A Comprehensive Introduction to The Triassic Period & Events

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Introduction to Triassic Period

Triassic Period *251 – 199.6 million years ago*	

Mean atmospheric O_2 content over period duration	ca. 16 Vol % (80 % of modern level)
Mean atmospheric CO_2 content over period duration	ca. 1750 ppm (6 times pre-industrial level)
Mean surface temperature over period duration	ca. 17 °C (3 °C above modern level)

The **Triassic** is a geologic period that extended from about 250 to 200 Mya (million years ago). As the first period of the Mesozoic Era, the Triassic follows the Permian and is followed by the Jurassic. Both the start and end of the Triassic are marked by major extinction events. The extinction event that closed the Triassic Period has recently been more accurately dated, but as with most older geologic periods, the rock beds that define the start and end are well identified, but the exact dates of the start and end of the period are uncertain by a few million years.

During the Triassic, both marine and continental life show an adaptive radiation beginning from the starkly impoverished biosphere that followed the Permian-Triassic extinction. Corals of the hexacorallia group made their first appearance. The first flying vertebrates, the pterosaurs, evolved during the Triassic.

Dating and subdivisions

The Triassic was named in 1834 by Friedrich Von Alberti from the three distinct layers (Latin *trias* meaning triad)—red beds, capped by chalk, followed by black shales—that are found throughout Germany and northwest Europe, called the 'Trias'.

The Triassic is usually separated into Early, Middle and Late Triassic Epochs and the corresponding rocks are referred to as Lower, Middle, or Upper Triassic. The faunal stages from the youngest to oldest are:

Upper/Late Triassic (Tr3)

Rhaetian	(203.6 ± 1.5 – 199.6 ± 0.6 Mya)
Norian	(216.5 ± 2.0 – 203.6 ± 1.5 Mya)
Carnian	(228.0 ± 2.0 – 216.5 ± 2.0 Mya)

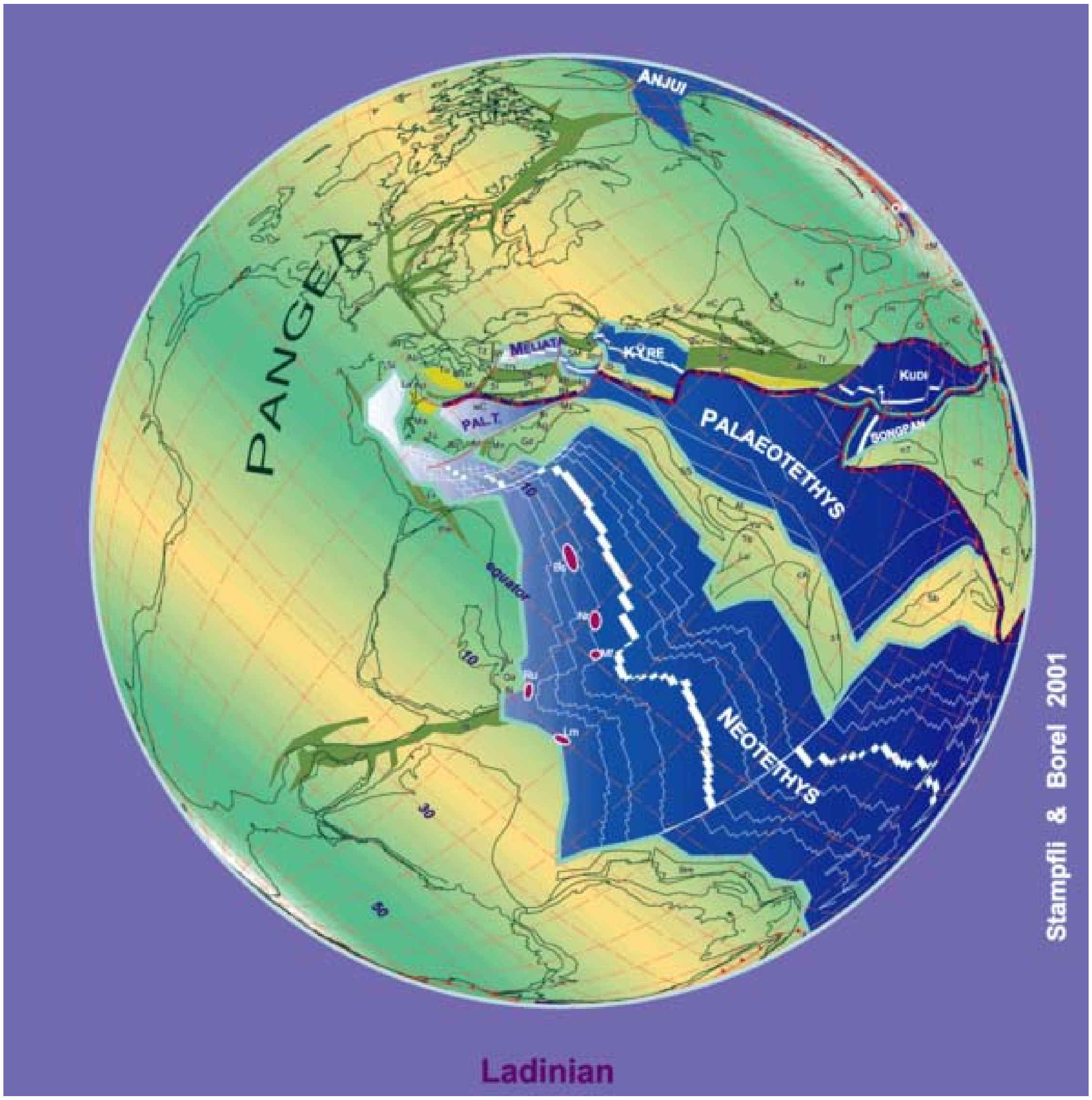
Middle Triassic (Tr2)

