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The Mesozoic Era - 1

The Mesozoic Era of the Phanerozoic Eon: 251 to 65.5 million years ago

Phanerozoic Eon
  Paleozoic Era
  Mesozoic Era
    Triassic Period
    Jurassic Period
    Cretaceous Period
  Cenozoic Era

Lasting little more than half the duration of the Paleozoic, the Mesozoic was a spectacular time. The generalized archosaurian reptiles of the Triassic gave way to the dinosaurs, a terrestrial megafauna the like of which the Earth has not seen before or since. While dinosaurs dominated the land, diverse sea-reptiles ruled the oceans, and invertebrates, especially ammonites, were extremely diverse. Pterosaurs and later birds took to the sky. Mammals however remained small and insignificant. Climatic conditions remained warm and tropical worldwide. The supercontinent of Pangea broke up into Laurasia and Gondwana, with different dinosaurian faunas evolving on each. During this era modern forms of corals, insects, new fishes and finally flowering plants evolved. At the end of the Cretaceous period the dinosaurs and many other animals abruptly died out, quite likely the result of an asteroid impact and associated extensive volcanism MAK020914

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The Mesozoic Era - 1

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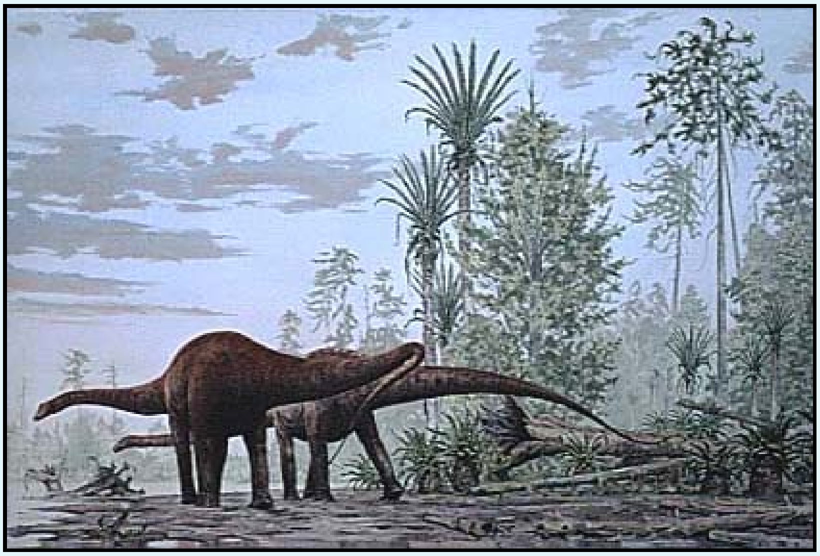


The supercontinent Pangea divides into Laurasia in the north and Gondwana in the south. The climate is hot and tropical worldwide. On land, the dinosaurs reign supreme. In the oceans are various kinds of marine reptiles, as well as ammonite and belemnite molluscs and many other invertebrate groups. Plants include ferns and gymnosperms. Mammals are small and insignificant, but probably numerically common.

The **Mesozoic Era** lasted more than 180 million years. During this time, many modern forms of plants, invertebrates, and fishes evolved. On land, dinosaurs were the dominant animals, while the oceans were populated by large marine reptiles, and Pterosaurs ruled the air. For most of this period, the climate worldwide was warm and tropical, and shallow seas covered low-lying landmasses. At the beginning of the Mesozoic, all of the world's continents were joined into the supercontinent of Pangea, which rifted into Laurasia in the north and Gondwanaland in the south. By the end of the era most of continents had separated into their present form.

The Mesozoic Era is divided into three periods, each lasting many millions of years: the Triassic, Jurassic, and Cretaceous. The **Triassic** saw the emergence of many modern invertebrate groups, and on land the archosaur reptiles replaced the therapsids. In the oceans Ichthyosaurs such as *Shonisaurus* became as large as whales. The**Jurassic** was the height of the dinosaur era, with giants such as *Brachiosaurus*, *Stegosaurus*, etc, and mammals tiny and shrew-like. Distinctive plants like ferns, Cycads, Bennettitales, and Cheirolepidiaceae conifers characterized the landscape. During the **Cretaceous** period, the first flowering plants appeared, birds and fish diversified, and new types of dinosaurs appeared. The climate cooled and unique dinosaurs evolved on different continents.

The Mesozoic era came to an end with the great terminal extinction event known as the K-T (Cretaceous-Tertiary) event.

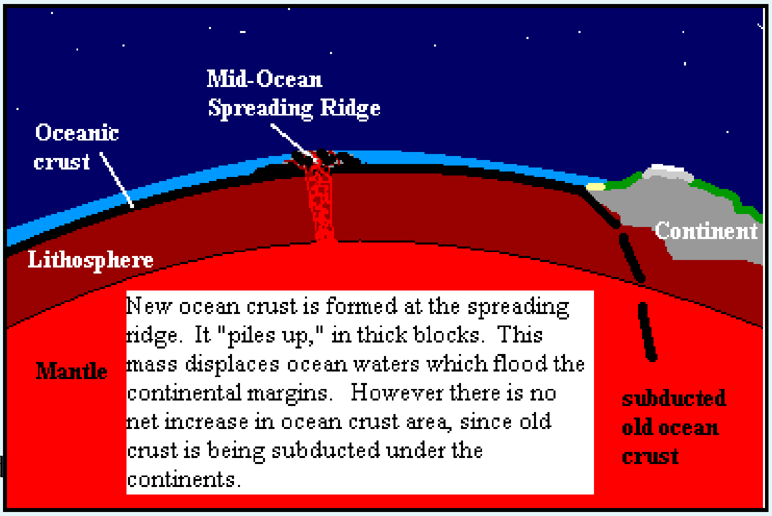
Image: illustration © Doug Henderson, reproduced with permission

The Mesozoic Era: Stratigraphy

Period	Epoch	Age	Range (Mya)	Duration (My)
Cretaceous K	Upper/late K2	Maastrichtian k6	70.6 - 65.5	5.1
		Campanian k5	83.5 - 70.6	12.9
		Santonian k4	85.8 - 83.5	2.3
		Coniacian k3	89.3 - 85.8	3.5
		Turonian k2	93.5 - 89.3	4.2
		Cenomanian k1	99.6 - 93.5	6.1
	Lower/early K1	Albian b6	112.0 - 99.6	12.4
		Aptian b5	125.0 - 112.0	13.0
		Barremian b4	130.0 - 125.0	5.0
		Hauterivian b3	136.4 - 130.0	6.4
		Valanginian b2	140.2 - 136.4	3.8
		Berriasian b1	145.5 - 140.2	5.3
Jurassic J	Upper/late J3	Tithonian j7	150.8 - 145.5	5.3
		Kimmeridgian j6	155.7 - 150.8	4.9
		Oxfordian j5	161.2 - 155.7	5.5
	Middle J2	Callovian j4	164.7 - 161.2	3.5
		Bathonian j3	167.7 - 164.7	3.0
		Bajocian j2	171.6 - 167.7	3.9
		Aalenian j1	175.6 - 171.6	4.0
	Lower/early J1	Toarcian l4	183.0 - 175.6	7.4
		Pliensbachian l3	189.6 - 183.0	6.6
		Sinemurian l2	196.5 - 189.6	6.9
		Hettangian l1	199.6 - 196.5	3.1
Triassic T	Upper/late T3	Rhaetian t7	203.6 - 199.6	4.0
		Norian t6	216.5 - 203.6	12.9
		Carnian t5	228.0 - 216.5	11.5
	Middle T2	Ladinian t4	237.0 - 228.0	9.0
		Anisian t3	245.0 - 237.0	8.0
	Lower/early T1	Olenekian t2	249.7 - 245.0	4.7
		Induan t1	251.0 - 249.7	1.3

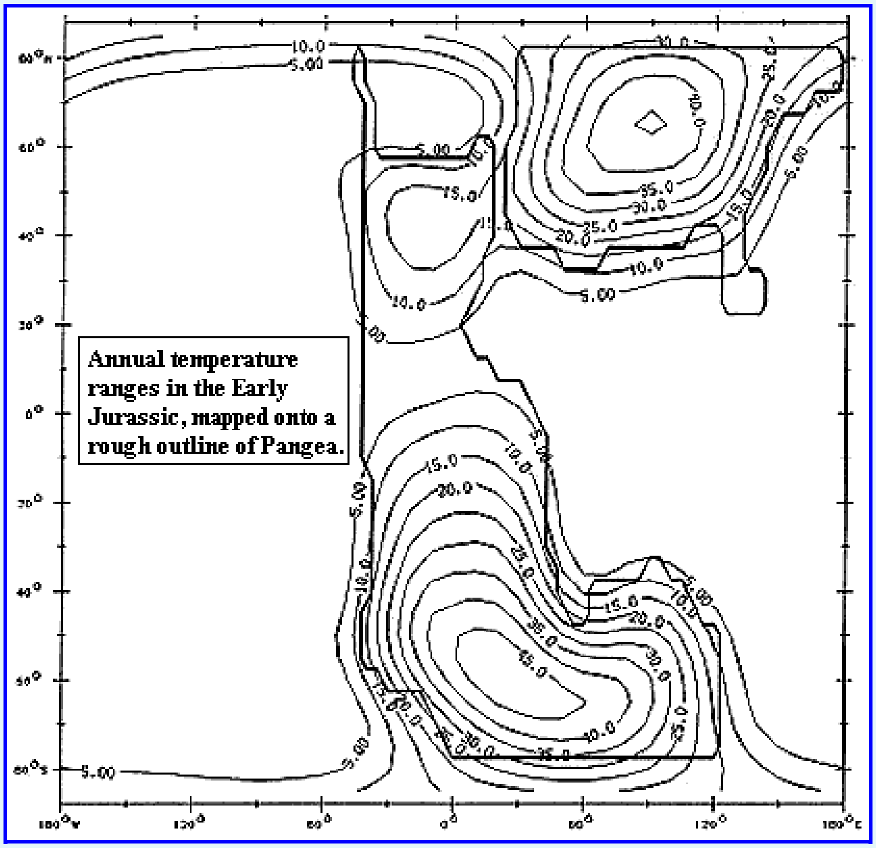
Mesozoic Climate

Some of the main outlines of Mesozoic climate are matters of general agreement, but almost no one is very satisfied with the explanations for what has been observed. Here's the usual story:



New ocean crust is formed at the spreading ridge. It "piles up," in thick blocks. This mass displaces ocean waters which flood the continental margins. However there is no net increase in ocean crust area, since old crust is being subducted under the continents.

The Triassic, particularly the first half of the Triassic, was dry and highly seasonal, with particularly large annual temperature variations in the vast continental interior of Pangea, the world-spanning continent of the Triassic. Low sea levels probably exaggerated these temperature extremes. Water acts as a heat sink -- it takes much more heat to warm a cup of water than it does to warm a cup of rock. Water also circulates, so that heat doesn't build up in one place. The net result is that water tends to stabilize temperatures. Land areas near the ocean are warmed or cooled by winds which pass over the ocean and by rains from evaporated ocean waters. It is generally agreed (a) that the low sea levels of the Triassic contributed to temperature extremes in the interior of Pangea and (b) that the interior of Pangea probably included huge areas of desert.



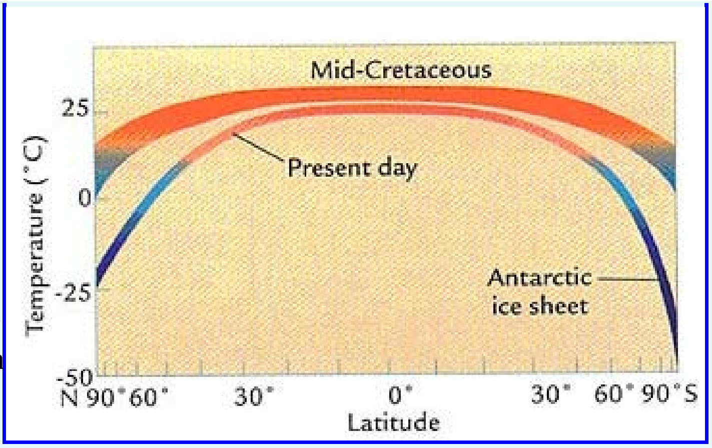
Annual temperature ranges in the Early Jurassic, mapped onto a rough outline of Pangea.

During the Jurassic, sea levels began to rise, probably due to an increase in sea-floor spreading. This seems paradoxical, but the mechanism is explained in the image. This caused flooding of large areas of the continents. As a result, the deserts began to retreat, and continental temperatures stabilized. Pangea also began to break up into smaller units, which brought more land area in contact with the ocean. The presence of nearby oceans also increased humidity, so that climates worldwide became wetter as well as warmer.

During the first half of the Cretaceous, this process continued. In addition two climate trends which began in the Jurassic became quite pronounced in the Cretaceous. The mechanism for these events is not fully understood. First, the temperature gradient from North to South became almost flat -- much more so than would be predicted from ocean circulation models. In other words, average temperatures were about the same everywhere on Earth, from the poles to the equator. Second, average temperatures were much higher than today, probably by about 10C°. Higher CO_2 (carbon dioxide) levels certainly played a part, but the paleoclimate data do not match theoretical predictions.

The later Cretaceous story is more complex, and more controversial. Many researchers, but not a real consensus, believe that sea temperatures near the equator may have become a bit *too* warm by the Aptian-Albian, perhaps actually incompatible with ocean life. In addition, some data suggest that land areas near the equator were not jungle- or forest-covered, that plant diversity was low, and that these regions were arid despite being close to the sea. Deep ocean circulation may also have broken down. That is, water continued to circulate horizontally, but not vertically. The deep oceans weren't getting oxygen, and "black shales" appeared in the Aptian-Albian and High Cretaceous. These are large volumes of organic matter in the oceans which never completely decomposed because of lack of deep ocean oxygen. Still, the north-south temperature gradient remained very flat.

Things cooled off a little during the End-Cretaceous, but it's unclear how much or how regularly. The climate at the very end of the Mesozoic is particularly controversial.



Unfortunately, the data only match this story to a limited degree, and there are internal inconsistencies. Here are a few of the problem areas.

1) If temperature extremes in the Triassic were as great as general circulation models predict, one would expect rather hefty ice-build-up in at least some polar regions. Glaciers leave a rather distinct geological signature, and we simply don't have any evidence of Triassic glaciers or polar caps.

2) Conversely, there is evidence of the kind of rapid sea level changes associated with polar ice in the Mid-Cretaceous, which is rather hard to accept. Miller *et al*. (2003).

3) CO_2 levels are usually invoked to explain Cretaceous warmth and the flat Cretaceous temperature gradient. This makes sense, since the very active mid-ocean spreading ridges might well have been associated with out-gassing of CO_2 from deep within the Earth. Unfortunately, neither the geology of the period nor the stable carbon isotope records really support the idea as well as they might.

4) Even the most sophisticated quantitative models can't reconstruct the flatness of the Cretaceous temperature gradient. Either our temperature estimates are off, or some important factor is missing from the models. Since dinosaurs and semi-tropical vegetation are known from within 10° of the Cretaceous poles, the problem is likely to be with the theory. A recent study of a mid-latitude continental interior (in eastern Russia) -- far from the ocean in even Late Cretaceous times, suggest that temperatures were very even and that these regions were damp and non-seasonal even in the Mid-Cretaceous.

Links: Mesozoic Dinosaurs - Enchanted Learning Software, Lecture 24-, Global Climate Change Student Guide, Pz-Mzclimate, Global Climate and Phytogeography in the Early Mesozoic, Pangaean climate during the Early Jurassic- GCM simulations and ..., The Vilui Basin and the Late Cretaceous Continental Interior ..., Mesozoic LAND ECOSYSTEMS, Geological Society - Abstracts.

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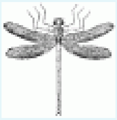
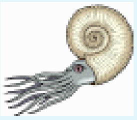
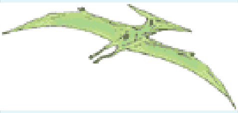
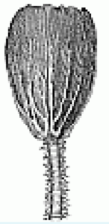
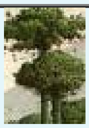
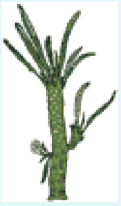
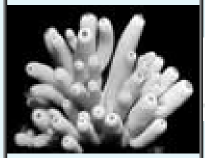
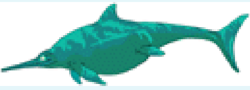
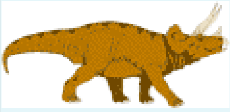
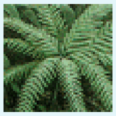
Mesozoic Life

 Dragonfly	 Bivalve	 Ammonite	 Belemnite	 Pterosauria	 Crinoid	 Araucariacean conifer	 Bennettitale
 Calcareous Sponge	 Ichthyosaur	 Plesiosaur	 Dinosaur	 Echinoid		 Fern	

If you're looking at this section, you may be a beginner without much previous knowledge. Of course, you may simply have been searching the web for an old Nirvana CD and you ran across this page because, as it happens, you're also a moron. In either case, it is unlikely that you have much background in Mesozoic zoology (or, for that matter, much taste in music). Accordingly, we'll keep this pretty basic and concentrate on the familiar tetrapods.

The Mesozoic came after the Paleozoic. The Paleozoic Era ended with the Permian Period, Benton (2003)

which ended with a sort of general meltdown, sometimes called the "PT" or "End-Permian" extinction. We still aren't certain exactly what happened, but the fact that much of central Siberia turned into a sort of volcanic bubble bath for a few million years didn't help. This was, bar none, the worst mass extinction in the last 600 My. Don't get this one confused with the "KT" extinction at the *end* of the Mesozoic -- the one which finished off the dinosaurs 200 My later. That was a sumo match by comparison. That is, it eliminated some very large and conspicuous folks very quickly, but it was all very fast and civilized.

The PT extinction dragged on for at least a few hundred thousand years and resulted in the loss of perhaps 98-99% of all species of animals. The survivors of the End-Permian radiated into a world that was rather empty, and the new life forms that evolved from those survivors were sometimes quite different from those whch had come before. For example, of all the therapsids (mammal ancestors) in the world at the end of the Permian, only a few cynodonts and dicynodonts were left. Not surprisingly, they multiplied like rabbits and spread out all over the world. As they did, they encountered environments and ecological challenges quite different from those in their South African (probably) home base. So, different populations evolved in different directions.

In addition, the great legion of their dinocephalian cousins had vanished completely, leaving those large-herbivore and carnivore jobs empty. Some of those slots were filled by newly modified cynodonts and dicynodonts; but, many of those positions were taken over by archosaurian reptiles, instead. So, not only were the surviving groups changed in composition, but the balance between them changed as well. Among the tetrapods, the newly expanded range of the archosaurs created an opening for the evolution of the archosaurian dinosaurs and pterosaurs, both of which appeared just a few million years after the PT extinction. These went on to drive the dicynodonts to extinction and reduce the cynodonts to a marginal population of small, furtive night-dwellers -- the mammals. A similar, but larger, set of vacancies in the marine job market created new opportunities for other major reptile lines, which evolved several different groups of specialized sea-going forms, including the sauropterygians (plesiosaurs and their kin), ichthyosaurs, and mosasaurs.


Dinilysia **(a Cretaceous snake)**

This same story could be told about molluscs and echinoderms and even plants, which suffered much less than animals from the effects of the PT events. In each case, one or two of the big groups were completely eliminated, the rest were changed, and the old ecological balances of the Paleozoic were very thoroughly unbalanced. The entire Triassic, and most of the Jurassic, was spent getting all that sorted out. At the end of this period -- about the Late Jurassic and earliest Cretaceous -- there was another burst of evolutionary creativity associated with rising seas and relatively warm, equable climate throughout the world. Familiar examples include birds, placental mammals and angiosperm (flowering) plants. Again, even more fundamental changes were going on in the sea: rudist molluscs, new types of sharks, planktonic foraminifera, and several new types of algae, to name but a few.

Both temperature and sea level reached maxima in Aptian-Albian time, or perhaps a little later. By this time, things were getting a bit too warm in the seas, and there was some climatic deterioration. The Late Cretaceous saw a remarkable evolution of smaller animals of all kinds, perhaps at the expense of the giants of earlier Mesozoic ages. So, for example, we find the first examples of modern lizards and snakes, and mammals which were probably primates.

Of course, all these vermin might have come to nothing if a small asteroid hadn't happened to land in Mexico, 65.5 Mya. But it did, and the cycle of disaster, evolution, dispersal, and recovery continued. Speaking of which, if you're *still* interested in that Nirvana CD, forget it. Sure, Cobain could have been the TS Elliot of the Twenty-First Century had he, likewise, taken a different path. But he didn't either, and its just no use pretending otherwise.

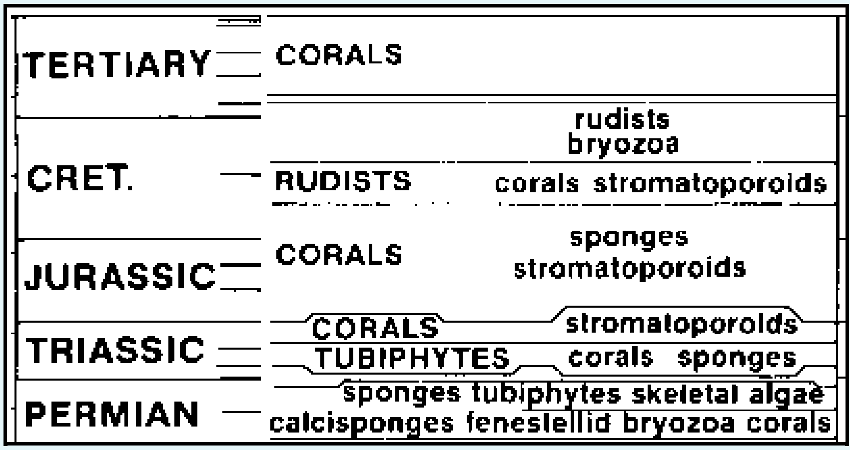
Mesozoic Reef Systems

It is easy to type "Mesozoic Reef Systems," just as it is easy to type the words "The History of the Asia." In both cases, it's a bit harder to say anything meaningful in a few words. We might try a few verbal pictures instead.

The Mesozoic began with the universal desolation of the end-Permian world. Most reef systems were devastated beyond recovery. The frothy and exhuberant dream castles of Late Permian calcareous sponge were were now in ruins -- crumbling blocks of lifeless rock, around which no fishes swam. Instead, there sprouted, here and there, the squat and flaccid mushroom shapes of pale stromatolites. These glowed a ghost-like green against the garish, toxic shades of fungal blooms which gnawed like ghouls opon the last decaying flesh of Permian life. The seas were weirdly clear. The rich planktonic rains of fusilinid forams, diatoms, and softer-bodied forms, uncounted and unknown, were gone. In deeper seas, the drifting galaxies of crystal radiolarian stars were swept away. All ocean life was strangled by anoxic waters reaching through unheard-of depths; and nothing lived that did not feed on death.

Almost two million centuries later it closed with a riot of shape and of form, leaving reefs made of corals and sponges and clams, leaving mountains of algae and snails, leaving brachiopods by the billion or more, leaving walls built by rudists on carbonate platforms with foraminiferan floors. For throughout the Triassic, Jurassic, Cretaceous, the oceans continued to rise. And as long as the waters continued to rise, the corals continued to grow. Like the rudists and algae and sponges and clams, they grew to the tops of their tropical seas, where the sun made a tropical glow.

While an interesting exercise, the attempt to deliver scientific information in blank verse suffers from certain unavoidable inefficiencies. We will therefore return to our regular bland diet of tasteless literary grits – with but with an occasional metrical lapse for particular pieces and bits. ATW040909.



TERTIARY	CORALS	
CRET.	rudists bryozoa	
	RUDISTS	corals stromatoporoids
JURASSIC	CORALS	sponges stromatoporoids
TRIASSIC	CORALS	stromatoporoids
	TUBIPHYTES	corals sponges
PERMIAN	sponges tubiphytes skeletal algae	
	calcisponges fenestellid bryozoa corals	

Image: Jurassic corals from **Jurassic Reef Park**

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The Mesozoic - 2

Phanerozoic Eon
  Paleozoic Era
  Mesozoic Era
    Triassic Period
    Jurassic Period
    Cretaceous Period
  Cenozoic Era

Marine Life in General

Mesozoic oceans were populated by a rich and diverse fauna of fish, reptiles, and a variety of cephalopod mollusks including the ammonites and the belemnites (nautiloids were also present but less common). Both these molluscan groups were adapted for speed and mobility. Fish were mostly slow moving heavy scaled ("ganoid") types, which were probably not as agile (teleosts only become predominant towards the later Cretaceous).

From the Jurassic onwards Plankton increased in diversity, with phytoplankton such as coccoliths, diatoms and silicoflagellates together with a zooplankton dominated by foraminifera and radiolarians. Arthropods such as the amphipod, decapod and isopod crustaceans together with nudibranch mollusks and the annelid and polychaete worms were also probably part of the plankton. MAK020428

Invertebrates

Annelida

The fossil record of Mesozoic annelids, like the fossil record of all annelids, is poor. We can only make a few, general remarks.

The end-Permian extinction more or less destroyed the entire Paleozoic benthic fauna. The Mesozoic benthic communities, developed an entirely new style, possibly (i.e., this is *complete* speculation) based on the very few anoxia-tolerant detritivores who would have flourished in the benthic carnage of the end-Permian. Whatever their origin, Mesozoic and Cenozoic benthic communities are dominated by infaunal (burrowing) deposit-feeders, rather than epifaunal suspension feeders. This was surely good for the annelids who are quite handy with low-oxygen, burrowing ways of making a living. Oligochaetes probably evolved in the Late Jurassic. However, they were unable to employ the usual annelid skills on land until the Late Cretaceous, when angiosperms began creating large quantities of humus, permitting the evolution of the oligochaete earthworms.

Brachiopoda

Brachiopods suffered greatly during the end-Permian extinction. They were able to make a considerable come-back during the Late Triassic, but ultimately declined and were ecologically replaced by bivalves. Their fate may have been tied to substrate. The brachiopods of the Late Triassic resurgence were strongly associated with carbonate shelves, the classic reef environment of the Late Paleozoic and Early Mesozoic. The rise in sea levels during the Jurassic and Early Cretaceous drowned these platforms on a global basis. That is, the residents of the carbonate platforms gradually found themselves too deep in the water column for sunlight to sustain photosynthesis, and the shelf ecosystems collapsed. This permitted the bivalves to "mussel" their way in, as they were better adapted to the soft and unstable sand & mud sea bottoms within the new photic zone. In fact, with the evolution of the rudists, the bivalves were able to make their own quick and sloppy reefs on even the softest substrate.

As a consequence, the surviving Mesozoic brachiopods became off-shore specialists, occupying deeper-water and more cryptic environments in crevices and on submarine cliffs below the photic zone. Some developed poisonous tissues. The more robust and globose terebratulides such as *Terebratella* and probably some species of *Tichosina* were free on the substrate. A few of these developed semi-infaunal strategies.

Mesozoic brachiopods, like many other invertebrates, show considerable differentiation between Tethyan (tropical) and Boreal (subtropical and temperate) types in the Late Triassic and Jurassic. Also like many other invertebrates, these distinctions broke down in the Cretaceous, as rising sea levels and flattened climate zonation homogenized most marine fauna.

Bryozoa

Early Mesozoic bryozoans were largely cheilostomes and cyclostomes. During the Early Cretaceous, however, the cyclostomes declined while cheilostomes diversified. The reasons for this replacement are unclear. Both suffered massive extinctions in Maastrichtian time, possibly coinciding with the more general KT extinctions. The cheilostomes rebounded during the Cenozoic. The cyclostomes generally did not. McKinney & Taylor (2001).

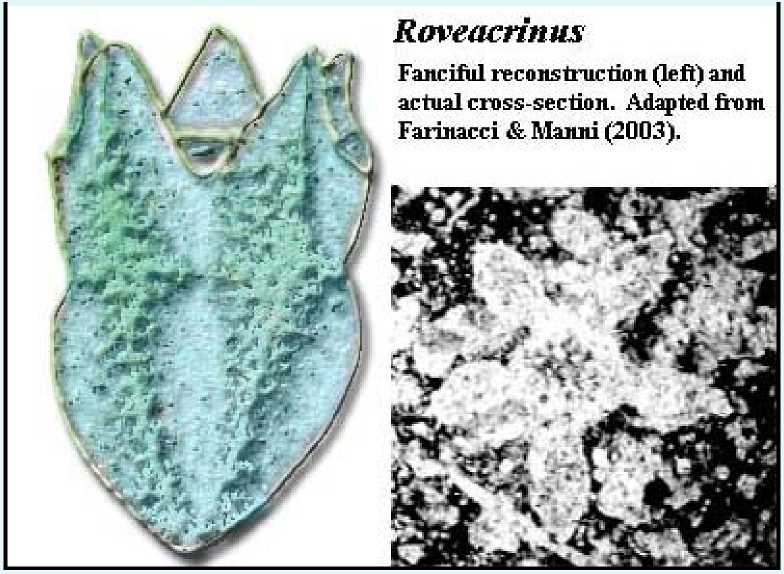
Cnidaria

Mesozoic cnidarians are mostly known from their greatest success story, the scleractinian corals. Several groups of scleractinians developed tight symbiotic relationships with photosynthetic zooxanthellae with a resulting huge boost to their productivity. The scleractinians suffered considerably from the drowning of the carbonate platforms on which their reefs were based during the Late Jurassic and Cretaceous. However, they recovered quickly after the KT extinctions.

A Santonian coral on which two smaller mushroom-shaped corals have grown.

Echinodermata

The End-Permian extinction at the end of the Paleozoic Era took a heavy toll on the stemmed echinoderms. The blastoids became extinct at that time and the crinoids suffered heavy losses. In general, Paleozoic echinoderms were epifaunal suspension and detritus feeders. Like so many high school students, their strategy was to sit more or less stationary on the sea bottom with their mouths open and wait for food to come to them. In the Mesozoic and Cenozoic, the echinoderms became more like undergraduates -- still bottom-feeders, but now willing to dig for it (infaunal detritus feeders) or, if sufficiently pressed, to go and hunt for it (armored herbivores and carnivores).



Roveacrinus

Fanciful reconstruction (left) and actual cross-section. Adapted from Farinacci & Manni (2003).

This use of rather heavy armor runs counter to a general trend among Mesozoic life forms to shed heavy plates and to depend more on speed, or on other behavioral adaptations for survival. However, behavioral strategies depend on having the neural equipment to select a response and adapt it to local conditions. Echinoderms are poorly adapted for this sort of thing because they are attractive, but brainless. So as time went on, echinoderms, like other attractive but brainless organisms, were increasingly forced to rely on heavy make-up, intimidating ornament, and a thick skin. The surviving crinoids, for example, were articulates, with rounded, closely fitting armor plates, usually bearing elaborate ornamentation. Some also gave up sessile life, left their stems behind, and became motile. These swimming crinoids, the Rovecrinidae, are discussed briefly elsewhere.

However, for the most part, the old crinoid fauna simply died out. The future of the Echinodermata lay with the Echinoidea and Asteroidea. Echinoids are rare in Paleozoic faunas, but radiated extensively during the Mesozoic and Paleogene. Paleozoic, and even Triassic, urchins have no compound plates, and the interambulacral plates are constructed in many columns **[1]**. These earliest sea urchins are generally small and lack strong spine development -- characters which developed over the course of the Mesozoic.

Porifera

Sponges as a whole did well and slowly diversified until the very end of the Mesozoic. However, this general trend is made up of varying fates of different groups of sponges. Demosponges and calcisponges recovered from the end-Permian extinction and dominated the reef fauna once more in many locations during the Late Triassic. However, they were gradually replaced by scleractinian corals. Hexactinnelids and some stromatoporoids continued as important frame builders for the coral reefs of Jurassic Europe. Demosponges and hyalosponges became more common in the Cretaceous. As sea levels rose, these sponges were sometimes able to thrive in regions which had become too deep for the corals. Mesozoic stromatoporoids (demosponges probably not related to the Paleozoic forms) were significant reef-builders in the Cretaceous. All types of reef-building sponges virtually disappeared at the KT boundary and never recovered. ATW040905

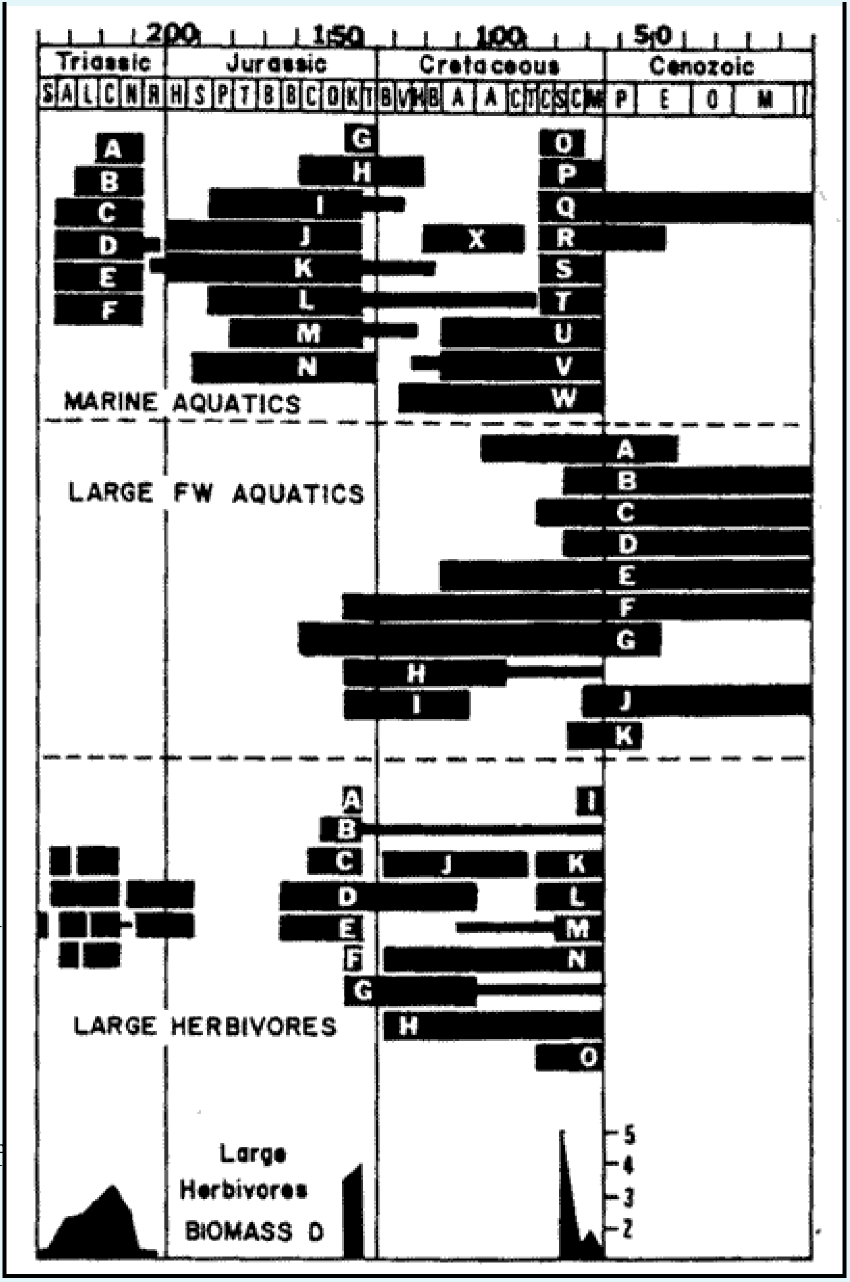
Vertebrates

Mesozoic Tetrapods

The Mesozoic era was an extremely long period of time, which saw the rise and fall of successive "dynasties" of life. At least half a dozen succesive evolutionary communities or empires of land vertebrates (tetrapods) can be distinguished. Identifying them by characteristic large herbivores, these can be called the lystrosaur (Earliest Triassic [Induan]), kannemeyeriid- traversodontid (primarily Gondwanan, though this may be sampling bias) (Early [Olenekian] to Late (Carnian) Triassic], plateosaur-vulcanodontid (Late Triassic [Norian] - Early Jurassic), sauropod- stegosaur (Middle to Late Jurassic), iguanodont- nodosaur (Early to Mid Cretaceous), and ceratopsian-hadrosaur (Late Cretaceous - Laurasia only, Gondwana was predominantly Titanosaurid, with Abelisaurid carnivores) communities or "empires". In the sea one finds what could be perhaps termed the mixosaurnothosaur (Mid Triassic), shastasaur (Late Triassic), ichthyosaur- plesiosaurid- rhomaleosaurid (Latest Triassic [Rhaetian] - Early Jurassic), ophthalmosaur-pliosaurid- metriorhynchid (Middle Jurassic-Early Cretaceous), and protostegid- elasmosaurid- mosasaur communities (Mid to Late Cretaceous).

The following diagram is from Fig. 3. of Dr Robert T. Bakker's 1977 paper "Tetrapod Mass Extinctions - A model of the regulation of speciation rates and immigration by cycles of topographic diversity" *in* A. Hallam, ed. *Patterns of Evolution as illustrated by the Fossil Record*, Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York, pp.439-68

Although subsequent research has modified some of the family rankings and stratigraphic correlations, the basic pattern remains.



Diversity of tetrapods, Early Triassic to Cretaceous. Standard marine stages are indicated by initials in boxes at top. Narrow extensions of bars indicate that the family is present but very rare. Families known from only one formation are omitted. Roman numerals at top show the successive "dynasties". Biomass D for large herbivores for Triassic taken from Fig. 2; D calculated for a few large Jurassic and Cretaceous samples from the following formations: 1, Tendaguru (Kimmeridgian); 2, Morrison (Kimmeridgian/Tithonian); 3, Old Man (Campanian); 4, Lower Edmonton A (Campanian/Maastrichtian); 5, Lower Edmonton B (Maastrichtian); 6, Lance-Hell Creek-Frenchman (latest Maastrichtian).

Family abbreviations:

Marine Aquatics: A = henodontids; B = pachypleurosaurids; C = mixosaurids; D= placocheliids; E = nothosaurids; F = shastasaurids; 0 = pliosaurids; H = metriorhynchids; I= rhomaleosaurids; J = ichthyosaurids; K = plesiosaurids and cryptoclidids; L = stenopterygiids; M = teleosaurids; N = rhamphorhynchids; O = protostegids; P = mosasaurids; Q = cheloniids; R = toxocheliids; S = ichthyornids; T = hesperornids; U = elasmosaurids; V = polycotylids; W = ornithocheirids (pteranodontids); X = ornithodesmids.

Large Fresh-Water Aquatics: A =amphisbaenids; B = varanids; C = pelomedusids; D = dermatemyids; E = crocodylids; F = trionychids; G = pholidosaurids; H = goniopholids; I = glyptopids; J = emyids; K = champsosaurids.

The sampling of non-marine tetrapods during the first eight stages of the Jurassic is so poor that the records are not worth plotting on this compilation.

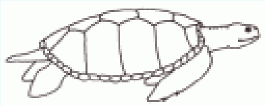
Large Terrestrial Herbivores: A = camarasaurids; B = diplodocids; C = stegosaurids; D = brachiosaurids; E = cetiosaurids; F = camptosaurids; G = hypsilophodontids; H = panoplosaurids; f = ceratopsids; J = iguanodontids; K = hadrosaurids; L = protoceratopsids; M = titanosaurids; N = pachycephalosaurids; 0 = euoplocephalids.

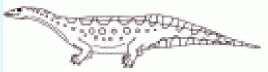
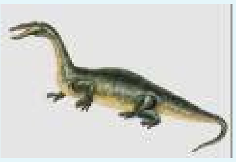
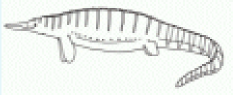
Marine Reptiles

illustration © Walking with Dinosaurs © 1999 ABC, BBC

During the Mesozoic era there were a number of lineages of marine reptiles. In comparison with the mammals, many more types of reptiles, having attained an existence on land, returned to the seas. Aquatic adaptation (whether freshwater, estuarine, or marine) is a common phenomenon among reptiles, due to their low metabolic rate, tolerance of anoxia and of low body temperatures, and easy ability to make use of fermentative metabolism for muscle activity. Moreover it does not require great structural or physiological changes, as indicated by the modern marine iguana. Reptiles move with a naturally sinuous motion, which is easily adaptable to swimming (as it comes originally from the swimming motion of the fish). In marine iguanas aquatic locomotion requires only one quarter the metabolic activity of terrestrial locomotion. When looked at this way, it is not surprising that reptiles have returned to the water, like their tetrapod and fish ancestors, whenever conditions were favourable.

The following is a list of aquatic reptiles, with some basic data. *Note*: Many of these pages are under construction or very incomplete. So here they are: the marvelous Mesozoic marine reptiles:

Picture	name	time-span	habitat	location	approx size	food
	**Plesiochelyidae**	late Jurassic [Kimmeridgian] to early Cretaceous	estuarine, near shore marine	Central to East Laurasia	shell c.75 cm???	invertebrates, fish, plant material?
	**Desmatochelyidae + Protostegidae**	Cretaceous **Desmatochelyidae** - Albanian to Maastrichtian **Protostegidae** - Turonian to Maastrichtian	open ocean	**Desmatochelyidae** - cosmopolitan **Protostegidae** - west Laurasia ("inland sea") only?	**Desmatochelyidae** - av. 1.2 meters (shell) **Protostegidae** - up to 4 meters long (*Archelon*)	jellyfish, other invertebrates, fish?
	**Toxochelyidae**	late Cretaceous (Coniacian to Maastrichtian)	open ocean	west Laurasia ("inland sea" to west Atlantic)	shell 60-120 cm	jellyfish, other invertebrates, fish?
		latest Cretaceous [Maastrichtian] to	open	Worldwide	75 cm to over 1	jellyfish, other

	**Cheloniidae**	Recent	ocean		meter long	invertebrates, fish?
	**Ichthyosauria**	Triassic to Jurassic, a few stragglers into the Cretaceous	open ocean	world wide	1 to 23 meters	mostly fish, also cephalopods, smaller reptiles
	**Placodontia**	Triassic	near shore marine	Tethys Sea	1 to 2.5 meters	probably shellfish (Bivalve mollusks)
	**Pachypleurosauridae**	Middle Triassic [Early Anisian to Ladinian]	estuarine, near shore marine	world wide	20 cm to 1 meter	fish, crustacea, etc
	**Nothosauridae**	Middle to early late Triassic [Anisian to Carnian]	near shore marine	world-wide	2 to 8 meters	mostly fish
	**Plesiosauria**	rare in the Triassic common in the Jurassic and Cretaceous	open ocean (a few estuarine species)	world wide	2 to 14 meters	fish, cephalopods, other reptiles
	**Mosasauroidea**	**Aigialosauridae** Late Jurassic to Early late Cretaceous (Tithonian to Turonian) **Mosasauridae:** late Cretaceous (Turonian to Maastrichtian)	open ocean	**Aigialosauridae:** Europe **Mosasauridae:** world wide	**Aigialosauridae:** av. 1 meter **Mosasauridae:** 2.5 to 17 meters	fish, cephalopods, other reptiles
	**Thalattosauria**	Triassic	near shore marine	Tethys Sea, also west Laurasia	about 1.5 meters	fish, crustacea etc
	***Nanchangosaurus***	earliest Middle Triassic (Early Anisian)	near-shore and estuarine	China	no info (~1 meter?)	probably fish, crustacea, etc
	**Teleosauridae**	Jurassic	estuarine, near shore marine	world wide	2 to 6 meters	mostly fish
	**Metriorhynchidae**	Jurassic to Early Cretaceous	open ocean	world wide	2 to 6 meters	mostly fish

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Mesozoic References

References

Benton, MJ & DAT Harper (1997), **Basic Paleontology**. Longman, 342 pp.

Blake, DB (2000), *The class Asteroidea (Echinodermata): Fossils and the base of the crown group*. **Amer. Zool.** 40:316–325. WWW

Blake, DB & BS Kues (2002), *Homeomorphy in the Asteroidea (Echinodermata); a new Late Cretaceous genus and species from Colorado*. **J. Paleontol.** 76: 1007–1013. WWW.

Cox, B., RJG Savage, B Gardiner & D Dixon (1988), **The Simon and Schuster Encyclopedia of Dinosaurs and Prehistoric Creatures : A Visual Who's Who of Prehistoric Life**. Simon & Schuster, 312 pp.

DeBraga, M. & RL Carroll (1993) *The origin of mosasaurs as a model of macroevolutionary patterns and processes*. **Evolutionary Biology** 27: 245-322.

Creisler, B (2000) ***Mosasauridae Translation and Pronunciation Guide*** iNet.

Farinacci, A & R Manni (2003), *Roveacrinids from the northern Arabian Plate in SE Turkey*. **Turkish J. Earth Sci.** 12: 209-214. **WWW.**

Jenkyns, HC & PA Wilson (1999), *Stratigraphy, paleoceanography, and evolution of cretaceous Pacific guyots: relics from a greenhouse Earth*. **Am. J. Sci.** 299: 341–392.

Lehmann, C, DA Osleger, IP Montañez, W Sliter, A Arnaud-Vanneau & J Banner (1999), *Evolution of Cupido and Coahuila carbonate platforms, Early Cretaceous, northeastern Mexico*. **GSA Bull.** 111: 1010–1029. **WWW**.

McKerrow, WS [ed.] (1978), **The Ecology of Fossils: An Illustrated Guide**. Duckworth.

McKinney, FK & PD Taylor (2001), *Bryozoan generic extinctions and originations during the last one hundred million years*. **Paleontol. Elec.**

Miller, KG, PJ Sugarman, JV Browning, MA Kominz, JC Hernández, RK Olsson, JD Wright, MD Feigenson & W Van Sickel (2003), *Late Cretaceous chronology of large, rapid sea-level changes: Glacioeustasy during the greenhouse world*. **Geology** 31: 585–588.

Tweet, J (2004) ***Thescelosaurus!*** iNet.

Williston, SW (1898) Mosasaurs, The University Geological Survey of Kansas, Volume IV, Paleontology, Part V, pp. 81-347

Notes

[1] The "tube feet" of sea urchins look like very short tentacles. You can see them moving between the spines of any live urchin. The tube feet are arranged in strips which run from the top of the urchin (apical disk) to the bottom. These strips are called *ambulacral zones*. The tube feet are connected to the urchin's internal water vascular system. The armor plates of the ambulacral zones are known, naturally enough, as *ambulacral plates*. The plates between the ambulacral zones are *interambulacral plates*. The ambulacral plates of many modern urchins are *compound*. That is, they are completely fused. The arrangement of ambulacral plates is an important tool of echinoid taxonomy. This is all explained, with figures and much additional information, at Skeletal morphology of regular echinoids from the **Natural History Museum (London)**. The invertebrate part of the NHM site, unlike the awful dinosaur section, is an informative resource and worth browsing at length.

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Triassic period

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Triassic Period

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The Triassic Period

The Triassic Period of the Mesozoic Era: 251 to 200 million years ago

Paleozoic
  Permian
Mesozoic
  Triassic
    Early Triassic
    Middle Triassic
    Late Triassic
  Jurassic
  Cretaceous

Introduction

In 1834 Friedrich August von Alberti recognized three distinctive formations in southern Germany. These are the Bunter (lower), Muschelkalk (middle) and Keuper (upper) formations, which he grouped into the Trias, and today this is called the Triassic System. The old term Trias is often used in Europe, even by English-speaking geologists. The Muschelchalk or "mussel limestone" contains many fossils of marine organisms.

The Triassic Period is the first geological period of the Mesozoic era or "Age of Reptiles". It was during this time that Archosauromorph ("ruling") reptiles achieved dominance on land, and many types of marine reptiles flourished in the seas.

Image: graphic from Naturmuseum Senckenberg (Centre for Biodiversity Research).

Triassic Climates and Continents

The Triassic saw the single vast supercontinent of Pangea straddling the equator. This was shaped rather like a giant "pac man". Where the mouth is the Tethys sea. All around Pangea was a huge ocean, Panthalassia. Yet Pangea had no sooner formed then it began tearing apart, with rift valleys developing between North America and the African portion of Gondwanaland. Large crustal blocks subside, creating physiographic basins. The Tethys Sea intrudes into Pangea from the east, leading to the division between Laurasia in the north and Gondwana in the south. The climate was warm but for the most part dry, and the middle of Pangea was very arid.

Stratigraphy

The original terminology of Bunter (lower), Muschelkalk (middle) and Rhaetic (upper) Triassic has been replaced by a more standardized series of ages, as follows:

Period	**Epoch**	**Age**	**Base (beginning)**	**Duration**
Jurassic	**Early Jurassic**	**Hettangian**	**199.6**	**3.1**
Triassic	Late Triassic	**Rhaetian**	**203.6 mya**	**4.0**
		Norian	**216.5 mya**	**12.9**
		Carnian	**228.0 mya**	**11.5**
	Middle Triassic	**Ladinian**	**237.0 mya**	**9.0**
		Anisian	**245.0 mya**	**8.0**
	Early Triassic (Scythian)	**Olenekian (Nammalian & Spathian)**	**249.7 mya**	**4.7**
		Induan (Griesbachian)	**251.0 mya**	**1.3**
Permian	**Lopingian**	**Changhsingian**	**253.8**	**2.8**

An older system is still widely used for the Early Triassic, referred to as the *Scythian*. In this system, the first age of the Triassic is the *Griebachian*, which is probably somewhat longer than the Induan. The Oleneckian is divided into the *Nammalian* (which is subdivided into *Dienerian* and *Smithian*) and the *Spathian Ages*.

Triassic Land Plants

Triassic land plants included a diverse assortment of plants characteristic of the "Mesophyta" ("middle flora" - from Late Permian to Middle Cretaceous). The great lycopod and cordaite trees of the Carboniferous and Permian were long gone, although smaller lycopods survived. *Calamites*-like forms were however still important, perhaps fulfilling the ecological role of bamboo today, with *Neocalamites* reaching fifteen meters in height. Ferns also continued to flourish, and dominated Triassic floras.

The great coal swamp lycopods, sphenopsids, and tree-ferns, which reproduced by spores and hence required moist habitats, didn't do too well in the dry Triassic climate. The drier climate - especially the arid interior - encouraged the evergreen conifers and other gymnosperms, which reproduced by exposed seeds and wind pollination. These include conifers (including many modern families), pteridosperms (such as *Dicrodium*, above), cycads, Bennettiales, and ginkgos [Gastaldo 1997]. Xeromorphic (dry adapted) characteristics were common, such as scale-leaved conifers and thick-cuticled pteridosperms and cycads [Behrensmeyer et al 1992 p.330]. Moister conditions meant plant life was more abundant in the coastal regions [McGowan iNet]. There were also several main biotic provinces, determined perhaps by climatic factors.

In spite of the single global landmass, Triassic terrestrial biotas were quite provincial, probably due to climatic rather than geographical factors: monsoon and extreme seasonality caused by symmetrical placement of Pangea over the equator. Biotas are thus divided into a northern, Pangean, and a southern, Gondwanan, province, with several overlaps such as India where Gondwanan flora occurs with Laurasian tetrapods* (land animals). The plant division is more marked than the animal one.

The Laurasian/Pangaean Flora

The Laurasian Flora is made up of; a mixture of primitive conifers - Voltziaceae and Lebachiaceae - along with cycads, bennettitales, ginkgos (especially in northern latitudes), ground and tree ferns, and sphenopsids. .The conifers and ginkgos seem to have been medium-sized to large trees that formed diffuse canopies.

The northern part of Pangea was lusher, with forests of tree-ferns and gingkoaleans, and forest-floors covered in luxuriant fern growth [McGowan iNet]. Araucariacean conifers were the predominate large trees in Laurasia, with primitive gingkoaleans (e.g. *Sphenobaiera* and *Glossphyllum*) and cycads as lower story and underbrush [Behrensmeyer *et al* 1992 p.334]. The equatorial region was less favorable for much of period and the forests down here were sparse, consisting of conifers (especially Araucariaceae) and cycads [McGowan iNet]. The situation improved during the late Triassic, with moist conditions that encouraged cynodont herbivores [Olsen, et al])

The Gondwanan Flora

The Permian *Glossopteris* flora disappears, to be replaced by the corystospermaceaeous seed-fern *Dicrodium*. *Dicrodium* occurs in all assemblages, from heath and broad-leafed forest to dry woodlands. Sometimes it is the only species present. Voltziacean and primitive podocarpaceous conifers, peltaspermaceous seed ferns, and some Laurasian cycads and ginkgos also occur in Gondwanan floras.

In some parts of Gondwana, trees were relegated to a secondary role by giant seed ferns which grew up to form the top storey of the forest, with smaller ferns forming the undergrowth. [McGowan iNet] Otherwise, voltziacean and primitive Podocarpaceae were the predominant conifers, especially during the middle and late Triassic [Behrensmeyer *et al* 1992 p.339]. The seed fern *Dicrodium* was ubiquitous for most of the period.

Different types of animals are associated with each floral type. In the south, therapsids like sheep-sized herbivorous Traversodonts predominated; in the north, archosaurs were more common.

Invertebrates

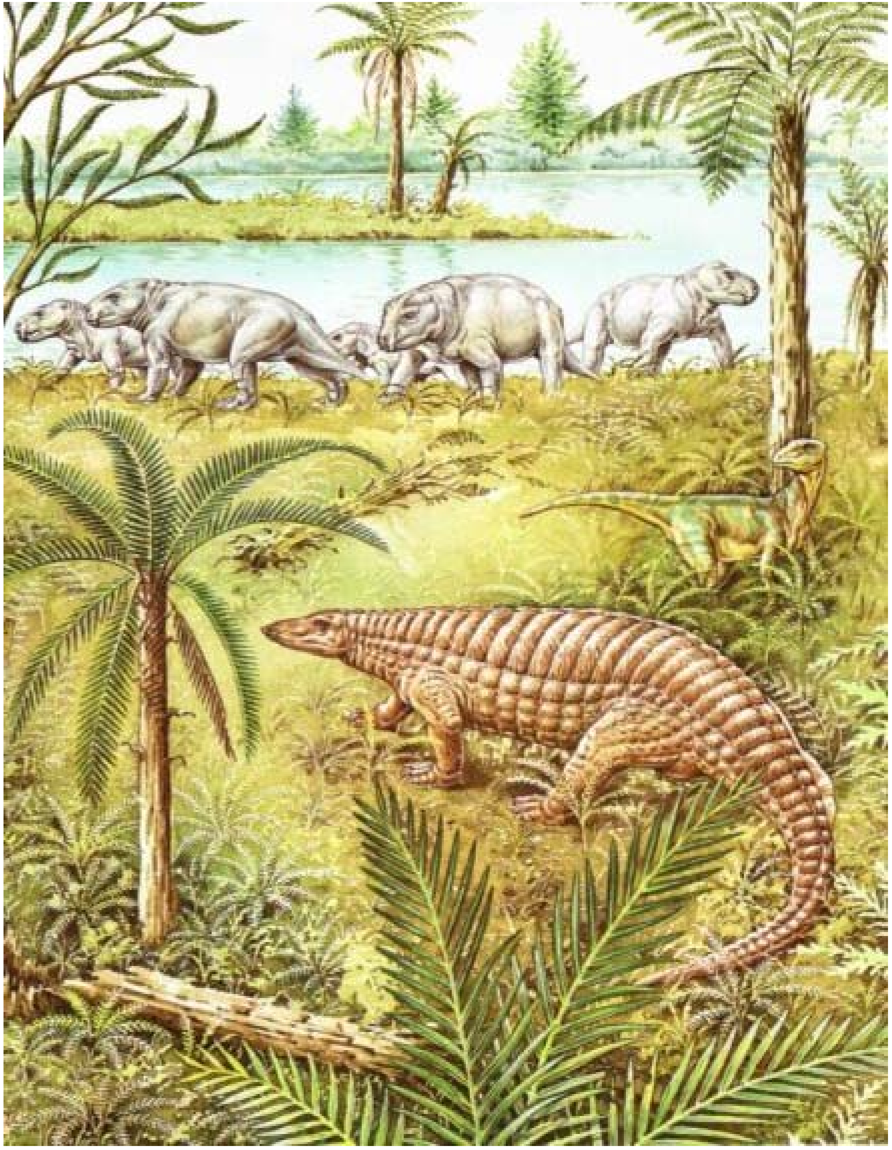
As regards the history of life on Earth, the Triassic period was significant for a number of reasons. This was a time of transition, in which many old forms of life died out, and new, and sometimes even modern, ones appeared. The fusilinid foraminifers, lacy bryozoans, rugose corals and trilobites that had characterized the late Paleozoic all disappeared.

Bivalves, ammonoids and brachiopods all recovered from the Permian extinction to dominate the Triassic. In the case of the brachiopods, Spirifid, Terebratulid, and Rhynchonellids are all well represented. Ammonoids include a huge number of families with ceratitic suture lines, these all evolved from a single lineage that survived the end-Permian extinction event. So diverse are these ammonoids that the Triassic could easily be called the age of Ceratites. In addition to the ceratites, other forms with more complex (ammonitic) suture patterns appear for the first time. The ammonoids are also joined by new groups of coloeids or squid-like forms, including the Belemnites, a group that was to become abundant during the Jurassic..

Most modern groups of invertebrates also appeared during the Triassic. A number of new orders of echinoderms (starfish, sea urchins and their relatives) evolve, although echinoids remain rare and of specialized types. Modern scleractinian corals appear, and in the equatorial Tethyean regions form small patch reefs no more than a meter high and often build on the decaying remains of sponge reefs. There are no massive reefs like those that exist today.

There are very little remains of phytoplanktonic. It is likely that the phytoplanktonic of the time were - soft-bodied forms, and hence they were not preserved as fossils.

Insects included many modern orders, as well as several extinct lineages. Little is known of other terrestrial groups of arthropods, but since they are known from both the Paleozoic and the later Mesozoic they must have been present.



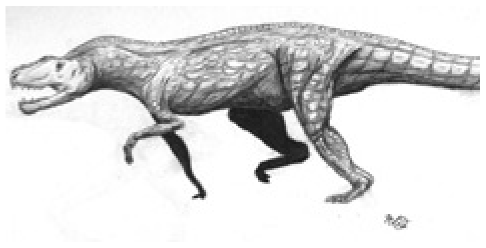
A scene from the late Carnian of south-west Pangea (Gondwana), as represented by fossil remains from the Ischigualasto Formation, San Juan Province, Argentina. In the foreground is the armoured thecodont *Stagonolepis*, about 2.5 meters in length. In the immediate foreground is the cycad *Pseudoctenis* (with palm-like leaves), and to the left of *Stagonolepis* another cycad, *Leptocycas* (resembling a small palm). A bit further back and to the right is the early ornithischian dinosaur *Pisanosaurus*, about a meter in length, standing under a Dicksoniaceous fern tree. Further back are a small group of large (up to 2 meters long) herbivorous cynodonts of the genus *Exaeretodon*, which existed in great numbers worldwide during the Carnian. In the far background are conifers. Dipteridacean ferns and *Dicrodium* pteridosperms (seed-ferns) provide a luxuriant undergrowth

Illustration from *The Cambridge Encyclopedia of Life Sciences*, ed. Adrian Friday & David S. Ingram, © Cambridge University Press 1985..

Vertebrates

During this time, aided perhaps by better adaptation to arid environments, the ectothermic ("coldblooded") archosauromorphs attained prominence over the endothermic ("warm-blooded") Therapsids or "mammal-like reptiles". Some of these archosauromorphs belonged to the Prolacertiformes, Archosauriformes, Trilophosauridae, and Rhynchosauria These basal archosauromorphs and archosaurs were a diverse group, that included several semi-aquatic crocodile-like forms (Proterosuchidae, Proterochampsidae, Phytosauridae), early lumbering semi-aquatic carnivores (Erythosuchidae), more advanced and active large terrestrial carnivores (Prestosuchidae, Ornithosuchidae, Poposauridae, and Raiusuchidae), small, active bipedal forms, armoured herbivores (aetosaurs), lightly built quadrupeds that were ironically related to true crocodiles, and many more.

Towards the end of the Triassic, several new and more advanced archosaur groups evolved from the earlier forms. These were the dinosaurs and the pterosaurs (which were closely related), and the small terrestrial sphenosuchian Crocodylomorpha, the "greyhounds" of the reptile world.



The late Triassic rauisuchian thecodont *Postosuchus*. Length 4 meters. Illustration © Robert Gay

There were also many types of small lizard-like non-archosaurian reptiles like Younginiformes and Paliguanids, but little is known of them. The procolophonids - stubby herbivorous lizards, were also very common. The rivers, ponds and lakes were populated by large temnospondyls, of which the Capitosauria were frequently one or two meters in length (the great *Mastodonsaurus* may have reached four or five meters), and Ceratodan lungfish were also common. In the seas were an unprecedented diversity of marine reptiles - the dolphin-like ichthyosaurs, the lizard-like pachypleurosaurs and thalattosaurs, the long-necked seal-like nothosaurs, walrus-like placodonts, the turtle-like henodonts, and the long-necked Pistosaurs. Most of these animals were seriously diminished by the end-Carnian extinction event (possibly caused by an extraterrestrial impact - a comet or asteroid). New forms of animal life evolved to take their place, or suddenly came into dominance after millions of years of obscurity. These included the archosaurian dinosaurs, pterosaurs ("flying reptiles"), and proto-crocodiles. Various forms of lizard-like diapsids (non-archosaurian reptiles) also appeared - choristoderes, and Eolacertians (including the gliding Kheunosaurs) and Sphenodonta, along with the first tortoises.

Following the extinction of many therapsids and parareptiles at the end of the Permian, new dynasties of synapsids arose. These included more advanced therapsids such a the cynodonts. Cynodonts had always been a minor group during the Permian, but they now diversified to a great degree. The dicynodonts were represented for the most part by a single family of large forms. The cynodonts were of small to moderate in size. The largest types (such as *Cynognathus*) only occurred during the earlier Triassic, although several large herbivore types (traversodontids like *Exaeretodon*, see illustration above) appeared later. They were distinguished by a number of mammalian traits. By the Late Triassic they had given rise to the mammals, although one family, the Tritylodontidae, were to continue right through to the Early Cretaceous.

The first true mammals also appeared at the end of the very end of the period. The mammals were to remain insignificant throughout the whole of the Mesozoic era and only come into their own after the extinction of the dinosaurs. The ancestors of small familiar animals like frogs and possibly also lizards also first appear at this time.

Vertebrates - The Land Vertebrate Zones

In a number of papers [Lucas 1998, Lucas 1999], Dr Spencer Lucas and coworkers present a Triassic tetrapod biochronology, in terms of common global faunas. (During the Triassic, the existence of a single landmass enabled most animals to wander very widely). This incorporates earlier biochronologies based on the South African (Karoo), West and East European Argentinean, Chinese, and North American sequences. The series is as follows.

Land Vertebrate Faunal Zones - stratigraphic correlation

Geological Age	Broom, Kitching, etc South Africa	xxxx Russia (Perm region)	Bonaparte Argentina and Brazil	Lucas China	Lucas & Hunt West USA	Huber et al East USA	Lucas Global
Rhaetian (and late Norian?)			Coloradian		Apachean	Cliftonian	Apachean
Norian					Revueltian	Neshanician	Revueltian
latest Carnian (late Tuvalian)			Ischigualastian **note**		Adamanian	Conewagian	Adamanian
early part of late Carnian (early Tuvalian)					Otischalkian	Sanfordian	Otischalkian
early Carnian? (or latest Ladinian)			Chanarian **note**				another LVF between the Berdyankian and Otischalkian?
Ladinian		Zone VII					Berdyankian
Early or Middle Anisian **note**		Donguz	Ningwuan			Economian	Perovkan
Late Olenekian / Early Anisian **note**	*Cynognathus* Zone	Zone VI (Bashkunchak)	Puestoviejan	Oedosian			Nonesian LVF
Olenekian		Zone V (Vetluga)		Fuguan			

Induan	(*Procolophon* Zone) *Lystrosaurus* Zone	(*Lystrosaurus* Zone equivalent)		Jimsarian			Lootsbergian **note**

Notes:

1 (according to Lucas, Adamanian only. However this is a highly endemic fauna, and may represent an ecological succession. Hence it is possible it spans several faunal ages)

2 tentatively placed by Lucas in the Berdyankian. However the known faunas of this period of endemic with little shared genera. Hence this attribution is provisional

3 according to Shishkin this would more likely be at least middle Anisian

4 according to Shishkin this would extend to at least early Anisian

5 according to Shishkin this would extend to early Olenekian

The following gives a list of some of the animals that occur at each faunal zone

Land Vertebrate Faunal Zones - representative genera

Geological Age	Land Vertebrate Faunal Zone	Tetrapod Index fossils
Rhaetian (and late Norian?)	Apachean	*Redondasaurus* (= *Pseudopalatus*?), *Redondasuchus*, *Riojasaurus*
Norian	Revueltian LVF	*Typothorax*, *Aetosaurus*, *Pseudopalatus*, *Nicrosaurus*, *Mystriosuchus*.
latest Carnian (late Tuvalian)	Adamanian	*Scaphonyx*, *Stagonolepis Ischigualastia*, *Rutiodon*, *Leptosuchus*, and *Smilosuchus*
earlier late Carnian (early Tuvalian)	Otischalkian	*Paleorhinus*, *Angistorhinus*, *Longosuchus* (= *Lucasuchus*, *"Stagonolepis" meadi*), *Metoposaurus*, *Doswellia*.
Ladinian (and part of the early Carnian?)	Berdyankian LVF	*Mastodonsaurus*, *Massetognathus*, *Stahleckeria*, *Dinodontosaurus*
Early or Middle Anisian	Perovkan LVF	*Eryosuchus*, *Eocyclotosaurus*, *Shansiodon*, *Scalenodon*, *Parakannemeyeria*, *Sinokannemeyeria*, *Kannemeyeria simocephalus*.
Late Olenekian / Early Anisian	Nonesian LVF	*Parotosuchus*, *Trematosuchus*, *Erythrosuchus*, *Cynognathus*, *Diademodon*, *Trirachodon*, *Kannemeyeria cristarhynchus*.
Induan	Lootsbergian LVF	*Wetlugasaurus*, *Tupilakosaurus*, *Luzocephalus*, *Lydekkerina*, *Procolophon*, *Lystrosaurus*, *Scaloposaurus*, *Thrinaxodon*, *Proterosuchus* (= *Chasmatosaurus*), *Prolacerta*

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The Early Triassic

The Early Triassic Epoch of the Triassic Period: 251 to 245 million years ago

Paleozoic
  Permian
    Lopingian
Mesozoic
  Triassic
    Early Triassic
      Induan
      Olenekian
    Middle Triassic
    Late Triassic
  Jurassic
  Cretaceous

Stratigraphy
Early Terrestrial Biotas

image courtesy of Mathematical Com

The later Early Triassic (Olenekian age) Archosauriform *Garjainia*, a member of the family Eyrthosuchidae. These large animals, which reached 3 meters and more in length, were the first big predators of the Mesozoic era.

Stratigraphy

The Early Triassic period is also known as the Scythian epoch. The following table shows the Scythian epoch's main subdivisions. Because this stage of Earth history did not last very long, we are only considering it in terms of its two main subdivisions, the Induan and the Olenekian. Nevertheless, this was a period of great change and drama, as whole new lineages and clades of animals radiated into the empty niches vacated by the Permian fauna, and the evolutionary battle for the supremacy of the land was waged. The hot dry Pangean deserts of the Triassic would witness the competition between the synapsid proto-mammals (therapsida) that had dominated the land uptil now, and the newly emerged archosaurian reptiles (thecodonts). And in the arid climes of the early Mesozoic, the reptiles had an obvious metabolic advantage, despite the superior locomation and care of young behavior of the mammals. MAK

Early Triassic (Scythian)	Olenekian	**Spathian**	
		Nammalian	**Smithian**
	Induan (=Brahmanian)		**Dienerian** (=Gandarian)
		Griesbachian (= Gangetian)	

Early Terrestrial Biotas

Early Triassic marine biotas were seriously impoverished. Recovery from the extinctions at the end of the Permian was slow for many groups. Many types of corals, brachiopods, molluscs, echinoderms, and other invertebrates had disappeared altogether, and many survivors remained hidden (possibly in geographically restricted environments) before returning as "lazurus taxa" during the middle or late Triassic.

With the extinction of many typically Paleozoic faunas, the most common Early Triassic hard-shelled marine invertebrates were bivalves, gastropods, ammonoids, echinoids, and a few articulate brachiopods. This mix of invertebrates constitutes the Modern Evolutionary fauna, even though most of these forms were also present in the Paleozoic Evolutionary Fauna. However, other typically Palaeozoic forms like Strophomenid Brachhiopods, Trilobites, Blastoids, and many type of Crinoids are gone.

On land, the period that followed the great Permian extinction was also an important time. The increasing aridity further contributed to the ascendency of the seed-bearing Gymnosperms over the spore-bearing plants.

As for the tetrapods, the few surviving reptiles became the ancestors of all later Mesozoic animals. The most common and widespread animal, *Lystrosaurus*, was a medium-sized herbivore, a dicynodont, a distant relative of the mammals. The only other large animals were the labyrinthodont (temnospondyl) amphibians and the semi-aquatic *Proterosuchus*, the latter in size, appearance, and habits, probably resembling a small (1.5 meter) unarmoured crocodile. We are used to thinking of prehistoric animals as all giant-sized - the great brontosaurus and tyrannosaurus of the Mesozoic for example; or the giant mammals of the last age (the Pleistocene). But at this particular period in the Earth's history all the animals were only moderately sized. Such a "Lilliput Effect" (which concerned both invertebrates [Price-Lloyd and Twitchett 2002] and veretbrates, may be the logical result of a big extinction event. Several million years further on in the Early Triassic, larger animals *did* appear; *Lystrosaurus* was replaced by the ox-sized *Kannemeyeria*, and large carnivores such as wolf-sized therapsid *Cynognathus* and the large archosaurs *Garjainia* (see illustration above) and *Erythrosuchus* also made their appearance. They were accompanied by many smaller animals, whilst many of the Permian hold-overs like the carnivorous Moschorhinids dissappeared (only teh lizard like Procolophonids flourished). These reptiles were the largest animals of their day (*Erythrosuchus* had a skull alone a meter in length), and were not surpassed in size until the rise of the bigger dinosaurs near the end of the Triassic.

These terrestrial animals were accompanied by various types of large temnospondyl amphibians belonging to the Capitosaur clade. In fact, the capitosaurs were to dominate the freshwater ecosystems for much of the Triassic. MAK

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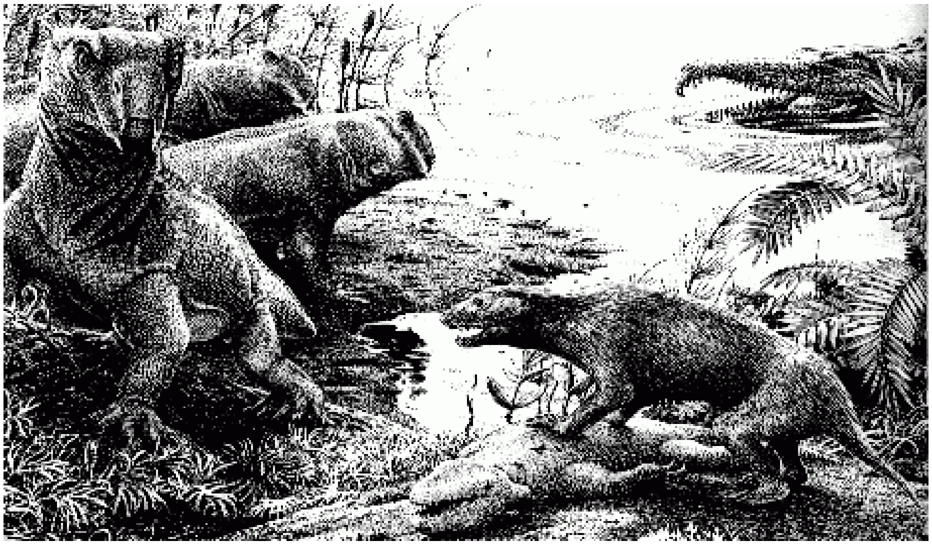
The Induan - 1

The Induan Age of the Early Triassic Epoch: 251 to 250 million years ago

- Paleozoic
  - Permian
    - Lopingian
      - Changhsingian
- Mesozoic
  - Triassic
    - Early Triassic
      - Induan
      - Oleneckian
    - Middle Triassic
    - Late Triassic
  - Jurassic

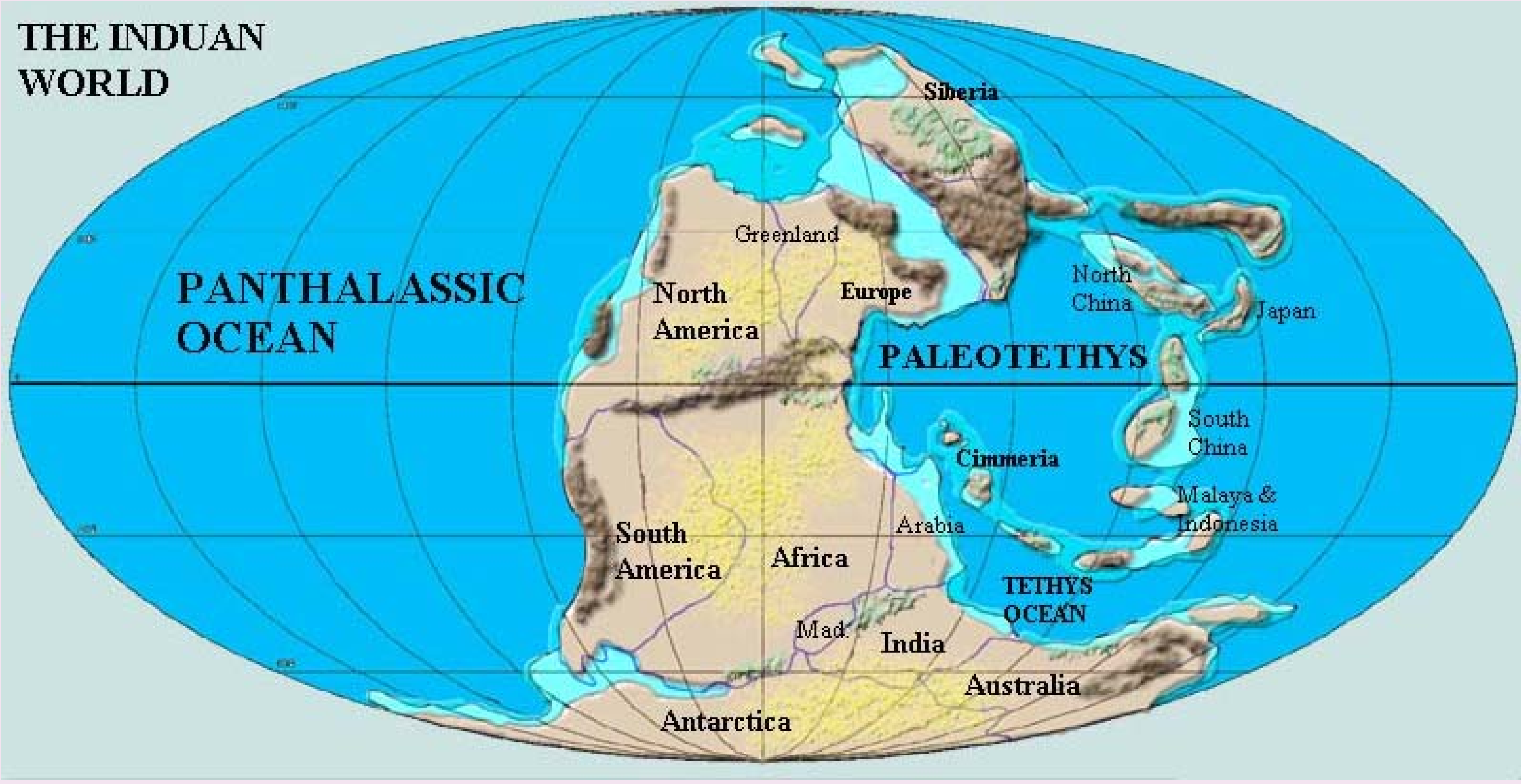
Introduction - Dawn of the Mesozoic

During the Induan age, the survivors of the greatest disaster the Phanerozoic biosphere had faced emerged to inherit the Earth. The Mesozoic Era had begun



The drawing above shows some of the animals that were around at this time. Many of these forms had a cosmopolitan distribution. All these animals are known from the Middle Beaufort *Lystrosaurus* Assemblage Zone (Karoo Basin of South Africa). The herbivores were squat quadrupedal forms, belonging to the genus *Lystrosaurus*, an animal a little over a meter in length (above, and left on the drawing on the right). The small (about 50 cm) carnivorous and insectivorous cynodont *Thrinaxodon* represents a more mammalian form; one is shown here about to feed on a dead temnospondyl amphibian. The semi-aquatic *Proterosuchus* (1.5 metres in length) populated the rivers and streams, these resembled small crocodiles but lacked the armoured scutes (note - in this drawing the *Proterosuchus* appears much too large; it was only a little longer than a large Lystrosaur and a fraction the weight, and is also incorrectly shown with armour on its neck).

The Geography of the Induan



The geology of the Induan is rather poorly known. There are relatively few Induan exposures, particularly for the early part of the Age. With respect to continental drift, the Induan seems to represent a brief hiatus, just before the tectonic storm that ripped Pangea apart. The great Tethys Rift had already whittled the Cimmerian lands and Southeast Asia from the Gondwanan landmass, but the Tethys Ocean remained small, and the rate of northward movement seems to have been relatively slow. The northern Siberian terranes were still accreting to the mainland, and North China and Amuria (just to the north of China) remained unconnected to Siberia.

We have indicated a continuous continental seaway separating Eurasia from Siberia, sometimes called the Meliata-Halstatt Ocean. This may be premature. However, this seaway was not a completely consistent feature and may have come and gone a number of times. Conversely, the Sundance Sea along the western continental margin of North America, is shown as a tiny indentation. It, too, came and went several times, and its size here is arbitrary.

The major geological event of the Induan, especially its earliest years, was the highly active vulcanism in Siberia and along what would become the equatorial rift separating North America and Europe from Africa and South America. Whether this caused or contributed to the end-Permian extinction is unknown, although many workers are confident that it did. Another contributing factor may have been the very low sea levels, certainly the lowest of the Mesozoic, and possibly the lowest of the entire Phanerozoic. ATW030627.

The Climate of the Induan

"The Morning After Death"

Of all the ages of the Earth, the Induan should by rights be near the top of the list of those attracting interest and investigation. This short age, a mere five million years at most (and much less according to some workers) is the first Age of the Mesozoic and occurred immediately after the greatest extinction of the Phanerozoic. Unlike the end-Cretaceous event which closed the Mesozoic, this was probably not caused by some singular catastrophe. Unlike the Verangian, Ordovician or Pleistocene Ice Ages, we cannot blame the sun or the weather or the temperature. The world itself seems to have become toxic in some as yet uncertain way.

There is very little agreement on the conditions which caused the extinction. A number of unusual conditions were present at the end of the Permian and seem to have continued well into the Induan. Not unexpectedly, we also find that the recovery of the world's animal life was also delayed until the last half of the Induan. In some areas, notably the marginal seas of Gondwana, recovery was even later. We can list these unusual factors, roughly in order of certainty, from most certain to hotly debated:

1. the climate was unusually dry, with vast areas of desert.

2. sea levels were very low.

3. the seas were anoxic. Not only was the deep sea depleted in oxygen, but even shallow waters were unaerated. For the period right around the beginning of the Induan, the oceans may have been without oxygen below 10-20m. The extent of anoxia and rate of recovery are unclear and may have varied from place to place.

4. the carbon dioxide content of the atmosphere was very high, possibly related to the vulcanism mentioned above.

5. the climate was intensely hot (or was periodically hot, or was periodically very hot, then very cold).

6. the level of atmospheric oxygen was unusually low.

7. the number of fungal spores found as microfossils was very high in at least some regions.

8. for one, or perhaps several, episodes, the stable isotope ratios of carbon and oxygen departed strongly from the norm.

9. the level of (presumably cosmic) radiation was unusually high for a relatively brief period.

Before continuing, we pause to note the interesting parallels between these conditions and, except for humidity, normal August weather in Houston, Texas. While the residents of Southeast Texas may lack the diversions provided by an active volcano system in the neighborhood, the busy refineries of Pasadena and Baytown are, happily, present to provide an equivalent injection of ever-changing organic and inorganic atmospheric spices to enliven the otherwise bland mixture of oxygen, nitrogen and inert gases on which other, less fortunate peoples are forced to subsist. Surely it is no coincidence that Houston, like Induan Earth, boasts very few dinocephalians, pareiasaurs, or Permian fauna of any kind -- at least during the summer months.

Provincial considerations aside, it remains unclear exactly what happened at the end of the Permian. Regardless of the precise causes, it would be equally interesting, and perhaps of even greater practical value, to understand how the system recovered during the early part of the Induan, in the first years of the Mesozoic. ATW030627.

Griesbachian Age (Early Induan) - Stratigraphic Stages

stage	Ammonid zone, tropical (tethyal and perigondwanal)	Ammanoid zone (boreal)	Conodont zone (tethyal)	Russian platform	Jungar Basin China
Early		**Bukkenites strigatus**	**Clarkina**		(not investigated)

Dienerian	**Ophiceras tibeticum**		**postcarinata**	**Riyabinsk member**	
Latest Griesbachian		**Ophiceras commune**	**Clarkina carinata**		**lower Jiucaiyuan Formation**
Late Griesbachian			**Isarcicella isarcica**		
Middle Griesbachian	**Ophoceras woodwardi & Ophiceras bandoi**		**Hindeodus parvus**	**Astashich member**	
Early Griesbachian	**Otoceras fissisellatum**	**Tomphociceras pascoei**			**Upper Guodikeng Formation**

table based on Kozur 1998

Life in the Induan

Marine Life

Induan marine biotas were very impoverished, and diversity in general was low. The ammonoids survived the extinction by the skin of theior proverbial teeth, with only a couple of genera making it through.

An interesting side-effect of this was a sudden revival of microbial mats (stromatolites) to reef and shallow subtidal environments during the early Induan (not unlike the situation during the Precambrian). Quite possibly this was because the invertebrate grazers that fed on them had been almost decimated by the end Paleozoic extinction. The respite was short-lived however and they soon dissapeared.

Terrestrial Biotas

Plants

The Permo-Trias sea level minimum and glaciation, and the associated aridity, led to diversification and dominance of the more woody and pollen-producing Gymnosperms over the Paleozoic spore-bearers. Seeds allowed them to spread into dry areas, remaining dormant until there was sufficient water for germination, while pollen allowed much wider dispersal.

Tetrapods

Earliest Triassic tetrapod faunas are described by Dr M.A. Shiskhkin (Russian Academy of Science), as follows:

"Permo-Triassic tetrapod extinction caused by global uplifting and aridization of the land resulted in a dramatic change and, to some extent, the reversal of the above mentioned faunal structure. It may be characterized as an increasing switch of tetrapod life towards aquatic habitats. As a consequence, during the earliest Triassic (Induan), the newly arisen temnospondyl amphibian families, though still exceeded by reptiles in diversity, become fairly abundant in some cases, especially the Lydekkerinidiae in Gondwanaland and the early Capitosauridae (along with their benthosuchid offshoots) in Western Laurasia. Secondly, in contrast to latest Permian, the role of main shared component in the communities of both supercontinents was overtaken by aquatic or semi-aquatic groups, such as lydekkerinid, tupilakosaurid and long-snouted trematosaurid temnospondyls, and cosmopolitan dicynodont reptile *Lystrosaurus*. Except for the latter genus, the herbivorous forms completely went extinct by that time. Another peculiar feature of the Induan biota is a miniaturisation of most forms. The end of this evolutionary phase, called 'the Lystrosaurus - lydekkerinid episode' (Shishkin and Ochev 1993) appears to be marked by the replacement of primitive procolophonid reptiles (Spondylolestinae) by the more advanced Procolophoninae. This event is recorded both in South Africa and Russia and is reliably corrrelated in the latter region with the Inuan-Olenekian boundary (Shishkin et al 1996). The procolophonid evolution in both areas proceeded in parallel and gives no clear evidence of intercontinental faunal linkage. In terms of local biozonation, the discussed episode corresponds to the earliest (*Tupilakosaurus*) grouping of the 'Neorhachitome' Fauna in Russia and lower part of the *Lystrosaurus* Zone in Africa."

Shiskhkin, Post-extinction events...

During this time, the world was still ruled by Therapsids. These had gained ecological dominance in lowland basins during the Middle and Late Permian, and this trend continued in the Early Triassic Lystrosaurid community type. Alongside these animals, and appearing for the first time, were the Archosaurs or "ruling reptiles", a group that was to later include dinosaurs, crocodiles, and Pterosaurs (flying reptiles or "pterodactyls"), as well as a number of other forms. Archosaurs are rare in the collections from the Lystrosaurus assemblage zone, being represented only by the aquatic crocodile-like proterosuchids and the terrestrial and lizard-like prolacertiforms. The cynodonts were all small insectivorous or carnivorous forms, which are placed in the family Galesauridae or Thrinaxodontidae.

In this earliest Triassic landscape, *Thrinaxodon*, the direct ancestor of mammals, and *Proterosuchus*, the direct ancestor of crocs, dinosaurs and birds, lived side by side, although one was terrestrial, the other semi-aquatic. As the Triassic period unfolded, the descendents of these two relatively small and early forms would vie for supremacy.

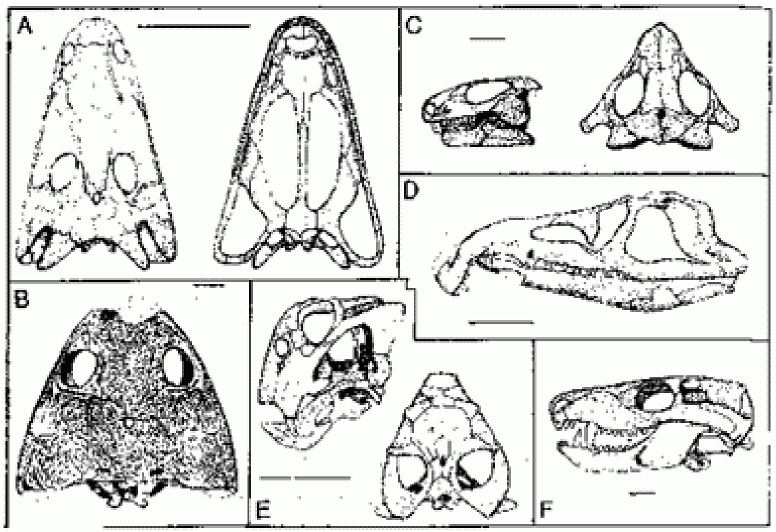


illustration from Lucas 1998

Lootsbergian index fossils: (A) *Wetlugasaurus*, (B) *Tupilakosaurus*, (C) *Procolophon*, (D) *Proterosuchus* (= *Chasmatosaurus*), (E) *Lystrosaurus*, (F) *Thrinaxodon*. Scale bars A, D, E are 10 cm; B and C are 1 cm.

Dr Spencer Lucas (ref) divides Triassic tetrapod evolutionary communities into into eight land-vertebrate faunachrons (LVF). The beginning of each LVF is defined by the first appearance datum (FAD) of a widespread tetrapod genus. The first of these is *Lootsbergian*, which is asosciated with the cosmopolitan dicynodont *Lystrosaurus*. It is mostly contemporous with the Induan epoch (equivalence at least in part with the Induan is indicated by the occurrence of characteristic Lootsbergian temnospondyls in ammonite-bearing Induan strata of the Wordy Creek Formation in eastern Greenland (Trümpy, 1961), although the FAD of *Lystrosaurus* is actually late Permian (perhaps middle Changhsingian). According to the Russian Palaeontologist M. A. Shiskhkin (ref), *Lystrosaurus* ranged well into the Early Olenekian, although this dating is disputed. However, one can suggest a generic and approximate equivalence between the *Lootsbergian LVF* and the Induan epoch

The following is Dr Lucas' description of the Lootsbergian and listing of characteristic fauna

"Lootsbergian time begins with the FAD of the dicynodont *Lystrosaurus*. The end of the Lootsbergian is equivalent to the beginning of the Nonesian, which is defined by the FAD of the cynodont *Cynognathus*. The Lootsbergian LVF is characterized by the *Lystrosaurus* Assemblage Zone in the Balfour (Palingkloof Member), Katberg and Burgersdorp (lower part) formations of the Karoo basin of South Africa (Groenewald and Kitching, 1995). The following tetrapod genera are restricted to Lootsbergian time and are widespread and/or common enough to be useful as index fossils: *Wetlugasaurus*, *Tupilakosaurus*, *Luzocephalus*, *Lydekkerina*, *Procolophon*, *Lystrosaurus*, *Scaloposaurus*, *Thrinaxodon*, *Proterosuchus* and *Prolacerta*.

The terms *Lystrosaurus* zone, beds or fauna have been applied to a wide geographic range of strata/fossils of Lootsbergian age. The most significant vertebrate fossil assemblages of Lootsbergian age are from the upper Guodikeng and lower Jiucaiyuan formations, Junggur basin, China; Heshanggou Formation, Ordos basin, China; lower part of Fremouw Formation, Antarctica; Panchet Formation, India; Vokhmian horizon of Vetluga Series, Russian Urals; and Wordy Creek

Formation, eastern Greenland."

Lucas, Tetrapod-based Triassic Timescale

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text by M.Alan Kazlev (MAK) and Augustus T. White (ATW)
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Paleozoic
  Permian
    Lopingian
      Changhsingian
Mesozoic
  Triassic
    Early Triassic
      Induan
      Oleneckian
    Middle Triassic
    Late Triassic
  Jurassic

An Induan Bestiary

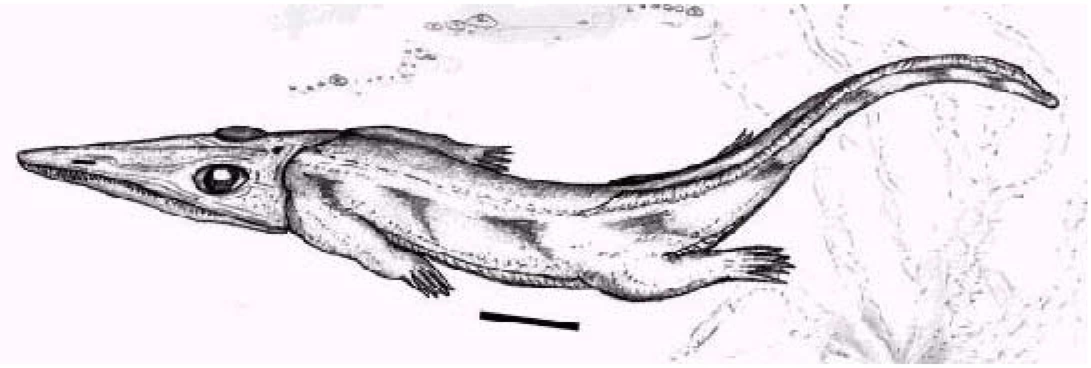


illustration © from Steyer 2002

The Temnospondyl Labyrinthodont amphibians were characteristic animals of this time. During the Triassic period these creatures experienced something of a rennaisance, and evolved along a number of parallel evolutionary lines. The great majority were semi-aquatic. Illustrated here is a juvenile *Wantzosaurus elongatus* (the scale bar is 4 cm), a member of the Trematosauridae and cousin (although belonging to a different subfamily) of the Lootsbergian index fossil *Luzocephalus* illustrated above. These animals were fresh-water and occasionally esturine and marine fish-eaters, with long crocodile or gharial-like snouts. As the adolescent *Wantzosaurus* shown here matures, its snout will become proportionally longer and thiner, although the rest of the head and body will not increase much.

