current opinion is that the original designation of a separate genus was correct.

Range: Late Cretaceous (Late Campanian) of North America (Alberta). [H01a], [L17].

Phylogeny: Tyrannosaurinae:: *Albertosaurus* + *.

Characters: up to 9m; ***Cranial:*** head narrow & moderately elongate [L17]; maxilla ventral margin "irregularly undulating" [L17]; nasal suture to frontal with lateral projections extending more posteriorly than medial projections [**$?**H01a]; promaxillary fenestra close to the maxillary fenestra; promaxillary fenestra anterodorsal to maxillary fenestra in adults [**$**H01a]; maxillary fenestra oval and separated from the antorbital fenestra by a wide bar of the maxilla; lacrimal horn anterior to descending ramus of lacrimal [H**$?**01a]; postorbital contacts lacrimal below orbit [**$?**H01a]; ventral pocket of ectopterygoid chamber strongly reduced [**$?**H01a]; ***Mandibular:*** surangular foramen present [L17]; ***Dental:*** 4 premaxillary teeth [L17]; premaxillary teeth typical tyrannosaurid (D-shaped, carinae, etc.) [L17]; 13 maxillary and 14 dentary teeth [L17]; first maxillary tooth incisiform [**$?**H01a] [L17]; other lateral teeth with anterior and posterior carinae (carinae serrated over entire length) laterally expanded [L17]; teeth replaced alternately, with new teeth arising medially, then displacing old root [L17]; ***Axial:*** vertebrae slight amphicoelous [L17]; vertebrae concave both laterally and ventrally [L17]; 11 dorsals, 5 sacrals & ~34 caudals [L17]; neural spines short [L17]; cervical neural spines excavated front & back, positioned posteriorly on centrum [L17]; cervical *zygapophyses* on robust processes [L17]; *parapophyses* directed posteroventrally from below prezygapophysis base [L17]; cervical ribs double-headed [L17]; posterior cervical ribs greatly elongated with large thin base and long complexly curved distal extremity (see image above) [L17]; dorsal diapophyses broad, well up on arch, directed dorsolaterally & somewhat posteriorly [L17]; dorsal *diapophyses* reinforced by thickened lamina of bone [L17]; dorsal neural spines increase length towards sacrum [L17]; dorsal neural spines extended anteriorly & posteriorly with medial lamina which may fuse to adjoining spine [L17]; dorsal vertebrae medial laminae terminally rugose, with numerous foramina & channels (ligaments?) [L17]; thoracic ribs double-headed, long & robust [L17]; thoracic rib heads straight & axially flattened between vertebral attachments [L17]; long, robust gastralia, distally elongated with "supplementaries" [L17]; gastralia meeting and overlapping on the ventral midline [L17]; gastralia continuous with thoracic ribs, forming almost unbroken band around entire abdomen [L17]; tail about half total length [L17]; caudal vertebrae with transverse processes ending with 14th caudal [L17]; distal caudals strongly interlocked with greatly elongated prezygapophyses [L17] **[3]**; chevrons intervertebral, with shape changing radically in distal vertebrae as shown in the image [L17]; distally, caudal centra lengthen, ventral concavity increases, prezygapophyses elongate, spines become lower [L17]; ***Forelimb:*** scapula strap-like & expanded at both ends [L17]; scapula acromial process very deep; coracoid plays relatively minor role in glenoid [CS01] [L17]; glenoid long, relatively narrow, with strong anterior rim [L17] but poorly developed medial wall [CS01]; glenoid rectangular [CS01]; notch in lateral margin of glenoid along scapula-coracoid suture [CS01]; coracoid thin, broad & roughly rectangular [L17]; forelimbs very small, ~25% length of hindlimb [L17]; humerus twice length of ulna [L17]; proximal humerus posteriorly concave [L17]; ulna triangular in cross section proximally [L17]; "stout *olecranon* process" [L17] **[5]**; radius somewhat rectangular in cross-section [L17]; 5 carpals, all small, rounded, flattened & relatively featureless [L17]; vestigial Mc III present [L17]; Mc I very short [L17]; metacarpal distal articular surface consisting of simple groove [L17]; manus phalangeal formula 23000, including unguals [L17]; phalanx I1 with twist along long axis [CS01]; phalanx I1 same length as McII [**$**H01a]; phalanx I2 much longer [L17]; ***Hindlimb:*** robust [L17]; ilium elongate, plate-like, with flat dorsal surface in lateral view and rounded ends [L17]; ilium longer anterior to *acetabulum* than posterior [L17]; *pubic peduncle* and region above acetabulum particularly massive [L17]; dorsal margin of ilium, both lateral & medial surfaces heavily marked by muscle attachments [L17]; pubis expanded posteriorly for broad articulation with ischium [L17]; pubic symphysis (not fused) at about 1/2 shaft length [L17]; large pubic foot, extending further posteriorly than anteriorly [L17]; prominent muscle scar on dorsal surface of ischial shaft [L17]; ischial foot absent [L17]; femur and tibia about same length [L17]; femoral head well set off from shaft [L17] **[6]**; greater trochanter continuous with head, but separated from lesser trochanter by deep groove [L17]; lesser & 4th trochanter both well-developed [L17]; tibia relatively robust; tibia angles forward distally [L17]; tibia with heavy muscular attachment process on proximal, anteromedial surface [L17]; large cnemial process on anterolateral surface [L17]; fibula small, with proximal expansion [L17]; astragalus with very broad ascending process [L17]; metatarsals long, with Mt III 2/3rds as long as tibia [L17]; arctometatarsus present [L17]; pes phalangeal formula 23450 [L17].

Notes: [1] There is considerable confusion about this taxon. For most of its history, it was treated as a junior synonym of *Albertosaurus*. Currently, it is treated as a separate genus. However, it is uncertain whether *Gorgosaurus* and *Albertosaurus* make up a clade, or whether they are separate branches from the main line of tyrannosaur evolution [H01a]. One of the difficulties is that most of the skull of the holotype was crushed and useless. **[2]** Lambe's original description in 1914 identified the manual digits as II & III (actually I & II). He corrects this error in his 1917 description. **[3]** Note how tightly the caudals would have been locked together, particularly in the distal tail. The distal half of the tail was probably a rigid, rod-like structure, held together not only by thetight zygapophyseal articulations, but by the beveled edges of the centra and the "stapling" effect of the intervertebral chevrons. Likely the tail could not have been dragged on the ground, even if the animal had wished to do so. **[4]** Another remarkable feature is the continuous abdominal armor of gastralia plus thoracic ribs. At least anteriorly, *Gorgosaurus* was almost literally barrel-chested, with the entire anterior abdomen and sides protected by a continuous hoops of bone. It is quite possible that this construction was necessary for protection, not against prey, but against the risk of falling, as discussed on a previous page. These springy bone hoops might have done much to absorb the shock of impact. Lambe also speculates that this elastic system might have served some respiratory function, which sounds reasonable, if speculative. In any event, he notes that the ribs were constructed so as to lock together when pushed, pulled or impacted, which would have served a shock-absorbing function all the better. **[5]** This is not at all clear -- either from the figures or the measurements of the bones given by Lambe. **[6]** Lambe notes that the curvature of the femoral head splayed the femur out, while compensating asymmetry of its distal condyles would have directed the shank medially. The net result was that *Gorgosaurus* was "bow-legged" but would have walked erect, not sprawled.

Images: all images from [L17].

Links: DinoData Dinosaurs G043 GORGOSAURUS; Gorgosaurus Fact Sheet - EnchantedLearning.com; GORGOSAURUS; Gorgosaurus (Dutch); gorgosaurus; Gorgosaurus; Webshots Community - Gorgosaurus libratus; All Gorgosaurus Gus Photos Photos; Media Information; Gorgosaurus libratus; Photographer Darren Tanke; Albertosaur Systematics.

References: Carpenter & Smith (2001) [CS01]; Holtz (2001a) [H01a], Lambe (1917) [L17]. ATW021216.

A *Gorgosaurus* Gallery: annotated figures from Lambe (1917)

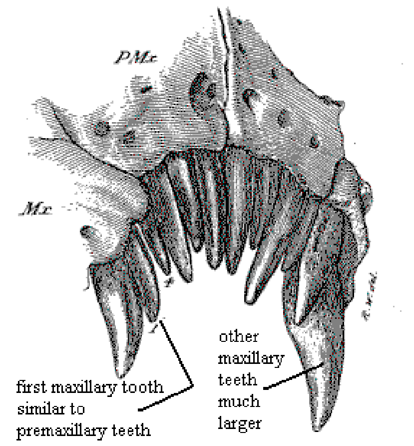
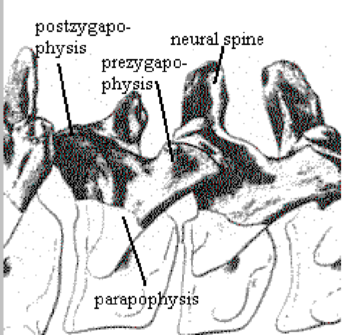
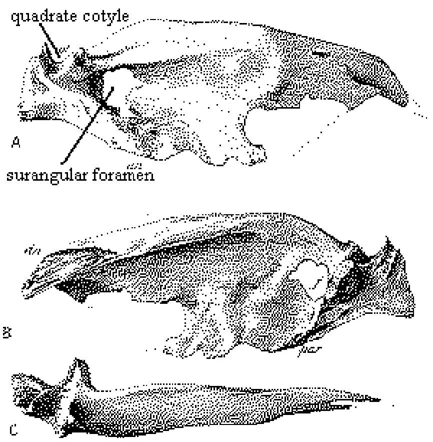


Figure 12. Premaxillary teeth of the type of *Gorgosaurus libratus*; anterior aspect ½ natural size. *Mx*, maxilla; *PMx*, premaxilla; 1, first maxillary tooth; 4, fourth premaxillary tooth.



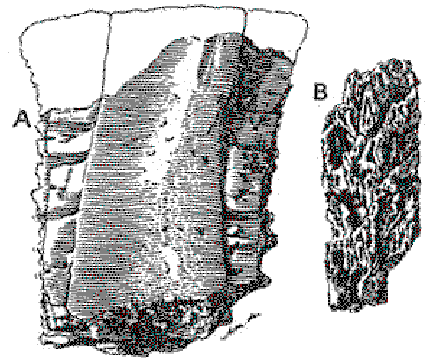
Gorgosaurus: cervical vertebrae V & VI in right lateral view

The cervical vertebrae were exposed on the surface, and only the neural arches remained. The centra shown above are Lambe's reconstruction.

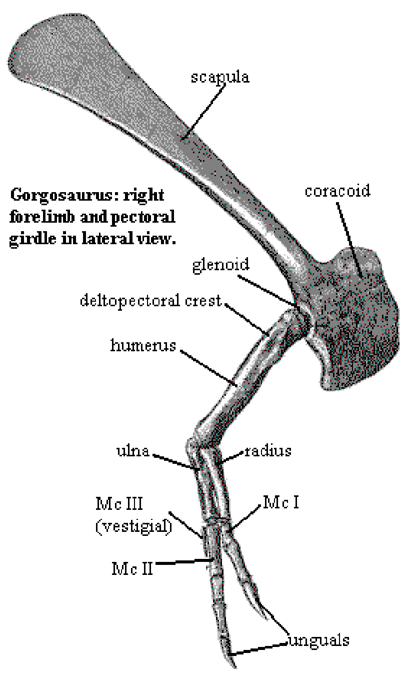


Gorgosaurus: surangular articular complex in lateral, medial and dorsal views. From Lambe (1917).

We are not skilful enough to describe the geometry of the surangular-articular complex properly. Accordingly, we have included Lambe's figure and the reader is left to her own devices.

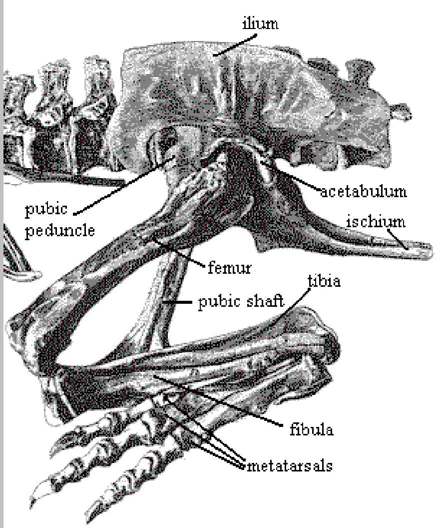


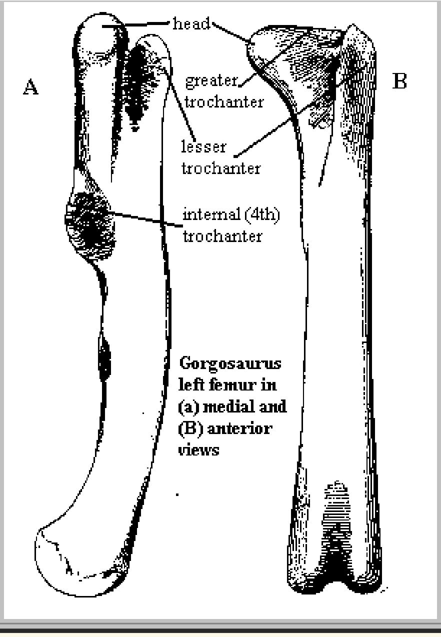
Detail of dorsal neural spine in (A) left lateral and (B) anterior views. The medial laminae sometimes fused to those of adjacent vertebrae.



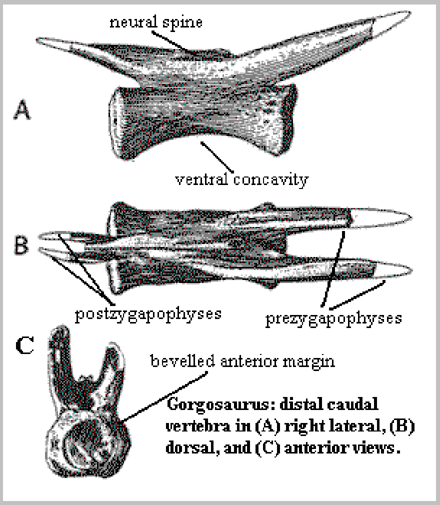
Gorgosaurus: right forelimb and pectoral girdle in lateral view.

Gorgosaurus left hindlimb and pelvic girdle

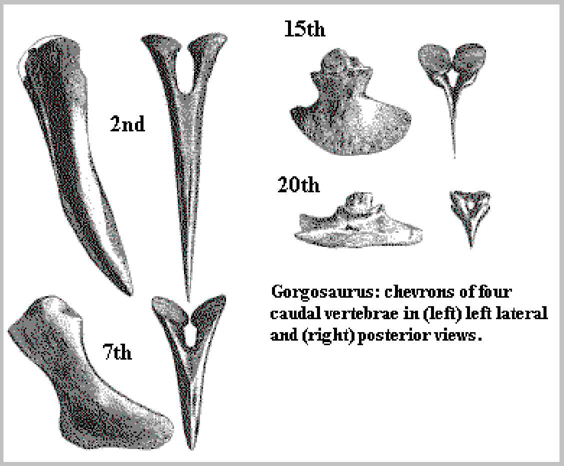




Gorgosaurus left femur in (a) medial and (B) anterior views



Gorgosaurus: distal caudal vertebra in (A) right lateral, (B) dorsal, and (C) anterior views.