Ladinian	(237.0 ± 2.0 – 228.0 ± 2.0 Mya)
Anisian	(245.0 ± 1.5 – 237.0 ± 2.0 Mya)

Lower/Early Triassic (Scythian)

Olenekian	(249.7 ± 0.7 – 245.0 ± 1.5 Mya)
Induan	(251.0 ± 0.4 – 249.7 ± 0.7 Mya)

Paleogeography



230 Ma plate tectonic reconstruction

During the Triassic, almost all the Earth's land mass was concentrated into a single supercontinent centered more or less on the equator, called Pangaea ("all the land"). From the east a vast gulf entered Pangaea, the Tethys sea. It opened farther westward in the mid-Triassic, at the expense of the shrinking Paleo-Tethys Ocean, an ocean that existed during the Paleozoic. The remaining shores were surrounded by the world-ocean known as Panthalassa ("all the sea"). All the deep-ocean sediments laid down during the Triassic have disappeared through subduction of oceanic plates; thus, very little is known of the Triassic open ocean. The supercontinent Pangaea was rifting during the Triassic—especially late in the period—but had not yet separated. The first nonmarine sediments in the rift that marks the initial break-up of Pangaea—which separated New Jersey from Morocco—are of Late Triassic age; in the U.S., these thick sediments comprise the

Newark Group. Because of the limited shoreline of one super-continental mass, Triassic marine deposits are globally relatively rare, despite their prominence in Western Europe, where the Triassic was first studied. In North America, for example, marine deposits are limited to a few exposures in the west. Thus Triassic stratigraphy is mostly based on organisms living in lagoons and hypersaline environments, such as Estheria crustaceans.

Africa

At the beginning of the Mesozoic Era, Africa was joined with Earth's other continents in Pangaea. Africa shared the supercontinent's relatively uniform fauna which was dominated by theropods, prosauropods and primitive ornithischians by the close of the Triassic period. Late Triassic fossils are found through-out Africa, but are more common in the south than north. The boundary separating the Triassic and Jurassic marks the advent of an extinction event with global impact, although African strata from this time period have not been thoroughly studied.

Climate

Middle Triassic marginal marine sequence, southwestern Utah

The Triassic climate was generally hot and dry, forming typical red bed sandstones and evaporites. There is no evidence of glaciation at or near either pole; in fact, the polar regions were apparently moist and temperate, a climate suitable for reptile-like creatures. Pangaea's large size limited the moderating effect of the global ocean; its continental climate was highly seasonal, with very hot summers and cold winters. It probably had strong, cross-equatorial monsoons.

Triassic flora as depicted in Meyers Konversations-Lexikon (1885-90)

Three categories of organisms can be distinguished in the Triassic record: holdovers from the Permian-Triassic extinction, new groups which flourished briefly and other new groups which went on to dominate the Mesozoic world.