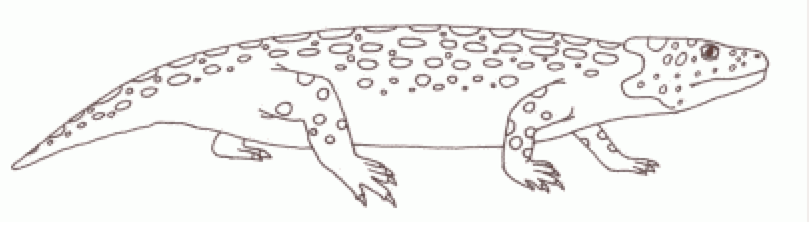
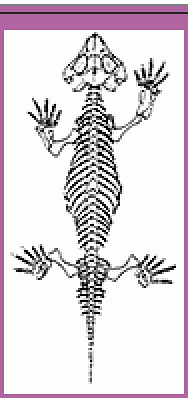
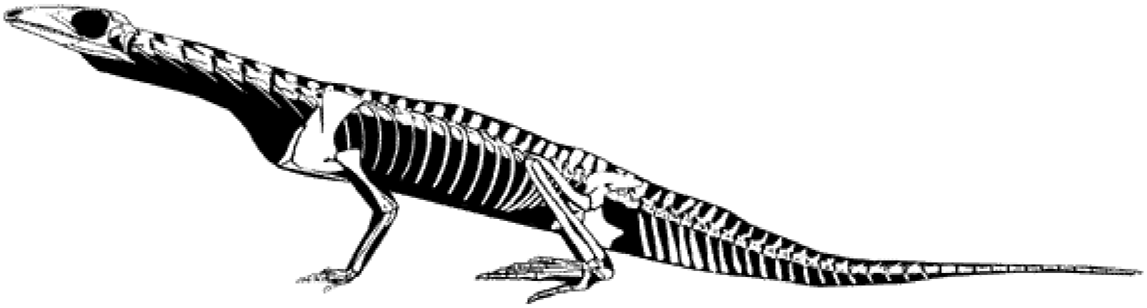


Illustration *above* © 2001 Vince R Ward - Prehistoric Pages
illustration *below right* after Colbert and Kitching 1975



Procolophon trigoniceps **Owen 1876 known from the Lystrosaurus zone, Beaufort Beds of South Africa and the equivalent Fremouw Formation of Antarctica (during the Triassic these two regions were quite close together) was a stout lizard-like herbivore with chisel-like teeth and a triangular-shaped skull. The whole animal reaxched about 30 cm in length. These little animals were actually cousins of the giant pareiasaurs of the middle and late Permian. Both belong to the clade "Parareptilia", which was a major group of Permian reptiles characterised by primitive skulls without any temporal openinings for musclke attachment. It was originally thought that the turtles (chelonida) evolved from *Procolophon*-like ancestor, but this is no longer considered the case.**

During the early Triassic the Procolophonidae were extremely diverse and widespread, and they remained an important part of terrestrial ecosystems right until the end of the Triassic. Unlike Theraspids, they preferred dry arid conditions Olsen *et al*. Were one to envisage a plump desert lizard that eats plants rather than insects, that would give a good picture of what *Procolophon* and its cousins were like.



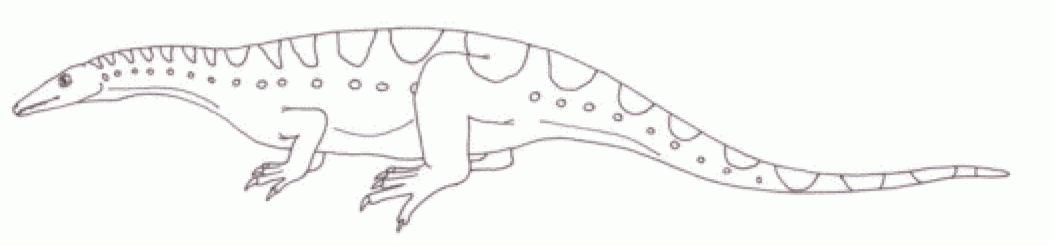


Illustration of skeleton (*top*) © David Peters; life restoration (*bottom*) © 2001 Vince R Ward - Prehistoric Pages

Prolacerta broomi **(Family Prolacertidae) was a medum-sized reptile, about a meter in length, whose fossil remains are known from the Lystrosaurus assemblage zone of South Africa and the Fremouw Formation of Antarctica. In habits and appearance it was probably very similar to a large lizard, apart from the enlrged hind legs, and doubtless filled the same ecological role in early Triassic Pangean ecosystems. But it was actually an early representative of the order Prolacertiformes; primitive members of the Archosauromorpha, the clan of "ruling reptiles" and their relatives. As medium-sized lizard-like forms with long hind legs for quick bipedal bursts of speed, the Prolacertiformes are little different in superficial appearance to the mostly Permian Younginiformes, and indeed both groups were for some time included under the (now no longer considered valid) Order Eosuchia. Details in osteology indicate however their relationships to the archosaurs**

Prolacerta broomi - artwork and some comments by Daniel Bensen.

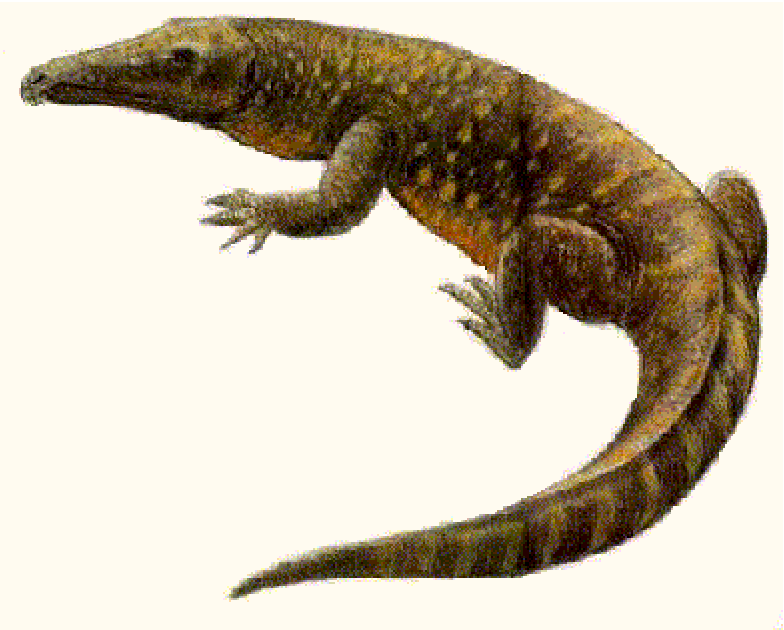


illustration by Steve Kirk - *Illustrated Encyclopedia of Dinosaurs and Prehistoric Animals*

Proterosuchus fergusi **from the Lystrosaurus zone, Beaufort Beds, of South Africa, was a primitive Archosauriforme, upto 1.5 metres in length, that lived a semi-aquatic, crocodile-like existence in a flood-plain pond environment, preying upon fish and labyrinthodont amphibians. Despite the superficial resemblence,** ***Proterosuchus*** **was actually rather more primitive then any crocodile, being a very early member of the (paraphyletic grade - not considered valid in cladistic phylogentics) group of reptiles called Thecodontia, the stem "ruling reptile" (archosaur) group from which all other forms developed. It was thus very close to the ancestry of all higher reptiles (Archosaurs) - crocodiles, dinosaurs, pterodactyls, birds, and a host of other types, all ultimately descended from this one type (or at least a creature very similiar to it).**

The taxonomy of this animal is rather confusing, owing to a large amount of material that has been given different names. ***Chasmatosaurus vanhoepeni*** **(=** ***Proterosuchus vanhoepeni*****),** ***Chasmatosaurus alexandri*****, and** ***Elaphrosuchus rubidgei*****, from the same locality, are now considered synonyms. [Welman 1998]. Similar but distinct species are known from Russia (*****Chasmatosuchus rossicus*** **and related forms, all poorly known), China (*****Proterosuchus yuani*****), India (*****Proterosuchus*** **sp.), and Australia (*****Tasmaniosaurus triassicus*****). [Lucas 1998; Early Triassic World - Vertebrates]. It seems that these animals had a worldwide distribution during the period from the Early Induan (if not Latest Permian) to Early Olenekian. All are members of the Family Proterosuchidae, which were apparently the only thecodonts of this time. Their extinction was probably due to competition from the larger and apparently also semi-aquatic Erythrosuchidae.**

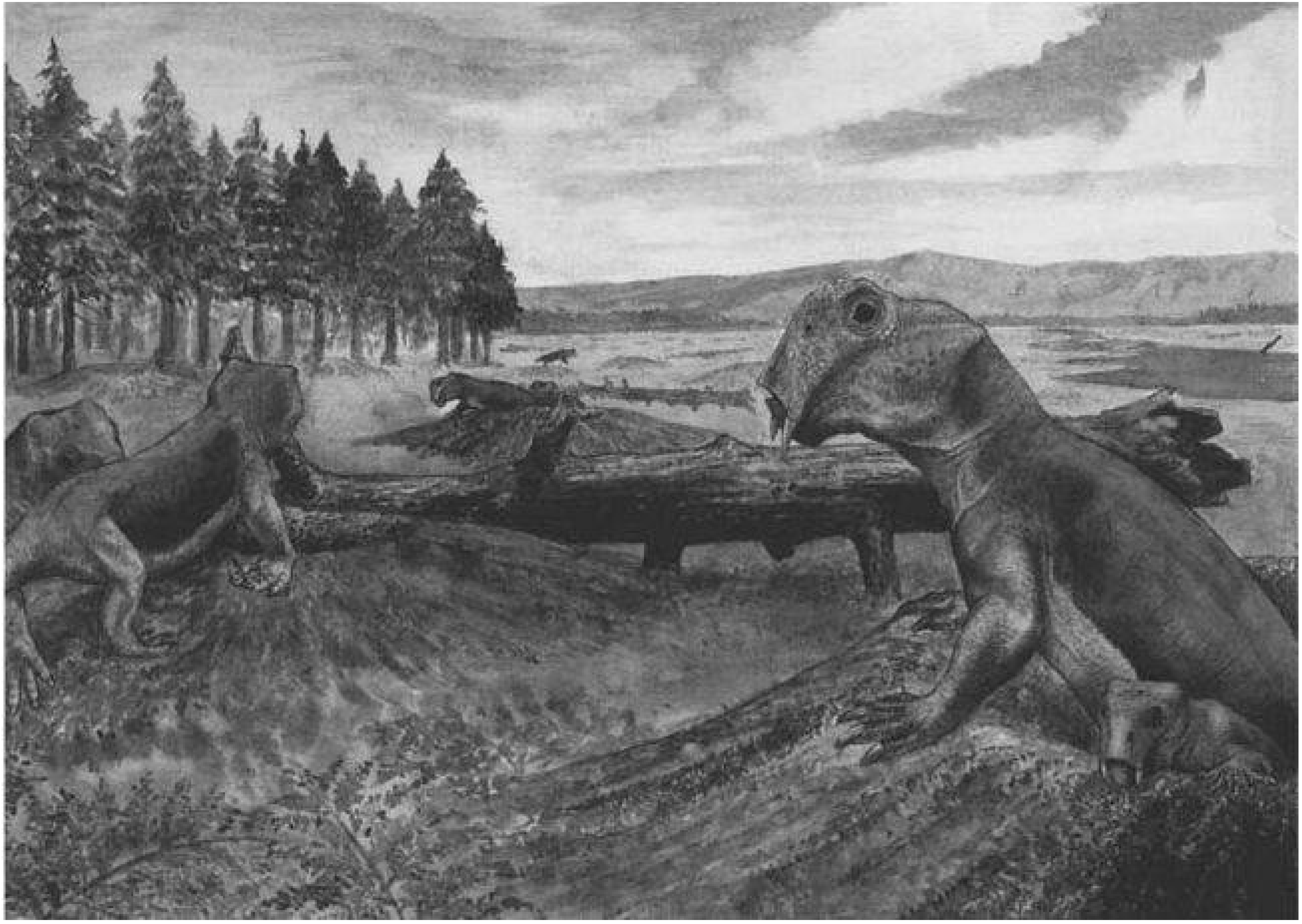


illustration © Seiji Yamamoto

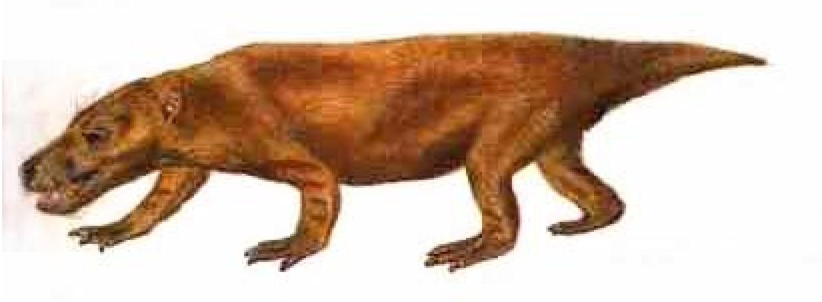
The herbivorous *Lystrosaurus*, a member of the dicynodont tribe, was the most ubiquitous and widespread animal during the earliest Triassic. They were squat quadrupedal forms, a little over a meter in length. Although originally thought to be semi-aquatic (a sort of miniature reptilian hippopotomus), study of functional morphology [King and Cluver 1991] indicates that *Lystrosaurus* was fully terrestrial and capable of burrowing; this is supported by paleoenvironmental observations [Retallack and Hammer 1996]. So, lthough frequenting aquatic waterside and thickly vegetated terrestrial settings, it is most likely that these animals could also survive in arid environments, and their association with river sediments is more an artifact of preservation (since these were the conditions animals were most likely to be preserved

***Lystrosaurus* gives its name to the Upper Beaufort *Lystrosaurus* assemblage zone (In the Karoo of South Africa). The Lystrosaurus assemblage zone fauna developed in a warm temperate lowland with seasonal floods in lacustrine fluvial environments. The basinal flora comprised mixed *Glossopteris* (tree-like, not illustrated here) and *Dicroidium* (the low fern-like plants, above), while extensive coniferous forests (background) may have occupied the basin periphery.**

A Note on Lystrosaur Species:
Although a number of species are known, these differ in only minor details, and some may still rturn out to be synonyms. The following species are listed on Early Triassic World - Vertebrates (only some of the synopnyms shown here):

***Lystrosaurus curvatus* (Owen 1876) (= *L. youngi*) - Lystrosaurus Assemblage Zone, Middle Beaufort Beds, South Africa South Africa; Halfmoon Bluff, Fremouw Fm, Antarctica; Junggar and Turpan Basin, Xinjiang, Jiucaiyuan Fm, Tunghungshan Series, China.**
***Lystrosaurus declivis* (Owen 1860) - Lystrosaurus Zone, South Africa**
***Lystrosaurus georgi* Kalandadze 1975 - Vetluga River, Nizhegorodskaya Region, central European Russia**
***Lystrosaurus hedini* Young 1935, Jiucaiyuan Formation, Tunghungshan Series, China.**
***Lystrosaurus mccaigi* Seeley 1898 (= L. putterilli, L. amphibius) - Lystrosaurus Zone, South Africa; Panchet Fm, India; Shenk Peak, Fremouw Fm., Antarctica,**
***Lystrosaurus murrayi* (Huxley 1859) (= *L. orientalis*, L. frontosus, Prolystrosaurus natalensis, L. broomi, L. rubidgei, etc); Lystrosaurus Zone, South Africa; Fremouw Fm, Coalsack Bluff, Antarctica; Panchet Fm, India; Jiucaiyuan Fm, China.**
***Lystrosaurus oviceps* Haughton 1915 (= *L. breyeri*) - Lystrosaurus Zone, South Africa;**
***Lystrosaurus platyceps* Seeley 1898 (= *L. andersoni*) - Lystrosaurus Zone, South Africa; Panchet Fm, India.**
***Lystrosaurus rajurkari* Tripathi & Satsangi 1963 - Panchet Fm, India**
***Lystrosaurus robustus* (Sun 1973) (= *L. latifrons*) Jiucaiyuan Fm, China**

***Lystrosaurus shichanggouensis* Cheng 1986 - Jiucaiyuan Fm, China.**
***Lystrosaurus weidenreichi* Young 1939 - Jiacaiyuan Fm, China**



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***Thrinaxodon liorhinus* Seeley 1894 was a fairly small (total length about 50 cm) early cynodont, known from the Lystrosaurus zone, South Africa, and the Fremouw Formation of Antarctica; a furry creature on the direct line to the mammals. Although technically a reptile, it would have appeared mammal-like in form. *Thrinaxodon* fed on large invertebrates and smaller vertebrates, and during the Olenekian gave rise to larger and more advanced forms like *Cynognathus*. It is usually placed in the (paraphyletic) family Galesauridae**

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The Olenekian

The Olenekian Age of the Early Triassic Epoch: 245 to 250 million years ago

Mesozoic
  Triassic
    Early Triassic
      Induan
      Olenekian
    Middle Triassic
      Anisian
      Landinian
    Late Triassic
  Jurassic

Links

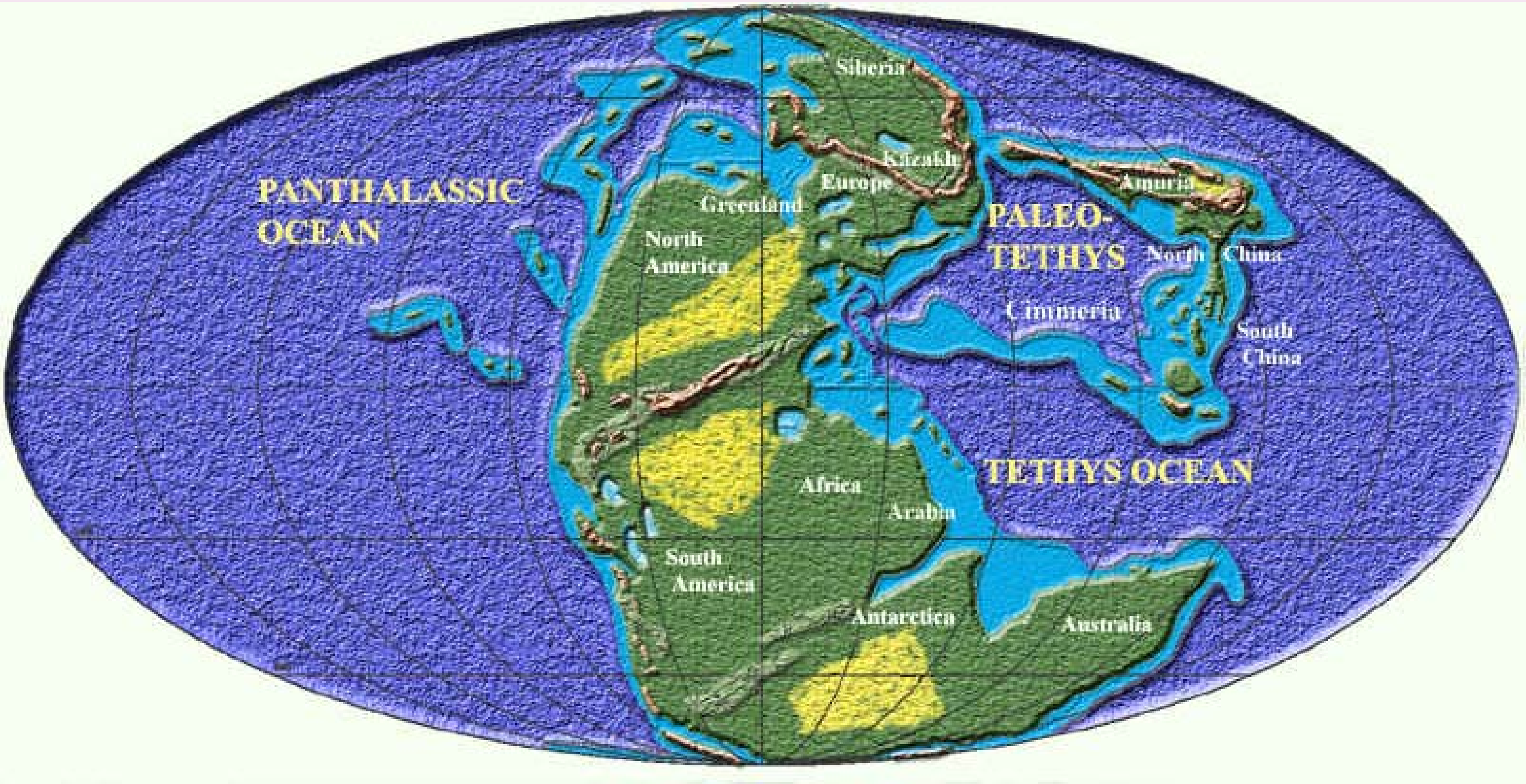
The Limits of the Olenekian

The Olenekian Age is named for the Олениок River in Siberia, where the type section occurs, and which we have probably spelled incorrectly. If so, it would not be the first muddled fact about this age, which has gone by an embarrassing number of names, particularly for such a modest span of time. The first half of the Olenekian has been referred to as the Late Nammalian, Smithian, or Ayaxian. The later Olenekian is (more or less) the Spathian or Russian. The entire Age is the same as the Late Scythian. Internationally recognized correlations have only been worked out in the last few years, and it appears that there is still much uncertainty, particularly for regions far from the type locality – which, unfortunately, includes most of the world.

The beginning of the Olenekian (Induan - Olenekian boundary) is marked by the first appearance of the conodont *Neospathodus waageni*. A great deal of Olenekian stratigraphy has historically been done using ammonoid biozones. The opening of the Oleneckian is also associated with the first appearance of a number of ammonoids, including *Flemingites* and *Euflemingites*. It occurs just before the end of the second Triassic normal magnetostratigraphic zone, and the peak of the first Triassic positive excursion of carbon isotope ^{13}C. The end of the

Olenekian, *i.e.* the Olenekian - Anisian boundary, is characterized by conodont zonation: the last occurrence of *Neospathodus homeri* and *N. symmetricus* and the first occurrence of *N. gondelloides*, *Chiosella timorensis* and *Neogondolella regalis*. Another indicator is a magnetostratigraphic shift from reversing polarity in the Late Olenekian to a long normal zone in the Early Anisian. Unfortunately, the absolute age of these terminal events is considerably less certain. It has been found, by various measures, to occur at anywhere from 240 to 247 Mya, with more recent measurements indicating older dates. As always, we have adopted the ICS/IUGS dates. ATW040206, rev'd ATW050429.

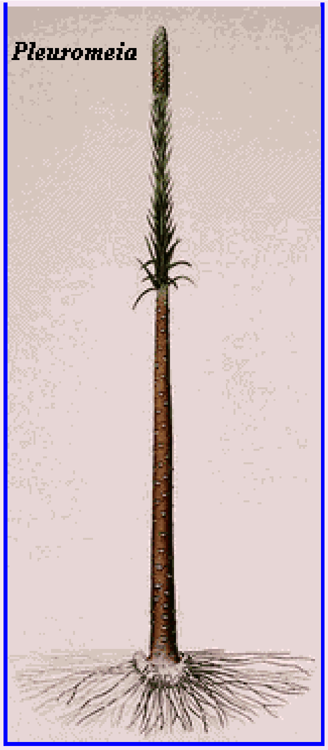
The Geography of the Olenekian



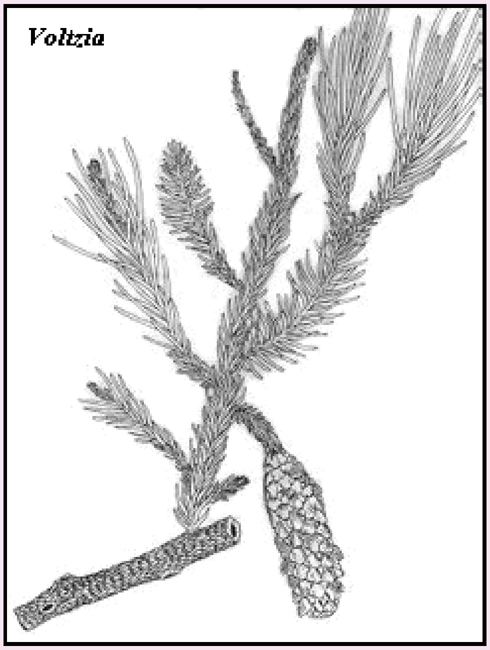
"Darkness Crumbles Away"[1]

Many discussions of the end-Permian extinction go something like this: "the seas became thoroughly deoxygenated, and most marine Metazoans died off. On land, many species also died off, but a number of critical (to us) tetrapods survived unchanged. The die- off may have been caused by climate, comet, vulcanism, or virus." The discussion then moves on to the evolution of archosaurs in the Middle Triassic. What gets left out here is the thing that really separates the end- Permian from every other mass extinction of the Phanerozoic -- the incredibly slow rate of recovery. In fact, reasonably normal ecosystems are not seen again until the last half of the Olenekian, about six *million* years after the extinction event(s). Just as interesting is the trajectory of the recovery. For over five million of those years, the recovery proceeded at a snail's pace. Then, in the space of just half a million years, the process accelerated, and the world's living systems recovered something resembling their Late Permian vitality.

This peculiar sequence of events was documented for a large terrestrial ecosystem by Looy *et al*. (1999) who examined the palynological record of the forests of Europe. In the Lopingian (Late Permian), Europe was covered in conifer forests. At the end-Permian, the conifers simply disappear. For the Induan and most of the Olenekian, the region was covered by *Pleuromeia*- dominated lycopsid stands. During this period, soil formation was low. Apparently the total biomass of lycopsids was not particularly



impressive, or the rate of erosion was unusually high. Probably both factors played a part, as there were few tree- sized species, and the soils would not have been strongly held. This may well have been a world- wide phenomenon, in view of the global absence of Early Triassic coal deposits. Then, late in the Olenekian, the lycopsids were rapidly replaced by a transitional flora of low, shrub- like, and rather simple conifers. Within half a million years, this was succeeded by open, *Voltzia*-dominated conifer forests, not so different from the original cover of the Lopingian.



The authors point out that the succession resembles the recovery patterns after the Wisconsin glaciation at the beginning of the Holocene -- but several thousand times slower. The comparison may be inexact. We do not yet know enough details of the Early Triassic recovery to attempt a rigorous comparison, and Holocene grasses are very unlike lycopsids. Still, the comparison is an interesting model. What could possibly have slowed a process which ought to have taken a few hundred years and stretched it out to five million? Climate is *not* the answer. Looy *et al*. point out that the same warm, semi- arid conditions are believed to have prevailed before, during and after the Early Triassic. They suggest that the appropriate conifers were all extinct and that tree- sized conifers simply needed time to re-evolve.

This explains too little. The Early Triassic recovery shows roughly the same trajectory everywhere -- probably. The uncertainties of Early Triassic stratigraphic correlation defeat any certain comparison. But marine invertebrates, temnospondyls, and tetrapods all show a recovery pattern similar to that of the pine forests. The timing might be similar because evolutionary events are somehow interrelated. However, there is no particular reason to think so. For example, East Asian radiolarian protists also show an extinction at the end-Permian, a depauperate population until the Late Olenekian, a Late Olenekian transitional community, and a characteristic Mesozoic community at the beginning of the Anisian. Suzuki *et al.* (2002). It's hard to think of a reason that Japanese radiolarian evolution would be correlated with European pine forests. As matters stand, there are no compelling explanations for the initial extinction, for the Earth's painfully slow convalescence, or for its much faster recuperation at the end of the Olenekian. ATW040207.

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[1] "Darkness Crumbles away.
It is the same old druid Time as ever,
Only a live thing leaps my hand ..."

Break of Day in the Trenches
Isaac Rosenberg (1916)

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The Middle Triassic

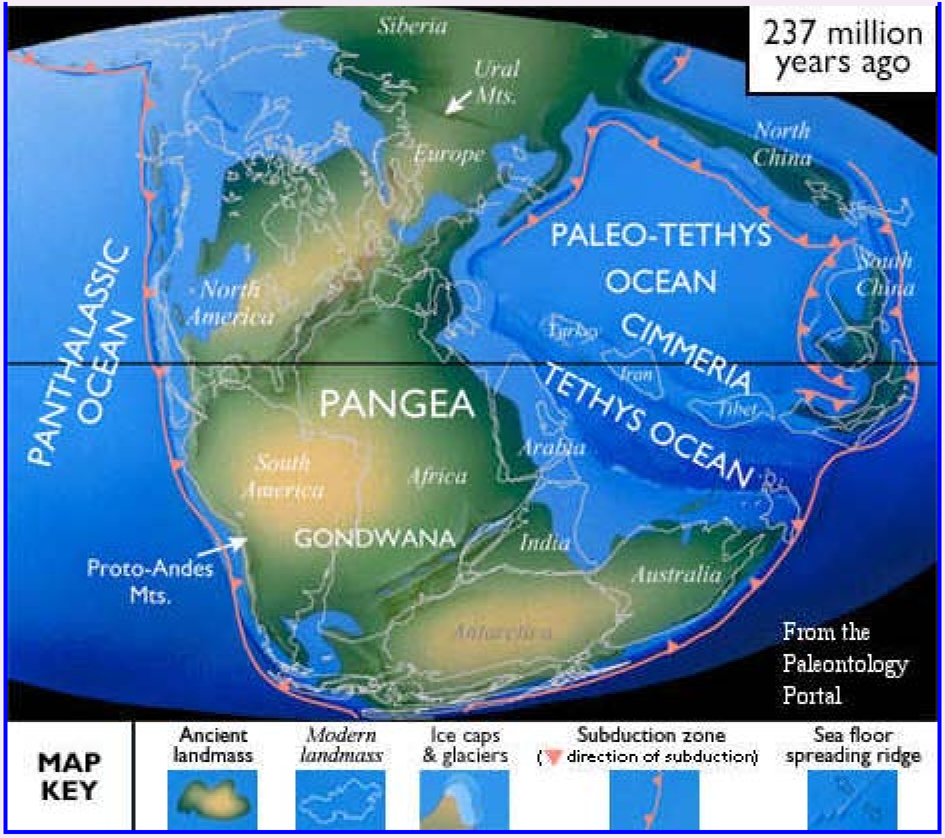
The Middle Triassic Epoch of the Triassic Period: 245 to 228 million years ago

Mesozoic Era
  Triassic Period
    Early Triassic Epoch
    Middle Triassic Epoch
      Anisian Age
      Landinian Age
    Late Triassic Epoch
  Jurassic Period

Introduction
Life in the Oceans
Life on Land

Introduction

By the Middle Triassic, a great crack had opened between Africa and the continent we can now call Eurasia, and a long arm of the Tethys Sea reached westward along southern Russia into what is now Germany and France. The lands of today's South Asia remained islands, largely submerged and well to the south of Eurasia. They formed the long Cimmerian ridge, which was drifting northward, separating the Old Tethys to the North, from the New Tethys, between the Cimmerian Ridge and Gondwana. These blocks had crumbled off the north coast of Gondwana in the first spasm of the tectonic shake-up which would destroy the world-continent of Pangaea by the end of the Mesozoic. The two Chinese cratons formed an irregular and incomplete eastern border to the Old Tethys, merging with the Cimmerian Ridge in the Southeast.



Directly across the Old Tethys, almost at right angles to the Cimmerian ridge, another fracture was also propagating westward, tearing Africa from Gondwana. In the far West and far South, however, little had changed. South America and Africa merged seamlessly together. India and Australia remained firmly attached to Antarctica in eastern Gondwana. The geological strains in the west were beginning to show in a series of undramatic fault valleys which tracked the old suture uniting Africa and Laurentia (Stanley, 1998), but the Atlantic Ocean was still far in the future. Laurentia and Eurasia still met in the north. A cool boreal ocean lay north of that landmass, surrounding the North Pole. At earlier times, the boreal ocean had sent a long finger south, forming a shallow sea between Eurasia and Siberia/Kazakh, sometimes even reaching the Old Tethys. But the merger of Eurasia and Siberia, with the rise of the Urals, had severed this antique connection. From Norway to the Lena River, the north coast of Eurasia was beginning to acquire its modern contour.

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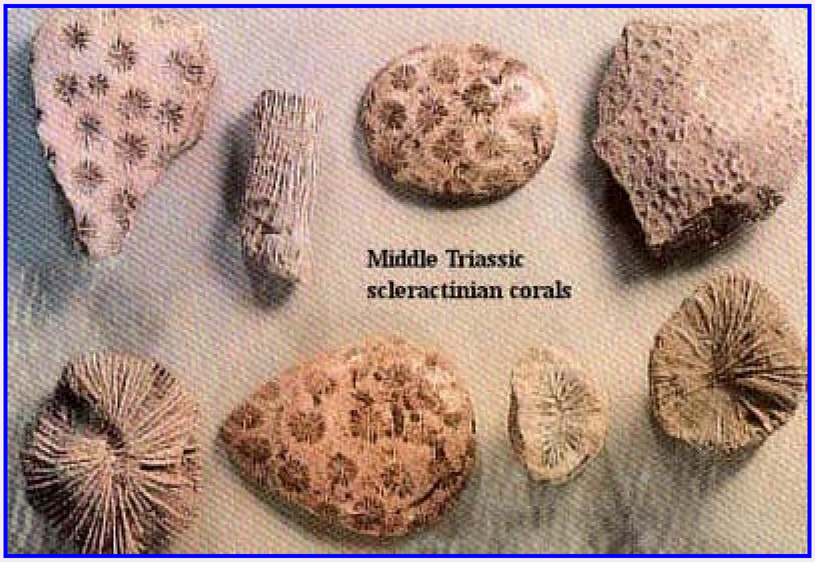
Life in the Oceans


Middle Triassic scleractinian corals

The Early Triassic recovery had been fitful and inconsistent. The Middle Triassic marks the return of better conditions for the whole biosphere, as well as the global radiation of a number of key groups which would dominate the remainder of the Mesozoic. Stanley (2003a); In the long run, perhaps the most important of these changes was the least conspicuous. The Middle Triassic saw the beginnings of the modern phytoplankton assemblage that forms the base of the entire marine food web. Falkowski *et al*. (2004). These included the first clearly identifiable dinoflagellates, which are found as organic walled cysts preserved in Middle Triassic continental margin sediments. Katz *et al*. (2004).

The recovery of reefs remained slow and sporadic, although increased ocean oxygen circulation now permitted some permanent gains. Stanley (1998). These gains were accomplished by calcareous sponges and mineralizing bacteria -- generally the first reef-builders to recover from disaster. However, further off-shore, particularly in the vast shallows around China, the first scleractinian corals had appeared. These animals formed small mounds no taller than 3m in the Middle Triassic (Stanley, 1998; Stanley 2003a), but they became a variably important element of reef communities from that time forward. While calcitic sponges did reasonably well, most other sponges, radiolarians, and all other organisms built on silicate skeletons, did very poorly.

Bilaterian animals recovered more slowly and less steadily. Several groups of crustaceans diversified (isopods, decapods). Others became extinct, including the problematic euthycarcinoids (Vaccari *et al*., 2004). Among mollusks, belemnites and various other neocephalopods appeared. Benton & Harper (1997). Gastropods became larger, but their total diversity may not have increased much above Early Triassic levels. Payne (2005). Conodont diversity declined, but the surviving species remained ubiquitous until the end of the Triassic.

Middle Triassic fishes were largely of neopterygian grade. In fact, even the more derived clades of neopterygian fishes (pycnodontiforms, pachycormiformes) are not known until the Late Triassic. The most significant event among fishes may have been the first appearance of neoselachian sharks (depending on how one defines the Neoselachii). Cuny *et al*. (2001); Maisey (1984).

The most famous marine organisms of the Middle Triassic, however, weren't fishes at all, but diapsid reptiles. The Middle Triassic was the epoch in which ichthyosaurs, placodonts, pachypleurosaurs, and nothosaurs all flourished. All of these groups evolved in the Early Triassic, but seem to have found the Middle Triassic European Tethys Seaway particularly congenial. In fact, the placodonts, pachypleurosaurs, and small nothosaurs are not often found in any other place or from any other time. Carroll & Gaskill (1985); Carroll (1988); Sander (1989). The Plesiosauria may well have been evolved nothosaurs, but the particular anatomical characteristics of plesiosaurs (including their great size) are not found until later in the Triassic. Carroll & Gaskill (1985). In addition to these reptiles, a few species of trematosaurid temnospondyls remained, at least some of which were marine. Steyer (2002).

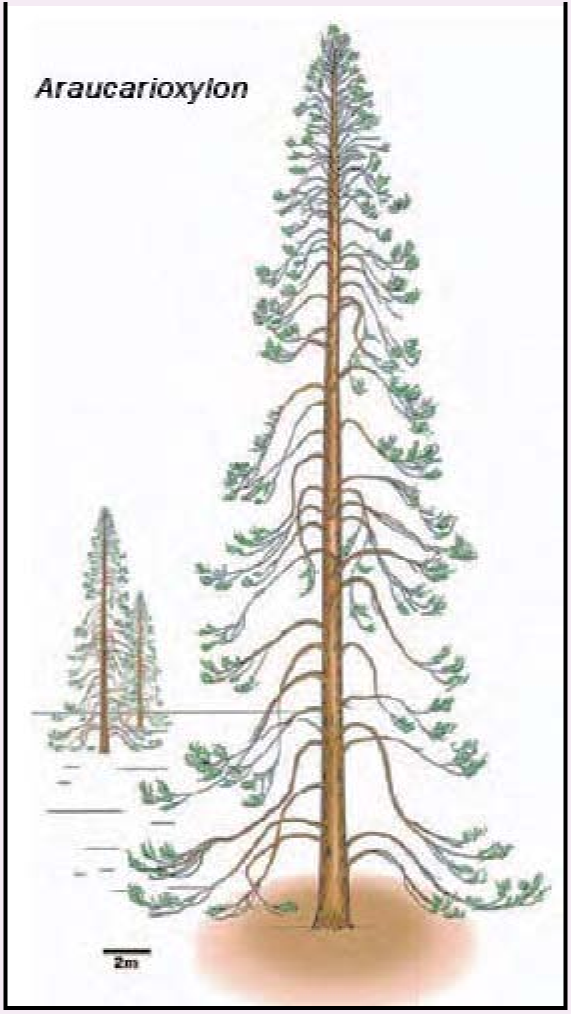
ATW080125

Life on Land

The plant cover of the Middle Triassic continued the recovery begun in the Olenekian. Commonly encountered large plants included sphenopsids, ferns, seed ferns, conifers, and cycads. Labandeira (1998). The conifers, in particular, radiated strongly, covering broad areas with open pine forests. This remained the general pattern through the remainder of the Triassic and Jurassic Periods.

Dipteran insects had appeared in the Early Triassic. They radiated with the recovery of the terrestrial plants; and the Middle Triassic saw the divergence of the fruit fly and mosquito lineages. Benton & Donoghue (2007). Other herbivorous insects also established themselves in the new forests, such as beetles, hemipterans, and an unknown insect which left cicada-like burrows. Labandeira (1998).

Temnospondyl amphibians remained an important element in swamp and fresh water settings, including types remarkable for large size (mastodonsaurs) or bizarre appearance (plagiosaurs). Damiani



(2001); Warren (1995). The earliest known turtle remains are also found in the Middle Triassic, and the existence of basal frogs and salamanders is likely.

However, the vast, dry inland areas of Pangaea favored a completely different fauna, known from localities like Ischigualasto and Los Cha�ares in South America. Lucas (1998); Sereno (1991). In such places, the early archosauromorphs evolved, including proterosuchids, erythrosuchids (Sereno, 1991), proterochampsids (Benton, 2004a), and others "whose obscure and uncouth names would only serve to oppress the memory and perplex the attention of the reader" (Gibbon, 1776). As Benton points out, the basal members of the Archosauromorpha were never numerous or widespread, with the outstanding exception of the rhynchosaurs (Carroll, 1988). However, by the Ladinian this lineage had produced the Crocodylomorphs and the Dinosauria. Sereno (1991).

These last were instantly (in a geological sense) successful. By the end of the epoch, the archosaurs had replaced synapsids as the dominant tetrapod group in terms of both biomass or diversity. Therocephalians became extinct. Dicynodonts began to decline, after a minor radiation which produced forms such as *Kannemeyeria*. Rubidge & Sidor (2001). However, a number of advanced cynodont groups, such as the probainognaths and tritylodonts continued. These groups began to converge toward forms of smaller size and simpler skull construction (Sidor, 2001), a trend which eventually produced the mammals.

ATW080126

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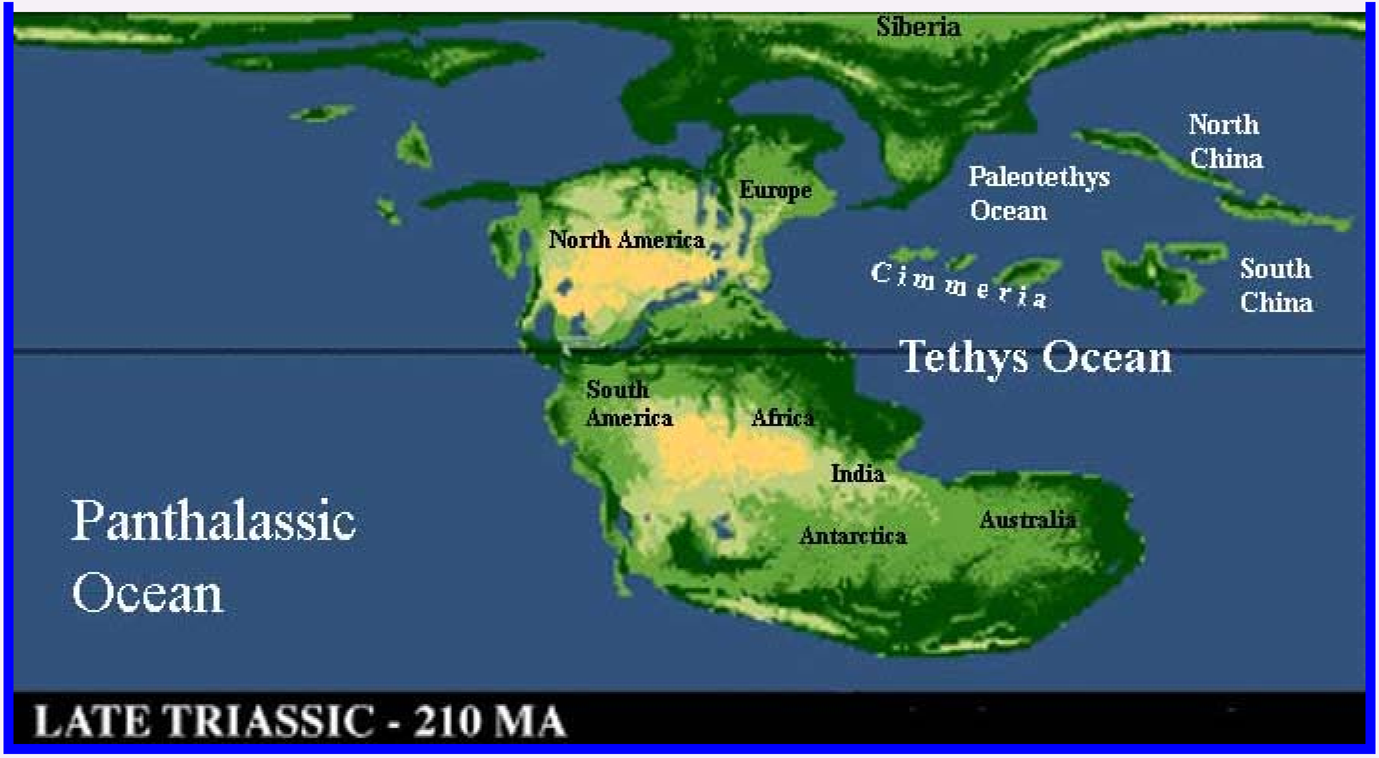
The Late Triassic

The Late Triassic Epoch of the Triassic Period: 228 to 200 million years ago

- Mesozoic Era
  - Triassic Period
    - Early Triassic Epoch
    - Middle Triassic Epoch
    - Late Triassic Epoch
      - Carnian Age
      - Norian Age
      - Rhaetian Age
  - Jurassic Period
    - Early Jurassic Epoch

- Geography
- Climate
- Life
  - The Late Sauropodomorph Revolution

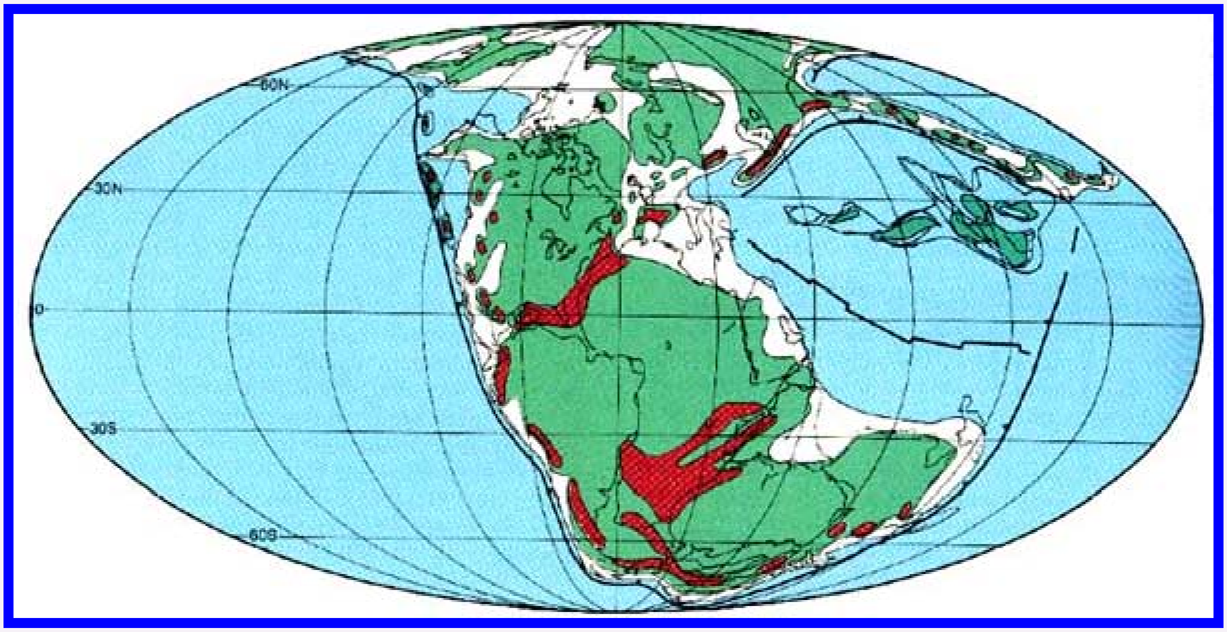
The Geography of the Late Triassic



Although rifts probably appeared in Pangea almost as soon as it was formed, the Late Triassic probably saw the first real cracks in the world- continent. This was particularly apparent around North America which began to separate from Europe, to the East, and from the old Gondwanan continents of Africa and South America to the South. In eastern North America, the Newark Supergroup reflects repeated cycles of rifting, basin fill (as lakes or seas invaded the rift valleys), followed by volcanic activity and more rifting. In the West, subduction of the sea floor continued under the western coast, with gradual addition of island arcs and microcontinents to the west coast.

Much the same process was occurring on the western edge of South America, although there was less accretion of new land. Subduction of oceanic crust under the west coast led to a rather irregular lifting of the broad coastal plain. By the end of the Late Triassic, the Andes had begun to form as the light oceanic crust melted below the margin of the craton and rose up to add to the mass of the continent.

By the Late Triassic, a permanent seaway -- what would become the Tethys Seaway – was already beginning to separate Africa from Europe and North America. Much of southern Europe was still attached to Africa at the beginning of the Late Triassic. However, by its end, a definitive fault line had propagated west from Arabia to Morocco, finally separating the last elements of Europe from Gondwana. At the same time, parts of North Africa were rapidly subsiding, resulting in the formation of a broad shallow sea, probably continuous with that which covered most of Europe. Parts of southern Africa, or the region where South America, Africa and Antarctica met, experienced enormous lava flows beginning in the Late Triassic and extending into the Jurassic. This presumably represent ted the beginning of the stresses which later led to the southern rift between Antarctica and India, on the one hand, and Africa and South America on the other.



The Late Triassic is rather poorly known in the remainder of Gondwana. The pattern of subduction which was discussed in connection with North and South America continued around the "back end" of Antarctica and, weakly, onto the West coast of Australia. The Cimmerian islands, the present Turkey, Iran and Tibet, broke completely free of the Australian craton and moved rapidly to the north. Eventually, these were to merge with the Chinese terranes, which had separated from Gondwana previously.

Finally, much of Europe and Russia were covered by the encroaching shallow waters of the Tethys. These became the home for the famous Triassic vertebrate fauna of Europe, including the sauropterygians (plesiosaur ancestors) and many key transitional actinopterygian species. At the same time, the broad, dry plains of equatorial Pangea provided a proving ground for a strange new group of lightweight, but large-bodied, archosaurs -- the dinosaurs.

Maps: *Right* from Lecture 9 I. The Triassic World. *Left*: from Triassic Times. ATW030322

The Climate of the Late Triassic

World sea levels were consistently low throughout the Triassic, and most of the vast landmass of Pangea was elevated and far from any water. There were no polar ice caps or continental glaciation. Not surprisingly, then, the climate of most of the world was intensely dry and hot. The deposition of large quantities of evaporites and calcretes along the new rift valleys, as well as in western North America testifies to the prevalence of desert conditions in much of the world. However, far southern Gondwana, northern Europe and Greenland were thickly wooded subtropical refugia for animals requiring a cooler, wetter environment. North China, on the other hand, was hot, but damp and tropical swamp and jungle -- a foretaste of a climatic regime that was to become much more prevalent as Pangea dispersed in the later Mesozoic.

These predominantly hot and dry conditions may have actually become worse during the course of the Late Triassic as volcanic activity, particularly the South African flows added conspicuously to global carbon dioxide levels. On the other hand, there is also evidence that the aridity of many coastal regions was seasonal. During some wet season, these same areas may have experienced considerable monsoonal rain. Unfortunately, this type of ecosystem often leaves a poor fossil record, since it supports relatively few large animals. ATW030322.

Late Triassic Life - A Time of Transition

On all levels, the Late Triassic was an age of transition. In the seas, the Ceratitidan ammonoids underwent a drastic and progressive decline from a mamximum diversity of 150 genera and subgenera during the Carnian, to 90 in the Norian, and only half a dozen in the Rhaetian [Teichert 1988 p.59]. The last of the straight-shelled nautiloids (belonging to the order Orthocerida/ Pseudorthocerida, depending on one's interpretation) that so typified the Palaeozoic seas also dissapeared after a brief Tethyan resurgence. But a single genus of nautilid, *Cenoceras*, survived to give rise to all later nautilids [Teichert 1988 p.57] . So did Phyllocerid ammonoids, although the relation between the Triassic forms and the Jurasisc newcomers are unclear [Teichert 1988 p.59].

The Norian oceans witnessed the first radiation of more advanced and lighter-scaled neopterygian fish at a time when more primitive and heavy scaled "chondrosteans" and "holosteans" paleopterygians were still preominant. [ref Andrea Tintori - Norian Fauna and Flora] However the more primitive types such as *Saurichthys* and *Birgeria*, along with hybodont sharks, remained as top preditors in the sea, as they were in fresh water. The late Triassic rivers also saw the last of the fresh-water Xenocanth sharks, which had been so important in Permo-Carboniferous freshwater environments

The Triassic marine reptile fauna is dominated by ichthyosaurs, both the mediumn to large, predominant Shastosaurs and the newer, more dolphin-like Parvipelvia. Not only were they diverse and widespread, but some shastosaurs grew to be the largest reptiles that ever lived; the Norian *Shonisaurus sikanniensis* was the size, literally, of a

illustration © Ron Garrett, used with permission

balleen whale.

On the other hand, other reptilian groups like the Pachypleurosaurs, Nothosaurs and Placodonts are clearly in decline, the former two dissappearing in the Carnian, the latter straggling through (with only one species) to the Rhaetian.

The Rhaetian also sees a radical replacement of typically Triassic marine reptiles with Early Jurassic forms. It seems likely that some sort of trophic turnover must have affected the marine food chain, leading to the exitinction of the gigantic shonisaurs and their smaller cousins, and enabling the evolutionary radiation of new types of ichthyosaurs and the first "nessie"-style plesiosaurs. This change is so dramatic that with the exception of a single genus of placodont ("reptilian walrus"), all Rhaetian marine reptiles are of the classic "Liassic" (early Jurassic) type.

On land typically Mesozoic-Cenozoic plants such as "modern" Conifers appeared during the end of the Late Triassic (Rhaetian), and the giant and throughout the Triassic common *Neocalamites* sphenopsids dissapeared.

A *Plateosaurus* browses for food, whilst a small anchisaur looks on nearby. Plants include ferns, cycads, and bennettitales
graphic from Earth History Resources

Of course it is the tetrapods that grab the most attention, and we have already briefly mentioned the amazing ichthyosaurs of this time. While on land, the Late Triassic was the beginning of the"'Age of Dinosaurs", and constitutes one of the most important faunal replacements among non-marine tetrapods. A number of important groups appeared suddenly in the (Late?) Carnian (phytosaurs, advanced pseudosuchia, small crocodylomorphs, dinosaurs and mammals), and Norian (pterosaurs), of which the pseudosuchian thecodonts and immediately took over the landscape, and phytosaurs the rivers and lakes. Dinosaurs remain mostest-sized and rare during the Carnian, but had filled many ecological niches by Norian and Rhaetian time, both herbivores and carnivores reaching large size (6 to 9 meters in the case of the herbivorous plateosaurs and melanorosaurs). The Norian also saw the decline of the Kannemeyerid dicynodonts, which were replaceed as megaherbivores by prosauropod and early sauropod dinosaurs, although continuing on for a while numbers in the wetter biomes of the equatorial and Gondwanan regions. The end-Rhaetian mass extinction saw the extinction of all the large pseudosuchian/crurotarsan "thecodonts" (even those that only appeared during the Carnian) and all but two or three families of large temnospondyl amphibian, leading to an even greater doiminance by dinosaurs as the Jurassic openeed. However, small protococodilian pseudosuchians (Sphenosuchia) continued through to the Jurassic quite happily, as did most lepidosaurian lizard-like forms and the equally lizard-like Choristodera, the little mammals, and several clades of small advanced cynodonts very close to the mammalian stem.

Early Late Carnian terrestrial and semi-aquatic tetrapod faunas were quite cosmopolitan as evidenced by the distribution of the phytosaur *Paleorhinus* and the metoposaurs *Buettneria*/*Metoposaurus*, but became more provincial during the latest Carnian and Norian [Hunt, et al, iNet], with the Rhaetian being the most provincial of all (which makes correlating fanas difficult) [Lucas 1998, Lucas 1999] During this time there were three broad biogeographic provinces - northern Laurasia (Europe, Greenland, and perhaps northeastern North America (indicated in the Newark Supergroup)), southern Laurasia and northern Gondwana (Western North America (Chinle), Morocco) and southern Gondwana (India, South Africa, Argentina, Brazil) [Hunt, et al, iNet]. MAK030909

Late Sauropodomorph Revolution

The sudden rise to dominance of the sauropodomorphs during the late Triassic was a real ecological revolution. Previously a rather minor element of the tetrapod fauna, sauropomorphs suddenly underwent an evolutionary radiation during the Middle Norian, and by the Late Norian, exept for a few types of aetosaurs in west Pangea, every large herbivore on Earth was a sauropodomorph. It was a monopoly that was to endure until the early Cretaceous in Laurasia, and the end of the Mesozoic in Gondwana

Can sauropodomorph success be explained in terms of what one might call the "Mammal model" (sudden extinction of competitors produces vacant ecological niches), the "Archosaur model" (environmental factors like climate change favour one group over another), the "Insect model" (a completely new adaption enables the type radiates into many ecological niches that were previously unfilled), or the "Teleost model" (the new type is simply a superior adaptive design and takes over from the less efficient rivals)? Current research seems to indicate there was no mass extinction [Hunt et al] which invalidates the "Mammal model". If there really was no dramatic global climate change [Olsen et al] such as was previously thought, that leaves out the "Archosaur model". And the fact that prosauropods were around for at least several million years during the Carnian (being found in the possibly early Carnian of Madagascar, although Lucas & Heckert 2002 argue for an early late Carnian date) without going anywhere seems likewise to cast doubt on the "Insect" and "Teleost" hypotheses.

Whatever the reason, the change in terrestrial megaherbivore biotas is so marked that Anderson and Cruikshank coin the term "Plateosaur/Melanorosaur empire" to distinguish the Norian and following Rhaetian land faunas from the preceeding Olenekian through to Carnian "Kannemeyeriid/Diademodontid empire" (Kannemeyeriid/Gomphodontid may be more correct, as *Diademodon* is mostly Olenekian). Zawiskie 1986 likewise refers to the equivalent "Rhynchosaur-Traversodontid Community" (which he describes as Gondwanan, it has since been found that elements of this community also occured in (at least Western) Laurasia) being replaced by the "Plateosaur Community"

This ecological revolution also meant a dramatic transformation in the way that animals processed their food - a switch from Mammal-Like oral chewing to Bird-like gastric mills (stomach chewing)

All the sauropodomorphs were herbivorous dinosaurs, with long necks and small heads. With the dissapearance of the Rhynchosaurs and Trilophosaurids (at the end of the Carnian) and the Therapsid (mammal-like reptile) Dicynodonts (during the Norian) and the decline of the Traversodonts, they became the dominant terrestrial herbivores. Whereas all of the earlier forms had strong jaws and teeth or horny beaks, the sauropodomorphs had tiny heads and weak jaws and teeth, and used gastric stones, like modern-day birds, to grind up food in the stomach. Here we see the replacement of mammal-like masticatory apparatus (strong jaws and teeth, which grind up the food in the mouth) with the bird-like emphasis on gastric stones.

Through the ascendancy of the early sauropodomorphs and their descendents the gigantic sauropoda, this bird-like "chewing" was to characterise the dominant herbivores for 80 to 100 million years (from the late Triassic to earliest Cretaceous), while the mammal-like chewing ornithopod dinosaurs, with their elaborate batteries of teeth were to remain as minor players, before suddenly diversifying in the middle and late Cretaceous, perhaps in response, as with the Triassic prosauropod success, to a change in climate and/or vegetation.

During this same period the genuine mammals also waited in the sidelines, as small nocturnal rodent-like creatures, until the extinction of the dinosaurs gave them space to undertake their evolutionary radiation after the end of the Cretaceous. But that is another story.

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The Carnian Age - 1

The Carnian Age of the Late Triassic Epoch: 228 to 217 million years ago

Mesozoic Era
  Triassic Period
    Early Triassic Epoch
    Middle Triassic Epoch
      Anisian Age
      Ladinian Age
    Late Triassic Epoch
      Carnian Age
      Norian Age
      Rhaetian Age
  Jurassic Period
  Cretaceous Period

Introduction

New Archosaur Clades (including the first Dinosaurs), and the First Mammals

The first of the three divisions that make up the Late Triassic period, the term Carnian Stage was introduced by Mojsisovics in 1869. It is named after the Carnic Alps in Europe. The alternative spelling Karnian is sometimes used but Carnian with a C is based on the Latin and therefore more correct.

The Carnian was an important time,

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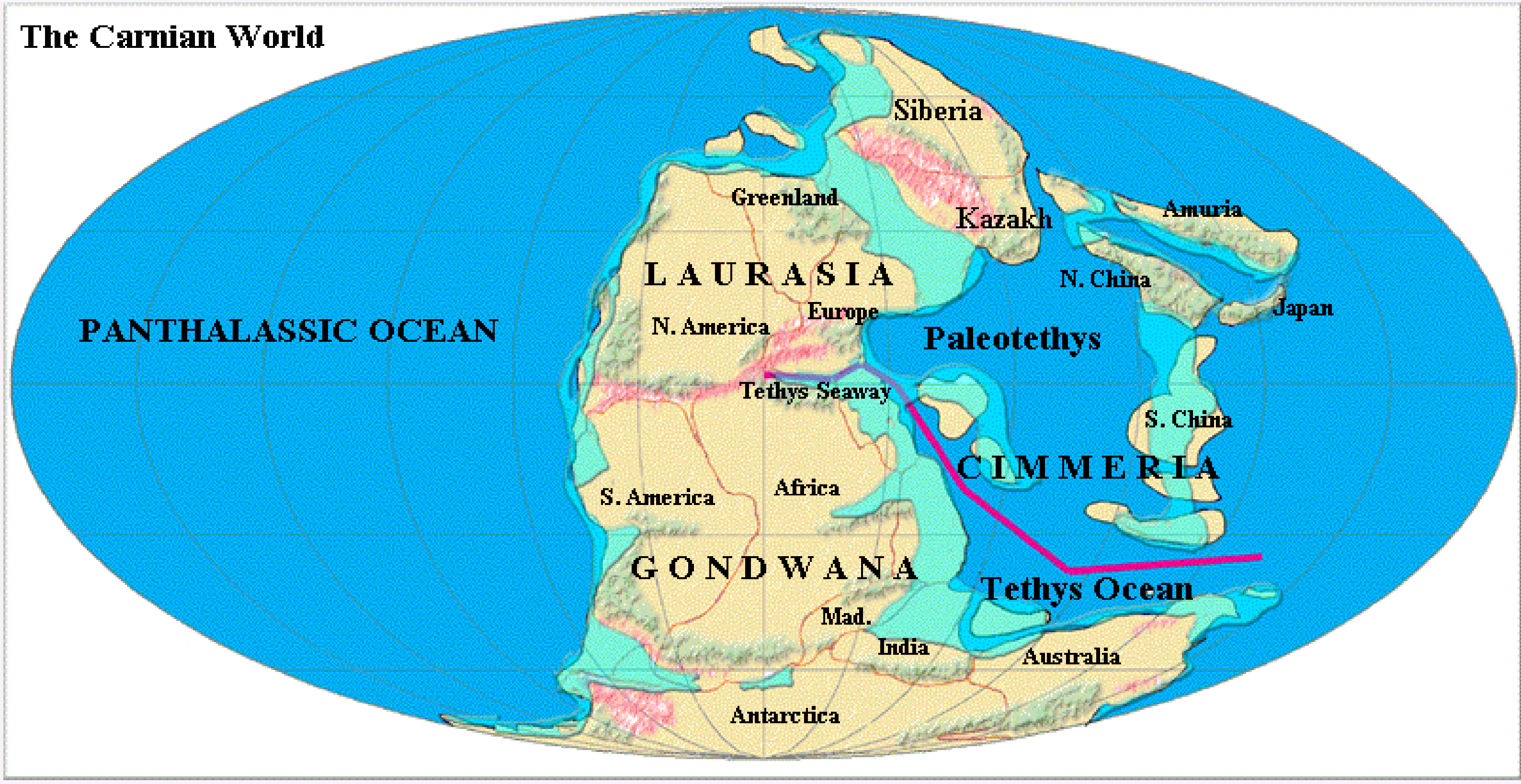
evolutionarily speaking. On the one hand the archosaurs - the "ruling reptiles" - have pretty much taken over the world, and include a whole host of large lizard-, crocodile-, and dinosaur-like forms. One the other hand, the therapsids or mammal-like reptiles have become progressively smaller. They are represented by several types, of which the small ictidosaurs continue on to give rise to mammals.

But the most significant creatures to appear are the dinosaurs. As yet they too were still rather small and insignificant: bipedal bird-like carnivores, insectivores, and herbivores. Most of the big animals of the time were not dinosaurs but dinosaur and crocodile-relatives, of the time: the phytosaur, ornithosuchid, prestosuchid, aetosaur, poposaur, and raiusuchid archosaurs.

As with the early Triassic world, many of these animals had world-wide distribution: the fauna of India, North America, South America, Africa, and Britain are seen from known fossils to be pretty much the same. There is however the beginning of a separation between the faunas of the North - the Laurasian supercontinent - and those of the South - the Gondwanaland supercontinent. Already, the land-masses, having barely united, were beginning to separate. Pangea itself was still to remain as a fairly coherent entity for 100 million years.

But several unique and evolutionarily very important forms did apparently develop in West Gondwanaland, or what is now South America. The earliest dinosaurs (*Eoraptor*, *Staurikosaurus*, etc), dinosaur ancestors (*Lagosuchus*), and crocodile ancestors (*Trialestes* and *Gracilosuchus* are known from this continent. So it seems that this was an important centre of evolution at this time.

The Geography of the Carnian



The Carnian Age may mark the high point of Pangea. This is a difficult point to identify since, like the Roman Empire, Pangea continued to grow at the margins long after it had begun to crumble from within. We lack a Triassic Tacitus to describe "the history of a period rich in disasters." Then again, Tacitus would undoubtedly have blamed the whole business on the decadence of the cynodonts, their loss of ancient virtues, the perfidy of the debased archosauromorphs, and the primitive virility and martial spirit of the early dinosaurs. Perhaps we are better off, after all, with the stodgy, but less judgmental language of plate tectonics.

The big news of the Carnian -- and of the entire Triassic -- was the spreading ridge in the south, which had sheared off small pieces of Gondwana and was busy driving these small "Cimmerian" plates north across the Paleotethys. The exact identity of the Cimmerian lands seems to be subject to some dispute. The list may include Iran, possibly Turkey, Tibet, Indonesia and Southeast Asia. Behind them, the spreading ridge left the "new" Tethys Ocean. As the eastern end of the ridge herded the Cimmerian blocks north, the western end began to drive a wedge between Laurasia and Gondwana. This gap was filled by a long, narrow, shallow sea, the Tethys Seaway. The Tethys Seaway is well-known for the distinctive vertebrates that evolved and lived within it, particularly the Sauropterygia and Ichthyosauria. By Carnian times, the Seaway and its fauna were well-established, although the permanent rift had not yet penetrated far to the west. In between, in the region sometimes called the Vardar Ocean, collisions were already taking place between small, northward moving blocks and the European craton. Subduction of the old sea floor of the Paleotethys under the southern margin caused lifting in southeastern Europe and southern Russia. Transverse faulting associated with the Tethyan rift seems to have caused geological chaos in central Europe. Geological maps of Central Europe in this period tend to look like political maps of the same area in the Eighteenth Century. Not surprisingly, there is considerable confusion about just what was happening when -- a subject to which we will return in the discussion of climate.

While a permanent rift had not yet developed between North America and Africa or South America, the region was tectonically active. This may or may not have included a Carnian "CAMP Event," a brief catastrophic lava flow at various points along the future rift line (the "Central Atlantic Magmatic Province"), lasting less than a million years. Certainly, there were significant lava flows in Morocco as well as at the Eastern end of the Seaway. However, volcanic activity was also present in Siberia and in southwestern Gondwana. The latter was associated with another major rift, which would separate Africa and South America, on the north, from Antarctica and India, on the south. In fact, by the Carnian, the Karoo rift system in southeast Africa was well-established, and shallow seas already filled most of the rift valley.

The Siberian vulcanism was, by contrast, probably associated with continental consolidation. By the Carnian, all of the various minor blocks around Siberia, including the large Kazakhian piece, had consolidated, and the whole thing was suturing itself to the eastern end of Laurasia. This created a brick wall in the northwest, an immovable object against which the irresistible force of the Tethyan spreading ridge was batting the Cimmerian and Chinese terranes. The result was a sort of train-wreck in the Far East which eventually created the megacontinent of Asia. However, these effects were only just beginning to be felt in the Carnian. ATW03051

The Climate of the Carnian

The Carnian appears to have been a turning point for a number of key environmental variables. Carbon dioxide was reaching a local maximum (at 250-300% of modern levels), and oxygen a local minimum (at about 50% of modern levels). Sea levels had been extremely low and quite stable since the end of the Permian. By the end of the Carnian, we see the first hints of a long-term rise in sea level which would last for a hundred million years, cresting in mid-Cretaceous times. Finally, the relatively stable, dry climates of the Early and Middle Triassic were shifting to the more strongly zonal, monsoonal climates of the Late Triassic.

There are numerous indications from the well-sampled exposures in the Chinle Formation (southwest US), the Newark Supergroup (Eastern US & Canada) and the shores of the Tethys Seaway in Europe, that a pulse of relatively humid conditions occurred during the Carnian. However, there are paradoxical indications, from the *same areas*, that the climate was unusually arid and intemperately hot. At some point, the Seaway itself appears to have experienced a "salinity crisis" (general evaporation) and a breakdown of the reef system.

Professor Paul Olsen and co-workers have proposed a possible solution to this problem which explains most, but not quite all, of the observations. Olsen's key observation, which seems obvious only in retrospect, is geographical. All of these well-sampled areas (a) lie along the Tethyan rift valley (b) on a more or less direct east-to-west transect (c) almost exactly on the Carnian equator. Thus, they are hardly a fair sample of what was going on in Pangea generally. Armed with this knowledge, we can sort things out fairly quickly. First, the conclusion that the Carnian was unusually arid comes from the presence of evaporites, salt deposits from evaporated seas. The stretching and transverse fracturing along the Tethyan rift zone naturally led to many short-term marine transgressions into the rift valley system before the final inundation. In between marine invasions, these temporary seas would dry out, leaving extensive evaporite deposits along the whole length of the rift from Arabia to Arizona. Because transverse fracturing was extensive, particularly in Europe, we may doubt that the timing of either evaporitic episodes or transgressions was the same in all places. For example, a brief survey of abstracts on the web yields three studies which agree that a major transgression, associated with humid conditions occurred in Carnian Italy. However, one says humid conditions appeared early in the Carnian, with the land later becoming arid. Another says the reverse. The third states that equable climates occurred in the middle of the Carnian, with a howling waste on both sides. The problem is probably not dating error, but sampling error. Along the complex and evolving system of transverse faults associated with the Tethyan spreading ridge, we may reasonably expect a great deal of local variation. In particular, evaporites are not a good indicator of climate under these conditions because the rather rapid changes in relative elevation of the splintered blocks causes temporary marine flooding and evaporation without any real change in climate or sea level.

Second, the Late Triassic did see the establishment of a zonal climate. Olsen proposes that a narrow equatorial tropic belt was already established by Carnian times. As Pangea drifted slowly northward, the lands around the Tethyan rift passed through this narrow climatic zone in just a few million years. The observed, asynchronous "pulse" of tropical climate was then a geographical artifact, not a temporal event. The equatorial belt, with its distinct, endemic ecosystem didn't disappear. It simply moved, with the equator, into the poorly known and deeply buried Late Triassic deposits of the southeastern US and northern Africa. This hypothesis is supported by the presence of flourishing higher-latitude, highly seasonal ecosystems (*e.g.* Ischigualasto & North China) roughly where one would expect other belts of moist conditions in a zonal world climate system.

The breakdown of the reef system in the Seaway need not have occurred during one single episode. In any case, the "event," if that is what it was, is coincident with a significant evolutionary change in reef systems. After the mass extinction at the end-Permian, the reef systems of the world were re-established (if we ignore the brief run of stromatolites in the very early Triassic) by calcareous sponges. Some time in the Middle Triassic, corals appeared. These began to replace sponges as the major reef organisms in the oceans of the world by the Late Triassic. Thus, what we see in the Seaway may be only some discontinuity in the faunal replacement of sponges by corals.

One of the more interesting things about the Carnian climate is that it has been modeled to moderately high resolution by one of the most complex computer programs known to man, the GENESIS project. One interesting prediction of the computer model is a very large seasonal temperature variation in the Pangean interior -- on the order of C 45�. This seems unreasonably large, but not completely out of the question. There is no easy way to test this prediction (or retrodiction, to be more precise), and it is probably inaccurate. Nevertheless, it is a useful reminder of one fact: there is simply no guarantee that the surface of the Earth always has been, or always will be, a place in which conventional tetrapods can comfortably survive. ATW030517.

Stratigraphy

The Carnian is the first of the three ages/stages of the Late or Upper Triassic. It is named after the Carnic Alps of Austria and Italy, by the Austro-Hungarian geologist and palaeontologist Johann August Georg Edmund Mojsisovics (1839-1907), in 1869. The alternative spelling Karnian introduced by Tozer in 1967 is not correct as it is based on German rather than Latin. [Harland W.B., *et al*]. Its base is defined by the first occurrence of the ammonoids *Daxatina* or *Trachyceras*, and of the conodont *Metapolygnathus polygnathiformis*. It ends at the base of *Klamathites macrolobatus* or *Stikinoceras kerri* ammonoid zones and the *Metapolygnathus communisti* or *M. primitius* conodont zones [ref GeoWhen database - Carnian] (which is also the start of the Norian). The Carnian is divided into two sub-stages, the older Julian and younger Tuvalian

But whilst marine correlation is pretty straight-forward, thanks to wide dispersal of pelagic and planktonic fossils like ammonoids and conodonts, correlating marine and terrestrial rocks - and hence organisms, can be more tricky.

Problem of Correlating the German Keuper series: There is some controversy over the dating of the terrestrial German Keuper, which itself serves as the standard for the other stratigraphic series, and the Marine ammonite zones. Two alternative correlations are offered. these are indicated here as A and B

sub-stage	ammonite zone (marine)	Zonation of German Keuper - interpretation A	tetrapod zones based on A	Zonation of German Keuper - interpretation B
Late Carnian	*Klamathites macrolobatus*	Schilfsandstein	T 15	Rotewand
	Tropites welleri			
	Tropites dilleri	Gipskeuper	T 14	Schilfsandstein
Early Carnian	*Sirenites nanseni*		T 13	
	Trachyceras obesum			Gipskeuper

Anderson & Cruikshank follow interpretation A, which shifts a large number of faunas into the early Norian; while Harland et al, Chaterjee, and Olsen and Sues go for interpretation B. Magnetostratigraphic evidence indicates the Schilfsandstein is latest Carnian in age (G. Hahn, "Palaomagnetische Untersuchangen im Schilfsandstein (Trias Km 2) Westeuropas". *Geol. Rundsch.* 73; 499-516). An important factor here is the discovery of *Paleorhinus* in marine (*dilleri* zone) strata, thus providing a critical tiepoint to the standard Alpine (Keuper) chronology. No doubt further discoveries will modify these correlations again. It really doesn't matter that much, because the uncertainty is only a few million years either way.

Marine and Terrestrial Straigraphy:

stage	sub-stage	ammonite zone (marine)	tetrapod zone	LVF (Land Vertebrate Age)	phytosaur zone (terrestrial)	Zonation of German Keuper
Carnian Age	Late Tuvalian	*macrolobatus*	T17	**Adamanian**	*Rutiodon*	Blasensandstein Kieselsandstein Rote Wand
	Early Tuvalian	*welleri*	T16			
		dilleri		**Otischalkian**	*Parasuchus*	Schilfsandstein
	Julian	*nanseni*	T15			
			T14			
		obesum	T 13			Gipskeuper

Notes:

Late Triassic Tetrapod Biochronology of Pangaea - Lucas, Hunt, & Huber, gives an important summary of tetrapod faunas of this period. Carnian-Norian biochronology, correlation and biotic events of the non-marine Triassic of North America - Huber, Lucas, & Hunt, - another interesting abstract by the same authors on this topic

Ammonite zones are based on Harland, Cox, Llewellyn, Pickton, Smith and Walters, (1982) *A Geological Time Scale* (Cambridge University Press)

Tetrapod zones is based on J. M. Anderson & A. R. I. Cruikshank, "The Biostratigraphy of the Permian and Triassic, Part 5, a review of the classification and distribution of Permo-Triassic Tetrapods," in *Paleontologica Africana*, **21**, 15-44 (1978); as modified according to LVF correlations in Lucas 1998 (ref below also)

LVF (Land Vertebrate faunachrons) according to S.G. Lucas, "Global Triassic tetrapod biostratigraphy and biochronology", *Palaeogeography, Palaeoclimatology, Palaeoecology* 143, (1998) pp.347-384

Phytosaur zones (and correlation German Keuper, south-west USA and India) are from Sankar Chatterjee, The Late Triassic Dockum Vertebrates; their stratigraphic and Paleobiological significance", in Kevin Padian (ed.) *The Beginning of the Age of Dinosaurs* (1986, Cambridge University Press), pp.139-150, modified according to above

Stratigraphic correlations (German Keuper, south-west USA, India and Argentina) are based on Anderson & Cruikshank, Chaterjee, and Paul E. Olsen and Hans-Dieter Sues, "Correlation of continental Late Triassic and Early Jurassic sediments, and patterns of the Triassic-Jurassic tetrapod transition", in Kevin Padian (ed.) *The Beginning of the Age of Dinosaurs* (1986, Cambridge University Press), pp.321-351

Terrestrial Biotas - Tetrapods

The Aetosaur-Rhynchosaur-Traversodontid Community

The Carnian terrestrial biotas were dominated by what I term the *Aetosaur-Rhynchosaur-Traversodontid Community*. This is so called because while almost all the previous elements of the *Rhynchosaur-Traversodontid Community* are present, they are now joined by the large, armour-plated and spiny aetosaurs (Family Stagonolepidae), one of the few groups to evolve herbivory.

This evolutionary biota, which lasted throughout the extent of the Late Carnian and into the following Early Norian age (early Carnian terrestrial faunas are very poorly known), saw a further diminishing of the therapsids, with only the traversodontids continuing in large numbers. The great kannemeyeriid dicynodonts that had remained the sole megaherbivore type throughout almost the entire Triassic, while still not uncommon, are now so diminished in diversity that in the Chinle local fauna only one big herbivore genus is common, the placerine kannemeyerid *Placerias gigas* (also called *Placerias hesternus*), and to the south in the Ischigualasto local fauna, the related *Ischigualastia jenseni*. However, new herbivores included not only the large aetosaurs but at least two lineages of small bipedal dinosaur.

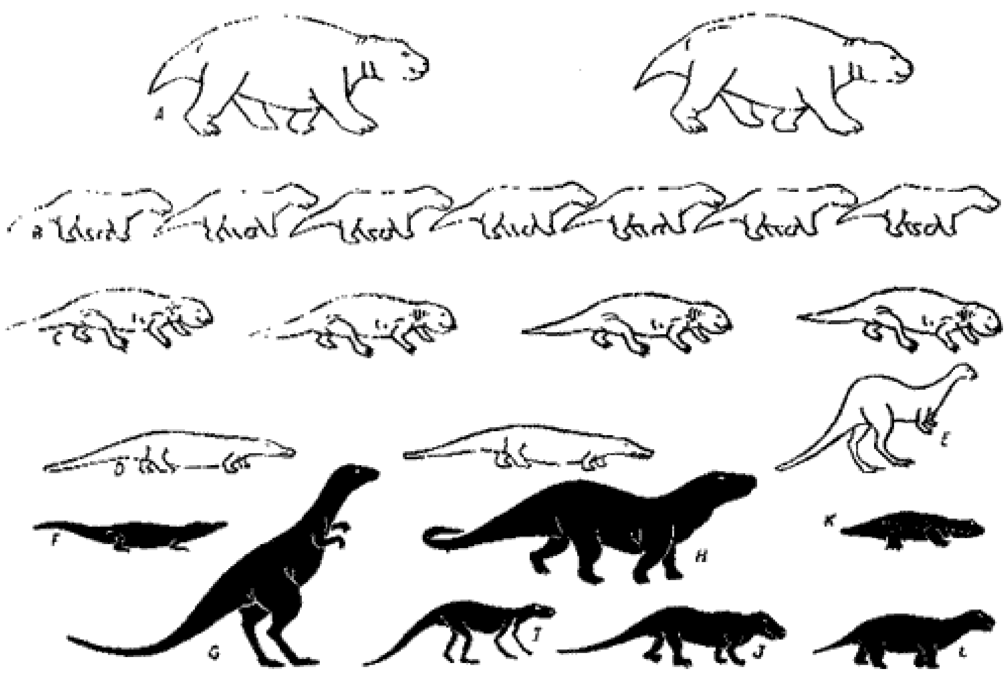


illustration from Bonaparte, 1982

A representative Aetosaur-Rhynchosaur-Traversodontid fauna - Late Carnian of South-West Gondwana (Ischigualasto Formation, Argentina) - showing approximate abundance. Herbivores in outline, carnivores in black
Key: A, Kannemeyeriidae; B, Traversodontiidae; C. Rhynchosauridae; D. Stagonolepidae; E, Gracilosuchidae, F. Proterochampsidae; G, Herrerasauridae ; H. Prestosuchidae; I, Trialestidae; J, Ornithosuchidae; K, Capitosauridae /

The archosaurian carnivores of the Middle Triassic are joined by new large forms like the poposuchids and ornithosuchids, both of which were

Mastodonsauridae and Chigutisauridae; L, Chiniquodontidae

facultative bipeds (i.e. capable of both bipedal and quadrupedal walking and running), several further small gracile terrestrially adapted crocodylomorphs, as well as the very first dinosaurs, all bipedal and mostly small, and represented by the three main dinosaurian lineages of Theropoda, Sauropodomorpha, and Ornithischia. Only the theropods are carnivorous, but these are represented by several families (Staurikosauridae, Herrerasauridae, and possibly Coelophysidae). All the archosaurs - herbivores and carnivores - had an efficient, vertical limb posture superior to that of the contemporary therapsids.

Meanwhile, the rivers, lakes and swamps were populated by new types of amphibians (metoposaurs, although possible ancestors are reported from the early Triassic [Steyer 2002]) and the astonishingly crocodile-like phytosaurian archosaurs, which, unlike their terrestrial relatives, had a primitive, typically reptilian sprawling posture.

Early Late Carnian (early Tuvalian) faunas were quite cosmopolitan as evidenced by the distribution of the parasuchian *Paleorhinus* and the metoposaurid *Buettneria*/*Metoposaurus* [Hunt, et al, iNet], but became more provincial during the latest Carnian.

It was previously thought that the Kannemeyeriid-Rhynchosaur-Traversodontid megaherbivore assemblage died out suddenly at the end of the Carnian epoch, victims of the most serious of several mass-extinctions that rocked the Triassic world. It now seems to be the case that some of these animals continued through to the early or middle Norian, and the extinction was more gradual.

Carnian Land-vertebrate Faunachrons

Dr Spencer Lucas (ref) divides Triassic tetrapod evolutionary communities into eight land-vertebrate faunachrons (LVF). Of these, the Berdyankian includes all of the Ladinian and possibly some of the early Carnian. The Otischalkian is a short period that encompasses the early part of the late Carnian, and the Adamanian the remainder of the Carnian. The following is a brief review of these stages, and the characteristic index fossils of each.

Early Carnian LVF

Whilst **early Carnian** marine vertebrates are well known from the Tethys, there are no *unambiguous* early Carnian terrestrial tetrapod-bearing formations. The Lower (Therapsid Assemblage) part of the Santa Maria Formation (Berdyankian LVF) may possibly be (or extend into) earliest Carnian, rather than a solely Ladinian as traditionally assumed. However the fauna is very endemic and so difficult to correlate. An apparently early Carnian assemblage has recently been collected from basal levels of the Isalo II in the southern Morondava Basin, near Sakaraha, in western Madagascar [Burmeister *et al* 2000]. These include the traversodontid *Exaerpeton* and other synapsids, possibly the earliest known prosauropod dinosaurs (or the earliest dinosaurs if the dating is correct), and the rhynchosaur, *Isalorhynchus genovefae*. Preliminary cladistic analysis of the latter suggests a placement between Middle Triassic rhynchosaurs from England and Tanzania, and the Late Carnian Hyperodepodon from Scotland and South America . [Flynn *et al* 1999]. There is a curious absence of the ubiquitous (from late Carnian onwards) phytosaurs and aetosaurs, although these both occur higher up in the stratigraphic sequence. However Langer *et al* 2000 reassigned *Isalorhynchus* to *Hyperodapedon*, and Spencer G. Lucas and Andrew B. Heckert [Lucas & Heckert 2002] argue that the Isalo II base is no older than Otischalkian (early late Carnian, see below)

Otischalkian LVF

The **Otischalkian** is defined as the interval from the FAD (First Appearance Datum) of the phytosaur *Paleorhinus*/*Parasuchus* up to (but not including) the FAD of the phytosaur *Rutiodon*. Among the widespread tetrapod index fossils of this time are the phytosaurs *Paleorhinus* and *Angistorhinus*, the aetosaur *Longosuchus*, the temnospondyl *Metoposaurus* and the small armoured archosaur *Doswellia* [Lucas 1998, Lucas 1999]. Some of these forms are illustrated on the left.

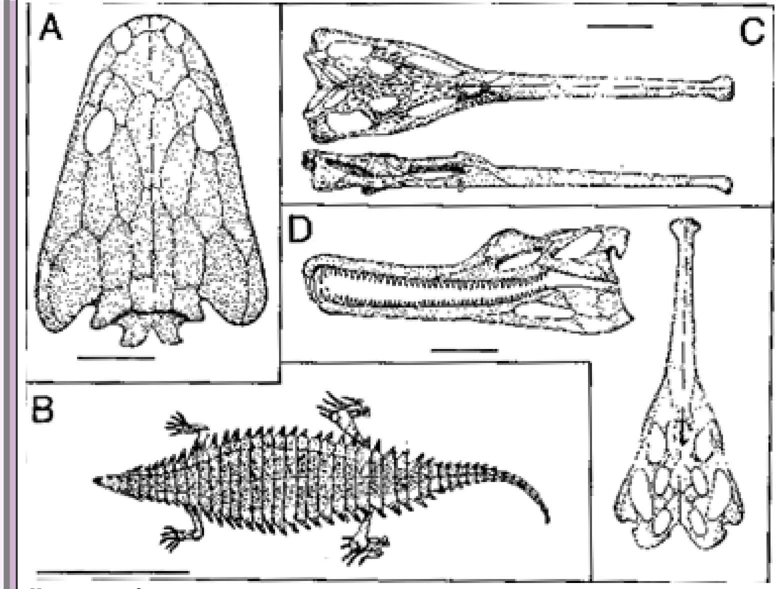


illustration from Lucas 1998

Otischalkian index fossils: (A) *Metoposaurus*, (B) *Longosuchus*, (C) *Paleorhinus*, (D) *Angistorhinus*, Scale bars A , C and D are 10 cm; B is 1 meter.

Included in the Otischalkian is the Chinle Group and correlatives in south-west USA (including the type fauna found in the Colorado City Member of the Dockum Formation, Chinle Group near the defunct town of Otis Chalk, Howard County, Texas), the equivalent Sanfordian interval of the Newark Supergroup basins of eastern North America; the Schilfsandstein, Kieselsandstein, Lehrbergschichten and Blasensandstein of the German Keuper; the Irohalene Member (T4) of the Timesgadiouine Formation, Argana Group, Morocco; and basal part of Maleri Formation, Pranhita-Godavari Valley, India. [Lucas 1998, Lucas 1999] The Ischigualasto Formation of Argentina and the upper Santa Maria Formation of Brazil are dated somewhat later, largely on the basis of the single taxon *Stagonolepis* (*Aetosauroides*), but the endemic nature of fauna makes correlation difficult, and it is not at all certain that the scrappy Santa Maria remains belong to the same species. Santa Maria forms differ on either the species or the generic level, which indicate either a high degree of endemism, or that the Upper Santa Maria Formation is slightly earlier [Bonaparte, 1982], or both

The Otischalkian is described as late Julian-early Tuvalian age based on *Paleorhinus* and *Metoposaurus* records in Tuvalian marine strata in Austria, palynostratigraphy, and magnetostratigraphy [Lucas 1998, Lucas 1999], or early Tuvalian only [Heckert & Lucas 2000]

Adamanian LVF

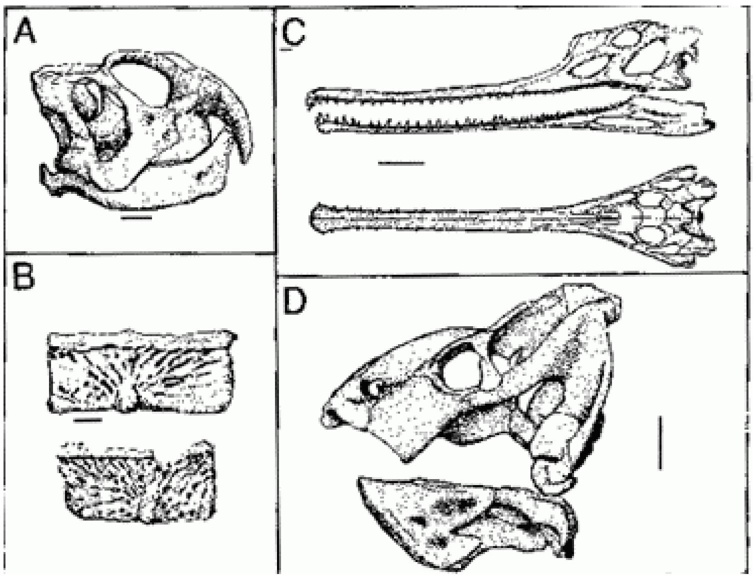


illustration from Lucas 1998

Adamanian index fossils: (A) *Scaphonyx*, (B) *Stagonolepis* (paramedian plates), (C) *Rutiodon*, (D) *Ischigualastia*, Scale bars A is 1 cm, B 3 cm, C and D are 10 cm.

The Adamanian succeeds the Otischalkian. The beginning of the Adamanian is defined as the FAD of the phytosaur *Rutiodon*, and it continues up to (but not including) the FAD of the phytosaur *Pseudopalatus*. Lucas 1998 and 1999 lists the tetrapod taxa *Scaphonyx* (=*Hyperodepedon*), *Stagonolepis* (including "*Aetosauroides*") and *Rutiodon*-grade phytosaurs such as *Leptosuchus* (possibly a synonym of *Rutiodon*), and *Smilosuchus* as useful Adamanian index fossils. However, Scaphonyx/Paradepedon/*Hyperodepedon*-grade rhynchosaurs are also reported from Otischalkian correlates in India and Eastern USA (Newark) [Lucas 1998]. And just because *Stagonolepis* is unknown from the Otischalkian of North America does not mean it did exist elsewhere at that time (diachronic appearance of the same species in different localities is a well-known phenomenon; e.g. the problem of correlating early Cambrian faunas [Brasier, 1989).

The Adamanian type vertebrate fauna is that of the Blue Mesa Member of the Petrified Forest Formation in the Petrified Forest National Park, Arizona, USA. Other major Adamanian-age vertebrate faunas are those of the Conewagian interval of the Newark Supergroup basins of eastern North America; Lossiemouth Sandstone Formation, Scotland; and the Ischigualasto Formation, Argentina and upper Santa Maria Formation, Brazil [Lucas 1998/1999]

(although as I suggested it is not impossible that these may not also extend earlier)

The Adamanian can be pretty reliably dated as latest Carnian (Late Tuvalian) based mostly on palynostratigraphy and magnetostratigraphy.