Gorgosaurus: chevrons of four caudal vertebrae in (left) left lateral and (right) posterior views.

Tyrannosaurini: Definition: *Tyrannosaurus* > (*Albertosaurus* or *Gorgosaurus*). Includes: *Daspletosaurus, Dinotyrannus?, Tarbosaurus, Tyrannosaurus*.

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

Phylogeny: Tyrannosaurinae: (*Albertosaurus* + *Gorgosaurus*) + *.

Characters: lacrimal horn absent; widely expanded occiput relative to snout width resulting in orbits having a forward-pointing component; ventrally deflected occipital condyle; intramandibular joint frozen by (a) supradentary overgrowing joint and fusing with coronoid (b) long process of prearticular articulating with both coronoid & splenial, (c) angular anterior process bridges gap ventrally; and (d) supradentary sends ridges between the teeth [HC00].

Links: Re- Dwarf Tyrannosaurs; Re- Tyrannosauridae; What's the difference between Tyrannosauridae, Tyrannosaurinae, ...; Nanotyrannus; Gigadispute..

References: Hurum & Currie (2000) [HC00]. ATW030425.

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checked ATW030425

Coelurosauria: Ornithomimosauria

Ornithomimus

Abbreviated Dendrogram

```
DINSAUROMORPHA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
               |--Tyrannosauroidea
               `--+--Coelurus
                   `--Maniraptoriformes
                      |--Ornithomimosauria
                      `--Maniraptora
                         |--Therizinosauroidea
                         `--+--Alvarezsauridae
                            `--+-
-Oviraptorosauria
                               `--+--+-
-Troodontidae
                                  |    `-
-Dromaeosauridae
                                  `--AVES
```

Contents

Taxa on this Page

1. Ornithomimosauria X

Descriptions

Ornithomimosauria: *Ornithomimus*, *Gallimimus*. Used here as *Ornithomimus* > real birds (i.e. = Arctometatarsalia)

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

Phylogeny: Maniraptoriformes **:** (*Ornitholestes* + Maniraptora) + *.

Characters: Gracile, cursorial, with (moderately?) long neck and tail; **$** enlarged, beak-like premaxilla; premaxilla with long posterior process separating maxilla from nasal [H+01]; long, shallow snout formed dorsally by elongated nasal; nares at tip of snout between premaxilla and nasal; elongated antorbital fossa with 2-3 fenestrae; very large orbits; bone capsule of unknown function at base of braincase; braincase and overlying frontals are strongly domed, sloping forward smoothly on the frontals and nasals and back sharply on parietals; postorbital skull short; squamosal with pneumatic recess [H00*]; lower temporal fenestra reduced; in derived species, quadrate slopes anteroventrally, lower jaw is offset anteriorly and articulates below the orbit (which might just explain the mystery capsule); **$** secondary palate created by maxilla and premaxilla; toothless in almost all species; premaxillary teeth incisor-like with both carinae of each tooth being placed along the same plane perpendicular to the main axis of the skull [H00*]; teeth, where present, lack serrations [H+01]; vertebrae 10+13+5-6+<40; caudals moderately elongated, with low spines & short ribs fused to centra; dorsals with taller spines; caudals have transverse processes proximally which apparently retrovert (and articulate?) distally; large pectoral girdle with especially large coracoid bearing posteroventral process & large tubercle for biceps; clavicles unknown & girdle may be mobile; sternum in 1 species.; **$** gracile, straight humerus with reduced deltopectoral crest [H+01]; ulna & radius adhere distally; carpals flat, reduced & perhaps could not flex;semilunate carpal block reduced or absent [H00*]; **$** long hand; **$** metacarpals equal length; **$** same for digits; **$** unguals straight, with weak flexor tubercles [H+01]; strongly probubic, with pubes fused;semicircular scar on posterior face of ischium {H00*]; tibia elongate [H+01]; **$** metatarsus elongated to ~80% length of tibia; **$** short, stout pedal digits; pes V absent [$MB89].

Note: **[1]** Ornithomimosaurs are often said to "resemble an ostrich," however the posture was quite different as currently reconstructed. **[2]** A recent report in **Nature** (Aug. 30, 2001) announces the discovery of keratinous beak fragments in *Gallimimus* suggesting a filter-feeding adaptation similar to a duck. **[3]** There is ongoing debate about whether some species were herbivores. The recent discovery of gastroliths is a strong argument in favor of this idea. **[4]** Characters ascribed to [H00*] are those which unite ornithomimids and tyrannosaurs.

Links: DD: Ornithomimosauria; Harpymimus; Garudimimus; Gallimimus; (all 3 from the high-quality Nakasato Museum site); ornithomimosauria cladogram; Gallimimus (life reconstruction); Ornithomimidae; VPTHEROPOD; Ornithomimosauria ; ; Untitled Document (Hungarian).

References: Holtz (2000) [H00], Hutt *et al*. (2001) [H+01], Mader & Bradley (1989) [MB89]. ATW 020128.

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checked ATW050619

Coelurosauria: Maniraptora

Troodonts, Oviraptors, Therizinosaurs & Dromaeosaurs

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--Metornithes
                  |--Alvarezsauridae
                  `--+--Oviraptorosauria
                     `--Paraves
                        |--Deinonychosauria
                        |   |--Troodontidae
                        |   `--Dromaeosauridae
                        `--AVES
```

Contents

Taxa on This Page

1. Maniraptora

Descriptions

Maniraptora: Maniraptoriforms closer to Daffy Duck than to *Ornithomimus*.
Padian *et al.* (1999).

Range: Early Cretaceous-Late Cretaceous of China & North America. Birds > bird mimics, *i.e.* Neornithes > *Ornithomimus*. Holtz (1996a).

Phylogeny: Maniraptoriformes: Ornithomimosauria + (*Ornitholestes* + * **:** Therizinosauria + Metornithes)

Characters: **$** prefrontal reduced or absent; distal 3/4 of tail stiffened; **$** enlarged sternum; **$** furcula present (? plesiomorphy?); **$** lateral shoulder joint; **$** arm 75%+ of presacral vertebral length; **$** bowed ulna; enlarged semi-lunate carpal; **$** enlarged manus digit 3; laterally flattened hand claws(?); some groups with retroverted pubes; no anterior expansion of pubic boot; **$** ischium <2/3 length of pubis; distal obturator process on ischium; anterior trochanter near or confluent with proximal end of femur; hyperextendable second digit of the foot, with enlarged ungual; feathers with vanes (?!).

Links: DD: Maniraptora; Maniraptoran Dinosaurs!; Avimimus; Selected Synapomorphies; theropods; maniraptora; Case for Maniraptorid Tyrannosaurs; A New Dinosaur Specimen With Feather-like Structures; Evolution, dinosaurs, BAND, BAMM, BCF, 2F, Cladistics, Birds, Secondary, Flightlessness, Archaeopteryx; The Theropod Ancestry of Birds; taxonomy; Coelurosauria - Paleontology and Geology Glossary.

Image: "Avimimids and Troodontids" © 2000 byDan Bensen and reproduced by permission. Key: from top left to bottom center: *Avimimus portentosus*, (*Kakuru kunjani*), *Sinornithoides youngi*, *Byronosaurus jaffei*, (*Borogovia gracilicrus*), *Troodon formosus*, (*Tochisaurus nemegtensis*), *Saurornithoides mongoliensis*, (*Saurornithoides asiamericus*), (*Saurornithoides isfarensis*), (*Saurornithoides junior*). Parentheses indicate reconstructions based upon scanty evidence.

Notes: The membership of this group, as well as its characteristics, is fairly unclear.

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checkedATW040810, revised MAK120307

Maniraptora : Therizinosauria

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauria
               |  |--Falcarius
               |  `--Therizinosauroidea
               |     |--Beipiaosaurus
               |     `--+--Alxasaurus
               |        `--Therizinosauridae
               `--Metornithes
                   |--Alvarezsauridae
                   `--+--Oviraptorosauria
                      `--Paraves
                         |--+--Troodontidae
                         |    `--Dromaeosauridae
                         `--AVES
```

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1. *Alxasaurus* X
2. *Beipiaosaurus* X
3. *Falcarius* X
4. Therizinosauria X
5. Therizinosauridae X
6. Therizinosauroidea X

Descriptions

Therizinosauria. *Falcarius*

Synonyms: Segnosauria Barsbold & Perle 1980, Segnosaurischia Dong 1992, Therizinosauridae Sereno 1998

Phylogenetic Definition: The most inclusive clade containing *Therizinosaurus cheloniformis* but not *Tyrannosaurus* *rex*, *Ornithomimus edmontonicus*, *Mononykus olecranus*, *Oviraptor philoceratops* or *Troodon formosus* (stem-based) (Zanno 2010)

Range: Cretaceous of NAm & East Asia

Phylogeny: Maniraptora **:** Metornithes + * **:** *Falcarius* + Therizinosauroidea).

Kirkland et al., 2005

Horizon: Lower Yellow Cat member of the Cedar Mountain Formation (Barremian), Utah

Phylogeny: Stem Therizinosauria.

Comment: Known from over 3000 complete or partial elements have been collected from the holotype locality, representing a mass death assemblage of hundreds of individuals in various growth stages, which makes *Falcarius* the most complete therizinosaurian yet found (Zanno 2010). A lightly built animal about 4 meters long, with a long neck and small head; unusually for theriznosaurs, the tail is very long The most primitive and ancestral therizinosaur yet known, it reveals the transition from primitive carnivory (a long-bodied small-headed, rather typical coelurosaur, think *Coelurus* or *Ornitholestses*) to herbivory (in this instance, the upright, short-tailed, ground sloth-like therizinosaurs).

Image: *Falcarius utahensis*, Utah Museum of Natural History. Photo by Paul Fisk, via Wikipedia, Creative Commons Share Alike

Links: Falcarius: bizarre sickle-cutter - Scott Hartman; Falcarius, Killer Dinos Turned Vegetarian - Utah Geological Survey; Dinosaur embraced vegetarianism : Nature News; Falcarius - Wikipedia MAK120307

Therizinosauroidea (=Segnosauria)

Range: Early Cretaceous (Barremian) - Late Cretaceous (Maastrichian) of China & North America.

Phylogeny: Therizinosauria **:** *Falcarius* + * **:** *Beipiaosaurus* + (*Alxasaurus* + Therizinosauridae).

Characters: 2-8 m long, <100-2000 kg; head unusually small; ant jaws toothless and form bill structure; teeth small, se , slightly flattened and (**$**) bulbous; braincase and vertebrae pneumatized; neck long and light; **$** cervicals elongate (?) and highly pneumatized, with **($)** widely-spaced zygapophyses; anterior dorsal vertebrae with tall neural arches; dorsal ribs flat & broad; 5-6 sacrals; tail somewhat short, anteriorly massive; scapula strap-like; large coracoid; forelimbs elongated; humerus massive with expanded ends in some spp; conspicuous, sharply peaked deltopectoral crest posteromedially on humerus (not all spp); manus variable, but generally large and bearing long claws, curved or uncurved; **$** very broad pelvis; ilia widely separated; ilia very deep above acetabulum and flare laterally; postacetabular ilia are short, with unique knob-like protruberances; pubes retroverted (*i.e.* opisthopubic); tibia 80%+ length of femur; fibula slender & closely appresed to tibia; **$** short metatarsus (<1/3rd length of tibia); broad, short, (**$**) 4-toed feet; foot claws (unguals) pointed, curved and laterally compressed; proximal end of 1st metatarsus reaches tarsus (?). Possible herbivores, and general form converges on prosauropods.

Links: DD: Therizinosauridae; Literature - Segnosauria; DIM - number 12; A therizinosauroid dinosaur with integumentary structures from China; Untitled Document; DGF, Geological Society of Denmark, Geologisk Tidsskrift Nr. 4, 1996.

Note: possibly originated in Central Asia. 010619.

Discussion: Greg Paul's reconstruction shows visually how weird these creatures truly were – so odd that for some years they were thought to be a Cretaceous relict of an early prosauropod lineage. In many ways, the Therizinosaurs do resemble some aberrant sauropodomorph. In other ways they are just as clearly Theropods. The head best illustrates this mixture. The skull is small, although not any smaller than that of reasonably close relatives, such as the Ornithomimosaurs. The front of the snout is usually curved downward. The front of the jaw is sometimes described as "bill-like," but there is little in the way of lateral expansion. Perhaps it is more like the offset jaw articulation of prosauropods -- designed to create a moving point of contact rather than single tearing force as in carnosaurs. The front of the jaw lacks teeth, which is a bit hard to explain. However, we have little idea what "soft" keratinous structures might have been present, such as a sharp tearing beak. The teeth, especially those in front, are somewhat chisel-like with a constricted base. This might be interpreted as the beginnings of a convergence toward the leaf-shaped teeth of sauropods. The teeth are also very numerous, recalling the beginnings of Ornithischian dentition, and are supplemented by sharp, curved denticles. This would be hazardous duty for a tongue! The back teeth are of a more indeterminate small-theropod grade. On the whole, the back teeth seem designed to cut or hold, while the front teeth sheared and the beak, if any, cut -- a real chimera.

The head is highly pneumatized and mounted on neck vertebrae which were also full of air holes. However the neck differs markedly from sauropods in that it is not heavily reinforced and was probably quite mobile. There are no exaggerated zygapophyses, interlocking caudal ribs or ossified tendons which would have held the neck rigid. The individual vertebrae are not elongated. These features suggest a relatively vertical posture, because there is no obvious way to hold the neck horizontally without continual muscular effort.

This impression is confirmed by the angled pelvis and general back-heaviness of the body. The arms are relatively slender, but long and probably heavily muscled. Both the large coracoids and the marked deltopectoral crest on the humerus suggest this, as do the enlarged ends of the arm bones. In fact, the thin central shaft of the humerus is the most difficult part of the arm to explain: perhaps a savings in weight at the expense of tensile strength. The enormous claws, particularly of *Therizinosaurus*, are also difficult to interpret. They seem almost too large for digging, and in *Alxesaurus* they are only slightly curved, a feature which would preclude digging against ordinary earth. One might speculate that these animals lived in a more arid, sand-dominated environment. Alternatively, the claws may have been specialized to strip bark or fronds from some locally common type of vegetation.

The pelvis is equally strange: enormously deep and wide, solidly fused to 5 or 6 vertebrae. The leg proportions tell us that this was no runner. Yet the pelvis would permit the attachment of huge leg, and possibly tail, muscles. The reversed pubic bones suggest additional room for the typical herbivore gut. However, as Paul has illustrated, a large gut hangs almost to the ground in the anticipated semi-vertical posture. At the same time, Therizinosaurs seem to have the classic dinosaur perforated acetabulum (the socket in the pelvis where the leg fits) with the back legs originating fairly close to the mid-line. Frankly, it is almost impossible to see how this arrangement of parts would fit together. Paul solves the problem by angling the femur about 20 degrees out from the mid-line. This leaves the femoral head at a reasonable place and angle to fit in the socket, but gives the animal an absolutely bizarre gait, something like a sumo wrestler -- very stable but not at all graceful. The feet are blocky and short, with an unusual 4 digits: not the usual sort of digging leg, which is longer. However, the probable short, curved claws would make good digging tools.