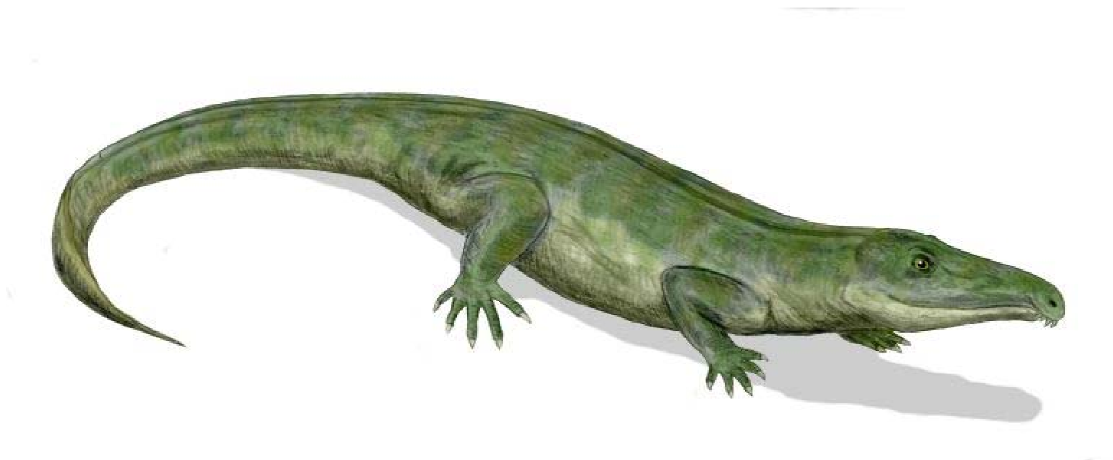
Flora

On land, the holdover plants included the lycophytes, the dominant cycads, ginkgophyta (represented in modern times by *Ginkgo biloba*) and glossopterids. The spermatophytes, or seed plants came to dominate the terrestrial flora: in the northern hemisphere, conifers flourished. *Glossopteris* (a seed fern) was the dominant southern hemisphere tree during the Early Triassic period.

Marine fauna

In marine environments, new modern types of corals appeared in the Early Triassic, forming small patches of reefs of modest extent compared to the great reef systems of Devonian times or modern reefs. The shelled cephalopods called ammonites recovered, diversifying from a single line that survived the Permian extinction. The fish fauna was remarkably uniform, reflecting the fact that very few families survived the Permian extinction. There were also many types of marine reptiles. These included the Sauropterygia, which featured pachypleurosaurs and nothosaurs (both common during the Middle Triassic, especially in the Tethys region), placodonts and the first plesiosaurs; the first of the lizardlike Thalattosauria (askeptosaurs); and the highly successful ichthyosaurs, which appeared in Early Triassic seas and soon diversified, some eventually developing to huge size during the late Triassic.

Terrestrial fauna



Reconstruction of *Proterosuchus*, a genus of carnivorous reptile, classified under Archosauromorpha, that existed in the Early Triassic period.

Coelophysis, one of the first Dinosaurs, appeared in the mid-Triassic

The Permian-Triassic extinction devastated terrestrial life. Biodiversity rebounded with the influx of disaster taxa, however these were short lived. Diverse communities with complex trophic structures took 30 million years to reestablish.

Temnospondyl amphibians were among those groups that survived the Permian-Triassic extinction, some lineages (e.g. Trematosaurs) flourishing briefly in the Early Triassic, while others (e.g. capitosaurs) remained successful throughout the whole period, or only came to prominence in the Late Triassic (e.g. plagiosaurs, metoposaurs). As for other amphibians, the first Lissamphibia, characterized by the first frogs, are known from the Early Triassic, but the group as a whole did not become common until the Jurassic, when the temnospondyls had become very rare.

Archosauromorph reptiles—especially archosaurs—progressively replaced the synapsids that had dominated the Permian. Although *Cynognathus* was a characteristic top predator in earlier Triassic (Olenekian and Anisian) Gondwana and both kannemeyeriid dicynodonts and gomphodont cynodonts remained important herbivores during much of the period. By the end of the Triassic, synapsids played only bit parts. During the Carnian (early part of the Late Triassic), some advanced cynodont gave rise to the first mammals. At the same time the Ornithodira, which until then had been small and insignificant, evolved into pterosaurs and a variety of dinosaurs. The Crurotarsi were the other important archosaur clade and during the Late Triassic these also reached the height of their diversity, with various groups including the phytosaurs, aetosaurs, several distinct lineages of Rauisuchia and the first crocodylians (the Sphenosuchia). Meanwhile the stocky herbivorous rhynchosaurs and the small to medium-sized insectivorous or piscivorous Prolacertiformes were important basal archosauromorph groups throughout most of the Triassic.