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text by M. Alan Kazlev (MAK) and Augustus T. White (ATW)
Last revised ATW030513, MAK030913

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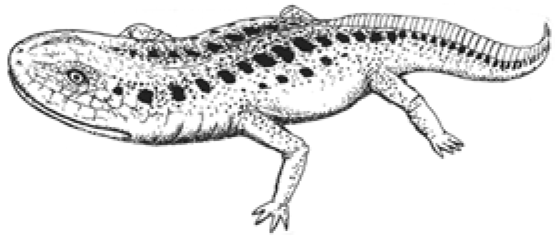
The Carnian Age - 2

A Carnian Bestiary - 1

Mesozoic Era
  Triassic Period
    Early Triassic Epoch
    Middle Triassic Epoch
      Anisian Age
      Ladinian Age
    Late Triassic Epoch
      Carnian Age
      Norian Age
      Rhaetian Age
  Jurassic Period
  Cretaceous Period

Pelorocephalus | *Metoposaurus* | *Leptopleuron* | *Shonisaurus* | *Henodus* | *Brachyrhinodon* | *Malerisaurus* | *Trilophosaurus* | *Hyperodapedon* | *Paleorhinus/Parasuchus* | *Angistorhinus* | *Saurosuchus* | *Ornithosuchus* | *Stagonolepis* | *Postosuchus* | *Erpetosuchus* | *Scleromochlus* | *Pisanosaurus* | *Herrerasaurus* | *Saltopus* | *Placerias* and *Ischigualastia* | *Exaeretodon* | *Microconodon* and *Dromatherium* | *Gondwanadon* and *Adelobasileus*



Dinosaurios y animales prehistoricos argentinos/Ischigualasto fauna

Pelorocephalus ischigualastensis **Bonaparte, 1975 was a chigutisaur, a type of temnospondyl amphibian known only from Gondwana/South Pangea. The late Carnian was the high point of these creatures; as well as several species from Argentina, there are two genera from the Upper Maleri Formation of India. These specialized short-headed amphibians were one of the very few labyrinthodonts to survive the end Triassic extinctions. During the Jurassic and Middle Cretaceous crocodiles are unknown and giant Chigutisaurids (3 to 5 meters) flourished in south-east Gondwana.** ***Pelorocephalus*** **was originally known as** ***Chigutisaurus*****, the genus from which the family derives its name. But whereas** ***Chigutisaurus*** **was named in 1948, the**

***Pelorocephalus* moniker goes back a further four years, to 1944, and hence has priority, under the formal rules of Linnean (binomial) nomenclature** Carnian species:

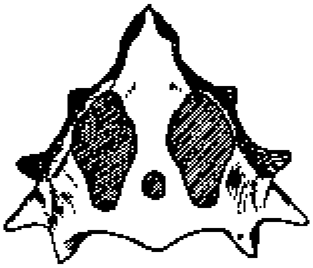
Pelorocephalus cacheutensis (Rusconi, 1953)
Pelorocephalus ischigualastensis Bonaparte, 1975 - Late Carnian - Ischigualasto Formation, San Juan Province, Argentina (Southwest Pangea)
Pelorocephalus mendozensis Cabrera, 1944 [= Chigutisaurus tunuyanensis Rusconi, 1948b , ??Otuminisaurus limensis Rusconi, 1948 [ref Marsicano 1996] (Latest Carnian/early Norian) - Cacheuta Formation Cerro Bayo, West-Central Argentina.
Pelorocephalus tenax (Rusconi, 1949)
Compsocerops cosgriffi Sengupta 1995 - Latest? Carnian, Upper Maleri Formation, Pranhita-Godavari Valley, India [ref. Lucas 1998]

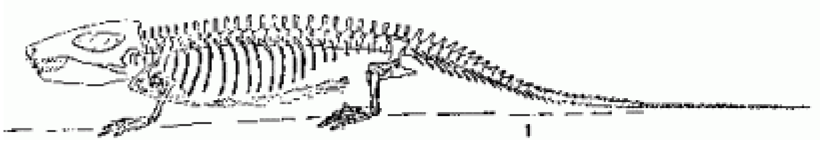
Kuttycephalus triangularis Sengupta 1995 - Latest? Carnian, Upper Maleri Formation, Pranhita-Godavari Valley, India [ref. Lucas 1998]

Links: Pelorocephalus ischigualastensis
References: Bonaparte, 1975

The Carnian temnospondyls were every bit as diverse as their Ladinian predecessors. In addition to the familiar mastodonsaurids (Cyclotosaurs) there were also several newcomers - the big metoposaurs and small latiscopids (both included under the same superfamily). No plagiosaurs are known from the Carnian but they must surely have been present, since their remains are found in both Ladinian and Norian deposits. The metoposaurs are one of the Carnian success stories. They appear to come seemingly from nowhere (although possible early forms are reported from the Induan [J.S. Steyer 2002) and attain near-global distribution. They were large aquatic forms (2 to 2.5 meters in length) with huge flattened skulls, very much like the Capitosauridae/Mastodonsauridae, but differing in details and proportion of the skull. The European (North Central Pangea) metoposaurs differ in small details from the North American and Indian (north-western and central southern Pangean) forms, which differ again from the central Pangean (Morocco) species. Although these have all been given different generic names, they are very similar and probably could equally be retained under *Metoposaurus*.

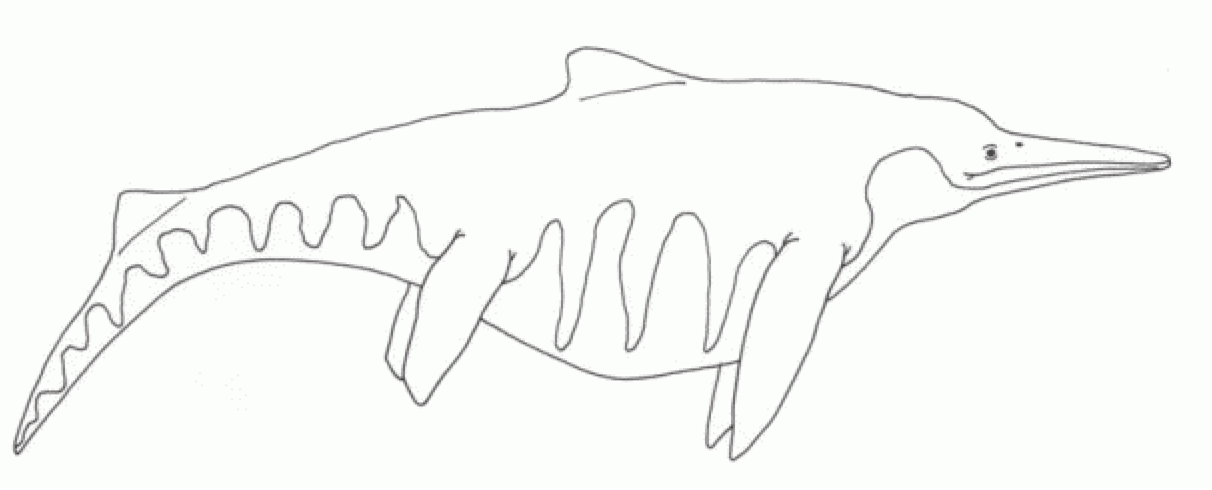
Shown here is *Buettneria perfecta*, a metoposaur whose fossil remains are known from both the Chinle Group and Newark Supergroup, North America (then west and central equatorial Pangea). Length of skull about 40 cm; overall length about 2 meters. Like almost all metoposaurs (apart from the aberrant small terrestrial *Apachesaurus*) these animals probably spent much of their time submerged in ponds, rivers, and swamps.





from Kuhn 1969 after Huene 1912 (skeleton) and 1956 (skull)

***Leptopleuron lacertinum*, known from the Lossiemouth Beds, Elgin, Scotland, represents yet another representative of the primitive (parareptile) reptilian herbivores called procolophonids. These stocky herbivorous desert "lizards" were a ubiquitous component of many Triassic terrestrial ecosystems, especially the more arid environments; which during late Triassic Pangea meant the higher and more desert-like latitudes [Olsen et al]. *Leptopleuron* was a fairly advanced form, as indicated by its broad spiny skull, and would seem to be closely related to the late Norian to Rhaetian *Hypsognathus*, as well as to several other little known Norian forms [Sues *et al* 2000]. This could all be placed in the family Leptopleuroninae Ivakhnenko, 1979. It would seem then that during the late Triassic the leptopleuronines completely replaced the older and less specialized procolophonines**



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During the Carnian epoch the Ichthyosaurs continued to flourish, a number of forms existing alongside each other. These have traditionally been classified under the families Shastasauridae and Shonisauridae, although more recent research has the shown these to be paraphyletic or even polyphyletic groupings, part of the clade Shastasauria, and the relationships between these various types not well known, owing to fragmentary material in the case of many forms. These were large animals, and grew progressively more so; "*Shastasaurus*" beginning at 3 meters and increasing to 10 meters in stratigraphically younger forms [Zittel, 1932 p.280]. *Shonisaurus* was even larger but exhibited a similar trend [Camp, 1980], so that the latest Carnian forms reached more than 15 meters. While one related Norian form was about 23 meters along, the largest Mesozoic marine animal known. It is possible that this rapid increase in size was encouraged by the vacant ecological niche left by the extinction of earlier large marine reptiles *Cymbiospondylus* and *Paranothosaurus*, but the shastasaurs grew much larger than their predecessors.

***Shonisaurus popularis* Camp 1976, from the Luning Formation of Nevada, is the best known of these late Triassic ichthyosaurs, as a number of almost complete skeletons have been found, and the largest animal of its time. The skull alone is 2.4 to 3.7 metres long; overall length is about 14.5 to 15.4 metres, and weight might be estimated at 30 to 40 tonnes. The tail is only slightly bent, and the paddles were unusually long for an ichthyosaur, and, also unique for this group, the fore and hind limbs were the same size (in most ichthyosaurs the forelimbs are larger). These whale sized reptiles were not as streamlined as their later Jurassic descendents, being transitional between the earlier, more elongate Triassic types like *Mixosaurus* and *Cymbiospondylus* and the Jurassic dolphin like forms. These Late Triassic ichthyosaurs probably fed on slow swimming heavy scaled chondrostean and holostean fish of the time, as well as other, smaller reptiles; certainly the giant Shonisaurus (above) with its long deep body would have been incapable of rapid bursts of speed, but seems to be designed more as a long distance endurance swimmer**
***Shonisaurus* is Nevada's state fossil**

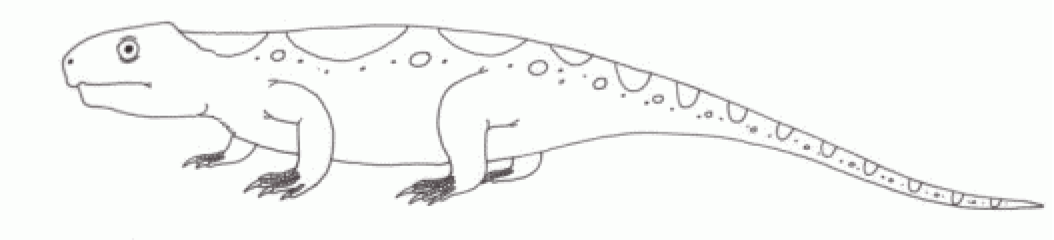
?*Shonisaurus silberlingi* Camp 1976 - Lower Luning Formation (= *S. popularis*?)
?*Shonisaurus mulleri* Camp 1976 - Middle Luning Formation (= *S. popularis*?)

***Shonisaurus popularis* Camp 1976 - Upper Luning Formation (or just Luning Formation if the above two are synonyms**
***Himalayasaurus tibetensis* Dong, 1972 - Norian (similar in size and form to *S. popularis* [Motani *et al* 1999])**

***S. silberlingi* represents the beginning of a lineage of shonisaurs that continue through the late Carnian. The next, larger, species in the series, found in a slightly younger stratigraphic level is *S. mulleri*, and *S. popularis* is the largest and most recent. Because of the fragmentary remains of the former tow it is now considered that they are probably synonyms of *S. popularis*, but it is not impossible for there to be a series of species replacing each other in a short interval of time.**
Reference: Camp, 1980

illustration by Steve Kirk, © from *Encyclopaedia of Dinosaurs and Prehistoric Animals*, Barry Cox, R.J.G.Savage, Brian Gardiner, Dougal Dixon,

***Henodus chelyops* Huene 1936 is known from a number of skeletons from the Gipskeuper (Early Carnian) of Tübingen, southern Germany. The only known non-marine placodont, it inhabited brackish or possibly freshwater lagoons, and may have fed on fishes and crustaceans as well as molluscs. As with the Ladinian *Placochelys*, it was a member of the Placodonta that had evolved to look like turtles, with a broad armoured carapace. The back and belly were covered with an armour of irregular, many-sided bony plates, the whole being completely covered with horn. The square toothless snout was equipped in life with a strong horny beak, another parallel with a modern turtle. Originally it was considered to be an advanced species, but recent research indicates that Henodus may actually represent a primitive form, and its late appearance in the fossil record explained by the fact that it was restricted to a peculiar environment that is not preserved in older rocks of the same region. [Rieppel and Zanon 1997). Henodus reached an overall length of about 1.2 meters.**
Links: Henodus Henodus - Dinoworld, Henodus - Pangea
References: *Dixon et al 1988*, Kuhn 1969, Naish 2000, Fauna der Obertrias (Mittel- und Oberkeuper)



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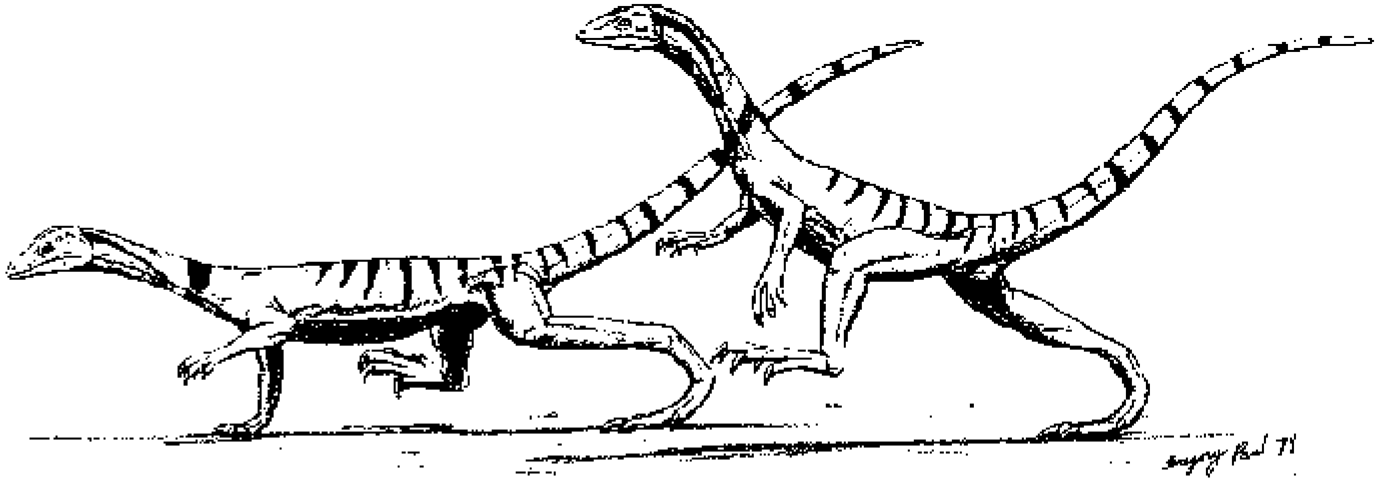
***Brachyrhinodon taylori* is one of the oldest known sphenodonts, a group that filled the important lizard ecomorph in the late Triassic and throughout the Jurassic, when true lizards remained less common. This little animal is remarkable for the brevity of the snout, which would seem to represent a specialized adaptation. It is known from poorly preserved casts in the Elgin sandstone, which makes exact relationships difficult to determine, and has been placed in its own subfamily Brachyrhinodontinae [Kuhn 1969], related**

to the Polysphenodontinae [Fraser 1986], or placed with *Polysphenodon* in a clade that includes *Clevosaurus* [Wu, 1994]. In any case, these little reptiles had already become a part of the small insectivore guild, and were clearly more widespread and diverse then their fragmentary remains indicate



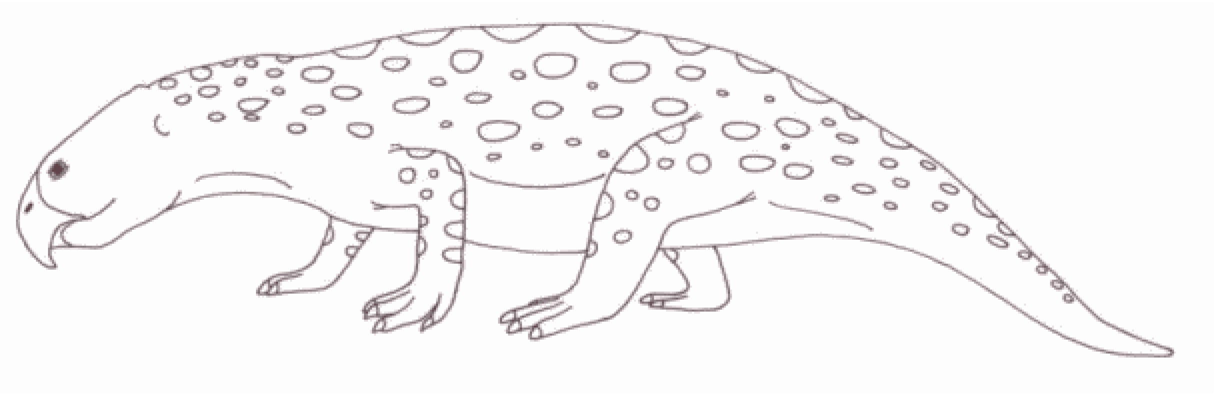
llustration by Gregory S Paul

***Malerisaurus* was a lizard-like prolacertiform, superficially not unlike the Induan *Prolacerta*, which averaged about 1.2 meters in length. It probably had rather similar habits to a large tropical lizard. The hindlimbs were larger than the front legs, indicating that, like Permo-Triassic Younginoformes and the modern fill-necked lizard of Australia, these animals could rear up on their hind limbs for an extra burst of speed. Feeding on invertebrates and small vertebrates, *Malerisaurus* itself fell prey to larger hunters. Two specimens of *M. robinsonae* were found preserved in the stomach cavity of a *Parasuchus* phytosaur.**

These animals were widely distributed during late Triassic times. *Malerisaurus robinsonae* Chatterjee 1980, illustrated here, is known from the early Late Carnian [Otischalkian] Maleri Formation, of the Pranhita-Godavari Valley, India. A very similar species, *M. langstoni* Chatterjee, has been found in strata of the contemporary Dockum Formation of Texas

llustration (such as it is) by M. Alan Kazlev

***Trilophosaurus buettneri* were large (length about 2.5 meters) herbivorous reptiles, with a body in the form of a large lizard, but with an incongruous-looking small turtle-like heads and a toothless beak. These sprawling reptiles appeared suddenly in the late Carnian and flourished briefly before dying out, although some small Norian forms from Europe may be related. *Trilophosaurus* is from the Otis Chalk, Dockum formation, Chinle Group, of Texas, USA (equatorial west Pangea) early Late Carnian [Otischalkian age]. *Trilophosaurus* this was at one time considered a euryapsid, owing to similarities of the skull to the aquatic reptiles like ichthyosaurs and plesiosaurs. In more recent decades, it has been conclusively shown that they are actually archosauromorphs, and their nearest relatives are the lizard-like Prolacertiformes (e.g. *Malerisaurus*) and stock-bodied rhynchosaurs (e.g. *Hyperodapedon*)**



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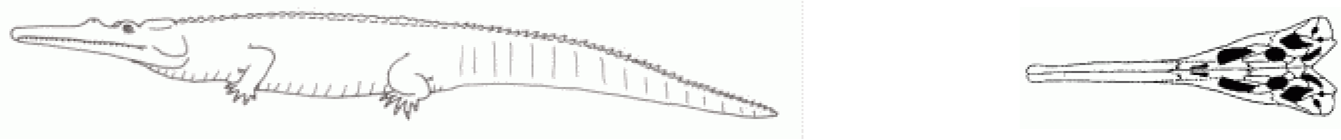
The Rhynchosauridae were a family of purely Triassic archosauromorphs that became particularly important during the Carnian age. All Carnian forms belong to the advanced subfamily Hyperodapedontinae, and most can be included in the genus *Hyperodepedon* Huxley, 1859. These were medium-sized terrestrial herbivores (Skull length about 20 cm; average overall length 1.3 to 1.5 meters), with stocky barrel-like bodies, broad heads and beaked jaws. There were two broad tooth plates on each side of the upper jaw, and these had a groove that matched the single tooth row on each side of the lower jaw, giving a very efficient cutting action. The heads were also much broader than their predecessors, to enable larger rows, and have the most advanced dentition of any rhynchosaurs.

Hyperodapedontines seem to have been extremely common (e.g. they are one of the main elements of the in the Ischigualasto fauna), attained world-wide distribution, and seem to have been specialized feeders on particular types of vegetation, such as dicrodium seed ferns, which were chopped into small pieces and then fermented in the large gut.

These extremely successful animals became completely extinct at the end of the Carnian, due to climate change and the extinction of their food source.
Originally the Hyperodapedontines were considered separate genera (*Scaphonyx*, *Hyperodapedon*, *Paradapedon*, etc) but the various species are so closely related as to belong in the same genus

H. genovefae **Buffetaut, early or late Carnian, Base of Isalo II, Madagascar (= *Isalorhynchus* [Langer *et al* 2000]) (most primitive species?)**
H. huenei **Langer & Schultz, 2000 [*Scaphonyx fischeri* Woodward, 1907, in partim] Late Carnian Brazil (most primitive species?)**
H. mariensis **(Tupi-Caldas, 1933) Late Carnian, Brazil**
H. huxleyi **Lydekker, 1881, early Late Carnian [Otischalkian], Maleri Formation, Pranhita-Godavari Valley, India (= *Paradapedon*)**
H. gordoni **Huxley, 1859, late Late Carnian (Adamanian), Lossiemouth Beds, Elgin, Scotland**
H. fischeri **(Woodward, 1907) sensu Langer & Schultz, 2000 [*Scaphonyx fischeri* Woodward, 1907; *Cephalonia*; *Cephalastron*; *Cephalastronius*; *Scaphonychimus*] Late Ladinian / ?early Carnian) Brazil. [nomen dubium?]**
H. sanjuanensis **(Sill, 1970) sensu Langer & Schultz, 2000 [*Scaphonyx sanjuanensis* Sill, 1970] Ischigualasto Formation, San Juan Province, Argentina (Southwest Pangea),**
"c.f. *Scaphonyx*" early Late Carnian, Sanfordian [= Otischalkian], Newark Supergroup [p.364-5]
References: Lucas & Heckert 2002; Mikko's Phylogeny - Rhynchosauria



drawing © 2001 Vince R Ward - Prehistoric Pages; skull from A. H. Müller, *Lehrbuch der Paläozoologie*

The fish, amphibians and smaller reptiles of the Carnian rivers and swamps frequently fell prey to animals that bore a remarkable resemblance to modern crocodilians. These were the rather inappropriately-named phytosaurs ("plant saurians" because the original describer believed that the mud fillings between the teeth sockets were actually thick herbivore teeth). These were large armoured semi-aquatic archosaurs with a

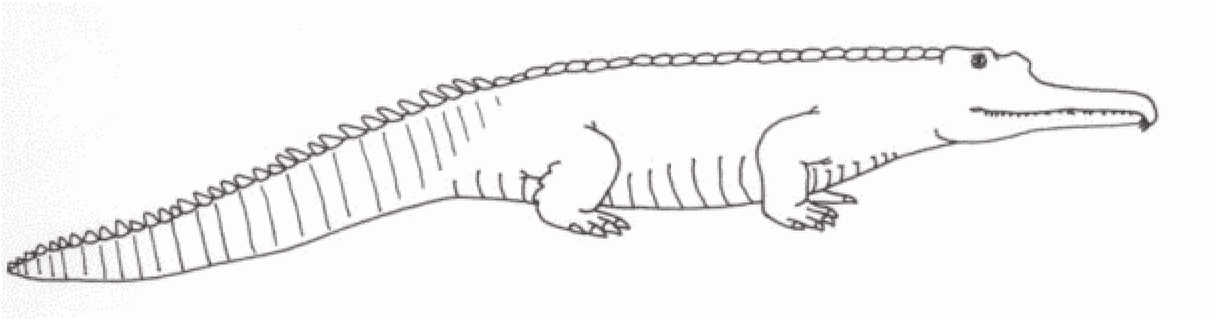
primitive ankle structure and sprawling posture (either these were hold-overs from early Triassic primitive forms, or degenerate descendents from later types).

The most primitive members of the Family Phytosauridae are represented by a number species of the genus variously known as *Parasuchus* and *Paleorhinus*. These were modest sized animals by phytosaur standards (skull length 60 to 80 cm, overall length about 2.5 to 3.5 meters), which means they were big enough to tackle just about anything in their environment, except a bigger phytosaur!

The various species of *Parasuchus* / *Paleorhinus*, which differ in only minor respects, such as proportions of the skull, are found in such widely distributed localities in North America, Europe, Morocco, and India, and hence represents a key index fossil for the Otischalkian interval. co-existed in tropical/equatorial northwest Pangea with other species of phytosaur. Not only did they eat fish and amphibians, but also any terrestrial reptiles foolish enough to approach too close, as indicated by the remains of *Malerisaurus* in the stomach region of one specimen from India (Chatterjee 1978)). The genus is more commonly known as *Paleorhinus*.

***Paleorhinus bransomi* (Williston 1904) - Pop Agie Formation, Chinle Group, Wyoming; Otis Chalk, Dockum formation, Chinle Group, Howard County, Texas (equatorial northwest Pangea) (= *P. scurriensis*, based on a partial skull that seems to be a juvenile of *P. bransomi*)**
***Paleorhinus ehlersi* (Case 1922) - (= *Promystriosuchus*) Dockum formation, Chinle Group, Texas; Irohalene Member of the Timesgadiouine Formation, Morocco (= tropical/equatorial Pangea)**
***Paleorhinus fraasi* (Kuhn 1932) (=Francosuchus) - Blasensandstein, Northesats Bavaria**
***Parasuchus hislopi* Lydekker 1885 - Maleri Formation, Pranhita-Godavari Valley, India**

References: Chatterjee 1978



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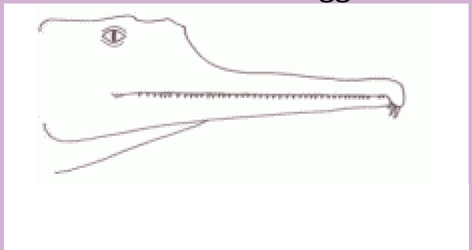
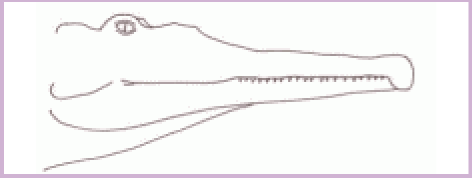
Angistorhinus was another of the early phytosaur genera. It was similar to *Parasuchus* but differed in having the nostrils located further back, towards and above the eyes. This was a more specialized condition that characterized all phytosaurs above the *Parasuchus* / *Paleorhinus* grade. Another development was that the rear teeth were compressed to blade-like sharp edges, while the front of the snout had cylindrical crushing-type teeth. This was the heterodont (different teeth types) condition, indicating further specialization over *Parasuchus* in feeding on large prey. The angistorhinines were also larger and more heavily built, with crocodile- or alligator-like skulls, characterized by a shorter, wider, deeper snout. These were huge animals by any standards; the skull length was generally about 120 cm; estimated overall length to 7 or 8 meters, more in *Angistorhinus megalodon*, a very large, short and heavy-muzzled form sometimes given its own genus (*Brachysuchus*), and which exceeded in size any living crocodile.

Angistorhinus was a contemporary of *Paleorhinus* (both early Late Carnian [Otischalkian] age), and its paleodistrubution ranged from equatorial northwest Pangea (Wyoming) to east equatorial Pangea (Morocco). However it is not known from either Europe (north Pangea) or India (south-east Pangea); it can be assumed that this bigger animal stayed closer to the tropical swamps then its smaller relative.



Angistorhinus alticephalus Stovall and Wharton 1936 - Otis Chalk, Dockum formation, Chinle Group, Howard County, Texas. Also reported from Morocco. Skull length 122 cm (type specimen) - shown when alive, left

Angistorhinus grandis Mehl 1915 - Skull length 90 to 120 cm Pop Agie Formation, Chinle Group, Wyoming;



Angistorhinus (Brachysuchus) megalodon Case 1929 - Skull length 124 cm (type specimen), Otis Chalk, Dockum formation, Chinle Group, Howard County, Texas - shown when alive, left (bottom)

Saurosuchus galilei and small fry

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

Saurosuchus galilei, whose remains have been found throughout the entire stratigraphic range of the Ischigualasto Formation, San Juan Province, Argentina (Southwest Pangea), was an enormous predator, as big as a full-grown Jurassic theropod dinosaur. Unlike sluggish sprawling present-day reptiles, Saurosuchus had an erect posture (shown by the elongate ischium and femur) and strong pneumatisation (air-spaces) in the vertebrae [Bonaparte 1970, p.668], which would indicate a metabolically advanced animal. Superior locomotive ability obviously conferred great adaptive advantages, and hence developed among a number of only distantly related archosaurs. (this posture developed in at least three or four distinct clades), and with increased stance came increased metabolic activity. And in this case enabled increase size as well. The skull alone was up to a metre in length, and the total animal exceeded 6 meters, and must of weighed around three-quarters of a tonne in large specimens.

Saurosuchus was also the last of its lineage, a family of large carnivorous pseudosuchians known as the Prestosuchidae. While the semi-aquatic phytosaurs are newcomers, the prestosuchids are holdovers from the Middle Triassic. These successful animals continue with only relatively minor change from the earlier Anisian and Ladinian ages. As they co-exist quite happily alongside other related but more advanced carnivores, such as rauisuchids, postosuchids ornithosuchids, and early theropod dinosaurs, it seems that these various top predators specialized in different ecological niches. It has recently been suggested, on the basis of comparison of the braincases of various archosaurs, the Prestosuchidae as previously defined are a grade of Pseudosuchia, with the true Prestosuchidae constituting only a few species. All of this taxonomic hair splitting meant nothing to the mighty Saurosuchus, who was without doubt top predator of its environment. This great carnivore would have fed upon the large kannemeyerid dicynodonts and the medium-sized rhynchosaurs and traversodontids, whose remains occur in the same formation.

Links: Digimorph - Saurosuchus galilei

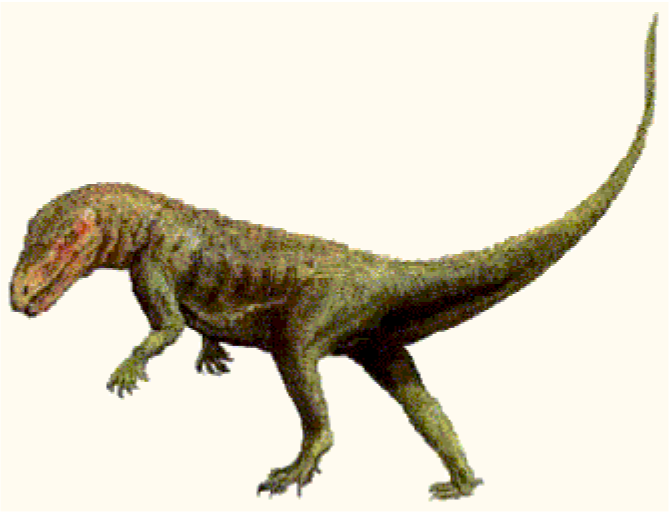


illustration by Steve Kirk, © from *Encyclopaedia of Dinosaurs and Prehistoric Animals*, Barry Cox, R.J.G.Savage, Brian Gardiner, Dougal Dixon,

Ornithosuchus longidens **was a large active terrestrial carnivore, 3 to 4 meters in length, whose remains are known from the Lossiemouth Beds, Elgin, Scotland (Northeast Pangea - Latest Carnian (Adamanian) age). This animal, which was at the top of its local food chain, belonged to the family Ornithosuchidae, a specialized taxon being known from both Scotland (Lauraisa) and Argentina (Gondwana). The name means "bird crocodile", which seems to nicely describe all the great archosaurs of Mesozoic, combining as they did features of both crocs and birds, although it is technically only used to describe this group. These were active, fast-moving animals, with fully erect and upright posture, just like dinosaurs, mammals, and Prestosuchia/Rausichia.**

Ornithosuchids are yet another of the many archosaurian lineages that constituting the confusing Triassic family tree of these animals. Like the phytosaurs, aetosaurs, and poposaurs, the Ornithosuchids appear seemingly out of nowhere during the Carnian (a possible ancestor has been suggested in the Ladinian genus *Gracilosauchus*, but even this small animal is of dubious relationships). They have been variously considered dinosaur ancestors (similarities in the skull meant that at one time *Ornithosuchus* was thought to be a primitive theropod dinosaur), crocodile relatives, and an separate branch of the Crurotarsi (the group that includes crocodiles and their Triassic cousins). Much of this confusion is due to the fact that Triassic archosaur relationships rest to a large degree on ankle structure, with some, like dinosaurs, having bird-like ankles, and others, like pseudosuchians, having croc-like ankles. The trouble with the ornithosuchids is that their ankle structure is very ambiguous, it can do either way. So these interesting animals have no clear relatives.

Early books illustrate *Ornithosuchus* as a theropod-like biped, with long strong legs and diminutive fore-arms. And whilst these creatures could indeed move on their hind legs (and probably did for bursts of speed) they were just as comfortable on all fours.

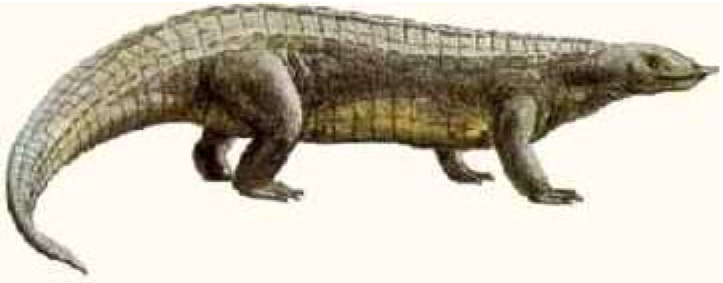


illustration by Steve Kirk, © from *Encyclopaedia of Dinosaurs and Prehistoric Animals*, Barry Cox, R.J.G.Savage, Brian Gardiner, Dougal Dixon,

The Aetosauridae or Stagonolepidae as they are also known, were an important family of Triassic tetrapods that first appear in the middle or late Carnian. *Stagonolepis* was a large animal, 2.5 to 2.7 metres in length; I would guess the adult weight at around 200 kg. The body is long and narrow, and the armor lacks the prominent spines of its cousins and contemporaries the desmatosuchines. This was a prominent and

widespread animal of the latest Carnian. Two or three species are known. *Stagonolepis robertsoni* Agassiz (from the Lossiemouth Beds, Elgin), from north-eastern Pangea (Scotland), *Stagonolepis wellesi* (= *Calyptosuschus*) (Long & Ballew) (Lower Blue Mesa member, of the Petrified Forest Formation) from equatorial western Pangea (Arizona and New Mexico), although the ranges may have overlapped; and *Stagonolepis scagliai* (=*Aetosauroides*) (Casamiquela 1960) from the Ischigualasto Formation, San Juan Province, Argentina. It has been suggested that material from *S. scagliai* may actually belong to one or other of the other two species, so possibly these may all only be subspecies or variations of the same cosmopolitan form; although cladistic analysis indicates *Aetosauroides* and *Stagonolepis robertsoni* are distinct (but related) species.

© BBC/ABC from Walking with Dinosaurs

***Postosuchus kirkpatricki* was a large heavily built animal, some 4 meters in length, known Dockum formation, Chinle Group, Howard Post County, Texas, USA and (Latest Carnian - Adamanian) the Bull Canyon Formation of east-central New Mexico (middle Norian); an animal at the top of its food chain. But *Postosuchus* has a somewhat chequered history hardly befitting its status as top predator of the Triassic floodplains. It was originally interpreted by its discoverer Sankar Chaterjee as a bipedal poposaurid and dinosaur ancestor (the poposaurids are now universally considered crocodile uncles), then reinterpreted as a quadrupedal rauisuchid by Long and Murry 1995. It is furthermore suggested now that the original specimen was based on a confusion of three distinct species, the rauisuchid *Postosuchus* (most of the skeleton), the poposaurid *Lythrosaurus langstoni* (part of the hip bones), and the small *Chatterjeea elegans* (the lightly built forelimbs), an animal of uncertain relationships (either rauisuchid, poposaurid, or member of a distinct family.**

The family Rauisuchidae seem to have evolved from "Prestosuchids" (inverted commas because in the phylogenetic methodology this is a paraphyletic group) like *Ticinisuchus* during the Middle Triassic (*Saurosuchus* is a late surviving Prestosuchian). They are a little more advanced than their prestosuchid cousins, and may in turn have given rise to the ancestors of poposaurs and aetosaurs. Because the various groups of medium to large terrestrial pseudosuchian carnivores are similar in build and general structure, they have often been confused with each other, and at one time with theropod dinosaurs as well. Especially regarding the membership of the Rauisuchidae and the Postosuchidae, this question is not resolved with certainty, with animals like *Postosuchus* and *Chatterjeea* being placed in one family or the other, or even sometimes (in the case of *Chatterjeea*) in a distinct family of its own

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text by M. Alan Kazlev (MAK) and Augustus T. White (ATW)
Last revised ATW030513, MAK030913
checked ATW050907

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Mesozoic Era
  Triassic Period
    Early Triassic Epoch
    Middle Triassic Epoch
      Anisian Age
      Ladinian Age
    Late Triassic Epoch
      Carnian Age
      Norian Age
      Rhaetian Age
  Jurassic Period
  Cretaceous Period

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Pelorocephalus | *Metoposaurus* | *Leptopleuron* | *Shonisaurus* | *Henodus* | *Brachyrhinodon* | *Malerisaurus* | *Trilophosaurus* | *Hyperodapedon* | *Paleorhinus/Parasuchus* | *Angistorhinus* | *Saurosuchus* | *Ornithosuchus* | *Stagonolepis* | *Postosuchus* | *Erpetosuchus* | *Scleromochlus* | *Pisanosaurus* | *Herrerasaurus* | *Saltopus* | *Placerias* and *Ischigualastia* | *Exaeretodon* | *Microconodon* and *Dromatherium* | *Gondwanadon* and *Adelobasileus*

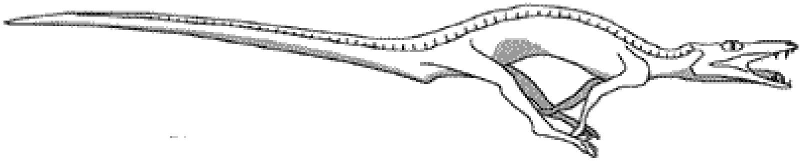


illustration © Paul E. Olsen, from Lecture 10 - Triassic: Newark, Chinle

Erpetosuchus granti **is a small (about 60 cm ion length) crocodylomorph known from four specimens from the latest Carnian Lossiemouth Sandstone Formation [Benton and Walker 2002]. A related but somewhat later (?early to mid Norian) species has more recently been found in the New Haven Formation of the Newark Supergroup, Connecticut Valley [Olsen *et al* 2000]. It can be assumed that these little animals had a wide distribution over much of northern Pangea at the time.**

The Erpetosuchids were lightly built, fast running (cursorial) animals with a fully erect dinosaur-bird-mammal type stance. They may have been either bipedal or (as illustrated above) lightly built quadrupeds. It is difficult to say more, as only the head and the front part of the body is known from the incomplete

remains. In any case, these little animals were the "greyhounds" of the Triassic. In proportions of the skull, neck and forelimbs *Erpetosuchus* is very similar to the later facultatively bipedal Rhaetian age sphenosuchian crocodylomorph *Terrestrisuchus*, as well as to the tiny ornithodiran *Scleromochlus* (also found at Lossiemouth), the Middle Triassic lagosuchid dinosauromorphs *Lagerpeton* and *Marasuchus*, and basal dinosaurs. All these animals represent an important element in the late Triassic terrestrial ecosystem as small active insectivores and predators of microvertebrates, and continued in this niche until the middle or late Jurassic, when they were replaced by coelurosaurian dinosaurs.

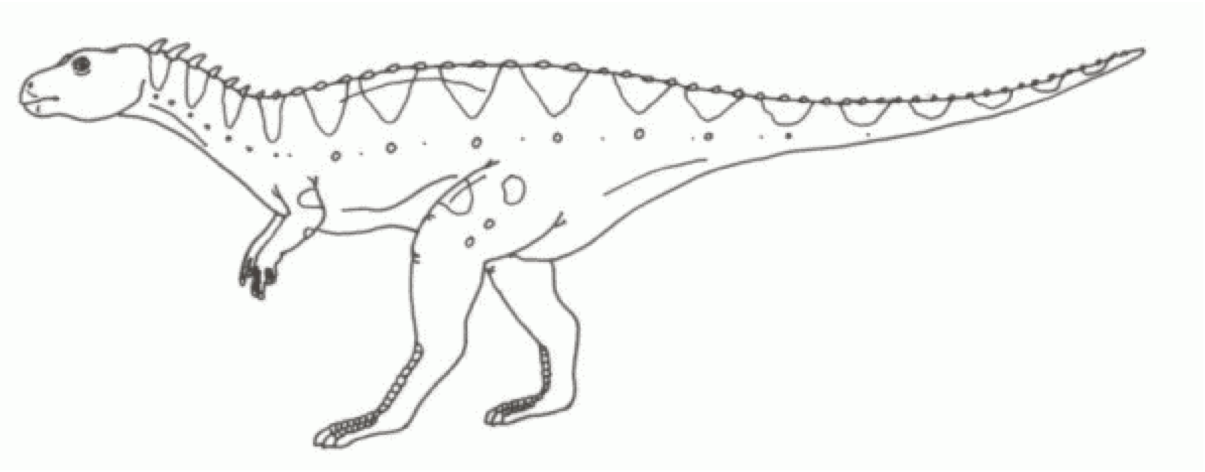
References/Links: Jeff Poling - Fossil of crocodile with erect stance found; Benton and Walker 2002

illustration © M. Shiraishi,

Saltopus elginensis is an enigmatic ornithodiran known from a single partial but still fairly complete skeleton from the Lossiemouth Sandstone of Elgin, Scotland. In life, this was a gracile, long-legged cat-sized animal about 60 or 70 cm long, with jaws equipped many small sharp teeth indicating a mostly insectivorous diet (although microvertebrates were also on the menu).

The fossil has not been adequately reexamined since its discovery in 1910, and the extremely poor preservation of the specimen makes it impossible to interpret unambiguously. So where *Saltopus* fits on the evolutionary tree is still debatable. It may be a non/pre-dinosaurian ornithodiran, such as a lagosuchid or a pterosaur relative like *Scleromochlus*, or a very early theropod dinosaur (the original reference to four sacral vertebrae (source of much confusion as dinosaurs have three and more basal archosaurs two) would seem to be an error, with the animal having the normal compliment of three), perhaps a primitive ceratosaur (It is similar in proportions to small Norian and later coelophysids), which makes it more advanced than *Herrerasaurus*. It may even be a juvenile of a larger animal. Whatever the case, the existence of this animal and others like it shows that the Carnian undergrowth was alive with many kinds of small active archosaurs.

References/Links: Mickey Mortimer - What is Saltopus?; DinoData - Saltopus; Paul 1988



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***Pisanosaurus* is a small dinosaur, about a meter in length, known from a single partial skeleton from the Ischigualasto Formation, San Juan Province, Argentina. One of the earliest known and most primitive of the ornithischian dinosaurs (Order Ornithischia), it is usually included under the family Fabrosauridae (a mostly early Jurassic group best known from South Africa) but is too poorly known to be place there with any certainty. The Fabrosauridae in fact are something of a garbage taxon for any basal or very primitive ornithischian dinosaurs.**

Recent microvertebrate collecting in the Upper Triassic Chinle Group of Texas, New Mexico and Arizona has shown that ornithischian dinosaurs were much more common and diverse during the Carnian than previously believed, with prosauropods. Carnian ornithischians of west and central equatorial and low latitude northern Pangea include a possibly carnivorous ornithischian of Chinle Otischalkian age, and a the following somewhat younger (Adamanian age - Latest Carnian) taxa: *Tecovasaurus murryi* (Chinle, the most widespread form); *Pekinosaurus olseni*, and *Galtonia gibbidens* (known from the Newark Supergroup but also from teeth in the Chinle) [Heckert & Lucas, 2001]. It seems that ornithischians originated during the early or middle part of the Carnian, and diversified rapidly during the late Carnian. All these animals were pretty similar; small, gracile, fast-running, and apart from the one curious exception, herbivorous.

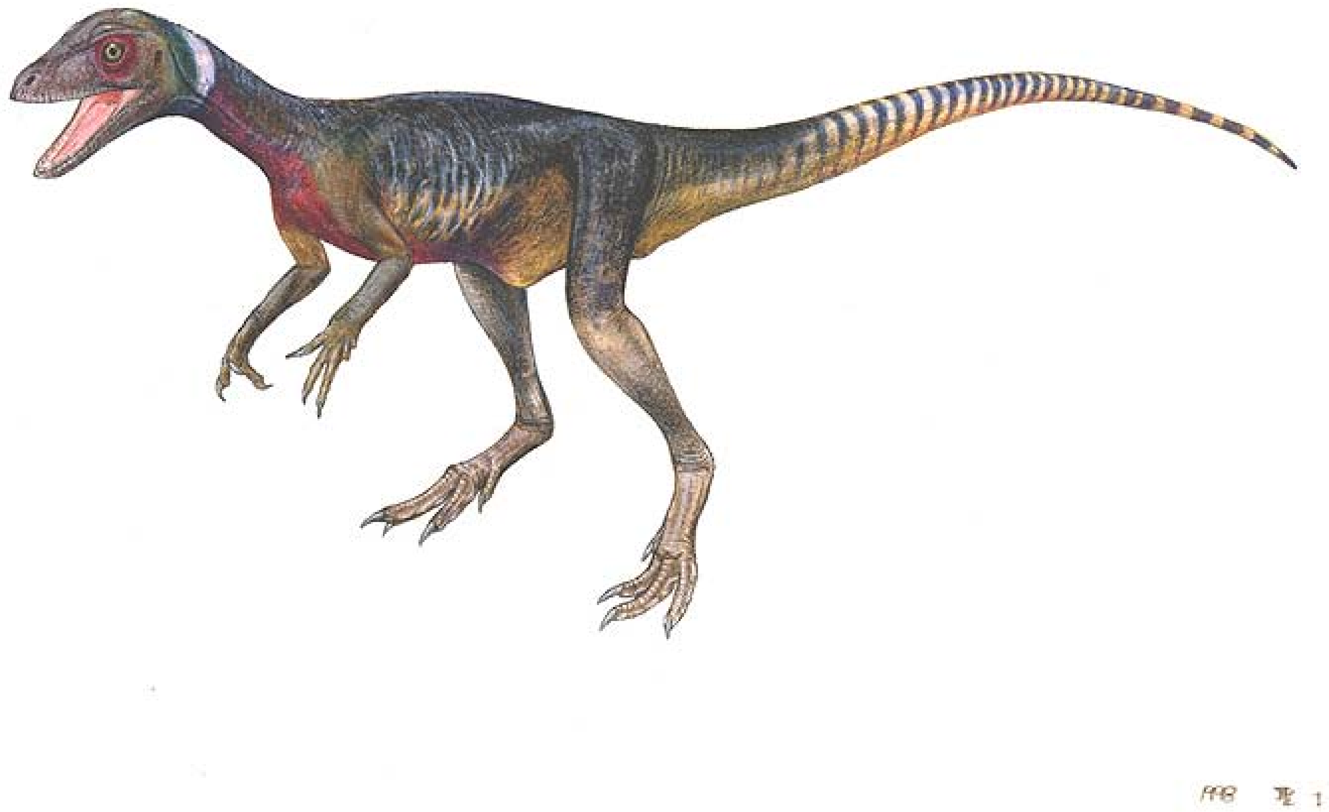
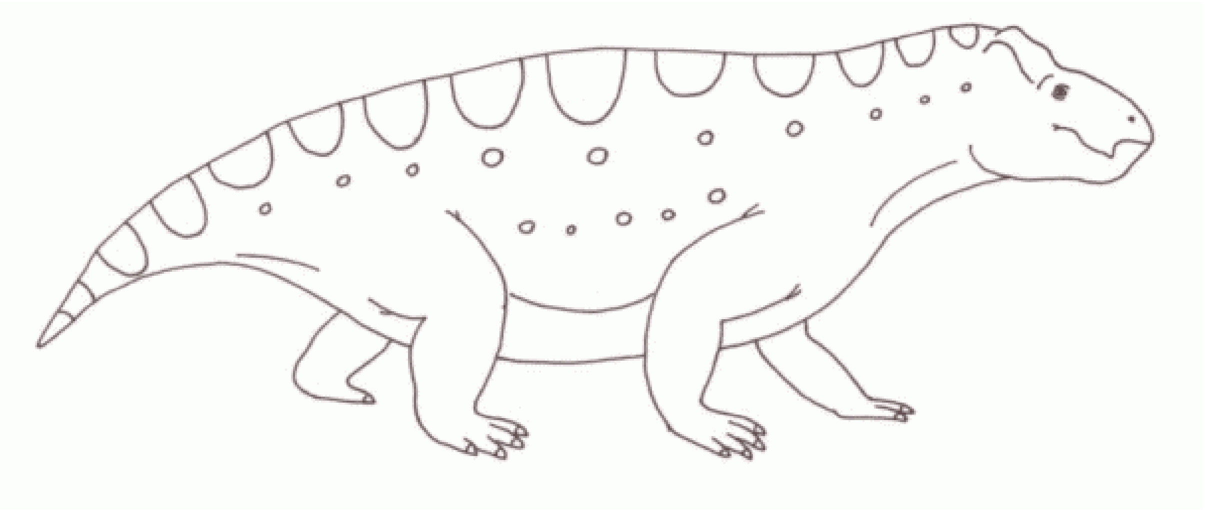


illustration © Seiji Yamamoto

Herrerasaurus ishigualastensis, known from the Ischigualasto Formation, San Juan Province, Argentina (Southwest Pangea), is a very primitive and early member of the theropod dinosaur clade, and the eponymous representative of the family Herrerasauridae. Since *Herrerasaurus* was found, other herrerasaurs have turned up or been relocated in this group. These include *Staurikosaurus* from the (slightly earlier?) Santa Maria Formation, Brazil, which Paul 1988 considers a more primitive animal, the Norian *Chindesaurus*, and the poorly known *Caseosaurus*, the two latter from North America. At one time it was thought that the herrerasaurs lay outside the rest of the dinosaur lineage [Benton 1990], but they were later (following publication of several papers by Sereno and Novas) considered pre-ceratosaurian theropods proper. These were all medium to large and active terrestrial carnivores, which were distinguished from the contemporary rauisuchians by their efficient bird-like digitigrade (standing on toes) stance. *Herrerasaurus* was one of the largest Carnian dinosaurs, with an estimated overall length of around 3.9 metres, and an adult weight of about 210 kg [Paul 1988]. Yet both early dinosaurs and pseudosuchians (Ornithosuchids, rauisuchids, and poposaurids) co-existed happily for many millions of years. It is likely that the slower and more heavily built pseudosuchians were ambush predators that fed on large or slow animals; and the more lightly built and fast-running herrerasaurs and Coelophysids were pursuit predators of small to medium-sized animals



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During the Late Carnian, the megaherbivore niche was still dominated by large kanneymeriid dicynodonts, as it had been throughout almost the entire Triassic (from the Olenekian age onwards). And although by the late Carnian they were still common, they were reduced in diversity, with only one species found in each local fauna. The best known species are *Placerias hesternus* (= *Placerias gigas*) of the Chinle Formation, Arizona, and south in the Ischigualasto local fauna of Argentina, has been found the related *Ischigualastia jenseni* (known only from the Lower Third of the Ischigualasto Formation [Bonaparte, 1970]). both members of the placerine tribe. *Placerias* is also reported from Morocco (which shares a number of points of similarity with the west North America fauna), and a "large dicynodont" is described from India [Lucas 1998].

The Placerines were sturdy animals, with an overall length of about 3.5 metres; a height of around 1.3 to 1.6 metres, and a short deep skull about 55 cm long, these stocky animals were the size of a modest hippopotamus, which they vaguely resembled. They easily massed over a tonne each. Some *Placerias* (presumably males) had tusks which were used for intraspecific display and combat, and also for digging through the soil in search of roots and tubers, as indicated by the wear facets (worn down tooth edges). [King & Cluver 1991]

Large numbers of *Placerias* have been found at a single quarry, which indicates, like the Jurassic and Cretaceous sauropod dinosaurs and the Cenozoic elephants, these large herbivores lived and traveled in herds, and they must have had a huge impact on the local environment.

Even though the Carnian dicynodonts are not as abundant as the contemporary traversodontids and rhynchosaurs, or even the Ladinian dicynodonts, the three groups together characterize the herbivore dynasty of the Middle and Early late Triassic, and supported a number of large carnivorous types, such as the prestosuchids, rauisuchids, and poposaurids. These large pseudosuchians, which reached 4 to 5 meters and more in length, were the only terrestrial predators strong enough to bring down a full-grown dicynodont, and even they would have had a difficult time of it.

References/Links:

BBC - Walking with Dinosaurs - Fact Files - Placerias

Paleo Photos - Placerias (mounted skeleton)

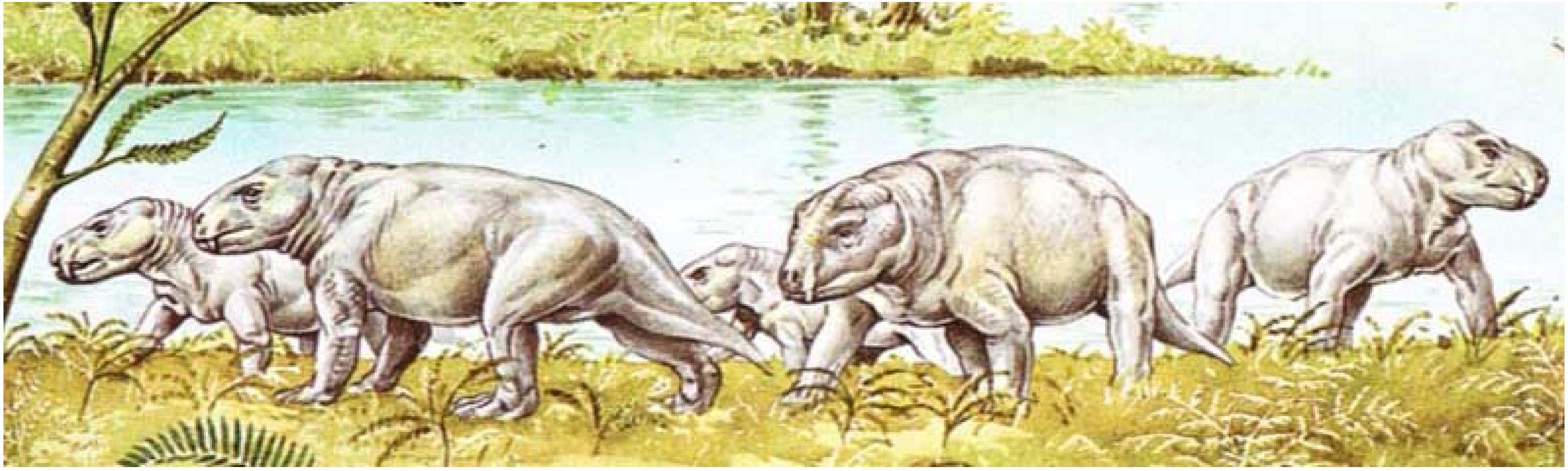


Illustration from *The Cambridge Encyclopedia of Life Sciences*, ed. Adrian Friday & David S. Ingram, © Cambridge University Press 1985.

One of the most common animals of the Carnian age was the large herbivorous traversodontid cynodonts of the genus *Exaeretodon*; known from the Gondwanan biogeographic province (Argentina, Brazil, India, and more recently [Depuydt 1998] Madagascar; with smaller and more distantly related forms from western Laurasia). These were the largest of the Traversodontidae, reaching nearly 2 meters in length, and probably weighing around 80 kilos live. They were also among the most mammalian of the group, with a mammalian hip indicating a more erect posture and limbs under the body; possibly also some steps towards coupling of locomotion and breathing [Hunt 1994-1997].

In the Ischigualasto Formation, San Juan Province, Argentina, *Exaeretodon frenguellii* Cabrera 1944 and the similar and comtemporary *Exaeretodon argentinus* Bonaparte 1962 (could these two species be sexual dimorphs?), along with the rarer and even larger *Ischignathus* were large, advanced herbivorous cynodonts and the most common members of the local fauna. [Bonaparte, 1970, Bonaparte, 1982] *E. argentinus* is not mentioned in more recent literature such as the papers by Lucas [e.g. Lucas 1998] and others, so perhaps it is a synonym of *E. freguelli*. In any case, these animals, like the contemporary rhynchosaurs, seem to have been abundant across Gondwana (southern Pangea), but strangely not in the north of the supercontinent, where smaller forms like *Arctotraversodon plemmyridon* and *Boreogomphodon jeffersoni* are found. *E. statisticae* Chaterjee is known from the Lower Maleri (early part of the Late Carnian) of India, and may be a junior synonym of *E. freguelli*.

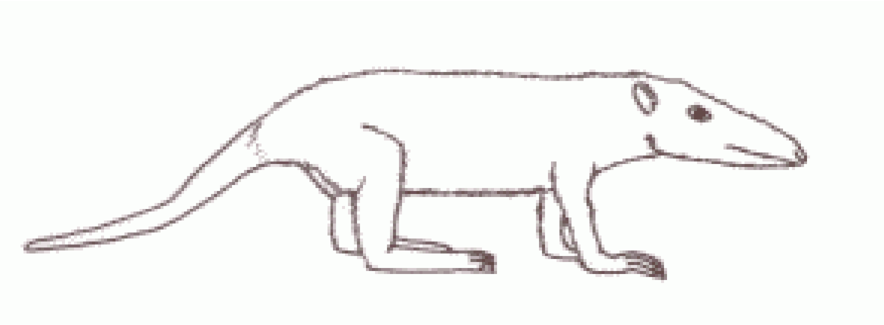
List of species:
***Exaeretodon* Cabrera, 1943**
?*E. argentinus* Bonaparte, 1962 (= *E. frenguellii*?)
?*E. vincei* (Bonaparte, 1963) [*Proexaeretodon* Bonaparte, 1963; = *E. frenguellii*?]
?*E. major* (Huene) Barbarena, 1974 [*Traversodon*? *major* Huene, 1935-42]
***E. frenguellii* Cabrera, 1943**
?*E. statisticae* Chatterjee, 1982 (= *E. frenguellii*?)
***E. riograndensis* Abdala, Barbarena & Dornelles, 2002**
E. sp. Madagascar

Links: Exaeretodon frenguellii (info sheet); Triassic Gomphodonts (more info), Digimorph - Exaeretodon (University of Texas CT Facility).

Microconodon tooth © Natural Canvas Fossils

***Dromatherium sylvestre* and *Microconodon tenuirostris* were tiny rat or shrew-like animals known from a few jaws and teeth from the Latest Carnian (Adamanian stage) of the Newark Supergroup of Eastern North America (North Carolina, Virginia, and Pennsylvania). Originally (during the 19th century) considered among the earliest and most primitive mammals, they were reinterpreted in the 1920s by G.G. Simpson. Their several supposedly unique mammalian features are shared by tritheledontids and other advanced cynodonts, and they are now best regarded as advanced or derived eucynodonts of uncertain affinities. [Sues 2001] A dromatherid has been reported from the Tiki Formation, India, and several problematic taxa known only from isolated teeth from the Late Triassic and Early Jurassic of Europe are also usually placed in the Dromatheridae [Luo *et al* 2002]**

Links/References: Trevor Dykes 2001-2003 Chiniquodontoidea,



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***Adelobasileus cromptoni*, known from a partial skull from the Latest Carnian (Adamanian) Tecovas Formation, West Texas, USA, is the most primitive and perhaps the earliest known mammal, intermediate condition between non-mammalian cynodonts and true Early Jurassic mammals. It also predates the earliest known tritylodontids and trithelodontids, unless the partial dentary called *Pachygenelus milleri*, from the contemporary (or earlier?) strata of the Dockum Formation, Texas [Chaterjee 1986], turns out to be a genuine trithelodontid. *Gondwanadon tapani* from the Tiki Formation, South Rewa Gondwana basin, Madhya Pradesh, India (?early Late Carnian). Claimed to be the earliest mammal, this specimen is based on a single tiny molar. Its attribution as a morganucodontid is very dubious, but it does seem to indicate that as early as the late Carnian there were tiny animals on the borderline between reptile and mammal scurrying through the undergrowth or in trees. The name means "Gondwana tooth". Exact systematical relationships of both these tiny animals are uncertain.**

Links/References: Trevor Dykes 2001-2003 Basal Mammaliaformes, Morganucodontidae and Hadrocodium

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The Norian Age - 1

The Norian Age of the Late Triassic Epoch: 217 to 204 million years ago

Mesozoic Era
  Triassic Period
    Early Triassic Epoch
    Middle Triassic Epoch
    Late Triassic Epoch
      Carnian Age
      Norian Age
      Rhaetian Age
  Jurassic Period
  Cretaceous Period

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  Invertebrates
    The Ammonoid Saga
  Vertebrates
    Rise of the Neopterygii
    Marine Reptiles - Ichythyosaurs
    Freshwater and Terrestrial Biota
    Terrestrial Tetrapod Succession
A Norian Bestiary
Links

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The early sauropodomorph dinosaur *Plateosaurus*; late Norian of middle-north Pangea. As the first of the large herbivorous dinosaurs, *Plateosaurus* and closely related genera seemingly come out of nowhere to completely dominate terrestrial communities across most of Pangea. The sauropodomorph dinosaurs reached lengths of 8 to 10 meters or more, and weights of 2 tonnes, making them even bigger than the kannemeyerid dicynodonts that had filled the megaherbivore niche for much of the Triassic. Looking at the heavy body, long neck, and small head, we see in *Plateosaurus* the beginnings of the evolutionary type that would culminate in the gigantic sauropod dinosaurs of the Jurassic and Cretaceous; one of the most successful and impressive evolutionary experiments the Earth has seen

Norian - Overview

The second of the three divisions that make up the Late Triassic period, the term Norian Stage was introduced by Mojsisovics in 1895 and Diener in 1926. The term Juvavic was at one time used. [Harland *et al*] The Norian stage was named after an ancient Roman province south of the Danube River in present-day Austria [Encyclop�dia Britannica]. It is named after strata in the Eastern Alps in Europe [Harland *et al*]. . Geologically speaking, the Norian Stage underlies the Rhaetian Stage and overlies the Carnian Stage, these three make up the Upper Triassic Series. Chronologically, the Norian succeeds the Carnian Age and is in turned followed by the Rhaetian Age

The Norian was an important period in the history of life on Earth, for it saw the rise to prominence of a number of Mesozoic organisms that had previously played only a minor role in life's drama, and the decline and disappearance of others that had passed their heyday.

Among the successes were the neopterygian fish (the teleosts and their immediate ancestors) in the seas, and theSauropodomorph dinosaurs (like *Plateosaurus*, above) on land. Among the losers were the ceratite cephalopods that, although still going strong, were experiencing a constant decline throughout the late Triassic [Teichert 1988 p.59], including a minor extinction event at the Lower to Middle Norian substage boundary [Krystyn, 2003) in the sea; and the formerly ubiquitous herbivorous therapsids (the large Dicynodonts and medium-sized traversodonts) on land. The success of dinosaurs over therapsids seems to be due to climatic factors; the increasing aridity meant that the moist biome that had enabled the therapsids to flourish had now become a narrow equatorial strip [Olsen *et al* 2001], bordered by deserts and semi-deserts to both north and south.

The Norian began as a world dominated by typically Carnian (and hence typically Triassic) forms on both land and in the sea. By the end of the age life, although retaining many earlier forms, was also well represented by clades that would continue to flourish and dominate for many tens or two hundreds of millions of years
MAK

Stratigraphy and Index Fossils

The Norian is the second of the three divisions that make up the Late Triassic period. The term Norian Stage was introduced by Mojsisovics in 1895 and Diener in 1926. It was introduced for the *Pinacoceras metternichi* and *Cyrtopleurites bicrenatus* ammonoid fauna of the pelagic Hallstatt Limestone facies in the Hallstatt area (Mojsisovics, 1869 cited in Kozur 2003, and Encyclop�dia Britannica]. The term Juvavic was at one time used. It is named after strata in the Eastern Alps. . In Europe there are three marine substages, which in ascending order are the Lacian, Alaunian, and Sevatian, which can be correlated worldwide with ammonoid and conodont biozones. The pdf diagram (by Gradstein *et al* 2004) shows the various geological and magnetostratigraphy divisions, and ammonoid, conodont, palynological, and land vertebrate (Lucas 1998) biozones, that make up the Norian.

The following is an integrated and obviously somewhat speculative table combines Gradstein, Ogg, Smith *et al* 2004, Benton 1994, Lucas and Hunt 1994 (table) and Lucas 1998. We have given our own suggestion as well. However the more precise tetrapod stratigraphic correlations are tentative and will no doubt be refined and modified with future research and discoveries.

Norian timescale

MYA	Age	Stage	Ammonoid Zone	Conodont Zone	Pollen Zone	Vertebrates (Lucas and Hunt 1994, Lucas 1998)	Vertebrates (Benton 1994)	Vertebrates (Palaeos suggestion)
205	Norian	Sevatian	*Gnomohalorites cordilleranus*	*Epigondolella bidentata*	*Rhaetipollis germanicus*	Apachean	NOR L1	**late Late Norian**
206								**early Late Norian**
207		Alaunian	*Mesohimavatites columbianus*	*E. serrulata*	*Limbosporites lundbladii*, *Ricciisporites tuberculatus*	Revueltian	NOR M2	**late Mid Norian**
208				*E. postera*				
209				*E. elongata*				**mid Middle Norian**
210				*E. spiculata*				
211			*Drepanites rutherfordi*	*E. multidentata*			NOR M1	**early Mid Norian**
212		Lacian	*Juvavites magnus*	*E. triangularis*	*Chasmatosporites* spp.			**late Early Norian**
213			*Malayites dawsoni*					
NOR E			**214**	*E. quadrata*			**early Early Norian**	
			215					*Stikinoceras kerri*
	216	*Metapolygnathus primitius*						

Norian Tetrapod Index Fossils

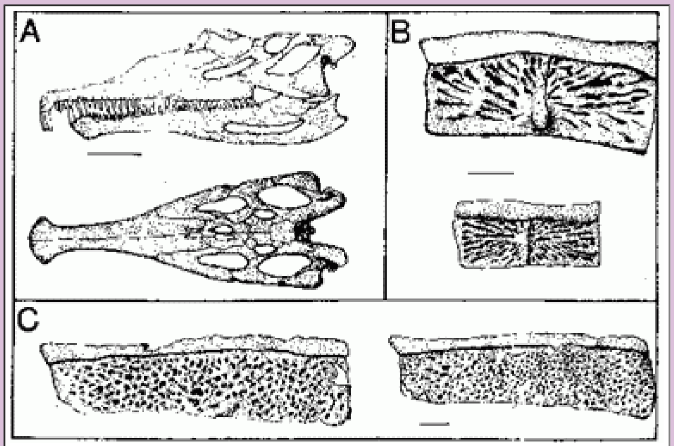


illustration from Lucas 1998

Revueltian index fossils: (A) *Pseudopalatus*/*Mystriosuchus* (another common and widespread genus is *Nicrosaurus*), (B) *Aetosaurus* paramedian plates, (C) *Typothorax* paramedian plates. [from Lucas 1998].

Dr Spencer Lucas (ref) divides Triassic tetrapod evolutionary communities into eight land-vertebrate faunachrons (LVF). Of these, the *Revueltian* assemblage is defined as beginning with the FAD (First Appearance Datum - earliest fossil occurrence) of the phytosaur *Pseudopalatus*, and ending (with the beginning of the following, Apachean, age), which the FAD of the phytosaur *Rendondasaurus*. The Revueltian is considered Norian on the basis of palynostratigraphy, magnetostratigraphy, and sequence stratigraphy. Certainly it corresponds to the later part of the early, and much of the middle Norian. The status of the late Norian is more dubious, since the point of beginning of the following, Apachean, LVF, although tentatively considered Rhaetian, may be in the Norian as well. Moreover, in the famous "Ghost Ranch" fauna (where *Coelophysis* occurs), both *Pseudopalatus*, and *Rendondasaurus* occur together [Ford, 2001, Irmis, 2001], which somewhat muddies the waters.

The following are some tetrapod type fossils from the Revueltian; they belong to two common archosauromorph ("thecodont") clades, the aetosaurs (which left many fossil armour scutes, even partial skeletons are obviously much rarer) and phytosaurs (which, being river and swamp dwellers were often preserved):

Tetrapod Stratigraphy of North America

According to Gradstein *et al* 2004, the Norian age lasted a fairly considerable period of time: 13 million years, which is almost a third the length of the entire Triassic, and longer than the Paleocene or the Oligocene epochs of the Cenozoic. As with the preceding Carnian, this stage can be subdivided as regards terrestrial tetrapods [see Anderson & Cruikshank 1978, Benton 1994, and Lucas 1998 for varying interpretations]. Problems with stratigraphic correlations remain; we have used Lucas and Hunt 1994 fig 20.5 (below) as a primary guide for the major tetrapod-bearing strata. According to this table, based on correlations of the non-marine Chinle group with the marine strata in western Nevada, none of the Norian tetrapod faunas of south-west USA are earlier than late early Norian (*Magnus* ammonite zone). In other words, there is a hiatus in the fossil record between the late Carnian (Adamanian land vertebrate age) and the early Norian (Revueltian land vertebrate age). This table is supplemented with the age attributions in Benton 1994; where the two differ I have used Lucas and Hunt 1994.

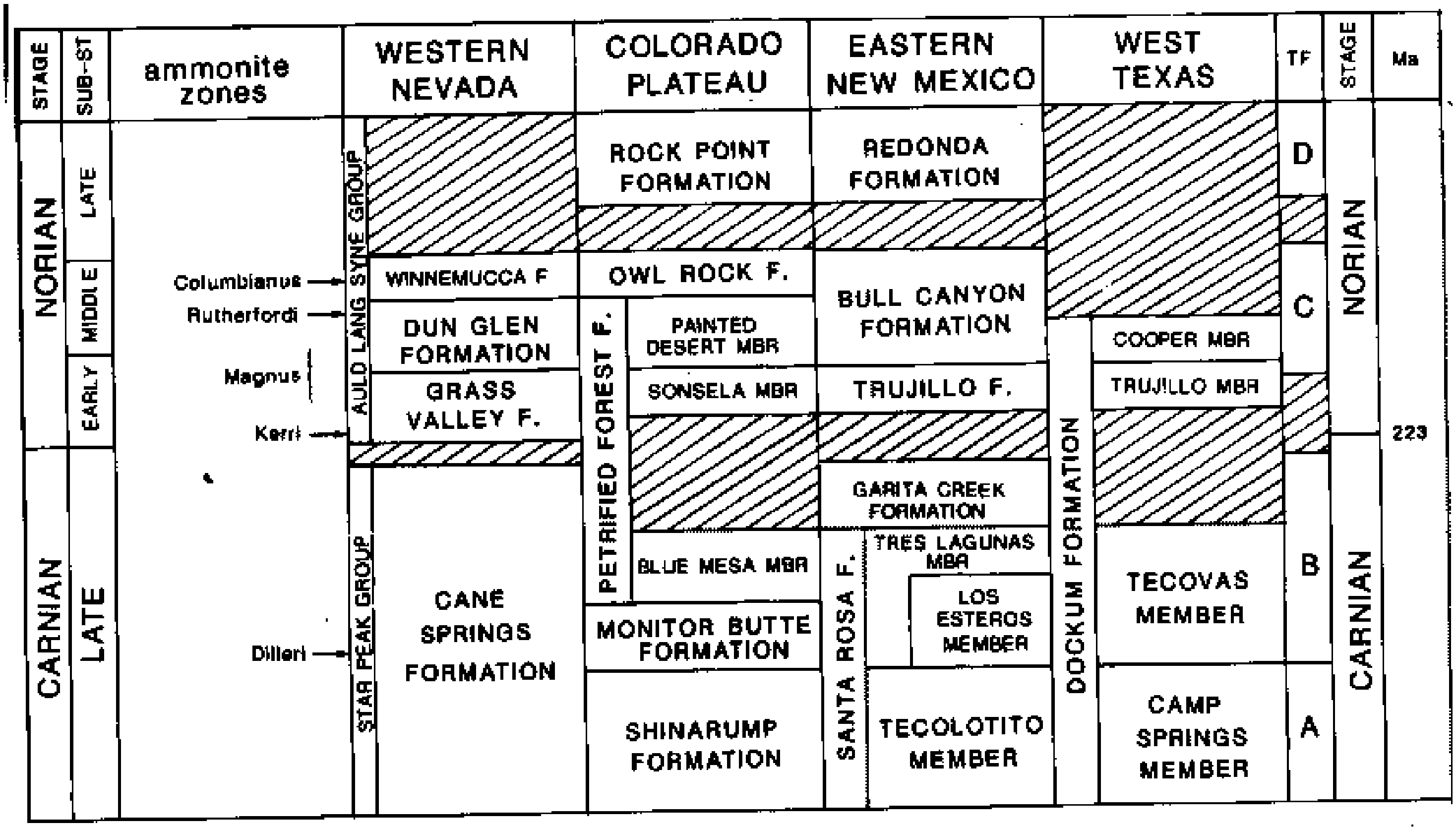


table from Lucas, S G., and Hunt, A P. 1994, The chronology and paleobiogeography of Mammalian Origins, p.343 in Fraser & Sues (eds.) *In the Shadow of the Dinosaurs: Early*

Mesozoic Tetrapods, Cambridge University Press, Cambridge.

The following is our attempt at a Norian timescale for North America, incorporating the above information.

Norian timescale (North America)

MYA	Age	Stage	Vertebrates	Arizona, Colorado Plateau	Eastern New Mexico	West Texas	East Coast USA		Tetrapod zone
205	Norian	Sevatian	**late Late Norian**	Rock Point Formation	Upper Redonda Fm.		Upper Passaic Formation and Upper Balls Buff / Upper Passaic Palynofloral Zone	Cliftonian	early *Redondasaurus* zone = (Early) Apachean Age
206			**early Late Norian**		Middle Redonda Fm.				
207		Alaunian	**late Mid Norian**		Lower Redonda Fm.				
208									
209			**mid Middle Norian**						
210				Owl Rock Fm.	Neshanician				
211			**early Mid Norian**	Upper Painted Desert Member				(Upper) Bull Canyon Formation (Lower)	*Typothorax* zone = Revueltian Age
212		Lacian	**late Early Norian**			Cooper Canyon Fm.	Lower Passaic Formation and Lower Passaic-Heidlersberg Palynofloral Zone		
213				Sonsela Member	Trujillo Fm.	Trujillo Fm.			
214			**early Early Norian**						
215									
216									

The Phytosaur-Aetosaur-Metoposaur vertebrate fossil assemblage of the west (Chinle Group and correlatives) is quite different to the capitosaur-prosauropod-turtle fauna of Europe and Greenland. But even the Newark Supergroup of eastern North America of Neshanician and Cliftonian represents a different fauna to that of the South-west. *Aetosaurus* and *Hypsognathus* are common (perhaps indicative of a drier climate), phytosaurs and large aetosaurs are rarer. In the south-east there is a relict Carnian-type fauna (including traversodonts and rare dicynodonts), populating a wet equatorial zone

The date of the *Typothorax* zone is Lower/early Norian in early papers by Hunt and Lucas which only attempt a stratigraphy of American faunas (see table in Benton 1994), and the *Redondasuchus* zone Middle and possibly Late Norian. In the later work which correlates other faunas (e.g. European) Lucas 1998 *Typothorax* zone becomes the Revueltian LVA, which now includes at least most or all of the Norian, and the *Redondasuchus* zone becomes the Apachean LVA, which now includes all of the Rhaetian. However if we assume an average tetrapod species life-span of 2 or 3 million years (as estimated for mammals and dinosaurs) it seems hard to believe that a single species of *Apachesaurus*, *Paratypothorax*, or *Hesperosuchus* each last some twenty million years or more! (Late Carnian + all of Norian + Rhaetian). Although it is conceivably possible (or not) that most later Triassic tetrapod faunas were unusually stable and long-lived, and it is also possible that the Gradstein *et al* 2004 chronology overestimates the length of the Norian, another explanation might be that due to Late Triassic provinciality (which increased as the period proceeded) meant that the North American and European faunas were not always simultaneous, so that *Aetosaurus*, say, occurred later in Europe than in south-west North America. This would allow an earlier occurrence for American Apachean faunas, and hence a more realistic lifespan of the occurring species.

The famous Ghost Ranch, New Mexico, fauna provides a good case study for difficulties in dating Late Triassic (or any prehistoric) vertebrates. This assemblage, which features not only the early theropod *Coelophysis* (perhaps the most famous of all Triassic dinosaurs) but a number of other forms as well, is traditionally dated at late Carnian or Early Norian. The presence of *Pseudopalatus* shows that it has to be post-Carnian. On the basis of the presence of the phytosaur *Redondasaurus* Lucas 1998 considers it (The revised international LVF series) to be Apachean (=?Late Norian to Rhaetian) age. As well as *Redondasaurus* and the advanced podokesaur *Syntarsus* sp., the fauna contains typically late Carnian (Adamanian) / early Norian elements, as represented by the sphenosuchian *Hesperosuchus agilis* [Clark *et al* 2000] and, supposedly, the aetosaur *Desmatosuchus haploceras* [See Ford, 2001 and Irmis, 2001 for a species list of this fauna - although of course this assumes that the identification of *Desmatosuchus* from this locality is correct). Hargrave 1999 considers the Coelophysis quarry to be "no younger than early Norian and is more likely near the Carnian/Norian boundary" on magnetostratigraphic evidence. On the other hand, the Rock Point Formation, in Whitaker (Ghost Ranch) quarry occurs, is just below (and possibly overlaps with the Latest Triassic to Earliest Jurassic Wingate Sandstone, which favours either a Rhaetian age or a Middle or Late Norian. Benton 1994 gives the age of the Rock Point Member of the Chinle Formation as Late Middle Norian. Pending more precise analysis, the date of the Whitaker quarry / Ghost Ranch fauna will remain somewhat debatable.

Tetrapod Stratigraphy of Europe and Asia

Norian timescale (Europe and Asia)

MYA	Age	Stage	Vertebrates	England & Wales	SW German Keuper	Greenland	North Italy	Thailand	Tetrapod zone
205	Norian	Sevatian	**late Late Norian**	Fissure Fillings (lower complex "A") ? ? ?	Knollenmergel	Fleming Fjord Formation: Ørsted Dal Member	(non tetrapod)		*Plateosaurus longiceps* zone
206			**early Late Norian**		Upper Stubensandstein				
207		Alaunian	**late Mid Norian**		Middle Stubensandstein		Zorzino Limestone	Huai Hin Lat Formation	*Mystriosuchus* zone
208							Forni Dolomite		
209			**mid Middle Norian**				(non tetrapod)		
210									
211			**early Mid Norian**		Lower Stubensandstein				*Proterochersis* zone
212		Lacian	**late Early Norian**		Lehrbergstufe, etc				
213									
214			**early Early Norian**						
215									
216									

A single broad fossil assemblage seems to occur in the Stubensandstein of the German Keuper; the Ørsted Dal Member of the Fleming Fjord Formation, Greenland; the Zorzino Limestone and Forni Dolomite, northern Italy; and as far east as Thailand (the Huai Hin Lat Formation). This wide-ranging fauna is characterized by the phytosaur *Mystriosuchus* (unknown in North America or Gondwana), the early chelonid *Proganochelys*, and (in Germany and Greenland) the prosauropod *Plateosaurus*. In the Keuper *Mystriosuchus planirostris* is found only in the Middle Stubensandstein, where it is common. It's occurrence in the Zorzino Limestone - dated to latest *columbianus* ammonite zone - provides a good marine tie-point. For this reason in the above table the Middle Stubensandstein is considered to be late Middle Norian/Alaunian. The Upper Stubensandstein (where *Mystriosuchus* is unknown; if that information is incorrect please contact me!) must therefore be early Late Norian/Sevatian, rather than Late Alaunian as it is usually shown (e.g. [Benton 1994].

Tetrapod Stratigraphy of Gondwana

Norian timescale (Gondwana)

MYA	Age	Stage	Vertebrates	Argentina	Brazil	Africa	India	Tetrapod zone
205	Norian	Sevatian	**late Late Norian**	Basal Los Colorados		Lower Elliot Formation	Dharmaran Formation	*Euskelosaurus* zone
206			**early Late Norian**					
207		Alaunian	**late Mid Norian**			Molteno Formation		
208								
209			**mid Middle Norian**					
210								
211			**early Mid Norian**				Lower Dharmaran Formation	
212		Lacian	**late Early Norian**					
213								? ? ? *Jachaleria* zone
214			**early Early Norian**					
215					Catturita Formation			
216								

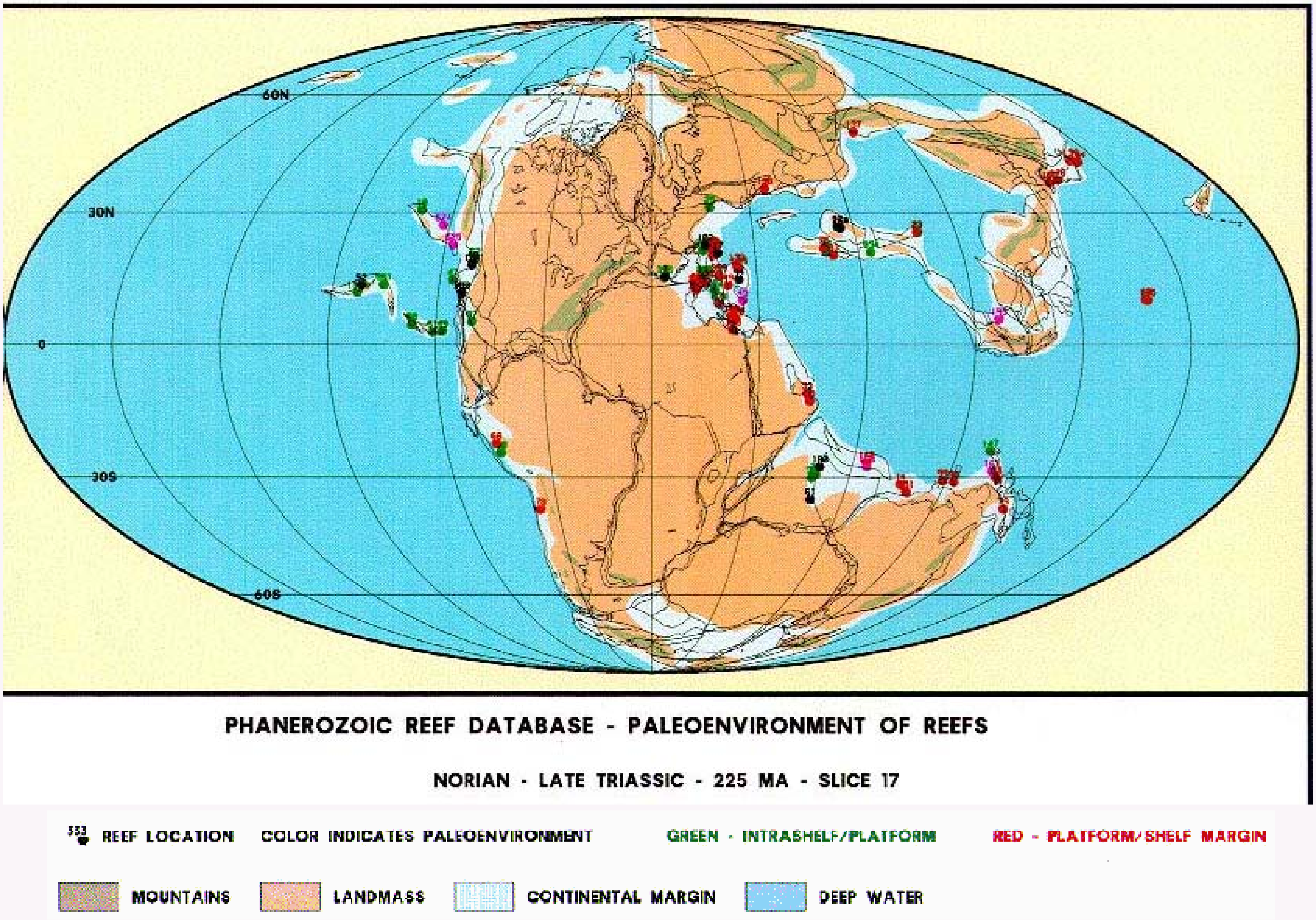
With the exception of southern Africa, Norian Gondwana faunas are not as well known as those of the preceding Carnian and following Rhaetian. Moreover, they are highly provincial. The large dicynodont *Jachaleria* is found in both Brazil (the " *Jachaleria* zone" of the Catturita Formation) and Argentina (Basal Los Colorados) and clearly was an important element in west Gondwana. The lower part of the Dharmaran Formation, India, reveals a hybrid fauna that combines Gondwanan (chugitosaurid) and Laurasian (phytosaurs, *Paratypothorax*) elements. The Lower Elliot Formation, which seems to Late Norian [Lucas and Hancox 2000] rather than (as usually stated on the basis of *Dicrodium* flora and traversodont therapsids) Late Carnian, there is a rich assemblage of large sauropodomorphs, including the earliest known true sauropods. This is somewhat similar to plateosaur-dominated fauna of Europe, but very different to the phytosaur-aetosaur-metoposaur assemblage that continues into the Rhaetian in North America

The Los Colorados of Argentina reveals a similar preponderance of large sauropodomorphs to Europe and Southern Africa. The dating of the Los Colorados (Argentina) is uncertain, and may be of either Late Norian or Rhaetian age. In view of its advanced "transitional" Early Jurassic elements we have chosen a date of Rhaetian for the Los Colorados (which therefore is considered in more detail in the next Unit). In any case, both these high southern latitudes show a fauna rich in sauropodomorph megaherbivores.

Norian Life

Marine Biotas

Norian Reefs - Diversification, Extinction, and Greater Diversification



map © Paleo Reef Database, E. FL�GEL, W. KIESSLING and JAN GOLONKA

During the Norian age, reefs are known from both the Tethys Seaway and the West Pangean / North American island-arc terranes. This is shown in the above map. The Tethyan reefs are on the right of the Pangean landmass (around the edge of the mouth of the "Pakman"), the American reefs on the left. The two provinces followed somewhat different histories

The Tethys-Panthalassan Reef Province:

As can be seen from the above map, reefs are distributed throughout a vast shallow Tethys seaway as well as around Panthalassan island outposts and terranes.

The Late Carnian-early Norian interval saw major reef extinctions here, with the loss of older sphinctozoid and coral species (90% of species dying out), but diversity was maintained with reciprocal replacement by new taxa, with reefs were characterized by a diversification of sponges and corals [Stanley 2001, with the emergence of the latter as reef builders [Stanley 2003]. These then in turn become extinct, possibly a result of a sudden global cooling, since the same period saw the extinction of tropical, low latitude ammonoids and their replacement by more cosmopolitan forms Krystyn, 2003). The early Norian Tethyan-Panthalassan reef systems are replaced by a much larger reef development during the latest Triassic (mid-Norian to Rhaetian), which extended up to 30�N and 35�S, coinciding with a major rise in global sea-level. At this time new higher taxa appear, sphinctozoid sponges diversify, and scleractinian corals come to dominate; these two groups constituting a new reef building consortium. These are associated with a diverse selection of other reef organisms. This was a period of worldwide expansion of carbonate platforms (limestone laid down by reef organisms) and maximum reef diversity [Stanley 2003].

The West Pangean Reef Province:

The Triassic reef record for West Pangean / North American island-arc terranes is poor prior to the Norian. The Norian saw a great expansion here, with latitudes similar to those of the Tethys, but beginning even earlier, in the earliest Norian, and continuing through to the Rhaetian . Rare subtropical Carnian patch reefs are known from the western Canadian craton. Although these reefs lacked the development and carbonates deposits of their Tethyan equivalents, these were still high diversity communities, of which at least half were Tethyan species [Stanley 2003].

During the Mid Norian there is the appearance in the West Pangean reefs of more Permian Lazarus taxa than in the Middle Triassic [Stanley 2001]; presumably these forms had remained rare and geographically isolated (Panthalassan volcanic islands might have served as refuges during times of crisis when the Tethys was affected [Stanley 2003]), and possibly Middle Norian conditions were similar to those of the Permian.

Invertebrates

The Ammonoid Saga

Ammonoids are important stratigraphic markers, because of their rapid evolutionary change. These shelled cephalopods (especially those of the Order Ceratitida) were so common and diverse during the Triassic that it has been suggested that this period be called the "Age of Ceratites". But by the Norian, the Ammonoids were on the wane, following their maximum diversity during the Carnian. During this period, ammonoids experienced both gradual change and more dramatic turnovers and occasional extinction events. New discoveries have however shown some unexpected results.

It was previously thought that the Carnian-Norian stage boundaries showed extinctions of many Carnian genera and new Norian forms that replaced them. But new data show considerable overlapping ranges of many genera considered previously as distinct boundary markers, and no extinctions on the family level are observed. (the same has been shown to be the case for the Ladinian-Carnian extinction. [Krystyn, 2003)

A strong turnover at the Lower to Middle Norian substage boundary, in which a tropitacean rich association of tropical, low palaeolatitude affinity is suddenly replaced by a Trachycerataceae dominated fauna of less palaeoclimatic restriction Krystyn, 2003) , seems to indicate a sudden climatic cooling. This was also a period of extinction and turn-over for reef organisms, as the Late Carnian-early Norian reefs made up of corals and sponges died out, to be replaced by the mid-Norian to Rhaetian associations involving sphinctozoid sponges and dominating corals. [Stanley 2001]

A more gradual faunal shift, with overlapping generic ranges, occurred at the Middle (=Alaunian) to Upper Norian (=Sevatian) substage boundary; which seems to be the period during which prosauropod dinosaurs came to dominate terrestrial ecosystems

A much larger extinction event occurs at the traditional Norian-Rhaetian stage boundary (i.e., top of the *Reticulatus* Zone) and is characterized by the demise of all trachyostracean ammonoids of the superfamilies Trachycerataceae, Clydonitaceae and, Tropitaceae. [Krystyn, 2003) As a result of this, the Rhaetian ammonoid fauna was much more impoverished.