One possible reconstruction is, again, that Therizinosaurs were essentially desert animals. The gait, large, square feet and very low center of gravity all contribute to generate great stability on uncertain, shifting surfaces. Additional balancing adaptations might be the long mobile arms, as well as the relatively large brain. The bulbous body shape minimizes surface area. The hands and feet might be capable tools for digging in loose or sandy soil for roots, for extracting small lizards or mammals, or for splitting the tough exterior of typical desert plants while avoiding any sharp protective spines or scales. The relatively short tail reflects that tails are a less adequate method of achieving balance in a more-or-less upright posture, since the tail's reduced horizontal distance from the center of gravity also reduces the effect of torque. The small gastroliths found in the gut of some therizinosaurs might evolve simply from the necessity of doing something with the sand and gravel inevitably eaten with a diet of roots or burrowing desert animals. Undoubtedly, there are other plausible reconstructions, but it is interesting to imagine a small group of therizinosaurs plodding slowly over a dune near sunrise, their crested heads lurching and darting about, perhaps covered in white feathers to reflect the sun, stopping occasionally to dig up roots or excavate the burrows of unlucky mammals, making their endless rounds of widely scattered or seasonal oases. ATW 010619.

Note added in Disproof: Russell & Dong (1993) note that there is an "association between therizinosaurids and relatively moist (fluvial and lacustrine) environment Asia." This generalization may hold up with *Beipiaosaurus* as well, since this early therizinosauroid was found in the notably lake-dominated Yixian. Xu *et al.* (1999). So its back to the drawing board on the ecological restoration in this Note, although the mechanical analysis still seems to hold up.

References: Currie (2000), Russell & Dong (1993); Xu *et al.* (1999).

Beipiaosaurus

Range: Early Cretaceous (Barremian) of China.

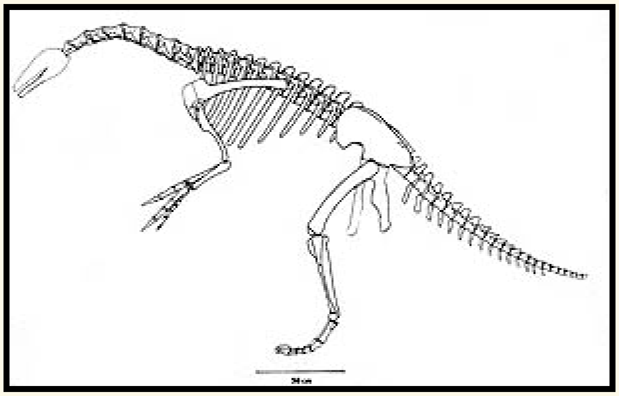
Phylogeny: Therizinosauroidea: (*Alxasaurus* + Therizinosauridae) + *.

Characters: ~2 m; **$** largest skull of Therizinosauroidea and (**$**) shortest, most bulbous tooth crowns; >37 teeth, with dorsally pointed, triangular interdental plates; cervical vertebrae with small, short spines; "fused posterior dorsals" (= pygostyle?); furcula widely arched; hpocleidium absent; semilunate distal carpal present; long hand (10% longer than femur); several features of hand said to be same as *Deinonychus*; manual unguals laterally comperssed & strongly curved; ilium with shallow anterior iliac process (similar to that of dromaeosaurs?); posterior andanterior processes of ilium equal; hindlimb short & stout; crest on the tibia; medial surface of fibula flat, without medial fossa; metatarsals III & IV compressed proximally; Mt V slender & strap-like; feet with three functional toes and splint-like proximal 1st metatarsal; integument with "proto-feather" filaments 5-7 cm in association with limbs; filaments contact bones; Xu *et al.* report possibly hollow and branching at ends.

Links: DD: BEIPIAOSAURUS inexpectus; DIM - number 1; theropode.pdf; Beipiaosaurus -- The Dinosauricon; Beipiaosaurus; Beipiaosaurus (Dutch); Dann Pigdon's Paleo Gallery @ Prehistorics Illustrated page 07; Dinosauria Translation and Pronunciation Guide B; Nieuwe therizinosauride (Dutch); Untitled; New feathered dinosaur found; Beipiaosaurus Fact Sheet - EnchantedLearning.com; *Beipiaosaurus* Recapitulated; A therizinosauroid dinosaur with integumentary structures from China.

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

Alxasaurus (= Alxasauridae)



Range: mid-Cretaceous (Albian) of China.

Phylogeny: Therizinosauroidea:: Therizinosauridae + *.

Characters: 4 m; 380 kg; >40 very small teeth on dentary; teeth extend to front of jaw; interdental plates probably present; cervical neural spines small & narrow; zygapophyseal articulations broad; centra amphiplatyan; cervical ribs not fused; 5 sacral vertebrae; short tail, but 13 caudal vertebrae with transverse processes; scapular blade very long and slender with little distal expansion; coracoid probably circular; arms slender & very long; relatively small deltopectoral crest on humerus; ~70 cm manual unguals; elongate ilium with moderate preacetabular expansion; femoral shaft slightly bowed; large, keeled "posterior" (prob. = greater) trochanter separated by cleft from "anterior" (lesser) trochanter; 4 functional toes.

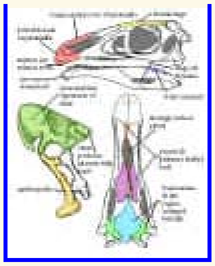
Links: DD Alxasaurus; Alxasaurus Printout- ZoomDinosaurs.com; Alxasaurus -- The Dinosauricon; Alxasaurus; PANGEA (Italian); DinoDictionary.com | A - Dinosaurs Page 2.

References: Currie (2000); Russell & Dong (1993).

Image: *Alxasaurus* reconstruction from Russell & Dong (1993).

Note: Russell & Dong diagnose *Alxasaurus* and the Alxasauridae by a number of features. However these are, as they state, almost certainly plesiomorphic. Thus, it may not be wise to recognize a separate family at this point based on a diagnosis which will almost certainly take in a paraphyletic group of stem therizinosauroids. 010619.

Therizinosauridae: *Erlikosaurus, Segnosaurus, Therizinosaurus*.



Range: Late Cretaceous (Cenomanian - Maastrichian) of China, Mongolia, & Central Asia.

Phylogeny: Therizinosauroidea:: *Alxasaurus* + *.

Characters: Larger therizinosauroids. Skull & jaw shallow & long; teeth absent from front of jaws; jaw curves downward in anterior; dentary shallow, with weak coronoid process; external mandibular foramen large; palate highly vaulted; long, posteriorly shifted vomers & palatines; vomers fused (?), forming *vertical* plate; pterygoids reduced rostrally; probable beak on premaxilla; external nares very long, with long nasal process of premaxilla; frontal very large dorsally; basicranium & otic region enlarged & highly pneumatized; cervical ribs fused to vertebrae; 6 sacral vertebrae with long transverse processes and ribs; humerus with both ends strongly expanded; long, massive deltopectoral crest; ligament pits on phalanges shallow; opisthopubic; ilium short with significant preacetabular expansion; postacetabular process very short, with knob-like caudolateral protruberance; femoral head turns at right angle with distinct neck; greater trochanter expanded and separated from lesser by cleft; 4th trochanter present as rugose crest; long ascending process of astragalus; astragalus with reduced condyles, only partly covering distal end of tibia; foot claws large, narrow, & curved.

Links: DD: Therizinosauridae; Question of Segnosaurs; Therizinosaurids; Segnosaurus (Dutch).

References: Barsbold & Maryanska (1990); Currie (2000).

Image: skull and palate of *Erlikosaurus*, pelvis of *Segnosaurus*. Both modified from Barsbold & Maryanska (1990).

Note: some of the characters above are from Barsbold & Maryanska (1990) based on materials even more skimpy than those known today. 010618.

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checkedATW040810, revised MAK120307