Among other reptiles, the earliest turtles, like *Proganochelys* and Proterochersis, appeared during the Norian (middle of the Late Triassic). The Lepidosauromorpha—specifically the Sphenodontia—are first known in the fossil record a little earlier (during the Carnian). The Procolophonidae were an important group of small lizard-like herbivores.

Archosaurs were initially rarer than the therapsids which had dominated Permian terrestrial ecosystems, but they began to displace therapsids in the mid-Triassic. This "Triassic Takeover" may have contributed to the evolution of mammals by forcing the surviving therapsids and their mammaliform successors to live as small, mainly nocturnal insectivores; nocturnal life probably forced at least the mammaliforms to develop fur and higher metabolic rates.

Coal

At the start of the Triassic period coal is noticeable by geologists today as being absent throughout the world. This is known as the "coal gap" and can be seen as part of the Permian–Triassic extinction event. Sharp drops in sea level across the Permo Triassic boundary may be the proper explanation for the coal gap. However, theories are still speculative as to why it is missing. During the preceding Permian period the arid desert conditions contributed to the evaporation of many inland seas and the inundation of these seas, perhaps by a number of tsunami events that may have been responsible for the drop in sea level. This due to the finding of large salt basins in the southwest United States and a very large basin in central Canada.

Immediately above the boundary the glossopteris flora was suddenly largely displaced by an Australia wide coniferous flora containing few species and containing a lycopod herbaceous under story. Conifers also became common in Eurasia. These groups of conifers arose from endemic species because of the ocean barriers that prevented seed crossing for over one hundred million years. For instance, Podocarpis was located south and Pines, Junipers and Sequoias were located north. The dividing line ran through the Amazon Valley, across the Sahara and north of Arabia, India, Thailand and Australia. It has been suggested that there was a climate barrier for the conifers. although water barriers are more plausible. If so, something that can cross at least short water barriers must have been involved in producing the coal hiatus. Hot climate could have been an important auxiliary factor across Antarctica or the Bering Strait, however. There was a spike of fern and lycopod spores immediately after the close of the Permian. In addition there was also a spike of fungal spores immediately after the Permian-Triassic boundary. This spike may have lasted 50,000 years in Italy and 200,000 years in China and must have contributed to the climate warmth.

An event excluding a catastrophe must have been involved to cause the coal hiatus due to the fact that fungi would have removed all dead vegetation and coal forming detritus in a few decades in most tropical places. In addition, fungal spores rose gradually and declined similarly along with a prevalence of woody debris. Each phenomenon would hint at widespread vegetative death. Whatever the cause of the coal hiatus must have started in North America approximately 25 million years sooner.

Lagerstätten

Triassic sandstone near Stadtroda, Germany

The Monte San Giorgio lagerstätte, now in the Lake Lugano region of northern Italy and Switzerland, was in Triassic times a lagoon behind reefs with an anoxic bottom layer, so there were no scavengers and little turbulence to disturb fossilization, a situation that can be compared to the better-known Jurassic Solnhofen limestone lagerstätte. The remains of fish and various marine reptiles (including the common pachypleurosaur Neusticosaurus and the bizarre long-necked archosauromorph *Tanystropheus*), along with some terrestrial forms like *Ticinosuchus* and *Macrocnemus*, have been recovered from this locality. All these fossils date from the Anisian/Ladinian transition (about 237 million years ago).

Late Triassic extinction event

The Triassic period ended with a mass extinction, which was particularly severe in the oceans; the conodonts disappeared and all the marine reptiles except ichthyosaurs and plesiosaurs. Invertebrates like brachiopods, gastropods and molluscs were severely affected. In the oceans, 22% of marine families and possibly about half of marine genera went missing according to University of Chicago paleontologist Jack Sepkoski.

Though the end-Triassic extinction event was not equally devastating everywhere in terrestrial ecosystems, several important clades of crurotarsans (large archosaurian reptiles previously grouped together as the thecodonts) disappeared, as did most of the large labyrinthodont amphibians, groups of small reptiles and some synapsids (except for the proto-mammals). Some of the early, primitive dinosaurs also went extinct, but other more adaptive dinosaurs survived to evolve in the Jurassic. Surviving plants that went on to dominate the Mesozoic world included modern conifers and cycadeoids.