At the base of the Rhaetian, defined by the FAD of *M. posthernsteini* and *C. suessi* / *C. amoenum*, a distinct faunal change can be observed not only for ammonoids, but also bivalves, brachiopods, conodonts and radiolarians. [Kozur 2003]

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The Norian Age - 2

Mesozoic Era
  Triassic Period
    Early Triassic Epoch
    Middle Triassic Epoch
    Late Triassic Epoch
      Carnian Age
      Norian Age
      Rhaetian Age
  Jurassic Period
  Cretaceous Period

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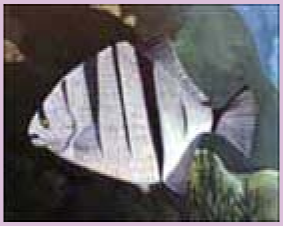
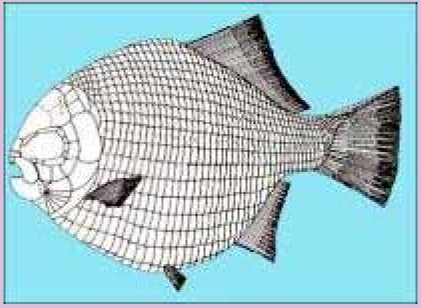
A Norian Bestiary
Links

Vertebrates

Rise of the Neopterygii

As for actinopterygian fish, the Late Triassic saw the first real radiation of Neopterygii, a radical ecological shift equivalent to the ascendancy of Teleosts during the Cretaceous. Significantly, more primitive forms - Chondrosteans and "Sub-Holosteans" - remain important, especially at the top of the food chain. In localities like the richly fossilferous Zorzino Limestone (Calcari di Zorzino), where at 50 genera have been described, all the large predators (*Birgeria*, *Saurichthys*) are chondrostean [ref Prof. Andrea Tintori, Norico Fauna and Flora]. The following are some representative Actinopterygia of this time. All the species illustrated here were contemporary, and lived in the European Tethys, during the middle of the Norian.

	 Subclass: Actinopterygii Infraclass: Neopterygii Division: "Holostei"	



Subclass: Actinopterygii
Infraclass: Neopterygii
Division: "Holostei"
Order: **Semionotiformes**
Family: Dapediidae (or Semionotidae)

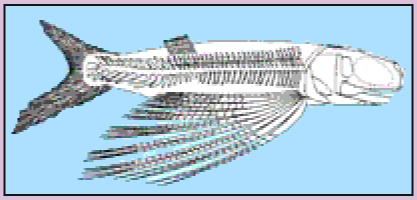
Dapedium noricum *Tintori 1982*

Size: length 8-9 cm Horizon: Zorzino Limestone
Age: Norian
Locality: Zogno, Italy (tropical Tethys)
Comments:
A common deep-bodied late Triassic and Early Jurassic durophagous fish. *D. noricum* is the smallest known species of the genus, it also differs from other species in the shape of the infraorbitals. References/Links: Dapedium by Prof. Andrea Tintori (also link to larger illustrations on this page)
illustration © Prof. Silvio Renesto, University of Milan - Vertebrate Palaeontology

Order: **Semionotiformes**
Family: Semionotidae

Sargodon tomiscus *Plieninger 1847*

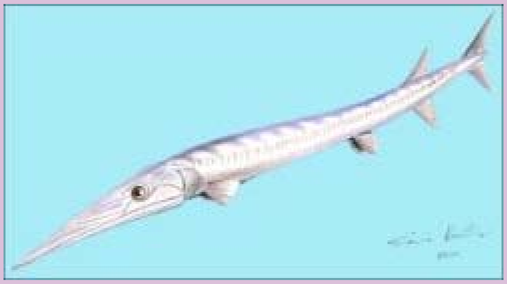
Size: length 30 cm to 1 meter
Horizon: Zorzino Limestone; Dolomia di Forni
Age: Norian
Locality: Brembilla; Endenna; Poscante; Cene; Valvestino; all Northern Italy (University of Milan - Vertebrate Palaeontology collection - see Norian localities page), also known from elsewhere in Europe (teeth of similar or same species also known from the Norian-Rhaetian of Europe, especially from bone-beds of England, France and Germany) (tropical and subtropical Tethys)
Comments:
The "big brother" of *Dapedium*, *Sargodon* was the largest of a number of species of durophagous (feeds on hard shelled food) or semi-durophagous fish of this region and time
References/Links: Sargodon by Prof. Andrea Tintori (also link to larger illustrations on this page)
illustration © Prof. Silvio Renesto, University of Milan - Vertebrate Palaeontology



Subclass: Actinopterygii
Infraclass: Chondrostei
Order: Luganoiiformes
Family: Thoracopteridae

Thoracopterus

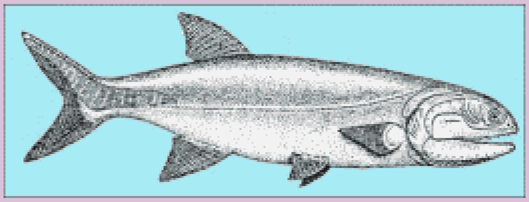
Size: Horizon and Locality: Carnian of Raibl (Italy) and Lunz (Austria), also known from the Norian of Italy (Tethys)
Comments:
The earliest known flying (actually, gliding) fish, and the only type known before the Cenozoic exocetids, with which they shared a similar lifestyle.
References/Links: Norico Fauna and Flora by Prof. Andrea Tintori
illustration © Prof. Silvio Renesto, University of Milan - Vertebrate Palaeontology



Subclass: Actinopterygii
Infraclass: Chondrostei
Order: Saurichthyiformes
Family: Saurichthyidae

Saurichthys seefeldensis and three new species

Size: the largest *Saurichthys* individuals from the Zorzino Limestone attain a length of 180 cm
Age: Norian
Horizon and Locality: Southern Calcareous Alps Comments:
Comments:
a ubiquitous form, known worldwide from the Early to Late Triassic, *Saurichthys* was the Triassic equivalent of a pike or barracuda. By Norian times, perhaps in response to selection pressure by the nimble newly emerging



Subclass: Actinopterygii
Infraclass: Chondrostei
Order: Palaeonosciformes
Family: Birgeriidae

Birgeria

Size:
Age: Early to Late Triassic
Locality: Spitzberg, Greenland, North America, Madagascar, Europe (Early Triassic)
Comments:
Like ***Saurichthys***, ***Birgeria*** was a large primitive form that nevertheless survived well as a dominant predator for a considerable period of time

Neopterygia, a number of advanced species of this genus had evolved, distinguished by a highly stiffened vertebral column, resulting in a greater springiness and hence faster acceleration. An ambush predator.

References/Links: Saurichthys by Prof. Andrea Tintori

illustration © Prof. Silvio Renesto, University of Milan - Vertebrate Palaeontology

References/Links:

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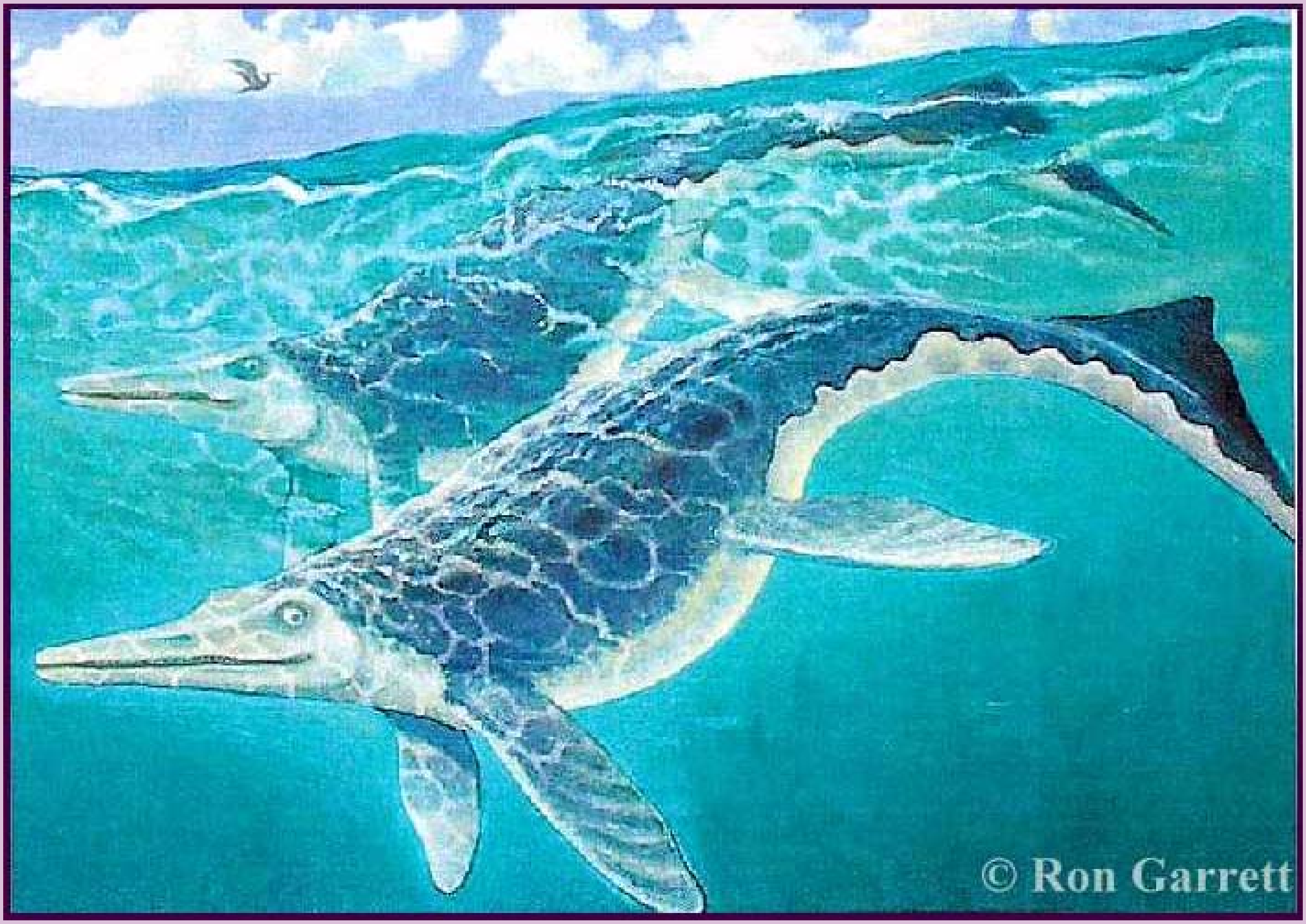
Marine Reptiles - Triumph of the Ichythyosaurs



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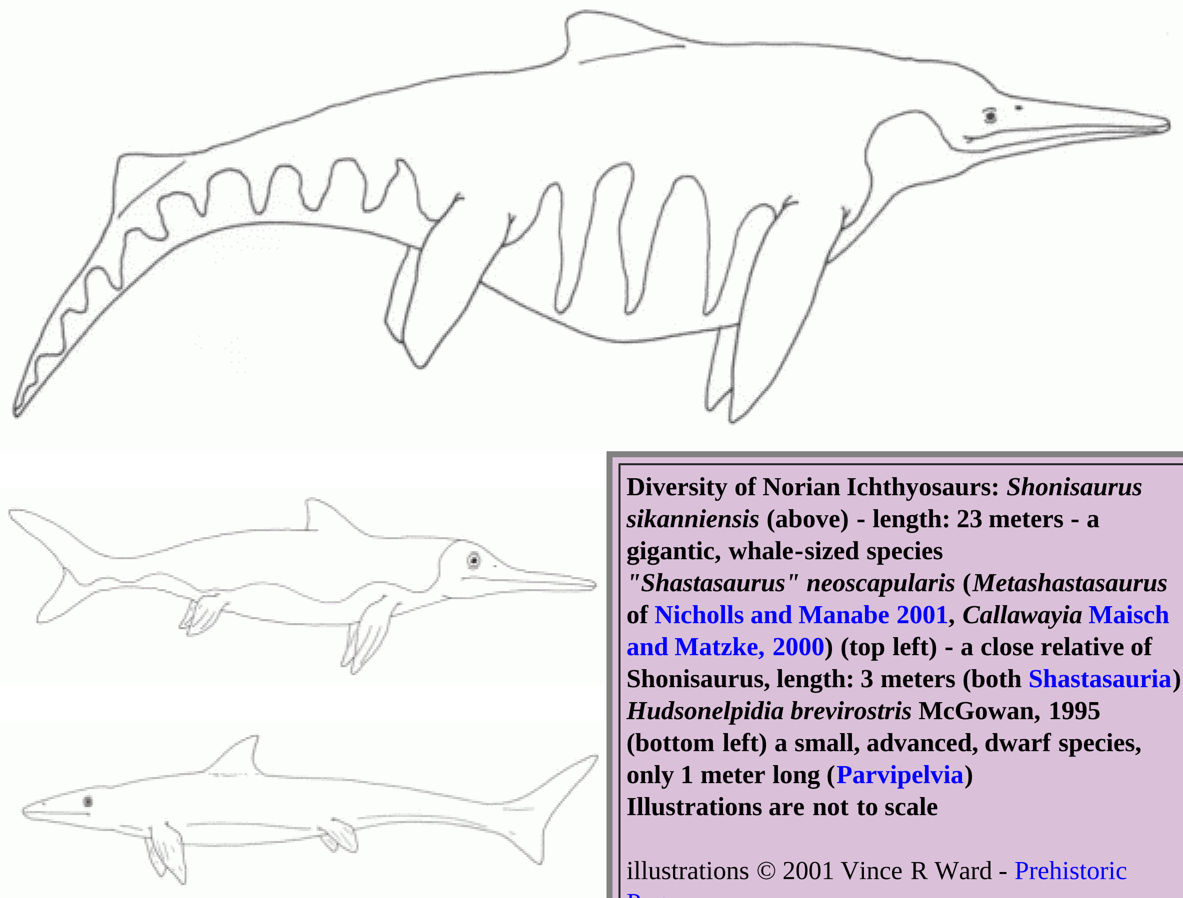
The warm Triassic seas are home to a rich marine fauna. Reefs of brilliantly coloured corals and sponges provide shelter for fish, Crustacea, and other animals. Rising upon the water column of the open seas we find the trophic food chain that has supported higher life on Earth for hundreds of millions of years. Warm sunlight nurtures phytoplankton, which supporting millions of tiny zooplanktonic organisms, which provide food for small fish.

These fish are in turn preyed upon by larger fish and the coiled-shell ceratite ammonoids and squid-like coleoid cephalopods. These in turn fall victim to the snapping jaws of small to medium-sized ichthyosaurs, marine reptiles not unlike modern dolphins, and averaging some 3 meters in length. But even these ichthyosaurs are not the top of the food chain. For ruling the Triassic waves in the earliest Norian, as it did in the late Carnian and will continue to do so throughout the Norian, is the mighty *Shonisaurus*, a whale-sized predator on anything smaller than itself. For a span of at least fifteen million years - from early Late Carnina to Late Norian and maybe beyond, these ichthyosaurs - far larger than any Cretaceous *T. rex* - will continue with only minor (species-level) change.

The great diversity of ichthyosaurs is indicated by



Diversity of Norian Ichthyosaurs: *Shonisaurus sikanniensis* (above) - length: 23 meters - a gigantic, whale-sized species
"*Shastasaurus*" *neoscapularis* (*Metashastasaurus* of Nicholls and Manabe 2001, *Callawayia* Maisch and Matzke, 2000) (top left) - a close relative of Shonisaurus, length: 3 meters (both Shastasauria)
***Hudsonelpidia brevirostris* McGowan, 1995 (bottom left) a small, advanced, dwarf species, only 1 meter long (Parvipelvia)**
Illustrations are not to scale

illustrations © 2001 Vince R Ward - Prehistoric Pages

fossil remains from the Sulphur Mountain and Pardonet formations of British Columbia. Late Triassic ichthyosaurs seem to have belonged to two distinct clades, the medium sized to gigantic shastasaurs, which were the more common group, and the (as yet still mostly) medium-sized Euichthyosauria, including *Californosaurus* and Parvipelvia; the latter being the ancestors of some later Rhaetian types that ushered in the age of "classic" Jurassic marine monsters.

There is some disagreement regarding the phylogenetic position of the shastosaurs; Nicholls and Manabe 2001 argue that the Shastasauridae form a monophyletic taxon, while Maisch & Matzke, 2000 present them as a grade - transitional between Middle Triassic and typical Early Jurassic forms - rather than a clade. Regardless of their exact status, these were often spectacular animals.

Norian Shonisaurs of the Himalayas

It is hard to believe that the mighty snow-capped Himalayas were once shallow sea beds where tropical invertebrates flourished, and above which fish swam and giant ichthyosaurs frolicked, but such is the case, and fossils found here indicate the continuity in time and wide (probably global) dispersion in space of the shastosaurian ichthyosaurs (specifically shonisaurs).

The partial skull and skeleton of *Himalayasaurus tibetensis* Dong, 1972 was collected from Norian marine strata near Mt Everest, at an altitude of some 4800 meters above sea-level [Lucas 2001 p.117]. *Himalayasaurus* is a clear descendent or close relative of the late Carnian *Shonisaurus popularis*, which it resembles closely in size and build. This species is distinguished by the cutting-edges on its flattened tooth crowns, which are otherwise unknown among ichthyosaurs. The large size (around 15 meters) and extensive cutting edges of the teeth indicate a diet of other tetrapods, and hence a lifestyle perhaps not unlike that of a modern killer whale [Motani *et al* 1999]. The 10 meter long *Tibetosaurus tingjiensis* Young, Lui & Zhang, based on a partial skeleton from the Tingi district of Tibet, is indistinguishable in the published diagnosis, and being from the same stratigraphic unit (Langjiexue Group) in nearby localities, are considered by Lucas 2001 p.118 to be synonyms. According to Motani *et al* 1999, the similarities between *H. tibetensis* and *S. popularis* are so small as to indicate the two forms belong to the same genus, the only clear difference between the two being the shape of the tooth crown. If the two species are congeneric, the name *Himalayasaurus* Dong, 1972 has priority over *Shonisaurus* Camp, 1976 (being earlier), and the shonisaur species would have to be renamed *Himalayasaurus*, although it is hoped this won't happen because the name *Shonisaurus* is already so well known! Maisch and Matzke, 2000 in contrast consider both *Himalayasarus* and *Tibetosaurus* as *nomina dubia*, while in their paper Nicholls and Manabe 2001 use the term *Shonisaurus*.

Whatever the exact identity of the Himalayan giants, it would be a pretty safe bet to consider them shastosaurs, and almost certainly Shonisaurs. The existence of very similar animals on opposite ends of Pangea (*Shonisaurus* is known from the Carnian of California and the Norian of Canada) need not surprise us. The great whales of today have no problem swimming across oceans, and 10 to 25 meter Shonisaurs would likewise have swum the Triassic Panthalassian ocean with ease.

Wherever you were in the late Triassic, if you had to go out into the open sea, at the right time, chances are you would glimpse one of these marvelous reptiles surfacing to breath, with a huge spray of water and foam.

Freshwater and Terrestrial Biota

Freshwater Faunas

Like the Carnian before it, the Norian age was both a time a change and a time of continuity.

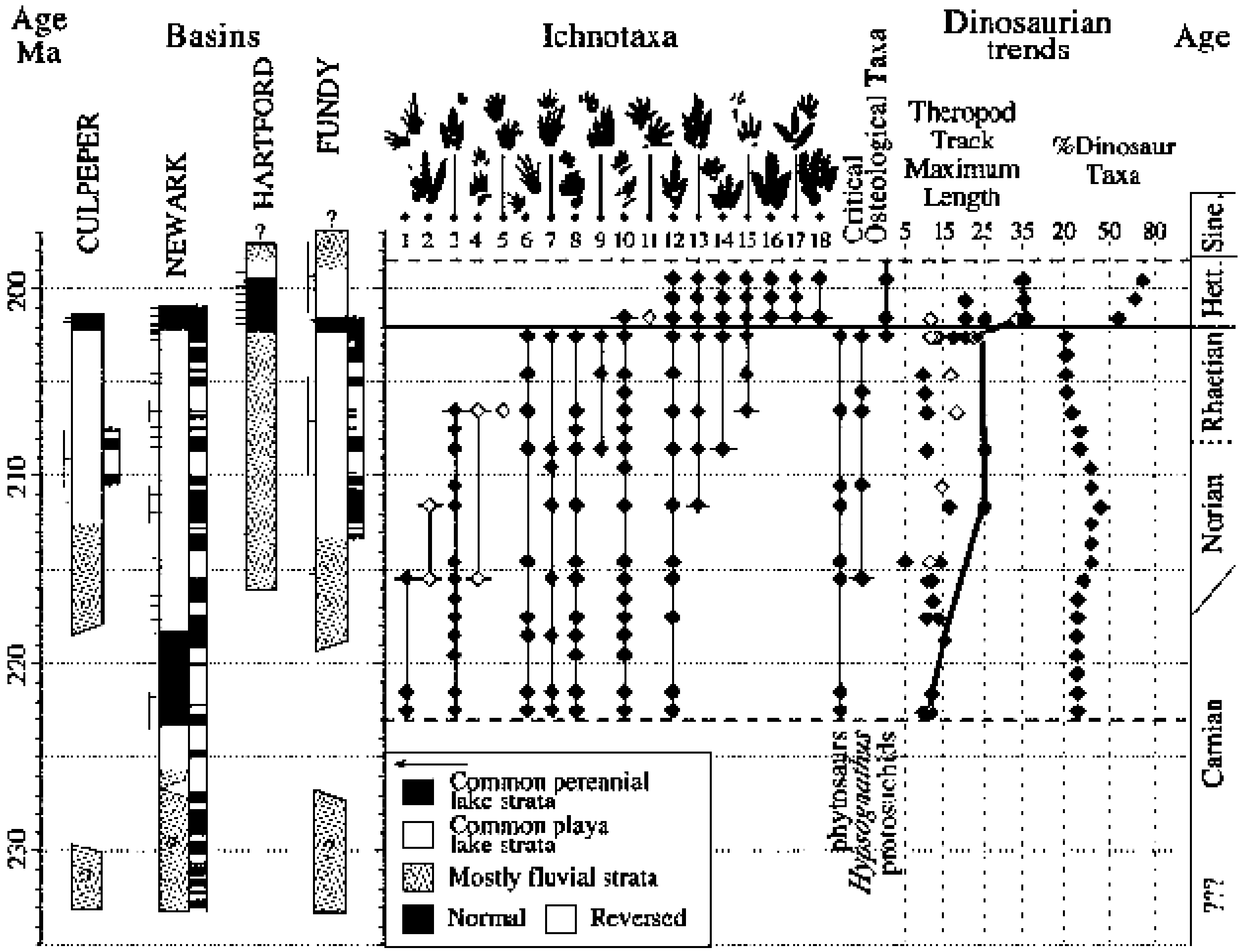
Norian freshwater faunas were little changed from those of the Carnian, including various invertebrates, a diverse selection of fishes, sharks, both chondrostian and primitive neopterygian actinopterygians, coelacanths and lungfish, and temnospondyl amphibians and phytosaurian reptiles. These latter, being at the top of the freshwater food chain, were more susceptible to environmental stress than fish and invertebrates. So we find that among the temnospondyls and phytosaurs a number of Carnian forms have disappeared, such as the metoposaurs and most of the phytosaurs (all belonging to the paraphyletic subfamily (or grade) Rutiodontinae, which experienced a dramatic turn-over, similar to the middle of the late Carnian phytosaur extinction. All Norian phytosaurs are of the subfamily Pseudopalatinae, which evolved from rutiodontines, and like them filled a diverse selection of ecological roles.

Terrestrial Tetrapods

Originally it was believed that there was a mass extinction at the end of the Carnian, even a meteor impact. However, it seems that some of the apparent extinctions were due to sampling bias, as continental drift means the moist environments that favour the typically Carnian biota are under-represented because the rich fossil localities now correlate with higher and more arid latitudes [Olsen et al]. In Eastern North America (centra Pangea) at least, Norian terrestrial assemblages differed little from those of the Latest Carnian (late Tuvalian / Adamanian)). Ichnotaxa (footprint taxa) found widely across the Newark Supergroup basins in this period include *Brachychirotherium* (rauisuchian), *Apatopus* (phytosaur), *Rhynchosauroides* (lepidosauromorph or basal archosauromorph) *Atreipus* (ornithischian dinosaur) and *Grallator* (coelophysid dinosaur) [Olsen and Huber 1998]. These taxa generally represent family or related generic groupings, rather than individual species.

This is not to say there was no turn-over at all. During the Norian age the fortunes of the many types of Carnian terrestrial herbivores seem to have declined. The common and cosmopolitan stagonolepine aetosaurs and hyperodopedontine rhynchosaurs, and the big lizard-like trilophosaurs (which in contrast were limited to western equatorial Lausasia), seem to have disappeared completely. The large kannemeyeriid dicynodonts are still present in moist equatorial West Pangea, as are the dog-like traversodontids. The large aetosaurs are replaced by small ones. The sauropodomorph and ornithischian dinosaurs and the small stocky lizard-like procolophonids are unaffected, and it seems that the extinctions were insignificant in comparison to the diversity of those that were unaffected. [Hunt, et al]

Unlike the semi-aquatic phytosaurs, terrestrial carnivores have done well. The late Carnian rauisuchian *Postosuchus kirkpatricki* continues into the early or middle Norian [Lucas 1998, Hunt et al], while the medium-sized predator guild was similarly little affected - herrerasaur dinosaurs are known in the Norian, and ornithosuchid "thecodonts", while unknown at this time, are represented in the Late Norian/Rhaetian Los Colorados of Argentina. sphenosuchid crocodylomorphs continue to flourish.



Correlation of four key basins of the Newark Supergroup showing the temporal ranges of footprint ichnogenera and key osteological taxa binned into 1-My intervals showing the change in maximum theropod dinosaur footprint length (line drawn through maximum) and percent at each 1-My level of dinosaur taxa. Short, horizontal lines adjacent to stratigraphic sections show the position of assemblages, and the attached vertical lines indicate the uncertainty in stratigraphic position. Solid diamonds indicate samples of footprints, and open diamonds indicate samples with 10 footprints. Horizontal, dashed gray lines indicate the limits of sampling; thick gray line indicates trend in maximum size of theropod tracks; ?, age uncertain. Ichnotaxa are as follows: 1, *Rhynchosauroides hyperbates* [Lepidosauromorph or primitive archosauromorph]; 2, unnamed dinosaurian genus 1 [Unknown dinosaur, perhaps herrerasaurid]; 3, *Atreipus* [Ornithischian dinosaur]; 4, *Chirotherium lulli* [Crurotarsan, possibly aetosaurid]; 5, *Procolophonichnium* [procolophonid parareptile]; 6, *Gwyneddichnium* [tanystropheid]; 7, *Apatopus* [Phytosaur]; 8, *Brachychirotherium parvum* [Rauisuchian]; 9, new taxon B [Crurotarsan, possibly crocodylomorph] (1); 10, *Rhynchosauroides* spp. [lepidosauromorphs]; 11, *Ameghinichnus* [Advanced synapsid, possibly trithelodontid]; 12, "*Grallator*" [Small theropod dinosaur]; 13, "*Anchisauripus*" [Small- to medium-sized, theropod dinosaur]; 14, *Batrachopus deweyii* [Crocodylomorph]; 15, "*Batrachopus*" *gracilis* [Crocodylomorph]; 16, *Eubrontes giganteus* [Large theropod dinosaur]; 17, *Anomoepus scambus* [Ornithischian dinosaur]; and 18, *Otozoum moodii* [Prosauropod dinosaur]. Stratigraphic and magnetostratigraphic columns and correlations are modified from (2). Details of vertebrate assemblages are given in supplemental data (3). Correlation with the other rift basin sequences is based on the larger scale magnetic polarity pattern, Milankovitch cycle stratigraphy, palynology, and basalt geochemistry (4). Ma, million years ago; Hett., Hettangian; Sine., Sinemurian..

[ref Olsen *et al* 2002 [Fig.1]

1. M. J. Szajna, B. W. Hartline, in *The Great Rift Valleys of Pangea in Eastern North America: Volume 2, Sedimen- tology and Paleontology*, P. M. LeTourneau, P. E. Olsen, Eds. (Columbia Univ. Press, New York, in press). back

2. P. E. Olsen, *Ann. Rev. Earth Planet. Sci.* 25, 337 (1997). back

3. Additional information is provided in the supplemental material available on Science Online at www.sciencemag.org/cgi/content/full/296/5571/1305/ DC1. back

4. . P. E. Olsen, R. W. Schlische, M. S. Fedosh, *Mus. North. Ariz. Bull.* 60, 11 (1996). back .

The dinosaurs were the big winners of the Norian, increasing in diversity and size. As can be seen from the above diagram, the theropods increase almost four-fold in linear dimensions from the early Tuvalian (mid Carnian) to the Mid Norian, while at least double the number of dinosaurian species are known from any one time span.

The Norian therefore was an age dominated by archosaurs. As we have seen, the larger synapsid herbivores - the lumbering Dicynodonts, and the traversodontid cynodonts - were now reduced in both diversity and range, confined as Carnian relics to a narrow wet tropical band, although still locally common. The medium-sized carnivorous chiniquodontids were replaced by much smaller, and more mammal-like, forms called Dromatheriidae, the ecological equivalent of a shrew. These advanced tiny cynodonts were probably very successful, but remain poorly known, because such tiny remains are only rarely fossilized.

Terrestrial Tetrapod Succession

As with the Carnian, the Norian is a long period of time (in fact it is the longest age in the Triassic, in terms of duration) that embraces several distinct tetrapod faunas. We find that a number of different ecological and biogeographic communities existed, developed, and were replaced by new communities, the most dramatic being the sauropodomorph takeover. A review of these is given here. As large predators are relatively rare, we have - following the "empires" of Anderson & Cruikshank 1978, Bakker 1977, etc - defined these by the most common herbivores or (in the case of the sphenodont lepidosaurs or common terrestrial metaposaur *Apachesaurus*) insectivores. They can be represented as follows:

Tetrapods of the Earliest Norian (Early Lacian Age)

Description of this first stage is very speculative, due to incomplete strata.

Following the Carnian-Norian turnover, there is an impoverished fauna. Of the large herbivores the rhynchosaurs, trilophosaurs, and stagonolepine aetosaurs are completely extinct, whilst dicynodonts and traversodonts have completely disappeared from the north-west and form eastern Pangea (but still found in in south-west Pangea). Of the carnivores the prestosuchids (represented by the single genus *Saurosuchus*) are also gone. Among the semi-aquatics , the rutiodontine phytosaurs and the large metoposaurs are extinct, replaced by nicrosaurs and cyclotosaurs (and chigutosaurs in the south). The dinosaurs are the big winners, with several new types appearing.

The West Pangean Aetosaur-Apachesaur Community: As explained, no Earliest Norian terrestrial faunas are known for sure from south-western North America. But it does seem that at some point, perhaps the end of the Carnian, some groups - like the rhynchosaurs and Trilophosaurs on land, and the rutiodontine phytosaurs and large metaposaurs in freshwater, disappeared from this region entirely. In fact, the rhynchosaurs and large metaposaurs seem to have died out worldwide, and no post-Carnian Trilophosaurs are known with certainty. However, a number of latest Carnian (Adamanian) species seem to have continued unchanged right through to the Late Early Norian, so we can assume that they were present at this time, even if fossils are absent. These species would include the large rauisuchian *Postosuchus kirkpatricki*, the large aetosaurs *Desmatosuchus haplocerus* and *Paratypothorax andressum*, the small metoposaurid *Apachesaurus gregorii*, and small podokesaur dinosaurs (*Coelphysis* or similar)

The Middle Pangean Metoposaur Community: To the north and east, in Central Laurasia, *Metoposaurus stuttgartensis* is known from the Lehrbergstuff of Stuttgart-Sonnenberg, Germany. This is the only known Norian metaposaur from Europe. Like *Apachesaurus* the fragmentary remains belonged to a relatively small animal [Milner 1994, p.11]. It seems then that metoposaurs had been drastically diminished at the end of the Carnian, with only a few specialized forms surviving. Interestingly, in Gondwana, Chigutosaurs take their place (as is evident from late Triassic deposits in India [****), in Europe it is the capitosaurs (*Cyclotosaurus*) that takes over.

The South-West Pangean Kannemeyeriid-Traversodont Community: In southern Brazil meanwhile, the Catturita Formation of Latest Carnian to Early Norian age, the highest level, informally called the Jachaleria Level [Scherer 1994] includes the kanneymererid *Jachaleria candelariensis* and the very primitive dinosaur *Guaibasaurus candelariensis* (which has features indicating affinities with both the sauropodomorph and the Theropoda, implying that it may belong to the ancestral group for both of them; it has been given its own family: the Guaibasauridae. Also found in the Catturita Formation is the earliest known Prosauropod proper, *Unaysaurus tolentinoi*; preliminary phylogenetic analysis indicates it to be closely related to the European *Plateosaurus* (Plateosauridae). [Leal *et al* 2004]

Tetrapods of the Late Early Norian (Late Lacian Age) - Age of the Aetosaurs and Small Dinosaurs - Early Revueltian

In the arid equatorial west, new advanced phytosaurs (*Pseudopalatus*) and aetosaurs (*Typothorax*) appear (although these may have evolved in the preceding stage and not been recorded because of absence of equivalent strata). And for the first time, both herbivorous and carnivorous dinosaurs grow as large as the bigger "thecodonts".

The West Pangean Aetosaur-Apachesaur Community: later Early Norian terrestrial faunas are so far only well known from the middle Chinle Group of south-western North America, where it seems that while some groups - like the rhynchosaurs and Trilophosaurs on land, and the phytosaurs and metaposaurs in freshwater, disappeared entirely, many of latest Carnian species seem to have continued unchanged, alongside a few newcomers. In the Cooper Canyon Formation of Texas we find a transitional Adamanian-Revueltian fauna characterized by the rauisuchians *Postosuchus kirkpatricki* and *Chatterjeea elegans*, the large aetosaur *Desmatosuchus haplocerus*, all late Carnian, as well as a small metoposaurid (perhaps this is *Apachesaurus* or a relative) and other temnospondyl amphibians, the advanced phytosaur *Pseudopalatus buceros*, the small ornithischian dinosaur *Technosaurus smalli*, and the procolophonid *Libognathus* [Small 2002]

In New Mexico the type Revueltian fossil assemblage of the Bull Canyon Formation in New Mexico is dated Early to Middle Norian, and probably extends over some time, as Hunt 1989 distinguishes two biochrons. The "Anaschisma (here = *Apachesaurus*?) -Belodon- (=*Pseudopalatus*) Typothorax-Desmatosuchus-Paratypothorax biochron" includes the rauisuchians *Postosuchus kirkpatricki* and *Chatterjeea elegans*, *Revueltosaurus* (formerly thought to be an ornithithischian dinosaur), a diverse aetosaur fauna consisting of *Typothorax coccinarum*, *Desmatosuchus* sp. and *Paratypothorax sp.*, the sphenosuchian *Hesperosuchus*, and the possible ornithischian dinosaur *Lucianosaurus wildi* [Hunt 1989, Lucas 1998].

The wide diversity of large aetosaurs suggests that they have taken over the role of big herbivore vacated by the trilophosaurs, rhynchosaurs, and dicynodonts with their disappearance from the region at the end of the Carnian.

A small prosauropod is known from fragmentary postcrania from the Cooper Member of the Dockum Formation of Texas, this was previously thought to be an ornithischian because of the presence of ornithischian teeth (Technosaurus) in this locality. However it seems the two animals were distinct [Hunt and Lucas 1994 p.236]. Neither ornithischians nor prosauropods seem to have been as common or important ecologically as aetosaurs, no more than a single species of ornithischian is known from any one locality, and these dinosaurs are rare throughout the Late Triassic [*ibid* p.236].

A significant new addition to these faunas is the large (5.5 meter) coelophysid theropod *Gojirasaurus quayi*, from the late early or middle Norian Cooper Canyon Formation of New Mexico. This was the first of the larger carnivorous dinosaurs, although it is unlikely it ever competed directly with the heavily built Rauisuchians of the time. It correlates with the appearance of larger theropod footprints in the Newark Supergroup during the middle Norian

See also Therrien and Fastovsky 2000 for a description of this and nearby Paleoenvironments (Table 2 in that document includes a list of species)

In this seasonally arid environments, the terrestrial metoposaur *Apachesaurus gregorii* makes up a common element, while the Carnian aquatic metaposaurs are either very rare or completely absent.

The Middle and East Pangean Aetosaur-Prosauropod-Proterochersid Community: The Lower Stubensandstein fauna of South-west Germany is very similar to that of the Upper Chinle or Upper Dockum of Western North America, and the associated Neshanician stage of the Newark Supergroup of eastern North America (New England, etc). Included here are basic pseudopalatine phytosaurs (*Nicrosaurus kampfi*), and the large aetosaur *Paratypothorax andressum* [Rauhut and Hungerbuhler 1998]. These are typical of Revueltian tetrapod assemblages of Lucas 1998. Dinosaurs are represented by the medium- to large-sized (4 to 6 meters long) prosauropod *Plateosaurus gracilis*, a species which would seem to be directly seem to have been directly ancestral to the later plateosaurs.

Temnospondyl amphibians (*Cyclotosaurus* and *Gerrothorax*), phytosaurs, and the earliest known turtles (*Proterochersis*) are all found. No doubt smaller animals were also present. (*Aetosaurus ferratus* dates from either the Lower or Middle Stubensandstein, the original location is not certain)

No ornithischians have as yet been found, indicating a different community or environment to that of the contemporary West Pangean (SW USA). The only indication of cosmopolitanism is the large aetosaur *Paratypothorax andressum* which occurs in both regions. Other elements are similar but not identical. There areCyclotosaur capitosaurs instead of Apachesaur metoposaurids, the phytosaur *Nicrosaurus* rather than *Pseudopalatus*, and prosauropods instead of ornithischians. These differences may be the result of geographic isolation between the two faunas.

A similar fauna occurs in southern Gondwana, since the lower part of Dharmaran Formation, India, which might tentatively be dated at around this time, includes *Nicrosaurus*, a *Paratypothorax*-like aetosaur, and prosauropods. [Lucas 1998]

Tetrapods of the Early Middle Norian (Early Alaunian Age) - Age of the Aetosaurs and Small Dinosaurs - Middle Revueltian

The West Pangean Aetosaur-Apachesaur Community: (continued). The upper Bull Canyon Formation in New Mexico represents the *Apachesaurus*-*Pseudopalatus*-*Typothorax* biochron. Filling the medium predator niche is *Chatterjeea elegans*, which continues from the earlier stage, and a new, small, advanced cynodont, *Pseudotriconodon chaterjeei*, appears. The ornithischian *Lucianosaurus* replaces *Technosaurus*. The upper Petrified Forest Member near San Ysidro might be the same age [Hunt 1989]. The aetosaur *Aetosaurus arcuatus* (I don't know if this occurs in the upper or lower parts of the formation) is known from both New Mexico and the Newark Supergroup of Eastern North America, indicating that, like its larger cousin *Paratypothorax andressorum* known from both western North America and Europe (although its long stratigraphic range (late Carnian to middle Norian) means it isn't of much help in determining age of the faunas) Hunt and Lucas 1992, these animals traveled widely cross northern Laurasia

Understanding the nature of vertebrate faunas of south-western North America depends on the interpretation of the stratigraphy. There is disagreement regarding whether the Whitaker (Ghost Ranch) quarry dates from the early Norian or the Rhaetian. If the latter, than the dinosaurs is *Eucoelophysis baldwini* whose fossil remains are known from the Upper Triassic Petrified Forest Formation of the Chinle Group in north-central New Mexico [Sullivan and Lucas 1999]. This was a small animal closely related to (either a near cousin or perhaps an ancestor) to *Coelophysis bauri* and the Hettangian *Syntarus rhodesiensis*. If the former than *Eucoelophysis* would be Latest Carnian in age. The type horizon of *E. baldwini* is the upper part of the Petrified Forest Formation, about 45 meters stratigraphically below the locality of the neotype of *Coelophysis bauri*.

The Central West Pangean Equatorial Aetosaur-Traversodont Community: During the Middle Norian a narrow swath around the Pangean Equator remains home to a persistent Carnian-type biotic province characterized by the presence of small herbivorous traversodont cynodonts, (*Plinthogomphodon*), rare kannemeyerid dicynodonts, the ubiquitous aetosaur *Aetosaurus* (*Stegomus*), a poposaurid rauisuchian similar to *Postosuchus*, the sphenosuchian crocodylomorph *Dromicosuchus*, and phytosaurs and temnospondyl amphibians. [Olsen et al]

Elsewhere, fossil footprints indicate the presence of lepidosauromorphs, tanystropheids, Phytosaurs, a possible herrerasaurid and both small and small- to medium-sized podokesaurid theropod dinosaurs [ref Olsen *et al* 2002].

Tetrapods of the Late Middle Norian (Alaunian) - Time of Transition - Late Revueltian

In places fairly large sauropodomorphs come to dominate the environment (certainly in the Keuper, and it can be expected elsewhere too). The Middle Stubensandstein of Germany, some of the fissure fillings of Bristol, England, the Ørsted Dal Member of the Fleming Fjord Formation, Greenland; the Zorzino Limestone and Forni Dolomite, northern Italy, share very similar faunas (including the same species, or closely related ones) and can probably be considered more or less contemporary.

This stage then sees the appearance of both advanced forms (e.g.*Mystriosuchus*) and, curiously, a resurgence of several primitive types (*Aetosaurus*, *Proganochelys*, and Thecodontosauridae - *Efraasia*)

The Middle and East Pangean Prosauropod-Proganochelyid-Aetosaur Community. To the east, in Central Laurasia, in the Middle Stubensandstein, which could be considered contemporary with the above, or nearly so, we find a sudden radiation of sauropodomorphs, which increase in both quantitative numbers and diversity. *Sellosaurus* is now joined by the small, rare *Thecodontosaurus* and the large (6 meters long) common *Efraasia*. Curiously both these species are of a more primitive, basal, type, and would appear to be immigrants, as they have no ancestors in the Lower Stubensandstein. Similarly, *Proterochersis* has disappeared, and is replaced, by a likewise more primitive form, *Proganochelys*

As for other reptiles, the advanced phytosaur *Mystriosuchus* now joins the more generalized *Nicrosaurus*. As with the dinosaurs, this is almost certainly an immigrant (perhaps from the Tethys, where it is also known), as no obvious ancestors are known. These genera were all provincial (however it has been suggested that Nicrosaurus also occurs in North America, although the interpretation of *buceros* as *Nicrosaurus* [Zeigler *et al* 2001] is controversial [see different interpretation in Hungerb�hler 2002 where it is considered *Pseudopalatus*], the aetosaur *Aetosaurus ferratus* is different in species but generically similar and again closely related to its west Laurasian counterpart. Here we also find the Rauisuchian *Teratosaurus* can be compared to *Postosuchus* and *Chatterjeea*.

Two small theropod dinosaurs are also known from this level, the small *Procompsognathus triassicus* and the medium-sized *Halticosaurus longotarsus*, the latter too fragmentary identify properly (*nomen dubium*).

These early dinosaurs lived alongside amphibians (Cyclotosaurus posthumus continues from the Lower Stubensandstein), aetosaurs, and new species of phytosaurs (*Mystriosuchus*) and sphenosuchids (Saltoposuchus).

This European (Central Laurasian) fauna extended as far as East Laurasia (Thailand), where one finds in the Huai Hin Lat Formation (dated as Norian on the basis of plants and ostracods [deBroin et al 1982) Actinopterygii, lungfish, the temnospondyl *Cyclotosaurus robustus*, indeterminate plagiosaurs, a distinct species of *Proganochelys* (*P. ruchae*) , and phytosaurs *Mystriosuchus* and "a *Beledon* [=*Nicrosaurus*) -like form" [Buffetaut et al 2000]

Marine and Terrestrial Reptiles of the Late-Middle Norian Tethys (Zorzino Limestone)

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Center-left (crawling into the water) is the placodont *Psephoderma alpinum*, behind which is the phytosaur *Mystriosuchus planirostris*, which also occurs in the Middle Stubenstein, while in the middle forground the thalattosaur *Endennasaurus acut�rostr�s* pokes its head

out of the water. In the left foreground is the insectivorous prolacertiform *Langobardisaurus pandolfii*, while in the right foreground the sphenodontid *Diphydontosaurus* stalks a beetle. In the middle background is the aetosaur *Aetosaurus ferratus* (known from this locality only from a small fragment of dorsal armour). To the right are the arboreal archosauromorphs *Drepanosaurus* and *Megalancosaurus*. Above fly several pterosaurs.

The Tethyan Pterosaur-Drepanosaur Community (*above*) When we move south to the Tethyan coast, and west to western Laurasia, we find another unique ecosystem. A distinct endemic fauna has been found at the Zorzino Limestone and Forni Dolomite in northern Italy, and represents a tropical coastal environment. Being marine sediments, these can be very accurately dated by ammonoid and conodonts. The Zorzino Limestone turns out to be very close in age to the Alaunian-Sevatian boundary, being placed in the younger part of the*Mesohimavatites columbianus* zone. The Forni Dolomite, also *Mesohimavatites columbianus* zone, is dated at Middle-Late Alaunian; it contains different species of Pterosaurs and so may be slightly older. The common presence of the aetosaur *Aetosaurus ferratus* and the phytosaur *Mystriosuchus planirostris* indicates that the Middle Stubensandstein and the Zorzino Limestone are probably the same age - Latest Middle Norian - or at least fairly contemporary.

The Thecodontosaur Sphenodont Community During the late Triassic and early Jurassic in middle north Pangea, Carboniferous limestone caves and crevices in presumably upland regions, served as traps into which animals would stumble into, fall, and be unable to get out. Eventually their bodies were mummified, preserved, and fossilized as the caves filled with sediments. These became the Anglo-Welsh (and French and German) limestone fissure fillings, which have provided fossil remains of a diverse range of small reptiles and early mammals. Although traditionally dated as "Rhaetic" or "Rhaeto-Liassic", it is now considered that many of these faunas are actually Middle or Late Norian, and some may be as early as the late Carnian onwards. In these regions away from the broad floodplains and braided streams that favoured the large sauropodomorphs, a provincial Thecodontosaur community developed, perhaps as a subset of a larger Prosauropod community. Its endemic nature makes this fauna difficult to correlate with that of larger middle and east Laurasia. Representative forms include Thecodontosaur sauropodomorphs, Sphenosuchid (*Terrestrisuchus*) crocodylomorphs, gliding lepidosaurs (Keuhnosaurus), sphenodonts, advanced cynodonts, early mammals, and other small animals. Comparisons are sometimes made between *Terrestrisuchus* and *Thecodontosaurus* and the Middle Stubensandstein *Saltoposuchus* and *Thecodontosaurus*, in order to suggest a similar date for the Bristol fissure fillings, but similarity does not guarantee they are contemporary; *Terrestrisuchus* is now considered distinct from *Saltoposuchus* [Fraser et al 2002], and the Stubensandstein "Thecodontosaurus" is too fragmentary to identify with that genus with certainty.

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Tetrapods of the early Late Norian (Sevatian) - Age of Sauropodomorphs

During this period (Late Norian to Rhaetian) large sauropodomorphs dominate most terrestrial environments (except the north-west). Often a single taxon will be very common: *Plateosaurus* in Europe / Central and North Laurasia, *Euskelosaurus* in Southern Africa / South Gondwana, and *Riojasaurus* in Argentina / South-West Gondwana. This is not to say that a number of other taxa are not often present as well, but these are always much fewer in number. Earlier types of aetosaurs and phytosaurs die out, while new phytosaurs, aetosaurs, and dinosaurs (*Syntarsus*) appear.

The West Pangean Aetosaur-Apachesaur Community: (continued). Animals of west equatorial Pangea seem to be best represented by the diverse remains discovered at the Whitaker (Ghost Ranch) quarry (Rock Point Member of the Chinle Formation, New Mexico), although a little to the north the Chinle Church Rock Member (Utah) might be considered a similar age [Benton 1994].

This can be considered then the earliest date of the Apachean Land Vertebrate Age, as indicated by the presence of the phytosaur *Redondasaurus* Lucas 1998]. Curiously, the predominance of large sauropodomorphs that characterizes the rest of the world is absent here, this indicates either locally distinct conditions or an incorrect date for these strata.

The Low Latitude Central-West Pangea Hypsognathus Community. Further east, and north of the high rainfall band, in what is now eastern USA (Newark Supergroup), the Laurasian desert continues, but here instead of the typical plateosaur community is a more restricted assemblage characterized by the procolophonid *Hypsognathus* [Lucas 1998], although fossil footprints indicate the presence of lepidosauromorphs, tanystropheids, Phytosaurs, Rauisuchians, crocodylomorph-like crurotarsans, advanced Crocodylomorphs, Ornithischian dinosaurs, and both small and small- to medium-sized podokesaurid theropod dinosaurs [ref Olsen *et al* 2002]. Curiously, ornithischians rather than sauropodomorphs seem to be the main herbivore here.

In Europe the Late (Upper) Stubensandstein witnessed a further increase in dinosaurs. *Plateosaurus* is ubiquitous, having descended from and replaced the earlier forms. It is represented by a single species, *Plateosaurus longiceps* (*P. trossingensis* is a junior synonym [Galton 2001, Galton 2002]) and accompanied by phytosaurs and the long-lived turtle *Proganochelys quendstedti*, which continues from the Early and Middle Stubensandstein. We can assume many other animals were also present, although they have not been preserved as fossils.

According to Dr Bob Bakker, the pattern of emergence of the anchisaur-plateosaur empire follows very closely that of the earlier lystrosaurid-kannemeyerid empire. As Bakker explains, in the faunal zone following the Carnian extinctions (13 in Fig. 2) prosauropod dinosaurs of several closely related families (T and U in Fig. 2) make up nearly all big herbivore specimens.

> "In any one local basin, the diversity appears to be very low, reminiscent of that of the *Lystrosaurus* Zone; usually one genus of big prosauropod dominates the collections, although various growth stages sometimes have been recognized as distinct genera (Rozdestvenski). Surprisingly, the top predators of these early prosauropod zones are holdovers from the mid-Triassic - ornithosuchid and rauisuchid thecodonts (H and L in Fig. 2). Advanced theropod dinosaurs take over this trophic role at the Triassic-Jurassic boundary"

This ecological community probably extended for some distance, since prosauropods and turtles are common in the Fleming Fjord Formation (Malmros Klint and �rsted Dal Members) of East Greenland, where a diverse assemblage of fossil vertebrates very similar to that of the middle Norian Stubensandstein of Germany has been found [Jenkins *et al* 1995, Lucas 1998] including fish, temnospondyl amphibians (*Gerrothorax*, *Cyclotosaurus*), turtles (c.f. *Proganochelys* sp.), sphendontids, aetosaurs (*Aetosaurus ferratus*, *Paratypothorax andressi*), a pterosaur, prosauropod (*Plateosaurus*) a theropod dinosaur and footprints, and several species of mammals (*Kuehneotherium*, c.f. *Brachyzostrodon*, and *Haramayavia*) . During the Late Triassic, Greenland and continental Europe were adjacent during time, and dinosaurs and other animals clearly migrated widely. The environment was controlled by Milankovitch cycles, with climatic conditions varying from humid to seasonal to arid. Because a number of animals of different time periods are represented, it is likely that several stratigraphic levels are represented here.

Tetrapods of the late Late Norian (Sevatian) - Age of Sauropodomorphs

The Middle Pangean Prosauropod-Proganochelyid (*Plateosaur*) Community In middle Laurasia (middle latitude north-central Pangea) the formerly mixed and diverse fauna becomes increasingly dominated by sauropodomorph dinosaurs at the end of the Norian. This appears to be a global trend. The Plateosaur community extended widely throughout all of central Laurasia, as the most common plateosaur species (*Plateosaurus longiceps*, not *P. engelhardti* as usually identified - see notes on *Plateosaurus*, below) is known from Germany, France, Switzerland and Greenland. At this time, the climate in Greenland was very lush, and a rich assortment of plant species thrived (some 200 species are known from the Scoresby Sound area of eastern Greenland, although this represents a stratigraphic sequence extended in time, so not all were contemporary) in the warm and wet (even though high latitude (45 - 50 degrees north) climate. Yet the genus *Plateosaurus* is found in this part of the world, from the Fleming Fjord Formation, just as in the deserts, and as we have seen is associated with typical Keuper species.

In Germany, the Knollenmergel is almost entirely dominated by Plateosaurs. Three species are known - the common *Plateosaurus longiceps*, the rare *Plateosaurus engelhardti* (known from Bavaria, probably a geographically distinct form), and a new genus and species *Ruehleia bedheimensis* [Galton 2001, Galton 2001b, Galton 2002] which however appears to be very similar to *Plateosaurus* [Headden 2003]. A fourth species of plateosaur, *P. erlenbergiensis* from this time is known from incomplete remains and hence indeterminate, it is probably a synonym of one of the others. But regardless of how many species one counts, there is little variation, and only one dominate species.

These large dinosaurs are accompanied by phytosaurs - *Angistorhinopsis ruetimeyeri* replaces the earlier *Mystriosuchus* and *Nicrosaurus* - and the ubiquitous early turtle *Proganochelys*. *Cyclotosaurus robustus* has been replaced by *Cyclotosaurus carinides*, and the palgiosaur *Gerrothorax pulcherrimus* by a related species, *Plagiosaurus depressus*

Thus we find in middle Laurasia (middle latitude north-central Pangea) the formerly mixed and diverse fauna becomes increasingly dominated by sauropodomorph dinosaurs at the end of the Norian. This appears to be a global trend. The Plateosaur community extended widely throughout all of central Laurasia, as the most common plateosaur species (*Plateosaurus longiceps*, not *P. engelhardti* as usually identified - see notes on *Plateosaurus*, below) is known from Germany, France, Switzerland and Greenland. At this time, the climate in Greenland was very lush, and a rich assortment of plant species thrived (some 200 species are known from the Scoresby Sound area of eastern Greenland, although this represents a stratigraphic sequence extended in time, so not all were contemporary) in the warm and wet (even though high latitude (45 - 50 degrees north) climate. Yet the genus *Plateosaurus* is found in this part of the world, from the Fleming Fjord Formation, just as in the deserts, and as we have seen is associated with typical Keuper species.

In the trees and the underbrush living alongside these large dinosaurs were many smaller animals. The locality of Saint-Nicolas-de-Port (Late Norian to Early Rhaetian in age) is famous for having yielded numerous mammal teeth.

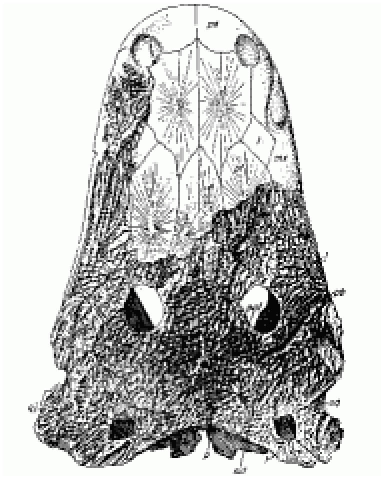
The South Pangean Melanorosaur-Sauropod (*Euskelosaurus*) Community: (High Latitude South Pangea) Going south to Gondwana, the Lower Elliott Formation of Southern Africa provides a glimpse of a rich assemblage of advanced early dinosaurs. The Lower Elliot is traditionally dated as Late Carnian on the basis of *Dicrodium* plants and the presence of typically Carnian elements like Traversodonts. However the advanced sauropodomorph elements indicate a later date [Lucas and Hancox 2000], and there is no reason why the dicrodium biota could not have continued in Gondwana well into the Norian.

In the Lower Elliott of Southern Africa (south Gondwana) then, we find a high latitude location with at least four different Proto-Sauropod and basal Sauropod genera (*Melanorosaurus*, *Euskelosaurus*, Blikanosaurus, and *Antetonitrus*). There are no mastodontosaurid (*Cyclotosaurus*) or plagiosaur amphibians; instead, brachiopods fill the role of medium to large semi-aquatic predator. Intriguingly, and adding to the distinct Gondwanan flavour of this community, large synapsid herbivores (a kannemeyerid dicynodont (represented by footprints) and the large cynodont *Scalenodontoides*) are also present, although rarer than the dinosaurs. The dominance of giant dinosaur herbivores (in this case *Euskelosaurus* is especially common) shows an ecological equivalence with the Plateosaur community to the north, and we can assume that these large animals were found worldwide. Again, the climate is seasonal monsoonal (savannah-like) to semi-arid. One also finds in Gondwana large rauisuchians - represented by *Fasolosuchus* in the west (Argentina) and "*Basutodon*" further south and east. Podokesaurid (= Coelophysid) theropods are indicated by the presence of numerous small to medium-large sized tridactyl footprints (*Grallator* and larger forms, the nomenclature of the latter (by Ellenberger 1970) is very oversplit.)

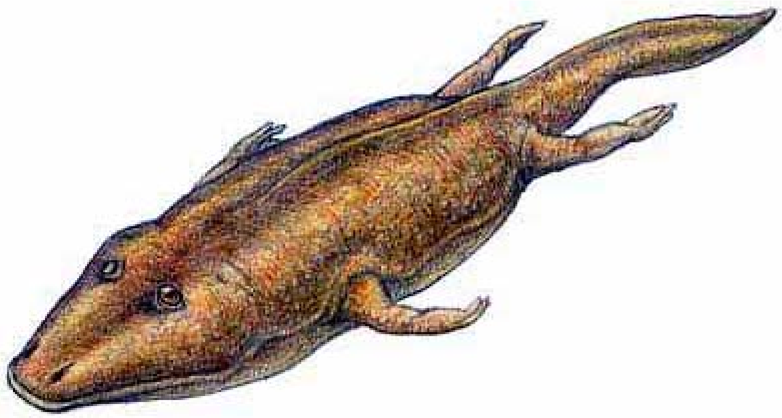
Also in Gondwana, the slightly younger (probably Rhaetian) Los Colorados of Argentina reveals a similar preponderance of large sauropodomorphs. It would seem likely in any case that the Sauropodomorph fauna continues through to the Rhaetian with little change; although the extreme provinciality of this time makes comparative dating difficult (so some formations attributed to Late Norian may be Rhaetian, and vice versa).

A Norian Bestiary

Cyclotosaurus | *Apachesaurus* | Gerrothorax | *Libognathus* | *Proganochelys* and *Proterochersis* | *Shonisaurus* | *Psephoderma* | *Kuehneosaurus* | *Planocephalosaurus* | *Drepanosaurus* and *Megalancosaurus* | *Mystriosuchus* | *Aetosaurus* | *Teratosaurus* and "*Basutodon*" | *Hesperosuchus*, *Dromicosuchus*, *Saltoposuchus*, and *Terrestrisuchus* | *Peteinosaurus*, *Eudimorphodon*, and *Preondactylus* | Agnosphitys | *Thecodontosaurus* | *Plateosaurus* | *Melanorosaurus* | *Euskelosaurus* | *Antetonitrus* | *Procompsognathus* | *Coelophysis* and *Eucoelophysis* | *Gojirasaurus* and *Liliensternus* | *Jachaleria (= Ischigualastia?)* | *Plinthogomphodon* and *Scalenodontoides* | *Pseudotriconodon*



Cyclotosaurus posthumus - skull length 53 cm
Stubensandstein (middle Keuper) of Pfaffenhofen, Bavaria
illustration from Welles and Cosgriff, 1965, p.43, from Fraas, 1913, pl.19



Cyclotosaurus sp. - illustration copyright © Satoshi Kawasaki - original page

With the drying of the climate across the Euramerican landmass, due to continental movement, the Metoposaurs die out, apart from the small terrestrial *Apachesaurus* of the western part of the northern Laurasia province. The Cyclotosaurs (family Capitosauridae or Mastodonsauridae) are more successful and continue to flourish in Europe. There the large *Cyclotosaurus robustus* of the Carnian has been replaced by the related *Cyclotosaurus posthumus* It differs from its predecessor in certain minor details, like a more narrower and more coarsely sculptured skull, a slightly narrower snout, and more lateral (sideways) nostrils [Welles and Cosgriff, 1965, p.45]. *Cyclotosaurus posthumus* is known from the Stubensandstein of Germany, the Fleming Fjord Formation of Greenland, and the Huai Hin Lat Formation of Thailand. It was a large animal, with a skull length of over half a meter, and an overall length of around two to two and a half meters in length. These animals probably lay quietly on the bottom of ponds and shallow rivers, snaring unwary passing fish and small aquatic tetrapods with a sudden opening of the huge mouth. While adults were probably large enough to be safe, the young would have fallen prey to the phytosaurs that frequented the same waterways.

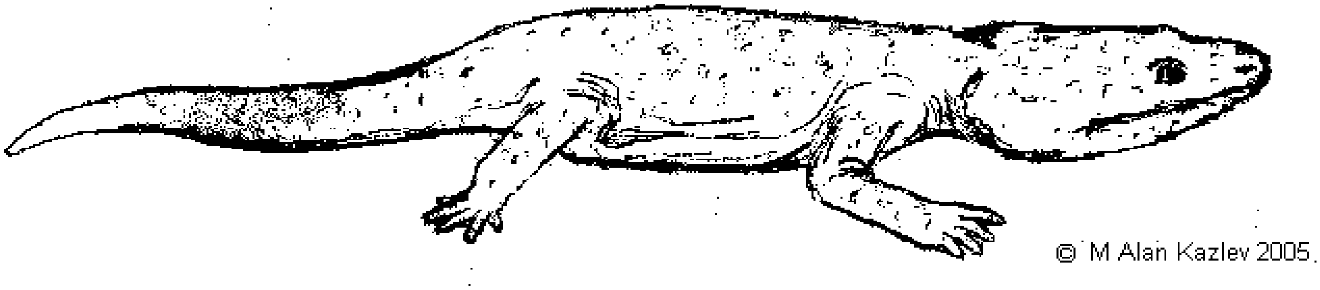
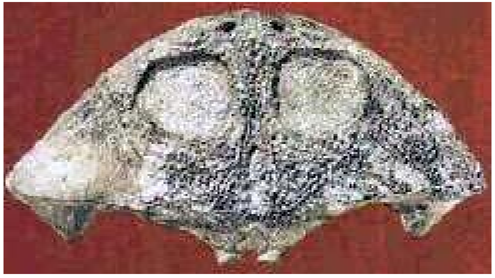


illustration by M.Alan Kazlev Creative Commons License 2005

Most Metoposaurs were large aquatic animals with large heads and small weak limbs. A prominent exception was the diminutive form (skull 25 cm or less) *Apachesaurus gregorii* (Hunt and Santucci 1993, Hunt 1998), known from abundant intercentra, several partial skeletons, partial skulls, clavicles and interclavicles found in the Chinle Formation of Arizona and New Mexico and the Dockum Group of Texas. *Apachesaurus* had a much more terrestrial habit than other members of its family, comparable perhaps to the Permian dissorophids. This animal is rare in the late Carnian (Adamanian), where large metoposaurs predominate, but is very common in the Norian of the American southwest [Milner 1994]. It is the most common element of the Painted Desert Member fauna (Chinle Formation). It appears to have been geographically restricted to that region, as it has not been found outside what was then western equatorial Pangea. It seems to have filled the ecological role of semi-aquatic insectivore/small carnivore.

The advanced temnospondyls *Plagiosaurus* and *Gerrothorax* were medium-large (around a meter long) short-headed amphibians of the family Plagiosauridae that lived alongside Cyclotosaurs and phytosaurs. They are known not only from the Ladinian to Rhaetian of Europe and (Norian) Greenland, but also the Huai Hin



Gerrothorax pulcherrimus, from the Stubenstein (Middle Norian) of Stuttgart, SW Germany; Fleming Fjord Formation of Greenland
illustration from the Staatliches Museum f�r Naturkunde - original page (pdf)

Lat Formation (Norian) of Thailand, and so can be assumed to have had a wide distribution throughout northern middle to north-east Pangea. Plagiosaurs were even better adapted to a totally aquatic existence than the cyclotosaurs; in fact the presence of gills means they were unable to live out of water at all. *Gerrothorax* fed on fish, invertebrates, and smaller amphibians and reptiles, while themselves falling prey to the phytosaurs with which they shared their environment. Indeed, considering that they seem to have had no natural defenses against phytosaurs, these large Temnospondyls did remarkably well throughout the entire period of the Late Triassic.

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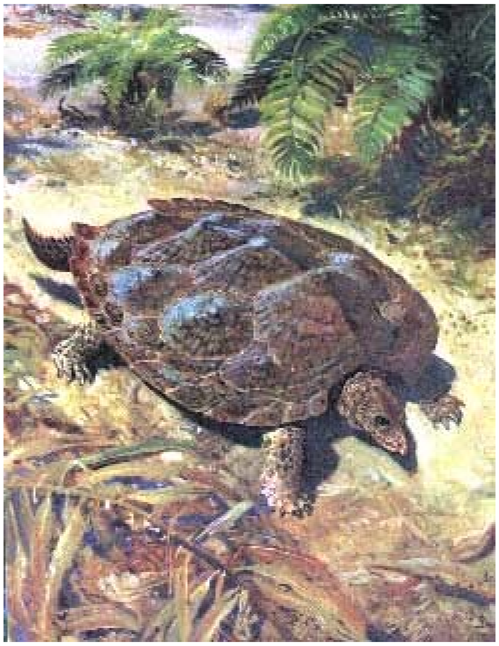
***Libognathus sheddi* is a representative of the advanced procolophonids; small, squat lizard-like reptiles which flourished in arid (desert or semi-desert) environments of the late Triassic [Olsen et al], and the first procolophonid to be described from the Late Triassic of the southwestern United States. *Libognathus*' remains were found in the late Early Norian of Cooper Canyon Formation (Dockum Group) near Post, Texas. It is one of a number of North American procolophonids represented solely by tooth-bearing jaws [Modesto S.P. ; Damiani R.J. ; Sues H. , 2002] These have provided an understanding of tooth replacement and implantation in procolophonids. The teeth set in sockets and firmly anchored by spongy hone of attachment (this is known as the protothecodont condition), and are replaced in a typical reptilian pattern. *Libognathus* is closely related to the Late Norian and Rhaetian *Hypsognathus* [Small 1997]**

The First Turtles



The Norian age was remarkable for the appearance of the Chelonia (turtles) which seem to have emerged out of nowhere. In the Lower and Middle Stubenstein of the German Keuper, they make up a large proportion of local fauna [Benton 1986]. Two species are known. *Proganochelys quendstedti* is the more common and well known, and a representative of the most primitive lineage of turtles (family Proganochelyidae). It is a largish chelonid, the overall animal being up to about a meter. The skull, although typically chelonid in its robust and solid construction, toothless jaws, horny beak, and other features, still retains a few primitive characteristics not found in more advanced forms, such as tiny teeth on the palate (roof of the mouth). The broad domed shell differs from that of later turtles only in the presence of small marginal spiky plates that projected outwards, and the openings being too small to withdraw the neck and legs into. Instead, the limbs were protected by the spiked plates, and the neck by spiny scales. This long-lived species, which has in the past also been known under the names *Psammochelys*, *Stegochelys*, and *Triassochelys*, continued to the end of the Norian (Knollenmergel). [Gaffney 1986] A related form is known from the Fleming Fjord Formation of Greenland [Lucas 1998]; it would not be surprising if this is the same species.

Illustration from *Life Before Man* by Zdenek V. Spinar, illustrated by Zdenek Burian

Proganochelys ruchae is a contemporary (Norian) species from Huai Hin Lat Formation of Thailand illustrates the wide (possibly worldwide) distribution of this genus.

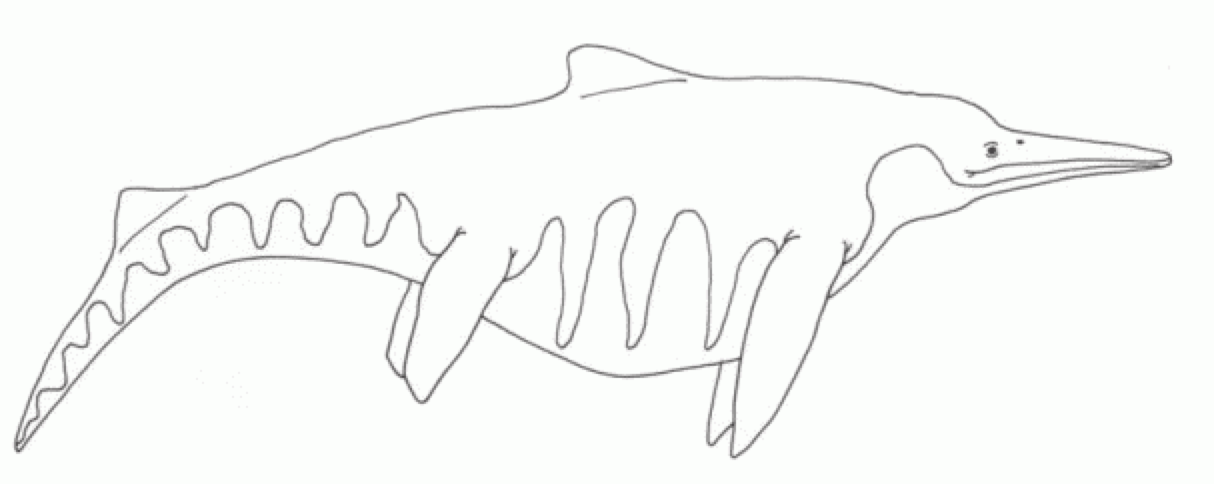
Despite appearing even earlier than *Proganochelys*, *Proterochersis robusta* is a more advanced form, the earliest known of the side-necked turtles or pleurodires. Unlike *Proganochelys* the lower shell or plastron has large openings to allow the limbs to retract (although the ability to retract the head and neck inside its shell did not develop, curiously, until the Cretaceous).

The presence of two very different types of turtles even at this time, and the implication of a third from the ghost-lineage formed by an intermediate Rhaetian form *Palaeochersis*, as well as the primitive Hettangian (early Jurassic) *Australochelys*, shows that the Chelonia had undergone an extensive evolutionary radiation in the early Norian, if not before. One might hazard a guess that their sudden appearance and abundance in the Norian was due to the disappearance of rivals or predators in the Carnian-Norian turnover. These early turtles clearly lived in a terrestrial environment [Joyce and Gauthier 2004], and it was only later in the Jurassic that the group moved to a semi- and fully-aquatic lifestyles.

Norian Chelonida

Proganochelys quendstedti	***Proganochelys ruchae*** *deBroin 1984*	***Proterochersis robusta*** *Fraas 1913*
Horizon & Locality: Middle and Upper Stubenstein and Knollenmergel of SW Germany; Fleming Fjord Formation of Greenland Age: late Middle to Late Norian Length: shell upto 56cm References: Gaffney 1986, Joyce and Gauthier 2004	Horizon & Locality: Huai Hin Lat Formation of Thailand Age: ?Middle Norian Length: -- References: deBroin et al 1982, deBroin 1984. However Gaffney 1986 considers this specimen too incomplete to identify as *Proganochelys*	Horizon & Locality: Lower Stubenstein of SW Germany Age: Late Early Norian Length: maximum carapace length of 33 cm References: Gaffney 1986

Giant Ichthyosaurs



Shonisaurus, the lord of the late Triassic seas. Length: 10 to 25 (or more) meters, known range, Late Carnian to Norian, distribution: Panthalassian (world-wide).
illustration copyright © M.Alan Kazlev 2005

In a dramatic scene from an episode of *Walking with Dinosaurs*, "the Cruel Sea", viewers saw a gigantic pliosaur swallow a theropod dinosaur. According to the WWD team, *Liopleurodon*, the giant pliosaur in question, was 25 meters long, the largest carnivore ever to live.

The truth is more disappointing. No pliosaur is known to have exceeded half that length, and 7 to 8 meters (the size of a modern adult killer whale) was standard. This would seem to be the optimal size of giant predatory marine animals.

However, during the late Triassic, there lived an animal that really *was* as big as the WWD pliosaur. This was *Shonisaurus sikanniensis*, whose gigantic remains is known from the Middle Norian Pardonet Formation, northeastern British Columbia. [Nicholls and Manabe 2004]

As well as being a lot bigger, *S. sikanniensis* differs from *S. popularis* in the shape of the scapula (shoulder bone) and relatively longer vertebral centra (indicating perhaps a more elongate body). Study of this new species, along with re-examination of *S. popularis*, indicates that *Shonisaurus* was not as deep-bodied as previously reconstructed. The teeth seem to have been present only in juveniles. The tendency towards toothless is found in some Jurassic ichthyosaurs as well.

Shonisaurus sikanniensis is the largest marine reptile known, and the largest forms are for that matter the largest type of reptile known (exceeding the biggest terrestrial sauropods in size), the largest carnivorous animal, and among the largest animals ever to live. It is considerably larger than the late Carnian *Shonisaurus popularis*, the previous record holder, perhaps an ancestor or close relative. A specimen collected by the Tyrrell Museum in 2000 is 21 meters long, and, incredibly, even larger specimens are known; putting these animals in the size range of the larger baleen whales [Nicholls 2003]. But unlike baleen whales, which are filter feeders, *Shonisaurus* was a carnivore, and very probably preyed on smaller (but still large) vertebrates, although it is not impossible that, like modern sperm whales, they may also have fed on giant cephalopods, assuming such existed at the time (coleoidea evolved in the Devonian, giant ammonites are known from the Cretaceous). The skull is massive, and the eye sockets alone are well over a meter across [Headden, 2004]. In life, had the largest eyes of any animal that ever lived.

The sunken carcasses of these giant animals supported whale bone-like chemosymbiotic communities, and provided nutrients for representatives of several different types of bivalves, including the Lucinidae and Thyasiridae, which are represented in modern and fossil cold seeps and in association with sunken carcasses, and *Halobia* and *Monotis*, which probably harboured chemosymbiotic bacteria [Johnston *et al* 2000]

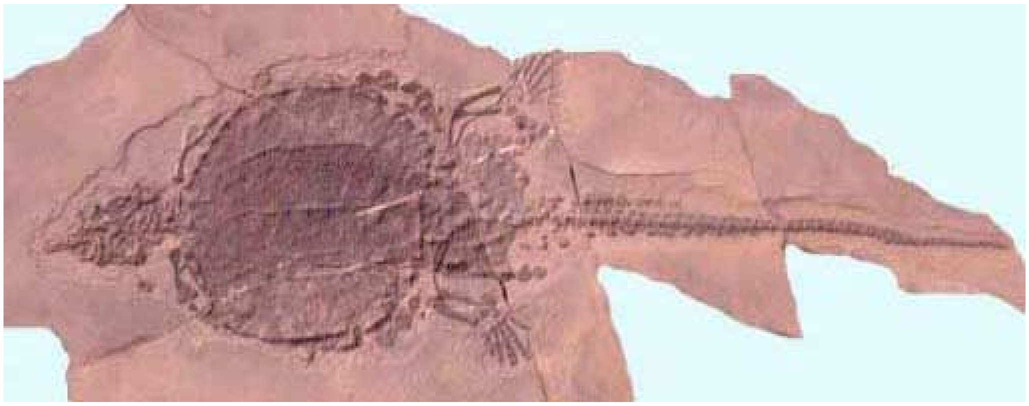
These huge ichthyosaurs were part of a diverse ecosystem, with at least five genera of ichthyosaurs represented in the Pardonet formation, the two most common being *Shonisaurus* and the related *Callawayia* [Nicholls 2003].

These gigantic animals seem to have became extinct at the end of the Norian, and were replaced by other, smaller, genera.

Clade: **Ichthyosauria**
Family: **Shastasauridae** (paraphyletic? [Maisch & Matzke, 2000] or not? [Nicholls and Manabe 2001])

Shonisaurus tibetensis *Dong, 1972* Horizon & Locality: Langjiexue Group of Tibet. Age: Norian Length: 10 to 15 meters Weight: to 40 tonnes Ecological Niche: Marine predator References: Motani *et al* 1999,Comments: = *Himalayasaurus tibetensis*; includes *Tibetosaurus tingjiensis* [see Lucas 2001 p.117]	***Shonisaurus sikanniensis*** *Nicholls and Manabe 2004* Horizon & Locality: Pardonet Formation of northeastern British Columbia. Age: Middle Norian Length: 21 meters and more Weight: ~100 tonnes and more Ecological Niche: Marine predator/super-	***Callawayia neoscapularis*** *Maisch and Matzke, 2000* Horizon & Locality: Pardonet Formation of northeastern British Columbia. Age: Middle Norian Length: 3 meters Ecological Niche: Marine predator References:/ Comments: *Metashastasaurus* of Nicholls and Manabe 2001, *Callawayia* Maisch and Matzke, 2000; it has been suggested that the name *Callawayia* represents a breach of the ICZN Code of Ethics.

predator
Reference: Nicholls and Manabe 2004
Comments: the largest known marine reptile



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Psephoderma alpinum (large)

Horizon & Locality: Calcari di Zorzino of Northern Italy
Age: Latest Middle Norian
Length: largest complete specimen is 180 cm long, but isolated teeth indicate it grew larger
Ecological Niche: ray-analogue - flattened bottom-dweller that fed on shellfish
Reference/Link:
Psephoderma

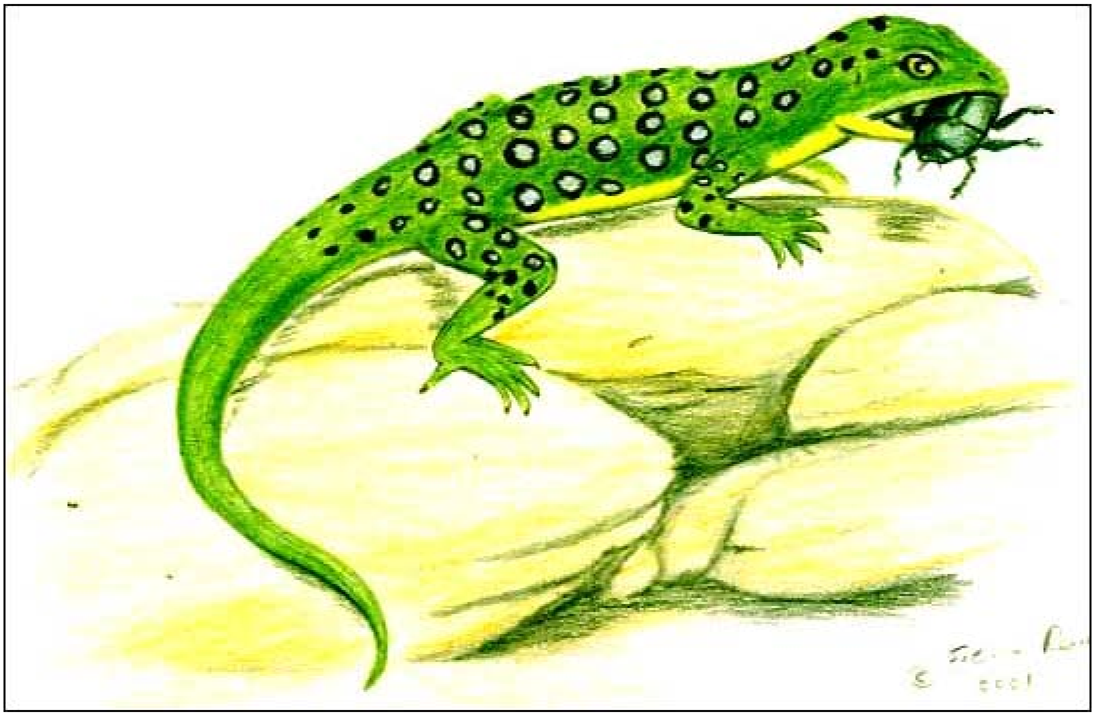
***Psephoderma alpinum*, is better known from the Rhaetian, but has also more recently been found in the late Middle Norian deposits. Like many of the Rhaetian forms, this early individuals lived in near-shore Tethys waters. However Norian specimens are at least 50% longer in linear dimensions than Rhaetic forms, so it is possible that these might be a different subspecies or even species. *Psephoderma* was a sort of reptilian ray, with a broad, flat body protected by a discoidal carapace. As with many other placodonts, the teeth are adapted to crushing shellfish, and it probably fed on mussels like *Isognornon* and *Modiolus*.**

illustration by Steve Kirk, © from *Encyclopaedia of Dinosaurs and Prehistoric Animals*, Barry Cox, R.J.G. Savage, Brian Gardiner, Dougal Dixon,

Kuehneosaurus

Horizon & Locality: Pant-y-ffynnon fissure filling, South Glamorgan, Wales.Age: Middle Norian?/late Norian? / Rhaetian?
Length: 65 cmEcological Niche: arboreal insectivore

Kuehneosaurus **is the epynomous representative of the Triassic gliding lepidosaurs or Kuehneosaurs. Although usually described as a lizard, and closely related, it nevertheless belongs to an earlier branch of the Lepidosauria, a lizard uncle rather than a true lizard, being equally related to both the Sphenodonta and the Squamata. Like its close relative the late Carnian** ***Icarasaurus*****, it glided from tree to tree using wings made from skin stretched over elongated ribs. This was the same adaptation acquired by the Permian basal diapsid** ***Coelurosauravus*** **and the recent gliding lizard flying dragon** ***Draco volans*****. The fact that three groups of small reptiles independently evolved the same characteristic shows the successful nature of this specialized adaptation**



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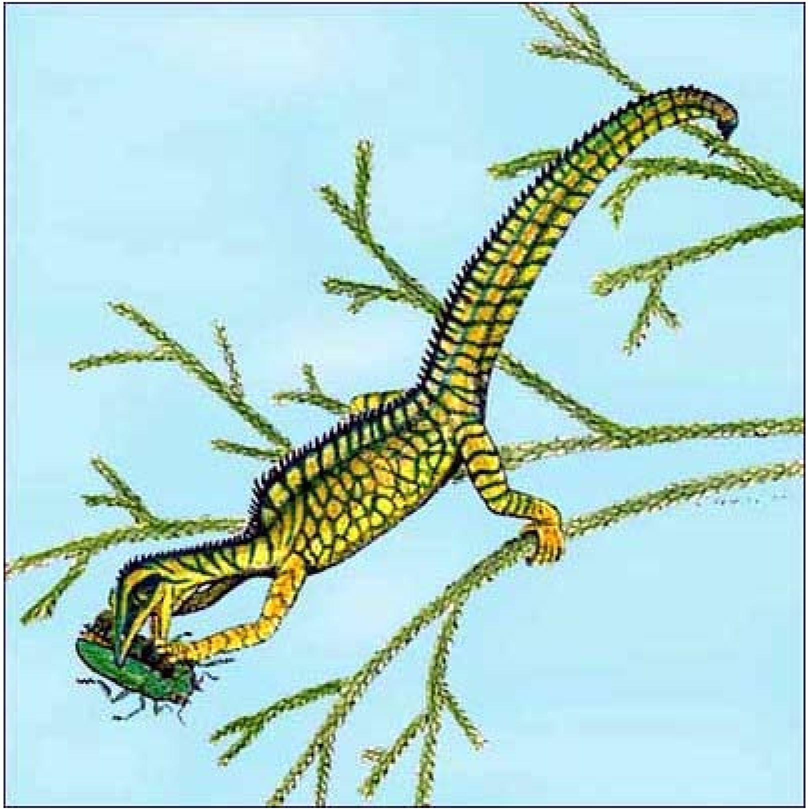
Diphydontosaurus avonis **and** ***Planocephalosaurus robinsonae*** **were very similar, very primitive Sphenodonta known from the Middle or Late Norian and Rhaetian of England and Wales (fissure fillings). Sphenodonts were both common and diverse during the Morian, and a number of species are known. These small animals were the Triassic equivalent of lizards; and in fact true lizards (Squamata) did not appear until the Middle Jurassic. There small size makes preservation difficult, and added to that there is "collector bias" in that large and obvious fossils are recovered more easily in favour of smaller and more modest (and often tiny and difficult to notice) remains. It is only in exceptional or carefully screened deposits that they are recovered.**

Diphydontosaurus **and** ***Planocephalosaurus*** **both belong to the paraphyletic family Gephyrosauridae, and constitute the most primitive grade of Sphenodonta**

A juvenile ***Diphydontosaurus*** **(illustrated above) belonging to a different species to** ***D. avonis*** **is also known from the latest-middle Norian of Tethyean Northern Italy, and is the only lepidosaur found in that locality. It seems that the Tethyan ecomorph was dominated by archosauromorphs, whereas the presumably drier inland and upland environments were frequented instead by Sphenodonts.**



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Among the more peculiar of the Norian lizard-like archosauromorphs (prolacertiforms) were the Drepanosauridae, a clade of reptiles that include the Tethyan *Megalancosaurus* and *Drepanosaurus* (known from the Dolomia di Forni and Calcari di Zorzino of Northern Italy), the west Pangean/Laurasian *Dolabrosaurus* (Dockum Formation) and *Hypuronector* (Lockatong Formation of New Jersey), and a number of other forms. Originally these animals were interpreted as aquatic swimmers because of the deep tail, but it is much more likely they were arboreal; the tail is laterally stiff and dorsoventrally mobile at its base. [Renesto, 2001]. *Megalancosaurus* is perhaps the best known form. It was about 30 cm in length, possessed long sharp hooked claws, opposable digits and a chameleon-like prehensile tail. The triangular, bird-like skull is set on a ling neck, and there is a sort of hump for muscle attachment at the shoulders. All of which gave this creature a rather strange appearance. *Drepanosaurus* was a bit larger and differed in some details; the skull is not known but the skeleton has parallels with the arboreal pigmy anteater, it is likely that Drepanosaurus used its large claws to break open bark to get at insects. Being small and living in an environment were preservation depending on their falling into water and being quickly buried in anoxic silt, these little diapsids were probably a lot more common than their few fossil remains indicate.. Links:

Megalancosaurus - Dr Silvio Renesto
Megalancosaurus preonensis - Dan Bensom

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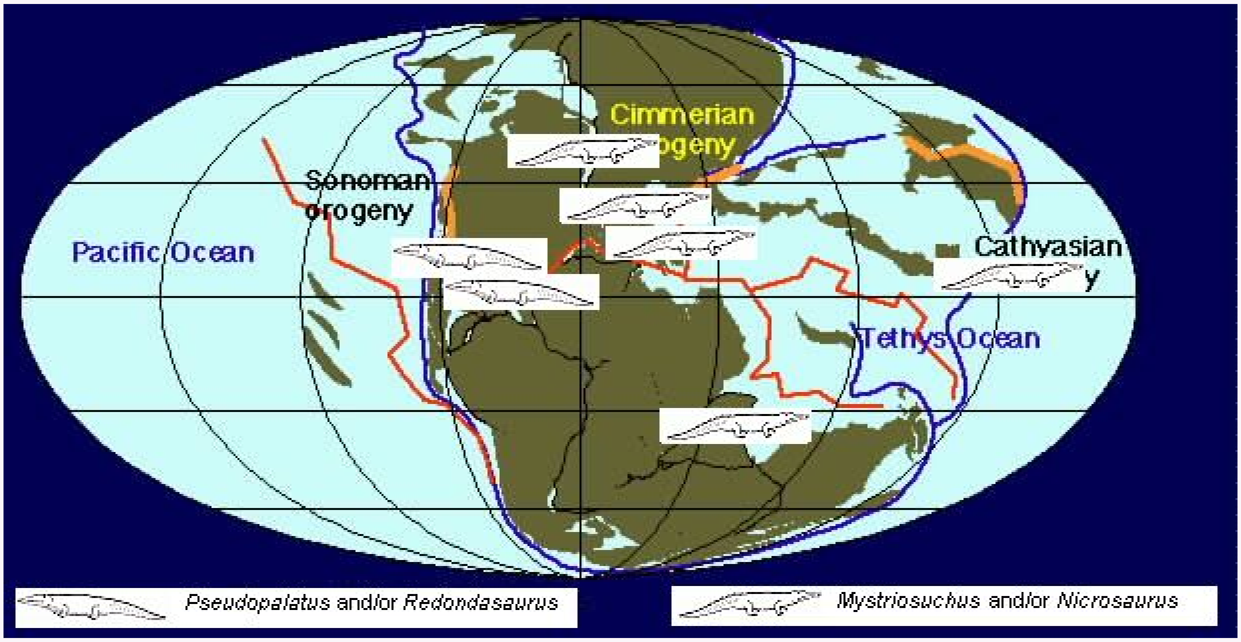
Archosaurs



Distribution of Norian phytosaurs
- map is by Dr. Ron Blakey

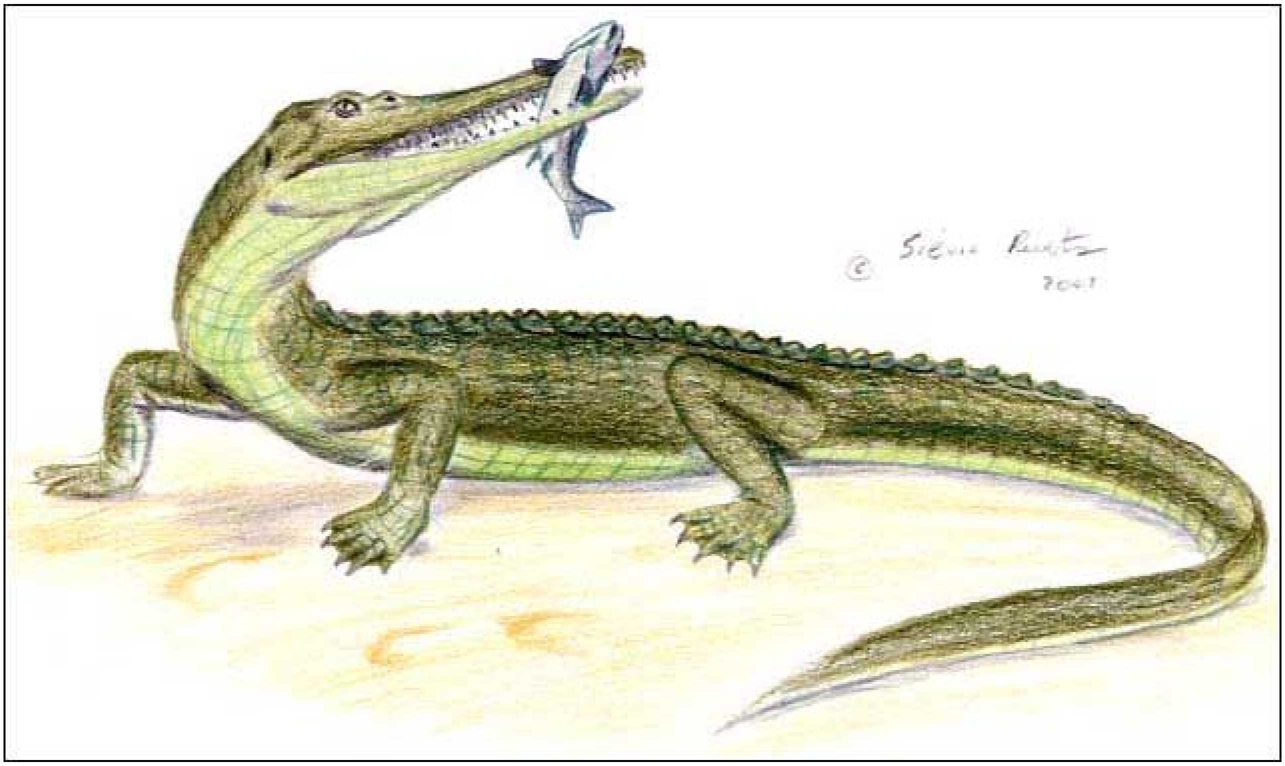
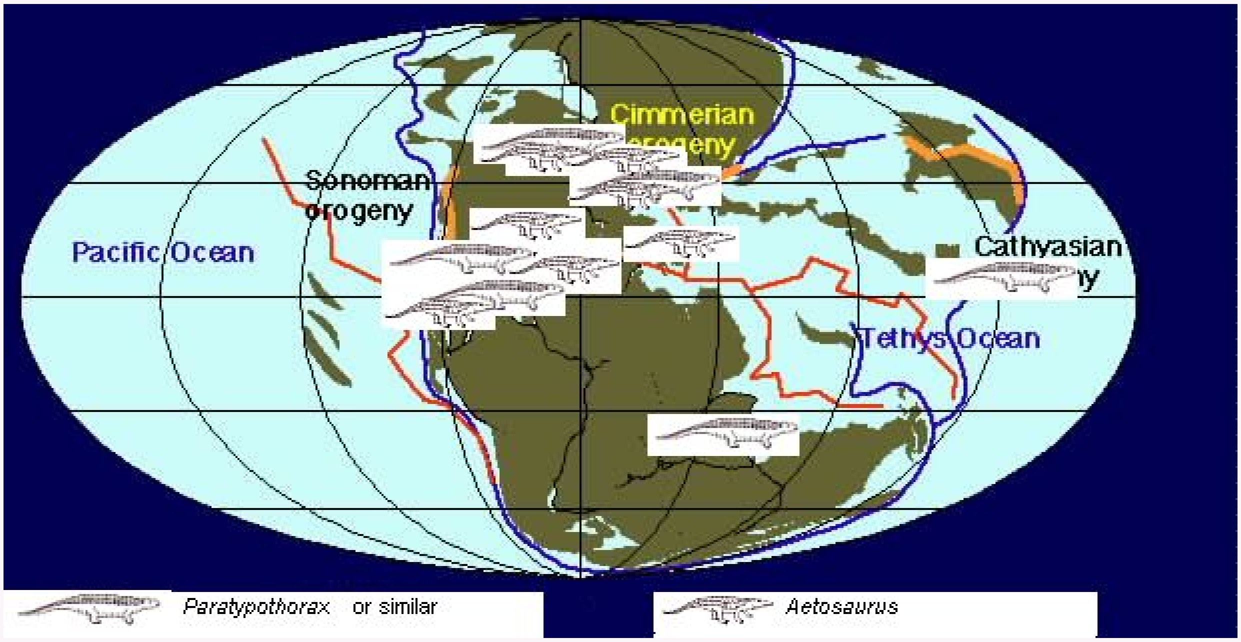


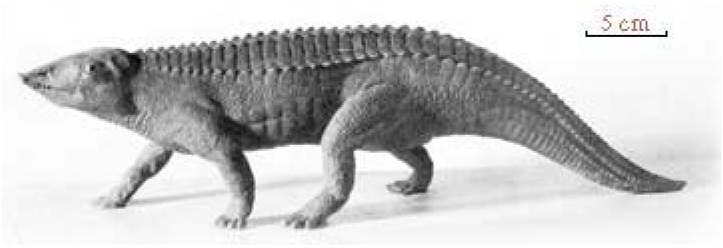
Illustration © copyright Silvio Renesto

Mystriosuchus was the most specialized of the long snouted phytosaurs; the Triassic equivalent (and probably precise ecological analogue) of the Tertiary to recent gavial. The skulls have a long, low, slender snout tipped with a pronounced spoon-like (hence the name "spoon crocodile") tusked "hook", and the teeth are all conical and similar in shape, indicating a fish-eating diet. Originally placed in its own subfamily, it is now known to be a specialized member of the subfamily Pseudopalatinae Hungerb�hler, 2002. This was a large phytosaur, about 4 meters in length, and also one of the later forms to appear. _Mystriosuchus_ is known from the Middle Stubensandstein (Middle Norian) of south-west Germany, Calcari di Zorzino of Northern Italy, and the Huai Hin Lat Formation of Thailand, and so can serve as useful index fossil. Significantly, it is absent from North America, showing that very different fauna lived in west Pangea from central and East Pangea.Two species are known, _Mystriosuchus planirostris_, illustrated above, and _Mystriosuchus westphali_ (formerly _Mystriosuchus plieningeri_), although there may very well be more in non-European localities.. Links:

Mystriosuchus - Dr Silvio Renesto.