Coelurosauria: Alvarezsauridae

Abbreviated Dendrogram

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DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--Metornithes
                  |--Alvarezsauridae
                  |  |--Alvarezsaurus
                  |  `--+--Patagonykus
                  |     `--Mononykinae
                  |--Oviraptorosauria
                  `--Paraves
                     |--+--Troodontidae
                     |  `--Dromaeosauridae
                     `--AVES
```

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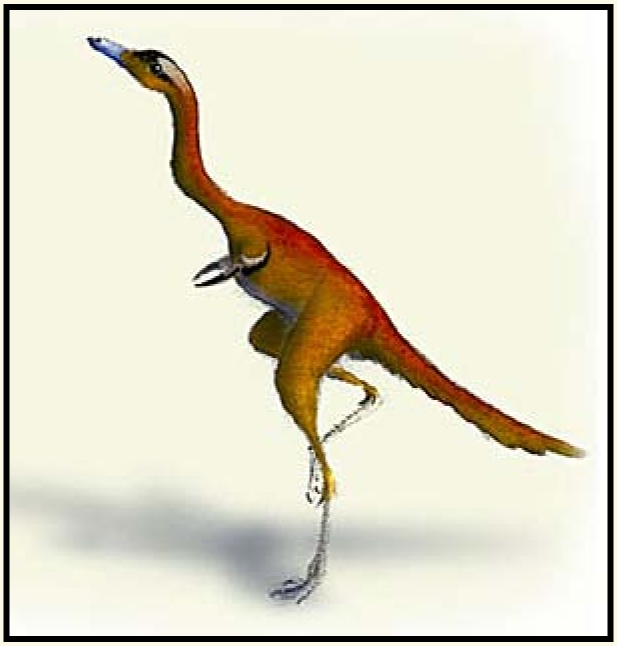
2. *Alvarezsaurus* X
3. Metornithes
4. *Patagonykus* X

Editor's note: this and the following page were originally included under the unit Aves. They have been relocated to the present unit following current understanding, which places the Alvarezsauridae stemward of (i.e. more basal than) true birds. However the text has not yet been revised. MAK120309

Alvarezsaurs: Arms, Flightlessness and Metabolism

Some of the strangest of early birds are the alvarezsaurs. These creatures were plainly flightless, and the nature of their flightlessness requires some special comment. The **Alvarezsauridae** are, conceptually, the very opposite of *Archaeopteryx*. The weirdness of *Archaeopteryx* is that it was plainly designed to fly, but had almost no birdlike features: no keeled sternum, little or no fusion of wrist or ankle bones; not much in the way of special skull adaptations, and so on. By contrast, the Alvarezsaurids have all these and more. The weirdness of the Alvarezsaurids is that, whatever they were adapted for, it was plainly*not* flight. One can envision any number of strange and wonderful keratinous or cartilaginous appurtenances for those short, but heavily muscled, single-fingered arms. However, it is beyond conception that any of them could ever have permitted *Mononykus* to fly.



As Henry Gee points out (in his usual pugnacious, but always eloquent, style) flight is very much a mixed blessing. It confers enormous advantages. However, at the same time, it demands an enormous dedication of energy and an enormous commitment of anatomical resources that might find "better" uses. Giving up on flight confers a large energy bonus and so, "the world is full of flightless birds." Gee (1999: 199); *see also* Feduccia (1999: 231).

But this may not be quite the same thing. The world is full of flightless birds which share certain characteristics. Feduccia (1999: 289). Cenozoic flightless birds do not have a keeled sternum. In fact, this is virtually the first anatomical "event" that occurs when flight is lost. Other relatively predictable adaptations are the development of an obtuse angle between the scapula and coracoid and the loss of the furcula. Since flightless birds are not constrained to minimize weight to the same extent as flying forms, they typically become, not only larger, but fatter at any given size. Feduccia (1999: 258-68). Modern flightless birds (mostly, but not entirely, ratites) also typically evolve in isolated locations, often islands where competition for a variety of niches is low. They have not competed well with other forms and tend to disappear or become marginalized fairly quickly once competition is introduced. Like adventitious plants, birds can fill ecological vacuums very quickly but are not necessarily robust competitors over the longer term.

Alvarezsaurids, by contrast, seem to represent a group that enjoyed considerable, long-term success in both Mongolia and Argentina, regions which are located on large continental land masses and were almost as remote from each other in the Cretaceous as they are today. Certainly alvarezsaurids did not have to compete with advanced rodents (the bane of many more recent flightless bird species), but their very broad geographic dispersion is notable. They plainly retained a keeled sternum and a robust pectoral girdle. The scapula - coracoid angle is problematic, but appears to have been only slightly obtuse in *Mononykus*, the most derived member of the clade. The clavicles (so far as I have been able to determine) are not known and the furcula may have disappeared. However, the alvarezsaurids remained, insofar as one can judge from bones, notably scrawny over the considerable size range from *Parvicursor* to *Mononykus* and did not put on weight like an elephant bird (Aepyornithiformes), or even a kiwi (Apterygiformes).

On the whole, the alvarezsaurids may point to a somewhat different pattern of evolution. The most striking difference is that the arms, while not useful for flight, were plainly useful for *something*. When neornithines become flightless, the pectoral apparatus is very quickly reduced -- a matter of generations, not megayears. Feduccia (1999: 266). The selective advantage in "bulking down" is strong because the flight muscles comprise an average of 20% of the body mass of even highly modified, flight-adapted neornithine birds. Even without the added weight of the pectoral girdle supporting flight, this represents an enormous metabolic commitment, and the energetic reward for losing it is a powerful selective advantage. Despite this selective pressure, alvarezsaurids seem to have lost the ability to fly while retaining much of the anatomical baggage that made flight so expensive. One of the principal advantages of flightlessness is the chance to get fat and lazy (i.e., to reduce basal metabolism and accumulate fat reserves). From all appearances alvarezsaurids did neither.

At this point, the perceptive essayist would introduce some startling insight into the lives of alvarezsaurids which would explain their strangeness. Unfortunately, nothing of the sort is on offer here. However, there is one possible evolutionary parameter that might be considered, given the exceedingly odd pattern of alvarezsaurid evolution. Perhaps the alvarezsaurids did not take full advantage of the metabolic advantage of flightlessness because there was less advantage to be had. If dinosaurs did not develop full endothermy until *after* the development of more advanced avian adaptations, then the energetics of secondary flightlessness simply didn't require the immediate loss of the flight apparatus and reduction of basal metabolism. Flight would be a short-term, anaerobic, hyper-exertion. The loss of flight would free up anatomical resources and open up "design" possibilities. It would not, however, involve as much in the way of immediate metabolic savings. The reduction in selective pressure could, in turn, slow down the process of de-adaptation for flight long enough to permit selection for some other forelimb function.

By contrast, it is noteworthy how few flightless neornithines have made any significant use of their forelimbs. Perhaps the only exceptions are auks, penguins and other birds which "fly" under water. The exceptions support the rule. It is perfectly possible to use wings for both flying and swimming (some petrels, razor-bills). Thus diving wings are an unremarkable adaptation because the development of such wings does not involve the same kind of geologically instantaneous vestigialization of the flight apparatus. The latter creates few opportunities for retooling.

Such a paradigm would go some way toward explaining one of the open questions about flight in *Archaeopteryx*. Flight, in efficient, neornithine birds, is terribly expensive. It is so expensive that the ability to fly is subject to enormous negative selection whenever circumstances permit survival without it. In the competition between the flying and non-flying descendants of island colonizers, the non-flyers seem to triumph in the blink of a geological eye. But, if this be true of efficient, highly derived neornithine flyers, how could a relatively inefficient, proto-archaeornithine almost-flyer ever overcome this negative selection and develop flight in the first place?

The answer that comes most easily to hand is that the selective advantage of flightlessness may have been less clear. The barrier might be lower because the energetic cost of flight did not include maintaining huge flight muscles at a constant internal temperature, with all that this entails. The proto-flyer's basal metabolism was already low. The gain from giving up flight muscle was not as compelling a selective argument as it later became. Indeed -- to crawl even further out on this limb -- it might be more sensible to suppose that the size and strength of the flight muscle later drove full Neornithine homeothermy, rather than the reverse. A bird fully committed to flight gains advantages by endothermy which would more than fully compensate for the energetic cost.

That half of the equation may be left for another day and another taxon. For the alvarezsaurids, who manifestly did lose flight, the net result of primitively lower metabolism would be what is actually observed: the flight apparatus was not lost, because it had not been all that expensive in the first place. Selection against flight was not the break-neck affair it is believed to be in the case of isolated island neornithines. Rather, the conversion was a slow and statistical process in which the flight apparatus was gradually converted to another use.

Now if we could only determine what that use was ...

Mononykus olecrans image courtesy of Daniel Bensen and T. Michael Keesey, whose scientific and artistic work, including this image or versions of it, may be accessed, respectively, at OPUS: Dinosaur and The Dinosauricon. (© as stated at those sites).

Metornithes: definition: *Alvarezsaurus* + Neornithes. Padian *et al.* (1999) [C95]

Range: from the Early Cretaceous.

Phylogeny: Aves: Archaeornithes + *: Alvarezsauridae + (Confuciusornithidae + Ornithothoraces)

Characters: **$** loss of "jugular" (jugal?) postorbital process [F+98]; **$** medial otic process of quadrate articulates with the prootic [F+98]; quadrate articulates with prootic and squamosal; **$** prominent ventral processes on cervicodorsal vertebrae [C95]; vertebral neural canal dorsoventrally wide relative to centrum depth [P+93]; **$** large rectangular sternum [P+93] [C95]; **$** sternum with ossified carina [C95] [P+93]; **$** ventral tubercle of humerus projects caudally and is separated from the humeral head by distinct "capital incision" (neck?) [F+98]; ulnar distal condyle present; **$** fused carpometacarpus [F+98] [P+93, but ambiguous] [C95]; **$** prominent antitrochanter on ilium (but wouldn't this be primitive?) [F+98] [P+93]; ischium > 2/3 length of pubis; **$** obturator process on ischium rudimentary or absent [F+98]; **$** pubic apron transversely narrowed with pubic symphysis restricted to distal one-third of shaft [F+98]; *compare* no pubic symphysis [P+93]; **$** loss of pubic foot [F+98] [P+93]; femur with undivided trochanteric crest [P+93]; femur with distal condyles nearly confluent below popliteal fossa [P+93]; **$** fibula does not reach tarsus [P+93].

Links: So here it is... my paper, open for discussion (very long; try to view it in maximum window breadth) (strange, but possible); Re: I'm back...; Re: Coelurus a maniraptoran (for how long?); THEM EARLY BIRDS; Re: Carpometacarpus.

References: Chiappe (1995) [C95]; Forster *et al*. (1998) [F+98]; Perle *et al*. (1993) [P+93].

Note: **[1]** It is interesting that the basic structure of the wing itself came first, *followed* by the reorganization of the limb girdle and musculature necessary to make really effective use of the wing in flight. **[2]** The tendency now is to put alvarezsaurids somewhere back in basal Maniraptora. See, e.g., Coelurosauria -- The Dinosauricon. In that case, its hard to tell what this clade contains. However, Mikko's site has a different definition (Neornithes > *Archaeopteryx*), attributed to Chiappe, which I like much better and which would preserve the utility of this clade. ATW020809.

Update: since the above was written, the evolutionary relationships of this clade has been totally revised, with all recent studies unanimously placing the Alvasauridae stemward of *Archaeopteryx* and Aves (Zhang et al 2008, Zanno et al 2009, Xu et al 2011, Lee & Worthy 2011). The following 2005 comment by Tim Williams, from the Dinosaur Mailing List pretty much sums up the resulting phylogenetic inversion:

> "...The discovery and or inclusion of one new specimen or one new taxon can shift taxa around and play havoc with topology. I seem to remember that _Mononykus_ once looked quite secure as a basal avialan more derived than _Archaeopteryx_, and there were plenty of papers arguing this point. Perle et al. (1993) erected the clade Metornithes under the assumption that _Mononykus_ (=_Mononychus_) was a bird more derived than _Archaeopteryx_. Subsequently, _Mononykus_ (and other alvarezsaurs) fell out of the Avialae. Now, with its current definition, Metornithes is bigger (more inclusive) than Avialae! If Metornithes had been defined as "all descendents of the most recent common ancestor of _Mononykus_ and _Passer_, but not _Archaeopteryx_", then Metornithes would disappear in the event that _Mononykus_ was found to be more basal than _Archaeopteryx_. In other words, once the avialan hypothesis for _Mononykus_ was no longer supported, the clade Metornithes (which was erected in the context of _Mononykus_ being a bird) would also expire."

For Paul 1988 and 2002, all maniraptors are neoflightless descendents of archaeopterygians. This is in agreement with Perle et al. 1993, but not with either earlier or more recent (e.g.Senter 2007) cladistic analyses of theropods and coelurosauria. In the standard hypothesis (birds evolved from troodont or dromaeasaur-like maniraptors), the original definition of Metornithes by Perle et al. (1993) as the clade containing *Mononykus* and Ornithothoraces, but not *Archaeopteryx* and non-avian theropods, becomes invalid. Because *Mononykus* and *Alvarezsaurus* belong to the same clade, Chiappe's (1995) definition of Metornithes as *Mononykus* + Neornithes is and Padian *et al.* (1999) definition are synonymous. Mickey Mortimer makes alvarezsaurids the sister taxon to the ornithominosaurs, and hence Metornithes synonymous with Maniraptoriformes. This differs from the consensus of current papers which place the Alvarezsaurs fully in the maniraprora, although it does recall Greg Paul's ornithomimids as neo-flightless birds. In any case, the close similarity between troodonts, dromaeasaurs, oviraptors, archaeopterygids, and alverezsaurs, with alverezsaurs in some regards appearing more bird-like than *Archaeopteryx*, shows how similar all these proto-birds were, as well as the nature of mosaic evolution and the way in which convergence, reversals, and other evolutionary artifacts make it difficult if not impossible to determine the extact relationships among the various proto-birds and dino-birds. MAK120306.

Alvarezsauridae: 1-2 m flightless birds with small arms. *Elaphrosaurus gautieri?* (see Mortimer), *Rapator?* (see Rapator ornitholestoides, large Aussie dinosaur -- or bird?)

Range: Late Cretaceous of South America, Mongolia & possibly Africa.

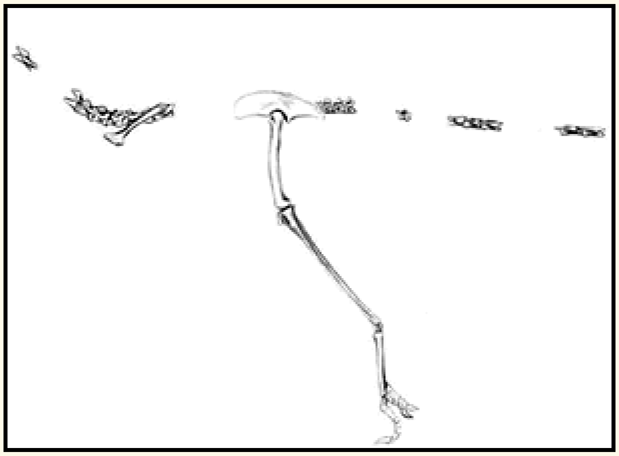
Phylogeny: Metornithes: (Confuciusornithidae + Ornithothoraces) + *: *Alvarezsaurus* + (*Patagonykus* + Mononykinae).

Characters: prenarial snout absent; upper jaw moveable on skull (i.e., without opening mouth); prefrontal large with broad orbital flanges; no postorbital-jugal contact; movable joint between quadratojugal and quadrate, no quadratojugal-squamosal contact; separate squamosal and braincase articulations of quadrate, tympanic recess opens within columellar recess (not paroccipital process); triradiate palatine; teeth present on dentary & premaxilla; maxilla without teeth; teeth with unserrated crowns; shortened vertebral spines; dorsal centra with very deep neural canal, approaching 50% centrum height; **$** sacrals procoelous [N97]; **$** posterior sacral centra ventrally keeled and laterally compressed [N97]; synsacrum with ~7 vertebrae; caudal count < 25-26; 1st (and distal?) caudal centrum (centra?) with ventral keel; caudals procoelous; tail moderately long (?); proximal chevrons long; caudal zygapophyses reduced & short; caudal hemapophyses not reduced; sternum rectangular; carinate sternum (carina small); glenoid does not face laterally; humerus very short; fused carpometacarpus; arms short, probably heavily muscled; humerus stout; in *M.*, large olecranon process and single large manual digit; **$** robust ungual on manus I with quadrangular articular surface [N97]; manual unguals with flattened ventral surfaces and distally displaced flexor tubercles; supraacetabular crest ends above acetabulum; pelvis with prominent antitrochanter; **$** iliac pubic peduncle slender [N97]; ilium pubic peduncle projects anteroventrally; iliac blades meet in the midline; ischium > two-thirds length of pubis; no contact between distal ends of ischia; legs very long, esp. in *M.*; fibula splint-like and incomplete; no medial fossa on proximal end fibula; primitively, at least one digit reversed (?).

Links: **DinoData: Mononykus**; **DinoData: Shuvuuia**; Link (Japanese); Mononykus (Nakasato); Nakasato ...Mononykus (forelimb); National Geographic ...1996; Lectures 19-20; Bonezone - Mark Norell; Alvarezsauria -- The Dinosauricon; polyphyletic Alvarezsauria assemblage; Arctometatarsalia and Alvarezsauria; \Elaphrosaurus\ gautieri identified as an ...... (and follow-ups thereto).

References: Novas (1997) [N97]. ATW011029.

***Alvarezsaurus*:** Bonaparte 1991. *A. calvoi* Bonaparte 1991.



Range: Late Cretaceous (Coniacian to Santonian) of South America.

Phylogeny: Alvarezsauridae: (*Patagonykus* + Mononykinae) + *.

Characters: ~2m & perhaps 20 kg; cervical pleurocoels present; last sacral & caudal vertebrae procoelous [N97]; caudal neural spines very low; tail very long; distal caudal elongate [N97]; single digit on forelimb (??); supraacetabular crest absent [N97]; femur 4th trochanter absent [N97]; fibula articulates (fuses?) distally with tibia [N97]; pes not arctometatarsalian [N97].

Notes: as [N97] points out, the forelimb of *Alvarezsaurus* is actually unknown, so that the peculiar alvarezsaurid claws may or may not be a synapomorphy of the Alvarezsauridae.

Links: Alvarezsaurus -- The Dinosauricon; Chamworks Dinosaurs & Such: Alvarezsaurus calvoi; DinoData Dinosaurs A090 ALVAREZSAURUS calvoi; ALVAREZSAURUS; Alvarezsaurus (Dutch); Alvarezsaurus.htm (Spanish); Alvarezsaurus page in The Natural History Museum's Dino Directory; DinoDictionary.com | A - Dinosaurs Page 2.

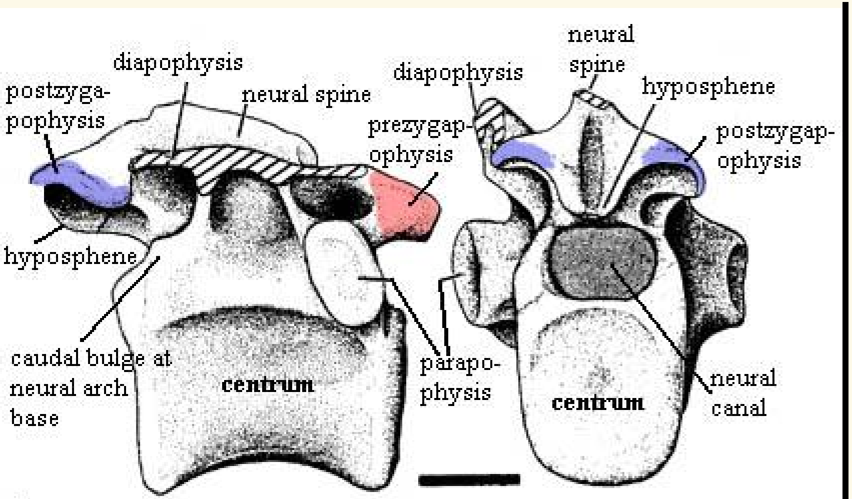
References: Novas (1997) [N97]. ATW020810.

***Patagonykus*:** *P. puertai* Novas 1996.

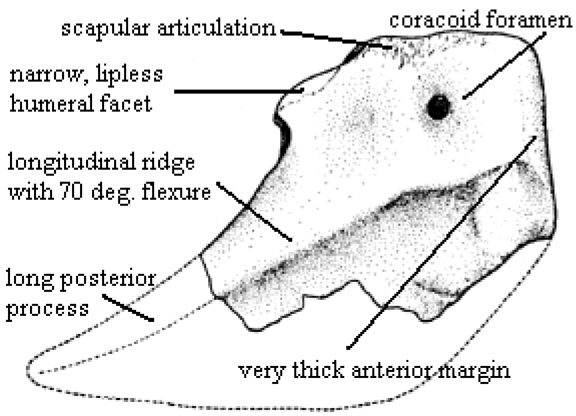
Range: Late Cretaceous (Turonian) of South America

Phylogeny: Alvarezsauridae:: Mononykinae + *.

Characters: cervical vertebrae with pleurocoels present; **$** dorsal vertebrae postzygapophyses with curved, tongue-shaped lateral margin [N97]; dorsal vertebrae without pleurocoels [N97]; dorsal vertebrae with accessory hyposphene-hypantra articulations;



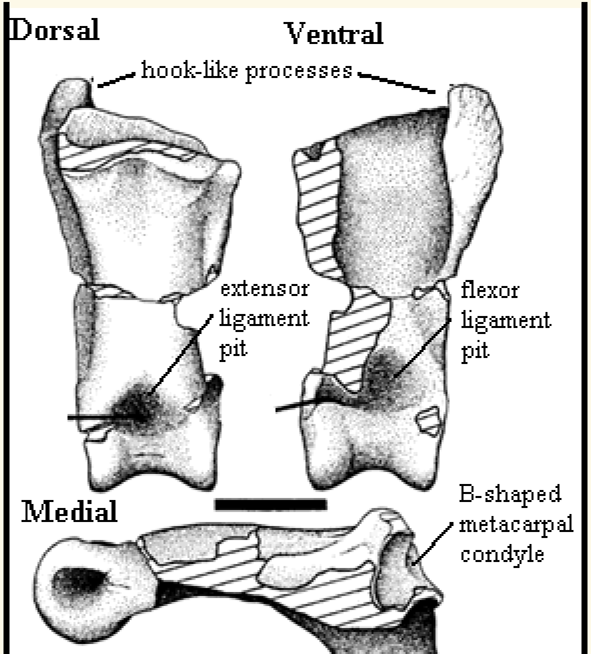
Patagonykus: dorsal vertebra in right lateral and posterior views. Scale = 10 mm. From Novas (1997).



***Patagonykus*: reconstruction of right coracoid in lateral view. From Novas (1997).**

hyposphenes present as deep and wide ridge between postzygapophyses [N97]; neural spines dorsally flat and elongated anteroposteriorly [N97]; dorsal parapophyses & diapophyses directed (i.e. the ribs were directed) laterally & slightly dorsal [N97]; **$** dorsal, sacral & caudal vertebrae with bulge at caudal base of neural arch [N97]; dorsal, sacral & caudal vertebrae procoelous [N97]; probably 5 sacrals [N97]; sacrals hollow, with thin periosteum [N97]; sacral centra narrow & deep [N97]; sacral transverse processes directed laterodorsally [N97]; posterior sacrals with ventral keel [N97]; anterior caudals similar to sacrals [N97]; caudal vertebrae with postzygapophyses much longer than in dorsals; distal caudals dorsoventrally flattened, with distinct grooves on ventral surface [N97]; **$** coracoid with transversely narrow humeral facet [N97]; coracoid posterior process long, flat & ventrally deep [N97];anterior margin is very thick [N97]; coracoid with long ridge, marking flexure of ~70 ° [N97]; forelimb very similar to *Mononykus* [N97]; humeral head convex, long & narrow (wide range of motion?) [N97]; humeral head may have been continuous with deltopectoral crest [N97]; **$** humerus internal tuberosity cylindrical & broadening distally [N97]; ends of both head and tuber smooth, convex & ringed with attachment scars [N97]; **$** humerus entepicondyle conical & projects strongly medially [N97]; humeral ectepicondyle separated from condyle by marked notch and strongly projecting almost distally [N97]; humerus with single, large, spherical distal condyle [N97]; ulna as in *Mononykus*, but even more robust [N97]; carpometacarpus has semilunate carpal fused to large MtI [N97]; **$** manual digit I phalanx 1 with proximomedial, ventrally-directed hook-like process(es) [N97]; digit is dorsoventrally flattened; supraacetabular crest prominent & projects laterally, but is restricted to dorsal part of acetabulum [N97]; ilium ischiac pedicel with raised antitrochanter [N97]; pubis with small obturator notch distal to articulation for ischium (with corresponding notch on ischium) [N97]; pubic symphysis and boot present [N97]; femoral anterior (= lesser) trochanter projects up to level of greater trochanter, but is separated by deep cleft [N97]; cleft continues as excavation separating anterior trochanter from femoral head [N97]; 4th trochanter present, with prominent foramen and slight depression for insertion of *m. caudofemoralis longus* [N97]; proximal femoral shaft laterally flattened [N97]; **$** "ectocondylar tuber of femur rectangular shaped in distal view" [N97]; tibia proximal articular surface almost flat [N97]; tibia with strong, but short cnemial crest [N97]; tibia with outer and inner condyles on posterior side, separated by deep, narrow notch [N97]; distal tibia closely appressed to astragalus but not fused [N97]; fibula articulates distally with tibia [N97]; fibula not in contact with calcaneum (*contra*? [N97]); astragalus fused to calcaneum [N97]; astragalus ascending process wide, but laminar & very (<1 mm) thin [N97]; metatarsals II & III partially fused [N97]; pes III not arctometatarsalian (vs. *Mononykus*) [N97].

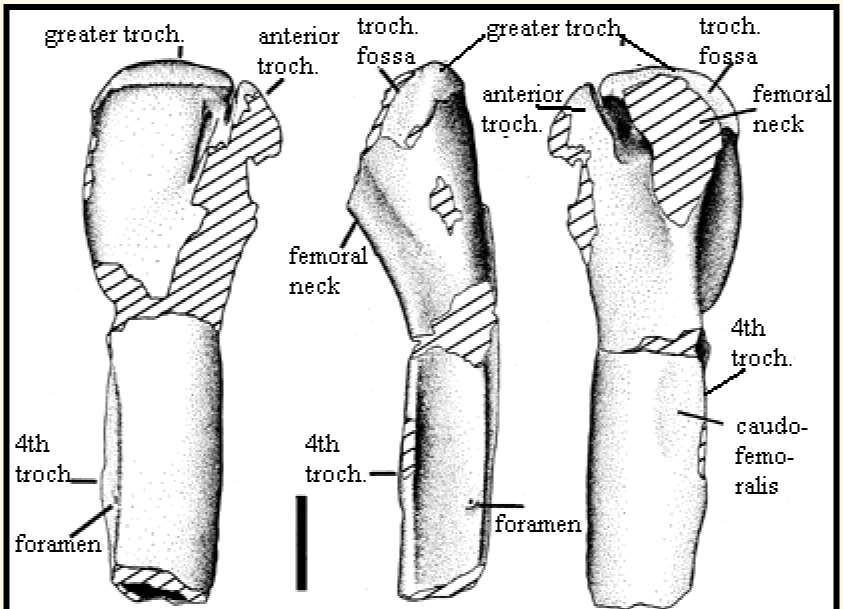
Note: [1] very fragmentary remains of a second, unnamed alvarezsaur were found with *Patagonykus*. [N97]. **[2]** It is very, very difficult to make sense of this arm -- even more difficult than in *Mononykus*. The humeral head seems to articulate comfortably with the coracoid facet only if the arm were sticking straight out sideways. In this position, it is hard to see how the humerus could



Patagonykus: right digit I, phalanx 1 from Novas (1997)

be rotated anteriorly, because of the long contact between coracoid and humeral head. If this is correct, the net result is that *Patagonykus* could only flap its arms up and down. The short, but powerful, claw and forearm would then appear to move -- rather uselessly -- in a sort of radial plane, between pointing anteriorly to pointing straight out sideways. Perhaps the creature makes better sense if we reconstruct it as a much fatter beast. This is also suggested by the dorsolateral angle of the rib articulations. The coracoids can then be placed on a broad, muscular breast and face more anteriorly than laterally. If we then rotate the right coracoid counterclockwise, the up-and-down motion becomes an in-and-out motion and the scapular blade points dorsolaterally, which looks about right and makes much better mechanical sense.

Links: DinoData Dinosaurs P049 PATAGONYKUS puertai; \Elaphrosaurus\ gautieri identified as an ......; PATAGONYKUS; Extinct Birds; The Dinosauria by DinosØMP; Patagonykus -- The Dinosauricon; The Theropod Ancestry of Birds; The Journal of Vertebrate Paleontology; Bruno Hernandez's Paleo Gallery @ Prehistorics Illustrated page 08; ALVAREZSAURIDAE (German); El mundo perdido de la Patagonia (Spanish); Argentina On View (Spanish); MEA592D Dinosaur Osteology: Lecture 6.



Patagonykus: proximal femur in lateral, posterior & medial views. Scale = 20 mm. From Novas (1977).

References: Forster *et al*. (1998), Novas (1997) [N97]. ATW020810.

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checked ATW050717

Coelurosauria: Mononykinae

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--+--Alvarezsauridae
                  |  |--Alvarezsaurus
                  |  `--Mononykinae
                  |     |--Mononykus
                  |     `--+--Parvicursor
                  |        `--Shuvuuia
                  |--Oviraptorosauria
                  `--Paraves
                     |--+--Troodontidae
                     |  `--Dromaeosauridae
                     `--AVES
```