What caused this Late Triassic extinction is not known with certainty. It was accompanied by huge volcanic eruptions that occurred as the supercontinent Pangaea began to break apart about 202 to 191 million years ago [(40Ar/39Ar dates)], forming the Central Atlantic Magmatic Province [(CAMP)], one of the largest known inland volcanic events since the planet cooled and stabilized. Other possible but less likely causes for the extinction events include global cooling or even a bolide impact, for which an impact crater containing Manicouagan Reservoir in Quebec, Canada, has been singled out. At the Manicouagan impact crater, however, recent research has shown that the impact melt within the crater has an age of 214±1 Mya. The date of the Triassic-Jurassic boundary has also been more accurately fixed recently, at 201.58±0.28 Mya. Both dates are gaining accuracy by using more accurate forms of radiometric dating, in particular the decay of uranium to lead in zircons formed at the impact. So the evidence suggests the Manicouagan impact preceded the end of the Triassic by approximately 10±2 Ma. Therefore it could not be the immediate cause of the observed mass extinction.

The number of Late Triassic extinctions is disputed. Some studies suggest that there are at least two periods of extinction towards the end of the Triassic, between 12 and 17 million years apart. But arguing against this is a recent study of North American faunas. In the Petrified Forest of northeast Arizona there is a unique sequence of latest Carnian-early Norian terrestrial sediments. An analysis in 2002 found no significant change in the paleoenvironment. Phytosaurs, the most common fossils there, experienced a change-over only at the genus level and the number of species remained the same. Some aetosaurs, the next most common tetrapods and early dinosaurs, passed through unchanged. However, both phytosaurs and aetosaurs were among the groups of archosaur reptiles completely wiped out by the end-Triassic extinction event.

It seems likely then that there was some sort of end-Carnian extinction, when several herbivorous archosauromorph groups died out, while the large herbivorous therapsids—the kannemeyeriid dicynodonts and the traversodont cynodonts— were much reduced in the northern half of Pangaea (Laurasia).

These extinctions within the Triassic and at its end allowed the dinosaurs to expand into many niches that had become unoccupied. Dinosaurs became increasingly dominant, abundant and diverse and remained that way for the next 150 million years. The true "Age of Dinosaurs" is the Jurassic and Cretaceous, rather than the Triassic.

Chapter- 2

Rhaetian and Triassic–Jurassic Extinction Event

Rhaetian

System	Series	Stage	Age (Ma)
Jurassic	Lower	Hettangian	**younger**
Triassic	Upper	**Rhaetian**	199.6–203.6
		Norian	203.6–216.5
		Carnian	216.5–228.0
	Middle	Ladinian	228.0–237.0
		Anisian	237.0–245.0
	Lower	Olenekian	245.0–249.7
		Induan	249.7–251.0
Permian	Lopingian	Changhsingian	**older**
Subdivision of the Triassic system according to the IUGS, as of July 2009.			

The **Rhaetian** is in geochronology the latest age of the Triassic period or in chronostratigraphy the uppermost stage of the Triassic system. It lasted from 203.6 ± 1.5 to 199.6 ± 0.6 million years ago. It was preceded by the Norian and succeeded by the Hettangian (the lowermost stage or earliest age of the Jurassic).

In this age, Pangaea began to break up, though the Atlantic Ocean was not yet formed.

Stratigraphic definitions

The Rhaetian is named after the Rhaetian Alps, a mountain chain stretching over parts of eastern Switzerland, northern Italy and western Austria. The stage was introduced in scientific literature by Austrian geologist Eduard Suess and German paleontologist Albert Oppel in 1856.

The base of the Rhaetian did not yet have a unanimously agreed upon definition in 2009. In the Tethyan domain, the base of the ammonite biozone of *Sagenites reticulatus* is used, in the boreal domain (where this species is not found) the base of the biozone of *Cochloceras amoenum* is used instead. The base is also close to the first appearances of conodont species *Misikella spp.* and *Epigondolella mosheri* and radiolarite species *Proparvicingula moniliformis*.

The top of the Rhaetian (the base of the Hettangian stage, the Lower Jurassic series and the Jurassic system) is at the first appearance of ammonite genus *Psiloceras*.