Distribution of the cosmopolitan Norian aetosaurs _Paratypothorax_ and _Aetosaurus_
- map is by Dr. Ron Blakey



The armoured Stagonolepidae (Aetosaurs) continue to flourish during the earlier part of the Norian, and are prominently represented by the eponymous *Aetosaurus*, a small but heavily armoured animal 0.7 to 1.5 metres in length. *Aetosaurus* is actually among the most primitive of the Aetosaurs (and probably qualifies for its own subfamily). At least two species are known. Being a prominent and widespread animal of the middle Norian of the central and east Laurasian (northwest to middle north Pangea) biogeographic region, and the with distinctive armour, *Aetosaurus* makes a useful index fossil. The American species was previously considered a separate genus, *Stegomus*. Aetosaurs are unknown from the Late Norian of Europe, but related forms continued in the west of Pangea through the Rhaetian.

The cosmopolitan nature of these aetosaurs continues the theme of the Ardamanian (Latest Carnian) when *Stagonolepis* had what must have been a worldwide distribution. From central (middle Keuper) and north to west (upper Chinle) Laurasia, one finds the large very advanced turtle like *Paratypothorax*, and the persistently primitive little *Aetosaurus*. [Lucas *et al* 1996]

Norian Rauisuchians

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Teratosaurus suevicus has had a rather strange history of discovery. The jaws of this rauisuchian were originally found with sauropodomorph bones (belonging to the species *Efraasia minor* (Huene, 1907-08)). It was thought that these belonged to the same animal, and it was reconstructed as an early theropod. It is now known to be a rauisuchian [Benton 1986b], perhaps a Poposaurid. Despite the appearance of large podokesaurian-grade theropod dinosaurs, these animals continued to serve as the dominant predator in terrestrial ecologies. Unlike the theropods, they were not fast runners, and probably ambushed their prey with a sudden rush (like their distant living cousins the crocodiles).

Teeth found in the Lower Elliot formation of Southern Africa can also be attributed to Rauisuchians; they were originally given the name *Basutodon ferox*. Because they are found associated with the common sauropodomorph *Euskelosaurus browni*, it was originally thought that these prosauropods were carnivorous. This is now known not to be the case; a fragment of jaw was discovered bearing the same type of teeth, and associated with large postcranial elements and bony plates (osteoderms), and these remains most likely are rauisuchian [Kitching and Raath 1984 p.114]. Nevertheless, the name *Basutodon* is still given a junior synonym for *Euskelosaurus*

As evidenced by both the giant Gondwanan *Fasalosuchus*, and the central Laurasian [Newark Supergroup] ichnospecies *Brachychirotherium parvum*, Rauisuchians continued to flourish right until the end of the Rhaetian age.

"Postosuchus"-like form Horizon & Locality: Durham sub-basin of the Deep River basin (Newark Supergroup) of Durham County, North Carolina Age: Middle Norian Length: 3 meters Link: The Predator in the Stone	***Teratosaurus suevicus*** Horizon & Locality: middle Stubensandstein = L�wenstein Formation) of south-west Germany. Age: Late Middle Norian Length: 3 to 4 meters?	***Basutodon ferox*** Horizon & Locality: Lower Elliot formation of Southern Africa Age: Late Norian to ?Rhaetian Length: ?

Norian Crocodylomorphs

When I was a kid growing up, my books on dinosaurs, when describing the Triassic period, featured drawings and descriptions of small bipedal thecodonts, looking like miniature theropod dinosaurs. Subsequent research has shown that these pseudosuchian thecodonts were actually proto-crocodiles (although on the outside they look nothing like crocodiles!), and rather than being bipedal they ran rapidly on four lithe legs. From the Late Carnian (Adamanian Age) through to the Sinemurian, lightly built sphenosuchians were an important medium-small predators on microvertebrates and large invertebrates.

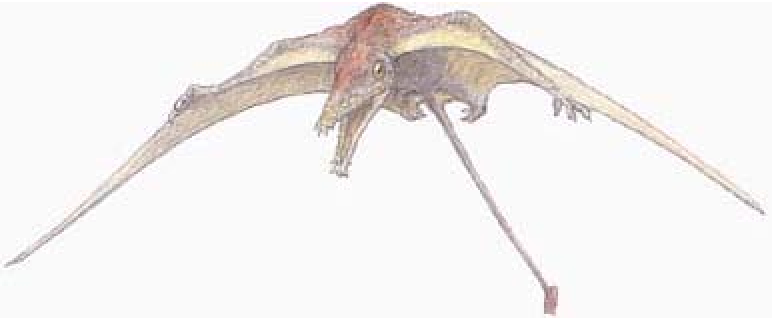
Terrestrisuchus gracilis - illustration by Steve Kirk, © from *Encyclopaedia of Dinosaurs and Prehistoric Animals*, Barry Cox, R.J.G. Savage, Brian Gardiner, Dougal Dixon,

It is not clear whether *Terrestrisuchus gracilis* from Anglo-Welsh fissure fillings, and *Saltoposuchus connectens* from the Stubenstein of Germany, are distinct but closely related forms, or simply growth stages of the same species [Clark *et al* 2000]. In any case, *Hesperosuchus*, *Dromicosuchus*, and *Saltoposuchus*/*Terrestrisuchus* form a tightly knit group. These slender animals were obviously very swift runners, and *Terrestrisuchus*, the best known and most illustrated (*see above*) has been described as "the greyhound of the Triassic". Clearly these animals competed with the podokesaurid theropods in the small predator niche, but inasmuch as the two groups lived quite happily side by side for some thirty million years or so, they must have filled different ecological niches.

The most recently discovered of these small crocodylomorphs, *Dromicosuchus grallator* [Sues *et al* 2003] was found preserved immediately underneath the skeleton of a rauisuchian, and this, along with apparent bite marks to the head and neck, indicate the two animals were buried together during the act of predation. It is however strange to imagine how a powerful rauisuchian can be killed in mortal combat with a lightly built sphenosuchid; a more likely explanation is that the two were killed and buried, perhaps by a sudden mudslide, just as the rauisuchian was dispatching its prey.

Norian Pterosaurs

Like turtles, pterosaurs are one of those groups of animals that appear in the middle Norian, seemingly out of nowhere. Four species representing three families are known from the Upper strata of the Dolomia di Forni and the slightly later Calcari di Zorzino of Northern Italy (Late-Middle Norian Age), indicating that the group already had an earlier history, perhaps during the earlier Norian (apparent reports have Late Carnian Dockum Pterosaurs have not been confirmed).



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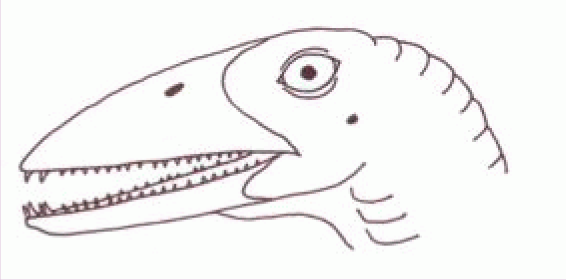
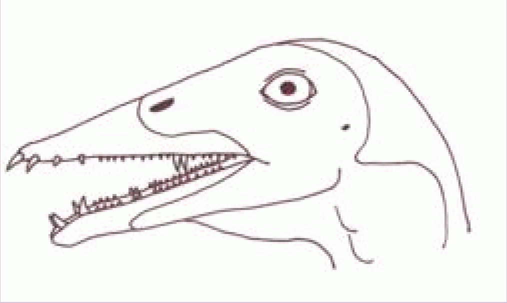
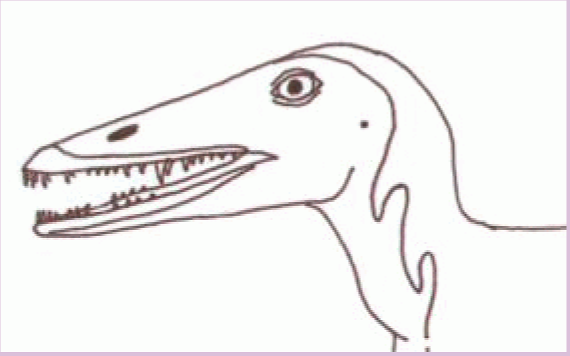


Peteinosaurus zambellii **is the smallest (wingspan of about 60 cm) and most primitive of the early pterosaurs. The wings are quite short, only twice the length of the hind legs, and there are numerous small teeth which are flattened laterally, This animal probably fed on large insects, which it caught on the wing, cutting up the tough chitin with its small blade-like teeth. Only the skeleton and lower jaw are known, so the reconstruction of the head on the left is speculative, although not implausible given this shape is based on the similarly sized insect-eating Jurassic Anurognathid pterosaurs. *Peteinosaurus* appears related or ancestral to the Early Jurassic *Dimorphodon*, and is therefore placed in the family Dimorphodontidae.**



Eudimorphodon **is so called because it has two types of teeth. The numerous small teeth have three or five cusps (points), a unique characteristic among Pterosaurs. There are also a number of larger, fang-like teeth. This was a largish pterosaur, with a wingspan of 1 to 1.75 meters. It was most likely a fish eater, like modern shore birds. The unusual teeth indicate that *Eudimorphodon* represented an early, specialized, evolutionary lineage. It is therefore given its own family: Eudimorphodontidae. This obviously common and widespread animal is known from the Norian of Greenland and Early Rhaetian of France as well as the late Middle Norian of Italy (Tethys)**

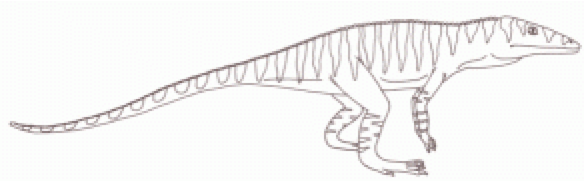


Preondactylus buffarinii **is among the largest and most advanced of these early forms, with a wingspan of 1.5 meters, it belongs to the family Rhamphorhynchidae. It shares a number of characteristics with the Toarcian *Dorygnathus*.**

Pterosaur portraits © 2001 Vince R Ward - Prehistoric Pages

Links: Eudimorphodon

Reference: Wellnhofer 1991 .



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Agnosphitys **is a small herrerasaur, superficially similar in size and appearance to *Scleromochlus*, presumably living a similar lifestyle. It is also the last known herrerasaur. These primitive dinosaurs survived alongside their more advanced podokesaur descendents**

Links: Agnosphitys (in Japanese), Agnosphitys cromhallensis by Brad McFeeters (sketch)

Agnosphitys cromhallensis *Fraser, Padian, Walkden & Davis, 2002*

Horizon & Locality: fissure assemblages of Cromhall, south-west England

Age: Mid/late Norian or ?Rhaetian

	Length: 60 cm Weigh: 650 gm Ecological Niche: medium-sized insectivore/ microvertebrate predator. Reference: Fraser et al 2002

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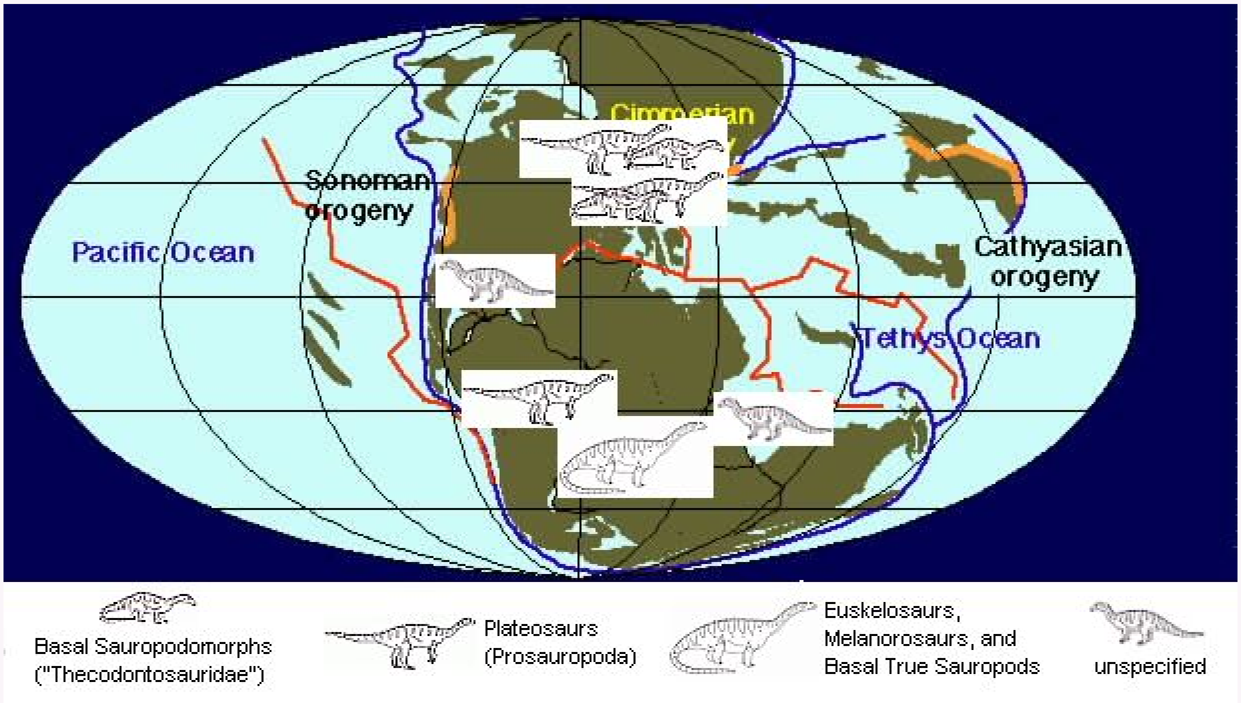
Rise of the Sauropodomorpha

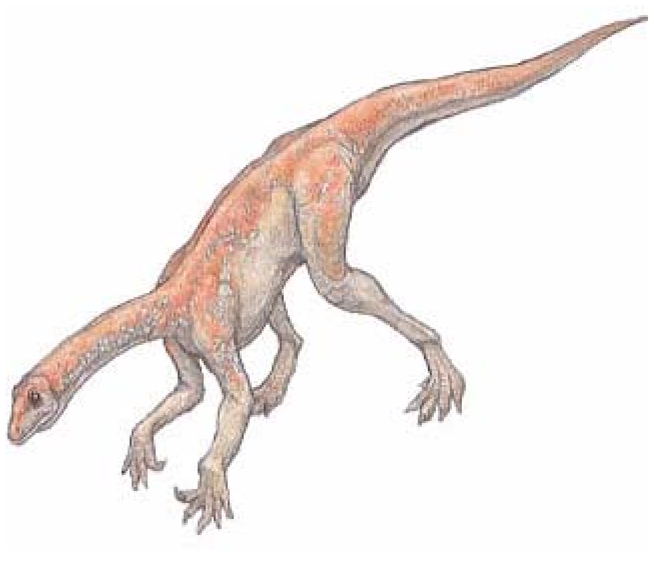


Distribution of Norian sauropodomorphs

- map is by Dr. Ron Blakey

The ecological turnover and dominance of the Archosaurs, specifically the dinosaurs, is particularly evident in the early representatives of the clade of herbivorous dinosaurs known as the Sauropodomorpha. Although small and insignificant throughout the Carnian and early Norian, during the middle Norian these early sauropodomorphs underwent an astonishing evolutionary radiation. It is not at all clear what triggered this. A combination of factors like vegetation and climate change (the prosauropods were better able to cope with aridity than the dicynodonts; although this assumes that there really was a global climate change in the Norian (which Olsen et al seem to indicate was *not* the case). It could hardly have been the absence of predators because large Rauisuchians were already present

These animals - thecodontosaurs, plateosaurs, and their kin - were all of a paraphyletic assemblage of early plant eating dinosaur formerly known as "Prosauropods", although the more accurate, if rather unwieldy term Basal Sauropodomorphs is used now. Prosauropod literally means "before the sauropods", because they were the ancestors and grand-uncles of the gigantic sauropods like *Brachiosaurus* and *Apatosaurus*. Indeed they resembled much smaller and lightly built versions of those better known animals. Previously a rather minor element of the tetrapod fauna, they underwent an evolutionary radiation during the Middle Norian, but it was really in the Late Norian and Rhaetian that they came to prominence. There seem to have been several different lineages, including persistently primitive thecodontosaurs (which don't seem to have changed much since the middle Carnian), the Prosauropoda proper, and the Sauropoda proper and their immediate ancestors (of which *Anchisaurus* is the most primitive albeit not the earliest known representative). As the Norian advanced the latter two of these clades diversified, with Prosauropods becoming Plateosaurs, Euskelosaurs, and Riojasaurs, and Anchisaur grade Proto-Sauropoda becoming Euskelosaurs, melanorosaurs, blikanosaurs, and True Sauropods.



Thecodontosaurus - illustration copyright © Satoshi Kawasaki - original page

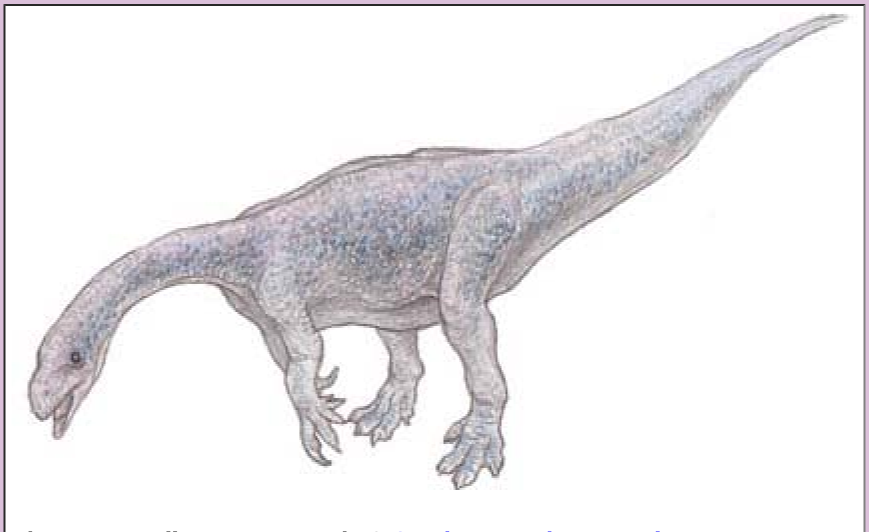
Thecodontosaurus antiquus is a small and very primitive dinosaur, near the base of the sauropodomorph tree, only a little more advanced then the late Carnian *Saturnalia*. The neck is short for a sauropodomorph, and the skeleton bears many primitive features. It is best known from Welsh Norian-Rhaetian "fissure fillings" but is also known from Durdham Down near Bristol in England, the late middle Norian (Middle Stubenstein) of southwest Germany [Benton 1986] (*T. hermannianus*), and has also been tentatively reported from Poland [ref Justin Tweet - Sauropodomorpha]. A very similar animal, *Agrosaurus macgillivrayi* Seeley, 1891, once thought to be the only known Australian dinosaur fossil from the late Triassic, later turned out to be mislabeled, and actually comes from England, and is a junior synonym of *Thecodontosaurus antiquus*. A new species *T. caducus*, has recently been described [Yates_2003). The presence of equivalent German forms like *Saltoposuchus* and *Thecodontosaurus* is sometimes used to argue for a Norian date for the English and Welsh fissure fillings but there is no way to date these for certain.

Efraasia, from the late middle Norian (Middle Stubenstein) of southwest Germany, is a closely related, slightly more advanced form than *Thecodontosaurus*, that is more than twice the linear dimensions. thecodontosaur grade dinosaurs then were an important part of the late Triassic fauna, although they do not seem to have survived the end-Triassic extinction. This persistently primitive type continued to exist quite happily alongside its giant plateosaur cousins, possibly inhabiting a specific niche environment in Europe.

Norian "Thecodontosauridae" (basal Sauropodomorphs)

Thecodontosaurus hermannianus *(Huene, 1907-08)* Horizon & Locality: Age: Late Middle Norian Length: ? Ecological Niche: Medium-sized Herbivore	***Efraasia minor*** *(Galton,1973)* Horizon & Locality: Middle Stubensandstein of Baden-Wurttemberg, SW Germany	***Thecodontosaurus antiquus*** *Morris, 1843* Horizon & Locality: Middle Stubensandstein of SW Germany Age: ?Middle or ?Late	***Thecodontosaurus caducus*** *Yates, 2003* Horizon & Locality: fissure fill in Pant-y-ffynnon Quarry, South Wales Age: ?Middle or ?Late Norian or ?Rhaetian

Comments: Known only from the partial maxilla (upper jaw bone), this basal sauropodomorph is too fragmentary to classify further, and there is nothing that specifies it belongs to Thecodontosaurus	Age: Late Middle Norian Length: 6 meters Ecological Niche: Dominant Large Herbivore	Norian or/to ?Rhaetian Length: 1.5 (juvenile?) to 2.6 meters Ecological Niche: Dominant Medium-sized Herbivore	Ecological Niche: Medium-sized Herbivore Reference: Yates 2003 Comments: known from juvenile specimens

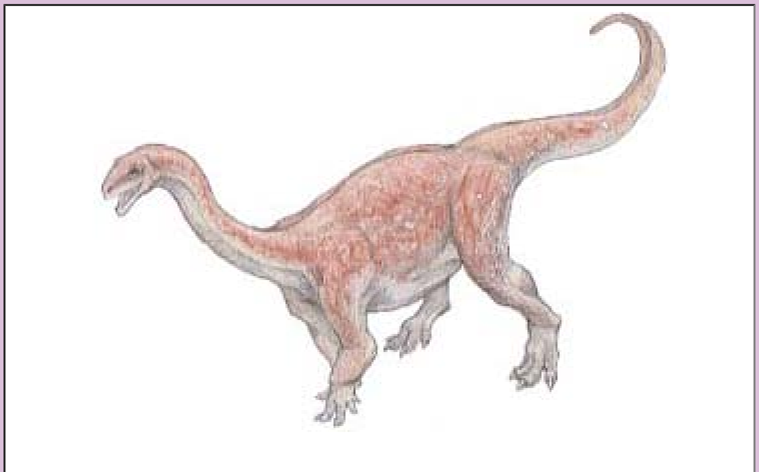


Plateosaurus - illustration copyright © Satoshi Kawasaki - original page

The animal traditionally referred to as *Plateosaurus engelhardti* Meyer, 1837 might actually be a different species, *Plateosaurus longiceps* (see notes on *Plateosaurus*). Regardless of what scientists finally decide its name should be, is the archetypal prosauropod, the best known German dinosaur, and, with *Coelophysis*, the best known Triassic dinosaur. It is known from the late Norian (Oberer Stubensandstein and Knollenmergel; Upper L�wenstein and Trossingen Formations) where it seems to have completely supplanted the earlier and more diverse Middle Norian (Mittlerer Stubensandstein) prosauropod fauna. This predominance may however be a preservation bias or the result of local conditions, and suggest immigration from elsewhere [Benton 1986]. Remains have been found from over 30 localities in an area of about 500km by 50km, including Franconia, Wuerttemberg, Thuringia and Saxonia-Anhalt. In Trossingen about 60 Plateosaurs have been found (approx. 100 finds). Altogether over 100 partial and complete skeletons and ten skulls are known, many of which have been attributed in the past to different species and even genera. *Plateosaurus has also been reported from the Switzerland, France, and Sweden, with a range possibly extending into the Rhaetian [ref. Justin Tweet - Sauropodomorpha]. It seems that the Plateosaurs were the predominant megaherbivores of their time, a role that continued into the following, Rhaetian age with the South American Riojasaurus*.

Norian Plateosaurs

Unaysaurus tolentinoi *Leal, Azevedo, Kellner, and Da Rosa, 2004)* Horizon & Locality: Catturita Formation of southern Brazil Age: Latest Carnian/early Norian Length: 2.5 meters Weight: 30 kg Ecological Niche: Medium-sized Herbivore Comments: skull and partial skeleton known	***Plateosaurus gracilis*** *(Huene, 1907-08)* Horizon & Locality: Lower and Middle Stubensandstein of Baden-Wurttemberg, Germany Age: Middle Norian Length: 4 to 6.5 meters Weight: 110 to 400 kg Ecological Niche: Large Herbivore Comments: also known as *Sellosaurus*; this is probably a more correct name cladistically speaking, since the genus Plateosaurus is almost certainly paraphyletic	***Plateosaurus longiceps*** *Jaekel, 1914* Horizon & Locality: Upper Stubensandstein of SW Germany, and Knollenmergel of Thuringen, Germany Age: Late Middle to Late Norian (to Rhaetian?). Length: 8 meters Weight: 1300 kg Ecological Niche: Dominant Large Herbivore Comments: a gracile form, includes the famous Trossingen plateosaur	***Plateosaurus engelhardti*** *Meyer, 1837* Horizon & Locality: Knollenmergel of Bavaria Age: Late Norian Length: 8 meters Weight: 1500 kg Ecological Niche: Large Herbivore Comments: the most heavily built and the most quadrupedal of the three species.	***Ruehleia bedheimensis*** *Galton, 2001* Horizon & Locality: Trossingen Formation = Knollenmergel, of South Thuringia, Germany Age: Late Norian Length: 8 meters Ecological Niche: Large Herbivore Comments: originally referred to Plateosaurus plieningeri,



Melanorosaurus - illustration copyright © Satoshi Kawasaki - original page

Melanorosaurus readi was a large (7.5 meters long) proto-sauropod. Some individuals, perhaps of a related species, are thought to have reached 12 to a whopping 15 meters in length, which would make them the largest land animals of their time, and indeed of the entire Triassic. The melanorosaurs lived alongside other sauropodomorphs like 8 meter long *Euskelosaurus browni*, and the earliest known sauropod *Antetonitrus ingenipes*, some 10 meters or more in length. The giants had arrived.

Great size has forced this gentle herbivore down on all fours; unlike Plateosaurus it could not walk on its back legs even if it wanted to do. The hips have four sacral vertebrates, as opposed to three in Plateosaurus and *Euskelosaurus*, making them stronger and better able to transfer force to and from the powerful hind legs. The femur or thigh bone is straight too, like an elephant's, to help take the weight, and Melanorosaurus certainly would certainly have matched an African elephant in size (assuming an 8 meter Plateosaurus weighed 1500 kg, and scaling up from there), while a 15 meter individual would have equaled a modest sized sauropod in bulk.

Traditionally, *Melanorosaurus*, *Riojasaurus*, and a number of other early four-legged forms were grouped in the family Melanorosauridae, but *Riojasaurus* is now considered a more primitive form.

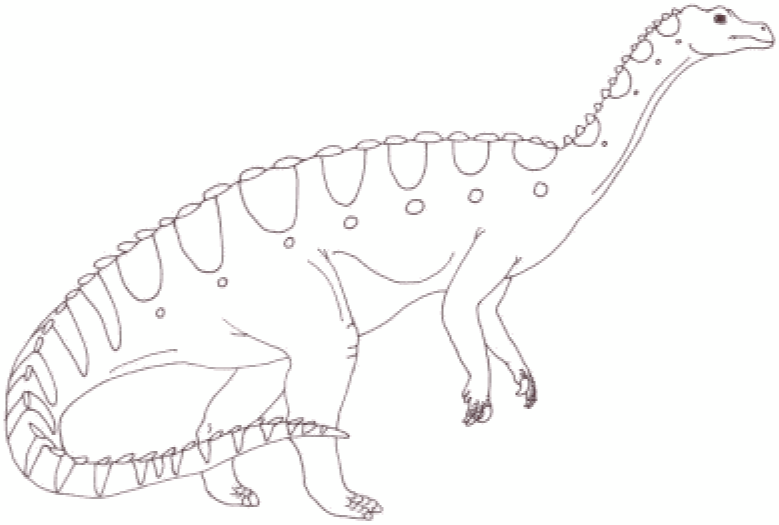


illustration © 2001 Vince R Ward - Prehistoric Pages

Euskelosaurus browni was a large (8 to 10 meters long) but fairly lightly built early sauropodomorph that was the commonest medium to large animal in its environment. It is known from the Lower Elliot formation (Late Norian) of South Africa, Lesotho, and Zimbabwe, and it clearly filled the same ecological role in Southern Gondwana that *Plateosaurus* did in central Laurasia (Europe and Greenland). It is quite likely that these animals were contemporaries, representing a worldwide sauropodomorph (Plateosaur-Melanorosaur-Protosauropod) community that continued from the Late Norian to the end of the Rhaetian, where there was an ecological turnover and a more diverse (but still dinosaur-dominated) biota took over.

Despite being such a common animal, the evolutionary relationships of *Euskelosaurus* are not clear. Originally it was considered a Prosauropod closely related to *Plateosaurus*, but more recently it has been considered a proto-sauropod [see Mortimer 2003 for suggested cladogram]). There is no doubt that the sauropodomorphs were a diverse and vibrant clade at this time, with a number of primitive and advanced lineages evolving in parallel.

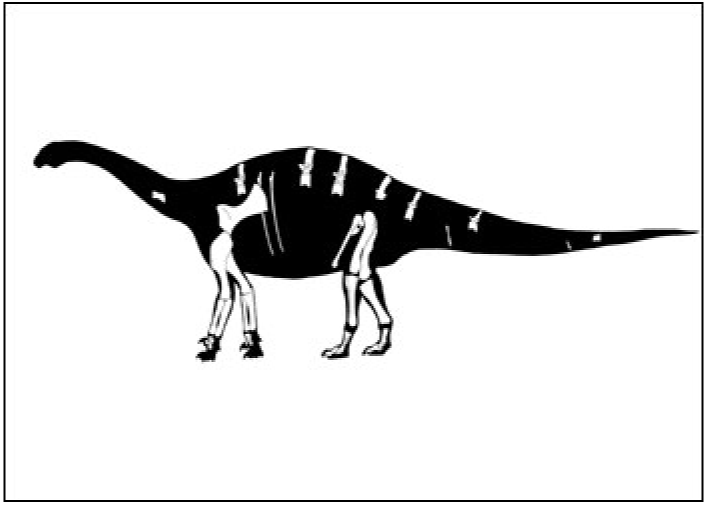
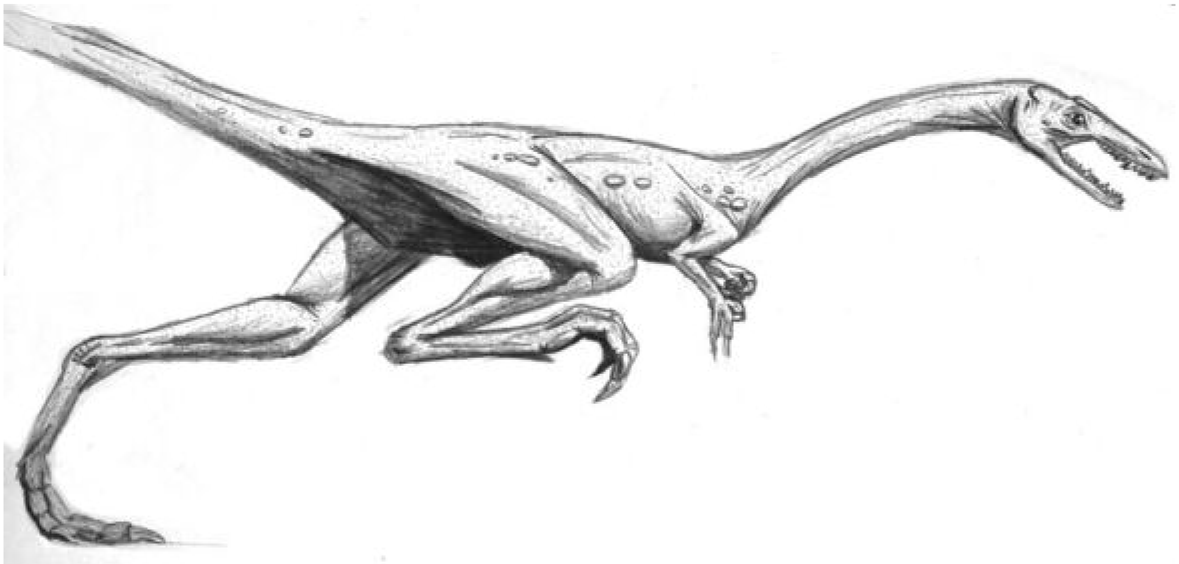


illustration © Adam Yates

Antetonitrus ingenipes, from the Lower Elliot Formation of South Africa, is the earliest known, and most primitive, true sauropod. This large (8 to 10 meters long), heavily built animal shows a mixture of primitive and advanced characteristics. Its fore and hind legs are of almost length and the foot is very short, indicating a slow, fully quadrupedal posture. Yet the fore-feet are also prosauropod-like, in that the thumbs retain a grasping ability. Possibly these large herbivores would rear up on their hind limbs, and use their forefeet and claws to pull down the branches of trees.

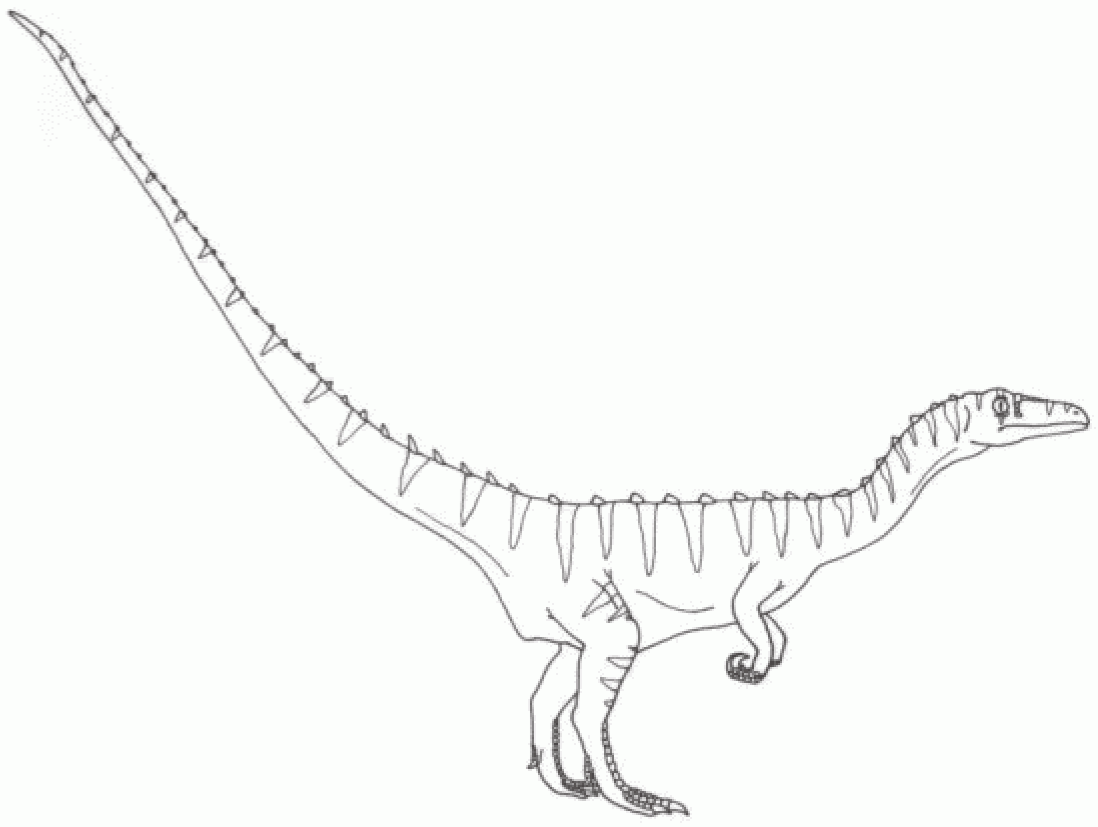
New dinosaur gives glimpse into the past



Procompsognathus triassicus image © Robert Gay

From the latest Carnian through to the later Early Jurassic (Toarcian), small podokesaurs played an important part throughout Pangea as small-medium sized terrestrial predators. Many of these belong to the

genera *Coelophysis*, so far known only from the SW USA. A number of types from the latest Carnian and Norian, previously included in the genus *Coelophysis*, have since been given different names but are closely related in structure, appearance, and obviously, habits and lifestyle. *Syntarsus* is a more advanced form with fused ankle-bones, has a much wider distribution - in the Norian it is known from both New Mexico and Wales (Pant-y-ffynnon fissure filling), and in the Hettangian from Lesotho and South Africa (Upper Elliot Formation). Many (although not necessarily all) of the small three-toed footprints that are called *Grallator* were probably made by these animals.



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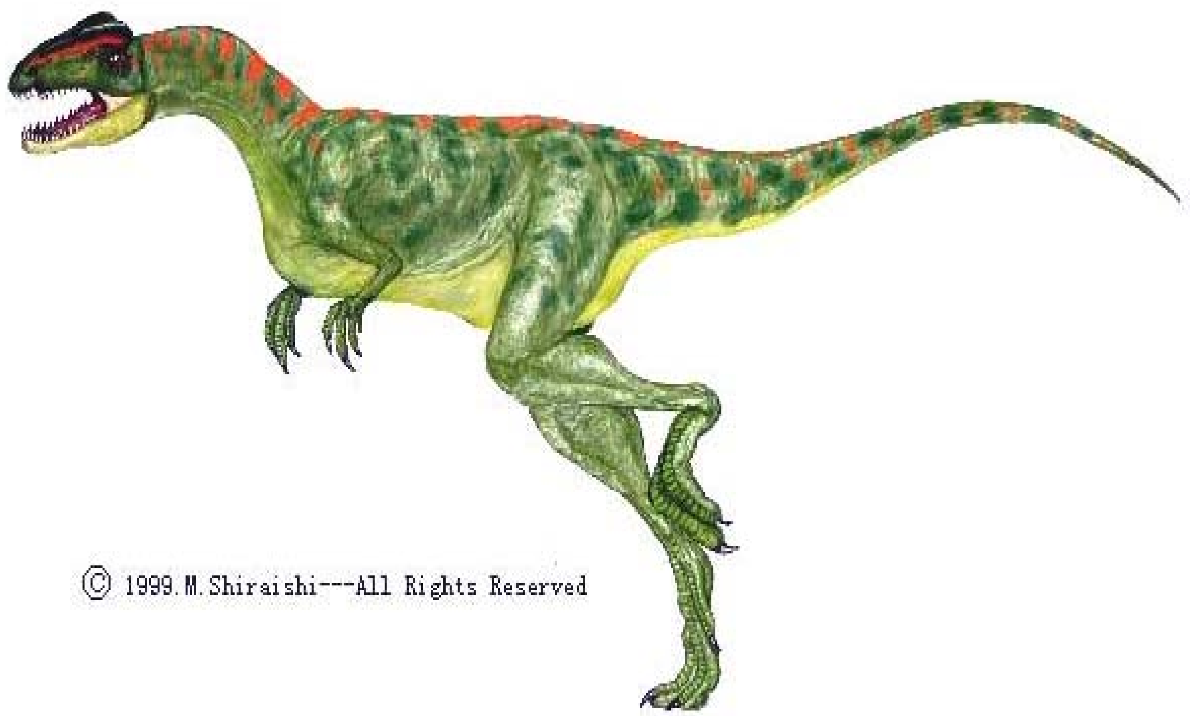


The Late Norian theropod *Liliensternus liliensterni*, artwork � M. Shiraishi

At 5 1/2 meters in length, *Gojirasaurus quayi* is the earliest known large theropod dinosaur. It is, appropriately, named after Godzilla (using the correct, Japanese pronunciation). Named after Godzilla (using the correct, Japanese pronunciation) this is the earliest known large theropod dinosaur. [Carpenter 1997]

Known from two (apparently, more on this shortly) sub-adult specimens, *Liliensternus liliensterni* is intermediate between the small (2.5 meters) and earlier latest Carnina/earliest Norian *Coelophysis* and the large 6 to 7 meters long) and later (Jurassic: Sinemurian) *Dilophosaurus* in anatomy. These were large graceful bipedal predators of the subfamily Dilophosaurinae (= Halticosaurinae). *Liliensternus* is probably a descendent from the earlier large podokesaurs like the upper Chinle *Gojirasaurus*; it represents a type that seems to have persisted with little change from the Middle Norian to the late Rhaetian, and which in turn - surviving the end-Triassic mass extinction, gave rise to the large dinosaurian carnivores of the Jurassic. They were also the first of the great dinosaurian carnivores.

***Liliensternus* has been found in association with *Plateosaurus* [Rauhut and Hungerbuhler 1998], and whilst healthy adult Plateosaurs were too big for the theropod to take on, the young, the old, or the sick or injured were another matter. Lilienstern ii probably stalked and followed plateosaur herds, waiting for an opportunity. In this they followed a different feeding strategy to the lie-in-wait rauisuchian predators like *Teratosaurus*.**

Although longer than most rauisuchian thecodonts, *Gojirasaurus* and *Liliensternus* were more lightly built; essentially scaled up versions of a small animal like *Coelophysis*. These large coelophysids also seem to have been rather less common than the thecodont (pseudosuchian) carnivores, which remain the main terrestrial terrestrial predators through till the end of the Triassic.

The traditional interpretation of animals like *Gojirasaurus* and *Liliensternus* is that they are sub-adults, as indicated by certain qualities in the skeleton, and that the full-grown theropod was some 7 meters or so in length (say the size of a large dilophosaurus). The problem here is that no large carnivore footprints (*Eubrontes*) occur until the earliest Jurassic [Olsen et al 2002]. So if there were half-tonne Norian theropods, where are their footprints? Instead, we see a sudden increase in theropod footprint size from small to *medium* during the Mid Norian (just at the time that *Gojirasaurus* appeared) and then another increase from medium to large at the earliest Hettangian (earliest Jurassic). I would suggest, as away of resolving this quandary (disclaimer - this is intended as rampant speculation only!), that maybe the 5 meter long so-called sub-adult *Gojirasaurus* and *Liliensternus* skeletons really were of *adult* animals, and that these creatures had neotonous features. Then, with the extinction of rauisuchians during the end Triassic, theropod dinosaurs quickly evolved to larger size and captured the ecological niche of top predator previously held by the "thecodonts"

Did climate change and increasing aridity kill off the once-abundant dicynodonts, as this image from the classic series *Walking with Dinosaurs* indicates?

Photo by Ian Macdonald from Walking With Dinosaurs - Placerias; © BBC/ABC from Walking with Dinosaurs

During the Norian the lived the last of the placerine Dicynodontia, members of the family Kanemyeriidae and the last known survivors of a long and successive lineage that stretched back to the Middle Permian. These large terrestrial herbivores weighed over a tonne each. It is possible that they were killed off by the increasing aridity which favoured the archosaurian metabolism, and may have even been forced to migrate long distances, as shown in the above still from the superb BBC series *Walking With Dinosaurs* . However Olsen *et al* 2001 argues that the apparent aridification of the Norian is just a sampling bias, and that these typically Carnian faunas continued into the Norian without suffering any decline. Certainly the traversodontid cynodonts continued right up until the end of the Triassic.

Jachaleria colorata; length of lower jaw 40 cm
illustration from Bonaparte 1970

Norian Dicynodonts are best known from South-west Gondwana (Argentina). A kannemeyeriid skull and complete jaws, identified as a new species by Bonaparte 1971 who named it *Jachaleria colorata*, is known from the Basal Los Colorados Formation, La Rioja Province Argentina (considered by Lucas 1998 to be Apachean = Rhaetian, but I would suggest more likely a Norian age). This was a large animal, the length of the lower jaw 40 cm [Bonaparte 1970 p.681] According to Bonaparte, *J. colorata* is the only tetrapod collected from the base of the Los Colorados Formation, which immediately overlies the (late Carnian) Ischigualasto. Lucas, 2001b states that *Jachaleria colorata* is a synonym of *Ischigualastia*. However, other recent papers (e.g. [Leal *et al* 2004] consider *Jachaleria* a separate genus.

Jachaleria colorata; drawing by M.Alan Kazlev

A similar form, *Jachaleria candelariensis*, is known from the early Norian [Scherer 1994, Leal *et al* 2004] (although Lucas 1998 suggests the date is Adamanian (latest Carnian)) Upper Caturrita Formation, Brazil. *J. candelariensis* is found together with the herbivorous cynodont *Exaeretodon* sp. In as much as *Jachaleria* (= *Ischigualastia*?) is reported from both the Upper Caturrita Formation (Early Norian?) and the basal Los Colorados (Late Norian?) it seems that these large animals continued quite happily in Southwest Gondwana at this time.

Other records of Norian kannemeyeriids include a dicynodont toe is known from the early or middle Norian Deep River Basin, Newark Supergroup, North Carolina Sues et al 2001, and footprints ({entasauropus") from the Late Norian Lower Elliot formation [Lucas and Hancox, 2000].

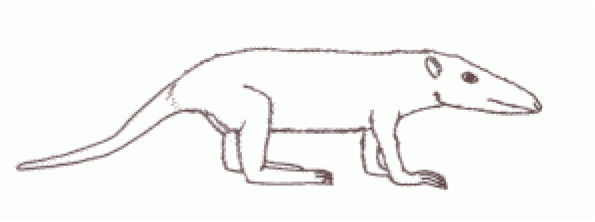
References/Links: **BBC - Walking with Dinosaurs - Fact Files - Placerias**

Traversodontid drawing © 2001 Vince R Ward - Prehistoric Pages

It was once thought that the herbivorous Traversodontid Cynodonts died out at the end of the Carnian. With the discovery of *Plinthogomphodon herpetairus* Sues et al 1999, this is now known not to be the case. The discovery of surprisingly common remains of this smallish (cat sized) animal in the Middle Norian Newark Supergroup, North Carolina (at the time equatorial Pangea) indicates that, unlike their dicynodont distant relatives, the Traversodontids were not affected by the Carnian-Norian turnover. *Plinthogomphodon* seems to be similar to the slightly earlier *Boreogomphodon* from the Latest Carnian of Virginia, and hence may well be a descendent or close relative of that animal.

A larger animal *Scalenodontoides macrodontes* is known from the Lower Elliot and Molteno Formations of Lesotho and South Africa (probably Late Norian). It shows that decent-sized traversodonts continued into the latest Norian at least, although these animals were no longer as abundant as in the past. [see also Trevor Dykes Triassic Gomphodonts] .

***Pseudotriconodon chatterjeei* Lucas and Oakes, 1988 was a member of the Dromatheriidae, related to the Latest Carnian *Dromatherium* and *Microconodon*. It lived several million years later, and somewhat to the east, being known from the Bull Canyon Formation, Chinle Group, East-Central New Mexico;**



Traversodontid drawing © 2001 Vince R Ward - Prehistoric Pages

Early or Middle Norian (Revueltian Age). These tiny shrew-like cynodonts, although poorly known, were probably an important part of the late Triassic terrestrial environment. In life they would have resembled small mammals, not reptiles. A related species, *Pseudotriconodon wildi* Hahn, Lepage & Wouters, 1984, is known from the fissure fillings of Saint-Nicolas-de-Port, France (Late Norian or early Rhaetian)

Links and References: Godefroit & Battail 1997; Lucas 1998 p.370; Trevor Dykes Chiniquodontoidea

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The Rhaetian Age - 1

The Rhaetian Age of the Late Triassic Epoch: 204 to 200 million years ago

Rhaetian - Overview

The Rhaetian is the last of three divisions in the Upper or Late Triassic. It was also the first Triassic Stage to be established (G�mbel 1859, cited in Kozur 2003). The Rhaetian Age succeeds the Norian Age and is followed by the Hettangian (earliest Jurassic). The name is derived from the Rhaetian Alps of Italy, Switzerland, and Austria, where rocks of this age are known. The stratotype (the defining section of rock formation) is the K�ssen beds at Kendelbachgraben, Sankt Wolfgang, Austria, where the bivalve *Rhaetavicula contorta* occurs. [Encyclop�dia Britannica]

On land, the Rhaetian saw the continuation of the rule of the dinosaurs among the megaherbivores that began in the late Norian. Other late Norian (Sevatian) floras and faunas seem to have continued with little change; so much so that the Sevatian Stage is sometimes taken to include the Rhaetian as well as the Late Norian [see e.g. Benton 1994]

The most significant thing in the history of life during the Rhaetian was the replacement of typically Triassic marine reptiles (nothosaurs and shastosaurs) with the classic dolphin-like ichthyosaurs and "Nessie"-style plesiosaurs . This change is so dramatic that with the exception of a single genus of placodont ("reptilian walrus"), all Rhaetian marine reptiles known are of the classic "Liassic" (early Jurassic) type.

The Rhaetian age and Triassic Period ended with a mass-extinction (possibly the result of an extraterrestrial impact) that killed off various taxa including some types of plankton, most reef-building organisms, the last of the pelagic conodonts and (assuming they hadn't died out earlier) the straight-shelled nautiloids, all the ceratites, the last of the placodonts, many types of bivalves, a number of amphibian and reptile types, and all non-dinosaurian and non-crocodylomorph archosaurs.

Stratigraphy and Index Fossils

The bivalve *Rhaetavicula contorta*, which was used to establish the Rhaetian (K�ssen Beds) is widespread in extra-Tethyan basins, such as the Germanic Basin, and, therefore, the Rhaetian was also widely used outside the Tethys. However the exact ammonoid definition was for a long time not resolved. This caused problems with the Norian-Rhaetian boundary within the Tethys and in other pelagic sequences, but the Rhaetian Stage was confirmed finally by the Triassic Subcommision in 1993. [Kozur 2003]

Stratigraphically, the base of the Rhaetian is defined as the "near lowest occurrence of ammonite Cochlocera, conodonts Misikella spp. and *Epigondolella mosheri*, and radiolarian *Proparvicingula moniliformis*." The end of the Rhaetian (and of the Triassic, and start of the Jurassic) is defined by the "lowest occurrence of smooth *Psiloceras planorbis* ammonite group." [Gradstein, Ogg, Smith, *A Geologic Time Scale 2004* - GeoWhen database - Rhaetian ICS Stage]

Rhaetian Index Fossils - Terrestrial

The Apachean LVF

Dating Rhaetian terrestrial faunas is difficult. Dr Spencer Lucas (ref) divides Triassic tetrapod evolutionary communities into eight land-vertebrate faunachrons (LVF). The last of these, the *Apachean* corresponds to at the Rhaetian, but may also include the later part of the Norian. It begins with the FAD of the phytosaur *Redondasaurus* and ends with the FAD of the crocodylomorph *Protosuchus*. The Redondo Member, which features the type Apachean fauna, is considered tentatively Rhaetian by Lucas 1998, but is referred to as middle to late Norian by both Benton 1994 and Hargrave 1999 This shows the difficulty of providing precise dating. Also, the endemic nature of the Redondo fauna makes it difficult to correlate with the fairly well-dated Stubensandstein and Rhaetian of Europe. For this reason it may not be impossible that the Apachean begins at around the later Middle Norian.

As well as by the Redonda Formation in east-central New Mexico, and the Ghost Ranch Whitaker quarry in the Rock Point Formation of the Chinle Group at Ghost Ranch, New Mexico (however this latter dated magnetostratigraphically as Late Carnian / Early Norian age by Hargrave 1999), the Apachean also includes the upper part of the Cliftonian assemblages, of the Newark Supergroup, the Coloradan Land Vertebrate Fauna of Argentina, and probably some of the fissure fill assemblages in the uppermost Mercia Mudstone Group and lowermost Penarth Group of England, Saint-Nicolas-de-Port and other vertebrate sites in France [Lucas 1998].

Late Norian and Rhaetian Marine Biotas

Fish

Study of the French Lons-le-Saunier site indicates a change in the marine faunas during the Rhaetian transgression, preferentially affecting the neoselachian sharks, which increase in abundance, and the durophagous bony fishes, which become dominated by the species *Sargodon tomicus*. [Cuny *et al* 2000]

Late Norian and Rhaetian Terrestrial Biotas -

Tetrapods

The Prosauropod-Sauropod Empire

As mentioned on the Norian page, the Norian terrestrial fauna represented two distinct and well-defined groups. The Early to Middle Norian shows similarities with the Carnian biota, as well as unique characteristics of their own, but are stratigraphically easily separated from both earlier and later communities. In contrast both large and small (i.e. European "fissure fillings") Late Norian tetrapods are difficult to separate from those of the Rhaetian, and terrestrial stratigraphy is often ambiguous (especially of Gondwana and Asia, where there are no common species with those of the well dated European series). These are usually just noted as "Upper/late Norian - Rhaetian". Dating of fissure fillings is even more difficult.

The main problem here is that unlike the late Carnian through to Middle Norian, the Late Norian and Rhaetian was a period of great provinciality, as far as tetrapods go, and it is rare to find even a single cosmopolitan genus. However, with the exception of North-West Pangean ecological communities, which - assuming the Redonda and Ghost Ranch fauna are of this period - still have a primitive "thecodont" (phytosaur-aetosaur) dominated aspect, all other major terrestrial ecosystems are sauropodomorph dominated. The Late Norian *Plateosaurus-Proganochelys* Community Type of the Oberer Stubensandstein and Knollenmergel is characterized by the large and abundant herbivore *Plateosaurus*, a dinosaur that persists into the Rhaetian, as do the plagiosaurs and phytosaurs that co-exist with it. The *Plateosaurus* community is ecologically very similar both to the Late Norian South African Lower Elliot Formation (protosauropods *Melanorosaurus* and *Euskelosaurus*, and early sauropod *Antetonitrus*), and the Rhaetian Argentinean Los Colorados (diverse large sauropodomorphs). Basal sauropods are also found in the Rhaetian of England (The 9 meter long *Camelotia borealis*) and the Rhaetian Nam Phong Formation, Thailand (the 6 meter long *Isanosaurus*). Even the isolated "fissure fillings" were characterized by sauropodomorphs - the small *Thecodontosaurus* is a very common element.

The Coelophysid Takeover

Ironically, while the evidence of skeletons indicates a continuing dominance by Sauropodomorphs, and the Los Colorados local fauna provides as diverse an assemblage as anything the Norian produced, the footprints of this period tell a different story. If this is anything to go by than the facts are clear - whereas the Norian witnessed the dramatic rise of the Sauropodomorpha, the Rhaetian saw the theropods emerge to dominance; although not yet very large theropods. Rhaetian footprint assemblages are predominantly theropod, and these replace the more diverse Norian assemblages. At this time "all faunas from footprint-bearing horizons are both less abundant and less diverse, and mainly consist of tridactyl bipeds (grallatorids)...*Apatopus*, the presumed phytosaur trackway, persists from the earlier (Carnian-Norian) section." [Haubold 1986 p.194] . This faunal displacement is especially apparent "in the Chinle Formation and the overlying Glen Canyon Group, in which three toed *Grallator* type tracks, attributed to early dinosaurs, become increasingly abundant, and increasingly large, as a function of stratigraphic height." [John Stear - Triassic Strata of the Colorado Plateau]. And according Lockley and Hunt (cited on that webpage)

> "Toward the end of the Triassic, in youngest Chinle Group sediments, small-sized *Grallator* tracks appear in association with a diverse assemblage of other archosaur tracks. Then in some of the very youngest Chinle layers (for example, the Sheep Pen Sandstone) these *Grallator* tracks become the dominant track type to the virtual exclusion of all other footprint types. We get the impression that the small dinosaurs were taking over. This impression if confirmed by the track record in the overlying strata of the Wingate Formation, where we find more medium-sized *Grallator* tracks, and very few other track types"

(Lockley and Hunt 1996 p. 103).

Rhaetian Terrestrial Communities

Rhaetian terrestrial faunas are with a few exceptions a lot more poorly known than those of the Norian - the following therefore is even more speculative a list than the Norian one.

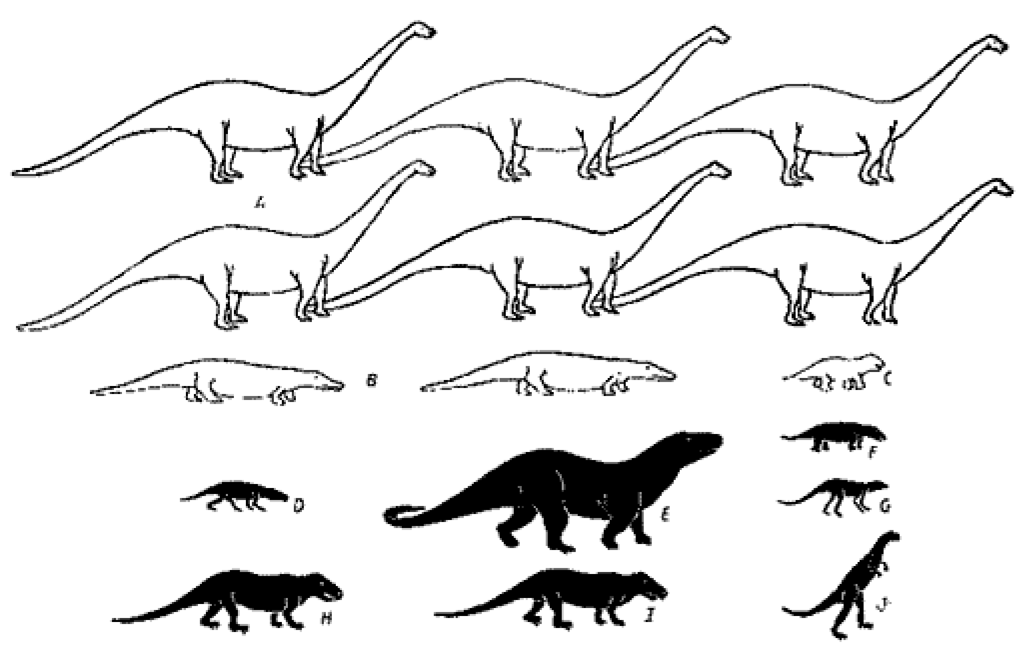

illustration from Bonaparte 1982

A representative Sauropodomorph fauna - Late? Rhaetian of South-West Gondwana (La Esuina Formation, Argentina) - showing approximate abundance. Herbivores in outline, carnivores in black
Key: A, Prosauropoda; B, Stagonolepidae; C. Tritylodontidae; D. Protosuchidae; E. Rauisuchids; F. Trithelodontidae; G. Sphenosuchidae; H. + I : Ornithosuchidae; J. Theropoda indeterminate (= ?)
from J.F. Bonaparte, 1982 "Faunal Replacement in the Triassic of South America"

Sauropodomorph (*Riojosaurus*)-Aetosaur Community. By far the best known Rhaetian assemblage is the Los Colorados Local Fauna found in the La Esuina Formation, Argentina. here we see a rich and diverse Sauropodomorph-dominated fauna featuring dinosaurs, other archosaurs, amphibians, turtles, and cynodonts, very much like the Middle and Late Norian assemblages of Europe, Greenland, Thailand, India (all The Prosauropod-Proganochelyid-Aetosaur Community - central-north to mid southern Pangea), and Southern Africa (here referred to as the Melanorosaur-Sauropod (*Euskelosaurus*) Community - South Pangea). The dinosaurian fauna combines both the prosauropod elements common in the north with the more advanced basal true sauropods of the south. However, the most common animal (*Riojosaurus*), is a Prosauropod like the northern *Plateosaurus*. The lack of any common faunal elements with the geographically very close Southern African Lower Elliot fauna indicates either a lot of geographic isolation (unusual when considering large and widespread animals) or rapid evolution, migration, and/or replacement over a short period of time.

Of especial interest in the Los Colorados Local Fauna is the presence of protosuchid crocodylomorphs and trithelodontid cynodonts. These are the only records of these animals in the Triassic; everywhere else they suddenly appear only in the Hettangian (earliest Jurassic). It has been suggested that this indicates that this fauna extends stratigraphically over some range - from Norian or Rhaetian to Hettangian. But this is made less likely by the fact that the typically Late Triassic *Riojasuchus* (an ornithosuchid) is found in association with *Hemiprotosuchus* (a protosuchid) [Bonaparte 1970]. So either ornithosuchids really did continue through to the earliest Jurassic, or this really is a transitional fauna. For the sake of dogmatic arrangement (never a good habit) we will here go with the latter hypothesis.

The upland **Thecodontosaur Community**, revealed in the fissure assemblages of Cromhall, south-west England, remains diverse and little changed from the Norian; if indeed the fissure fillings from Pant-y-ffynon were (Middle or Late?) Norian. We find here again numerous Thecodontosaur small sauropodomorphs, diverse lizard-like sphenodonts, a species of *Terrestrisuchus* distinct in some respects from the type species (*Terrestrisuchus gracilis*) from Pant-y-ffynon, advanced cynodonts, early mammals, and a small herrerasaur *Agnosphitys cromhallensis* [Fraser et al 2002]

Similar assemblages are known from nearby regions of central Pangea. A recently discovered locality in Luxembourg, palynologically dated to Rhaetian age, shows a diverse range of animals, including Phytosaurs, Pterosaurs, possible Ornithischia, Cynodontia and Haramiyidae, Morganucodontidae and Kuehneotheriidae mammals. [Godefroit *et al* 1998]. And shark teeth (Synechodus rhaeticus, "Hybodus" minor, which is shown to be a Synechodontiforme, not a hybodont) and an ornithischian dinosaur tooth have been found at a new palynologically dated Rhaetian locality at Lons-le-Saunier (Jura, France). [Cuny *et al* 2000]

Aetosaur Community Further west again [Redonda Fm,

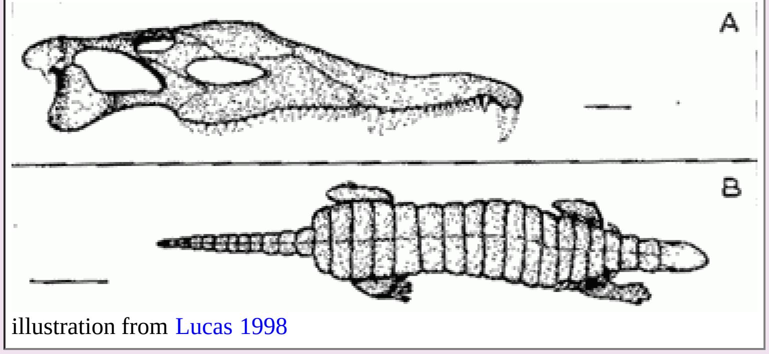

illustration from Lucas 1998

Tetrapods from the Redonda Fm: (A) *Redondasaurus*, (B) *Redondasuchus* scale bars: (A) 10 cm, (B) 20 cm

New Mexico], and one finds large advanced phytosaurs (*Redondasaurus* - two species (*R. bermanii* and *R. gregorii*) and medium-sized aetosaurs a little like the latest Carnian *Desmatosuchus*, but only half the linear dimensions (*Redondasuchus reseri*), as well as a large unnamed aetosaur (= *Paratypothorax*?), the metoposaur *Apachesaurus gregorii*, a rauisuchian, a sphenosuchian, a procolophonid, a sphenodont, theropod dinosaurs, and a possible cynodont [Lucas 1998]. The aetosaurs are the only medium to large herbivores - a feature typical of early Norian faunas, and there are no sauropodomorphs. So either this is a conservative relict community, or it dates from an earlier period.

The End Triassic Turnover and Bolide Impact

That the extinction of the dinosaurs and many other forms of life at the end of the Mesozoic was brought about through an extraterrestrial impact (comet or asteroid) is a popular, persuasive, but not yet universally accepted hypothesis. However a worldwide iridium layer, associated with a "fern spike" (ferns being able to regenerate in burned regions more quickly than angiosperms and gymnosperms) certainly points to some sort of worldwide catastrophe, and it has been suggested that the Chicxulub crater off Mexico provides evidence of a "smoking gun". A more comprehensive explanation is that many life forms - especially those like dinosaurs that were at the top of the food chain and so highly vulnerable to environmental fluctuations - had been highly stressed for some time by Indian vulcanism (the "Deccan Traps") and the asteroid simply executed the *coup de grace*. The wiping out of the dinosaurs at the same time enabled the mammals - which had at that time been flourishing albeit still small - to emerge and take over the large terrestrial niches for the first time.

There was a similar extinction event at the end of the Triassic which killed of the large Crurotarsi ("thecodonts") and allowed dinosaurs to rule as the single large terrestrial animal clade throughout the Mesozoic. While the Manicouagan in northeastern Canada is usually cited as the impact crater in this instance, it is now considered a little too early in age, and the Triassic/Jurassic (and for that matter the Jurassic/Cretaceous) boundary appears to involve multiple impacts [see Asteroid/Comet Impact Craters and Mass Extinctions by Michael Paine]. Even so, Olsen *et al* 2002 have recently found evidence of a K-T-type simultaneous peak in iridium traces and fern spores:

"Fine-scale correlation (left) between the Iridium anomaly and fern spike from the Jacksonwald syncline section of the Newark basin. The average Iridium anomaly is based on four localities along strike within the Newark basin, each of which have an Ir anomaly in similar positions. The duration of the interval, as based on the linear extrapolation of accumulation rates, is derived from an astronomical calibration of the entire composite Jacsonwald syncline section. [see supplemental data] Percent spore data are averaged from three sections (S. J. Fowell *et al.*, *Geol. Soc. Am. Spec. Pap.* 288, 197 (1994).). Details of vertebrate assemblages and data averaging methods are given in the supplemental data. cly, claystone; md, mudstone; ss, sandstone."

text and graphic © P. E. Olsen, D. V. Kent, H.-D. Sues, C. Koeberl, H. Huber, A. Montanari, E. C. Rainforth, S. J. Fowell, M. J. Szajna, B. W. Hartline, 2002 [ref Olsen *et al* 2002 [Fig.2]

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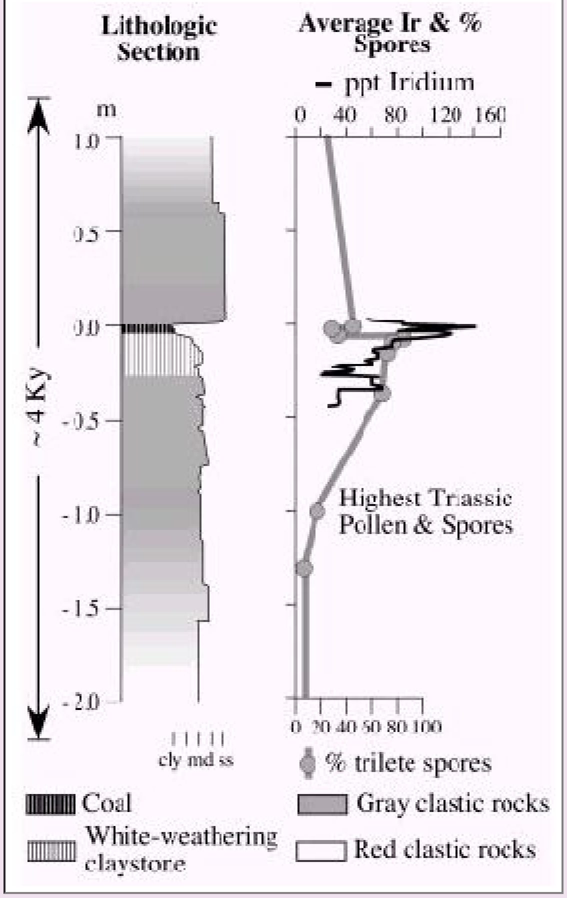
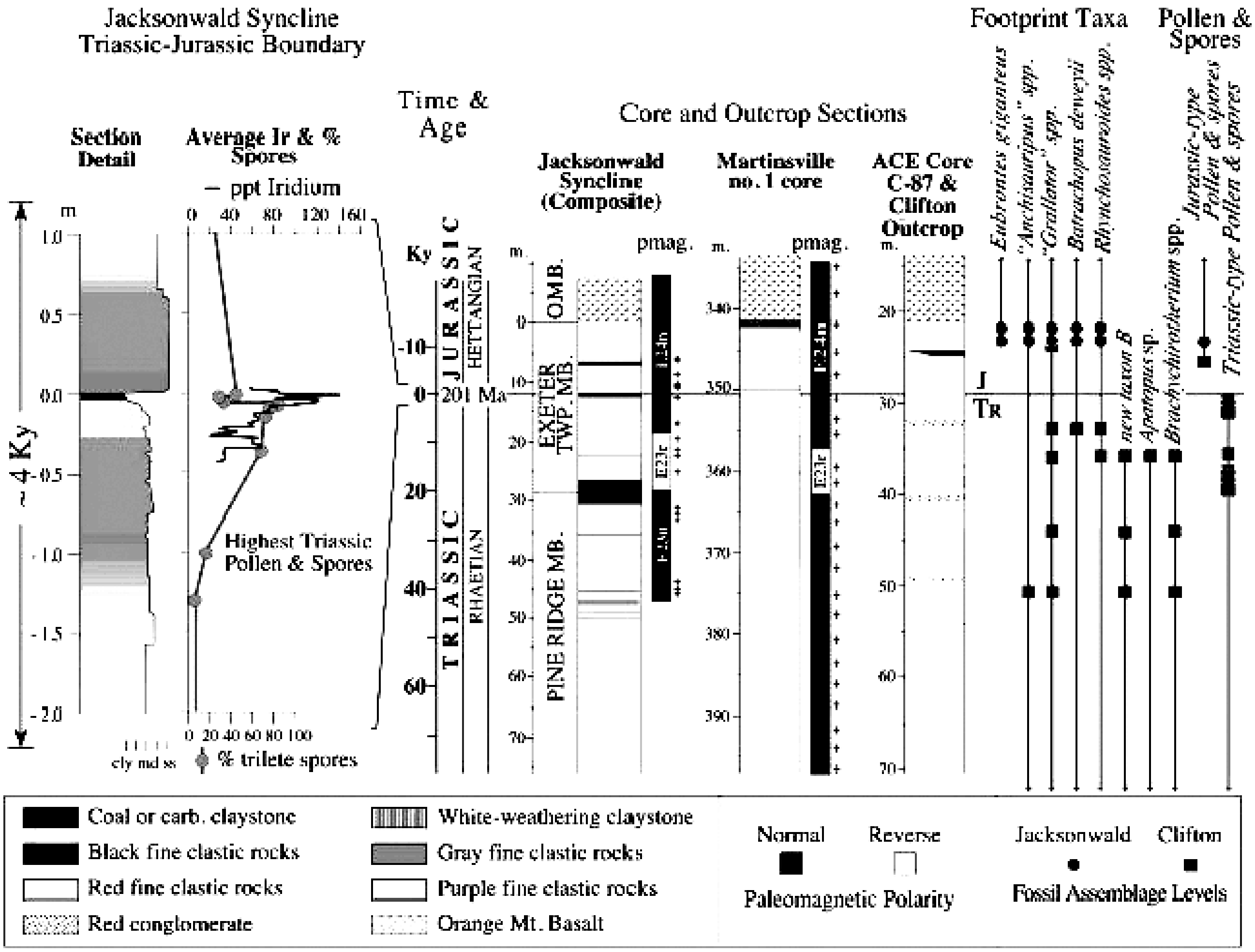


Below this iridium layer are late Triassic (Rhaetian) pollen and spores, immediately above there is the transition to typically Jurassic flora. Equally interesting is a similar transition among tetrapods, as indicated by a sudden transition in types of footprints (and hence types of animals (track makers) who left them). In the following diagram, (reading from left to right under "Footprint Taxa" *Eubrontes giganteus* is made by a large theropod dinosaur, "*Anchisauripus*" a small- to medium-sized theropod, "*Grallator*" a small theropod like *Coelophysis* or *Syntarsis*, *Batrachopus deweyii* a crocodylomorph (sphenosucian?), *Rhynchosauroides* spp. lepidosauromorphs , new taxon B a crurotarsan, possibly crocodylomorph, *Apatopus* sp. by phytosaurs, and *Brachychirotherium* spp. by rauisuchians. It can be seen that the typically Triassic archosaurs end just below the boundary, whilst large theropods (perhaps this is *Dilophosaurus*) appear very soon after. Just as mammals were only able to grow large once the dinosaurs had disappeared, theropod dinosaurs, although reaching a decent medium size as early as the middle Norian, were only able to grow really big once the other big predators - in this case the phytosaurs and rauisuchians, had disappeared.



"Detail of boundary section in the Jacksonwald Syncline Composite section as well as correlation to two other Newark basin boundary sections, paleomagnetic polarity data, and footprint and pollen and spore assemblage distribution. "New taxon B" is the term applied to an unnamed form by S. M. Silvestri, M. J. Szajna, *New Mexico Mus. Natural Hist. Sci. Bull.* 3, 439 .(1993), and cly, md, and ss, refer to claystone, mudstone, and sandstone, respectively...Interval of time represented by Jacksonwald syncline detailed section based on linear extrapolation from the average accumulation rate implied by the astronomical calibration of the Jacksonwald syncline composite section. Correlation throughout the Newark basin is based on the distinctive magnetic polarity and cycle stratigraphy and the basalts."

text and graphic © P. E. Olsen, D. V. Kent, H.-D. Sues, C. Koeberl, H. Huber, A. Montanari, E. C. Rainforth, S. J. Fowell, M. J. Szajna, B. W. Hartline, 2002
[ref Olsen *et al* 2002 [Supplementary Material, Fig.4]

.

Unlike the situation on land (and in keeping perhaps with the idea of several closely spaced impacts), marine fossil evidence indicates the extinction was not a single simple event. Barras 2002, studying the marine trace fossil record in England and Austria, finds that the extinction event in Austria seems to begin at an earlier stage than in England, and the fauna takes a lot longer to recover. England shows heavy bioturbation (hence, activity of many invertebrates that burrow in the mud etc) immediately prior to the Late Rhaetian extinction horizon, with *Diplocraterion*, *Arenicolites*, and *Rhizocorallium* recorded. There is then a short interval of unbioturbated sediments above the extinction horizon, indicating that for a period the seas were impoverished of life. Then strongly bioturbated sediments reappear before the boundary between the Rhaetian and the *planorbis* zone of the lower Hettangian (earliest Jurassic). However, *Rhizocorallium* does not re-appear until the upper planorbis zone (Middle Hettangian), while *Diplocraterion* and *Arenicolites* do not re-appear until the following, upper angulata zone (latest Hettangian). *Diplocraterion*, on its re-appearance, is significantly smaller than its pre-event counterparts. [Barras 2002] This "Lilliputian effect" also characterizes organisms in the aftermath of the great Permian extinction [Price-Lloyd and Twitchett, 2002]

The Rhaetian sediments of Austria show a somewhat different pattern. They are thoroughly bioturbated some 60 metres below the Rhaetian/Hettangian boundary, with *Rhizocorallium*, *Diplocraterion*, and *Zoophycos* recorded. Immediately below the boundary itself, however, these ichnotaxa are absent. Above the boundary, laminated or layered - which means deposited with little or no stirring up of mud and sediment - sediments are common throughout the Hettangian, and here the Rhaetian trace-fossils are not recorded in until the middle Sinemurian. [Barras 2002]

A Rhaetian Bestiary

Gerrothorax | *Hypsognathus* | *Palaeochersis* | *Leptonectes* | *Thallasodraco* | *Psephoderma* | Clevosaurus | *Pachystropheus* | Riojasuchus | Neoaetosauroides | *Fasalosuchus* | *Terrestrisuchus* | *Riojasaurus* | *Isanosaurus* | *Zupaysaurus* | *Microscalenodon* | *Meurthodon* | Tricuspes | *Hallautherium* and *Helvetiodon*| *Thomasia*

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The common large Norian temnospondyl *Cyclotosaurus* disappears from central north Pangea in the Rhaetian, although the plagiosaurs continue; in fact they are more successful than ever, and are represented by the advanced genus *Gerrothorax*. A typical species of this time is *Gerrothorax rhaeticus* from the Rhaetic of Scania, Sweden. These large (meter long) and successful short-headed amphibians led a totally aquatic existence; in fact the presence of gills means they were unable to go ashore at all. Apart from being completely aquatic, there really wasn't much difference in appearance or habits between Plagiosaurs and the brachiopods and chigutosaurids of southern Pangea, and they were probably the direct ecological equivalent. *Gerrothorax* fed on fish, invertebrates, and smaller amphibians and reptiles, while themselves falling prey to the phytosaurs with which they shared their environment. Indeed, considering that they seem to have had no natural defenses against phytosaurs, *Gerrothorax* and other large temnospondyls did remarkably well throughout the entire period of the Late Triassic.

At the end of the Rhaetian, plagiosaurs disappear completely, whereas the brachyopids and chigutosaurids continue with little change. Perhaps conditions following the bolide impact were more severe in the northern hemisphere

illustration by Steve Kirk, © from *Encyclopaedia of Dinosaurs and Prehistoric Animals*, Barry Cox, R.J.G. Savage, Brian Gardiner, Dougal Dixon,

***Hypsognathus* was a common, successful, stocky little animal that was widespread in central west Pangea. It was the last and perhaps the most specialized of the procolophonids, with bony spines behind the skull, perhaps for protection against predators. Although the illustration shown above presents it as smooth skinned, it is just as likely to have been spiny, like the extant thorny dragon. This was probably the only defense these**

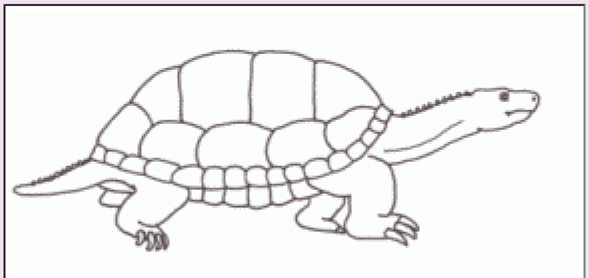
Clade: **Parareptilia**
Family: **Procolophonidae**

Hypsognathus

Horizon & Locality: Passaic Formation of New jersey, and correlative strata in Connecticut and Nova Scotia.

inoffensive animals had. Nevertheless they were remarkably successful, filling in the small herbivore niche, as they had since the earliest Triassic. Hypsognathus died out completely with the end Rhaetian extinction event, and no procolophonids are known from the Jurassic. It is not clear why these little animals, which had been so successful and widespread for so long, should completely disappear. Perhaps the bolide impact and "nuclear winter" killed off the plants on which it depended. In any case, with the disappearance of the procolophonids, the small lizard herbivore niche remained vacant for much of the Jurassic

Age: Late Norian to Latest Rhaetian
Length:
Community: Hypsognathus
Ecological Niche: Terrestrial (desert/semi-desert) herbivore
Reference:



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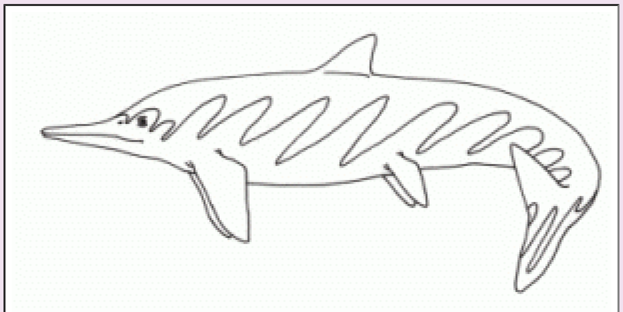
***Palaeochersis talampayensis*is an early turtle known from the Rhaetian Los Colorados fauna of Argentina. In the scheme of turtle evolution, *Palaeochersis* is the sister group to the pleurodires and cryptodires - more advanced than *Proganochelys* (although with a similar long tail) but, interestingly, more primitive than *Proterochersis*, despite the latter's earlier date. This shows how incomplete the fossil record of early turtles still is, with a number of "ghost lineages" still to be filled in.**

Like the Norian Proganochelyidae, *Palaeochersis* was a strictly terrestrial form, as indicated by the short forelimbs. (*Proganochelys quenstedti* and *Palaeochersis talampayensis* are the only early Chelonida with forelimbs preserved) [Joyce and Gauthier 2004]. And as with *Proganochelys*, shared its environment quite happily with large sauropodomorphs and medium-sized aetosaurs; these three plant eaters each grazing at different levels, and hence not competing with each other.



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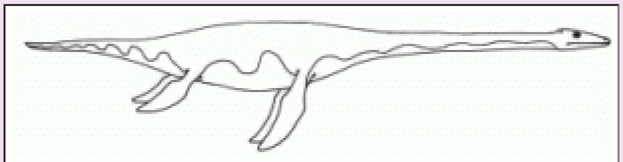
During the Rhaetian Ichthyosaur evolution proceeded rapidly. The Parvipelvia suddenly radiated into a number of lineages (although only a few are known from fossils; the rest are "ghost lineages") following the sudden extinction of the mighty shastosaurs. *Leptonectes tenuirostris*, previously known as *Leptopterygius*, from the Rhaetic and Lower Lias of England and France, is typical of this evolutionary radiation. This intermediate grade ichthyosaur was a large marine predator appeared in the Late Rhaetian but would continue right through to the Sinemurian (Jurassic). It is the earliest known member of the paraphyletic family Leptopterygidae



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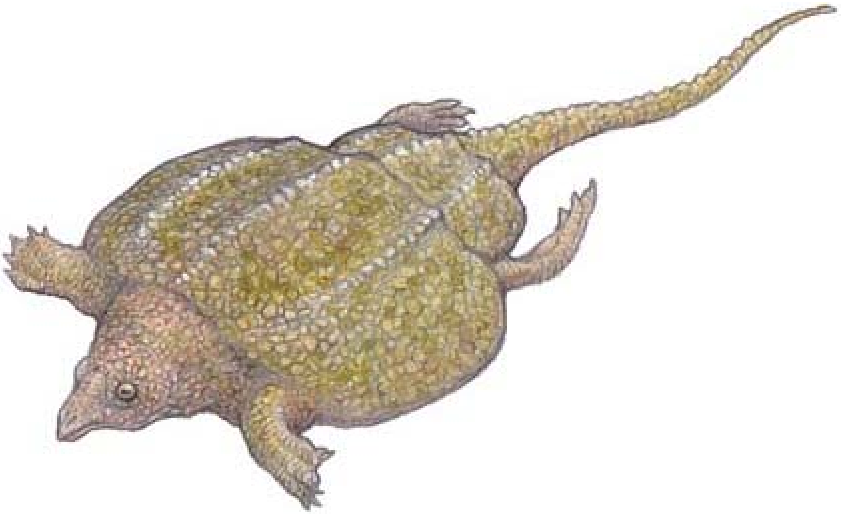
As well as advanced ichthyosaurs, the Rhaetian saw the radiation of an important new wave of Sauropterygia - the Plesiosauria. *Thalassiodracon hawkinsi* is one of the most primitive and earliest known plesiosaurs. This was a small animal, in life only about 2 to 3 meters long, known from the Rhaetic and Lower Lias of Somerset, England. It lived alongside other early representatives of the group, like *Eretmosarus*, which was about 3 meters long. Despite their long necks, both these animals are included in the "Pliosauria" on the basis of other features of the skull and skeleton. These animals survived into the earliest Jurassic, as part of a classic Rhaeto-Liassic marine biota. There is of course no guarantee that the poorly known stratigraphically earlier specimens belong to the same species as the later, Hettangian and Sinemurian forms



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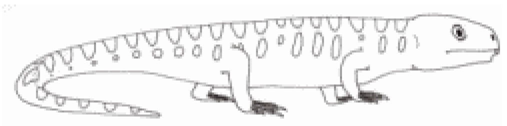
***Psephoderma*, which is known from the late Middle Norian through to the late Rhaetian of the Tethys ranging through to Central Laurasia (England, presumably via shallow sea), is the last of the placodonts. If its cousin *Placodus* was a walrus analogue, and *Henodus* a turtle analogue, this unusual but quite successful animal was the reptilian equivalent of the modern ray. The body is very broad and flattened. The discoidal carapace armour is in two parts, making the animal more mobile, there is a long thin tail, which does not seem to have been used in swimming. As with many other placodonts, the teeth are adapted to crushing shellfish. The main shell or carapace is made up of a large number of interlocking hexagonal osteoderms, while a smaller shell or caudal plate covers the pelvis and base of the tail. At least two species are known: the Tethyan *P. alpinum* and *P. anglicum* from the Rhaetian of England. [Naish 2000]**

Links:

Psephoderma

Rhaetian Placodonts

Psephoderma alpinum	***Psephoderma anglicum***
Horizon & Locality: Rhaetian of the Southern Alps Age: Rhaetian Length: 1.25 meters	Horizon & Locality: Rhaetian of England Age: Late Rhaetian Length:



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***Clevosaurus hudsoni* was a small insectivorous sphenodontan, the remains of which are known from British fissure fills. It served as the lizard analogue of the latest Triassic; true lizards would not appear until the Middle Jurassic. This animal was more advanced than its Norian predecessors such as *Clevosaurus minor*, and is similar to forms found in the early Jurassic (Lower Lufeng series) of China [Fraser, 2004]. It seems to be a common Rhaetian form, and its stratigraphic range appears to be restricted to that age, which would make it a useful index fossil. However more work needs to be done before the microvertebrates of the Anglo-Welsh fissure deposits can be reliably dated.**

***Clevosaurus* lived alongside *Diphydontosaurus*, a rather more primitive sphenodontian of the family "Gephyrosauridae". Without doubt, the Norian and Rhaetian fauna was very diverse, with a number of kinds of small lizard-like reptiles scurrying over rocks and hiding nooks and crannies in the late Triassic landscape.**

Continued on Next Page

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The Rhaetian Age - 2

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    Early Triassic Epoch
    Middle Triassic Epoch
    Late Triassic Epoch
      Carnian Age
      Norian Age
      Rhaetian Age
  Jurassic Period
    Early Jurassic Epoch
      Hettangian Age
      Sinemurian Age
      Pliensbachian Age
      Toarcian Age
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    Late Jurassic Epoch
  Cretaceous Period

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A Rhaetian Bestiary

Pachystropheus rhaeticus from the Late Rhaetian Penarth Group of South-West England, is the earliest known example of the Choristodera. It represents one of a number of lizard-analogues that populated the Late Triassic (others include sphenodonts, Prolacertiformes, and drepanosaurs, and kuehnosaurs). Much later In the Late Cretaceous and Early Tertiary, choristoderes will experience a brief resurgence as semi-aquatic crocodile-like reptiles.