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1. Mononykinae X
2. *Mononykus* X
3. *Parvicursor* X
4. *Shuvuuia* X

Descriptions

Mononykinae: Laurasian alvarezsaurs. Unnamed North American form [HC98]

Range: Late Cretaceous (Campanian - Maastrichtian) of North America & Mongolia [HC98]

Phylogeny: Alvarezsauridae:: *Patagonykus* + *: *Mononykus* + (*Parvicursor* + *Shuvuuia*).

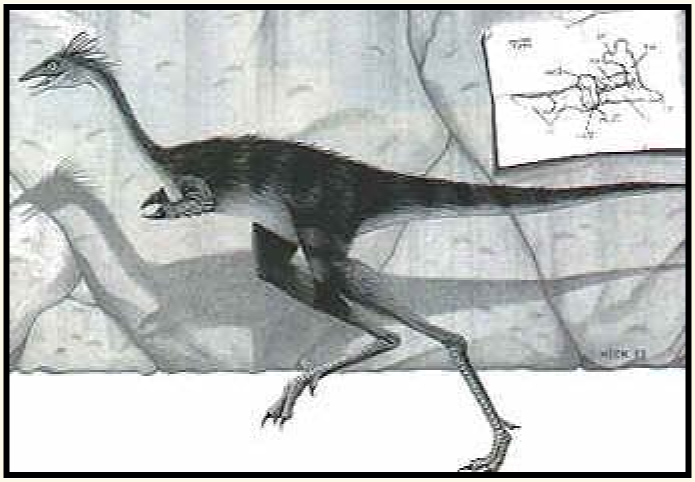
Characters: hyposphene-hypantrum articulations absent; semilunate distal carpal covers all metacarpals (but how many are there?); ischial shaft lies along posterodorsal surface of pubic shaft, embraced in a groove towards proximal end [HC98]; pubic & ischial shafts of roughly equal length [HC98]; pubis body laterally compressed, laterally concave & medially convex [HC98]; pubis with prominent anteriorly directed preacetabular tubercle [HC98]; pubis *opisthopubic* forming angle of ~50° relative to *iliac peduncle* [HC98]; lesser & greater trochanters fused; *popliteal fossa* on distal femur closed distally by condyles; medial cnemial crest on proximal tibia; distal tibia with distinct condyles separated by tendinal groove on anterior surface; ascending process of astragalus slender, covering only lateral half of anterior tibia surface; Mt III does not reach proximal end of tarsus (fully arctometatarsalian).

Note: As noted by Hutchinson & Chiappe (1998), the apparent Late Cretaceous migration of alvarezsaurids from South America to Laurasia is consistent with some kind of temporary land bridge between North and South America during the Late Cretaceous. The same odd pattern of exotic Gondwanan species has been noted, for example, in connection with the appearance of titanosaurs in Laurasia.

Links: 415780a-s1.doc.

References: Hutchinson & Chiappe (1998) [HC98]. ATW020811.

Mononykus: *M. olecrans* Perle *et al*. 1993.

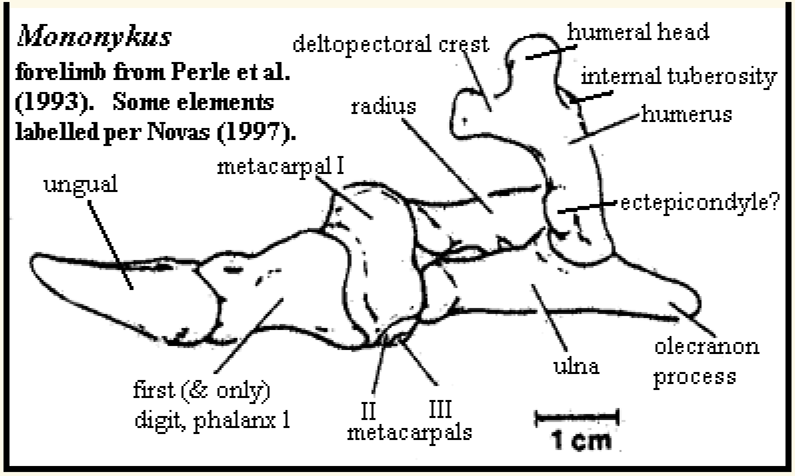


Range: Late Cretaceous (Campanian to Maastrichtian) of Mongolia (Nemegt & Djadokhta Formations)

Phylogeny: Mononykinae: (*Parvicursor* + *Shuvuuia*) + *.

Characters: ~90 cm; orbit connected with infratemporal fenestra [C95]; caudal & rostral tympanic recesses; accessory maxillary fenestra absent [P+93]; quadrate articulation anterior to otic recess [P+93]; maxilla *edentulous* [P+93]; small teeth on dentary and/or premaxilla [P+93]; teeth sharply pointed, laterally compressed, with distal & mesial carinae which broaden from tip to base [P+93]; long neck; vertebrae with very large neural canal [P+93]; caudal zygapophyses long, but not spanning adjacent centra [P+93]; cervical & dorsal vertebrae opisthocoelous [P+93] (*contra*, [N97]); one posterior dorsal vertebra biconvex [P+93]; sacral vertebrae procoelous & transversely compressed [P+93]; posterior sacral vertebrae sharply keeled [P+93]; 19+ caudals [P+93]; proximal caudals with elongate hemal arches [P+93]; furcula unknown [P+93]; sternum longer than wide (as in birds) with thick carina [P+93]; coracoid not expanded ventrally [P+93]; humerus with large *pectoral crest* [P+93]; humerus with large proximal ventral tuberosity [P+93]; humerus with single distal condyle [P+93]; ulna & radius with very short shafts [P+93]; ulna with long, prominent *olecranon* process [P+93]; massive fused wrist (*carpometacarpus*) with at least 3 metacarpals and 1 distal carpal [P+93]; one robust manual digit (digit I) [P+93]; digits II & III vestigial or absent [P+93]; robust ungual on digit I [P+93]; ilium with flat, horizontal posterior wing with shallow brevis fossa [P+93]; antitrochanter present [P+93]; ischium very slender [P+93]; opisthopubic [P+93]; pubic shaft proximally triangular in cross-section [HC98]; pubes & ischia do not meet in distal symphyses [P+93]; pubic "boot" absent [P+93]; long legs; femoral anterior & greater trochanters fused (as birds) [P+93]; depression near 4th trochanter for *m caudofemoralis* as in *Patagonykus* [N97]; popliteal fossa bounded distally by condyles [P+93]; "tibiotarsus" with medial cnemial crest [P+93]; tibia and proximal tarsals partially fused (tibiotarsus) in one specimen, but unfused in another [P+93]; tibiotarsus with fibula small and distally fused to tibia; metatarsals not fused [P+93]; metatarsal III limited to distal third and triangular in cross-section (extreme arctometatarsaly) [P+93]; Mts II & IV elongate, Mt I small & Mt V reduced to a splint [P+93]; phalangeal formula 23450 [P+93];

Note: short arms and powerful muscles suggest fossorial lifestyle, but long legs inconsistent with this. Perhaps it was insectivore, attacking termite mounds. It would then, easily, have been the world's all time fastest and most nimble termite



specialist.

Links: Mononykus; Nakasato Virtual Museum Mononykus (forelimb); DinoData Dinosaurs M134 MONONYKUS; National Geographic Magazine: July 1996 @ nationalgeographic.com; Mononykus -- The Dinosauricon; Paleontology and Geology Glossary: Mo; Mononykus (Dutch); Mike Fredericks' Paleo Gallery @ Prehistorics Illustrated page 07; 'Nisarg' - A Birdlike Dinosaur?; Mononykus - Suite101.com.

Notes: [1] many of the features cited as diagnostic by Perle *et al.* later turned out to be common to all alvarezsaurids.

References: Chiappe (1995) [C95]; Hutchinson & Chiappe (1998) [HC98]; Novas (1997) [N97]; Perle *et al*. (1993) [P+93]. ATW020811.

Parvicursor: *P. remotus* Karhu & Rautian 1996.

Range: Late Cretaceous (Campanian) of Mongolia

Phylogeny: Mononykinae:: *Shuvuuia* + *.