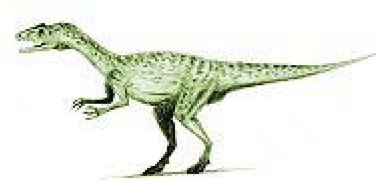
In the Tethyan domain, the Rhaetian contains two ammonite biozones. The highest ammonite biozone is that of *Choristoceras marshi*, the lower one that of *Rhabdoceras suesii*.

Life

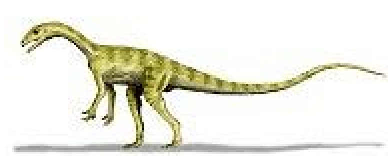
Dinosauria

Dinosaurs of the Rhaetian

Taxa	Presence	Images
• *Agnosphitys*		
• *Agrosaurus*		
• *Liliensternus*		
• *Pantydraco*		
• *Thecodontosaurus*	Norian/Rhaetian	



Liliensternus



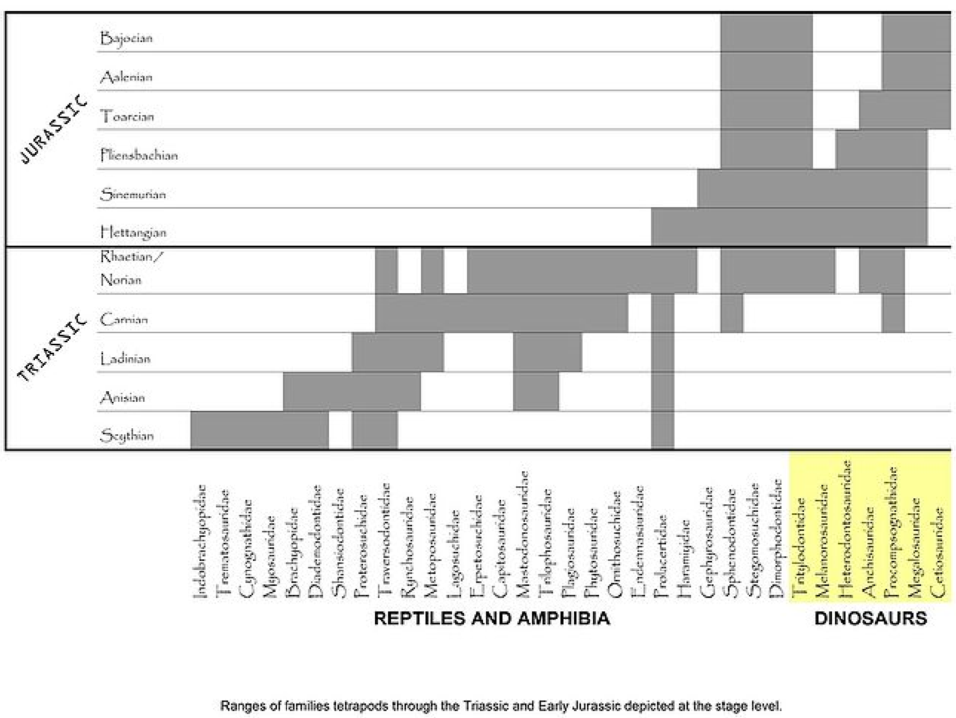
Pantydraco

Mammaliaformes

Mammaliaformes of the Rhaetian

Taxa	Images
• *Eozostrodon* • *Haramiya* • *Megazostrodon*	 *Megazostrodon*

Triassic–Jurassic extinction event



Ranges of families tetrapods through the Triassic and Early Jurassic

The **Triassic–Jurassic extinction event** marks the boundary between the Triassic and Jurassic periods, 199.6 million years ago and is one of the major extinction events of the Phanerozoic eon, profoundly affecting life on land and in the oceans. A whole class (conodonts), twenty percent of all marine families and all large crurotarsans (non-dinosaurian archosaurs), some remaining therapsids and many of the large amphibians were wiped out. At least half of the species now known to have been living on Earth at that time went extinct. This event vacated ecological niches, allowing the dinosaurs to assume the dominant roles in the Jurassic period. This event happened in less than 10,000 years and occurred just before Pangaea started to break apart.

Statistical analysis of marine losses at this time suggests that the decrease in diversity was caused more by a decrease in speciation than by an increase in extinctions.