Pachystropheus's identification as a choristodere 45 million years earlier than the next oldest representation of the group supports the validity of cladistics as a tool for suggesting the diversity of extinct organisms in terms of Ghost lineages. [Storrs and Gower 1993]

Angistorhinopsis ruetimeyeri (also known as *Rutiodon ruetimeyeri*, although true *Rutiodon* is limited to the latest Carnian [Lucas 1998] is a large long-snouted form known from the latest Norian and Rhaetian and Europe, where it replaces the earlier genera the earlier *Mystriosuchus* and *Nicrosaurus* in the same way that in south-west North America *Redondasaurus* replaces *Pseudopalatus*. It is not known however if *Anghistorhinopsis* and *Redondasaurus* are related. *Anghistorhinopsis* was originally named by von Huene for its supposed resemblance to the Latest Carnian genus *Angistorhinus* Later (in 1936) he erected the family Angistorhinidae to include

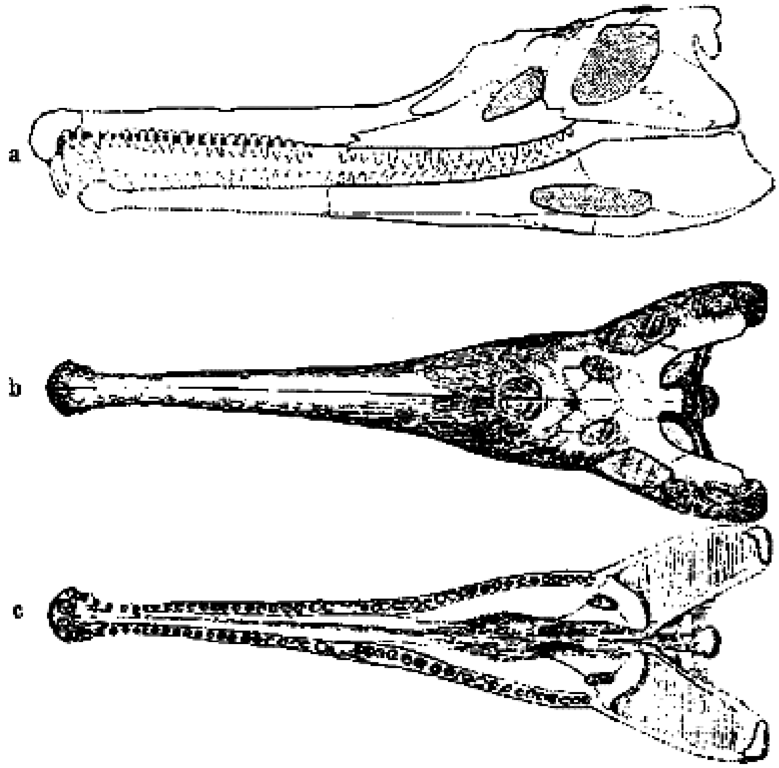
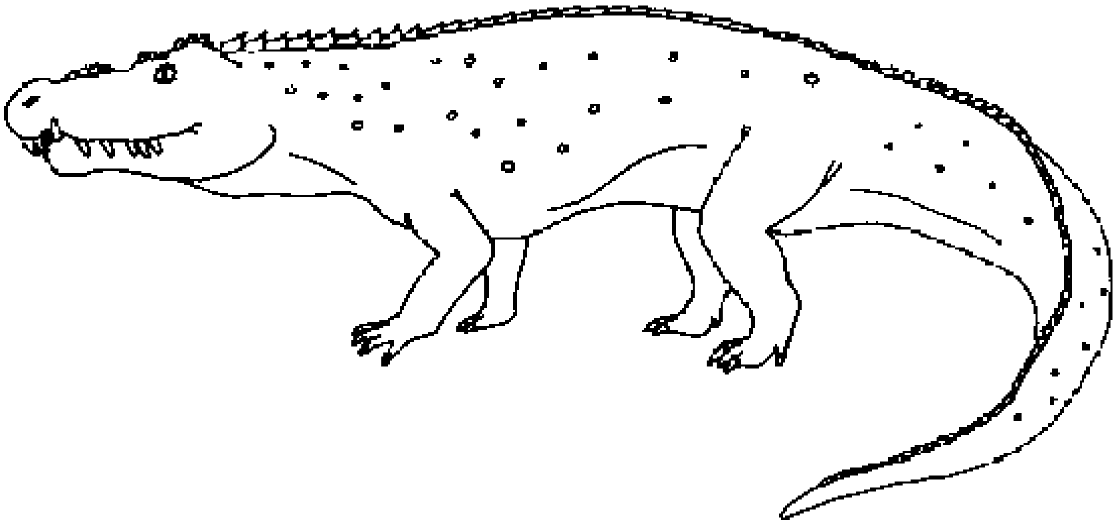


illustration from xxxx

Promystriosuchus, *Angistorhinus* and *Angistorhinopsis*. *Promystriosuchus* [Creisler 1996]., but this would seem to be an artificial grouping, although the name Angistorhinidae is still sometimes used. In nay case, the presence of *Angistorhinopsis ruetimeyeri* in the German Rhaetian (and similar teeth in the French early Rhaetian deposits of Saint-Nicolas-de-Point [Sigogneau-Russell and Hahn 1994]) shows that these large animals continued to flourish throughout the latest Triassic.



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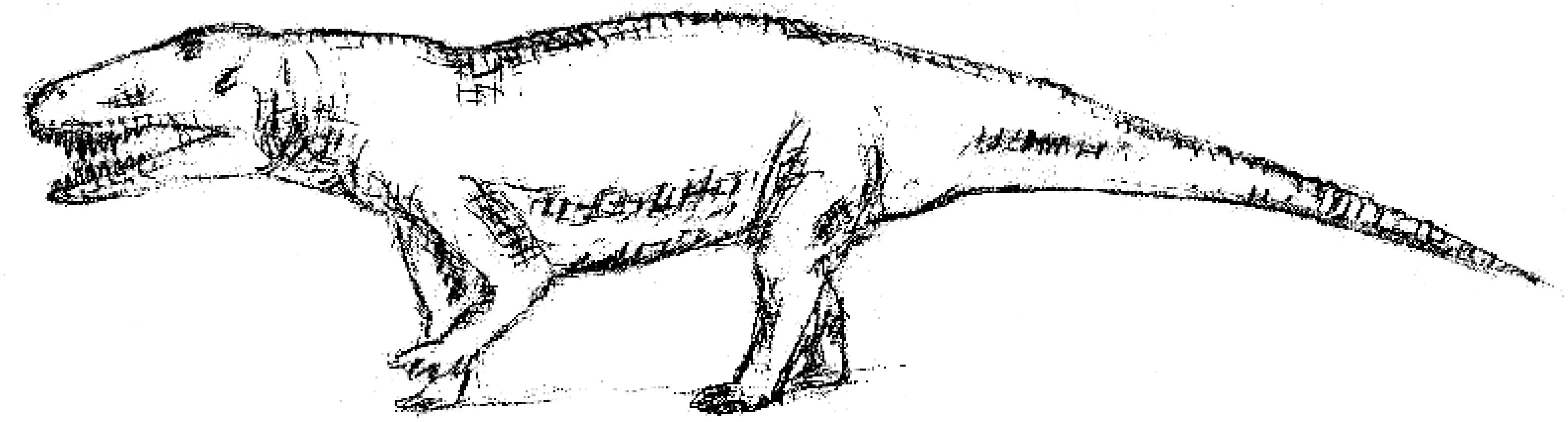
Riojasuchus **was a medium-sized terrestrial carnivore, about 2 meters in length. This animal was a cousin of the Late Carnian *Ornithosuchus*, although a bit smaller in size. These were active, fast-moving animals, with fully erect and upright posture, just like dinosaurs, mammals, and Prestosuchia/Rausichia.**

Riojasuchus **has been found associated with *Hemiprotosuchus*, *Pseudohesperosuchus*, and c.f. *Tritylodon* [Bonaparte 1970]**



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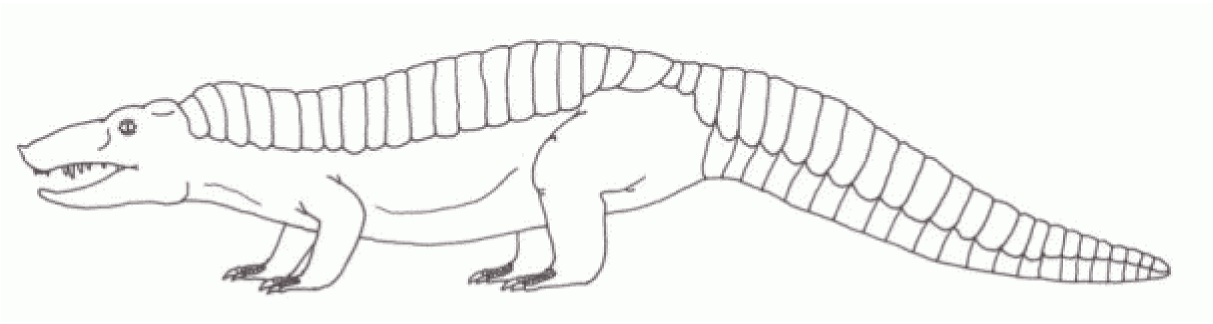
Fasolasuchus tenax was one of the last of the Rauisuchians, and also the largest. This animal had a skull alone that was 1.3 meters in length, which, assuming similar proportions with Saurosuchus, means an overall length of 8 or 10 meters, the size of a large theropod dinosaur. In fact, apart from the large theropods, *Fasolasuchus* was perhaps the largest fully terrestrial predators ever (both large phytosaurs and "super crocs" were bigger, but they were also semi-aquatic). It is likely that this animal was specialized for feeding on large sauropodomorphs, which raises the question of whether similar giant rauisuchians lived elsewhere.

In the (Late Norian) Lower Elliott formation of South Africa a jawbone (maxilla) and the ends of a femur have been attributed to a giant (allosaur-sized, about 1.5 tonnes) Herrerasaur (*Aliwalia rex*.) In view of the fact that no theropod of this size is known from Triassic rocks (whereas giant Rauisuchians are) it is more likely that this is a *Teratosaurus*-like chimera, with the maxilla belonging to a large rauisuchid. In view of the close geographic and temporal proximity, this may well imply that *Aliwalia* was a close relative (perhaps even belonging to the same genus) as *Fasolasuchus* [Bonaparte 1976, Bonaparte 1981, Bonaparte 1982]



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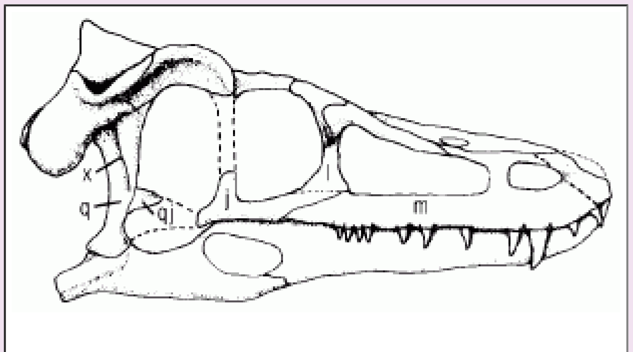
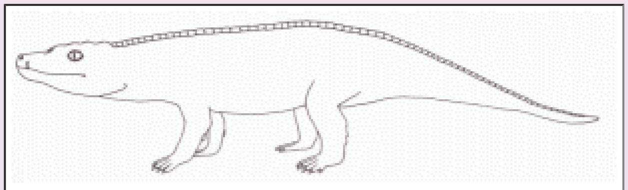
Although common and widespread from the Carnian to the middle Norian, the Aetosaurs seem to have declined thereafter. In Europe no aetosaur is known from later than the Middle Norian, and it seems that the group was limited to western Pangea. *Neoaetosauroides engaeus* Bonaparte 1967 is known from postcrania, jaws, and skull fragments the Upper beds of the Los Colorados Formation (Latest Norian and/or Rhaetic) , La Rioja Province, Argentina, where it is found associated with *Riojasaurus* [Bonaparte 1970]. It was a small and persistently primitive aetosaur, about 1.5 meters in length. Along with the large and advanced *Paratypothorax*, found to the north (Chinle Formation of North America), and the small *Redondosuchus*, these are the only aetosaurs known from the Late Norian/Rhaetian.



Pseudohesperosuchus jachaleri, from the Los Colorados formation of Argentina, was a Gondwanan representative of the graceful and lightly built sphenosuchians that were an important element in the late Triassic - early Jurassic terrestrial microvertebrate faunas. The lightly built skull is elongate and slender, as are the limb bones. *Pseudohesperosuchus* was probably similar in appearance to, and closely related to, the European *Saltoposuchus*/*Terrestrisuchus*. *Pseudohesperosuchus* has been found associated with *Riojasuchus*, *Hemiprotosuchus*, and c.f. *Tritylodon* [Bonaparte 1970] illustration from Clark *et al* 2000



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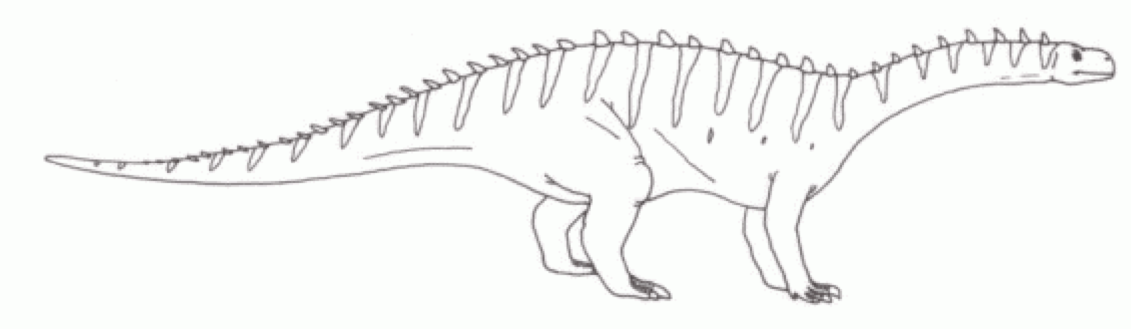
Hemiprotosuchus leali **is another reptile known from the rich fossil assemblages of the Los Colorados formation of Argentina. It is the earliest known representative of the Protosuchidae, a group otherwise known only from the Jurassic. The presence of such a typically early Jurassic form in the latest Triassic shows the transitional nature of the Los Colorados fauna.** ***Hemiprotosuchus*** **differed from its distant crocodylomorph cousin and contemporary** ***Pseudohesperosuchus*** **in its shorter, more massive, and typically protosuchian skull. If it is typical of its group, the limbs were shorter too, and the body stockier.** ***Hemiprotosuchus*** **differs from the early Jurassic** ***Protosuchus*** **in the presence of an opening before the eyes, a "primitive" archosaurian feature.** ***Hemiprotosuchus*** **has been found associated with** ***Riojasuchus*****,** ***Pseudohesperosuchus*****, and c.f.** ***Tritylodon*** **[Bonaparte 1970]. The presence here of** ***Riojasuchus*** **(family Ornithosuchidae) shows that these must be Triassic deposits, because the ornithosuchids, like other large "thecodonts" (Crurotarsal) are completely unknown after the Rhaetian**



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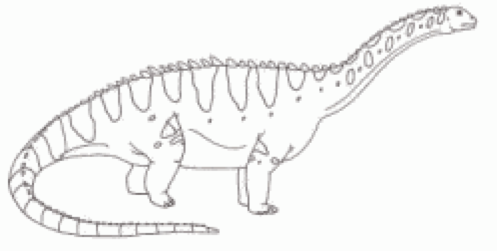
Riojasaurus incertus **was a large (length 6 to 10 meters) and common animal known from over twenty partial skeletons and a single skull, from the Los Colorados [sometimes considered late Norian but more likely (in view of advanced faunal elements) Rhaetian] of Argentina. It seems to have been the dominant herbivore of the Southwest Gondwana, the ecological equivalent of the Late Norian to Rhaetian** ***Plateosaurus*** **and the Late Norian (to Rhaetian?)** ***Euskelosaurus*****, which we can assume were contemporary. Although for some time considered a typical melanorosaurid` - perhaps on the basis of its large size and quadrupedal stance, it is now known to be a Prosauropod sensu stricta (plateosaur). It is clear that there were a large number of sauropodomorph lineages evolving parallel to each other during this period.**

This gentle giant must have lived in large herds, sharing its environment with other sauropodomorphs like the plateosaur ***Coloradisaurus brevis*** **and the early sauropod** ***Lessemsaurus sauropoides*****, along with smaller archosaurs like Neoaetosauroides. But even their large size could not protect them from the gigantic rauisuchian** ***Fasolasuchus*****, the only real predator of these large herbivores**



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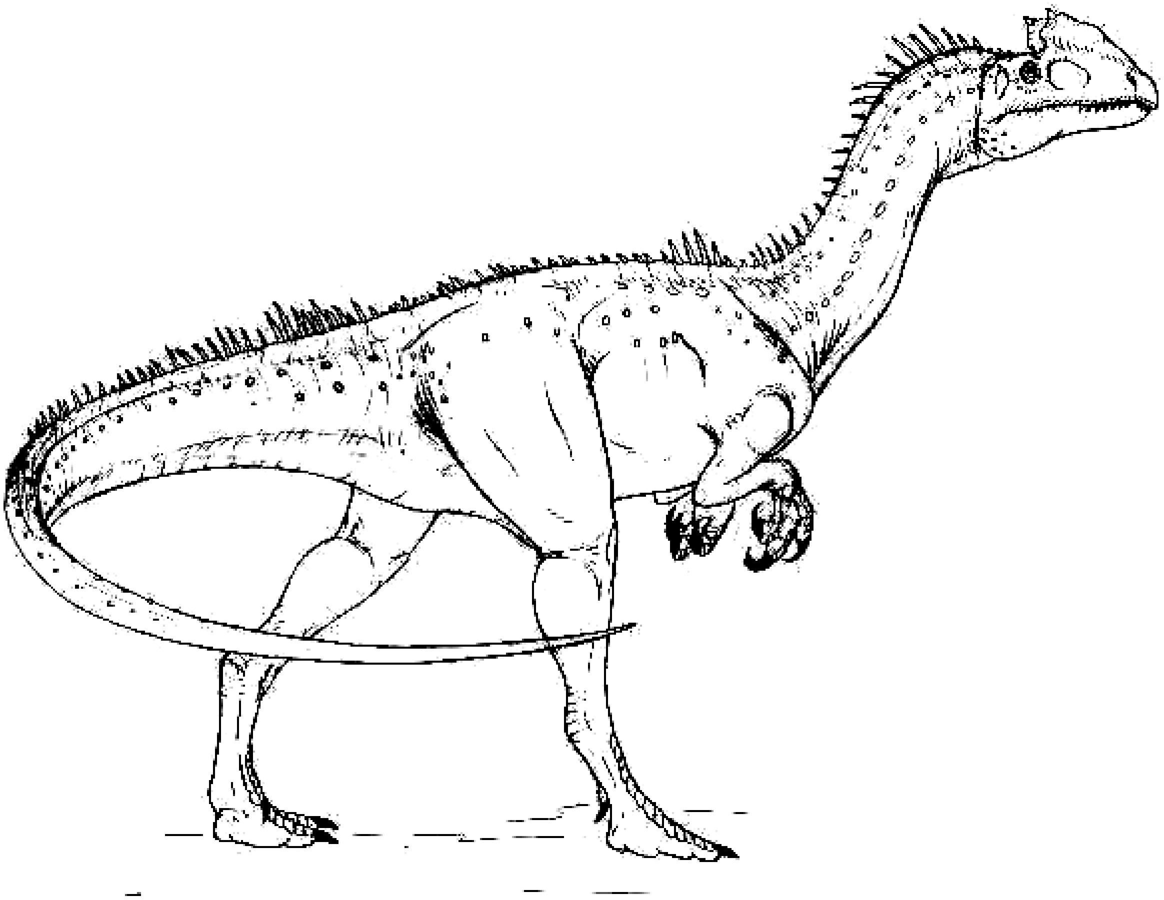
Isanosaurus attavipachi**, from the Rhaetian Nam Phong Formation of Thailand, is one of the earliest-known sauropods [Mortimer 2000]. Its partial postcranial remains provided the first osteological evidence of pre-Jurassic sauropods. Since the discovery of the even earlier Antetonitrus, it is no longer considered the earliest sauropod Holtz 2003.** ***Isanosaurus*** **differs markedly from prosauropods and confirmed the cladistic hypothesis of a fairly long period of sauropod evolution during the Triassic [Buffetaut et al 2000]. The animal is estimated to**

have been about 6.5 meters long when alive, and seems to have been a sub-adult

***Isanosaurus* was not the only early sauropod or proto-sauropod of its time. The 9 meter long *Camelotia borealis* from the Rhaetian of England is a rather poorly known (some assorted postcrania) Melanorosaurid, or possibly a basal sauropod. And *Lessemsaurus sauropoides*, based on a partial vertebral column from Los Colorados, Argentina, was originally considered a melanorosaurid but is now considered an early true sauropod close to Antetonitrus.**

Isanosaurus by Luis Rey



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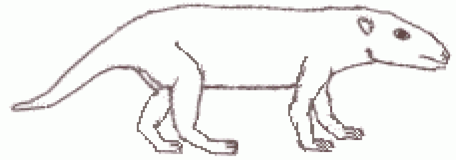
Zupaysaurus rougieri* is a large (skull estimated total length 45cm) early theropod recently (2003) described from the Los Colorados Formation, La Rioja Province, Argentina [Arcucci and Coria 2003]. It was originally though to have been the earliest known and most basal tetanuran, but it now seems to be a coelophysoid that independently evolved certain tetanuran characteristics. The neck was quite long, and the head decorated by paired crests (probably for intra-specific display). These animals would have fed on smaller sauropodomorphs, and the young of larger animals like *Riojasaurus



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Not all Traversodontidae were large. *Microscalenodon*, known from isolated teeth from the Rhaetian fissure deposits of Belgium and France, was a rare late surviving tiny traversodont, which presumably filled the same role as small rodents. It was probably about the size of a shrew or a small mouse

Microscalenodon nanus *Hahn, Lepage & Wouters, 1988*

Horizon & Locality: Gaume, Habay-le-Vielle, Belgium and Saint-Nicolas-de-Point in France
Age: Late Norian/early Raetian to Rhaetian
Length: about the size of a mouse
Material: isolated teeth
Ecological Niche: small rodent
References: Godefroit Battail 1997, Trevor Dykes, Triassic Gomphodonts;

Traversodontidae, an internet directory


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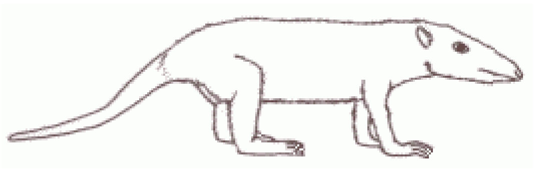
Although it is known only from isolated teeth, that is enough to tell that *Meurthodon* was a giant among Rhaetian synapsids (cynodonts and proto-mammals). Based on the size of the largest fossil teeth, this critter might have reached 30 to 40 centimetres in length. It was big enough to have fed not only on invertebrates but also on smaller vertebrates.

Because nothing is known of this animal other than some postcanine teeth - which show similarities to both the advanced Carnian cynodont *Therioherpeton* and the basal mammal Sinemurian *Sinoconodon*, it is difficult to know where it belongs on the synapsid evolutionary tree. The molars are more advanced and mammal-like than those of *Therioherpeton* in that they have two roots, but not yet at the mammal level. So it is not possible to determine whether Meurthodon is a very advanced cynodont or a true early mammal, and it has been provisionally referred to the Dromatheriidae, although - in view of its large size, it may also be an advanced and late-persisting member of the Therioherpetidae

After *Meurthodon*, no synapsid carnivore would exceed the size of a large mouse until the late Jurassic.

Meurthodon gallicus *Sigogneau-Russell D & Hahn G, 1994*

Horizon & Locality: Saint-Nicolas-de-Point in France
Age: Late Norian/early Rhaetian
Length: 30 to 40 cm
Material: isolated teeth
Ecological Niche: insectivore / small carnivore (probably nocturnal)
References: Sigogneau-Russell and Hahn 1994, Trevor Dykes, Triassic Cynodonts; Chiniquodontoidea, an internet directory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The Dromatheriidae were a group of tiny insectivorous cynodonts very close to the mammals ins structure, and known only from isolated teeth. *Tricuspes tuebingensis* E. v. Huene, 1933, *Tricuspes sigogneauae* Hahn, Hahn et Godefroit, 1994, *Tricuspes tapeinodon* Godefroit & Battail 1997, and *Pseudotriconodon wildi* Hahn G, Lepage J & Wouters G, 1984 are all known from the fissure fillings of Saint-Nicolas-de-Port, France (Late Norian or early Rhaetian), and are also known from Luxembourg, Germany, and (*Pseudotriconodon* sp.) Belgium. Clearly there was a very diverse and common mammal-like cynodont and proto-mammalian microfauna prominent at this time. For data on these little animals (such as there is) we can do no better than refer the reader to Trevor Dykes coverage on the Dromatheriidae, which also includes the original journal reference listing of each species, along with other information.

References: **Godefroit & Battail 1997; Trevor Dykes Chiniquodontoidea,**


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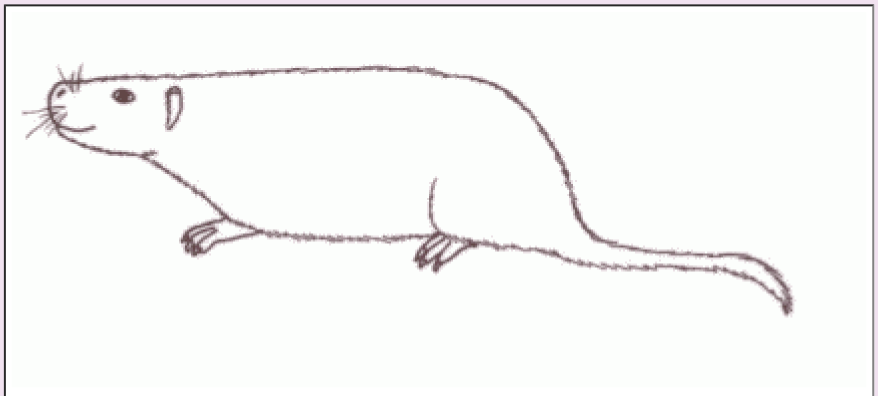
The morganucodontids - represented by genera like *Eozostrodon*, *Morganucodon*, *Hallautherium*, *Helviotodon*, and *Brachyzostrodon*, from Anglo-Welsh fissure fillings and Rhaetic (or latest-Norian-Rhaetic) deposits and bone-beds of Greenland, Switzerland and France - were the most primitive of the true mammals. Along with the haramiyids, they were the most common of the early mammalian taxa during the Latest Norian and Rhaetian, although, as with all these tiny animals, they are known chiefly from isolated teeth. These shrew-like and probably nocturnal insectivores must have been an important element in the microvertebrate fauna, rustling through the undergrowth of central north Pangaea. Although traditionally included in the order Triconodonta on the basis of dental characteristics, they appear to be far more primitive than later Jurassic members of the group. morganucodontids seem to have ranged in size from 30 to 90g, the equivalent of between one and four standard house mice. For more details, see Trevor Dykes Mesozoic

MAMMALS; Basal Mammaliaformes, Morganucodontidae, Megazostrodontidae and *Hadrocodium*, an internet directory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***Thomasia* is a representative of a group of very early mammalian herbivores that with one exception (*Haramiyavia*) are known only from isolated cheek teeth found in the fissure fillings of France, England and Germany. Rather confusingly, the name *Haramiya* Simpson, 1947 was given to upper teeth, and *Thomasia* Poche, 1908 to lower teeth, and it was thought that these belonged to different animals. *Haramiya* became better known, and lent its name to the family Haramiyidae and the order Haramiyida. Recently it has been argued that these are the same animal, and so the newer name, *Harimiya* becomes a junior synonym for *Thomasia* (which, being the older name, has priority). The change of name does not cover supra-generic nomenclature, so the names Haramiyidae and Haramiyida remain valid.**

Because these broad cheek teeth resemble those of recent voles, it is usually reconstructed as a miniature vole. Of course there is guarantee this is what it actually looked like, and study of *Haramiyavia* will no doubt provide a different picture. It is however most likely that it was a herbivore, living on low growing vegetation.

Haramiyids were originally considered ancestral to the multituberculates, an important group of rodent-like mammals of the Mesozoic and early Tertiary. The current majority view rejects this position, and considers them an early mammaliform offshoot unrelated to multituberculates, although a persisting minority view retains their relationship with the multituberculates, or sees them as a paraphyletic ancestral grade of multituberculates.

These animals seem to have been quite common but limited to north-central Pangea. A number of species known from the Late Norian/early Rhaetian to Sinemurian of central-north Pangea (Western Europe): *Thomasia antiqua* (Late Norian/early Rhaetian to ?Sinemurian of England & France & Switzerland - see data panel, right), *Thomasia hahni* Late Norian/early Rhaetian of Germany, *Thomasia moorei* (Late Norian/early Rhaetian to ?Sinemurian of England & France & Switzerland), *Thomasia wouteri* (Rhaetian of Belgium), *Haramiyavia clemmenseni* (Late Triassic ?or Early Jurassic of eastern Greenland) (the best known member of the family, known from a jaw with teeth in place, and some postcrania, sometimes placed in its own family), *Mojo usuratus* (Rhaetian of Belgium, sometimes considered related to the near to the multituberculate family Paulchoffatiidae, although this is debatable), and *Theroteinus nikolai* (Late Norian/early Rhaetian of France). For more details, see Trevor Dykes Mesozoic MAMMALS; Haramiyida, an internet directory

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References

Anderson, JM & ARI Cruikshank (1978), *The Biostratigraphy of the Permian and Triassic, Part 5, a review of the classification and distribution of Permo-Triassic Tetrapods*. **Paleontol. Afr.** 21: 15-44.

Arcucci, Andrea B & Coria, Rodolfo A., 2003. A new Triassic carnivorous dinosaur from Argentina. Ameghiniana 40(2): 217 - 228.
Rhaetian - Zupaysaurus

Bakker, RT (1977), *Tetrapod Mass Extinctions - A model of the regulation of speciation rates and immigration by cycles of topographic diversity*, **in** A Hallam [ed.], **Patterns of Evolution as illustrated by the Fossil Record**. Elsevier, pp. 439-68.
Norian - Tetrapods

Bakker, RT (?), *The Need for Endothermic Archosaurs*, **in** RDK Thomas & EC Olson [eds.], **A Cold Look at the Warm Blooded Dinosaurs**. **AAAS Select. Symp.** 28: 366.

Colin Barras, The ichnofossil record across the Triassic/Jurassic Boundary, Palaeontologiacl Association 46th Annual Meeting, Department of Earth Sciences, University of Cambridge, December 15-18, 2002 (**Annual Conference Abstracts**)
Rhaetian - The End Triassic Turnover and Bolide Impact

Behrensmeyer, AK, JD Damuth, WA Dimichele & H-D Sues (1992), **Terrestrial Ecosystems Through Time : Evolutionary Paleoecology of Terrestrial Plants and Animals**. U. Chicago Press, 568 pp.

Triassic

Benton, MJ (1983), *Dinosaur success in the Triassic: a non-competitive ecological model*. **Quart. Rev. Biol.** 58: 29-55.

Benton, M.J, 1986, "The Late Triassic tetrapod Extinction Events"; in *The Beginning of the Age of Dinosaurs*. Kevin Padian, ed., Cambridge University Press, pp.303-321
Norian - The Dinosaurian Revolution, Norian - *Proganochelys*, Norian - *Aetosaurus*, Norian - *Plateosaurus*

Benton, M.J., 1986b The Late Triassic reptile Teratosaurus- a rauisuchian, not a dinosaur. Palaeontology 29: 293-301
Norian - *Teratosaurus* and *Basutodon*

Benton MJ (1990) *Origin and interrelationships of Dinosaurs*, **in** DB Weishampel, P Dodson & H Osm�lska [eds.], **The Dinosauria**. U. Calif. Press. Carnian - *Herrerasaurus*

Benton MJ (1994), *Late Triassic to Middle Jurassic extinctions among continental tetrapods: testing the pattern*, **in** Fraser & H-D Sues (eds.) **In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods**, Cambridge Univ Press, pp.366-397 Norian - the Terrestrial Tetrapod Succession, Rhaetian - Overview, The Apachean LVF.

Benton MJ (2004), *Origin and relationships of Dinosauria*, **in** DB Weishampel, P Dodson & H Osm�lska (eds.), **The Dinosauria** [2nd ed.]. U. Calif. Press. pp. 7-20. Middle Triassic.

Benton MJ & PCJ Donoghue (2007), *Palaeontological evidence to date the tree of life.* **Mol. Biol. Evol.** 24: 26�53. Middle Triassic.

Benton MJ & DAT Harper (1997), **Basic Paleontology**. Addison Wesley Longman, 342 pp. Middle Triassic.

Benton, MJ & AD Walker (2002), ***Erpetosuchus****, a crocodile-like basal archosaur from the Late Triassic of Elgin, Scotland*. **Zool. J. Linn. Soc.** 136: 25-47. **Alt. Title:** DB Norman & DJ Gower [eds.], **Archosaurian Anatomy and Palaeontology: Essays in Memory of Alick D. Walker.** (all abstracts this issue)) abstract. Carnian - *Erpetosuchus*

Bonaparte, JF (1970), *Annotated List of the South American Triassic Tetrapods*, **in Second Gondwana Symposium, Proceedings and Papers**. Council of Scientific and Industrial Research, Pretoria.
Carnian - *Placerias* and *Ischigualastia*, Carnian - *Exaeretodon*, Norian - Jachaleria, Rhaetian Terrestrial Communities, Rhaetian - *Riojasuchus*, Rhaetian - *Neoaetosauroides*

Bonaparte, JF (1975), *Sobre la presencia del laberintodonte* ***Pelocephalus*** *en la Formaci�n Ischigualasto y su significado estratigr�fico*. **Actas I Cong. Argent. Paleont. Estrat.** 1. Carnian - *Pelorocephalus*

Bonaparte, JF (1976), *Un nuevo rauisuchidae de la Formaci�n Los Colorados,* ***Fasolasuchus tenax****, La Rioja, Argentina. (Archosauria-Thecodontia)*. Manuscrito, Tucum�n.
Rhaetian - *Fasolasuchus*

Bonaparte, J.F.. 1981. escripci�n de *Fasolasuchus tenax* y su significado el la sistem�tica y evoluci�n de los Thecodontia. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"l 3: 55-101.
Rhaetian - *Fasolasuchus*

J.F. Bonaparte, 1982, "Faunal Replacement in the Triassic of South America", *Journal of Vertebrate Paleontology* **2 (3):** 362-371, December 1982
Carnian - Tetrapods, Carnian - *Exaeretodon*, Rhaetian Terrestrial Communities, Rhaetian - *Fasolasuchus*

Bonaparte, J.F., 1982 b. Classification of the Thecodontia. Geobios Mem. Spec. 6, 99-112.
Carnian

Brasier, W.D. 1989 "Towards a biostratigraphy of the earliest skeletal biotas", in J.W. Cowie & M.D. Brasier eds. *The Precambrian-Cambrian Boundary*, Clarendon Press, Oxford,
Carnian

"Norian Stage" Encyclop�dia Britannica from Encyclop�dia Britannica Premium Service., 2003.
Norian - Overview, Norian - Stratigraphy, Rhaetian - Overview

Buffetaut, E., Suteethorn, V., Cuny, G., Tong, H., Le Loeuff, Jean., Khansubha, S., Jongautchariyakul, S., 2000, The earliest known sauropod dinosaur, Nature 407, 72 - 74 (2000); doi:10.1038/35024060
Tetrapods of the Late Middle Norian, Rhaetian - Isanosaurus

Burmeister *et al* 2000 Burmeister, K. C., J. J. Flynn, J. M. Parrish, R. L. Whatley, and A. R. Wyss. 2000. Biostratigraphic and biogeographic implications of new middle to Late Triassic fossil vertebrates; Morondava Basin, Madagascar. [PDF file] Abstracts of the 2000 Meeting of the Western Association of Vertebrate Paleontologists, Museum of Northern Arizona, Flagstaff.
Carnian - Tetrapods

Camp, C.L. 1980, Large ichthyosaurs from the Upper Triassic of Nevada. Palaeontographica Ser. A. 170: 139-200
Carnian - *Shonisaurus*

Carpenter K, (1997), *A giant coelophysoid (Ceratosauria) theropod from the Upper Triassic of New Mexico, USA*, **Neues Jahrb. Geol. Pal., Abh**. 205: 189-208. Norian - *Gojirasaurus* and *Liliensternus*.

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

Carroll RL & P Gaskill (1985), *The nothosaur* ***Pachypleurosaurus*** *and the origin of plesiosaurs*. **Phil. Trans. Roy. Soc. Lond.** 309: 343-393. Middle Triassic.

Caudle N (2000), *The Predator in the Stone*, **Endeavors**. Norian Rauisuchians, Norian - *Plithogomphodon*.

Chatterjee, S. 1978. A primitive parasuchid (phytosaur) reptile from the Upper Triassic Maleri Formation of India. Palaeontology. 21 (1): 83-127.
Carnian - *Paleorhinus*

Ralph Chapman, 1995 Greenland, Dinosaur Mailing List

Sankar Chaterjee 1986, "Late Triassic Dockum vertebrates: their stratigraphc and paleobiolographic significance"; in *The Beginning of the Age of Dinosaurs*. Kevin Padian, ed., Cambridge University Press,
Carnian - *Adelobasileus* and *Gondwanadon*

Barry Cox, R.J.G. Savage, and Brian Gardiner, Dougal Dixon, 1988 Collins/MacMillan Illustrated Encyclopedia of Dinosaurs and Prehistoric Animals
Carnian

Ben Creisler 1996, Phytosauria Translation and Pronunciation Guide, iNet
Rhaetian - *Angistorhinopsis*

Clark, J. M., Sues, H.-D. & Berman, D. S., 2000: A new specimen of Hesperosuchus agilis from the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph archosaurs. Journal of Vertebrate Paleontology: vol. 20, #4, pp. 683-704
Tetrapods of the Late Norian, Norian - *Saltoposuchus*

Cuny G, A Hunt, JM Mazin & R Rauscher (2000), *Teeth of enigmatic neoselachian sharks and an ornisthischian dinosaur from the uppermost Triassic of Lons-le-Saunier (Jura, France)*. **Pal�ont. Zeit**, 74: 171-185. Rhaetian Marine Biota - Fish, Rhaetian Terrestrial Communities.

Cuny G, O Rieppel & PM Sander (2001), *The shark fauna from the Middle Triassic (Anisian) of North-Western Nevada*. **Zool. J. Linn. Soc.** 133:285-301. Middle Triassic.

Damiani RJ (2001), *A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli: Stereospondyli)*. **Zool. J. Linn Soc.** 133: 379�482. Middle Triassic.

Depuydt P (1998), Re: anyone a Madagascar expert?, Dinosaur mailing list. Carnian - *Exaeretodon*

Falkowski, PG, ME Katz, AH Knoll, A Quigg, JA Raven, O Schofield & FJR Taylor (2004), *The evolution of modern eukaryotic phytoplankton*. **Science** 305: 354-360. Middle Triassic.

Flynn JA, JM Parrish, B Rakotasamimanana, WF Simpson & AR Wyss (1999), *A Triassic fauna from Madagascar, including early dinosaurs*. **Science** 286: 763-765. Carnian - Tetrapods.

Tracy L. Ford, 2001, RE: Ghost Ranch fauna, Dinosaur Mailing List.
Tetrapods of the Late Norian

Fraser, N.C. 1986, New Triassic Sphenodontids from South-West England and a review of their classification, Palaeontology, vol.29, part 1, pp.165-186
Carnian - *Brachyrhinodon*

Fraser, N. C., Padian, K., Walkden, G. M. & Davis, A. L. M. 2002. Basal dinosauriform remains from Britain and the diagnosis of the Dinosauria. Palaeontology 45, 79-95. abstract
Tetrapods of the Late Middle Norian, Rhaetian Terrestrial Communities,

Fraser, N.C. 2004, Assemblages of small tetrapods from British Late Triassic fissure fillings, in Fraser & Sues (eds.) In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods, Cambridge University Press, Cambridge.
Rhaetian - *Clevosaurus*

Gaffney, E. S., 1986, "Triassic and Jurassic turtles"; in *The Beginning of the Age of Dinosaurs*. Kevin Padian, ed., Cambridge University Press,
Norian - *Proganochelys*,

Galton, 2001. Valid species of prosauropod dinosaurs from the Upper Triassic of Germany. JVP 21(3) 52A.
Norian - The Dinosaurian Revolution - A Case Study

Galton, P. M. 2001. Prosauropod dinosaurs from the Upper Triassic of Germany. In Colectivo Arqueologico-Paleontologico de Salas, C.A.S. (Eds.): "Actas de las I Jornadas Internacionales sobre Paleontologia de Dinosaurios y su Entorno (Proceedings of the 1st International Symposium on Paleontology of Dinosaurs and their Environment)", Burgos (Spain), 25-92.
Norian - The Dinosaurian Revolution - A Case Study

Galton, Peter M., 2002 The prosauropod dinosaur Plateosaurus Meyer, 1837 (Saurischia: Sauropodomorpha; Upper Triassic). II. Notes on the referred species. � Revue Pal�obiol., 20 (2) (2001): 435-502; Gen�ve.
Norian - The Dinosaurian Revolution - A Case Study

Gastaldo RA (1997) *Plant Associations of the Mesophytic*. Triassic.

Gibbon E (1776-1788), **The History of The Decline and Fall of the Roman Empire** [1996 Project Guttenberg ed.] 6vv. Middle Triassic.

Godefroit P & B Battail (1997), *Late Triassic cynodonts from Saint-Nicolas-de-Port (north-eastern France)*. **Geodiversitas** 19: 567-631. **abstract**. Norian - *Pseudotriconodon*.

Godefroit P., Cuny G., Delsate D. et Roche M. (1998) - Late Triassic vertebrates from Syren (Luxemburg). N. Jb. Geol. Pal�ontol., Abhandlungen, 210(3): 305-343.
Rhaetian Terrestrial Communities

F.M. Gradstein, J.G. Ogg, A.G. Smith *et al*.: Geologic Time Scale 2004. Cambridge University Press (see The 2004 Time Scale - web site
Norian - Stratigraphy and Index Fossils, Rhaetian - Stratigraphy and Index Fossils

Eric Hargrave, 1999, Paleomagnetism of the Chinle Formation at Ghost Ranch , New Mexico: Age constraints for Coelophysis bauri , University of Puget Sound.
Tetrapods of the Late Norian, The Apachean LVF

Harland W.B., *et al*., "A Geologic Time Scale 1989," Cambridge University Press: Cambridge UK, Revised Edition, 1990.
Carnian - Stratigraphy, Norian - Overview,

Haubold, Hartmut, 1986, "Archosaur footprints at the terrestrial Triassic-Jurassic transition"; in *The Beginning of the*

Age of Dinosaurs. Kevin Padian, ed., Cambridge University Press, pp.189-202
Rhaetian - The Coelophysid Takeover

Jaime A. Headden, 2003 Re: YEAH!!! Sauropodomorph Phylogeny! - Archives of the Dinosaur Mailing List
Norian - The Dinosaurian Revolution - A Case Study

Jaime A. Headden, 2004, RE: Info on some less well known taxa Dinosaur Mailing List Archive
Norian - Shonisaurus

Heckert, A.B. & Lucas, S.G. 2000, Global correlation of the Triassic theropod record. Gaia 15. 63-74.
Carnian - Tetrapods

Heckert, A.B. & Lucas, S.G. 2001, North America's oldest herbivorous dinosaurs, Rocky Mountain (53rd) and South-Central (35th) Sections, GSA, Joint Annual Meeting, Session No. 12, Paleontology, Stratigraphy, and Sedimentology abstract
Carnian - *Pisanosaurus*

Thomas R. Holtz, 2003RE: oldest sauropod found
Rhaetian - Isanosaurus

Huber P., Lucas S.G. & Hunt A.P., 1996, Carnian-Norian Biochronology, Correlation and Biotic Events of the Nonmarine Triassic of North America.
Norian - *Aetosaurus*

Hungerb�hler, A. 2002, The Late Triassic Phytosaur Mystriosuchus Westphali, With A Revision of the Genus. *Palaeontology*, March 2002, vol. 45, no. 2, pp. 377-418(42) abstract / abstract
Tetrapods of the Late Middle Norian, Norian - Mystriosuchus

Hunt, A.P. 1989, Vertebrate biochronology of late Triassic red beds in New Mexico, AAPG Bulletin (American Association of Petroleum Geologists) ; Vol/Issue: 73:9; AAPG Rocky Mountain Section meeting; 1-4 Oct 1989; Albuquerque, NM (USA) abstract
Tetrapods of the Early - Middle Norian

Hunt, Adrian P., 1998 Preliminary Results of the Dawn of the Dinosaurs Project at Petrified Forest National Park, Arizona, National Park Paleontological Research, Tech Rept. 3
Norian - Apachesaurus

Hunt, Adrian P. and Lucas, Spencer G. 1992. The first occurrence of the aetosaur Paratypothorax andressi (Reptilia, Aetosauria) in the western United States and its biochronological significance. Palaeontologische Zeitschrift, Band 66, Heft 1/2 . pp. 147-157, 5 fig. abstract
Tetrapods of the Early - Middle Norian

Hunt, A.P., and Lucas, S.G., 1994. Ornithischian dinosaurs from the Upper Triassic of the United States. pp.227-241 in Fraser & Sues (eds.) In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods, Cambridge University Press, Cambridge.
Tetrapods of the Early to Middle Norian

Hunt, A. P., and Santucci, V.L., 1993. The record of Late Triassic dinosaurs at Petrified Forest National Park. Petrified Forest National Park Research Abstracts. in Santucci, V.L., (ed.), National Park Service Technical Report NPS/NRPEFO/NRTR- 93/11: 97, p. 14.
Norian - Apachesaurus

Hunt, A. P., Santucci, V.L., and A. J. Newell Late Triassic vertebrate taphonomy at Petrified Forest National Park, NPS Paleontological Research Vol. 2
Tetrapods of the Early to Middle Norian

Hunt, A P., Lucas, S.G. Huber, P., and Lockley, M. G., Faunal evolution in Late Triassic, nonmarine tetrapods (abstract)
Late Triassic - Biotas, Carnian - Tetrapods, Norian - Tetrapods

Kathleen Hunt, 1994-1997, Transitional Vertebrate Fossils FAQ (Talk-Origins Archives)
Carnian - *Exaeretodon*

Randall Irmis, 2001, RE: Ghost Ranch fauna, Dinosaur Mailing List. a list of fauna from the Rock Point from "Late Triassic Tetrapods from the Southwest Unitied States" by Long and Murray, 1995 (NMMNH Bulletin 4).
Tetrapods of the Late Norian

Ian Jenkins, 2000, "Gorgonopsid ecomorph niche-filling after the P-Tr extinction by 'aeluromorph' moschorhinid therocephalians: a finite element approach." PalAss Annual Conference Abstracts 2000, University of Edinburgh, 17-20 December 1999
Induan

Farish A. Jenkins, Jr., Neil H. Shubin, William W. Amaral, Stephen M. Gatesy, Charles R. Schaff, Lars B. Clemmensen, William R. Downs, Amy R. Davidson, Niels Bonde and Frank Osb�ck Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland. MoG Geoscience, vol. 32 1995, synopsis
Norian - Middle Norian Tetrapods

Paul A. Johnston, Christopher J. Collom, Elizabeth L. Nicholls, Makoto Manabe, 2000, A "whale bone-like" chemosymbiotic bivalve community associated with carcasses of giant ichthyosaurs, Pardonet Formation (Upper Triassic), British Columbia, Canada **PDF document**
Norian - Shonisaurus

Joyce WG & JA Gauthier (2004), *Palaeoecology of Triassic stem turtles sheds new light on turtle origins*. **Proceedings: Biological Sciences**; Volume 271: abstract. Norian - *Proganochelys*, Rhaetian - *Palaeochersis*.

Katz ME, ZV Finkel, D Grzebyk, AH Knoll & PG Falkowski (2004), *Evolutionary trajectories and biogeochemical impacts of marine phytoplankton*. **An. Rev. Ecol. Evol. Syst.** 35: 523-556. Middle Triassic.

King GM & MA Cluver (1991), *The aquatic **Lystrosaurus**: An alternative lifestyle*. **Hist. Biol.** 4: 232-341. Induan, Carnian - *Placerias* and *Ischigualastia*.

Kitching, J.W. & Raath, M.A. (1984). Fossils from the Elliot and Clarens Formations (Karoo Sequence) of the Northeastern Cape, Orange Free State and Lesotho, and a Suggested Biozonation Based on Tetrapods. *Palaeont. afr.* 25: 111-125.
Norian - *Teratosaurus* and *Basutodon*

H. W. Kozur, "Some aspects of the Permian-Triassic boundary (PTB) and of the possible causes for the biotic crisis around this boundary", in *Palaeogeography, Palaeoclimatology, Palaeocology* **143**, 1998, pp.227-72
Induan

Kozur, H.W. 2003, Micropaleontological definition of the Norian-Rhaetian boundary, Abstract - PDF, from Extinction Events, Faunal Turnovers and Natural Boundaries Within and Around The Late Triassic - Mirror
Norian Stratigraphy, Rhaetian - Overview, Rhaetian - Stratigraphy and Index Fossils

B. Krebs, 1976, Pseudosuchia, in O. Kuhn, Ed. *Handbuch der Palaeoherpetologie Teil 13: Thecondontia*, Gustav Fisher-Verlag, Stuttgart

Oskar Kuhn, 1969 *Handbuch der Palaeoherpetologie, Teil 9: Proganosauria, Bolosauria, Placodontia, Araeoscelidia, Trilophosauria, Weigeltisauria, Millerosauria, Rhynchocephalia, Protorosauria*, Gustav Fisher-Verlag, Stuttgart
Carnian - *Leptopleuron*, Carnian - *Henodus*, Carnian - *Brachyrhinodon*

Krystyn L (2003), *Upper Triassic substage boundaries and their ammonoid record: divided between gradation, faunal turnover and extinction* **Extinction Events, Faunal Turnovers and Natural Boundaries Within and Around The Late Triassic** (absrtact). Norian - Overview, Norian - Reefs, Norian - Ammonoids.

Labandeira CC (1998), *Early history of archropod and vascular plant associations*. **Ann. Rev. Earth Planet. Sci.** 26: 329-377. Middle Triassic.

Langer MC, M Boniface, G Cuny & L Barbieri (2000), *The phylogenetic position of **Isalorhynchus genovefae**, a Late*

Triassic rhynchosaur from Madagascar. **Ann. Pal�ont.** 86: 101-127. Carnian - Tetrapods; Carnian - *Hyperodapedon*.

Luciano A. Leal, Sergio A.K. Azevedo, Alexander W.A. Kellner and �tila A. S. Da Rosa. 2004., A new early dinosaur (Sauropodomorpha) from the Caturrita Formation (Late Triassic), Paran� Basin, Brazil. Zootaxa 690: 1-24.
Tetrapods of the Early Norian (Lacian Age), Norian - *Jachaleria*

Lockley, M., and Hunt, A. (1996). Dinosaur Tracks and Other Fossil Footprints of the Western United States.
Rhaetian - The Coelophysid Takeover.

Looy CV, WA Brugman, DL Dilcher & H Visscher (1999), *The delayed resurgence of equatorial forests after the Permian-Triassic ecologic crisis*. **Proc. Nat'l. Acad. Sci.** 96: 13857-13862. Olenekian.

Lucas SG (1998), *Global Triassic tetrapod biostratigraphy and biochronology*. **Palaeogeog. Palaeoclimat. Palaeoecol.** 143: 347-384. Carnian, Induan, Late Triassic, Middle Triassic, Norian Rhaetian, Triassic.

Spencer G. Lucas, 1999, A Tetrapod-based Triassic Timescale, Albertiana 22, February 1999.
Late Triassic - Biotas, Induan, Carnian - Tetrapods, Norian Tetrapod Index Fossils - The Revueltian LVF, Triassic,

Spencer G Lucas, 2001, Age and Correlation of Triassic Tetrapod Assemblages from Brazil, *Albertania* **26** p.17
Norian - *Jachaleria*

Lucas S.G. & Hancox P.J., 2000, Tetrapod-based correlation of the nonmarine Upper Triassic of Southern Africa. Albertiana 25, pp.5-9. [pdf]
Norian - *Jachaleria*

Lucas S.G. & Heckert A.B., 2002, The Hyperodapedon Biochron, Late Triassic of Pangea. Albertina 27
Carnian - Tetrapods; Carnian - *Hyperodapedon*

Lucas, S G., and Hunt, A P. 1994, The chronology and paleobiogeography of Mammalian Origins, pp.335-351 in Fraser & Sues (eds.) In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods, Cambridge University Press, Cambridge.
Norian - the Terrestrial Tetrapod Succession

Lucas, S G., Hunt, A P., Huber, P, 1996, Late Triassic tetrapod biochronology of Pangaea, Triassic Jurassic Working Group - Abstract
Norian - *Aetosaurus*

Spencer G. Lucas and Robert M. Sullivan, 1996, Fossils provide a Pennsylvania standard for part of Late Triassic time , *Pennsylvania Geology*, Vol. 27, no. 4, Winter 1996 pp. 7-13 (or pp.10-16)

Luo Z-X, Z Kielan-Jaworowska, & RL Cifelli (2002), *In quest for a phylogeny of Mesozoic mammals*. **Acta Pal Pol.** 47: 1-78. Carnian - *Dromatherium*.

Maisey, JG (1984), *Higher elasmobranch phylogeny and biostratigraphy.* **Zool. J. Linn. Soc.** 82: 33-54. Middle Triassic.

McGowan C, Never Mind the Dinosaurs - Other Mesozoic Life - plants Triassic.

Maisch, M. W. & Matzke, A. T. 2000. The ichthyosauria. Stuttgarter Beitraege zur Naturkunde. Serie B. Geologie und Palaeontologie. [print] 2000; (298): 1-159. abstract here
Norian - Ichythyosaurs, Norian - *Himalayasaurus*, Norian - *Callawayia*

Claudia A. Marsicano, 1996 Otuminisaurus limensis rusconi, 1948: a problematic Temnospondyl amphibian from the Triassic of Argentina, Journal of Vertebrate Paleontology, 1996, 16(4): 785-786 [abstract]
Carnian - Pelorocephalus

Milner, A.R. 1994, Late Triassic and Jurassic amphibians: fossil record and phylogeny, pp.5-22 in Fraser & Sues (eds.) In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods, Cambridge University Press, Cambridge.
Norian - *Apachesaurus*

Modesto S.P. ; Damiani R.J. ; Sues H. , 2002, A reappraisal of *Coletta seca*, a basal procolophonoid reptile from the Lower Triassic of South Africa, Palaeontology, September 2002, vol. 45, no. 5, pp. 883-895(13) abstract
Norian - *Libognathus*

Mickey Mortimer, 2000 Details on Isanosaurus attavipachi - Dinosaur mailing list archives
Rhaetian - Isanosaurus

Mickey Mortimer, 2003 Re: YEAH!!! Sauropodomorph Phylogeny! - Archives of the Dinosaur Mailing List
Norian - *Euskelosaurus*

Ryosuke Motani, Makoto Manabe, and Zhi-Ming Dong, 1999, The status of *Himalayasaurus tibetensis* (Ichthyopterygia) [pdf], Paludicola2(2):174-181 June 1999
Carnian - *Shonisaurus*, Norian - *Himalayasaurus*

Murry, P.A. 1986. Vertebrate paleontology of the Dockum group, western Texas and eastern New Mexico. In *The Beginning of the Age of Dinosaurs. Faunal Change across the Triassic-Jurassic Boundary* (K. Padian, Ed.), pp. 109-137. Cambridge Univ. press, Cambridge, UK.

Darren Naish, 2000, Placodonts: the bizarre 'walrus-turtles' of the Triassic - Oceans of Kansas Website
Carnian - *Henodus*, Rhaetian - *Psephoderma*

Darren Naish, 2001 Mandasuchus, Callawayia, Thyreophoran, Dinolist Archives
Norian - *Callawayia*

Elizabeth L. Nicholls (speaker) 2003, Triassic Icthyosaurs from British Columbia - the west coast of Pangea, abstract
Norian - Ichythyosaurs, Norian - Shonisaurus

Nicholls, E. L. & Manabe, M. 2001. A new genus of ichthyosaur from the Late Triassic Pardonet Formation of British Columbia: bridging the Triassic-Jurassic gap. **Canadian Journal of Earth Sciences** 38, 983-1002. abstract
Norian - Ichythyosaurs, Norian - *Himalayasaurus*, Norian - Shonisaurus, Norian - *Callawayia*

Elizabeth L. Nicholls, and Manabe, Makoto, 2004, Giant ichthyosaurs of the Triassic - a new species of Shonisaurus from the Pardonet Formation (Norian: Late Triassic) of British Columbia, *Journal of Vertebrate Paleontology*, 24(4):838-849 abstract
Norian - Shonisaurus,

Novikov, Igor V. & Sennikov Andrey G. :- The Tikhvinskoye continental Early Triassic locality: geological setting, fauna and flora - a short but informative on-line essay

Paul E. Olsen, Hans-Dieter Sues, and Mark A. Norell, First record of Erpetosuchus (Reptilia: Archosauria) from the Late Triassic of North America, Journal of Vertebrate Paleontology, 2000, 20(4):633-636
Carnian - Erpetosuchus

Olsen, P. E. and Huber, P., 1998, The oldest Late Triassic footprint assemblage from North America (Pekin Formation, Deep River basin, North Carolina, USA). Southestern Geology, v. 38, no. 2, pp. 77-90.
Norian - Tetrapods

P. E. Olsen, D. V. Kent, H.-D. Sues, C. Koeberl, H. Huber, A. Montanari, E. C. Rainforth, S. J. Fowell, M. J. Szajna, B. W. Hartline, 2002 Ascent of Dinosaurs Linked to an Iridium Anomaly at the Triassic-Jurassic Boundary, Science vol 296 17 May 2002 - PDF document - also supplemental material
Norian - Tetrapods, Norian - *Gojirasaurus* and *Liliensternus*, Rhaetian

Olsen, P. E., Schneider, V., Sues, H.-D., Peyer, K, M., and Carter, J. G., 2001, Biotic provinciality of the Late Triassic equatorial humid zone. *Geological Society of America, Abstracts with Programs*, v. 33, no. 2, p. A-27. (**abstract**)
Carnian - *Leptopleuron*, Norian - Overview, Norian - Tetrapods, *Libognathus*, Norian - Jachaleria

Paul GS (1988), **The Predatory Dinosaurs of the World**, Simon & Schuster. Carnian - *Saltopus*; Carnian - *Herrerasaurus*

Peyer K, JG Carter, H-D Sues, & PE Olsen (2001), *An articulated poposaurid rauisuchian from the Triassic Deep River Basin, North Carolina*. **Geol. Soc. Am., Abstr. with Prog.** 33: A-27.

Payne JL (2005), *Evolutionary dynamics of gastropod size across the end-Permian extinction and through the Triassic recovery interval*. **Paleobiology** 31: 269-290. Middle Triassic.

Price-Lloyd N & RJ Twitchett (2002), *The Lilliput Effect in the aftermath of the end-Permian extinction event*. **Pal. Assoc 46th An. Mtg.: Cambridge, Dec 15-18, 2002** (**Abstr.**). Early Triassic, Rhaetian - The End Triassic Turnover and Bolide Impact.

Rauhut, O.M.W. & A. Hungerbuhler, 1998, A review of European Triassic theropods. *Gaia* 15. 75-88 pdf
Norian - The Dinosaurian Revolution - A Case Study, Norian - *Aetosaurus*, Norian - Gojirasaurus and *Liliensternus*

Silvio Renesto, 2001, Re: "Hypuronector limnaios" Dinosaur Archives
Norian - *Megalancosaurus*

Retallack, G. J., and Hammer, W.R. 1996, Paleoenvironment of the Triassic therapsid Lystrosaurus in the central Transantarctic Mountains, Antarctica. Marine and terrestrial geology and geophysics, Antarctic Journal of the United States Review
Induan

Rieppel, O. and Zanon, R. T. 1997. The interrelationships of Placodontia. *Historical Biology* 12: 211-227.
Carnian - *Henodus*

Rozdestvenski AK (1965), *Growth changes in Asian dinosaurs and some problems of their taxonomy*, **Paleont. Zh.** 1965: 95-109 (in Russian). Norian - Tetrapods.

Rubidge, BS & CA Sidor (2001), *Evolutionary patterns among Permo-Triassic therapsids*. **Ann. Rev. Ecol. Syst.** 32: 449-480. Middle Triassic.

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

Scherer CMS (1994), *Análise faciologica e bioestratigrafica do Triassico Superior (topo da Formação Santa Maria) na região de Candelaria-RS*. Instituto de Geoci�ncias, Universidade Federal do Rio Grandedo Sul, M.Sc. Thesis, l00p. Tetrapods of the Early Norian (Lacian Age), Norian - *Jachaleria*.

Sereno PC (1991), *Basal archosaurs: phylogenetic relationships and functional implications*. **Soc. Vert. Paleont. Mem.** 2: 1-53. Middle Triassic.

Shiskhkin MA (1997), *Post-extinction events in the land tetrapod communities during Permo-Triassic faunal turnover* (abstract): http://www.gli.cas.cz/_abstr/0000003b.htm (3.9.1997). Induan.

Shishkin, M.A. & Ochev, V.G., 1993. The Permo-Triassic transition and the early Triassic history of the Euramerican tetrapod fauna. *Bull. New Mexico Nat. Hist. and Sci.*, Vol. 3, pp. 435-437.
Induan

Shishkin, M.A., Rubige, B. & Hancox, J., 1995. Vertebrate biozonation of the Upper Beaufort Series of South Africa - a new look on correlation of the Triassic biotic events in Euramerica and southern Gondwana.*Sixth Symp. on Mesozoic Terr. Ecosystems and Biota*, Beijing, China Ocean Press, pp. 39-41.
Induan

Shishkin MA, B Rubidge, J Hancox (1996), *Comparison of tetrapod faunal evolution during Early Triassic in Eastern Europe and South Africa*. **Abstr. 9th Bien. Conf. S. Afr. Pal. Soc**. 1996.

Sidor CA (2001), *Simplification as a trend in synapsid cranial evolution*. **Evolution** 55: 1419-1442. Middle Triassic.

Sigogneau-Russell D & Hahn (1994), *Upper Triassic microvertebrates from Central Europe*, in Fraser & Sues (eds.), **In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods**, Cambridge Univ. Press, pp.197-213. Rhaetian - *Angistorhinopsis*, Rhaetian - *Meurthodon*.

Small, B. J.; 1997, A new procolophonid from the Upper Triassic of Texas, with a description of tooth replacement and implantation, *Journal of Vertebrate Paleontology*, 1997, 17(4):674-678; abstract
Libognathus

Bryan J. Small, 2002, Cranial anatomy of *Desmatosuchus haplocerus* (Reptilia: Archosauria: Stagonolepididae), Archosaurian anatomy and palaeontology. Essays in memory of Alick Walker, Zoological Journal of the Linnean Society, Volume 136 Issue 1 September 2002 doi:10.1046/j.1096-3642.2002.00028.x abstract
Early Norian Tetrapods

Stanley, George D. 2001 Changes among reef ecosystems during the early Mesozoic, NAPC Abstracts June 26 - July 1 2001 Berkeley, California
Norian - Reefs

Stanley GD (2003), *Major events in the evolution of Triassic reef ecosystems*, **in Extinction Events, Faunal Turnovers and Natural Boundaries Within and Around The Late Triassic - Mirror** (abstr). Norian - Reefs, Norian - Ammonoids.

Stanley GD (2003a), *The evolution of modern corals and their early history.* **Earth-Sci. Rev.** 60: 195-225. Middle Triassic.

Stanley, SM (1998), **Earth System History**. WH Freeman & Co., 615 pp. Middle Triassic.

Steyer JS (2002), *The first articulated trematosaur 'amphibian' from the Lower Triassic of Madagascar: implication for the phylogeny of the group*. **Palaeontology** 45 4: 771-793. Induan, Middle Triassic.

Storrs GW & DJ Gower (1993), *The earliest possible choristodere (Diapsida) and gaps in the fossil record of semi-aquatic reptiles*, **J Geol. Soc.**, 150: 1103-1107(5) abstract Rhaetian - Pachystropheus.

Sues, Hans-Dieter, 2001. On Microconodon, a Late Triassic cynodont from the Newark Supergroup of Eastern North America. Bulletin of the Museum of Comparative Zoology. 10 October, 2001; 156 (1): 37-48.
Carnian - *Dromatherium*

Hans-Dieter Sues, Paul E. Olsen, and J. G. Carter, 1999, A Late Triassic Traversodont Cynodont from the Newark Supergroup of North Carolina, Journal of Vertebrate Paleontology, 19(2):351-354 abstract
Norian - *Plinthogomphodon*

Sues, H.-D., Olsen, P. E., Scott, D. M. & Spencer, P. K., 2000: Cranial osteology of Hypsognathus fenneri, a Latest Triassic procolophonid reptile from the Newark Supergroup of Eastern North America. --Journal of Vertebrate Paleontology: Vol. 20, no.2, pp. 275-284
Carnian - *Leptopleuron*

Sues, P. E., Olsen, P. E., Carter, J. G., and Peyer, K., 2001, A remarkable Triassic tetrapod assemblage from the Deep River basin of North Carolina. *Geological Society of America, Abstracts with Programs*, v. 33, no. 2, A.-27. (abstract)

Norian - Dicynodonts, Norian - *Plinthogomphodon*

Sues, H.-D., Olsen, P. E., Carter, J.G, and Scott, D. M. 2003 A new crocodylomorph archosaur from the Upper Triassic of North Carolina. Journal of Vertebrate Paleontology: Vol. 23, no.2, pp. 329-343 abstract
Norian - *Saltoposuchus*

Robert M. Sullivan and Spencer G. Lucas, 1999, Eucoelophysis baldwini, a new theropod dinosaur from the Upper Triassic of New Mexico, and the status of the original types of Coelophysis Journal of Vertebrate Paleontology, 1999, 19(1):81-90 abstract
Tetrapods of the Late Norian

Suzuki N, N Akiba & H Kanoh (2002), *Late Olenekian radiolarians from bedded chert of Ashio Terrane, Northeast Japan, and faunal turnovers in Western Panthalassia during Early Triassic.* **J. China Univ. Geosci.** 13: 124-140. Olenekian.

Curt Teichert 1988, "Main Features of Cehalopod Evolution", in *The Mollusca vol.12, Paleontology and Neontology*

of Cephalopods, ed. by M.R. Clarke & E.R. Trueman, Academic Press, Harcourt Brace Jovanovich, Late Triassic - Biotas, Norian - Overview,

Therrien, F., and Fastovsky, D.E., 2000 Paleoenvironments of Early Theropods, Chinle Formation (Late Triassic) Petrified Forest National Park, Arizona, pdf document. PALAIOS Volume 15.3 , pp.194-211
Tetrapods of the Early Norian

Trümpy R (1961), *Triassic of East Greenland*, **in** GO Raasch (ed.), **Geology of the Arctic**. Univ. Toronto Press. pp. 248-254. Induan.

Vaccari NE, GD Edgecombe & C Escudero (2004), *Cambrian origins and affinities of an enigmatic fossil group of arthropods*. **Nature** 430: 554-557. Middle Triassic.

Wall WP, AP Hunt & VL Santucci, *A preliminary biomechanical analysis of Phytosaur life habits*

Vince R Ward The Prehistoric Data Files - Reptiles listing in PDF format. Former http://www.angellis.net/Web/PDfiles/repgens.htm.

Warren AA (1991), **in** PV Rich, JM Monaghan, RF Baird, TK Rich, EM Thompson & C Williams (eds.), **Vertebrate Paleontology of Australia** Pioneer Design Studio, pp.605-702.

Warren AA (1995), ***Plagiosternum granulosum*** *E. Fraas: a plagiosaurid temnospondyl from the Middle Triassic of Crailsheim, Germany*. **Stuttg. Beit. Naturk. B** 229: 1-8. Middle Triassic.

Welles SP & J Cosgriff (1965), **A revision of the labyrinthodont family Capitosauridae**. Univ. Calif. Press. Norian - Cyclotosaurus posthumus.

Wellnhofer, P., 1991: The Illustrated Encyclopedia of Pterosaurs. --Salamander Books Ltd., London, 1991, pp. 192
Norian - *Peteinosaurus*, *Eudimorphodon*, and *Preondactylus*

Welman, J, 1998, The taxonomy of the South African Proterosuchids (Reptilia, Archosauromorpha) Journal of Vertebrate Paleontology, 18(2):340-347 **abstract**
Induan

Westphal, F. 1976 "Phytosauria" in O. Kuhn, Ed. *Handbuch der Palaeoherpetologie Teil 13: Thecondontia*, Gustav Fisher-Verlag, Stuttgart

Wu, X-C. 1994: Late Triassic-Early Jurassic sphenodontians from China and the phylogeny of the Sphenodontia. in Fraser, N. C. & Sues, H-D. 1994: In the Shadow of the Dinosaurs. --Cambridge University Press, New York. 1994
Carnian - Brachyrhinodon

Yates, A.M. (2003) A new species of the primitive dinosaur Thecodontosaurus (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. JSP 1: 1-42.
Norian - *Thecondontosaurus*

J.M. Zawiskie, 1986 "Terrestrial vertebrate faunal succession during the Triassic", in Kevin Padian ed., *The Beginning of the Age of Dinosaurs - faunal changes across the Triassic-Jurassic boundary*, Cambridge University Press, Cambridge

Zeigler, Kate E., Lucas, S. G., Heckert, A. B., and Hunt, A. P. 2001, The Phytosaur Nicrosaurus buceros in the Upper Triassic of the Chama Basin, North-Central New Mexico, abstract
Tetrapods of the Late Middle Norian,

Zittel, Karl A. von, 1932. Text-book of Palaeontology vol. II, 2nd English revised edition, translated and edited by Charles R. Eastman, Revised with additions by Sir Arthur Smith Woodward. MacMillan and Co, Ltd, London **buy**
Carnian - *Shonisaurus*

Jurassic period

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Jurassic Period

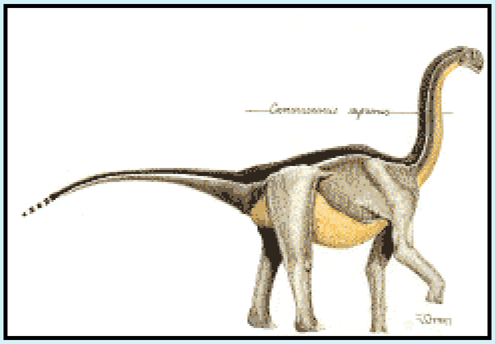
The Jurassic

The Jurassic Period of the Mesozoic Era: 200 to 146 million years ago

- Phanerozoic
  - Mesozoic
    - Triassic
    - Jurassic
      - Early Jurassic (Lias)
      - Middle Jurassic (Dogger)
      - Late Jurassic (Malm)
    - Cretaceous

- Jurassic
  - Introduction
  - Geography
  - Stratigraphy
  - Life
    - Plankton
  - Resources
  - References

Introduction



The second of the three divisions that make up the Mesozoic era, the Jurassic period saw warm tropical greenhouse conditions world-wide, shallow continental seas, the break-up of Pangea, cosmopolitan flora and fauna, and the triumph of the majestic dinosaurs and the great sea reptiles.

The name *Jurassic* comes from the Jura Mountains on the border of France and Switzerland (actually an extension of the Alps into eastern France), where rocks of this age were first studied. In 1795 Alexander von Humbolt described massive limestone formations of the Jura Mountains in Switzerland as the *Calcaire de Jura*, or *Jura-Kalkstein* ("Jura Limestone"), which he wrongly believed were older than the (Triassic) Muschelkalk. Between 1796 and 1815 William Smith published geological maps featuring strata that were referred to by William Buckland in 1818 as the *Oolite Formation* or *Oolitic Series*. These were divided into Lower, Middle and Upper Oolites. In 1822 Conybeare and Phillips named the underlying strata as the Lias. From this Alexander Brongniart used the term *Terrains Jurassiques*, although only for the "Lower Oolite" The names Lias and Oolites continued to be used in Britain until quite recently.

In 1839 Leopold von Buch formally named the rocks described by von Humbolt as the Jurassic System, from whence the term has come into general use.

The immense wealth of fossils in Jurassic sediments of Britain (especially ammonites) meant that biostratigraphic zonation was further advanced for Jurassic sediments than for other periods. The terms used to divide the Jurassic Period into early, middle and late - Lias, Dogger, and Malm, are ones that originally referred only to English sediments.

The fact that the remains of many dinosaur and sea reptile remains have been found from the early nineteenth century on contributed to the Victorian imagination regarding "antediluvian monsters."

Much more recently, the word Jurassic has become a household word with the success of Speilberg's rather absurd movie about genetically resurrected dinosaurs, *Jurassic Park*, based on a disappointing novel by Michael Crichton of the same name (actually the novel starts out quite well, but quickly slides into fantasy). Ironically most of dinosaurs featured in Jurassic Park actually lived during the following, Cretaceous, period. But then *Cretaceous Park* just doesn't have the same ring now, does it.

Images: *Camarasaurus supremus* © **Brenner Fishman**

Jurassic Geography

The Jurassic saw disintegration of Pangea that began in the Triassic continuing apace. The supercontinent begins to rotate, but the different components of the huge mass rotated at different rates and then in different directions, forming rift valleys. One of these opened the southern part of the North Atlantic Ocean and continued westward into the Gulf of Mexico. This was North America drifting westward, opening the Gulf of Mexico, forming the central Atlantic. As Greenland-North America separate from Europe-Africa and slide over the Pacific Ocean floor, mountain-building events are triggered that created the North American Cordillera (the Rocky Mountains and the Sierra Nevada). A huge arc was built on western North America and the Nevadan orogeny begins. Cimmeria begins its collision with Laurasia to form the Cimmerian orogeny.

In Gondwana the initial narrow split between South America and Africa that began during the Triassic widened into a configuration resembling the present-day Red Sea. New sea floor formed along the nascent South Atlantic. This lengthened into a long, narrow seaway between South America and Africa. The Western side South America was subducted by an opposing oceanic plate. A great rift separates Antarctica from the southern ends of South America and Africa, developing an arm that extends eastward from South Africa along what is presently the eastern side of India, which began drifting northward.. Volcanoes located along these rifts erupted and issued huge amounts of basaltic lavas. The separated segments of Gondwanaland move slowly northward, turning gently counter-clockwise. Early rifting along the Australia-Antarctica join provided moist forested conditions that became coal deposits.

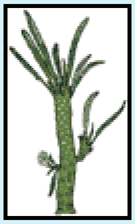
During the Jurassic the extent of the oceans was far more widespread then they had been in the Triassic. The Jurassic sea level rose and flooded large portions of the continents. Shallow epi-continental seas spilled out of the Tethys and Proto-Atlantic and spread across Europe, leaving a rich sedimentary record of limestone with fine clastics adjacent to the highlands. These warm shallow seas were home to a rich diversity of life. The spreading ocean crawled across Russia and into what is now the Arctic Sea before retreating at the end of the period. Meanwhile much of central North America was flooded by wide sea way that at its height extended into central Utah. This continent-wide embayment has been dubbed the Sundance Sea, and was fringed by strips of continental land on three sides.

Stratigraphy

Period	Epoch (sub-period)	Age	When began	Duration
Cretaceous	**Early Cretaceous**	Berriasian	146	5.3
	Late Jurassic (Malm) 15 My	**Tithonian**	151	5.3
		Kimmeridgian	156	4.8

Jurassic 54 My		**Oxfordian**	161	5.6
	Middle Jurassic (Dogger) 14.4 My	**Callovian**	165	3.5
		Bathonian	168	3.0
		Bajocian	172	3.9
		Aalenian	176	4.0
	Early Jurassic (Lias) 24.0 My	**Toarcian**	183	7.4
		Pliensbachian	190	6.6
		Sinemurian	197	6.9
		Hettangian	200	3.1
Triassic	**Late Triassic**	Rhaetian	204	4.0

Jurassic Life



On land gymnosperm plants were well represented. The superficially palm-like Cycadophyta (Cycads) were so abundant and diverse that the Jurassic period could well be called "the Age of Cycads" Some cycads were tall palm-like trees with rough branches marked by leaf scars, and pinnate (fern-like) leaf fronds. Other, unrelated forms, the equatorial flowering Bennettitales, were the most important group of shrubby trees, with short and stubby with squat bulbous trunks from the top of which the fronds grew.

Conifers continued to be the most diverse large trees, and included representatives of the extant (still living) families Araucariaceae, Cephalotaxaceae, Pinaceae, Podocarpaceae, Taxaceae, and Taxodiaceae, along with the extinct equatorial Cheirolepidiaceae. Ginkgos were important, particularly in mid to high northern latitudes. Dicksoniaceous tree ferns and Caytoniaceous seed ferns were relatively successful plants in the shrubby tree size range. The Cyatheaceae tree ferns may have (and still do) reach(ed) heights of 20 meters. Osmundaceous, matoniaceous, and dipteridaceous ferns were probably the dominant undergrowth and small plants. Lycopods remained relatively insignificant and sphenopsids were represented by the small (and still surviving "living fossil") *Equisetum* or "horsetail"

In the seas there was a great diversity of invertebrates. Sponges, corals, bryozoa, gastropods, bivalves, and ammonoid (*left*) and belemnite cephalopods all flourished, the latter two groups becoming the dominant nektonic invertebrates for the rest of the Mesozoic.

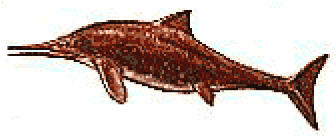
Brachiopods and Crinoids continued, but with nowhere like their Paleozoic glory.

Freshwater bivalves (clams), snails, and branchiopod Crustacea were common. On land, numerous groups of herbivorous insects were present, including the orders Orthoptera, Hemoptera (among which were the superfamilies Cicadelloidea and Fulgoroidea (leafhoppers), Psylloidea (plant hoppers), Pentatomoidea (shield bugs), and Cimicoidea (plant bugs)), Thysanoptera (thrips), Coleoptera (beetles, including most extant groups) and primitive Hymenoptera (sawflies). Pulmonate snails, millipedes, scorpions, spiders and mites were certainly present, but are not known from fossils.

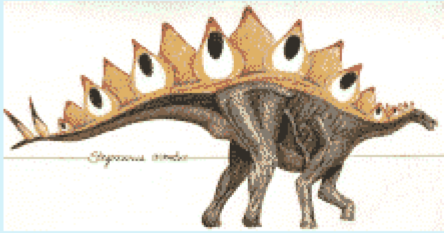
As for the vertebrates, modern shark groups begin to appear. Bony fish are still mostly the intermediate heavy scaled holostean type, although the first teleosts appear early in the period. The gigantic *Leedsichthys*, a huge, scaleless filter feeder, reached 10 or even 30 meters in length, and filled the same ecological role as modern baleen whales.

On land, a few basal tetrapods struggled on, but most amphibians were of essential modern types (frogs and newts), although the most primitive representatives of those orders.

Sphenodont lepidosaurs took the same ecological role as lizards do today. Crocodiles were abundant and diverse, and included marine, semi-aquatic and even a few small lizard-like terrestrial forms.



In the oceans new types of ichthyosaurs replaced their Triassic predecessors. The cousins of the Triassic nothosaurs, the long-necked plesiosauroids and short-necked pliosauroids, were also common. All these marine reptiles, filled similar ecological roles to cetaceans of the Cenozoic. In the air were various types of pterosaur, these were mostly small to medium-sized forms, all were endothermic with a covering of fur.

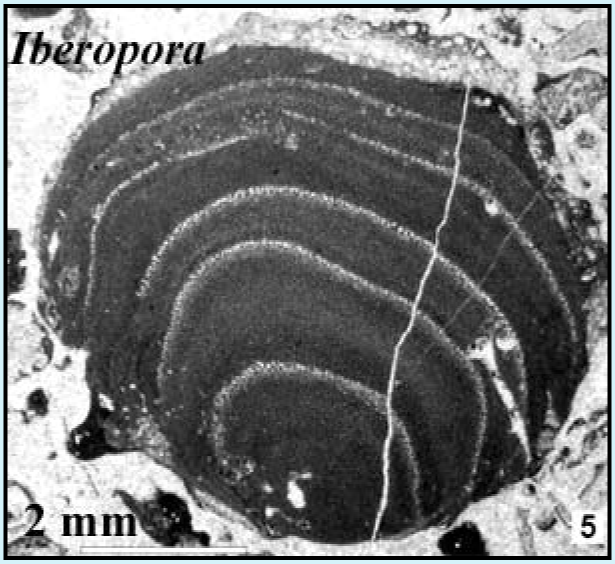


Dinosaurs were diverse and abundant, and their was a rich megafauna of huge sauropods (including a number of families - Euhelopidae, Cetiosauridae, Brachiosaurus, Camarasaurs, Diplodocidae, etc), reaching many tons in weight, and the more modestly sized Scelidosauridae, Stegosauridae, and the camptosaurid iguanodonts. The browsing pressure these great beasts exerted on the vegetation must have been tremendous, although there is continuing argument whether the dinosaurs were ectotherms, endotherms, homeotherms, gigantotherms, or (as seems most likely) some combination of all of the preceding. Obviously, the higher their metabolism the greater the selection pressure they would have exerted on the contemporary vegetation. Along with the giant herbivores there were also the small fleet-footed "fabrosaurs", scutellosaurs, and hypsilophodontids, the "gazelles" of the dinosaurian world. These plant eaters were kept in check by a variety of carnivorous (theropod) dinosaurs, including small lightly built coelophysids, compsognathids, and ornitholestids, and larger (from several hundred kilos to several tons in weight) dilophosaurids, Ceratosauria, Torvosauroidea, and Allosauridae. Some of the smaller carnivores developed feathers and took to the air, these were the proto-bird Archaeornithes.

A few tritylodontid therapsids straggled on, but it was a diverse assemblage of Mesozoic Mammals that played an important part of the microvertebrate fauna, filling the same ecological role as Insectivora and rodents do today.

Macroplata illustration by Steve Kirk - *Illustrated Encyclopedia of Dinosaurs and Prehistoric Animals*, ed.. Barry Cox, © 1988 Marshall Editions

Plankton



There must surely have been something special about the Jurassic oceans. Of the dozen or so types of planktonic organisms with a fossil record, at least four either first evolved or experienced massive radiation during Jurassic: coccolithophorids (evolved latest Triassic), diatoms (evolved Late Jurassic), dinoflagellates (radiated Jurassic), planktonic foraminifera (?evolved or radiated Jurassic), and ostracodes (radiated Jurassic). Most plankton groups experienced greater prominence yet in the Cretaceous. However, there seems to have been -- literally -- something in the water during the Jurassic. That "something" may simply have been lots of free calcium with which to build shells and tests; but, that would not explain the ostracodes and microcrustaceans that also seem to have found the Jurassic seas particularly congenial.

Nor were these the only marine groups who left Jurassic microfossils. The "modern" coralline group of the Rhodophyta (red algae) evolved in the Jurassic. They are called *modern* to distinguish them from the Paleozoic corallines. The current view is that the modern and Paleozoic corallines are unrelated. However, the otherwise unidentifiable Middle to Late Jurassic *Iberopora* may be a late member of a transitional taxon. Schlagintweit (2004). It would be useful to be more certain, since it has been suggested that the "something in the water" was the rhodophytes themselves -- or, rather, their chloroplasts. All of the new photosynthetic forms of the Jurassic were "red," with chloroplasts of the red algae type, with chlorophyll c, rather than the chlorophyll b of green plants and green algae (Chlorophyta). Falkowski *et al*. (2004). It is almost certain that these chloroplasts were "adopted" from red algae by some secondary symbiosis, rather than by descent from the Rhodophyta. Grzebyk *et al*. (2003).

Both of the last cited papers are from the Coastal Ocean Observatory Laboratory at Rutgers so (although it pains us to fall victim to so obvious a linguistic ploy) we'll refer to them as the COOL group. The COOL workers offer two reasons to explain why the ocean is "red." First, the Mesozoic rhodophyte chloroplast was a sturdy, self-reliant sort of plastid which had retained a much greater amount of its own DNA, and thus had greater genetic independence from its host. Consequently, by the Mesozoic, it was much easier for the red chloroplast to trade symbionts than it might have been for some debased, decadent green chloroplasts, which had surrendered most of its genetic control to its hosts. Second, the COOL group notes that red and green species are associated with different trace element requirements. The "red" elements are cadmium, cobalt and manganese, while the "green" elements are copper and iron. This leads the COOL group into a somewhat confused discussion of ocean anoxia and its effects on trace element availability. We suggest that they are correct about trace elements, but for the wrong reasons. Marine iron concentrations are largely dependent on continental weathering. Iron is high when the winds drop iron-bearing dust weathered from barren, arid inland areas. The rising seas and humid, equable conditions of the Mesozoic strongly reduced the availability of marine iron. It is not really necessary to invoke anything more complicated; however, we may also note that sulfides produced at the highly active Mesozoic mid-ocean ridges would also draw down dissolved iron as insoluble pyrite.

The Jurassic was also, in a small way, a good time for acritarchs. Acritarchs are just curiously shaped organic casings, without any particular phylogenetic identity. The Jurassic variety are probably some type of radiolarian-like protist and may have nothing at all to do with the Paleozoic acritarchs.

For radiolarians of the more conventional type, the Jurassic was also favorable. The Jurassic radiation of radiolarians was largely a radiation of the Spumellaria in the latter half of the Jurassic. *Pantanellium*, shown in the image, is a rather typical spumellarian. There is some speculation that this Late Jurassic recovery from a long period of decline may have been due to the availability of planktonic foraminifera as a food source. However, this remains speculation. Most radiolarian work in the Mesozoic is limited to identifying taxa for stratigraphic purposes. Surprisingly little has been done on their paleoecology or evolution.

Image Credits: *Iberopora* from Schlagintweit (2004). *Pantanellium* from **The Oceans** course at the Univ. of Texas at Dallas.

Links: Coralline Algae - Homepage of Michael Rasser; Radiolaria (MIRACLE site).

Resources

Links

The Jurassic period

Jurassic Reef Park - all that you would ever need to know about Jurassic reefs. A really great site!!!

Earth History Resources - Jurassic - graphics and some basic text info

Jurassic - in German and English

Jurassic - Dr Ron Blakey's Global Earth History - paleogeography and continental drift

Jurassic Period

The Jurassic Period - Enchanted Learning

The geology of Northamptonshire - England's Jurassic County

Notes & References

[1] These are both common Bajocian genera. The particular species shown here are Early Jurassic.

Benton, MJ & DAT Harper (1997), **Basic Palaeontology**. Longman, 342 pp.

Cornet, B & NG McDonald (1995), *A new cheirolepidiaceous conifer from the Lower Jurassic of North America*. unpub. MS. **WWW**.

Eble, GJ (1999), *Contrasting evolutionary flexibility in sister groups: Disparity and diversity in Mesozoic heart urchins*. **Santa Fe Inst. Working Paper** #99-04-026. **WWW**.

Falkowski, PG, O Schofield, ME Katz, B Van De Schootbrugge & AH Knoll (2004), *Why is the land green and the ocean red?* **in** H Therstein & JR Young [eds.], **Coccolithophores: from Molecular Processes to Global Impact**. Elseveir, pp 429-453.

Grzebyk, D, O Schofield, C Vetriani, & PG Falkowski (2003), *The Mesozoic radiation of eukaryotic algae: The portable plastid hypothesis*. **J. Phycol.** 39: 259–267.

Radwanska, U & A Radwanski (2003), *The Jurassic crinoid genus **Cyclocrinus** D'Orbigny, 1850: still an enigma*. **Acta Geol. Pol.** 53: 301-320.

Ruban, DA (2004), *Diversity dynamics of Early–Middle Jurassic brachiopods of Caucasus, and the Pliensbachian–Toarcian mass extinction*. **Acta Palaeontol. Pol.** 49: 275–282. **WWW**.

Schlagintweit, F (2004), ***Iberopora bodeuri** Granier & Berthou 2002 (**incertae sedis**) from the Plassen Formation (Kimmeridgian–Berriasian) of the Tethyan Realm*. **Geol. Croat.** 57: 1-13.

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Early Jurassic - The Liassic Epoch

The Early Jurassic Epoch: 176 to 200 million years ago

The age of great sea reptiles - meanwhile dinosaurs rule the land

A scene from what is now Germany, during this time a shallow continental tropical sea populated by various types of marine reptiles, fish, invertebrates, and flying reptiles
see Toarcian Age
image from American Museum of Natural History - Timelines Exhibit

Moving now from the Triassic to the Early Jurassic, we find that the dinosaurs have attained dominance, while most of the other Triassic types of animals have died out in two major Triassic extinctions - the mid-Carnian and the terminal Rhaetic. Apart from one or two early types, the dinosaurs seem to have been unaffected by these extinction events.

As the Jurassic Period opened, Italy, Greece, Turkey, and Iran were attached to the North African portion of Gondwanaland. The climate was warm and moister than during the Triassic. Reptiles were the dominant form of animal life and experienced a great adaptive radiation. In the oceans various types of ichthyosaurs and plesiosaurs evolved. In the air the pterosaurs began to diversify. On land many Triassic dinosaurs (prosauropod herbivores and coelophysid carnivores) continued, while a number of new forms (giant sauropods and armoured scelidosaurs) evolved. Under the feet of the dinosaurs rodent-like tritylodontid Therapsids co-existed with primitive shrew-like mammals and lizard-like sphenodont reptiles. Crocodiles appeared also, but they were mostly aquatic forms.

During the early Jurassic then, evolution seems to have polarised: on the one hand there were the ruling land animals, the great dinosaurs, which filled the ecological roles now taken up by medium-sized and large mammals; on the other hand the first mam-mals had appeared, and together with the tritylodont Therapsids they filled the small rodent and insectivore niche. The mam-mals were to remain small and individually insignificant - comparable to shrews, mice and rats of today - although doubtless very significant ecologically, for the 135 million years of the dinosaurs reign.

Early Jurassic (Liassic Epoch)	Toarcian
	Pliensbachian
	Sinemurian
	Hettangian

Jurassic Floras of Gondwanaland

> "During the Early Jurassic on the southern continents, Gondwanan floras came to resemble more closely those of the northern continents. Typically equatorial groups like Bennettitales and Cheirolepidiaceae, along with dipteriaceous and matoniaceous ferns, became more important components of the Gondwanan flora. Major differences between Jurassic floras of Gondwana and Laurasia included the relative paucity of Ginkgoales and Czekanowskiales and the greater importance of podocarpaceous conifers in the southern regions, although podocarps are known from Laurasia as well."
>
> *Terrestrial Ecosystems Through Time*, pp.349-352

Marine Invertebrates

Molluscs

Bivalves	Ammonites	Belemnites
		
Gryphea - coiled oysters	squid like body but possessing a coiled shell	squid-like marine cephalopods, possessing an internal shell

Marine Reptiles

In the several million years following the Rhaetic extinction of the last armoured placodonts and great Shastosaurs, a new dynasty of marine reptiles, consisting of new types of ichthyosaurs, plesiosauroids and pliosauroids, and fish-eating crocodles, quickly evolved and diversified.

The Ichthyosaurs included a number of types of streamlined medium-sized (2 to 3 meter long) animals, similiar in size and appearance to modern Dolphins, although their body-design and ectothermic metabolism indicated they were sprinters rather than endurance swimmers, and larger predatory types (family Leptopterygiidae), attaining 5 to 9 meters in length, and ecologically comparable to modern toothed whales.