Characters: [1] small form ~1 m; vertebrae without pleurocoels [KR98]; all vertebrae with low neural spines [KR98]; all dorsal vertebrae opisthocoelous [KR98]; hyposphene-hypantrum articulations absent [KR98]; dorsal vertebrae with somewhat triangular articular surfaces (broader dorsally than ventrally) [KR98]; some dorsal vertebrae with ball in socket articulations; prezygapophyses short & do not reach level of anterior margin of centrum [KR98]; only 1st sacral vertebra is laterally compressed & carinate [C+98] [KR98]; 2nd & 3rd sacrals are broad & not carinate [KR98]; free caudals are procoelic and proximal caudals are laterally compressed [KR98]; caudal prezygapophyses long & extend beyond level of anterior margin of centrum [KR98]; anterior sacral vertebra with ventral keel [S+02]; **$** pubic elements fused near acetabulum [KR98]; **[2]** dorsal part of acetabulum is medially concave [KR98]; **$** acetabular foramen diameter <50% diameter of acetabular cavity [KR98]; ilium strongly expanded laterally dorsal to acetabulum [KR98]; pubic & ischial shafts closely appressed & directed posteroventrally [KR98]; no pubic symphysis [KR98]; **$** proximal femur curved strongly in anterior direction [KR98]; femur with major & minor trochanters fused in single crest [KR98]; **$** femur with 4th trochanter absent [KR98]; **$** popliteal fossa open distally, separating distal femoral condyles [KR98]; **$** tibiotarsus >1.5x length of femur [KR98]; single prominent cnemial crest [KR98]; only a spike of fibulae remains (rest fused with tibia), flattened proximally [KR98]; astragalus ascending process shifted laterally and proximal part fused with tibia [KR98]; extreme arctometatarsaly with Mt III only 25% length of others [KR98]; pes IV <50% length of metatarsal IV [S+02]; phalangeal formula 1?3450? [KR98]; unguals moderate size, roughly equal size and slightly curved [KR98].

Notes: [1] Karhu & Rautian (1998) proposed a new family, Parvicursoridae, to include only *Parvicursor*, to the exclusion of *Mononykus*. For various reasons, this has not been generally followed. The diagnostic characters of the proposed family have been treated here as characters of *Parvicursor*. **[2]** In other words, the acetabulum actually cuts into the top of the ilium. This feature, combined with the considerable curvature of the top of the leg, suggests that *Parvicursor* habitually stood (or squatted!) in a very odd position, with the proximal femur perhaps actually above the level of the pelvis. Consistent with this hypothesis of strange posture, the articulations between the femur and tibiotarsus (not described above) are also unusual, with the lateral articulations protruding much more strongly than, and apparently at a distinct angle from, the medial articulation [KR98].

Links: PARVICURSOR; DinoData Dinosaurs P047 PARVICURSOR remotus; Parvicursor -- The Dinosauricon.

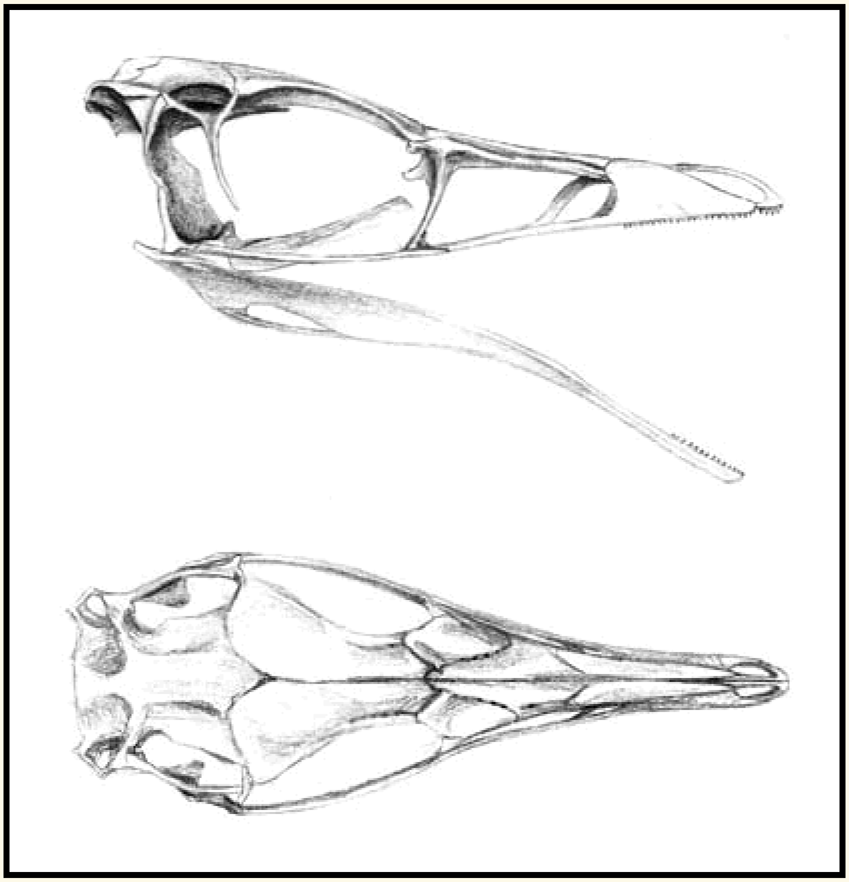
References: Chiappe *et al*. (1998) [C+98]; Karhu & Rautian (1996) [KR96]; Suzuki *et al*. (2002) [S+02]. ATW031113.

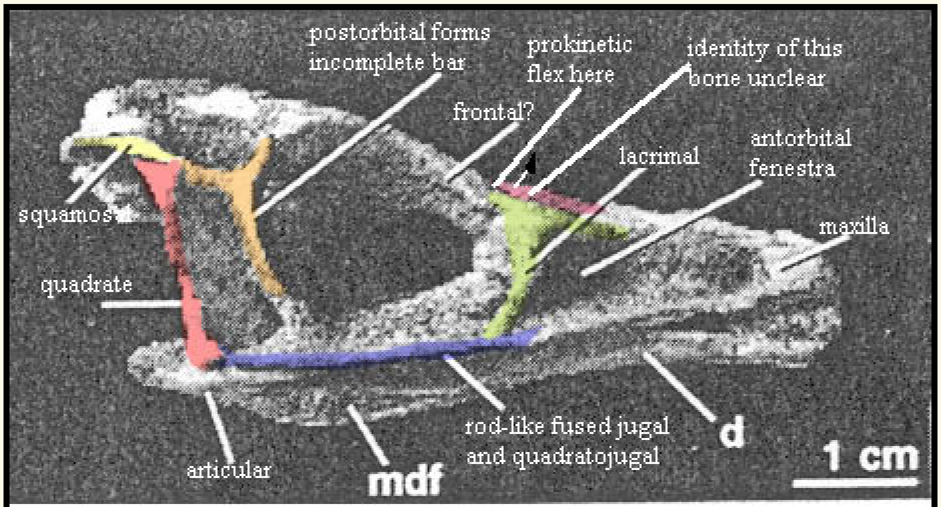
Shuvuuia: *S. deserti* Chiappe *et al.* 1998.

Range: Late Cretaceous (Campanian) of Mongolia.

Phylogeny: Mononykinae:: *Parvicursor* + *.

Characters: nares terminal [C+98]; maxilla forms most of lateral rostrum [C+98]; prokinesis with mobility where rostrum reaches braincase [C+98]; prefrontal? (or ectethmoid?) very large [C+98]; lacrimal with long anterior process and small posterior process [C+98]; orbit large [C+98]; postorbital forms incomplete postorbital bar [C+98]; jugal does not contact postorbital [C+98]; jugal & quadratojugal fused to form jugal bar [C+98]; quadratojugal does not contact squamosal [C+98]; quadratojugal forms mobile joint with quadrate (clasps quadrate in small, unsutured Y-shaped terminus) [C+98]; quadrate has separate articulations with quadratojugal and squamosal [C+98]; quadrate tall & slender [C+98]; squamosal triradiate & not incorporated into braincase [C+98]; paroccipital processes short & not perforated by caudal tympanic recess [C+98]; foramen magnum large [C+98]; occipital condyle very small & posteriorly directed [C+98]; caudal tympanic recess & columellar recess confluent [C+98]; *basipterygoid processes* elongated & almost vertical [C+98]; palatine elongate & triradiate, lacking jugal process [C+98]; coronoid absent [C+98]; numerous teeth on premaxilla and on maxilla up to anterior 1/3 of antorbital fossa [C+98]; teeth in continuous groove in dentary [C+98]; cervical centra with large pneumatic foramina [C+98]; 1st sacral not carinate [C+98]; humerus deltopectoral crest confluent with humeral head [C+98]; pubis circular in cross-section [C+98]; pubic shaft laterally compressed [HC98]; femur and tibiotarsus bowed [C+98];$ distal tibiotarsus with sharp ridge on the medial margin [C+98]; proximal tarsals and metatarsals less fused than in *Mononykus & Parvicursor* [C+98]; ß-keratin (feather protein) present by immunology, ultrastructure and (less convincingly) mass spectroscopy [S+99].





Shuvuuia skull in right lateral view from Chiappe et al. (1998). Note quadrate articulations (a) squamosal & postorbital (b) jugal & quadratojugal (c) articular. A 4th articulation with the braincase occurs internally.

Links: DinoData Dinosaurs S070 SHUVUUIA deserti; Shuvuuia Fact Sheet - EnchantedLearning.com; Shuvuuia deserti; OLogy; Shuvuuia -- The Dinosauricon; SHUVUUIA DESERTI (Dutch); ScienceDaily Magazine -- Researchers Announce Discovery Of Skulls Of Bizarre Animals Showing Advanced Stage In Transition Between Dinosaurs And Birds; Bird Dinosaur Link; Fighting Dinosaurs | American Museum of Natural History; \Feathered\ Dinosaurs.

References: Chiappe *et al*. (1998) [C+98]; Hutchinson & Chiappe (1998) [HC98]; Schweitzer *et al.* (1999) [S+99]. ATW020811.

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Coelurosauria: Oviraptorosauria

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--Metornithes
                  |--Alvarezsauridae
                  `--+--Oviraptorosauria
                     `-Paraves
                        |--Deinonychosauria
                        |      |--Troodontidae
                        |      `--Dromaeosauridae
                        `--Avialae
                           |-
-Scansoriopterygidae
                           `--AVES
```

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1. Oviraptorosauria X

Oviraptors are Birds?!

This is the teaching of Maryanska *et al.* (2002). This view has, thus far, met with a rather chilly reception among dinofolk. On initial reading of the paper, one may be suspicious. A number of key taxa, particularly alvarezsaurs, are scored, but not used in the analysis. Further, there is no comparison with neornithines or any other birds closer to neornithines than *Confuciusornis*. However, a little work suggests why. If neornithines are entered into the data matrix used by the authors, and the omitted taxa are included, the results are extremely strange. The overall topology is this:

```
Maniraptora
|--Alvarezsauridae
`--+--Therizinosauria
   `--Aves
      |--Archaeopteryx
```

```
    `--+--+--Troodontidae
       |  `--Dromaeosauridae
       `--+--Oviraptorosauria
          `--+--Confuciusornithidae
             `--Neornithes
```

Just as confusing, *Avimimus* and *Caudipteryx* are basal oviraptors. Undoubtedly, at some point, this will all be explained. After flirting briefly with this topology, we have returned to a more conventional view. ATW031103.

Oviraptorosauria

Oviraptor is frequently cited as an example of a bird-like dinosaur. Yet, for some reason, typical life reconstructions have missed one potential bird-like feature. The front surfaces of both jaws clearly show the typical rough, pitted markings of horn-like keratin material, quite possibly a beak. There is no reason to assume that the shape of the structure conformed closely to the shape of the bone. See, for example, the illustration at Oviraptor. While very good art, the bull-dog like cropped face that it shows would lose most of the nutritional value from whatever those odd jaws were designed to crack: nuts, eggs, fruit, or delicious crunchy lizards. Whatever it was, the good stuff would flow freely out the sides. What use is half a mouth? Would selection really favor an eye that was so close to things with sharp edges, whether egg shells or claws? Bone makes a very effective device for crushing and cutting. It would be completely superfluous to cover it with a layer of keratin merely to assume the same shape and function. It is more plausible to invent a long, tough curved beak from thin air (for, as usual, the keratin has dissolved without leaving fossil evidence) than to imagine otherwise.

Another problem with the available life reconstructions starts from the position of the arms girdles. *Ingenia is* a miniature (1.5 m) version of *Oviraptor* without some of the cranial bells and whistles. The body structures are very much the same. The Nakasota specimen shows a bony sternum (breast bone) like a bird. Above and/or in front of the sternum are the coracoid bones of the arm girdle, and above those the fused clavicles (furcula). The whole thing makes a rather neat package for both muscle attachment and at least some level of protection. The problem, when one does this, is that the big scapulas don't line up in a pretty way with the ribs and the vertebral column. See the close-up. Note how the scapulas stick up and away from the rib cage in the upper corners of the picture. Part of the problem here is that the anterior part of the spine may have been mounted too low (see the lateral view) for reasons that are not clear. Even so, *Ingenia* would have had remarkable shoulder blades.

A partial solution might be to give the beast a more vertical stance, leaning somewhat forward from the "shoulders." The clawed arms reach up in a natural position to protect the neck. The back bows outward and back, the neck swings forward somewhat, and the coracoids are raised slightly, which forces the scapulas to lie more closely with the body wall. This seems as if it would make reasonable fighting-threatening stance, with the chest armor facing the adversary. Running (and Oviraptorians would seem likely runners), the body assumes the forward, less balanced posture in which it is normally shown.

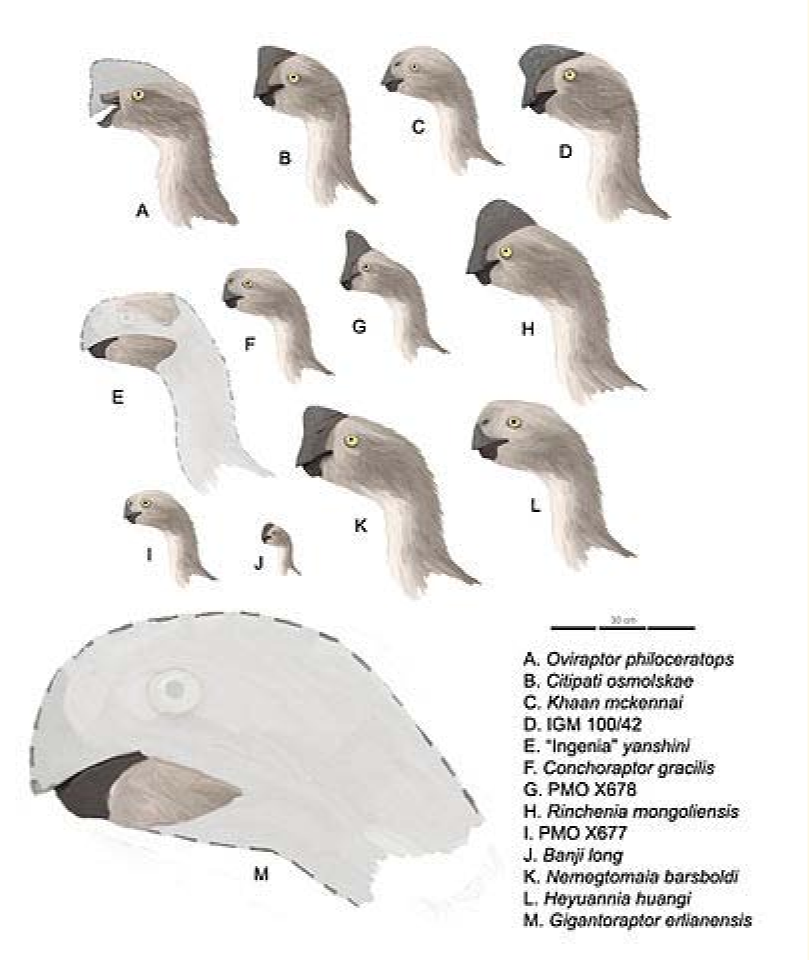
Descriptions

Oviraptorosauria: *Oviraptor*. LCA *Oviraptor* + *Chirostenotes*.

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

Phylogeny: Maniraptora:: Therizinosauroidea + *.

Characters: Small to medium (1-4 m) sized, lightly built, with a bizarre jaw. **$** deep skull; skull strongly



fenestrated; **$** jaws toothless, forming large base for attachment of presumed horny beak; jaws deep & short; nares high; orbits fairly large; cranial domes or crests in some species which may have had additional horn sheaths; infratemporal fenestra large & square [M+02]; foramen magnum larger than occipital condyle [M+02]; maxilla and premaxilla form secondary palate which may bear a central projection articulating with a similar projection on the central articular process; **$** strong medial process on articular; **$** upper margin of lower jaw arched; **$** dentaries with two long posterior processes; in effect, the lower jaw forms one narrow, centrally peaked (= "coronoid eminence" [M+02]), blade which may have articulated medially with the roof of the broader upper jaw; intramandibular joint absent; vertebral formula 10+13+6+~40; centra pneumatized, including anterior caudal vertebrae; hypapophyses present on caudal & dorsal vertebrae [M+02]; tail short overall (a 2000 article in *Nature* reports a specimen with a possible pygostyle, or at least a series of fused caudals); scapula thick, flat (in *O. philoceratops*, has process to articulate with clavicle); clavicles robust and fused (furcula); marked delto-pectoral crest on humerus; ectepicondyle more prominent than entepicondyle [M+02]; semilunate carpal present; three fingers with sharply curved , laterally compressed unguals; unguals with pronounced lip above articulation with penultimate phalanges; propubic; ilium deep in *O. philoceratops* but not others; pubis long, with small boot; ischium bears large obturator process; greater trochanter prominent, but 4th trochanter reduced; some species are arctometatarsalian; 4 toes, 3 weight-bearing; foot unguals relatively small & weakly curved. Several specimens found on nests with eggs, now believed to be their own.

Image: Profiles of all oviraptorids with known skull material, including identification key and scale bar. By Matt Martyniuk, via Wikipedia, Creative Commons Attribution

Links: DD: Oviraptorosauria; Oviraptor (striking life reconstruction of head without beak); Oviraptor philoceratops; Ingenia (another gorgeous Nakasota Museum display); Part One [Overview]; Primitive forms and Caenagnathids; oviraptorosauria; Untitled Document; Dann's Dinosaur Info

References: Currie (2000); Maryanska *et al*. (2002) [M+02]. ATW010617.

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Coelurosauria: Paraves

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--Metornithes
                  |--Alvarezsauridae
                  `--+--Oviraptorosauria
                     `--Paraves
                        |--Deinonychosauria
                        |   |--Troodontidae
                        |   `--Dromaeosauridae
                        `--Avialae
                           |-
-Scansoriopterygidae
                           `--AVES
```