Several explanations for this event have been suggested, but all have unanswered challenges:

- Gradual climate change or sea-level fluctuations during the late Triassic. However, this does not explain the suddenness of the extinctions in the marine realm.
- Asteroid impact, but no impact crater has been dated to coincide with the Triassic–Jurassic boundary (the impact responsible for the annular Manicouagan Reservoir occurred about 12 million years before the extinction event).
- Massive volcanic eruptions, specifically the flood basalts of the Central Atlantic Magmatic Province (CAMP), would release carbon dioxide or sulfur dioxide and aerosols, which would cause either intense global warming (from the former) or cooling (from the latter).

The isotopic composition of fossil soils of end Triassic and Early Jurassic has been tied to a large negative carbon isotope excursion (Whiteside et al. 2010). Carbon isotopes of lipids (*n*-alkanes) derived from leaf wax and lignin and total organic carbon from two sections of lake sediments interbedded with the CAMP in eastern North America have shown carbon isotope excursions similar to those found in the mostly marine St. Audrie's Bay section in England; the correlation suggests that the end-Triassic extinction event began at the same time in marine and terrestrial environments, slightly before the oldest basalts in eastern North America but simultaneous with the eruption of the oldest flows in Morocco (Also suggested by Deenen et al., 2010), with both a critical CO_2 greenhouse and a marine biocalcification crisis. Contemporaneous CAMP eruptions, mass extinction and the carbon isotopic excursions are shown in the same places, making the case for a volcanic cause of a mass extinction. The catastrophic dissociation of gas hydrates (suggested as one possible cause of the largest mass extinction of all time, the so-called "Great Dying" at the end of the Permian Period) may have exacerbated greenhouse conditions.

Chapter- 3

Norian

The **Norian** is a division of the Triassic geological period. It has the rank of an age (geochronology) or stage (chronostratigraphy). The Norian lasted from 216.5 ± 2.0 to 203.6 ± 1.5 million years ago. It was preceded by the Carnian and succeeded by the Rhaetian.

Stratigraphic definitions

The Norian was named after the Noric Alps in Austria. The stage was introduced into scientific literature by Austrian geologist Edmund Mojsisovics von Mojsvar in 1869.

The Norian stage begins at the base of the ammonite biozones of *Klamathites macrolobatus* and *Stikinoceras kerri* and at the base of the conodont biozones of *Metapolygnathus communisti* and *Metapolygnathus primitius*. A global reference profile for the base (a GSSP) had in 2009 not yet been appointed.

The top of the Norian (the base of the Rhaetian) is at the first appearance of ammonite species *Cochloceras amoenum*. The base of the Rheatian is also close to the first appearance of conodont species *Misikella spp.* and *Epigondolella mosheri* and the radiolarid species *Proparvicingula moniliformis*.

In the Tethys domain, the Norian stage contains six ammonite biozones:

- zone of *Halorites macer*
- zone of *Himavatites hogarti*
- zone of *Cyrtopleurites bicrenatus*
- zone of *Juvavites magnus*
- zone of *Malayites paulckei*
- zone of *Guembelites jandianus*

Palaeontology

- Synapsids
- Aetosaurs
- Dicynodonts
- Phytosaurs

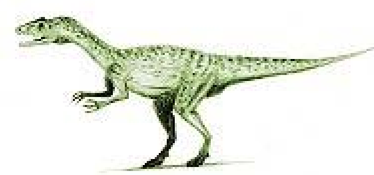
Dinosaurs

Dinosaurs of the Norian

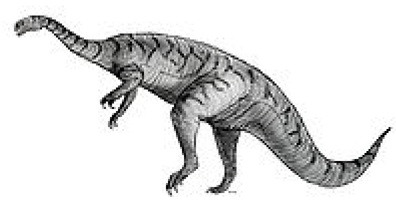
Taxa	Presence	Location
Agnosphitys		
Coelophysis	Late Carnian to early Norian	Ghost Ranch, New Mexico, USA
Halticosaurus		
Liliensternus		
Plateosaurus		
Sellosaurus		
Thecodontosaurus	Norian/Rhaetian	