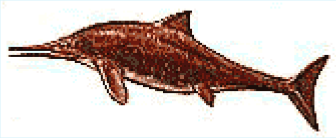
The Plesiosaurs were another diverse group, including both small and giant forms. Foremost among them were the Rhomaleosauridae, large but primitive pliosaurs with powerful crocodile-like jaws and medium-length necks. Reaching upto 7 meters in length, these animals shared the role of top marine predator with the Leptopterygiid ichthyosaurs. But already the plesiosaurs were beginning to evolve into the familiar long-necked small-headed Plesiosauroidea and the larger headed, short necked, streamlined Pliosauroidea that were to inhabit the oceans for the rest of the Mesozoic era.

The third party of Mesozoic marine reptiles, the Teleosaurid crocodiles, appeared in a rapid evolutionary radiation only at the end of the early Jurassic (Toarcian epoch). Theye were to continue as a success story until the end of the Jurassic, but were less common during the Cretaceous, dying out early into the period.

Order Ichthyosauria

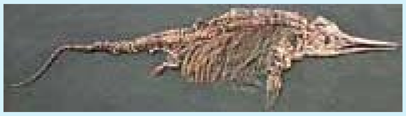
Family Leptopterygiidae
Temnodontosaurus
length 9 metres
giant marine preditor
drawing by Dr Bob Bakker

Hettangian to Sinemurian



Family Ichthyosauridae
Ichthyosaurus
length 2 metres
common small marine fish-eater

Rhaetic to Sinemurian



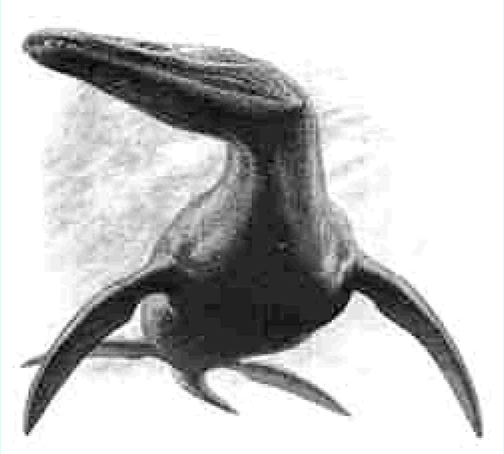
Family Stenopterygiidae
Stenopterygius
length 2 to 3 metres
common small marine fish eater
Image: **www.fosilien.de**

Toarcian

Order Plesiosauria

family undetermined
("Pliosauridae")
Eretmosaurus
length 3 to 4 metres long-necked fish eaters

Rhaetic to Sinemurian



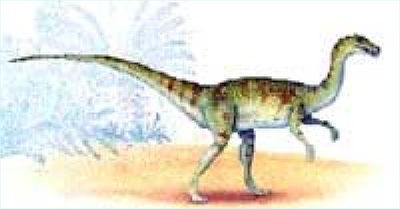
family Rhomaleosauridae
Rhomaleosaurus
length 3 to 7 meters
large to very large marine carnivores fed on other vertebrates - crocodile-like mode of feeding

Hettangian to Bathonian

family Plesiosauridae
Plesiosaurus
length about 3 metres: long-necked fish eaters

Hettangian? to Toarcian

Order Crocodylia



Hesperosuchus
family Sphenosuchidae
length 120 cm active small terrestrial
insectivores and carnivores
Image: **Wiley Interscience**

Carnian to Pliensbachian

family Protosuchidae
Protosuchus
length 60 cm to 1 metres

active small terrestrial carnivores
Image: Atlas Virtual da Pré-História

Rhaetic to Toarcian

family Teleosauridae
Steneosaurus
length 2 to 3 meters armoured marine fish-eaters

Toarcian to Valanginian

Early Jurassic herbivorous animals

" Early Jurassic herbivorous tetrapod assemblages were dominated by prosauropods, cynodont synapsids, and a variety of mostly small ornithischian dinosaurs. The latter included, in addition to the Fabrosauridae, the Heterodontosauridae and the armored Scelidosauridae. The Heterodontosauridae were bipedal forms that foraged 1 meter above the ground. The skull was sturdily built and had a well-developed dentition with robust, closely spaced cheek with distinct wear facets along the length of the tooth row. These dinosaurs would have been capable of processing relatively plant material. The Selidosauridae were quadrupedal forms characterized by robust, leaf-shaped teeth with high-angle double wear facets. Their foraging range was probably within 1 meter above the ground. The Tritylodontidae were small to medium-sized, extremely

mammal-like cynodont synapsids, which persisted well into the Middle Jurassic. They had multcuspid cheek teeth that met in complex occlusion and an extensive palinal power stroke, well suited for shredding fibrous plant material. These quadrupedal forms foraged within a meter above ground level. The structure of the shoulder girdle and forelimb suggests capability for digging, and wear on the enlarged incisors is consistent with digging for underground plant parts."
Terrestrial Ecosystems Through Time, pp.356-7

Early Jurassic terrestrial carnivores

Family Coelophysidae
Dilophosaurus weatherii length 6 meters - weight 300 to 500 kg Sinemurian-Pliensbachian
Image: © Alison Jeffs, from **Science Views**, by permission.

With the Rhaetian extinction of the basal Rauisuchia, the Dilophosaurine theropods emerged as the top predators of their day. The first of the great dinosaurian carnivores, the Dilophosaurs were active, graceful animals, easily able to tackle the contemporary prosauropods, vulcanodontid sauropods, and scelidosaurs that made up the main herbivorous fauna of the times. The double crest on the top of the head was probably a sexual display device.

Therapsids and Mammals

During the early Jurassic then, evolution seems to have polarised: on the one hand there were the ruling land animals, the great dinosaurs, which filled the ecological roles now taken up by medium-sized and large mammals; on the other hand the first mammals had appeared, and together with the Tritylodontid Therapsids they filled the small rodent and insectivore niche. The mammals were to remain small and individually insignificant - comparable to shrews, mice and rats of today - although doubtless very significant ecologically, for the 135 million years of the dinosaurs reign.

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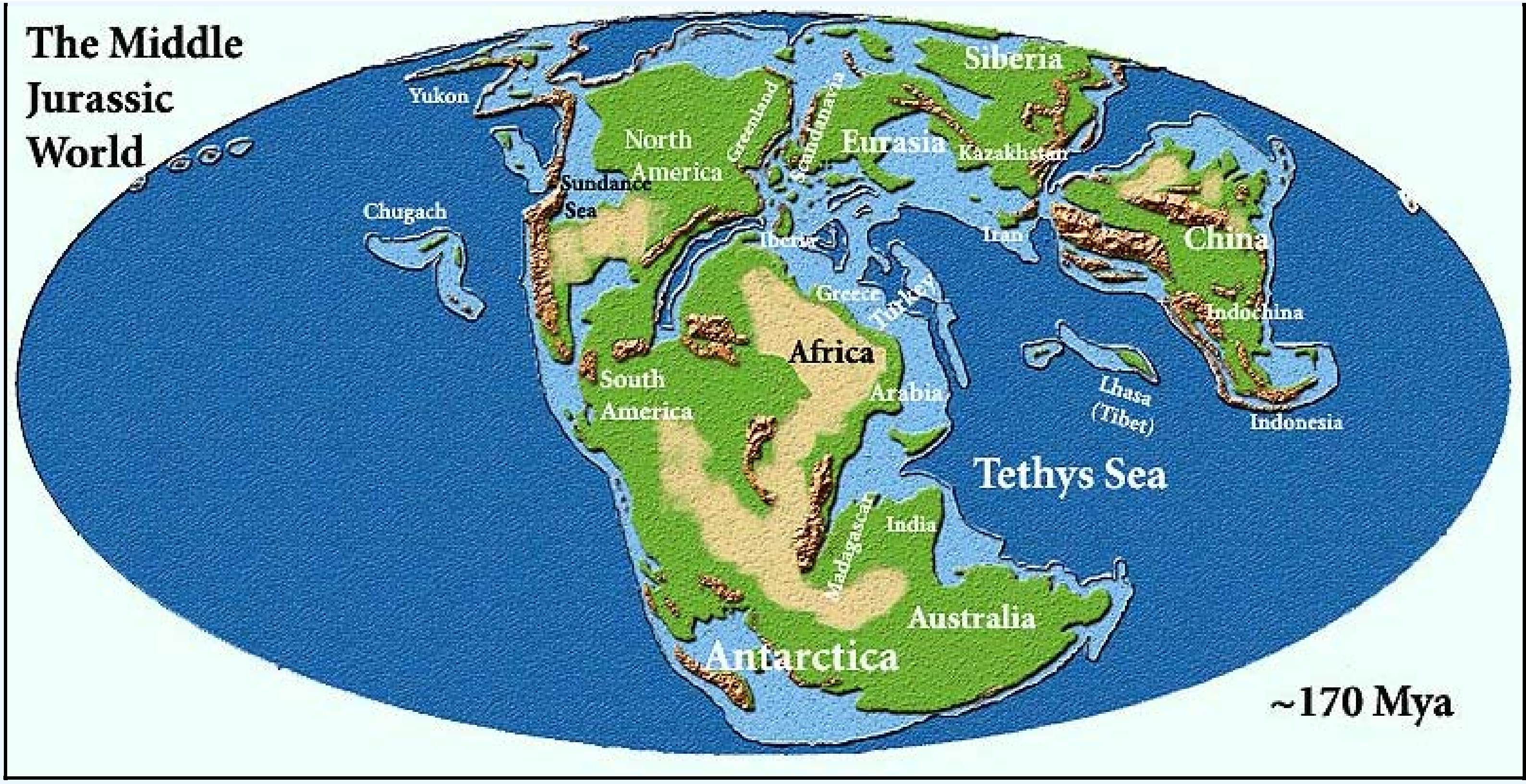
The Middle Jurassic

The Middle Jurassic Epoch of the Jurassic Period: 176 to 161 million years ago

- Phanerozoic
  - Mesozoic
    - Jurassic
      - Early Jurassic
      - Middle Jurassic
        - Aalenian Age
        - Bajocian Age
        - Bathonian Age
        - Callovian Age
      - Late Jurassic
    - Cretaceous

- Middle Jurassic
  - Stratigraphy
  - Geography

Middle Jurassic Geography



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Middle Jurassic Stratigraphy

Middle Jurassic	Callovian Age
	Bathonian Age
	Bajocian Age
	Aalenian Age

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The Bajocian

The Bajocian Age of the Middle Jurassic Epoch: 172 to 168 million years ago

Phanerozoic
  Mesozoic
    Jurassic
      Early Jurassic
      Middle Jurassic
        Aalenian Age
        Bajocian Age
        Bathonian Age
        Callovian Age
      Late Jurassic
    Cretaceous

The Bajocian Age
  Introduction
  Life
    Other Invertebrates
      Annelida
      Brachiopoda
      Cnidaria
      Echinodermata

Introduction

The Bajocian Age was originally supposed to be the lowest one third of the "Oolite" (Middle Jurassic). Thus it was first referred to, by William Smith, no less, as the "Under Oolite." (Later the business of naming strata fell into the hands of persons who disapproved of Anglo-Saxonisms, and it became the "Inferior Oolite.") As often happens in geology, this naive first intention was corrupted by other, equally well-intentioned, folk trying to square the original intention with new data. The three parts of the original Middle Jurassic Series are no longer of exactly equal size, and it became necessary to squeeze a *fourth* "third" (the Aalenian) between the Bajocian and the Toarcian. As currently defined, the Bajocian begins at the level where the ammonite *Hyperlioceras* replaces the Aalenian *Lioceras* near the old lighthouse of Cabo Mondego, on the Atlantic coast of Portugal, not far from Figueira da Foz and the ancient (pre-Roman!) university town of Coimbra.

The Bajocian marks the opening of the South Atlantic, at least so we are told. If this were actually the case, there would *be* no Aalenian ammonites at Cabo Mondego. Probably what is intended is that the Bajocian marks the first period during which the North American and African cratons were separated by a measureable amount of deep-ocean crust. The South Atlantic itself was already perhaps 500 km wide, a long arm of the Tethys reaching southwest from Central Europe (since much of southern Europe was still part of Africa). *See* the Middle Jurassic map. In North America, the Sundance Sea covered large parts of the American and Canadian West. That region was also subject to ocasional large volcanic eruptions, as small terranes sutured themselves to the west coast from Southern California to Alaska.

Bivalves and brachiopods were both present in large numbers (together with the inevitable ammonites and belemnites) abundance around the reefs. These reefs were of the Early Mesozoic type in which scleractinian corals grew on a framework filled in by calcareous sponges. These probably looked much more like modern reefs than the rudist-dominated reefs of the later Mesozoic. Crinoids were still an important part of the fauna, although far less so than in Paleozoic times. Infaunal crustaceans shared the benthic domain with bivalves as they do today. The large marine fauna, by contrast, would have been rather strange. It included a mixture of early teleosts with many surviving non-teleosts, modern (Neoselachian) sharks, but also numerous ichthyosaurs and plesiosaurs. The seas were also "greener" than they are today, *i.e.* the green algae chlorophyll b-based life dominated over the red algae and chlorophyll c-based autotrophs. So, for example, the first tentatively planktonic foraminifera were just beginning to appear during the Bajocian.

On land, the vegetation generally consisted of conifers, cycads, ginkgos, ferns and horsetails. Many of the most familiar insect orders of today had not yet evolved, *e.g.*, ants, termites and advanced roaches. On the other hand paleopterans -- dragonflies and their cousins -- were far more common. Since there were as yet no birds, flying insect predators were probably much more common. Small mammaliformes also helped control the insect population. The dinosaurs already dominated the large terrestrial niches. *Cetiosaurus* and *Rhoetosaurus* show the increasing importance of sauropods, while *Lufengosaurus* was one of the last of the prosauropods. Basal coelurosaurs were common theropods.

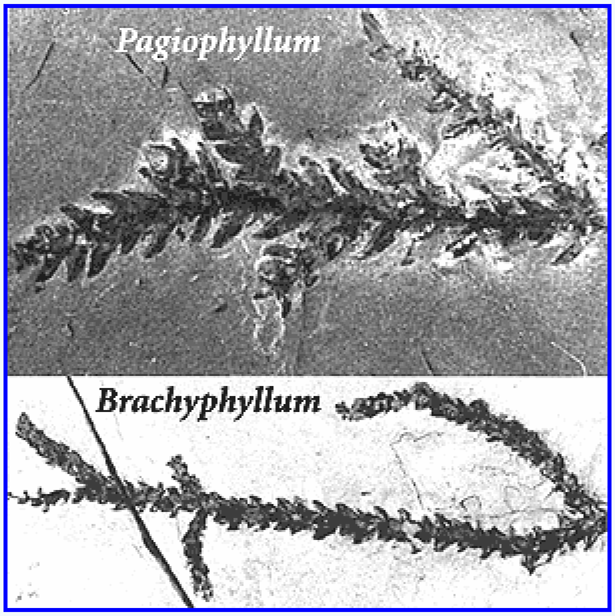

Image credit: (a) *Hyperlioceras* from **Echinologia**. (b) *Cetiosaurus* from **Yahoo!** *Pagiophyllum* and *Brachyphyllum* (conifers) from Cornet & McDonald (1995) **[1]**.

Links: DinoData Timeperiods Bajocian, Aalenian - Bajocian - GCR block, EARLY STRATIGRAPHIC RECORD AND MAJOR EVOLUTIONARY CHANGES OF THE ..., Image catalog, Bajocian to Oxfordian palynology of the Poland, My Fossils from Figueira da Foz, Radiolaria and Geological Age, Ammonites stratotyp stratotype bajocien bajocian.

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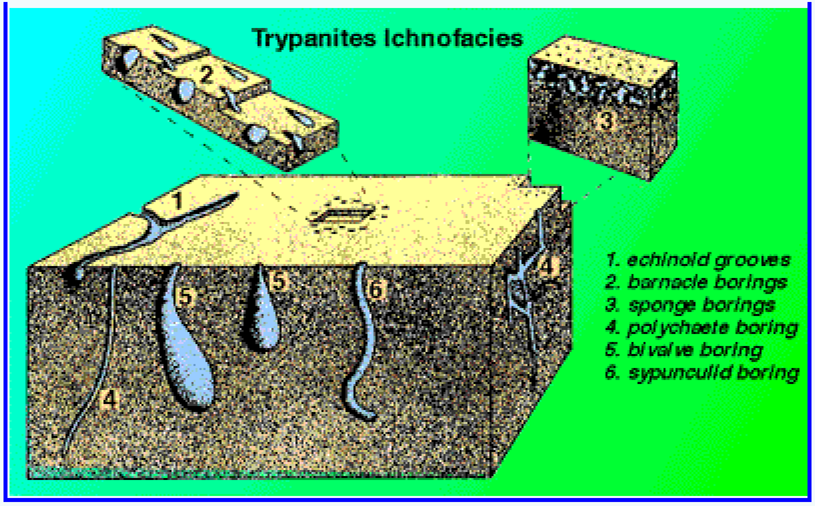
Bajocian Life

Other Invertebrates

Annelida

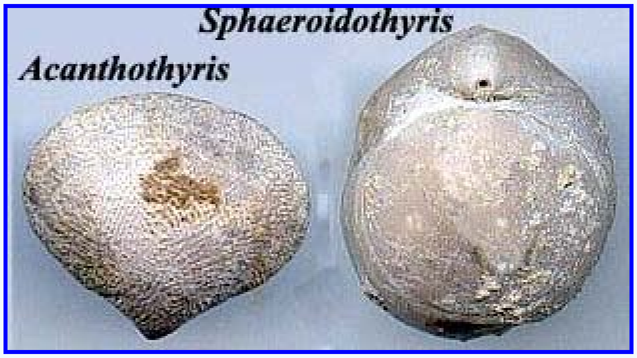
As usual, annelid fossils are rarer than galliform molars. However, Bajocian sediments frequently bear the long, narrow, slightly curved, and sometimes branched borings known as *Trypanites*. These are generally attributed to polychaete predators.



Brachiopoda

Typical Bajocian brachiopods are various species of the genera *Acanthothyris* and *Sphaeroidothyris*. The two in the image are actually Bathonian, but we're hoping you can't tell the difference.

Tethyan brachiopods suffered near extinction at the end of the Pleinsbachian in the Early Jurassic. In the early Bajocian, brachiopods recovered most of this lost diversity, only to lose most of their gains towards the end of Bajocian. This cycle of boom and bust characterizes Mesozoic brachiopods. Bivalves show similar cycles, but the changes are not as dramatic. Ruban (2004). Consequently, the bivalves had greater genetic resources to call on at the beginning of each cycle, and so gained steadily on brachiopods over the course of the next hundred million years.



As an aside, we occasionally wonder about the actual synchrony of these events on a worldwide scale. Who ordered this? Do we really need to invoke the invisible hand of mass extinction to explain anything here? Brachiopods evolved to fill a particular niche. They were, and are, suspension feeders specialized for areas of clear water, relatively low-energy, and stable substrates. Given those conditions, they are spectacular at turning detritus into biomass and are relatively impervious to the perils of depth, temperature, and predation. The brachiopod minimum daily requirements were very common in the Cambrian, reasonably common in the Ordovician, and relatively less common in the Mesozoic -- particularly in the heavily studied Tethyan area.

Mass extinction studies are normally done with a maximum resolution of ±1 My. In fact, we can't usually be much more precise than that for *any* event in the Jurassic. But all that's required for a global "mass extinction" is a *single* year with some combination of serious volcanoes, a few monster storms and some toxic algal blooms. Unlikely? Sure, but a lot can happen in two million years. Our idea of what is "likely," based on our own miniscule life span, really isn't a consideration. At least on a local level, "mass extinctions" probably happen every few centuries. If bivalves had had even the slightest long-term genetic advantage over brachiopods in responding to such events, the entire taxon would, in geological terms, have vanished faster than an assistant prof. with a two-year grant to study body-surfing in Hawaii.

For long-term, incremental faunal changes, we need to look for long-term, incremental environmental changes. The environmental factors needed for a happy brachiopod are well-understood. The reduced availability of those factors in the Mesozoic is likewise well understood. Why, in the name of Bill Occam's long mustache, do we need to invoke some pointlessly convoluted genetic explanation? Brachiopods don't suffer from "racial senescence," moral decadence, or a wasting disease. In their own part of ecospace, they can still lick any bivalve in the house with one lophophore tied behind their backs (if they had backs, that is). Their only problem is that, like a lot of the stratigraphers who study brachiopods, they're well-qualified specialists in a field that simply has fewer openings than it used to have.


Unidentified Jurassic crinoid from England -- possibly Late Jurassic

Cnidaria

Scleractinian corals peaked as reef builders during the Bajocian or somewhat later, depending on exact location. After this point, the rising seas began to drown the carbonate platforms around the Tethys which were their normal habitat. However, in the Bajocian, coral reefs were thriving even in areas well outside the tropics, from the Paris Basin all the way south to Tanzania, as marine conditions invaded the growing gap between Africa and East Gondwana (Madagascar, India and Antarctica). The coral belt also stretched from Iberia east to at least Kazakhstan and presumably China. For some reason, corals are very rare along the west coast of North America at this time, even in the warm, shallow waters of the Sundance Sea.

Echinodermata


The innapropriately named *Disaster granulosus*

The Bajocian marked a turning point for two large taxa of echinoderms. For the crinoids, it was virtually the last age in which stalked crinoids contested for dominance of shallow-water habitats. Radwanska & Radwanski (2003) report that the Bajocian 1-2 cm diameter North European "stalk ossicles" known as *Cyclocrinus* are actually the branched roots of some monster crinoid whose exposed parts have never been identified. They speculate that storms of unusual size may have been responsible for decimating these populations. We note, in addition, recent evidence that a lower mantle plume was tossing the Arabian plate around at the time. Magmatic inclusions all over eastern Eurasia show the strains this was putting on the neighborhood. These data have special interest for the preceding discussion of brachiopods. At any event, these last shallow-water crinoid communities were replaced by bivalves at the end of Bajocian time.

For the heart urchins, the Bajocian was the beginning of a period of major renewal. After near-extinction at the end of the Permian, the Irregularia had puttered along, and a handful of rare species are known from the Triassic and Early Jurassic. In the Middle Jurassic, the dominant, and perhaps sole, genus bore the inauspicious name of *Disaster*. Notwithstanding the name, *Disaster* was a great success. It soon diversified into a number of new forms, which gave rise two whole new orders in the Neocomian: the Holasteroidea and the Spatangoida. Eble (1999).

Porifera

The usual doctrine for the Mesozoic is that Triassic sponge reefs were replaced by the "advanced" scleractinian corals. In the Middle Jurassic, that order was actually reversed. The Bajocian marine transgression (a time when the sea rose to cover previously dry land) was the first step in the drowning of the marine carbonate platforms on which the corals grew. As the waters rose, the coral reefs grew further from their optimum level of sunlight. Coral growth slowed down. As the corals began to grow less aggressively,hexactinellid and lithistid sponges began to reappear, forming mixed sponge-coral reefs. This was a pattern seen all over western Europe in the Bajocian and subsequently elsewhere.

Image Credits: *Trypanites* from **Urme Fosile** (Dr. Sorin Filipescu, Univ. Babes-Bolyai, Romania), adapted from Benton & Harper (1997). *Acanthothyris* and *Sphaeroidothyris* from **The Jurassic Fossil Room**. Crinoid from **Discovering Fossils**. *Disaster* from the Natural History Museum's **Echinoid Directory**.

Links: CHECKLIST OF Jurassic BRYOZOANS; Burton Bradstock - Geology Field Trip Guide

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Palaeos: Mesozoic

Jurassic Period

Late Jurassic Epoch

LATE JURASSIC

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Late Jurassic - The Malm Epoch

The Late Jurassic Epoch: 161 to 146 million years ago

The Acme of the Dinosaurs

- **Phanerozoic**
  - **Mesozoic Era**
    - **Jurassic Period**
      - **Early Jurassic Epoch** (Lias)
      - **Middle Jurassic Epoch** (Dogger)
      - **Late Jurassic Epoch** (Malm)
        - **Oxfordian Age**
        - **Kimmeridgian Age**
        - **Tithonian Age**
    - **Cretaceous Period**
      - **Early Cretaceous Epoch**
      - **Late Cretaceous Epoch**

Late Kimmeridgian/early Tithonian dinosaurs of West Laurasia
image from American Museum of Natural History - Timelines Exhibit Dinosaurs from left to right are two individuals of the primitive theropod *Ceratosaurus* (6 meters), the ornithopod herbivore *Camptosaurus* (5 meters), the giant long necked sauropod *Barosaurus* (20 to 25 meters), in the background, and the small bird-like theropod *Ornitholestes* (2 meters) lower right

The late Jurassic period sees the evolution of some of the greatest dinosaurs of all. The sauropods continue to flourish and to diversify, as the older Mid-Jurassic cetiosaurids are replaced by a diverse Late Jurassic fauna of camarasaurs, Brachiosaurs, and diplodocids. Some of these creatures attained tremendous size. Thegiraffe-like *Brachiosaurus* reached 22 metres and weighed 15 tonnes and more. The *Seismosaurus*, a more slender animal, exceeded 40 metres in length

In addition there were many other types of animals around at this time: a number of different types of mammals, crocodiles, turtles, lizards, frogs, flying reptiles (Pterosaurs), marine reptiles, and the first birds (*Archaeopteryx*).

Late Jurassic (Malm Epoch)	Tithonian Age
	Kimmeridgian Age
	Oxfordian Age

Biogeographic Provinces

Much can be gleaned of the biogeography of this ancient world by studying the distribution of the dinosaurs. Four localities of importance as regards fossil remains are known: central North America (the Morrison formation of the South-West), East Africa (Tendaguru formation of Mkwoa wa Mtwara, Tanzania), Europe (scattered localities mainly in England, France, Bavaria, and Portugal), and China (especially the Upper Shangshaximiao Formation of Sichuan Province). Smaller vertebrates and invertebrates are also known in abundance from France and Bavaria. A comparison of the types of creatures from these localities shows often the same family, and sometimes even the same genus, is represented in different localities, showing that, just as in the preceding Triassic period, the world was a much more biotically uniform place than it is now. This is due to the fact that all the continents had merged into a single landmass. Yet high sea levels broke this supercontinent into a series of large islands, causing regional differences and faunal as well as floral provinces.

The following faunal (and megafaunal) provinces can be tentatively distinguished:

West Laurasian: - see top of page: Probably everyone is familiar with the great American dinosaurs of the Jurassic: the huge Brontosaurus (more properly called *Apatosaurus*), its slender cousin *Diplodocus*, the large carnivores *Allosaurus* and *Ceratosaurus*, and the striking plated *Stegosaurus*. Alongside these were a number of smaller herbivores and carnivores (*Camptosaurus*, *Dryosaurus*, *Ornitholestes*, etc). In this megafauna sauropods predominated, and were primarily of the diplodocid and camarasaurid families, with a few haplocanthosaurs (especially early on) and the occasional huge Brachiosaur (in fact the Brachiosaurs were bigger here than anywhere else). As Dr Bob Bakker has shown, the West Laurasian dinosaurs exhibited a tendency to increase in size, possibly caused by increasingly harsh and arid conditions, so that by the mid Tithonian they were truly gigantic. Then they suddenly died out, leaving a number of small dinosaurs, mammals, and lower vertebrates to carry on.

West Gondwanaland. West Gondwanaland (e.g. Africa) had a fauna very similar to that of North America, with many types of dinosaurs in common. The theropod *Ceratosaurus*, the diplodocid *Barosaurus*, and the ornithopod *Dryosaurus* occur on both continents. But the Laurasian *Camarasaurus* is absent, and the mighty *Brachiosaurus*, which is rare in North America (West Laurasia), is the most common sauropod in the Tendaguru formation (West Gondwana). However, it appears to be a distinct genus (designated *Giraffititan*) from the West Laurasian form. The small stegosaur *Kentrosaurus* closely resembles primitive European and Chinese forms, but is quite unlike the large and advanced American *Stegosaurus*. Pterosaurs are known too, these belong to the same genus (*Rhamphorhynchus*) that inhabited the islands of Europe. There were also several types of dinosaurs that were Gondwanan endemics as well. Of significance were *Dicraeosaurus* (a small short-necked persistently primitive diplodocoid sauropod), *Torniera* (a medium-sized sauropod, possibly ancestral to the Cretaceous Titanosauridae), and the poorly known ceratosaur *Elaphrosaurus*. These three taxa indicate the development of a unique Gondwanaland fauna.

Central Laurasia: Whereas Africa and North America were large landmasses, Europe during the Jurassic seems to have consisted of a number of large islands separated by shallow sea. A number of different types of dinosaurs have been found in Portugal. They include not only most "standard" Jurassic types (brachiosaurids, Stegosaurs, megalosaurs, etc) but also small nodosaurid ankylosaurs [armoured dinosaurs]). As with the early Jurassic scelidosaurs, this latter group are almost totally indigenous to Europe (which may well be the centre of evolution of these armoured dinosaurs) during the Jurassic period. But during the following early Cretaceous period they spread throughout the globe. The first protobirds like *Archaeopteryx* also inhabited the islands of Europe, no doubt benefiting from the isolation from large predators and tendency to evolutionary novelty that small islands provide.

East Laurasia and **East Gondwana:** Animals on the Eastern part of the world-continent remained quite different to those of the west. Stegosaurs were exceedingly diverse in China, and include both primitive and advanced forms. They lived alongside basal (ancestral) marginocephalians, persistently primitive euhelopid sauropods and Triassic holdovers like tritylodontid therapsids and short-headed brachyopid labyrinthodonts. Similar chigutosaurid labyrinthodonts must have lived in East Gondwanaland (Australia) as well, because they are known there from both the Early Jurassic and the middle Cretaceous. Allosaurids are also known from the Late Jurassic of China and the middle Cretaceous of Australia, indicating that these carnivores were able to wander widely over the Earth's surface (unlike the euhelopid sauropods which are not known outside of China).

Fossil-bearing Stratigraphic Table

note: although the dating of marine sediments is generally well worked out with ammonite zones, the dating of terrestrial (including dinosaur containing) sediments is often a *lot* more speculative, because there is no standard of ammonites or other marine organisms to go by. So the dinosaurian correlations listed on this table (four right-hand columns) may or may not have lived at this precise time, although they certainly lived somewhere around that period. I haven't even attempted to correlate the Chinese dinosaurian faunas - estimates of their age range from Oxfordian to Tithonian - i.e. the entire span of the late Jurassic! The megafauna there is however generally more primitive than that of North America, which may indicate it would be earlier rather than later - perhaps later Oxfordian or Kimmeridgian rather than Tithonian. Then again it may not!

standard age	**subdivision**	**est. time mya**	**equivalent dinoflagellate zone**	**ammonite zone**	**Europe (England)**	**Europe (Portugal, France, &Germany)**	**North America (Morrison Fm)**	**Tanzania Africa (Tendaguru Fm.)**
Tithonian	**Portland-ian**	145 146 147	***Dichadogonyaulax culmula***	*Subcraspedites lamplughi* *Subcraspedites preplicomphalus* *Subcraspedites primitivus* *Titanites oppresus* *Titanites anguiformis* *Galbanites kerberus* *Galbanites okusensis* *Galbanites glaucolithus* *Progalbanites albani*	**Purbeck Beds** ——— **Portland Beds**	unnamed units France	small faunas following megafauna extinction	
	"Late Kimmerid-gian" (= Lower, Middle, and part of Upper Tithonian)	148	***Gonyaulacysta perforans***	***Virgatopavlovia fittoni*** *Pavlovia rotunda* *Pavlovia pallasiodes* ***Pectinatites pectinatus***	**Upper Kimmeridge Clay**		***Apatosaurus ajax* zone**	
		150	***Gonyaulacysta longicornis***	***Pectinatites hudlestoni*** ***Pectinatites** wheatleyensis* ***Pectinatites scitulus*** ***Pectinatites elegans***	**Middle Kimmeridge Clay**	**Solenhofen Limestone (Bavaria)**	***Camarasaurus lentus* zone**	**Upper Saurian Bed** Upper Transitional Sands Lower Transitional Sands **Middle Saurian Bed**
Kimmeridgian	**(Late)**	151		***Aulacostephanus autissiodorensis***	**Lower Kimmeridge Clay**	**Lithographic stone, Cerin (France)**	***Haplocanthus* zone**	
		152	***Epiplosphaera bireticulata***	***Aulacostephanus eudoxis*** ***Aulacostephanoides mutabilis*** ***Rasenia cymodoce***				
	(Early)	153				unnamed units, France and Portugal		
		154	***Stephanelytron redcliffense***	***Pictonia baylei***				
Oxfordian	**Late Oxfordian**	155 156		***Amoeboceras rosenkrantzi*** ***Amoeboceras regulare*** ***Amoeboceras serratum*** ***Amoeboceras glosense***	**Ampthill Clay**			
	Middle Oxfordian	157		***Cardioceras tenuiserratum*** ***Cardioceras densiplicatum***	**Coralline Oolite**			
	Early Oxfordian	158	***Wannaea fimbriata***	***Cardioceras cordatum*** ***Quenstedtoceras mariae***	**Upper Oxford Clay**			
a	**b**	**c**	**d**	**e**	**f**	**g**	**h**	**i**

notes:

col. (a) gives the standard series of "Ages" or "Stages". This is the time division beneath "epoch" on the geological/stratigraphic time-scale). I consider these time-divisions (and the others of the Mesozoic) to be "epochs", because with spans (in the case of the Tithonian and Oxfordian) of around 5 or 6 million years or so each they are closer in duration to epochs than to "ages" (which at least in the Cenozoic are shorter - say in the order of one to three million years).

col (b) gives the sub-divisions (what I would term "ages"). This follows W. B. Harland *et. al*, 1982, *A Geologic Time Scale*, p.29, apart from the subdivision of the Kimmeridgian into Early and Late, which is based on casual references in Weishampel *et al* (*The Dinosauria*), and comments under "Late Kimmeridgian" which are from Thomas Holtz's post to the Dinosaur mail list. This indicates that the Tithonian could perhaps be subdivided into four ages, the Early, Middle, earlier Late, and Portlandian (later Late), each lasting around one or two million years or so.

col (c) is a purely extravagant and fanciful correlation of these stages given in terms of millions of years ago, on the basis of combining the dates given by Harland, Armstrong, Cox, Lorraine, Smith and Smith, *A Geologic Time Scale 1989*; and Gradstein, Agterberg, Ogg, Hardenbol, van Veen, Thierry and Huang "A Triassic, Jurassic and Cretaceous time scale". It is intended as a very approximate guide and should not be taken too seriously.

col (d) gives marine Dinoflagellate zonation, according to W. B. Harland *et al.*, 1982, *A Geologic Time Scale*, p.29

col (e) gives marine Ammonite zonation, according to W. B. Harland *et al.*, 1982, *A Geologic Time Scale* p.29, and *British Mesozoic Fossils*, pp.15-16

col (f) presents a simplistic representation of the general stratigraphic marine sequence from England, on the basis of W. B. Harland *et al.* p. 28, and *British Mesozoic Fossils*, pp.15-16

col (g) gives some terrestrial strata (many of which are unnamed). The famous Solnhofen limestone where *Archaeopteryx* and many other animals have been found preserved is given as only "?Kimmeridgian" by Weishampel *et al* (*The Dinosauria*) but "Lower [=Early] Tithonian" by Wellnhofer. The age of the Lithographic Limestone of Cerin, where many small crocodilians and other small vertebrates have been found, is given as "Late Kimmeridgian" by Weishampel *et al*.

col (h) gives the zonation of dinosaurs from the Morrison formation, according to Robert Bakker (see e.g. *The Dinosaur Heresies*, p.400). The stratigraphic correlation of each of these stages is pure fancy on my part. The date of the Morrison formation is given as "Kimmeridgian-Tithonian." by Weishampel *et al* (citing Dodson, Behrensmeyer and Bakker "Taphonomy of the Morrison and Cloverly Formation of the western United States" in *Ecosystèmes Continentaux du Mésozoïque*, Mémoires de la Société Géologique de France, no.139,), but Greg Paul gives the age uniformly as Tithonian, and Peter Wellnhofer has Tithonian likewise for Como Bluff (= *Camarasaurus lentus* zone) and Dry Mesa (=*Apatosaurus ajax* zone).

col (i) gives the zonation of the Tendaguru formation, [ref. D. Russell *et al*]. In that article the authors write: "Marine sandstones within the Tendaguru Beds contain ammonites indicative of an Upper Kimmeridgian-Tithonian age for the two main dinosaur-producing units (Aitken 1961)" [p.169] and "The morphological difference between barosaurs and dicraeosaurs above and below the marine sands suggest that the *Trigonia smeei* Bed (that separates the Middle and Upper Saurian Beds) was deposited over an interval of the order of one million years." [p.172]. However, Weishampel *et al* , also quoting Aitken, W.G., 1961 [Geology and Palaeontology of the Jurassic and Cretaceous of southern Tanganyika, *Geological Survey of Tanganyika, Bulletin* 31] give the age of the Tendaguru as simply "Kimmeridgian". Greg Paul gives it as "Tithonian", and Peter Wellnhofer has only a cautious "Upper Jurassic" for the Upper Saurian Bed.

References

- *British Mesozoic Fossils*, 2nd Ed., British Museum (Natural History), London, 1964
- Robert Bakker, 1986, *The Dinosaur Heresies*, p.400 (Longman)
- W. B. Harland, A.V. Cox, P. G. Llewellyn, C.A.G. Pickton, A.G. Smith and R. Walters, 1982, *A Geologic Time Scale* Cambridge University Press (unfortunately I don't have the later edition on me)
- Gregory S. Paul, 1988, *Predatory Dinosaurs of the World*, Simon & Schuster
- D. Russell, P. Béland, & J.S. McIntosh, 1980, "Paleoecology of the dinosaurs of Tendaguru (Tanzania)" in *Ecosystèmes Continentaux du Mésozoïque*, Mémoires de la Société Géologique de France, no.139, pp.169-175
- David B. Weishampel, Peter Dodson, and Halszka Osmólska, eds., 1988, *The Dinosauria*,
- Peter Wellnhofer, 1991, *The Illustrated Encyclopedia of Pterosaurs*, Crescent Books, New York, p.107
- Re. Portlandian - Thomas Holtz

miscellaneous comments

The term "Malm epoch" is used by W. B. Harland et al., in *A Geologic Time Scale*, to refer to the third division of the Jurassic Period (i.e. the

Late Jurassic). "Malm" was originally part of the three-fold division of Jurassic rocks in Britain, but has since become a more universal term (thanks to the accident of history that modern geology and paleontology started in Britain).

Personally I feel "epoch" (which is usually used to refer to periods like the Eocene, Oligocene etc) is inappropriate for a division on this scale (over 20 million years) and I would prefer "sub-period"

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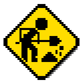 This page is not yet ready

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Cretaceous period

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Cretaceous Period

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The Cretaceous Period - 1

The Cretaceous Period of the Mesozoic Era: 146 to 65.5 million years ago

Mesozoic
  Triassic
  Jurassic
  Cretaceous
    Early Cretaceous I (Neocomian)
    Early Cretaceous II (Aptian-Albian)
    Late Cretaceous I (High Cretaceous)
    Late Cretaceous II (End-Cretaceous)
Cenozoic
  Paleogene

Introduction

In 1822 the Belgian geologist D'Omalius d'Halloy gave the name *Terrain Cretace*, for the chalk and rock outcrops of the Paris Basin, and for similar deposits in Belgium and Holland and traceable also from England eastward into Sweden and Poland.

This term "Cretaceous" "chalk-bearing" (from *Creta*, the Latin word for chalk) later came to be used. The famous White Cliffs of Dover, are typical of this rock formation. Extensive chalk deposits were laid down in Europe and parts of North America during this period. The chalk itself is actually formed from the shells of countless micro-organisms.

William Smith had previously mapped four strata between the lower clay (= early Tertiary) and the "Portland Stone" (= late Jurassic), namely White Chalk, Brown or Grey Chalk, Greensand, and Micaceous Clay or brick earth (later referred to as Blue Marl or Gault). In 1822 Conybeare and Phillips arranged these in two groups, the Chalk and the earlier strata, a division that has remained to the present day. In 1841 Leymerie introduced the term Neocomian for the lower division. Senonian was coined by d'Orbigny in 1842 for the later Cretaceous. The name "Gallic" has also been used for times that do not fall conveniently into either of the above two categories.

Cretaceous Geography

Much of the land masses are covered by shallow continental oceans and inland seas. Europe, Asia, Africa and North

America are all a series of islands. Marked regional differences in floras and faunas between the northern and southern continents developed, and indeed there were even differences in flora and fauna from continent to continent.

The breakup of the world-continent Pangaea, which began during the Jurassic, continued apace.

The Cretaceous saw the lengthening and widening of Atlantic Ocean, which especially spread further south, while the Alps were formed in Europe. India broke free of Gondwanaland and became an island continent, much like Australia is now. Africa and South America split apart, Africa moving north and closing the gap that was once the Tethys sea. The continents began to take on their modern forms.

Cretaceous Stratigraphy

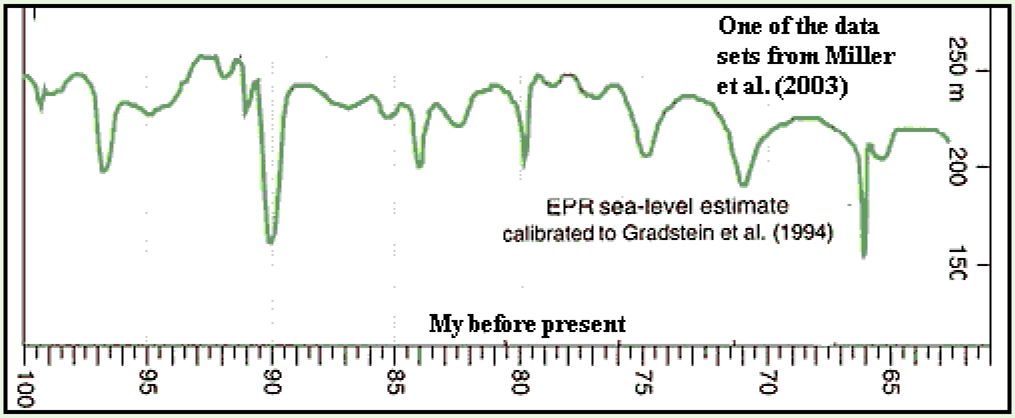
Period	**Epoch (ICS, with added subdivision)**	**Harland Epoch**	**Age**	**ICS Base**	**ICS Duration**
Paleogene	Paleocene: 9.7 My	Paleocene	**Danian**	**65.5**	**3.8**
Cretaceous 80.0 My	Late Cretaceous II (End-Cretaceous) 18.0 My	Senonian	**Maastrichtian**	**70.6**	**5.1**
			Campanian	**83.5**	**12.9**
	Late Cretaceous I (The "High Cretaceous") 16.1 My		**Santonian**	**85.8**	**2.3**
			Coniacian	**89.3**	**3.5**
		Gallic	**Turonian**	**93.5**	**4.2**
			Cenomanian	**99.6**	**6.1**
	Early Cretaceous II (Aptian-Albian) 25.4 My		**Albian**	**112.0**	**12.4**
			Aptian	**125.0**	**13.0**
	Early Cretaceous I ("Neocomian") 20.5 My		**Barremian**	**130.0**	**5.0**
		Neocomian	**Hauterivian**	**136.4**	**6.4**
			Valanginian	**140.2**	**3.8**
			Berriasian	**145.5**	**5.3**
Jurassic	Late Jurassic: 15.7 My	Malm	**Tithonian**	**150.8**	**5.3**

This site originally used the Harland three-fold division of the Cretaceous into Neocomian, Gallic, and Senonian Epochs. As of this writing (040911) we are in the process of gradually converting to the ICS system, which recognizes only Early and Late Cretaceous epochs. Unfortunately, the ICS Cretaceous epochs are unreasonably long for our purposes, so we have taken the further step of dividing both of them into two.

Our "Neocomian" division is based largely on climatic considerations. This "Early Early Cretaceous" demi-epoch was a time of steadily rising seas and temperatures. According to one source, the ocean temperature increased an almost unbelievable 17 C° over the Early Cretaceous, and the bulk of this must increase must have occurred in the Neocomian division. The Aptian-Albian division continued the Neocomian trend, but at a slower rate. The Aptian-Albian is also the interval that produced the definitive Cretaceous dinosaur clades. These dinosaurs dominated the large herbivore guild in the Late Cretaceous: the ornithischian iguanodonts (including hadrosaurs), Ceratopsia (e.g. *Triceratops*), and various saurischian titanosaurs. In the oceans, a final radiation of pliosaurs also occurred at about this time.

The Early Late Cretaceous ("High Cretaceous") was marked by several critical events. The first was the widening Atlantic rift. The Atlantic Ocean: (a) had become wide enough to become a complete barrier to east-west dispersal over its entire length, except in the far north, and (b) was circulating meaningful amounts of ocean water north and south. The initial results seem somewhat paradoxical. On the one hand, the High Cretaceous experienced unprecedented uniformity of ocean temperatures from pole to pole, suggesting very good horizontal mixing of ocean waters. On the other hand, it is well known for sporadic deep ocean anoxia, which would indicate poor vertical mixing. It is tempting to speculate on the causes of this peculiar set of events. One strong line of evidence implicates methane and/or carbon dioxide outgassing. But most of this data comes from the Atlantic basin. In due course, we will have enough information from the Pacific to give us a better global perspective.

The second major event of the High Cretaceous was angiosperm dominance. Angiosperm plants had begun to spread at least as early as the middle Neocomian. However, during the High Cretaceous, angiosperms reached some critical mass or critical stage of development and became the dominant type of plant in most parts of the world. Finally, the long, gradual increase in sea levels which began in the Triassic reached its peak in the High Cretaceous.

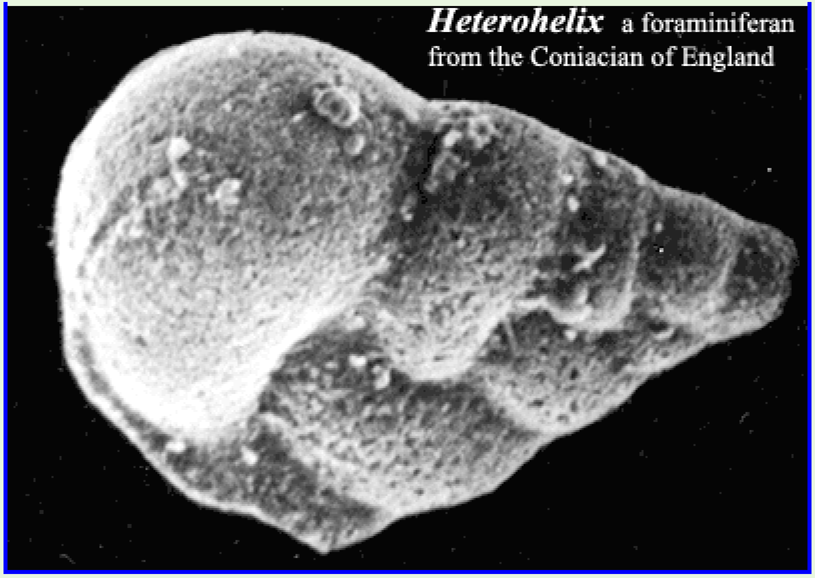


During the End-Cretaceous, sea levels began to retreat after 165 million years of advances. Miller *et al.* (2003) have recently reported that the peak and decline of sea levels in the Late Cretaceous is punctuated by a number of sudden, drastic, marine regressions. Apparently, the oceans retreated quite quickly, and, almost as quickly, returned to more or less their former depths. The pace of these changes appears to have been below the limit of geological resolution for their core samples, i.e. about <500Ky. Miller *et al*. state that their data are consistent only with the formation of short-lived, but rather extensive ice sheets in Antarctica. This conclusion is almost -- but not quite -- irreconcilable with what we know about Late Cretaceous climate. Miller's group coordinates data from a number of different regions in arriving at this result. While these sequences are diverse, they still cover only the Atlantic and Tethyan regions. Once again, we are badly in need of data from the Pacific Basin.

Cretaceous Life

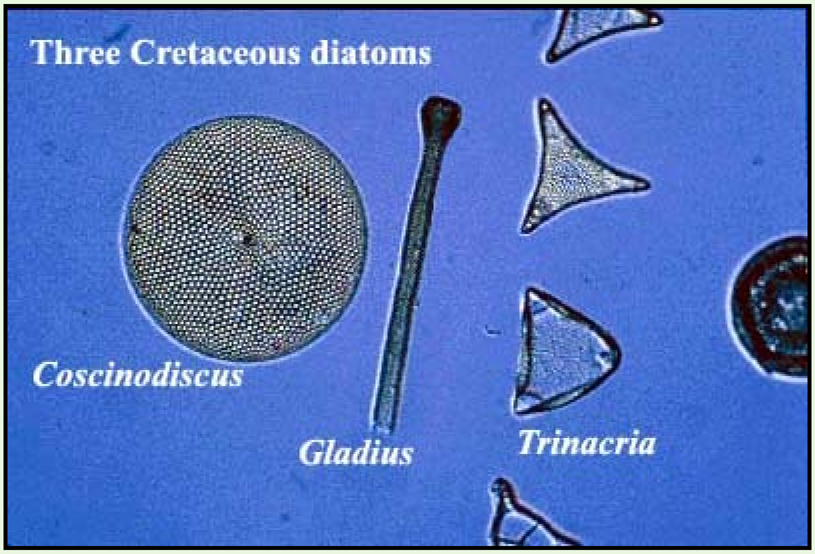
Small Stuff: Plankton &Microorganisms

The Cretaceous was as long and eventful for microorganisms as it was for nearly everything else. For terrestrial macro-organisms, the critical factor may have been the gradual spread and eventual domination of angiosperm plants in the Late Cretaceous. For marine macro-organisms, the driver may have been the gradual rise of sea levels over the course of the Early Cretaceous. We are pleased to report that this happy karmic balance is retained in microorganisms, which experienced great changes related to various events (not all of which are understood) over the middle Cretaceous,



specifically the Aptian-Albian episode and the earlier part of the High Cretaceous.

The main drivers at this time may have been changes in ocean chemistry, probably associated with the very active mid-ocean ridges of the time. Ocean crust was forming at a record rate, with all the usual geological belching and stretching that accompanies such events. Water temperatures became exceedingly, perhaps excessively, hot. Methane and carbon dioxide levels may have increased, and perhaps spiked at far above Early Mesozoic levels. Something seems to have happened to deep ocean circulation, since anoxic conditions prevailed at depth and black (poorly oxidized) shales formed from partially decomposed organic matter at several points during this middle part of the Cretaceous. Ocean fishes can often swim away from unpleasant environments. Single-celled organisms are bit more limited in their responses to deteriorating neighborhoods. Like reef biota or small grocery stores, they tend to adapt or die. Many died, but many adapted.



One trend which is likely related to these events is the mineralization of many microorganisms. Whether unmineralized versions of these organisms were present before the mid-Cretaceous, is sometimes hard to tell. However, beginning in the Aptian-Albian, we see a sharp increase in the diversity and biomass of marine organisms with mineralized skeletons. This bears remembering because that is *exactly* what happened during the only other time in Phanerozoic history when the sea floor spread at this rate -- the Cambrian Explosion of Cambrian Epoch 2. At that time, the biological first response was the evolution of the "small shelly fauna" of small, mineralized creatures. At the same point in the Cretaceous episode, we find new foraminifera, new coccolithophores and other armored algae (*e.g.*, silicoflagellates), and diatoms. We will briefly cover these forms and, finally, the Crenarcheota. This is a group so odd and so cryptic that their very existence was unknown until about 1998. Yet they are common in many oceans and may have played a major role in the events of the mid-Cretaceous.

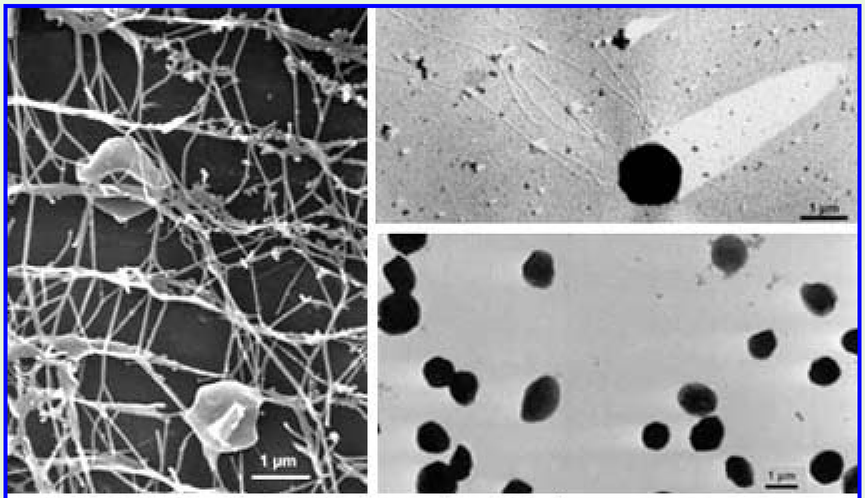
Foraminifera: of all the groups we will discuss, the forams were the least changed by the events of the Cretaceous. These are amoeboid protists with which evolved in the Early Cambrian -- possibly as part of the original small shelly fauna. They extend pseudopods through holes in their shell (or, more properly *test*), to feed on bacteria and small food particles, like radiolarians. *See, e.g.,* Acantharea. Also like radiolarians, they frequently live in symbiosis with photosynthetic protists, typically dinoflagellates. In the earliest forms, the test is formed simply by gluing together foreign particles. Simple shells appear in the Devonian, and the group gradually became planktonic, rather than benthic, over the course of the Mesozoic. A major turnover of planktonic foraminifera occurred, associated with many extinctions, during the first Ocean Anoxic Event ("OAE") of the mid-Aptian. The net result was a great diversification of planktonic forms with elaborate calcareous tests. *See, e.g.*, the image of *Heterohelix*.

Diatoms: Diatoms are eukaryotic, photosynthetic microorganisms that, today, are


Unidentified coccolithophore (probably Recent)

found in both fresh and salt water bodies throughout the world. They are said to account for the majority of marine primary productivity, and as much as 20% of the total photosynthetic activity on Earth. Yet they did not exist in any numbers prior to the mid-Cretaceous.

Calcareous nanoplankton: The Cretaceous Period was named for the great Late Cretaceous chalks of Northern Europe. These were formed from the tests of calcareous nanoplankton (armored algae), of which the best known are the coccolithophores. Nanoplankton with mineralized "armor" are known from the Late Triassic or Early Jurassic. Their fortunes seem to be tied rather directly to sea levels, so that their abundance peaked in the Late Cretaceous -- perhaps a bit later than the Aptian-Albian events we are discussing -- but perhaps not. It is not possible to make quantitative comparisons with much precision. Coccolithophores are responsible for some algal blooms today. One trigger for their rapid growth appears to be dissolved iron, which is often a limiting nutrient for algal growth. One school holds that iron released by new continental crust may have been responsible for massive blooms leading to the Mid-Cretaceous black shales and anoxic deep-ocean conditions. At any rate, some of the recoverable organic compounds from the black shales are biomarkers for haptophyte algae, a group that includes the coccolithophores. Bralower *et al.* (2002).

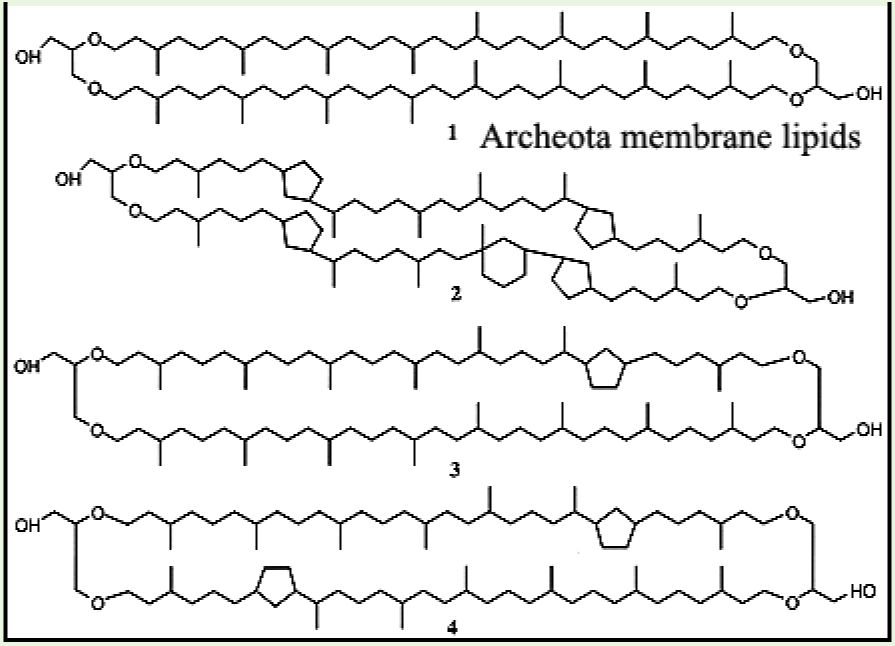


Three different species of Archeota

Why? The evolutionary "why" is a relatively easy question to answer. Tests provide some degree of physical protection, can be used to keep the cell in easy proximity to symbiotes, provide an ion reserve, can be used in at least two ways to control buoyancy, and allow extracellular storage of useful materials, among other advantages. The more difficult issue is why this became possible in the mid-Cretaceous and not before. What ocean chemistry made it easy to adopt such a difficult -- but ultimately useful -- piece of baggage?

Unfortunately, the answers involve rather complex geochemistry, which we are in no position to evaluate. One factor may have been the very low ratio of magnesium to calcium in Cretaceous seawater. This is another characteristic of the mid-Cretaceous which also applies to the Early Cambrian and was caused by the tendency of new ocean crust to lock up magnesium and release calcium. Calcite is nicely stable. Even an inefficient (evolving) test producer can work with calcite in a high-calcium sea, since calcite will hold together and doesn't require much maintenance.

The Mysterious Archeota: One recent hypothesis explains some (not all) of the weirdness of the Mid-Cretaceous with even greater weirdness -- The Archeota. The Archeota are one of the two principle divisions of the Archaea. The Archaea, in turn, are the sister group of the Eukarya. The Archeota were discovered in the 1990's. They are quite small, and tend to live in slightly less bizarre environments than other Archaea. In particular, they tend to be thermophiles, but do not require anything like the hellish conditions under which other



Archaea live. They cannot be cultured on conventional media. However, some can now be raised on a substrate of living sponges from which Archeote cells can be recovered in sufficient numbers and purity to do serious biochemistry. Although still poorly known, Archaeotes appear to be ubiquitous in the oceans. Schouten *et al*. (2000).

The critical finding is this: up to 80% of the recoverable organics from the black shales appear to be breakdown products from the unique membrane lipids of the Archeota. Any biochemist will assure you that these are very peculiar molecules. Unfortunately, the black shale organics are not these complete molecules, but even the breakdown products of these odd, cyclic diglycerol dialkylethers with inserted cyclopentane rings, are quite distinctive. It is not completely clear to us that these are precisely the same products described by Kenig *et al*. (2003) from both Archean (c. 2000 Mya) and modern sediments, but they seem closely related.

To add one more ingredient to the mix, it has recently been reported that archeotes mediate marine methane metabolism. Schouten *et al*. (2003). Specifically, archeotes work in tandem with sulfate- reducing bacteria to produce carbon dioxide and hydrogen sulfide from methane and sulfates under anaerobic conditions. The Mid-Aptian OAE, at least, is associated with a massive release of methane and an apparently large spike in world temperatures. This methane was, presumably, the abiotic product of processes in the mantle and was released during the frenzy of mid- ocean ridge spreading which occurred at this time. It is thus reasonable to speculate that the release of methane and associated temperature increase of the Mid-Aptian acted to trigger massive blooms of some relatively low temperature (for a thermophile) archeote and its sulfate reducing symbiotes. These microorganisms would eventually eliminate the excess methane, saving the Earth from long-term over-heating; but, in the process, would also generate enough toxic hydrogen sulfide to kill everything within a rather large radius of the archeote bloom.

It's a thought, anyway. But it still doesn't explain why everything developed silicate or calcite tests at this time.

Image Credits: *Heterohelix* from the **MIRACLE site** of University College, London. Cretaceous diatoms from the **Cushman Foundation for Foraminiferal Research**. Archeotes from **Ciència Hoje**. Archeote lipids from Damsté *et al*. (2002).

Links: Tectonics and plankton evolution during the Mid-Cretaceous; Foraminifera; CALCAREOUS MICROFOSSILS; Chapter 12, part 6, Lecture Notes, Life of the Mesozoic, Levin ..; Cretaceous nannoplankton evolution and diversity.

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The Cretaceous Period - 2

Mesozoic
  Triassic
  Jurassic
  Cretaceous
    Early Cretaceous I (Neocomian)
    Early Cretaceous II (Aptian-Albian)
    Late Cretaceous I (High Cretaceous)
    Late Cretaceous II (End-Cretaceous)
Cenozoic
  Paleogene

The Cretaceous
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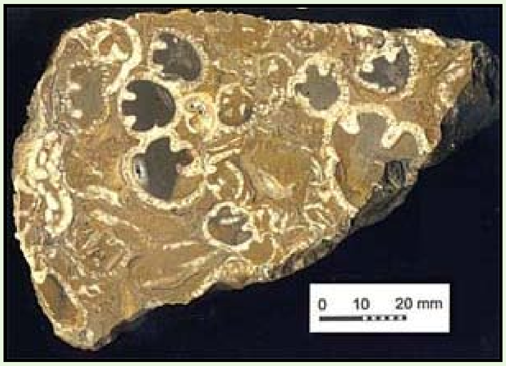
Cretaceous Reefs

See how the fates their gifts alot:
A is happy. B is not.
Yet B is worthy, I dare say
Of more prosperity than A . . .
But should A perish?
That should he --
That is, assuming I am B.

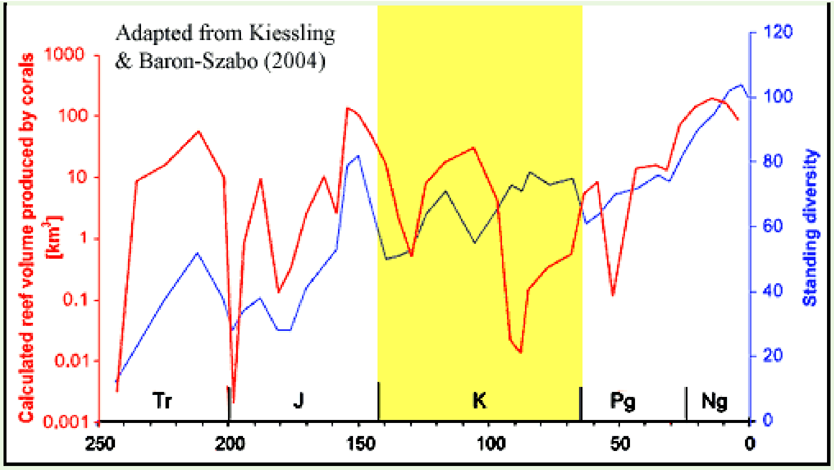
-- William S. Gilbert, **The Mikado**



Aberrant bivalve mollusks, known as rudists, dominated Cretaceous reefs. You can find more information, as well as clumsy evasions and outright speculation, in the sections on the Neocomian and the Aptian. Here, after some perfunctory remarks, we're going to take up the fate of another legion of reef builders, the scleractinian corals. We focus on corals, not only because they are important today, but also to investigate the role of ecological competition in evolution.

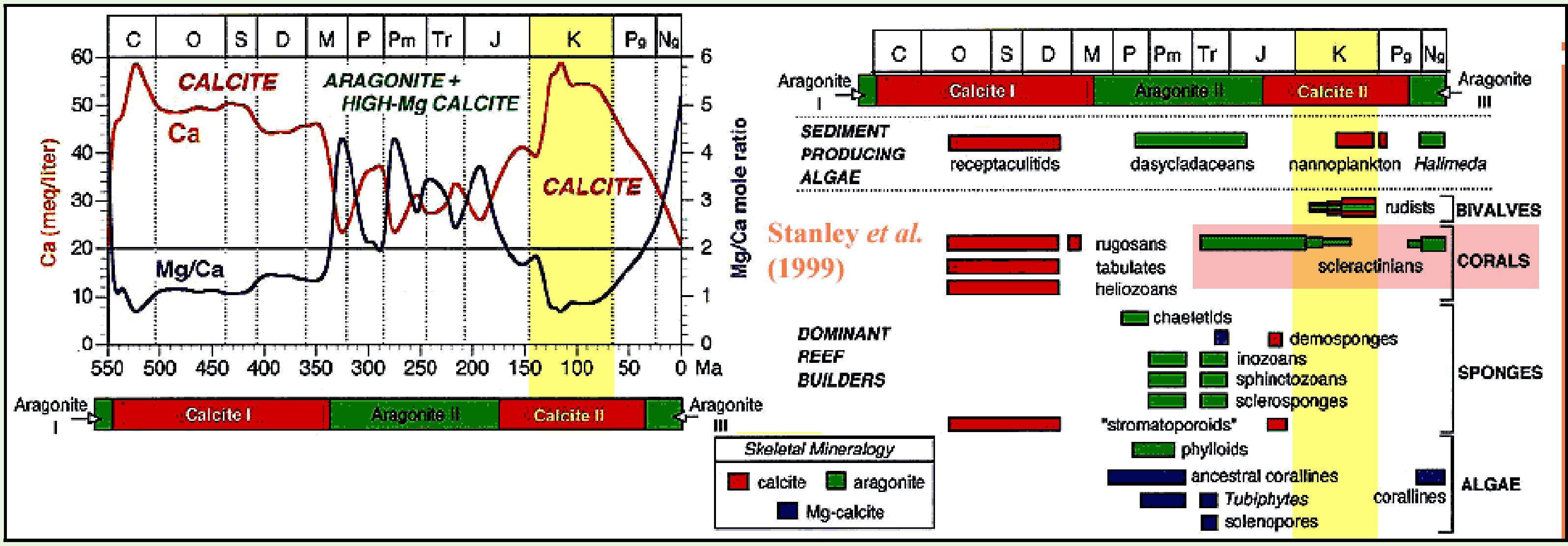
Here's the problem. In the old days -- perhaps before 1980 or so – most scientists believed that evolution was driven largely by competitive exclusion: the "nature red in tooth and claw" school of evolutionary theory. Taxon B replaced A because it was bigger, badder, and more "fit." Gradually, the pendulum swung the other way, as evidence accumulated suggesting that blind luck, climate, and environmental factors played an enormous role. Today, orthodoxy requires every paper to conclude that B replaced A only because A was already going to hell in a hand basket for environmental reasons. It is now considered very bad taste to contemplate that B might have been better at anything, or more "fit," than A, or even to admit that A and B actually competed for anything.

It may be simple perversity, or the fact that we are bad-tempered and easily irritated, but it is striking that these two views of the engines of evolution just happen to parallel the educational orthodoxy of academia, as it has changed over the years. Our suspicions are aroused because so much of this discussion seems to be over semantics, rather than science. Consider some examples. If I say that B is more fit than A, might I mean that, by chance, the environment changed in a way that promoted B's survival over A? Alternatively, if I relate that A was already near-extinct before B moved in, didn't B still have to out-compete C, D, and E for the open slot? As always, we meticulously avoid taking any position on the underlying philosophical positions. The problem here is that both philosophical positions seem to be getting in the way of a more dispassionate assessment of the data.



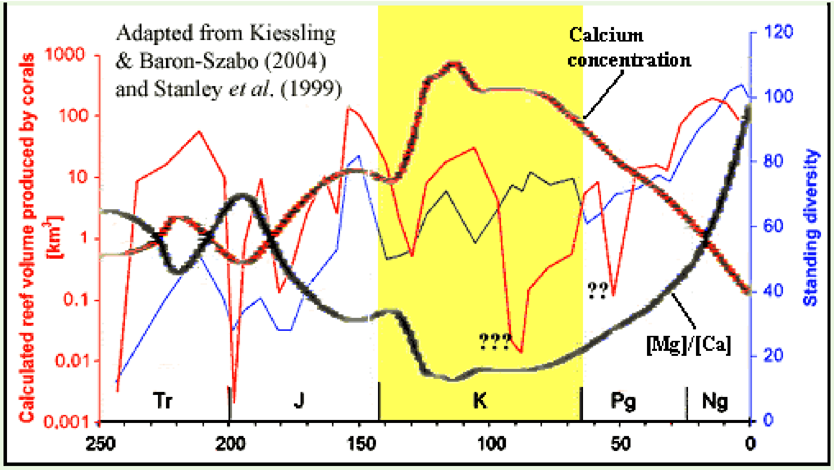
It turns out that Cretaceous corals are an interesting study for these purposes for two reasons. First and foremost, some very good studies have been done over the last few years by some rather careful workers. It's nice to have good data. Second, there's no dispute that corals were rather marginal reef-builders in the later Cretaceous and that rudist bivalves occupied the center stage. What can we say about competition and co-existence in this system?

We focus first on Kiessling & Baron-Szabo (2004). These authors were mainly interested in re-examining some quantitative conclusions reached by Sepkoski relating to the effect of the KT extinction on corals. In the process, they pull together the data shown in the figure, largely from previous work **[1]**. This graph charts coral reef formation rates (productivity) and coral diversity over the course of the Mesozoic. Note that the scale for reef productivity rate is logarithmic, so that the strong peaks and valleys in the reef productivity graph are even more dramatic than they appear at first glance. For the Cretaceous, coral diversity showed a slight, but relatively steady increase. Coral reef productivity was low throughout the Cretaceous; but it was essentially zero during the Late Cretaceous, except at the very end of the epoch. For our purposes, the more interesting pattern is the correlation between diversity and productivity. For *all* epochs except the Late Cretaceous and Paleocene, productivity and diversity are closely correlated. For the 50 My comprising the Late Cretaceous and Paleocene, the relationship is reversed. What's going on? Rather than answer our rhetorical question, we will deepen the mystery, or at least the confusion, by producing another messy, compound graph:



One of the most successful efforts to explain the ups and downs of reef-building taxa relies on marine calcium- magnesium balance. These two divalent cations (Ca^{++} and Mg^{++}) are chemically similar and may substitute for each other in crystal structures. This substitution has some biological importance, since the calcium atoms in the calcium carbonate ($CaCO_3$) of shells may be partially substituted by magnesium. This mixed material is called *high-magnesium calcite*. Perhaps more importantly, calcium carbonate can crystallize in one of two ways, calcite and aragonite. When magnesium levels are high, aragonite is the favored crystal form. Aragonite is less stable than calcite. However, organisms that are able to use aragonite have an advantage when magnesium levels are high. This is shown in the graph above, adapted from Stanley *et al.* (1999). The left half shows calcium levels and the magnesium/calcium ratio aver the entire Phanerozoic. The right half shows the dominant reef builders over the same scale. In broad, the correspondence between ion balance and reef-builder communities is remarkable. Reef-builders seem to be adapted to use either calcite or aragonite in their structural framework. When the calcium- magnesium ratio changes, so do the reef-builders.

But perhaps a closer look is warranted. The "aragonitic" scleractinian corals seem to have done remarkably well in the Early Cretaceous, all things considered, particularly in view of the fact that calcium levels were at an all-time high. Stanley *et al*. show the scleractinian corals petering out over the Early Cretaceous, presumably in response to changing ion balance. But we have a dark and suspicious nature. Out of curiosity, we combined the graphs of Kiessling & Baron-Szabo together with the data from Stanley *et al*. for the Mesozoic.


Adapted from Kiessling & Baron-Szabo (2004) and Stanley *et al.* (1999)

The results are quite peculiar. From the beginning of the Mesozoic, right through the Early Cretaceous, all of our metrics are closely correlated: coral diversity, coral biomass, and calcium concentration -- almost precisely the opposite of the conclusions of Stanley *et al*. That is, the graph shows that early Mesozoic corals were *not* happy with magnesium. To the contrary, coral diversity and biomass follow *calcium* levels very closely. As with the diversity/biomass curves, this correlation falls apart in the Late Cretaceous. Then, after the Paleocene, the correlation reverses. Diversity and biomass follow each other, with both rising as calcium levels fall.

How do we explain all this? Should we, perhaps, have stuck to showing pretty pictures of ammonites and blown off the temptation to look at the actual data? Too late for that now, I suppose.

But the case is not hopeless. First, we can tease apart the biomass and diversity curves. Corals occur as solitary and colonial forms. It is the colonial forms -- or some of them -- that contribute to global reef biomass. The data from Kiessling & Baron-Szabo show clearly that the Cretaceous and Paleogene were actually moderately happy times for scleractinian corals, with slow but steady increases in diversity. But, what the data also indicate is that the Late Cretaceous and Late Paleocene were really rotten times for a particular ecological (*not* phylogenetic) group of corals, the reef builders.

The simplest explanation for these data is competitive exclusion by rudists. Rudist diversity really escalated beginning in Aptian-Albian time and ended, abruptly, at the KT. The rudists didn't devour scleractinians, or hold any personal grudges. They just took up room in an increasing number of reef ecospaces. It shouldn't be a surprise that solitary corals continued to thrive as before. This happened precisely because the engine was competitive exclusion of a particular ecotype, not an environmental stressor applicable to corals generally.

With that background, the calcium curve makes more sense. We need only abandon the untenable belief that Early Mesozoic corals were magnesium lovers. The data are simply to the contrary. Scleractinian diversity and biomass follow the calcium curve from the first appearance of scleractinians, at the beginning of the Middle Triassic, right through the Neocomian. However, the big calcium spike of Aptian-Albian time did not result in a corresponding spike in coral biomass because rudist competition was already beginning to take hold, suppressing the recovery. The complex pattern around the KT is probably a combination of various effects, which cannot easily be untangled at this level of temporal resolution. These effects would include:

a) The initial diversification of several new families of truly aragonite corals, such as the Flabellidae, Meandrinidae, and Dendrophyllidae Stanley (2003);
b) The KT extinction itself;
c) The removal of rudist competition across the KT;
d) The gradual reduction in calcium concentrations over the End-Cretaceous; and
e) The resulting replacement of Mesozoic calcite genera by Cenozoic aragonitic genera.

The bottom line seems to be that, to the extent one can separate environmental and competitive effects in this system, both are important. However, competition and environmental effects may be limiting in different ways and at different times. It is interesting that coral and rudist communities managed to coexist for about 40 My in the Early Cretaceous, presumably by ever-finer partitioning of the available ecospace. However, at some point, competitive exclusion became the dominant mode. These data suggest that coral families adapted to prefer aragonite did not evolve until the end of the Mesozoic. Prior to that time, scleractinian corals preferred high calcium levels. So, Cretaceous ion balances cannot explain their retreat in the face of rudist competition.

Images: Rudist reef cross-section from the **M08313 Sedimentology** site of Oxford Brookes University.

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Other Cretaceous Life

plants

Although the Jurassic floras of ferns, cycads, and conifers continued, the most dramatic occurrence during the Cretaceous, was the first appearance of the flowering plants, the angiosperms. By the end of the Cretaceous, a number of modern plant forms had evolved.

marine invertebrates

Ammonites, belemnites (*left*), other molluscs were abundant, as were sponges, bivalves and echinoids. Several new groups of Echinoids appear during this time, and the families Echinocorythidae and Spatangidae become abundant. The brachiopods meanwhile declined in diversity. Higher crustaceans such as lobsters become common. Corals were of essentially modern types. Modern gastropod groups (especially Neogastropods) appear. These differ from all previous gastropods by being largely carnivorous, and, like the Mesogastropods, are easily able to live in sandy environments.

The normally conservatively coiled ammonoids take on bizarre shapes, which was at one time attributed to a sort of racial senility. This idea is no longer considered valid. In addition to uncoiled ammonoids, and normal coiled forms, both with complex suture patterns, there are those types found in areas of North Africa, Syria, South America and southern USA in which the suture-lines had become simplified so that they closely resembled those of the Triassic Cerratites. These are, naturally, called "pseudo-ceratites".

Cretaceous reefs are largely made up of rudists, huge bivalves with one cone-shaped valve and the other reduced to a small lid-like structure. A single animal could be a meter in height. Rudists grew rapidly, most certainly with the help of symbiotic algae. The early Cretaceous forms like *Monopleura* and *Caprotina* were replaced during the later Cretaceous by *Hippurites*, whose growth-habit paralleled that of Rugose corals. Especially in the Mediterranean region, these were an important part of the marine ecosystem.


Univ. of Michigan Exhibit Museum of Natural History -- Life Through the Ages Diroama

A Cretaceous underwater scene, showing a diversity of cephalopods Two squid-like belemnites swim slowly among the seaweed (upper left). To the right, the large ammonite *Placenticeras* (with shells reaching 50 cm in diameter) rests on the sandy sea-floor. A number of straight-shelled *Baculites* (their shells curiously reminiscent of the early Paleozoic nautiloids) rest with their shells vertical and their bodies on the surface, although in life they would of spent much of their time slowly cruising over the sea bottom. In the center is the strange, loosely spiraled ammonite Helioceras (just above the dashes in the text), which probably did live mostly on the bottom, unless it was planktonic. A large gastropod crawls over the sand at the lower left. Graphic from Earth History Resources.

fish

Modern teleost fishes become widespread around the middle and especially towards the end of the period, and modern sharks also appear during this time.

terrestrial invertebrates

The appearance of flowering plants greatly stimulated insect evolution, as the plants used insects for pollination. Many modern groups of insects appeared and began to diversify, including the oldest known ants and butterflies.

Amphibia:


Apart from a single lineage of giant temnospondyls confined to the rift valleys of south-east Gondwana, the amphibians are represented only by existing groups such as frogs and salamanders

Reptilia (non-archosauria)

The chelonia (turtles and tortoises) are common, and include representatives of both living and extinct groups. Some marine forms attained enormous size, such as the 3 meter *Archelon*.


The tuatara-like Sphenodontia are much reduced, their ecological role being taken by the Squamata (lizards and snakes). One line of aquatic lizards evolve into gigantic marine forms, the predatory Mosasauridae, with lengths of up to 10 meters and more.

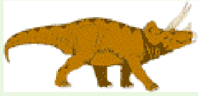
The Ichthyosauria are greatly reduced, with only a single family straggling through to the early part of the late Cretaceous. It is likely that they were unable to adapt to the new fast-swimming teleost fish. They died out long before the Cretaceous ended.

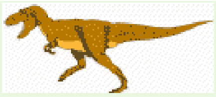

Plesiosaurs are represented by a number of new forms, including the Polycotylidae, Cimoliasauridae, and huge long-necked Elasmosaurids (*left*).

Crocodiles

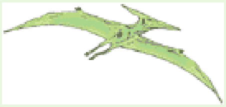
Modern crocodilians (Eusuchia) evolve for the first time, while a number of more primitive Mesouchian groups continue. The sea crocodiles die out early in the Cretaceous. The warm tropic conditions however are good news for the fresh-water crocs, some of which (e.g. *Sarcosuchus*, *Deinosuchus*) attain huge size. These gigantic crocodiles doubtless fed on unwary dinosaurs in the same way that large modern crocodiles will grab an ungulate mammal (such as a zebra or wildebeest) that approaches the water to drink.

Dinosaurs and birds


Like the Jurassic, the Cretaceous Period is distinguished in the popular imagination by the presence of great dinosaurs, marine reptiles, and flying pterosaurs. Many new types of dinosaurs evolved at this time. Among the greatest of the giants, the brachiosaurs and diplodocids died out, while new sauropod dinosaurs, specifically the Titanosauria, continued to flourish in Gondwanaland, but became rare in Laurasia. The plated Stegosauria were replaced by the heavily armoured Ankylosauria. The Ceratopsia (horned dinosaurs) evolved and flourished in Asiamerica but (apart from one or two questionable forms) are unknown elsewhere. The Pachycepalosauria seem to have been similarly limited in distribution. Curiously, the most abundant and diverse of the Cretaceous herbivores were the unarmoured ornithopod dinosaurs, specifically the hypsilophodontids and iguanodontian lines, all of which achieved cosmopolitan distribution.



Among the theropod carnivores there was an astonishing radiation of large and small bird-like forms, ranging from the giant carcharodontosaurs, spinosaurs, and Tyrannosaurs, through the medium-sized sickle-clawed deinonychids to the bird-like ornithomimosaurs and the enigmatic segnosaurs. Alongside these medium to large forms were an extraordinary range of birds and dinosaur-like protobirds. Indeed, during the Cretaceous it would have been impossible to tell where dinosaurs ended and birds began, such is the continuum between them.



The birds seem to have pushed the Pterosaurs (flying reptiles) progressively to extinction. As the Cretaceous progressed the Pterosaurs declined steadily, until at the end of the period only one or two aberrant giant forms (*Pteranodon*, *Quetzelcoatlus*) remained.

Many new mammal groups also appeared during this time, including the three living groups of mammals (placentals, marsupials and monotremes) which appear during the mid Cretaceous.

The Cretaceous-Tertiary Extinction

The Cretaceous and the entire Mesozoic was brought to an end by one of the greatest mass extinctions of all time, the K-T event or terminal Mesozoic extinction. About one half of all animal families died out, including dinosaurs, many marine reptiles, several lines of archaic birds, the ammonoid and most belemnite cephalopods, rudist clams, and many microorganisms.

Links

Links

The Cretaceous Period

The Cretaceous Period

Cretaceous map(50.9 kb)

Geophysicists model the Cretaceous motions of Australia

More Links: **Enchanted Learning** and **Wikipedia** have good, very accessible pages on the Cretaceous. **Cretaceous Tethyan Stratigraphy** has detailed stratigraphic information and some maps. The **USGS** covers North American stratigraphy, at a less technical level. **All things Cretaceous** has very well-organized links and some connecting material. We find the tone of the site irritatingly slick -- but, then, we are very easily irritated. ATW060107

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Early Cretaceous I (˜ Neocomian)

The First Part of the Early Cretaceous Epoch of the Mesozoic Era: 146 to 125 million years ago

Jurassic
  Early Jurassic
  Middle Jurassic
  Late Jurassic
Cretaceous
  Early Cretaceous I (Neocomian)
    Berriasian
    Valanginian
    Hauterivian
    Barremian
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  Late Cretaceous

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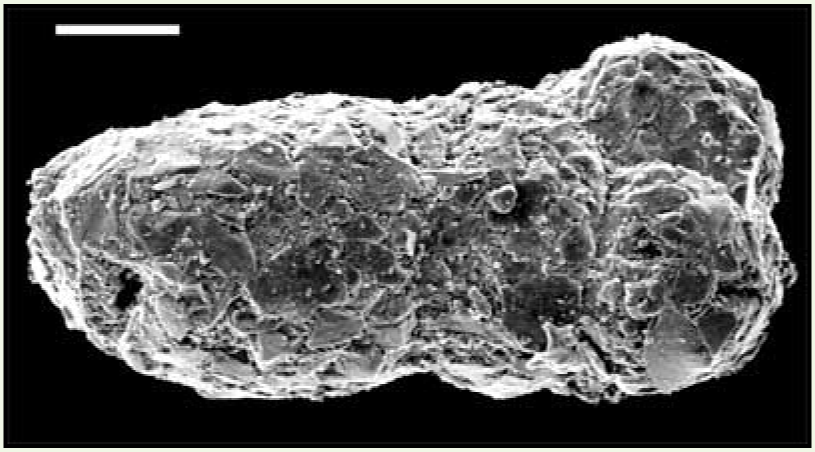

The Early Cretaceous, as defined by the International Commission on Startigraphy, is 46 my long -- simply too long an interval to conveniently deal with as a single epoch. Our original solution on this site was to use an older system which divided the Cretaceous into Neocomian, Gallic and Senonian Epochs. However, as we are now trying our best to conform to ICS nomenclature, this is inconvenient. The Gallic includes parts of both the Early and Late Cretaceous, and tends to throw off the whole system. Accordingly, this page is now devoted to an arbitrary first half of the Early Cretaceous, including the Berriasian, Valanginian, Hauterivian, and Barremian Ages. We will continue to call this the "Neocomian" for convenience. However our demi-epoch is somewhat larger than the traditional Neocomian, which does not include the Barremian. Our new and improved Neocomian is a particularly convenient division, since it leaves the Aptian-Albian interval as a distinct demi-epoch. This second half of the Early Cretaceous is, as we will see in due course, a very different and distinctive time period.

Image: The Barremian brought the beginning of the great Cretaceous flowering of the Foraminifera. The image shows *Bulbobaculites*, one of these new forams. The scale bar is 100µ. The image is from the extensive catalog of images and information compiled by David Haig at **Barremian - Turonian Foraminifera from the Southern Carnarvon Platform**. This appears to be a part of an even larger site, the **BioStrat Gallery**, which houses a number of such collections. ATW040811.

The Break-Up Of Pangea

For perhaps 300 million years, terrestrial animal types had been global in extent, there being only a single supercontinent, Pangea, across which creatures could freely roam. Now, for the first time, a seperation of continents had produced global geographic isolation, and provincialism and a unique faunas appeared on different landmasses. This, the last period of dinosaurian evolution, was also the period of their greatest diversity, although only a fraction of the types (mainly latest Cretaceous Western North American and Asian forms) are known.

It was only during the early Cretaceous period that the supercontinent of Pangea began to break up. This is indicated by map where we see the continents finally beginning to separate and take on their present forms. AsC.B. Cox explains:

> "A spreading axis gradually extended clockwise round Africa until it was almost completely isolated, and India began its long northward journey....Shallow seas separated Asia from Europe, and penetrated far towards the centre of North America.....The gap between North...and South America may have widened somewhat..., and any archipelagic connection between the Americas may have become rather more...difficult as a dispersal route for terrestrial animals." [p.76]

As the centrifugal process of continental fragmentation gets underway, the continents of Gondwana began to break and separate. And as there was a process of diversification of the land-masses, so there was also of diversification of animal-life; both in numbers of different kinds and in their geographical isolation. For the first time, real provincialism appears. Of interest is the fact that India has started to break away from the rest of Gondwanaland, to become an island continent all on its own. India in fact was to become the Australia of the Mesozoic. MAK

Timescale

Harland Epoch	**ICS Epoch**	**Age**	**ICS Base (mya)**	**Duration**
Gallic	**Late Cretaceous**	Cenomanian	**99.6**	**6.1**
	Early Cretaceous (Pt. 2)	Albian	**112**	**12.4**
		Aptian	**125.0**	**13.0**
	Early Cretaceous (Pt. 1)	Barremian	**130.0**	**5.0**
Neocomian		Hauterivian	**136.4**	**6.4**
		Valanginian	**140.2**	**3.8**
		Berriasian	**145.5**	**5.3**

Late Jurassic	**Late Jurassic**	Tithonian	**150.8**	**5.3**

ICS (2004). Geowhen Database

ATW040811.

Climate

We are accustomed to hearing that the climate of the Mesozoic was hot and humid -- like August in Houston, Texas, but lasting about 200 million years. Those who find this boring and oppressive will be relieved to know that the climate of the Neocomian was not so predictable. In fact, temperatures dropped through the Late Jurassic to produce what was, by Mesozoic standards, an "ice-house" world during parts of the early Neocomian. This "ice house" would still seem relatively warm (and, yes, even humid) by comparison with the dry and frigid standards of our own day; but the dinosaurs found it rather brisk, none the less. The poles had small permanent ice caps, and snow probably fell on the cool temperate forests that surrounded the poles. This was the coldest portion of the entire Mesozoic.

We know that things warmed up fairly rapidly after the middle of the Berriasian, but the warming trend may have faltered during the Valanginian. Our knowledge of the Valanginian climate is full of uncertainties. The indications are that the Valanginian included a sharp cold snap severe enough to reduce sea levels due to a (probably brief) build-up of polar ice. There are also paradoxical indications of a temperature spike and of deep ocean anoxia, on the one hand, and increased ocean primary productivity, on the other, during the Valanginian. These have have left the matter in doubt. Notwithstanding this brief and uncertain reversal, world temperatures climbed rapidly after the Valanginian, possibly increasing as much as 17° C. before the end of the Early Cretaceous (i.e., the better-known heat wave of the middle Aptian).

Links: There are a number of good web sites which touch on the cimate of the Neocomian. Among these are: Early Cretaceous; Early Cretaceous Climate; Climate History; BBC - Science & Nature - Dinosaurs; CLIMATE-OCEAN ISOTOPIC SIGNALS FROM LATE Jurassic-EARLY Cretaceous ...; Ocean Drilling Program- Leg 198 Preliminary Report; OZ fossils - The Age of Reptiles - The Climate. ATW040811, revised ATW041102.

Neocomian Life

The Neocomian is best known for the first appearance of flowering plants. During Neocomian time itself, the angiosperms probably did not amount to much, as the image suggests. Nevertheless, they became a detectable part of the flora and would go on to dominate the world's vegetation by the end of the Cretaceous. The development of flowers led immediately to their

co-evolution with insects. So we begin to see specialized pollinators evolving from several insect clades.

Even more important -- to us, at least -- the Neocomian was probably the time in which therian mammals evolved and diversified into placental and marsupial clades, and no doubt other groups which have left no Cenozoic descendants. Birds likewise became common in this period, as did cerapod dinosaurs -- the hypsilophodonts, heterodontosaurs, and, by the end of the Neocomian, iguanodonts.

The Neocomian may have been the high point of the pterosaurs, with such large and specialized types as *Ornithocheirus*, and of the Mesozoic breeds of turtles, which produced some enormous forms. It was the last period in which ichthyosaurs were at all common in the oceans.

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Neocomian Reefs

A Late Cretaceous rudist reef from France. Note that most of the "reef" is composed of mud and sand between the stalks of the rudist shells.

During the Neocomian, rudist reefs began to dominate over more conventional reefs formed by scleractinian corals. Coral reefs were the predominant form in the Jurassic, just as they are today. Rudists "reefs" are not quite reefs, and the rudists themselves are certainly not corals. Rudists are actually a group of aberrant bivalve mollusks which became extinct at the end of the Cretaceous. More about rudist reefs in general may be found in our discussion of Aptian Reefs. Many sources state that rudist reefs didn't become important until the Aptian-Albian, but this depends on where you look. The Central Tethyan region -- roughly between Arabia in the southeast to France in the Northwest -- was Rudist Country as far back as the Berriasian. However, areas such as the Caribbean Basin were dominated by corals until the Aptian.

The difference may be related to mode and speed of growth. We don't know much about the speed of rudist growth as such. However, rudists probably made quick, sloppy structures. They trapped sediment between "stalks," to form a "reef" out of sand and silt. Corals do it the hard way. A coral reef is built, entirely of calcareous tests, grown and deposited cell by cell, over millenia. The entire reef is biogenic. This is slow work. We may imagine, then, rudists moving in like weeds whenever something happened to disrupt the standing crop of coral. They would quickly overgrow the old framework, covering everything over with sand, silt, and fragments of shell and thus preventing the old, complex, high-diversity communities from re-establishing themselves -- a bit like suburban housing developments, in fact.