Contents

Taxa on This Page

1. Paraves
2. Deinonychosauria X

Anchiornis huxleyi, a troodontid maniraptoran coelurosaur from the late Jurassic of China.
Digital artwork by Nobu Tamura, via Wikipedia, GNU Free Documentation/Creative Commons Attribution

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Descriptions

Paraves Birds > Oviraptors

Possible or actual synonyms: Eumaniraptora, Deinonychosauria (if troodontids sensu latu are paraphyletic)

Range: From Late Jurassic

Phylogeny: Metornithes **:** Alvarezsauridae + (Oviraptorosauria + * **:** Deinonychosauria + Avialae)

Comments: the clade that includes true birds and the most bird-like dinosaurs. Traditionally and almost universally, Paraves is divided into two major sub-groups: Avialae, including Archaeopteryx and co, and Deinonychosauria, which includes the dromaeosaurids and troodontids. To the present author this seems like an artificial distinction based on external morphology (Archaeopteryx being a highly advanced and specialised form), and it is quite likely that Deinonychosauria as presently defined is a paraphyletic taxon; e.g. Archie may have evolved from stem Troodonts like *Anchiornis* (which would make the Troodontidae as presnetly defined paraphyletic as well, a not implausible premise); hence the lack of resolution in our phylogeny.

The following paragraph is copied from Wikipedia, due to editorial laziness and lack of time - MAK120306

The ancestral paravian is a hypothetical animal; the first common ancestor of birds, dromaeosaurids, and troodontids which was not also ancestral to oviraptorosaurs. Little can be said with certainty about this animal. The work of Turner et al 2007 suggested that the ancestral paravian could not glide or fly, and that it was most likely small (around 65 centimeters long and 600–700 grams in mass). But the work of Xu et al 2003, Xu & Zhang 2005 and Hu et al 2009 provide examples of basal and early paravians with four wings, including members of the Avialae (*Pedopenna*), Dromaeosauridae (*Microraptor*), and Troodontidae (*Anchiornis*). - Wikipedia

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Deinonychosauria LCA *Deinonychus* + *Troodon*

Range: Late Jurassic? Early Cret to Late Cret of NAm, As, Eur, S Am

Phylogeny: Paraves **:** Avialae + * **:** Troodontidae + Dromaeosauridae)

Comments: includes the two groups of coelurosaurs with a switchblade second toe claw, dromaeasaurs and troodontids. Xu et al 2011 include Archaeopteryx here, this is rejected by Lee & Worthy 2011. If however the Jurassic *Anchiornis* and *Xiaotingia* are stem paraves rather than stem deinonychosaurs (Xu et al 2011) or stem troodonts (Lee & Worthy 2011) then the Deinonychosauria is limited to the Cretaceous. MAK120311

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Coelurosauria: Dromaeosauridae

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--Metornithes
                  |--Alvarezsauridae
                  `--+--Oviraptorosauria
                     `--Paraves
                        |--Deinonychosauria
                        |    |--Troodontidae
                        |    `--Dromaeosauridae
                        `--Avialae
                            |-
-Scansoriopterygidae
                            `--AVES
```

Contents

Taxa on This Page

1. Dromaeosauridae X

Velociraptor mongoliensis, a typical dromaeosaur from the late Cretaceous of Mongolia.
Artwork by Matt Martyniuk, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share-alike

Introduction: Dromaeosaurs are considered dinosaurs, very close to the bird boundary (see *The Mistaken Extinction*). Greg Paul argues that they evolved from Archaeornithines -- the so-called "Secondary Flightlessness" (2F) hypothesis. For reasons which are not clear, this theory is very popular among educated amateurs, but finds little support among academic paleontologists. In either case, this shows how evolution is not about distinct types, but rather a gradation with countless intermediate stages.

These small to medium-sized predators were made famous through Hollywood fantasy. Everyone will remember them from *Jurassic Park*, Of course the *Jurassic Park* velociraptors were far larger than the typical species (two to three times the linear dimensions), scaly-skinned in a very un-maniraptoran reptilian manner, and, as befitting their cinematic black hatted villain role, had to be portayed as evil and menacing as possible. They were also able to turn door-knobs and open doors! [adapted from MAK, but with a different slant. AKW, revised MAK120307]

Descriptions

Dromaeosauridae (=Deinonychosauria): *Velociraptor*, *Utahraptor*.

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

Phylogeny: Deinonychosauria **:** Troodontidae + *

Characters: Small (2-3m), lightweight predators. Interdental plates present but fused; tall, slender vertical

process post to jaw articulation; brain fairly large; tail with thin anterior processes from pre-zaps & hemal arches (tail stiff, but not rigid); furcula present; ossified sternum; arms relatively long; "grasping" hand; pubis retroverted & parallel with ischium; short and unspecialized metatarsals; pes 2 with large raptorial claw, strongly curved and twice length of any other claw; probably feathered. Total mass perhaps 20 kg.

Links: DD: Dromaeosauridae; Dromaeosaurid Anatomy (excellent discussion of functional anatomy); Velociraptor (skull) and Nakasato Virtual Museum Velociraptor (skull) (Nakasato); Fighting Dinosaurs (same); Bambiraptor Home; The Court Of B.feinbergi (many detailed images of *Bambiraptor*); Dromaeosauridae; What is a Raptor?; The Fernleaf: Karen Carr; A New Dinosaur Specimen With Feather-like Structures; Pretty Butte Paleontology: Catalog of Dromaeosauridae Fossils; ???????? Dromaeosauridae; Re: Dromaeosauridae (was Troodontidae); DINOSAURS: Family Dromaeosauridae; dromaeosauridae; DROMAEOSAURIDAE (German); Arts-Letters.com | Dino Database - Glossary; Deinonychosauria (Dinosauricon); Deinonychosauria; ZOO-PAGE :: Dinosaorusi; Raptors; gaiaphyl.pdf; Feathered dinosaurs..

Image: *Sinornithosaurus* (reconstruction in Graves Museum by Brian Cooley) photograph by Michael Corriss (retouched by ATW) and reproduced by permission.

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checkedATW040810, revised MAK120307

Coelurosauria: Troodontidae

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--Metornithes
                  |--Alvarezsauridae
                  `--+--Oviraptorosauria
                     `--Paraves
                        |--Deinonychosauria
                        |   |--Troodontidae
                        |   `--Dromaeosauridae
                        `--Avialae
                           |-
-Scansoriopterygidae
                           `--AVES
```

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1. Troodontidae X

The *Archaeopteryx*-like troodont *Jinfengopteryx elegans*, from the Early Cretaceous of China.
Artwork by Matthew Martyniuk, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

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Descriptions

Troodontidae: *Byronosaurus, Saurornithoides, Sinornithoides, Sinovenator, Troodon.*

Range: Early Cretaceous (Late Jurassic?) to Late Cretaceous of China and North America.

Phylogeny: Deinonychosauria **:** Dromaeosauridae + *

Characters: ~2m long; skull long & low; premaxilla forms dorsoventrally flattened internarial bar [M+03**$**]; maxilla with broad shelf which contributes to palate; enlarged elongate maxillary fenestra; maxilla broadly contacts naris; nasals narrow posteriorly; skull roof peaks over orbits; **$** sharp sagittal crest; quadrate pneumatic, with pneumatopore on posterior face [M+03**$**]; occiput, basal tubera reduced & located directly below occipital condyle, close to midline [M+03**$**]; basisphenoid without ventral pneumatic recess [M+03**$**]; laterosphenoid, postorbital process with possibly pneumatic pit [M+03**$**]; large brain; lateral depression for middle ear; elaborate craniofacial sinus system; inflated parasphenoid (*contra* [M+03); jaw symphyses narrow but U-shaped; dentary foramina inside lateral groove which does not reach symphysis [M+03**$**]; large number of teeth on maxilla and and dentary (~100 total) [M+03**$**]; interdental plates absent; somewhat heterodont, with anterior teeth smaller and more chisel-shaped (posterior teeth are typically theropod); anterior dentary teeth in continuous groove, with alveoli confluent [M+03**$**]; teeth bear posterior serrations (also anterior serratrions in some spp.) (*contra* [M+03]: not in *Byronosaurus*); most distal posterior serration forming tip of tooth; **$** teeth with constriction between root & crown; teeth with large hooked denticles (may be absent from basal forms [M+03]) (functional significance of these unusual tooth characters is unknown); all vertebrae except distal caudals bear well-developed pockets for attachment of interspinous ligaments (absence on caudals may be **$**); trunk vertebrae with long, slender transverse processes [M+03**$**]; 6 sacral vertebrae; distal caudals with neural groove & no spine; transverse processes also absent from distal caudals; elongate caudal prezygapophyses; chevrons flattened in distal caudal (tail stiffened?); strap-like scapula with small acromion process; coracoid bears prominent biceps tubercle; pubic foot longer anterior to the shaft; **$** lateral knob-like trochanter on femur; fibula reduced to splint; **$** fusion of astragalus and calcaneum; tall ascending process of astragalus; **$** laterally compressed metatarsal II, markedly shorter than Mt III & IV; long, strongly arctometatarsalian III; metatarsal IV stout; tongue-like extension of articular surface on metatarsal III; **$** modified pes II allowing retraction of enlarged ungual (?); since second ungual normally retracted, foot functionally two-toed.

Links: DD: Troodon; National Geographic Magazine: July 1996 @ nationalgeographic.com; Troodontidae (rather dated UCMP page); Troodontidae -- The Dinosauricon; Re- Troodontidae (misfits); Troodontidae and All That Jazz; Troodontidae (Mikko's Phylogeny).

References: Makovicky *et al.* (2003) [M+03].

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Coelurosauria: Avialae

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--Metornithes
                  |--Alvarezsauridae
                  `--+--Oviraptorosauria
                     `--Paraves
                        |--Deinonychosauria
                        |   |--Troodontidae
                        |   `--Dromaeosauridae
                        `--Avialae
                           |-
-Scansoriopterygidae
                           `--AVES
```

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1. Avialae
2. Scansoriopterygidae X

Scansoriopteryx heilmanni, a tiny proto-bird from the late Jurassic of China.
Artwork by Matthew Martyniuk, via Wikipedia, GNU Free Documentation/Creative Commons Attribution

Illustrating the complex character of evolution at the dino to bird boundary, here are a group of arboreal proto-birds, or possibly very early true birds, known mostly from the fossil remains of tiny, sparrow-sized juveniles.. They have been variously considered as more primitive than (Zhang et al 2008, Lee & Worthy 2011), or more advanced than (Xu et al 2011), *Archaeopteryx*. Although universally classified as Avialae close to*Archaeopteryx*, and hence to tryue birds, their precise evolutionary relationships are uncertain MAK120307

Descriptions

Avialae. Daffy Duck > *Deinonychus antirrhopus*.

Range: From Late Jurassic

Phylogeny: Paraves **:** Deinonychosauria + * **:** Aves + Scansoriopterygidae

Comments: The clade that includes all birds and their immediate proto-bird ancestors and relatives. The almost unanimous position among paleontologists is that *Archaeopteryx* is more derived than *Deinonychus*. Two rare dissenting hypotheses are paleornithologist Alan Feduccia (who reject a dinosaur origin for birds) Triassic archosaur origin, and Greg Paul's popular (among lay-enthusiasts) neoflightless theropod hypothesis (*Deinonychus* as a descendant of *Archaeopteryx* rather than a cousin). More recently, Feduccia has modified his stance and now argues (like Greg Paul) that the very birdlike Dromaeosaurids and Oviraptorosauria, are actually neo-flightless avian lineages, probably more derived than Archaeopteryx, that through homoplasy associated with loss of flight and secondary acquisition of cursoriality, converged with theropod dinosaurs (Wikipedia). So far, cladistic evidence does not support the neo-flightless hypothesis MAK120307

Scansoriopterygidae. *Epidexipteryx*, *Scansoriopteryx*

Range: Late Jurassic of China

Phylogeny: Avialae **:** Aves + *

Comments: from Wikipedia: Scansoriopterygids can be characterized by their extremely elongated third fingers, which are longer than the first and second digits of the hand (in all other known theropods, the second finger is the longest). Other features shared within the group include short and high skulls with down turned lower jaws and large front teeth, and long arms. Tail length, however, varied significantly among scansoriopterygids. Epidexipteryx had a short tail (70% the length of the torso), anchoring long tail feathers, while Scansoriopteryx had a very long tail (over three times as long as the torso) with a short spray of feathers at the tip. All three described scansoripterygid specimens preserve the fossilized traces of feathers covering their bodies (Czerkas & Yuan 2002, Zhang et al 2008)

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Coelurosauria: Classification

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--Metornithes
                  |--Alvarezsauridae
                  `--+--Oviraptorosauria
                     `-Paraves
                        |--Deinonychosauria
                        |   |--Troodontidae
                        |   `--Dromaeosauridae
                        `--Avialae
                           |-
-Scansoriopterygidae
                           `--AVES
```

Contents

Suborder Coeluria (= Coelurosauria)

Traditional classification

As with other pages in this series, the current page is intended to provide an evolutionary-Linnaean rank-based taxonomy. But as one subgroup of Coelurosauria, the Manirapora especially, has always been defined and analysed cladistically, providing a linnaean interpretation invokes a somewhat retro feel, rather like the Steam Punk genre created by science fiction writers William Gibson and Bruce Stirling, in which in an alternative 19th century, computer programmers inserted punch cards in steam-powered babbage engines, and which has since developed into an entire literary artistic subculture fashion style and aesthetic. MAK120306 120506

Image: Datamancer's Steampunk laptop

Infraclass Archosauromorpha Huene, 1946 (*cont.*)

Order[1] Theropoda Marsh, 1881 (*cont.*)

Suborder[2] Coeluria Marsh, 1881 (= Coelurosauria Huene, 1914) mostly small lightly built forms, but also include two specialised lineages, the tyrannosaurs and ornithomimids, as well as the ancestors of birds, Mid Jur to End Cret

Family Coeluridae Marsh, 1881 monotypal, includes only *Coelurus fragilis*, late Jur of Nth Am

Family Compsognathidae Cope, 1871 small lightly built theropods, covered with protofeathers, rather similar to a flightless *Archaeopteryx*, Late Jur to Mid Cret. Irioonically these minature theropods are cloesley related to the largest of the coelurosaurs, the tyrannosaurids

Dilong, *Eotyrannus*, *Stokesosaurus*, etc proto-tyrannosaurs or tyrannosaur ancestors, not assigned to family rank [3]

Family Proceratosauridae Rauhut, Milner & Moore-Fay, 2010 primitive tyrannosaurs, including a range of crested forms - Mid Jur to Mid Cret of Laurasia

Family Dryptosauridae Marsh, 1890 poorly known late Cret tyrannosaurids

Family Tyrannosauridae Osborn, 1906 large to gigantic coelurosaurs known from Laurasia; advanced froms have diminutive forearms but powerfully built skulls and jaws

Alectrosaurus and other genera (not assigned to subfamilies) primitive tyrannosaurs

Subfamily Tyrannosaurinae advanced Tyrannosaurs

Tribe Albertosaurini Currie, Hurum & Sabath, 2003 relatively lightly built (but still very large) tyrannosaurs, latest Cret of Nth Am

Tribe Tyrannosaurini advanced, heavily built Tyrannosaurs, latest Cret of Asia & Nth Am

Family Ornithomimidae Marsh, 1890 the ostrich dinosaurs or ostrich mimics, Mid to late Cret of Asia & Nth Am.

Archaeornithomimus, Pelecanimimus, etc primitive ornithomids not assigned to a subfamily

Subfamily Garudimiminae Barsbold, 1981 monotypal family (here, subfamily) for the genus *Garudimimus*, Mid Cret of Mongolia

Subfamily Harpymiminae Barsbold & Perle, 1984 monotypal family (here, subfamily) for the genus *Harpymimus* Mid Cret of Mongolia

Subfamily Ornithomiminae advanced ostrich dinosaurs

Family Deinocheiridae Osmólska & Roniewics, 1970 monotypal family based on a single enigmatic pair of giant forearms, resembling ornithomid arms

Family *Ornitholestidae* Paul, 1988 either a coelurosaur or a primitive maniraptoran

Suborder[4] Protoavia Paul 1988 (= "non-avian" Maniraptora Gauthier, 1986)[5] - advanced, very bird-like theropods, alternatively, may be flightless dino-birds descended from Archaeopteryx-grade ancestors.

Infraorder Therizinosauria

incertae sedis: a number on unplaced genera, which could be placed in several monotypal or paraphyletic families: Falcarius, Beipiaosaurus, etc

Family Alxasauridae Russell & Dong, 1995

Family Therizinosauridae Maleev, 1954

Infraorder "Alvarezsauria" - yes we know it only contains one family

Family Alvarezsauridae Bonaparte, 1991 - bird-like, thumb-clawed, small coelurosaurs - Late Cret of EAs, Eur, NAm and SAm

Subfamily Alvarezsaurinae

Subfamily Patagonykinae

Subfamily Mononykinae (= Parvicursorinae) - specialized alvarezsaurids with a pinched foot, Late Cret of EAs and NAm

Infraorder Oviraptorosauria - bizarre, beaked, herbivorous or omnivorous coelurosaurs, Early to Late Cret of EAs and NAm

incertae sedis: a number on unplaced genera, which could be placed in several monotypal, monophyletic or paraphyletic families or subfamilies: *Caenagnathasia, Caenagnathus, Incisivosaurus, Protarchaeopteryx*

Family Caudipteridae
Family Oviraptoridae
Subfamily Oviraptorinae - More powerful arms, shorter stouter legs, Late Cret of EAs
Subfamily Elmisaurinae - Shorter arms, longer legged oviraptors, Late Cret of EAs and NAm
Subfamily Ingeniinae
Family Oviraptoridae Barsbold, 1976
Order Archaeopterygiformes (Class Aves) = Infraorder Deinonychosauria (Order Theropoda) [6]
Family Troodontidae Gilmore, 1924
Family Dromaeosauridae Matthew & Brown, 1922
Subfamily Microraptorinae - small four-winged aboreal glidings forms
Subfamily Unenlagiinae - long-snouted west gondwanan dromaeosaurs
Subfamily Dromaeosaurinae - large and heavily built dromaeasaurs
Subfamily Saurornitholestinae - similar to velociraprtorines
Subfamily Velociraptorinae - classic dromaesaurs - *Deinonychus, Velociraptor* etc
Infraorder or Order unspecified
Family Scansoriopterygidae

Hybrid classification

This section is another of our now discontinued and impractical attempt to integrate the rank-based Linnaean and the phylogeny-based Cladistic systems of organising the nartural world. The following key is used:

- **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 more on this (and the original reason behind these pages), see the Theropoda - Classification MAK120306 120312

Parainfraclass Archosauromorpha Huene, 1946 (*cont.*)
Paraorder Theropoda Marsh, 1881 (*cont.*)
Parasuborder Coeluria Marsh, 1881 (= Coelurosauria Huene, 1914) mostly small lightly built forms, but also include two specialised lineages, the tyrannosaurs and ornithomimids, as well as the ancestors of birds, Mid Jur to End Cret
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Dilong, Eotyrannus, Stokesosaurus, etc proto-tyrannosaurs and tyrannosaur ancestors
Evofamily Proceratosauridae Rauhut, Milner & Moore-Fay, 2010 primitive tyrannosaurs, including a range of crested forms - Mid Jur to Mid Cret of Laurasia
Holofamily Dryptosauridae Marsh, 1890 poorly known late Cret tyrannosaurids
Holofamily Tyrannosauridae Osborn, 1906 large to gigantic coelurosaurs known from Laurasia; advanced froms have diminutive forearms but powerfully built skulls and jaws
Alectrosaurus and other genera (not assigned to subfamilies) primitive tyrannosaurs
Holosubfamily Tyrannosaurinae advanced Tyrannosaurs
Holotribe Albertosaurini Currie, Hurum & Sabath, 2003 relatively lightly built (but still very large) tyrannosaurs, latest Cret of Nth Am
Holotribe Tyrannosaurini advanced, heavily built Tyrannosaurs, latest Cret of Asia & Nth Am

Holofamily Ornithomimidae Marsh, 1890 the ostrich dinosaurs or ostrich mimics, Mid to late Cret of Asia & Nth Am.

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Holosubfamily Ornithomiminae advanced ostrich dinosaurs

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Suborder Protoavia Paul 1988 (= "non-avian" Maniraptora Gauthier, 1986) - advanced, very bird-like theropods, alternatively, may be flightless dino-birds descended from Archaeopteryx-grade ancestors.

Holoinfraorder Therizinosauria

incertae sedis: a number on unplaced genera, which could be placed in several monotypal or paraphyletic families: Falcarius, Beipiaosaurus, etc

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Holofamily Therizinosauridae Maleev, 1954

Monoinfraorder "Alvarezsauria" - yes we know it only contains one family

Holofamily Alvarezsauridae Bonaparte, 1991 - bird-like, thumb-clawed, small coelurosaurs - Late Cret of EAs, Eur, NAm and SAm

Monosubfamily Alvarezsaurinae

Parasubfamily Patagonykinae

Holosubfamily Mononykinae (= Parvicursorinae) - specialized alvarezsaurids with a pinched foot, Late Cret of EAs and NAm

Holoinfraorder Oviraptorosauria - bizarre, beaked, herbivorous or omnivorous coelurosaurs, Early to Late Cret of EAs and NAm

incertae sedis: a number on unplaced genera, which could be placed in several monotypal, monophyletic or paraphyletic families or subfamilies: *Caenagnathasia, Caenagnathus, Incisivosaurus, Protarchaeopteryx*

Monofamily Caudipteridae

Holofamily Oviraptoridae

Ambisubfamily Oviraptorinae - More powerful arms, shorter stouter legs, Late Cret of EAs

Ambisubfamily Elmisaurinae - Shorter arms, longer legged oviraptors, Late Cret of EAs and NAm

Holosubfamily Ingeniinae

Family Oviraptoridae Barsbold, 1976

Paraorder Archaeopterygiformes (Class Aves) = Infraorder Deinonychosauria (Order Theropoda)

Evofamily Troodontidae Gilmore, 1924

Holofamily Dromaeosauridae Matthew & Brown, 1922

Evosubfamily Microraptorinae - small four-winged aboreal glidings forms

Holosubfamily Unenlagiinae - long-snouted west gondwanan dromaeosaurs

Parasubfamily Dromaeosaurinae - large and heavily built dromaeasaurs

Evosubfamily Saurornitholestinae - similar to velociraprtorines

Holosubfamily Velociraptorinae - classic dromaesaurs - *Deinonychus, Velociraptor* etc

Infraorder or Order unspecified

Holo? or Evo? Family Scansoriopterygidae

Notes

[1]Theropoda is conventially paced as a suborder of Order Saurischia Seeley, 1887. But since the three dinosaurian groups (Theropoda, Sauropodomorpha, and Ornithischia) all diverged at the same time and remained consistently distinct and diverse lineages, we felt that Theropoda should be promoted to Ordinal status

[2] With Theropoda becoming an order, previous infraorders now become suborders.

[3] Only a few taxa are listed here. The Tyrannosaurs include not only the familiar *T. rex* and similar species, but also a diverse range of Mid Jurasisc through to Mid Cret forms with more conventional theropod or coelurosaur proportions; because this new research into the evolutionary relationships of Tyrannosaurs uses rank-free cladistic analysis, no linnaean supra-generic taxa have been erected for them in most of the published literature.

[4] Suborder has been chosen as the linnaean rank for Protoaves, in keeping with the rest of the theropod

classification. This would represent a more advanced (bird-like) taxon than Coeluria. Alternatively, a fully ordinal rank could be used, either within superorder Dinosauria or in Class Aves. The latter option would apply especially if Greg Paul's Neoflightless theropod hypothesis were to be accepted..

[5] Maniraptora includes not only bird-like dinosaurs birds as well, so strictly speaking it should only be used in a monophyletic context. But as Although phylogenetic nomenclature (confusingly) uses the same names as Linanean/evolutionary nomenclature, but in a different context (only allowing monophyletic taxa, emphasising extant crown group definitions etc) we could strictly speaking go the other way and borrow a monophyletic term for a non-cladistic paraphyletic definition. Greg Paul's almost identical term, coined two years later, has the advantage of being Linnaean from the start. Unfortunately Paul's terms have no official nomenclatural standing, as they are not acconpanied by formal descriptions. That doesn't matter though, because the present page, and for that matter the whole of palaeos, is informal as well (which is half the fun!).

[6] In traditional Linnaean classification, the extant birds (Class Aves) are divided into a whopping thirty or so extant orders. The unusally high ranking reflects the influence of ornithologists in 19th century natural history; as Romer somewhere points out, were this any other group they would probably be considered families (or today, given the current tendency to taxonomic inflation, superfamilies). We have here followed Greg Paul (1988) in grouping *Archaeopteryx* with the deinonychosaurs; in Paul's evolutionary systematic approach, Deinonychosauria would becomes a junior synonym for a paraphyletic Archaeopterygiformes. MAK120306

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Coelurosauria Dendrogram

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--Metornithes
                  |--Alvarezsauridae
                  `--+--Oviraptorosauria
                     `-Paraves
                        |--Deinonychosauria
                        |   |--Troodontidae
                        |   `--Dromaeosauridae
                        `--Avialae
                           |-
-Scansoriopterygidae
                           `--AVES
```

Contents

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
       |
       COELUROSAURIA MH
       |?--Gasosaurus
       `--+--Compsognathidae •X
           |--Tyrannosauroidea X ToL, MH, Th
           |  |--Eotyrannus •X
           |  `--Tyrannosauridae X
           |     |--Alectrosaurus •X
           |     `--Tyrannosaurinae X
           |        |--+--Albertosaurus •X
           |        |  `--Gorgosaurus •X
           |        `--Tyrannosaurini •X
           `--+--Coelurus •X
              `--Maniraptoriformes
                 |--Ornithomimosauria •X MH
                 `--+--Ornitholestes •X
                      `--Maniraptora Th
                          |--Therizinosauria •X Th
                          |  |--Falcarius •X
                          |  `--Therizinosauroidea •X
                          |     |--Beipiaosaurus •X
                          |     `--+--Alxasaurus •X
                          |        `--Therizinosauridae •X
                          `--+--Alvarezsauridae  •X
                              |  |--Alvarezsaurus •X
                              |  `--+--Patagonykus •X
                              |     `--Mononykinae •X
                              |        |--Mononykus  •X
```

```
|        `--+--Parvicursor •X
|           `--Shuvuuia   •X
`--+--Oviraptorosauria •X MH
   `--Paraves
      |--Deinonychosauria •X
      |  |--Troodontidae •X , Th
      |  `--Dromaeosauridae •X Th
      `--Avialae
         |--Scansoriopterygidae •X
         `--AVES
```

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Coelurosauria References

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--SAUROPODOMORPHA
   `--THEROPODA
      |
      `--COELUROSAURIA
         |--Tyrannosauroidea
         `--+--Ornithomimosauria
            `--+--Maniraptora
               |--Therizinosauroidea
               `--Metornithes
                  |--Alvarezsauridae
                  `--+--Oviraptorosauria
                     `-Paraves
                        |--Deinonychosauria
                        |   |--Troodontidae
                        |   `--Dromaeosauridae
                        `--Avialae
                           |-
-Scansoriopterygidae
                           `--AVES
```

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