Our guess about rudist development is reasonably well substantiated by geology. The Tethys was notably unstable during the Neocomian, as Europe was cracked and splintered by the growing Tethys Seaway. In addition to geological activity, the region also seems to have been pounded by frequent, severe storms. Finally, the region experienced three periods of rapid sea level increase: (1) early Valanginian to early Hauterivian (this episode may have occurred in two stages), (2) middle Hauterivian, and (3) late Hauterivian to early Barremian. During these periods, the carbonate slopes on which coral reefs had developed "drowned." That is, the sea rose and the platforms came to be submerged below the zone optimal for photosynthesis. Because of the high relief of the sea bottom (e.g., abrupt cliffs caused by faulting) the corals couldn't grow into shallower water.

This was a sort of worst case for reef stability, and this is one of the areas to which rudists spread earliest in the Cretaceous. In fact, within the Tethyan realm, conditions were a little worse yet toward the eastern end, in present-day eastern Europe. Conditions comparable to the later mid-Cretaceous black shales are particularly well known in this region from well within the Neocomian. Not surprisingly, this seems to have been the original home of the rudists. They are known in this sector from the Late Jurassic, and they became the dominant reef-builders at the very beginning of the Neocomian.

On the other side of the proto-Atlantic, in the future Gulf of Mexico, we see a very different pattern. A great barrier reef stretched from Texas to the southern tip of Florida. The northern Gulf of Mexico was sheltered from the ocean on all sides. No violent tectonic forces were active beyond a gentle tug (extensional stretching) as the Yucatan attempted to turn in slow circles like a cat preparing for a serious nap. Sea levels also rose here, but the topography was so flat that growth on the northern margin easily kept pace with drowning to the south. This is practically ideal reef territory, and we see no rudists at all until the Aptian, when temperature extremes may have stressed the coral communities beyond endurance. A similar pattern is seen on the coast of what is now Nova Scotia. As we might expect, complex, intermediate patterns are observed in France, Jamaica, and Venezuela where rudists established themselves in the Hauterivian or Barremian.

In short, the rudists seem to be a classic case of evolution by adventitious specialization. They are not more "fit" than corals. Indeed, they eventually lost out to the corals. However, they could grow quickly and thus move in whenever the coral reefs suffered a setback. They then established themselves to the exclusion of the former owners. A good deal of "competitive replacement" in evolution must actually work this way -- not by head-to-head competition, but by slipping in the back door while no one is home.

Image credit: reef image from **Sedimentology MO8313** course materials, Oxford Brookes University (lots of good stuff on reefs of all kinds at this site).

The New Dinosaurs

The dinosaurian megafauna of the Neocomian was very different to that of the Late Jurassic. Gone are the diverse cetiosaurid, omeisaurid, and diplodocid sauropods, the range of spined and plated stegosaurs, and the ornitholestid, ceratosaurid, torvosaurid, and allosaurid guilds that fed upon them. In their place are titanosaurs, *Iguanodonts* (left), polacanthid ankylosaurs, primitive ceratopsians, the strange semi-aquatic spinosaurs, and an astonishing range of small and large coelurosaurs, including a number of new clades (Ornithomimosaurs, Dromaeasaurs,

Troodonts, Therizinosaurs, Tyrannosaurs) that clearly seem to have arisen from the poorly known maniraptors of the late Jurassic, and of course a huge radiation of birds, taking the place of small and medium-sized pterosaurs. Other dinosaurs continued with relatively little change - brachiosaurs and dicraeasaurs among the sauropods and hypsilophodonts among the ornithopods - while others again, like the stegosaurs, were greatly reduced in number.

In his classic work *The Dinosaur Heresies*, Dr Bob Bakker suggests that the replacement (in Laurasia) of Sauropods by Ornithischia (iguanodonts and ankylosaurs) was brought about through angiosperm evolution, itself triggered by selection pressures from dinosaurian feeding, with the slow growing conifers that the sauropods fed upon being replaced by fast-growing and fast regenerating angiosperms, which in turn became food for the new low-browsing ornithischian dinosaurs. But this hypothesis, persuasive and fascinating as it seems, ignores the fact that titanosaurian sauropods continued as the predominate dinosaur clade in Gondwana right until the end of the Mesozoic, and that Angiosperms themselves did not become an important part of the floral community until the Campanian (near the end of the Cretaceous). Nevertheless, it is quite likely that selection pressures and feedback loops between dinosaurs and the vegetation they fed upon may have been an important contributing factor in the evolution of Mesozoic plants and of course of the dinosaurs themselves.

In the late Jurassic, with the exception of China (presumably geographically isolated) with its unique omeisaur-stegosaur megafauna, dinosaurs were very similar from one continent to the next, differeing only at the species and generic level. But in the Cretaceous the break up of Pangea and the resulting island continents led to the start of a growing provincialism, in contrast to the uniformity of the Jurassic world. Psittacosaurs and therizinosaurs flourished in Asia, and hypsilophodonts, polacanthids, and brachiosaurs diversified in Europe and North America. Other clades like iguanodonts and titanosaurs seem to have been universal. As the Cretaceous progressed, the various continents would each become home to a distinctive fauna.

Iguanodon at a waterhole - illustration © BBC/ABC from Walking with Dinosaurs

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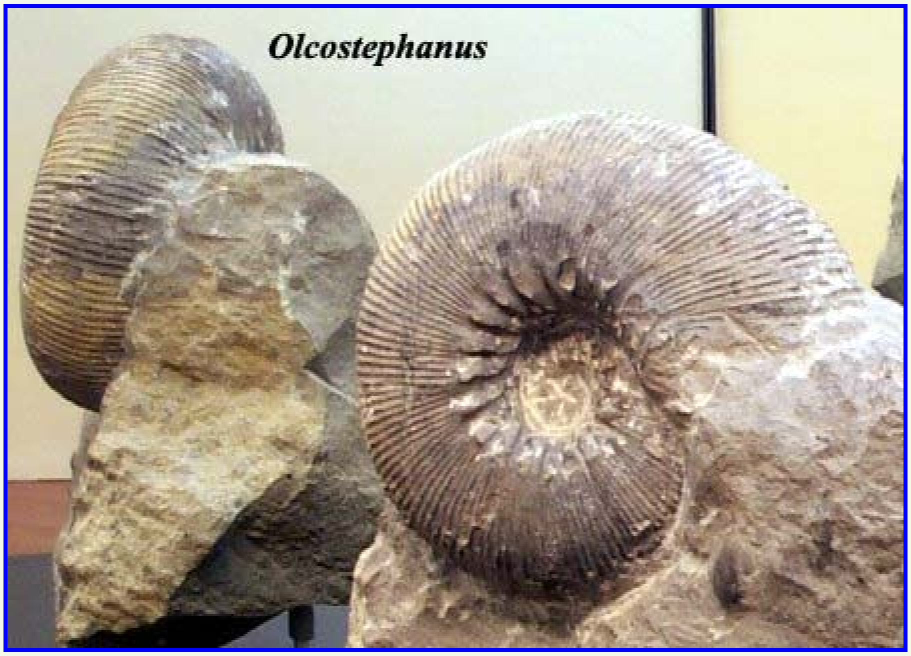
The Valanginian Age

The Valanginian Age of the Early Cretaceous Epoch: 140 to 136 million years ago

Cretaceous
  Early Cretaceous I (Neocomian)
    Berriasian
    Valanginian Age
    Hauterivian
    Barremian
  Early Cretaceous II (Aptian-Albian)
  Late Cretaceous

The Valanginian
  Introduction
  Life

Introduction to the Valanginian

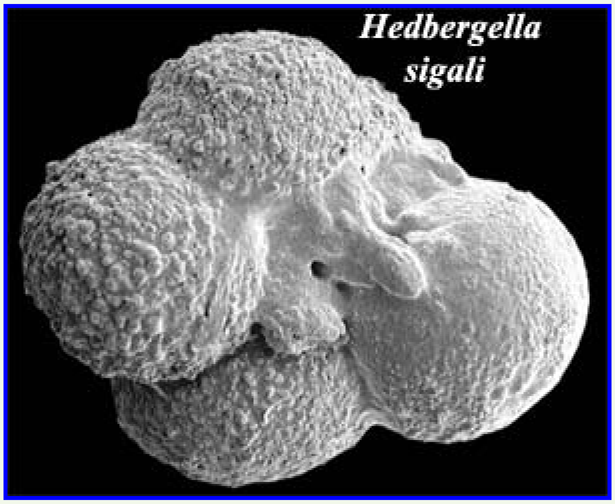


For a miserable little four million year interval, less than 1% of the Phanerozoic, the Valanginian has proven to be a complex and difficult Age. New dinosaurs emerged to rule the land, defining clades that would dominate for millions of years, such as the characteristic ornithopod herbivore *Iguanodon*, swiftly achieving ecological dominance, and the large and heavily armoured *Hylaeosaurus*, the first of the big ankylosaurs, and *Dromaeosauroides*, the earliest known Dromaeosaurid. Other contemporary forms like the brachiosaur *Pelorosaurus* and high spined theropod *Becklespinax* are less well known. These dinosaurs inhabited a land dominated by gymnosperms (e.g. pine forests), but a few angiosperms (flowering plants) were also beginning to appear. In lagoons and shallow coastal regions, possibly in freshwater as well, lived the small plesiosaur *Leptocleidus*, a late survivor of the Rhomaleosaur clade. The seas were inhabited by large ammonoids like *Olcostephanus*, bivalves like

Bruchia, and (in selected areas) some of the early rudist reefs.

In fact, we know who the players were with a good deal of certainty. We also have the script. We know who was going where in an evolutionary sense. What we don't have is the scenery. That is, our knowledge of the state of the oceans, the climate and atmosphere is fragmentary and sometimes contradictory. Here's a brief run-down of what we think we know.

The Valanginian was a period of transition between the relatively cold time at the end of the Jurassic to the "greenhouse" world which continued for the rest of the Cretaceous. Unlike most of the Mesozoic, the Valanginian world was quite seasonal, and climate was regional. That is, there seem to have been distinct climate zones – although what those climates actually were is much less certain. These climate zones are reflected in distinct "boreal" faunas in both the Northern Tethys (future North Atlantic) and Northwest Pacific provinces. These faunal regions both began to break down as rising seas created new north-south passages.



For sea levels were rising, as they did with some consistency throughout the Jurassic and the first half of the Cretaceous. During the Valanginian, there were two periods of rising seas: at the very base of the Valanginian, and during the later Valanginian. Very recently, it has been learned that these events were accompanied by smaller-scale versions of the Ocean Anoxic Events which began in the mid-Aptian. Black shales, signaling deep ocean anoxia, have been found in both the Central Tethys (Europe) and the western Pacific provinces **[1]**. Another similarity to the mid-Aptian is a recently-discovered early diversification of foraminifera. Finally, there are indications of a possible temperature spike, a milder, and possibly regional, version of the flash heating of the oceans in the Aptian.

Thus the Valanginian presents paradoxical indications of cold oceans and hot, regionality of climate and fauna and later globalization, essentially Jurassic oceans in some areas, with Aptian conditions in others. Its all beginning to fit a consistent pattern, but the pattern is complex.

Image credits: *Olcostephanus* from **3D-Fossils.com**. *Hedbergella sigali* from the **MIRACLE site** of University College, London. *H.* sigali is actually of Hauterivian or Barremian age, but it is closely related to the Valanginian *H. aptica*.

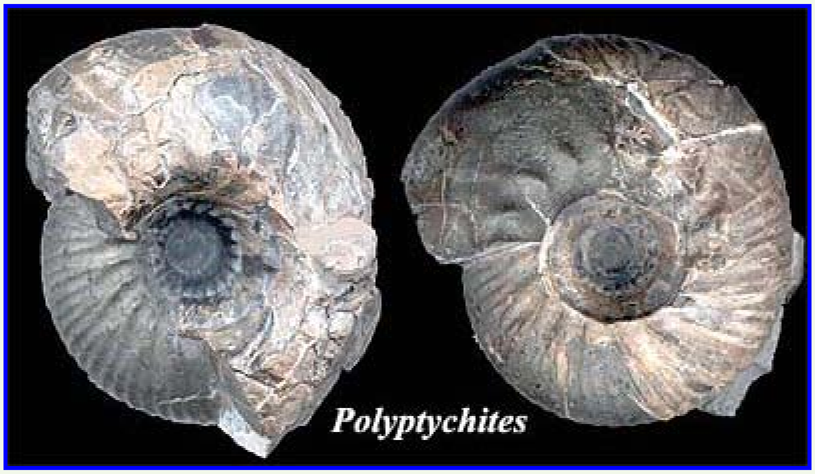
Links: DinoData Timeperiods Valanginian; The Plesiosaur Site - Chronological List of Taxa -Valanginian; Geotimes - May 2004 - Outsourcing geology (Valanginian black shales); Nannofossil carbonate fluxes during the Early Cretaceous ... (more on black shales); DISCUSSION AND CONCLUSIONS (same); October 22, 2001 (and yet more); Annual Conference Abstracts 2001 (boreal Tethyan fauna); ePIC- The Greenland-Norwegian Seaway- A key area for understanding ... (boreal Tethyan fauna); 224 (same); Tauka and Zuravievka Terranes of the ... (boreal Pacific fauna briefly discussed); CCOD Abstracts (changes in plankton); Ocean Drilling Program- Leg 198 Preliminary Report (temperature spike?);

Valanginian Life

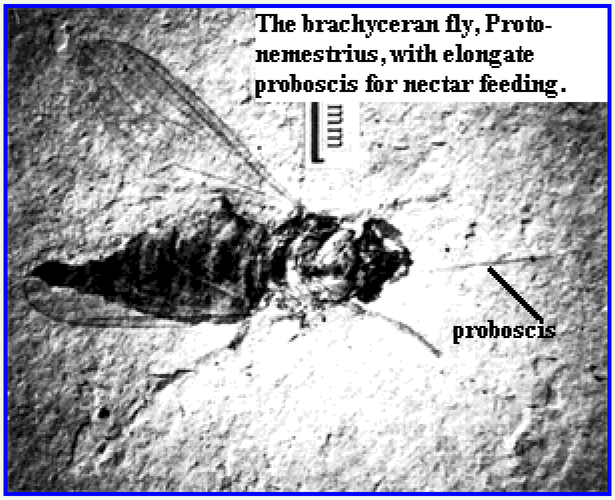
The transitional nature of the Valanginian shows itself only in small ways, with a few outstanding exceptions. One of those exceptions is the first radiation of Foraminifera. The forams had been around for some time as simple, benthic "agglutinated" forms. Only in the Cretaceous did they become a major component of the plankton. The first sign of this development came in the Valanginian, with the evolution of the Hedbergellids, such as *H. sigali*, shown above. A few new coccoliths, such as *Watznaueria barnesae* also appeared for the first time.

One British marginal marine site is described in the following terms:

Invertebrate faunas included simple and compound corals, calcareous sponges and bryozoa, abundant bivalve molluscs, such as oysters, smooth terebratulid and ribbed rhynchonellid brachiopods, gastropods (snails), asteroids (starfish), echinoids (sea urchins) and crinoids (sea lilies). Microscopic organisms included foraminifera, ostracods and phytoplankton (dinoflagellates and coccolithophorid algae). Lobster- and shrimp-like crustaceans often produced burrows within sediments, preserved as trace fossils. Belemnites, relatives of the ammonites, were abundant and along with fish were probably the main food of the aquatic reptiles, which were the largest vertebrate animals in the sea. These included ichthyosaurs, plesiosaurs, pliosaurs, crocodiles and turtles. The fish included both holostean and teleostean bony fishes, and sharks and rays. On land, dinosaurs were advanced; mammals formed a minor but increasingly important part of the fauna. Land plants of particular prominence were the gymnosperms, notably conifers, cycads, ginkgoes, ferns and horsetails. Insect life included dragonflies. Berriasian, Valanginian, Hauterivian, Barremian - GCR block



We should add that the crustaceans weren't just lobster-*like*. This was the age of the first real clawed lobsters. Bivalve molluscs were well represented by countless species of *Bruchia* and *Aucella*, as well as early rudists. As is usual in the Mesozoic, cephalopods in general, and ammonites in particular, are grossly over-represented in the fossil record. Some representative types are: *Baculites*, *Belemnites*, and the ammonites *Thurmanniceras*, *Karakaschiceras*, *Olcostephanus*, *Polyptychites*, and *Jeanthieuloyites* -- not to mention many, many others. Galeomorph sharks, including early carcharinids, also appeared in the seas at this time. However, it is obvious they had not yet learned the top predator job very well, since we are still burdened with this interminable litany of Valanginian ammonites.


The brachyceran fly, Protonemestrius, with elongate proboscis for nectar feeding.

On land, fern-dominated floras continued to dominate, with pine forests important in many areas, and large horsetails holding the wetlands together. However -- and here is the second major exception -- angiosperms appear for the first time in the fossil record. No fossil angiosperm plants have yet been recovered from the Valanginian, but angiosperm pollen becomes a distinct part of the terrestrial microfossil assemblage.

On and around these plants were the first oonopid spiders, caddisflies (Trichoptera), and the first advanced cockroaches. Consistent with the probable presence of angiosperms, we also see brachyceran flies, which may have been among the first pollinating insects. Ren (1998) **[2]**. The roaches, in particular must have been fairly numerous (why is this not surprising?) since coprolites attest to the presence of some organism which appears to have specialized for eating them.

New and old species of dinosaur overlapped in the Valanginian. We have mentioned some of them in the general introduction. In the Valanginian, iguanodonts overlapped with stegosaurs. Allosaurids overlapped with both *Tyrannosauroids* and one of the first dromeosaurs, *Dromaeosauroides bornholmensis*. In fact, *all* of these types co-existed in Europe during the Valanginian! Among mammal-kind, the Valanginian was mostly the age of triconodonts. For example, *Gobiconodon* is Valanginian. However, it is likely that therian mammals not only existed, but were diverging into placental and marsupial forms. At least early representatives of both types are found in slightly younger sites.

Gobiconodon

Image credits: *Watznaueria barnesae* from **The Calcite Palace**; *Polyptichites* from **1996-2000 University of Rochester Arctic Expeditions**; *Protonemestris* from Ren (1998). *Gobiconodon* from **Carnegie Online** of the Carnegie Museum.

Links: Cretaceous CLIMATE-OCEAN DYNAMICS- FUTURE DIRECTIONS FOR IODP (forams); Mesozoic Mammals; Triconodonta, an internet directory (*Gobiconodon*); AGP, Volume 47, Number 3-4, 1997 (ammonites); Proceedings-1998 (insects); Flower (insects); Current Issue (insects); Dinosaur Genera List update #199 (dinosaurs); Another new dinosaur (dinosaurs); WEALDEN DROMAEOSAURS, JOSH TV STAR (dinosaurs); Mesozoic Mammals; Triconodonta, an internet directory (mammals); Time Line (NC) 2 (mammals).

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[1] Possibly, this supports the speculation about non-biogenic, mantle-derived methane and Archeota discussed elsewhere.

[2] Ren refers to these fossils as Jurassic. The levels of the Yixian Fm. in which they were recovered have more recently been dated as Valanginian.

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The Berriasian Age

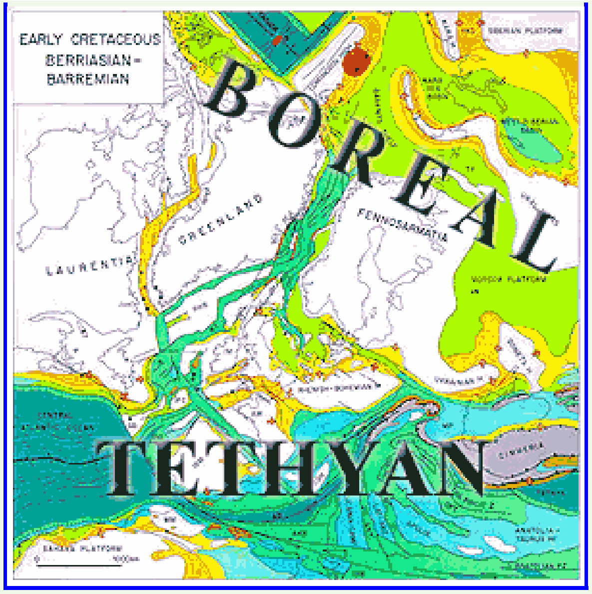
The Berriasian Age of Neocomian Time: 146 to 140 million years ago

Jurassic
  Late Jurassic
    Oxfordian
    Kimmeridgian
    Tithonian
Cretaceous
  Early Cretaceous I (Neocomian)
    Berriasian Age
    Valanginian
    Hauterivian
    Barremian
  Early Cretaceous II (Aptian-Albian)
  Late Cretaceous

Introduction to the Berriasian

The Berriasian is the first age of the Cretaceous. By the Berriasian, East Gondwana (India, Australia and Antarctica) had separated cleanly from West Gondwana (Africa and South America); and, by the end of the Age, India was beginning to break from East Gondwana. The Tethys had long since split the Gondwanan lands from the Northern lands, although the situation in the Caribbean Basin was complex. The Pacific Plate was growing, but still quite small, and the entire western margin of North and South America was fringed with volcanic island arcs. Zharkov *et al*. (1998).

The cooling trend of the Late Jurassic continued into at least the middle of the Berriasian, and the poles may have borne small permanent ice caps, with glaciers at higher elevation in East Gondwana. The Atlantic and Ural connections between the Tethys and the northern sea were still well in the future, so that the Middle latitudes of the Northern hemisphere were thermally isolated and quite cool, at least by Mesozoic standards. Chumakov (2003).



Most of the characteristic life forms of the Cretaceous had not yet evolved or were insignificant, including angiosperms, mosasaurs, therian mammals, hadrosaurs, rudists, calcareous plankton and planktonic foraminifera. Dinosaurs were represented by *Brachiosaurus*, *Camptosaurus*, *Iguanodon*, and a number of weird and poorly known transitional forms such as *Echinodon*, *Embasaurus*, *Nuthetes*and *Stenopelix*. Teleost fish were present, but not yet in their Cenozoic forms, and the dominant marine reptiles were *Cimoliasaurus* and *Cryptocleidus*.

Image credits: *Camptosaurus* from the College of Eastern Utah Museum site. Map from the American Association of Petroleum Geologists site.

Links: The Plesiosaur Site - Stratigraphy; DinoData Dinosaurs Timeperiods Berriasian; anrepeap.

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Stratigraphy

Studies of the Berriasian and the Jurassic-Cretaceous boundary interval have been concentrated, particularly, in the area of the great former ocean of Tethys. This was the largest single geographical unit of the time and its rocks and fossils give the best possibilities for wide and consistent correlations. In the earliest Cretaceous, this gigantic ocean divided Laurasia from Gondwana, and Berriasian marine sediments are widespread from Mexico to the Russian Far East and Japan via north Africa, Europe, Crimea, Arabia, Iraq, Iran and Tibet.

Early research on the Berriasian was, in fact, not in Tethys nor even on marine sedimentary rocks, but on nonmarine strata. The English Purbeck Formation is largely of Berriasian age, though it extends down into the Tithonian (Portlandian) and up into the Valanginian. And it was the Purbeck Formation and its rich molluscan and vertebrate fauna (mammals, lizards, pterosaurs, crocodilians etc) that took the attention of famous geologists such as De la Beche, Buckland, Webster and Fitton. Brongniart, in 1829, labelled these beds as part of the Jurassic, in the "Purbeckien" stage, a name officially suppressed in the 1960s: whereas D'Orbigny relegated the "Purbeckian" to the Cretaceous.

When geologists started to study marine sequences of this age in Tethys, the focus moved for a time, particularly, to the limestones of southern France, and a new name was introduced, Berriasian (after the village of Berrias in the Ardèche region: Coquand, 1869). As stratigraphers now view things, the Berriasian defines the lowest Cretaceous and its base delimits the Tithonian, the top of the Jurassic. Unfortunately, the section at Berrias has no macrofossils near where the boundary might be expected, and so specialists have been busy looking for better, more fossiliferous, sections that show the uppermost Tithonian and lowest Berriasian.

Historically, in the Mediterranean parts of Tethys, the Berriasian has been described as consisting of athe following ammonite zones and subzones:

Fauriella boissieri Zone	*Thurmanniceras otopeta*
	Tirnovella alpillensis
	Berriasella picteti
	Malbosiceras paramimounum
Tirnovella occitanica Zone	*Dalmasiceras dalmasi*
	Berriasella privasensis

	Tirnovella subalpina
Pseudosubplanites grandis Zone	*Pseudosubplanites grandis*
	Berriasella jacobi

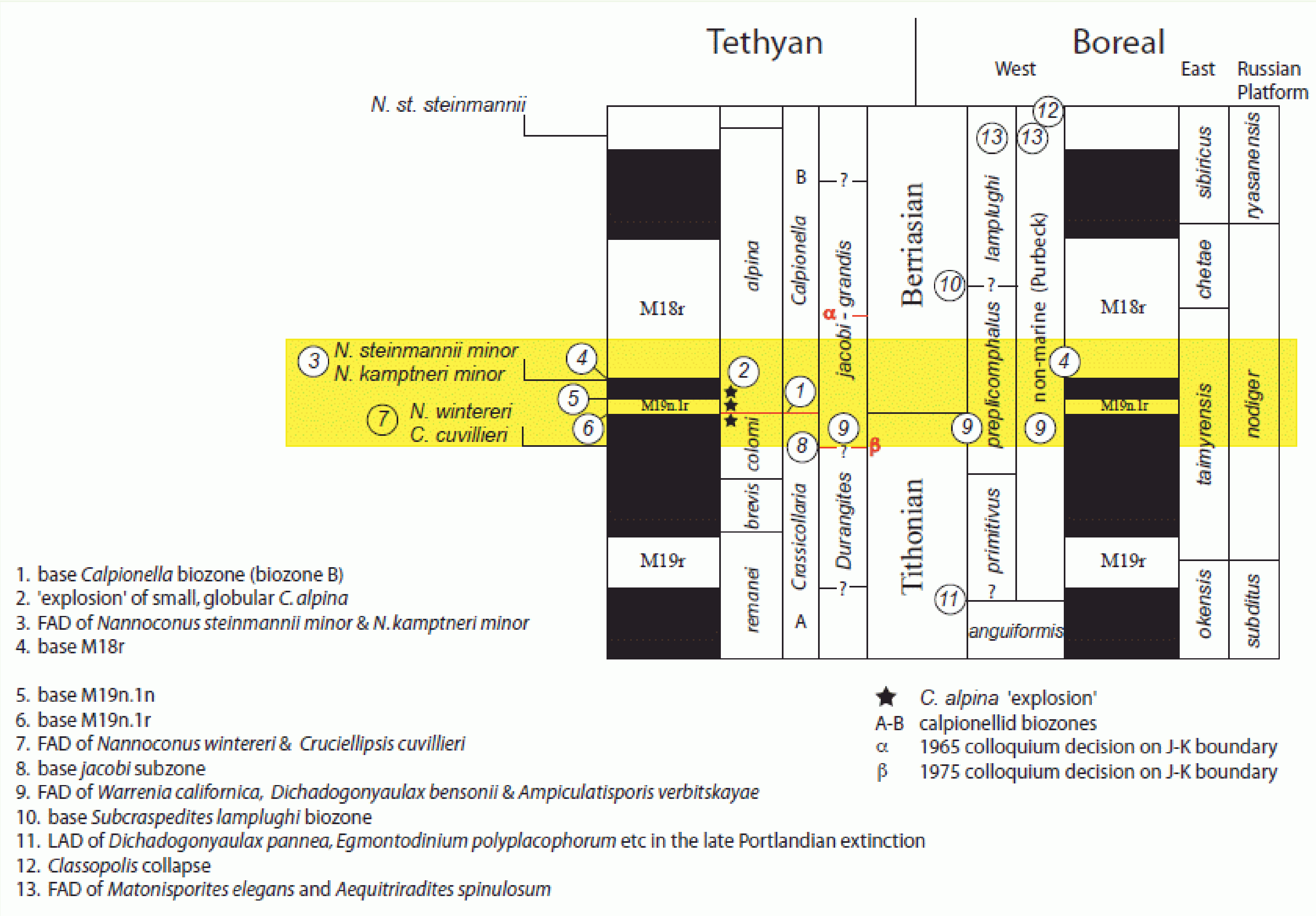
At two international meetings on the Cretaceous, stratigraphers considered the best level to place the base of the Berriasian, and formally voted that the base of the *grandis* and *jacobi* subzones afforded the optimum levels for this. Unfortunately, some of the best sections for the J/K boundary have few or no ammonites in the critical interval. Therefore, in the last thirty years, micropaleontology has become more and more important, as microfossils are more consistently present and much more common than ammonites in many profiles in Tethys. To the precision of microfossil ranges has been added another stratigraphic tool, magnetostratigraphy, which is being applied to key sections.

The latest Jurassic and earliest Cretaceous rocks are complicated and hard to decipher outside Tethys, as J/K palaeogeography is quite complicated. The more extensive late Jurassic seas had withdrawn from large areas and earlier seaways had closed. Some regions were periodically connected with Tethys, but others were isolated, and some that had been sea had become freshwater lakes and land, as in England, Germany and Poland with the Purbeck beds, which only have rare levels with marine fossils. Non-marine rocks of this age are also well-developed in Mongolia and China. Some areas nearer to the paleo-poles had limited endemic biotas (Siberia, Antarctica, Canada). Others had oceanic connections that sometimes allowed faunal migration, but they were very distant from Tethys (e.g. Argentina) and had their own particular marine faunas Some were landlocked basins with low biotic diversity (Russian Platform), and others have suffered subsequent extreme tectonic disruption (Japan). The challenge and task with all these areas is to correlate with the better documented sequences in Tethys.

A global reference profile for the base of the Berriasian (a GSSP) is under active consideration by theInternational Subcommission on Cretaceous Stratigraphy (ISCS) of IUGS, and a range of contender GSSP localities are currently being studied in detail by the ISCS's Berriasian Working Group.

Several markers are being employed to refine correlations and to work towards definition of a widely useable base for the Berriasian Stage. These include, particularly, calpionellids, calcareous nannofossils, such as *Nannoconus*, ammonites, palynological datums and magnetostratigraphy. Depending on which final fossil markers are employed to define a boundary , in magnetostratigraphic terms, it is likely to be between the base and top of magnetozone M19n. The calibration of markers, such as *Nannoconus steinmannii minor*, *N. kamptneri minor*, and *Calpionella alpina*, with precisely fixed magnetozones gives greater precision in trying to identify the best position for a boundary.

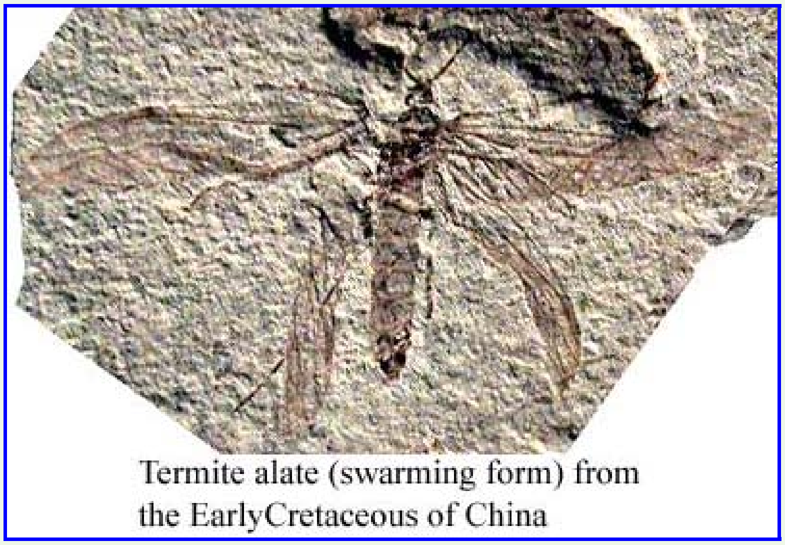
Bill Wimbledon 130211



Markers useful in defining the Jurassic-Cretaceous Interval (yellow band). Adapted from Wimbledon et al 2011 p.299, fig.1

Berriasian Life

Arthropods

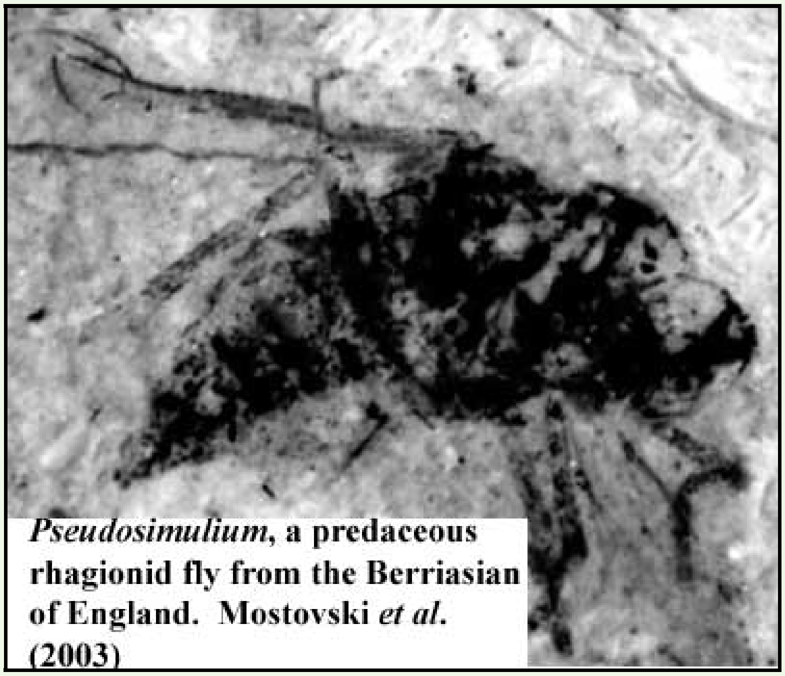

Termite alate (swarming form) from the EarlyCretaceous of China

Generally speaking, the Cretaceous was not a good time for arthropods (although it is not easy to be certain, because of the usually miserable fossil record). The clear exception are the Crustacea who produced both lobsters and shrimp at some point in the earliest Cretaceous. Sadly, such essential condiments as butter, tomato sauce, and horseradish were not yet available in the Berriasian.

Chelicerates nearly became extinct in the Cretaceous, at least by comparison to their large diversity in the Paleozoic and Cenozoic. However, spiders were present and the remains of a number of orb-web weavers are known from the Berriasian. These spiders may have benefited from the large number of flying insects. The flying insect jobs were dominated by

Diptera. In fact, it was an age of flies. Since many modern neopteran insect groups had not yet become important, flies occupied a large number of niches in which they are now marginal, including the job of nipping at vertebrates (absent gnats, midges and mosquitoes). Mostovski *et al*. (2003). When angiosperms arrived later in the Neocomian, it was these flies with suctorial mouthparts which first evolved as pollinators.

Two important clades of insect recyclers are first found in the Berriasian. The first of these are the Scarabaeoidea, the stag, scarab and dung beetles. They are probably of Jurassic origin, but diversified in the Berriasian. Krell (2000). A far more important development was the evolution of termites (Isoptera), which evolved from the ancient cockroach lineage (Blattaria) during, or just before, the Berriasian. Mayhew (2002).


***Pseudosimulium*, a predaceous rhagionid fly from the Berriasian of England. Mostovski *et al.* (2003)**

Bear in mind that wood recycling had been handled almost exclusively by fungi since the Mississippian. The fungi do a very thorough job, but they're slow. *Lignin* is a fiendishly complex molecule, and generates an amusing variety of toxic phenols if it isn't digested in just the right way. Termites can't actually digest lignin themselves, but the termite gut is a very complex ecosystem which plays host to an entire battery of bacterial and protist symbiotes which cooperate to get the job done rather quickly. *C.f.* Oxymonadida (one of the main protist groups involved in this industry). The advent of termites would likely have changed the entire forest food chain. Prior to termites, dead or fallen trees would have remained in place for many years as they were slowly consumed by rot. Termites recycle the nutrient content of wood much faster and convert it into insect biomass. This would not only permit faster recovery of woodlands from storm, fire and (perhaps) sauropod damage, but would open up vast new opportunities for small insectivores. One might suspect that the rapid spread of the opportunistic and aggressive angiosperms and the diversification of insectivorous therian mammals just after the Berriasian was not a coincidence. Thus, we may have mutant cockroaches to thank for the existence of both ourselves and our main food supplies.

Image Credits: termite from Fossilmall.com. *Pseudosimilium* from Mostovski *et al*. (2003).

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The Aptian Age

The Aptian Age of the Early Cretaceous II: 125 to 112 million years ago

The Aptian was a long age, the second-longest of the Mesozoic. It was also an eventful time. Unlike some geological ages, it is not at all difficult to find important events in the Aptian. A spike occurred in an already rapid rate of ocean spreading in the Atlantic. This, for the first time, opened the Atlantic Ocean wide enough to allow significant mixing of waters across the equator. This is associated, in some as-yet undetermined manner, with: (a) the first in a series of Ocean Anoxic Events which extended into the Santonian, and (b) with a probable massive release of methane about 117 Mya. This last event -- or something else -- caused a dramatic increase in temperatures in the mid-Aptian (Jenkyns & Wilson, 1999), and a significant turnover of land fauna in the Late Aptian and across the Aptian-Albian boundary. The Aptian saw the first ceratopsians, almost the last stegosaurs, the enormous *Sauroposeidon* and the diminutive *Gobiconodon*, the simultaneous evolution of the first of the swift, unarmored iguanodont- hadrosaur group, and the definitive members of nature's ultimate tanks, the nodosaurs.

Image: *Gobiconodon* from Validosta State University's **Virtual Museum of Fossils**.

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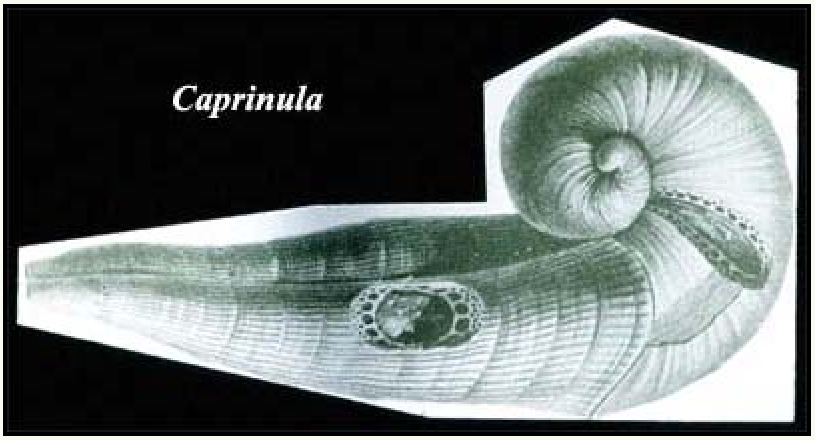
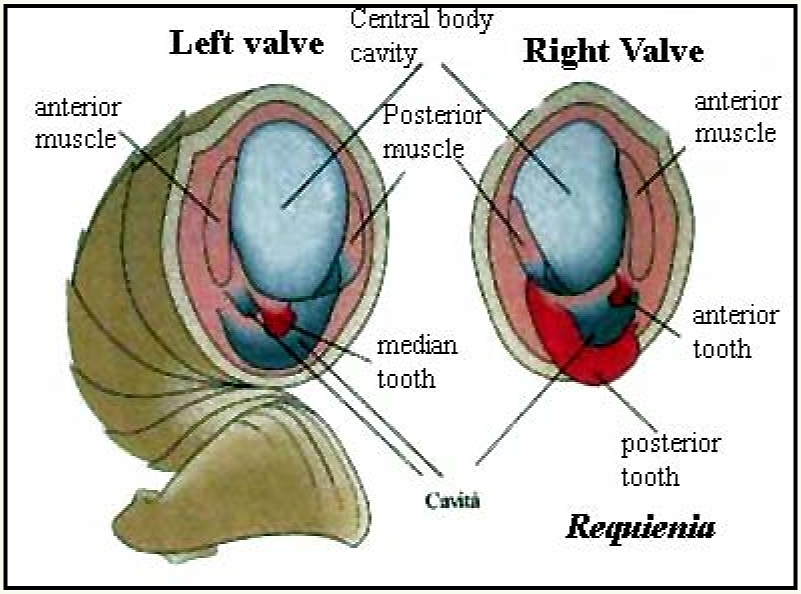
Aptian Reefs



Aptian reefs were typically composed of rudists. In spite of their name, rudists were probably no less civil than the scleractinian corals they replaced. Indeed, it is the rudists who have suffered from a singular lack of courtesy from ill-bred geologists, who rejoice in pointing out that rudist masses are not really "reefs." Technically, this may be correct. The rudists tended to trap sediment between their long, ribbed lower valves, which stood up from the sea floor like the stalks of some horrible mutant celery. Thus, rudist reefs were not entirely composed of biogenic carbonates like a coral reef. They contained substantial amounts of sand and mud, in addition to encrusting calcareous algae and other oddments. Yet it is surely impolite to harp on these occasional indiscretions of the distant past.

Rudists were, in fact, aberrant bivalve mollusks. Consider an ammonite, or nautiloid. Now, since this is a bivalve, imagine a creature with two such shells curling in opposite directions, like the horns on a ram's head. Finally take one (or sometimes both) of the coiled horns and straighten it out. The result should look something like *Caprinula*, shown in the image. The left valve became an elongate stem anchored in the sea floor. The right valve could take on any number of morphologies -- from a simple, flat, operculum (like the "lid" on the exhaust pipe of a diesel truck) to any one of the peculiar morphologies adopted by single-shelled mollusks. "Teeth" mounted on the valves formed the articulation between them. The internal structure, so far as it has been worked out, was more or less like that of conventional bivalves. *See* the image of *Requienia*. The animal itself occupied only the upper part of the lower valve, the remainder of the lower section being sealed off with horizontal partitions.



Rudists diverged from other bivalves some time in the Jurassic. The earliest were Requinidae which were still usually somewhat coiled. The formation of Aptian rudist reefs may have been driven by -- or may have driven -- the evolution of the Capridae, like *Caprinula*, and other new forms of rudist. This brief bloom of rudist diversity ended before the close of the Aptian-Albian and was not resumed until well into the High Cretaceous. Rudist diversity collapsed during the Maastrichtian, and the entire taxon became extinct at the end of the Mesozoic.

These earlier rudists are frequently associated with other faunal indicators to form a characteristic "Urgonain" facies. In Urgonian deposits, rudists are often found in association with masses of tests from large foraminifera, such as *Orbitolina* and *Choffatella*, the presence of which is an indicator of Aptian-Albian age. Lehmann *et al*. (1999). A well-known example is the reef enclosing the Shuaiba Formation limestone reservoirs of the United Arab Emirates, one of the richest oil-producing systems in the world. Urgonian facies are also characterized, negatively, by the absence of ammonites and belemnites. These absence indicators may simply reflect the fact that these early rudist reefs were usually products of shallow water, or even intertidal, environments.

Corals may also be associated with rudist reefs -- possibly only those reefs far from the equator. It has been argued at some length that equatorial surface waters during the Aptian heat wave approached 30° C. and were lethal to corals. Thus, this first generation of rudist reefs may have gotten its start because the seas were simply too hot for corals to thrive.

Links: Drome and Provence (however, we question the statement that *Hippurites* was present in the Aptian), Patch reefs in the limestones of the Altamira Formation ... (the formation which also created the canvas for an unknown Late Pleistocene artistic genius) , Bild constratatal (great site on rudists), Hippurites taburnii (more on rudists).

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Palaeos: Mesozoic

CRETACEOUS PERIOD

Παλαιός

Aptian-Albian

APTIAN-ALBIAN

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Early Cretaceous II (Aptian-Albian)

The Later Early Cretaceous Epoch: 125 to 99.6 million year ago

Cretaceous
- Early Cretaceous I (Neocomian)
- Early Cretaceous II (Aptian-Albian)
  - Aptian Age
  - Albian Age
- Late Cretaceous

Aptian-Albian (Early Cretaceous II)
- Stratigraphy
- Life
  - Other Invertebrates
    - Annellida
    - Brachiopoda
    - Bryozoa
    - Echinodermata
  - Land Vertebrates

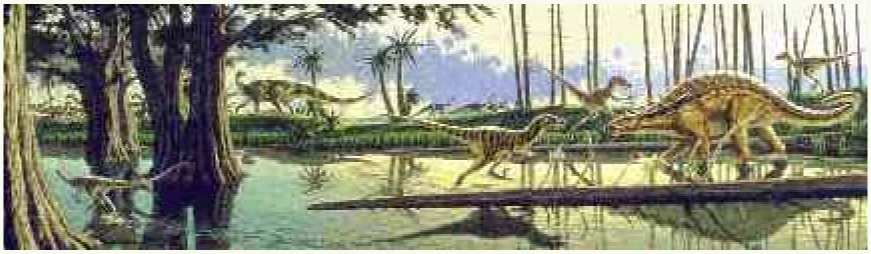


image from American Museum of Natural History

The Cashenranchian dinosaur fauna
(illustrated above)

Stratigraphy

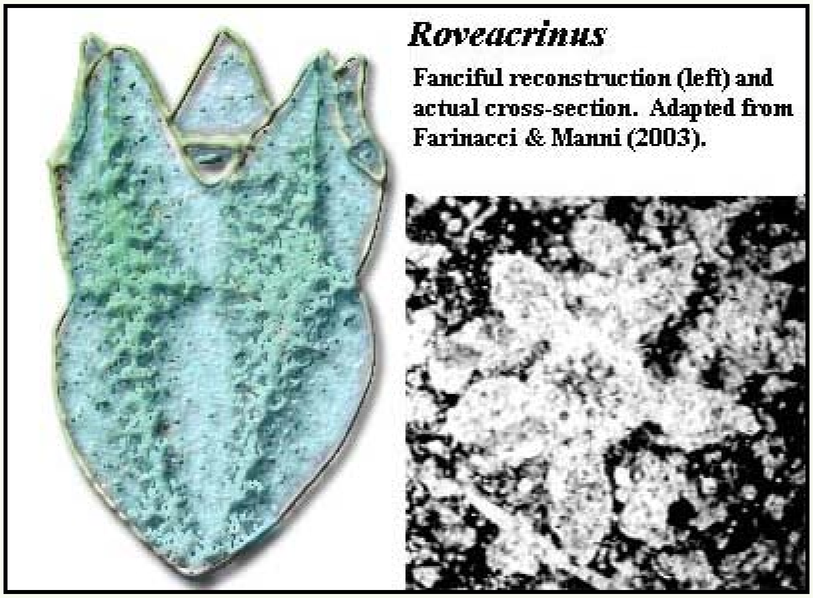
Epoch	Age	ICS Base (Mya)	ICS Duration (My)
Late Cretaceous I (High Cretaceous)	**Cenomanian**	**99.6**	**6.1**
Early Cretaceous II (Aptian-Albian)	Albian	**112**	**12.4**
	Aptian	**125**	**13.0**

Early Cretaceous I (Neocomian)	**Barremian**	**130**	**5.0**

Life

Invertebrates

Echinodermata



Roveacrinus

Fanciful reconstruction (left) and actual cross-section. Adapted from Farinacci & Manni (2003).

Echinoderms are well-represented in Albian microfossils in the Gault Fm of southern England. A number of excellent examples may be found on the website of the late Jim Craig (now maintained by Fred Clouter) at Echinodermata_Home. Note the unusually high proportion of ophiuroidian remains. These include some fragments of a *Nielsenicrinus* which must surely have been a monster in life. Echinoids are well represented and essentially modern. *See*, these examples of the sea urchins *Macraster*, *Heteraster* and *Hemiaster*.

The Asteroidea went through a process of rapid evolution and diversification during the Early and Middle Jurassic. This resulted in some fundamental changes in the organization of the arms associated with the transfer of the ampullae to the interior of the arms. Blake (2000). This change may have been associated with some unusual selective pressure. In any case, starfish are not frequently found in the Neocomian, and it is only in the Aptian-Albian that the Asteroidea again become common fossils. At this point, all of the remaining forms are essentially modern types and fall easily into well-characterized Recent families. *Id.*

Among the Crinoidea, the Aptian-Albian is especially noteworthy for the Roveacrinidae. These are odd, tiny, stemless, forms. Both nektonic and benthic forms are known, although both were motile to varying degrees. The benthic roveacrinids are characterized by the presence of flanges and spines, and by limited arm mobility. Nektonic roveacrinids have a large dorsal cavity, good arm mobility, and typically have very little ornamentation. They are first known from the Hauterivian (later Neocomian), bloomed in the Aptian-Albian, and flourished in the High Cretaceous before becoming extinct. Farinacci & Manni (2003).

Annelida

As you might expect, little is known of annelid evolution in the Mesozoic, since annelids rarely leave fossils. One exception are the serpulid tube worms which add a calcareous cement to their tube walls. The worms themselves are never recovered, but the tubes are frequently preserved in shallow marine sediments. In some cases, useful ultrastructural details can be made out. However, recrystalization and weathering make these details unrecoverable in Mesozoic or Paleogene remains. Two extremely common forms are shown in the image. These are better known from slightly younger strata in the High Cretaceous. However, they are common enough in the Aptian-Albian of the North American Interior Sea.

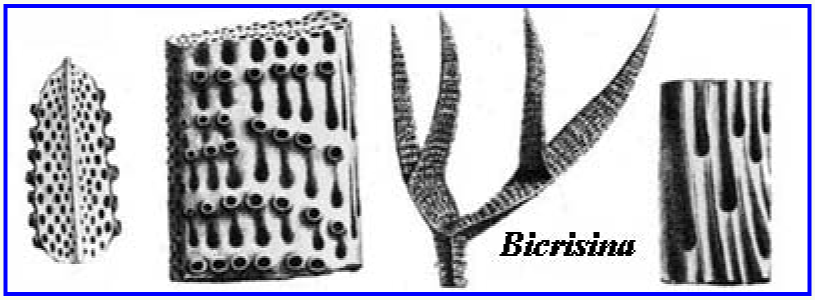
Two common Aptian-Albian annelids from North America

Brachiopoda

Brachiopods continued their slow and stately progression toward probable oblivion, a march that continues to this day. The Aptian Albian was the high point of a Late Jurassic to End-Cretaceous family of rhynchonellids known as the Cyclotherididae, and is marked by the appearance of the common genera *Burrirhynchia* and *Septatoechia*. Other "new" brachiopods include *Orbirhynchia*.

Image: *Burrirhynchia* from **Associació Amics de la Paleontologia de Morella**.

Bryozoa



Unlike some other large invertebrate taxa, it is a simple matter to determine what genera of Bryozoans are known from any part of the Cretaceous. *See* **Checklist of Cretaceous Bryozoa**, compiled in incredible detail by Prof. Alan Horowitz of Indiana University. It is a little harder to say anything meaningful about them.

The Aptian-Albian was perhaps the high point of the Cyclostomata, which were extremely diverse, with at least 70 known genera. These are mostly tube-like forms, well integrated and often branching. Benton & Harper (1997). *Bicrisina*, shown in the image, is a typical example. Another cyclostomate bryozoan, *Cellulipora*, from the same period, had an encrusting growth pattern. These and other encrusting bryozoans were significant reef builders in the Aptian-Albian and High Cretaceous.

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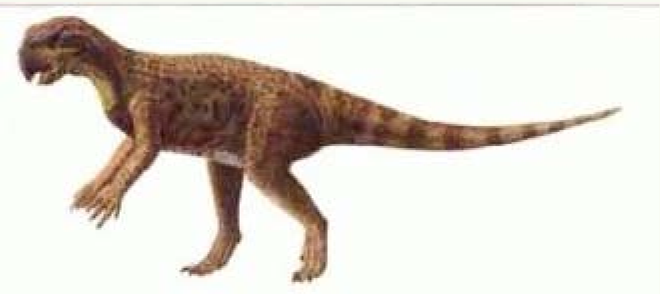
Land Vertebrates

On land, animals seem to have migrated and spread widely, despite provincialism. The presence of spinosaurids and iguanodontians on at least three continents) indicates the swamp system was very extensive and connected at certain periods of time. It is unlikely that specialized, advanced, spinosaurids might have traveled and migrated very far form their natural habitat.

A number of tetrapod provinces could be suggested:

Central Asian (East Laurasia)



What is now China and Mongolia were host to a distinctive tetrapod fauna, charcterised by the Sinochelyid turtle *Peishanemys*, mesosuchian crocodiles, advanced hadrosaur-like iguanodonts (*Probactrosaurus*, *Altirhinus*), the abundant small ceratopsian *Psittacosaurus*, the strange herbivorous Therizinosaurs (*Alxasaurus*, *Nanshiungosaurus*), and large (by Mesozoic standards) triconodont mammal *Gobiconodon*. This is basically a continuation of the earlier central Asian fauna, although with some changes among the big herbivores. Sauropods are now very rare, and the stegosaurs that had earlier been present have also disappeared (although the dating is difficult, so these form may actually have continued into the Aptian); the large herbivore guild now dominated by iguanodonts and therizinosaurs. Large theropods are present but poorly known; *"Alashansaurus" maortuensis* may have been related to the Tyrannosauroidea. It is not impossible that several lineages of tyrannosauroid-like animals may have developed from earlier forms at this time.

Psittacosaurus illustration by Steve Kirk - *Illustrated Encyclopedia of Dinosaurs and Prehistoric Animals*, ed.. Barry Cox, © 1988 Marshall Editions

"Cashenranchian" - North American (West Laurasia)

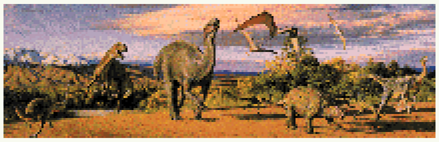
North America's endemic Aptian-Lower Albian dinosaur fauna features specialized allosaurids like *Acrocanthosaurus*, a diversity of dromaeosaurs, and herbivorous *Sauropelta*, *Tenontosaurus*, and *Pleurocoelus* sauropods. This megafauna differs strikingly from the more famous late Jurassic and late Cretaceous dinosaurs. It has been documented from the Cloverly Formation, Arundel Formation, Trinity Group, and Cedar Mountain formation. The term Cashenranchian has been proposed for it (from the Cashen Ranch, in southern Montana, where this fauna is well developed in the Cloverly Formation).

Climatically, the Barremian through Albian in the western North America represents a dry savanna, and water-loving Euro-Gondwanan predators like spinosaurids may have been ecologically excluded. Conditions however were wetter to the east. During the Cenomanian the west become much wetter with many extensive swamps.

North African (West Gondwana)

During the Mid-Cretaceous (Aptian to Cenomanian) a unique fauna of enormous dinosaurs evolved on a large island of what is now northern Africa. We tend to think of the *Tyrannosaurus* as being the largest land carnivore, but at this time there were no less than three different evolutionary lines of *Tyrannosaurus*-sized (12 metres and more in length) types of predators in this region alone: spinosaurs, carcharodontosaurids, and deltadromeids. These great predators preyed on the many kinds of herbivores, especially the giant Sauropoda, such as *Rebbachisaurus*, *Brachiosaurus*, and *Aegyptosaurus*. Also inhabiting this environment were large (3 to 6 meter)lungfish and gigantic (10 to 15 metre) *Sarcosuchus* crocodiles; a genus also known from South America (at the time part of a single biome and landmass)

Polar (East Gondwana)



During the Aptian-Albian, what is now Australia was located very near the South Pole. Although the climate was not as harsh as it is in today's Antarctic, the animals and plants of this environment still had to endure some freezing weather in winter and six months of darkness. Many unique animals inhabited this environment, including large temnospondyls, nocturnal hypsilophodontid and dwarf allosaurid dinosaurs, and the ancestor of the modern duck-billed platypus.

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The High Cretaceous: Late Cretaceous I

The Early Late Cretaceous Epoch: 99.6 to 83.5 Million Years Ago

- **Cretaceous**
  - **Neocomian** Early Cretaceous I
  - **Aptian-Albian** (Early Cretaceous II)
  - **High Cretaceous** (Late Cretaceous I)
    - **Cenomanian Age**
    - **Turonian Age**
    - **Coniacian Age**
    - **Santonian Age**
  - **End Cretaceous** (Late Cretaceous II)

an ankylosaur herbivore is menaced by
a tyrannosaurid predator
from American Museum of Natural History Timelines Exhibit

Stratigraphy

	Epoch	Age	sub-age	time MYA	Land Mammal Age (North America)	Terrestrial Vertebrate age (Asia0	date A	date B
		Maastrichtian	Late	65	Puercan		65.3	
				66 67	Lancian			

Late **Cretaceous**	**Late Cretaceous II** **"End-Cretaceous"**		**Early**	**68** **69**		**Nemegtian**	69.7	
				70 **71**	**Edmontian**			71.3
		Campanian	**Late**	**72**		**Nem.** *or* **Barun.**	72.1	
				73 **74** **75** **76** **77** **78** **79** **80**	**Judithian**	**Barungoyotian**		
			Early	**81**			81.1	
				82	**Aquilian**	**"Djadochtian"**	??	
				83				83.5
	Late Cretaceous I **"High Cretaceous"**	**Santonian**	Late	**84**				
			Early	**85**				85.8
		Coniacian	**Late**	**87**				
			Early	**89**				89.9
		Turonian						
		Cenomanian						

dating A: Land-Mammal Age table (former site), and A Quantitative North American Mammalian Time Scale (former site) by John Alroy.

dating B "A Triassic, Jurassic and Cretaceous time scale," by Gradstein, F.M., F.P. Agterberg, J.G. Ogg, J. Hardenbol, P. van Veen, J. Thierry and Z. Huang. 1995.in pp. 95-126 of W.A. Bergrgren, D.V. Kent, M.-P. Aubry & J. Hardenbol (eds.), *Geochronology, Time Scales, and Global Stratigraphic Correlation*. SEPM Special Publication No.54.)

Life

Plants

In the middle Permian the gymnosperm-dominated Mesophytic flora emerges (although Mesophytic type plants go back to the Carboniferous, just as some Paleophytic plants survive even to this day), and this flourishes right up until the middle and later Cretaceous. At this time, when the dinosaurs and other Mesozoic animals are in full swing, the current, angiosperm-dominated Cenophytic flora emerges (in fact Angiosperms appear in the later Early Cretaceous, but do not become predominant until the later Cretaceous). The Cenophytic flora continues quite happily through the great K-T extinction that eliminated the dinosaurs and many other forms of animal life (including some marsupial mammal and early bird types), although some modern biome-types like grasslands only appeared very recently (during the Miocene epoch). MAK010115.

Links

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Palaeos: Mesozoic
Cretaceous Period
Παλαιός
Late Cretaceous I
Santonian Age

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The Santonian Age

The Santonian Age of the Late Cretaceous Period: 85.8 to 83.5 million years ago

- Cretaceous
  - Early Cretaceous I (Neocomian)
  - Early Cretaceous II (Aptian-Albian)
  - Late Cretaceous I (High Cretaceous)
    - Cenomanian
    - Turonian
    - Coniacian
    - Santonian Age
  - Late Cretaceous II (End-Cretaceous)
    - Campanian

- The Santonian
  - Geography
  - Climate
  - Life
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    - Mosasaurs
    - Hadrosaurs
    - Pterosaurs & Birds
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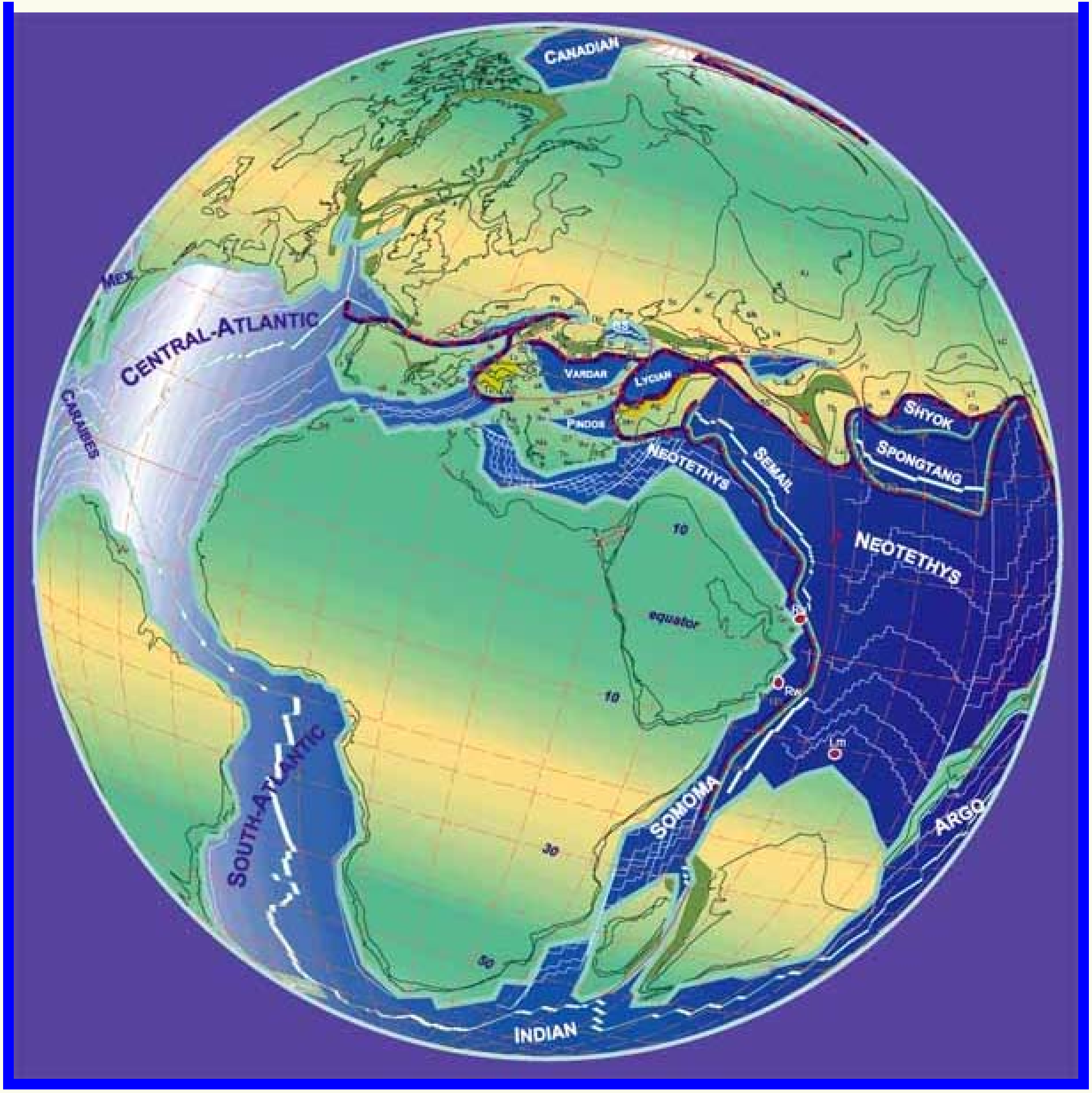
Geography of the Santonian

The geography of the Santonian seems to be a contentious subject. One version of the African and Mediterranean region is shown here. This map shows the position of the tectonic plates, with modern shorelines superimposed for reference. However, the Santonian was a time of extremely high sea levels --



perhaps the highest ever -- and much of the area shown as "land" would have been covered by shallow seas. You may get an idea of the proportions by looking at the PaleoMap Project map of the Late Cretaceous (Cenomanian). Dr. Blakey's maps of the Late Cretaceous are perhaps the best overall representation.

On the whole, the globe was beginning to look quite familiar by the Santonian, with a few exceptions. The Atlantic was narrower than in modern times. In fact, there may be some dispute as to whether the South Atlantic was entirely open yet. Some residual contact between the continental shelves of South America and Africa may have remained. However, the Central Atlantic was certainly open. The situation north of the Central Atlantic is less certain. Probably, an open seaway continued right up to the North Pole through the Labrador Sea. The Atlantic waters were certainly connected with the Pole by way of the North American Interior Seaway, which cut right through the center of the North American continent. South America, and even perhaps Africa, also held substantial inland seas.

Although the Atlantic was becoming quite recognizable, Southern Europe was still a confused and poorly understood collection of microplates, most of which were submerged, as were large sections of Eurasia. TheTethys Seaway through this region remained well open, and a strong westerly current swept from the Tethys, out across the Labrador Sea to South America. The Arabian peninsula remained tightly bound to Africa. India, which would one day close the Eastern end of the Tethys, was still far away. At this point in time, India was just separating from Madagascar and beginning its sprint (by geological standards) toward South Asia.

Eastern Asia had, by this time, consolidated, although Japan was probably still well to the South of its present position, perhaps just north of the equator. Australia was firmly locked to Antarctica, which was a bit east of its present position. The Pacific was far larger even than its present size, since most major land masses were still fairly well bunched near their Pangean positions.

Across the Pacific, the Sevier orogeny was beginning to build the Rocky Mountains in earnest, just as the Andes were becoming a major mountain chain in South America. The present Central America was open ocean. However, North and South America may have been sporadically joined through the Caribbean Arch.

Image: from Geodynamic evolution of the Alpine Tethys. ATW030206.

Climate of the Santonian

The Santonian may have been an age of storms. This speculation is admittedly our own, but there are several, independent lines of evidence that point to this conclusion.

First, several conditions were extremely favorable to the formation of cyclonic storms. World temperatures were both hot and uniform. There is considerable disagreement about the pattern of temperature change in the Late Cretaceous, but there is no doubt that it was very warm by modern standards. The Santonian is particularly noted for its *even* temperatures. That is, the average temperature varied little from pole to pole. It is not clear why this should be so, but the evidence from isotope ratios and the distribution of planktonic microfossils (and dinosaurs, for that matter!) is very clear. We may add to this mixture the highest sea levels the world had ever experienced, at least during Phanerozoic times. The net result is millions of square kilometers of open ocean, much of it shallow and easily warmed, baking to temperatures over 26.5° C., the critical water temperature for hurricane formation. Because temperatures were hot, humid, and uniform, we would be unlikely to see temperature inversions or complex upper air flows (causing vertical wind shear), both of which tear hurricanes apart before they can form.

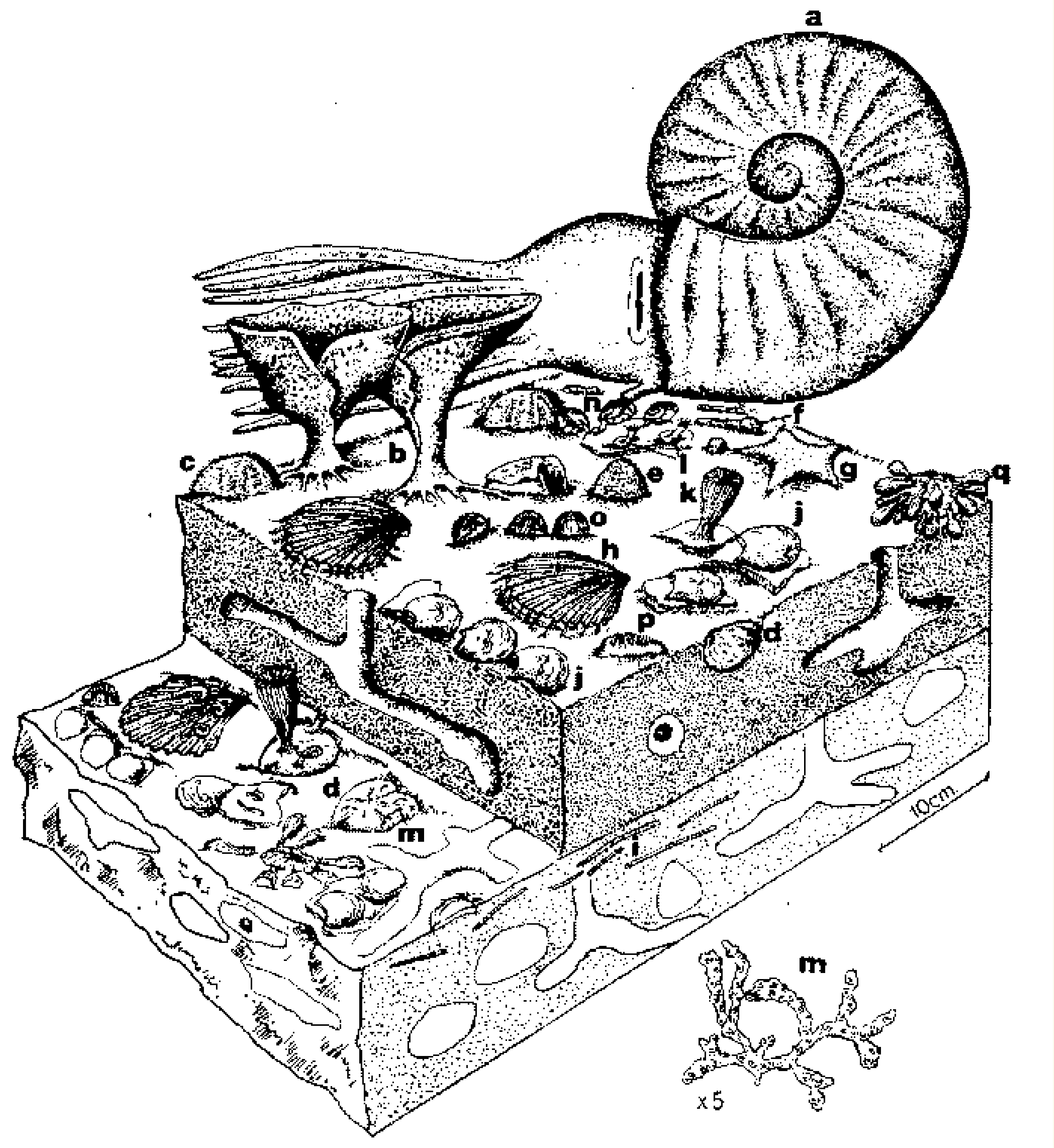
Second, the Santonian was notable for the controversial phenomenon of black shales. Black shales are dark layers of poorly oxidized decomposed organic matter on the ocean floor. There has been much discussion of the reasons for supposed Ocean Anoxic Events (OAEs) which caused these materials to accumulate. The supposition generally is that hot, uniform ocean surface temperatures created very stable layering of the oceans, depleting the oxygen in cooler deep ocean waters. However, OAEs seem to be made up of very short intervals of anoxic accumulation. We will not get far into this highly technical debate. The point we wish to make is that one possible reason for the perceived pattern of OAEs is that organic matter accumulated in large bursts and was buried quickly, before it could decompose. This might occur where giant storms washed enormous amounts of continental plant material into the ocean within days. This hypothesis accounts for both the presence and pattern of black shales. It also accounts for recent findings in Venezuela which show long periods of black shale accumulation outside the established Atlantic OAEs. Venezuela is roughly where one might expect ordinary tropical storms to make landfall in the Santonian. The presence of black shales in this region, *outside* the known temporal range of OAEs is consistent with hurricane events as the root cause of black shale accumulation.

Third, we know of another direct measure of storm activity, this time from North America. Dr.James Lamb of North Carolina State University has sampled Santonian vegetation in the Southeastern United States and along the north coast of the Gulf of Mexico. He finds that the northern Gulf differs from most contemporary sites because the tree-sized vegetation is dominated by pines. He believes that this is due to the influence of storm activity which periodically cleaned out the entire crop of standing trees, allowing the faster-growing pines to maintain an unstable dominance over angiosperm trees in this region. If correct, this provides relatively direct evidence of very large storm activity on a reasonably regular basis.

Much of the recent literature has been devoted to examining the relationship between OAEs and long cycles in Earth's orbit around the sun. This may well be the case, as these cycles have large, if poorly understood, effects on Earth's weather. But whatever the root geophysical cause, we suggest that the immediate cause was sudden accumulation of vast amounts of organic debris through hurricane activity. The climatic conditions and physical evidence point to the Santonian as an age of violent storms. ATW030205.

Representative Ecological Communities

The following reconstruction of a Santonian *Micraster Chalk Community* is from W. S. McKerrow *The Ecology of Fossils*



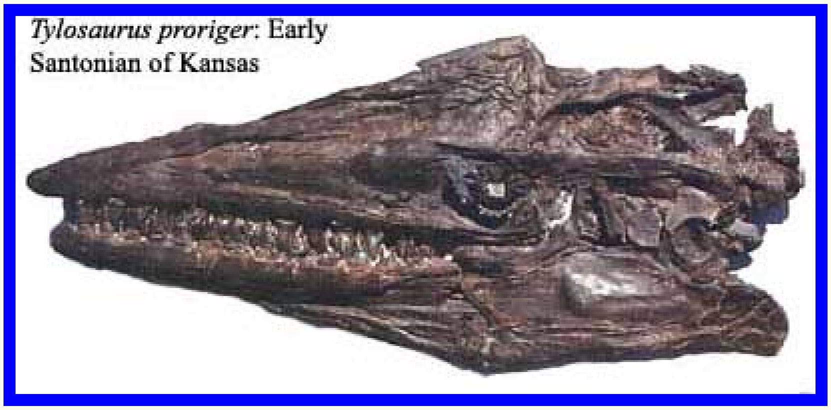
Santonian Micraster Chalk Community

a *Parapuzosia* (Mollusca - Cephalopoda - Ammonoidea)
b *Ventriculites* (Porifera - Hyalospongea)
c *Echinocorys scutata* (Echinodermata - Echinoidea)
d *Micraster* (Echinodermata - Echinoidea)
e *Conulus albogalerus* (Echinodermata - Echinoidea)
f *Baurgueticrinus eltipticus* (Echinodermata - Crinoidea)
g *Mitraster hunteri* (Echinodermata - Asteroidea)
h *Spondylus spinosus* (Mollusca - Bivalvia - Pterioida)
i *Inoceramus* fragments (Mollusca - Bivalvia - Pterioida
j Pycnodonte vesicutaris (Mollusca - Bivalvia - Pterioida - Oyster)
k Parasmilia centralis (Cnidaria - Anthozoa: Scleractinia)
l serpulids (Annelida)
m bryozoans (Bryozoa)
n Gibbithyris (Brachipoda - Articulata: Terebratulida)
o *Cretirhynchia* (Brachipoda - Articulata: Rhynchonellida)
p *Ptychodus* tooth (Vertebrata - Chondrichthyes)
q *Tylocidaris clavigera* (Echinodermata - Echinoidea)

> "The reconstruction of this fauna assemblage is based on a highly fossiliferous soft Santonian chalk on the Kent coast. Faunas of this general composition occur throughout much of the English Upper Chalk, but elsewhere faunal densities are very much lower.
>
> The chalk has been intensively bioturbated, but is so pure that burrow outlines are difficult to detect. Bottoms were probably thixotropic or semi-fluid, and the faunal elements present show adaptations to this habitat. All but the largest aragonitic organisms are absent.
>
> Benthic elements frequently adapted themselves for living on soft bottoms: they sometimes developed long spines to spread the weight of the shell, as in the case of the pectinid *Spondylus* **[h]**, or club-shaped spines, as with the cidarid echinoid *Tylocidaris* **[q]**. Inoceramids are scarce; when present they have often developed a bowl-like lower valve, or are vastly expanded and flattened. Shell debris provided hard substrates which were heavily encrusted by bryozoans **[m]**, serpulids and oysters; they may also have provided a substrate for some brachiopods. Other brachiopods such as *Cretirhynchia* **[o]**, lay loose on the sediment surface when adult. Echinoderms are a prominent element of these faunas and shown here are *Micraster* **[d]**, an infaunal or semi-infaunal deposit feeder; *Conulus* **[c]** and *Echinocorys* **[c]**, which probably lived partly buried, ploughing through sediment and feeding on detritus; the cushion star *Mitraster* **[g]** and the crinoid *Bourgueticrinus* **[f]**. Nekton are represented by the giant ammonite *Parapuzasia* **[a]** which reaches a diameter close to 2 metres, and by teeth of the mollusk-eating fish *Ptychodus* **[p]** (tooth), probably responsible for much of the fragmentation of inoceramids and other shells."

© xxxx - W.J. Kennedy "Cretaceous", in W.S. McKerrow (ed.) *The Ecology of Fossils* pp. 318-9

The Mosasaur Success Story Continues


Tylosaurus proriger: Early Santonian of Kansas

Although these huge marine lizards had only first appeared a few million years earlier, they had already by Santonian times attained a great ecological diversity. The three subfamilies continue and each are well represented in the Niobrara Chalk.

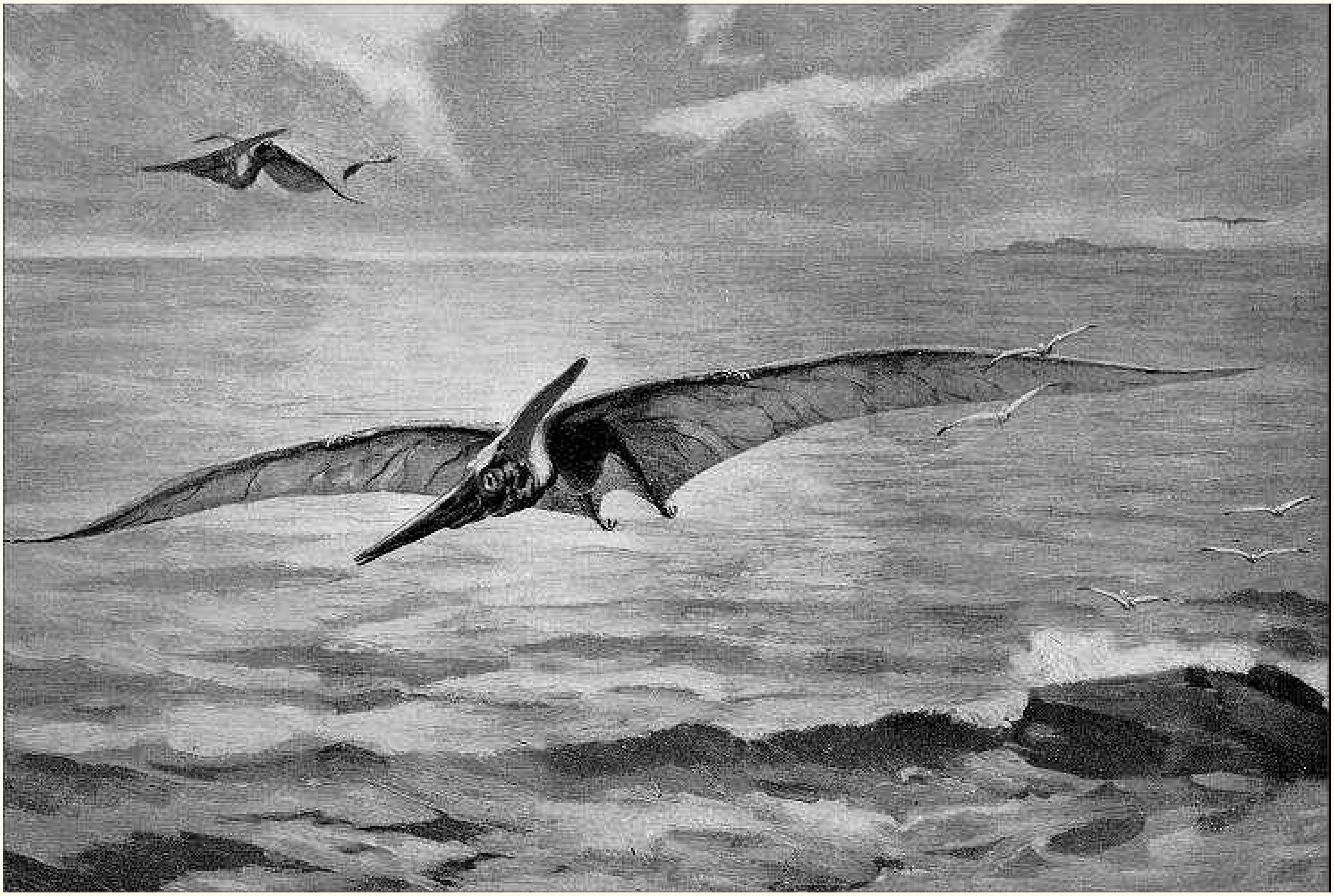
Clidastes propython is a primitive member of the subfamily Mosasaurinae [DeBraga and Carroll 1993 p.252]. It was the smallest mosasaur of the North American inland sea, with an average length of about 4 meters, and a slender elongated body and a relatively short flattened tail. The end of tail features expanded neural spines that created a tail-fin, although the existence of an additional soft-tissue fin (as possessed by sea-snakes) to further enlarge the end of tail is debatable. In any case *Clidastes* was a fast swimmer, and possibly able to dive to fairly great depths [Creisler 2000]

Tylosaurus propriger is a very large mosasaur, with lengths of up to 10 to 12 meters and a skull alone of upto a meter or more. (*Tylosaurus* skull illustrated above). Clearly this was the dominant animal in its environment. It is representative of the second subfamily, Tylosaurinae. It is named for its long projecting snout, or rostrum, which projects past the front teeth in the upper jaw; and may have been similar in function to the "ram" or "beak" (Lat. *rostrum*) that the ancient Greeks and Romans mounted on the prow of warships to sink enemy vessels. Tylosaurus might have use its snout to ram and stun prey, defend against sharks or other predators, and battle rivals of its own species. [Creisler 2000]

Platecarpus ictericus - A medium-sized species, 4.3 meters in length, *Platecarpus* belongs to the most advanced subfamily of mosasaurs, the Plioplatecarpinae. This was a common species in the Inland Sea that became the Niobrara chalk deposits. The flattened tail is as long as the body, and the animal swum with a sinuous motion, while the broad feet were used for steering [Cox et al pp.88-89]. Although the thick fossilized eardrums would seem to indicate a deep-diving capacity [Williston 1898], these animals appear to have been adapted to life in shallow water as an ambush predator [Creisler 2000] MAK030211

Some Technical Notes on Mosasaurs

Pterosaurs and Birds



The giant pterosaur *Pteranodon ingens*, with a wingspan of 7 meters, dwarfs the toothed shore birds (*Ichthyornis*) with which it shared its environment

from Early Images
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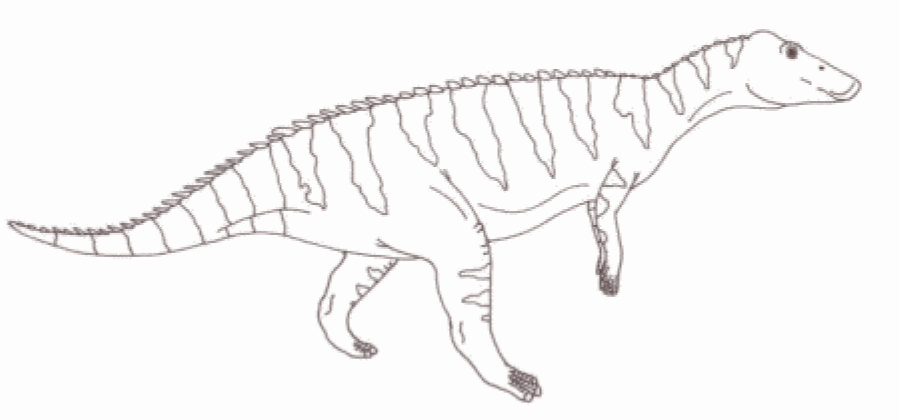
Throughout the Cretaceous, pterosaurs grew larger, while the ecological niche of smaller fish and insect-eaters that during the Jurassic was occupied by Rhamphorhynchid and other small pterosaurs is now occupied by true birds.

Hadrosaurid Dinosaurs



drawing © 2000 Vince R Ward - Prehistoric Pages

It can be assumed that Santonian dinosaurs were not very different to those of the preceding Coniacian age, but seem to be poorly represented in the fossil record. Mongolian sediments seem to be either older (Coniacian or at latest Early Santonian) or younger (Middle Campanian onwards), although admittedly the stratigraphy is still uncertain. Brazilian dinosaurs may also tentatively be of Santonian age although again the dating is not certain. The Nequen Formation of Argentina may be either Coniacian or Santonian. So the only certain dinosaurs of this age are a few rare specimens from the Niobrara that were washed out to sea before being fossilized, and even their the dating may be anywhere from Middle Santonian to Early Campanian.

The Laurasian Hadrosauridae, which go back as far as the Cenomanian, were wide-spread but primitive, as indicated by *Claosaurus agilis* from the Niobrara of Kansas (sketch, above) a small (3.5 meters long) animal known from a mostly complete postcranium and some skull fragments. *Claosaurus* is one of the most primitive hadrosaurids known, as it retains of the first metatarsal, which all other hadrosaurids for which the foot is known have lost. [Tweet iNet]. It may be compared with Asian species such as *Arstanosaurus* of the Bayn Shireh Formation (Svita), Gobi Desert, Mongolia (probably Turonian or Coniacian), *Gilmoreosaurus mongoliensis* and *Bactrosaurus johnsoni* from the Iren Dabasu Formation of Inner Mongolian (dating uncertain, perhaps anywhere from Turonian to Campanian). *Gilmoreosaurus* was a large animal (possibly upto 8 meters), with an iguanodont-like skull, that represents the beginning of, or is prior to, the hadrosaurine lineage. *Bactrosaurus* (4 to 6 meters long) is almost as primitive, and stands at the base of lambeosaurine (hollow-crested duckbills) evolution. The very primitive *Telmatosaurus transylvanicus* (Nopcsa, 1899), a smallish (5 meters long) animal known from fragmentary skulls and postcrania from Romania, France and Spain, lived much later, during the late Maastrichtian, but had an Iguanodont-like skull and is one of the few known European hadrosaurs. The contemporary Argentine *Secernosaurus koerneri*, only 3 meters long, may have been at a similar level of organization and is one of only two known Gondwana hadrosaur species

It seems then that during or prior to (perhaps in the Turonian or Coniacian) this time, primitive hadrosaurs migrated widely, colonizing Eastern Laurasia (Europe and Eastern North America), and Gondwana. While the center of Hadrosaurid evolution, like ankylosaurid, ceratopsid, pachycephalosaurid, tyrannosaurid, and maniraptoran evolution, remained the huge Asiamerican island (a long strip of land from Mongolia through to Western Canada and down to Mexico), these other regions, dominated by a saurischian Titanosaurid-Abelisaurid megafauna, proved a welcoming environment for the very primitive Hadrosaurs, which persisted seemingly with little change right up until the end of the age of the Dinosaurs. MAK030211

Links

Links

Late Cretaceous - Dr Ron Blakey's Global Earth History

Oceans of Kansas - Mike Everhart's world-class site, which includes a great deal of material about the Niobrara (mid Santonian to Early Campanian)

Colorado Niobrara Formation fossils - from the Itano website

Santonian (Late Cretaceous) Cephalopods - photos of some large ammonites - from Kevin Bylund's Old Calamari - Fossil Cephalopods in Utah website

Upper Cretaceous Sharks & Rays of Kansas - Mike Everhart

Chronological List of Taxa -Santonian - from The Plesiosaur Site

DinoData - Santonian - list of dinosaurs from this period (*note* - because of uncertainty in stratigraphic dating, not all the species listed on the page are necessarily of this time-period

Between the Devil and the Deep Blue Sea - Brandi Berry provides a short description of a number of taxa from the Niobrara

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References

Boetius A, K Ravenschlag, CJ Schubert, D Rickert, F Widdel, A Gieseke, R Amann, BB Jorgensen, U Witte & O Pfannkuche (2000), *A marine microbial consortium apparently mediating anaerobic oxidation of methane*. **Nature** 407: 623-626.

Bralower, TJ, IP Silva & MJ Malone (2002), *New evidence for abrupt climate change in the Cretaceous and Paleogene: An Ocean Drilling Program expedition to Shatsky Rise, northwest Pacific*. **GSA Today** 12: 4–10.

Chumakov, NM (2003), *Trends in global climate changes inferred from geological data*. **Strat. Geol. Corr.**, 12: 117–138.

Damsté, JSS, WIC Rijpstra, EC Hopmans, FG Prahl, SG Wakeham, and S Schouten (2002), *Distribution of membrane lipids of planktonic Crenarchaeota in the Arabian Sea*. **Appl. Env. Microbiol.** 68: 2997-3002.

Kenig, F, D-JH Simons, D Crich, JP Cowen, GT Ventura, T Rehbein-Khalily, TC Brown, & KB Anderson (2003), *Branched aliphatic alkanes with quaternary substituted carbon atoms in modern and ancient geologic samples*. **Proc. Nat. Acad. Sci. (USA)** 100: 12554–12558.

Kiessling, W & RC Baron-Szabo (2004), *Extinction and recovery patterns of scleractinian corals at the Cretaceous-Tertiary boundary*. **Palaeogeog. Palaeoclimatol. Palaeoecol.** 214: 195– 223.

Krell, F-K (2000), *The fossil record of Mesozoic and Tertiary Scarabaeoidea (Coleoptera : Polyphaga)*. **Invert. Taxon.** 14: 871–905.

Kuypers, MMM, P Blokker, J Erbacher, H Kinkel, RD Pancost, S Schouten & JSS Damsté (2001), *Massive expansion of marine Archaea during a Mid-Cretaceous oceanic anoxic event*. **Science** 293: 92-95.

Mayhew, PJ (2002), *Shifts in hexapod diversification and what Haldane could have said*. **Proc. R. Soc. Lond. B**

01PB0885 (on line ed.)

Miller, KG, PJ Sugarman, JV Browning, MA Kominz, JC Hernández, RK Olsson, JD Wright, MD Feigenson & W Van Sickel (2003), *Late Cretaceous chronology of large, rapid sea-level changes: Glacioeustasy during the greenhouse world*. **Geology** 31: 585–588.

Mostovski, MB, AJ Ross, R Szadziewski & W Krzeminski (2003), *Redescription of **Simulidium priscum** Westwood and **Pseudosimulium humidum** (Brodie) (Insecta: Diptera: Rhagionidae) from the Purbeck Limestone Group (Lower Cretaceous) of England*. **J. Sys. Palaeontol.** 1: 59–64.

Ren, D (1998), *Flower-associated Brachycera flies as fossil evidence for Jurassic angiosperm origins*, **Science** 280: 85-88.

Schouten, S, EC Hopmans, RD Pancost & JSS Damsté (2000), *Widespread occurrence of structurally diverse tetraether membrane lipids: Evidence for the ubiquitous presence of low-temperature relatives of hyperthermophiles*. **Proc. Nat. Acad. Sci. (USA)** 97: 14421-14426.

Schouten, S, SG Wakeham, EC Hopmans, & JSS Damsté (2003), *Biogeochemical evidence that thermophilic Archaea mediate the anaerobic oxidation of methane*. **Appl. Env. Microbiol.** 69: 1680-1686.

Stanley, GD (2003), *The evolution of modern corals and their early history*. **Earth-Sci. Rev.** 60: 195-225.

Stanley, SM, LA Hardie & MK Blaustein (1999), *Hypercalcification: Paleontology links plate tectonics and geochemistry to sedimentology*. **GSA Today** 9(2): 1-7.

Wimbledon W.A.P., Castellato C.E., Rehakova D., Bulot L.G., Erba E., Gardin S., Verreussel R. M.C.H., Munsterman D.K., Hunt C.O. (2011) Fixing a basal Berriasian and Jurassic/Cretaceous (J/K) boundary - is there perhaps some light at the end of the tunnel? *Rivista Italiana di Paleontologia e Stratigrafia*. Vol.117. no.2. P.295-307
Berriasian - Stratigraphy

Zharkov, MA, IO Murdmaa & NI Filatova (1998), *Paleogeography of the Berriasian–Barremian Ages of the Early Cretaceous*. **Strat. Geol. Corr.**, 6: 47–69.

Notes

[1] The figure combines data from two separate figures in Kiessling & Baron-Szabo (2004).

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