Images

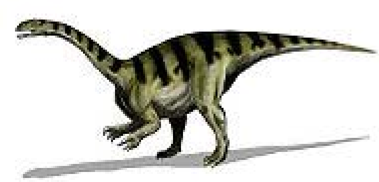
Coelophysis



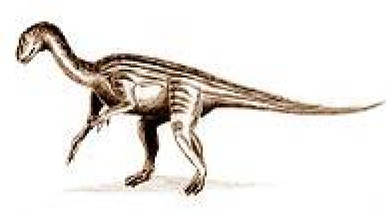
Liliensternus



Plateosaurus



Sellosaurus



Thecodontosaurus

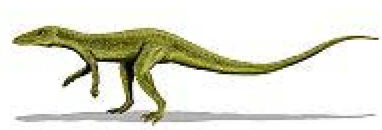
†Pterosaurs

Pterosaurs of the Norian

Taxa	Presence	Location	Description	Images
• *Eudimorphodon* • *Peteinosaurus*				 *Eudimorphodon*
• *Preondactylus*				 *Preondactylus*

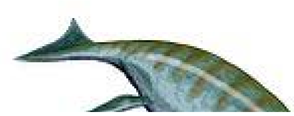
Crocodylomorphs

Crocodylomorphs of the Norian

Taxa	Presence	Location	Description	Images
• *Saltoposuchus*				 *Saltoposuchus*

†Ichthyosaurs

Ichthyosaurs of the Norian

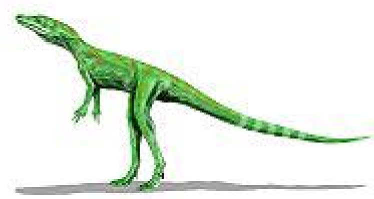
Taxa	Presence	Location	Description	Images
Shonisaurus 1. *Shonisaurus*				

popularis

Shonisaurus

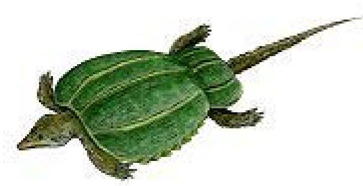
†Dinosauromorphs (non-dinosaurian)

†Non-dinosaurian dinosauromorphs of the Norian

Taxa	Presence	Location	Description	Images
• *Dromomeron*				 *Dromomeron*
• *Eucoelophysis*		New Mexico		

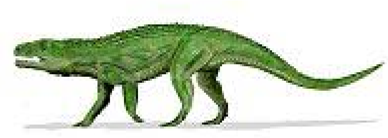
†Placodonts

Placodonts of the Norian

Taxa	Presence	Location	Description	Images
• *Psephoderma*				 *Psephoderma*

†Crurotarsans (non-crocodylomorph)

†Non-crocodylomorph Crurotarsans of the Carnian

Taxa	Presence	Location	Description	Images
• *Basutodon*				 *Teratosaurus*
• *Teratosaurus*				

Chapter- 4

Carnian

The **Carnian** (less commonly, **Karnian**) is the lowermost stage of the Upper Triassic series (or earliest age of the Late Triassic epoch). It lasted from about 228.7 till 216.5 million years ago (Ma). The Carnian is preceded by the Ladinian and is followed by the Norian. Its boundaries are not characterized by major extinctions or biotic turnovers, but a climatic event (known as the Carnian Pluvial Event) occurred during the Carnian and seems to be associated with important extinctions or biotic radiations.

Stratigraphic definitions

Alluvial plain red clays of the Travenanzes formation, upper Carnian, the Dolomites, northern Italy

Brotheotrachyceras brotheus from the San Cassiano Formation, Val Badia, Dolomites, Southern Alps. This ammonoid is an index fossil for the lower Carnian

The Carnian was named in 1869 by Mojsisovics. It is unclear if it was named after the Carnic Alps or after the Austrian region of Carinthia (*Kärnten* in German). The name, however, was first used referring to a part of the Hallstatt Limestone cropping out in Austria.

The base of the Carnian stage is defined as the place in the stratigraphic record where the ammonite species *Daxatina canadensis* first appears. The global reference profile for the base is located at the *Stuores-Wiesen* near Badia (Abtei) in the Badia Valley in the region of Südtirol, Italy.

The top of the Carnian (the base of the Norian) is at the bases of the ammonite biozones of *Klamathites macrolobatus* or *Stikinoceras kerri* and the conodont biozones of *Metapolygnathus communisti* or *Metaolygnathus primitius*.

Dating and subdivisions

There is no established, standard usage for the Carnian subdivisions, thus, while in some regional stratigraphies a two-substage subdivision is common:

- Julian
- Tuvalian

others prefer a three-substage organization of the stage as follows:

- Cordevolian
- Julian
- Tuvalian

The Carnian spans from 228.0 ± 2.0 to 216.5 ± 2.0 Ma in the proposed geologic time scale by Gradstein et al. (2004). These dates are interpolated, because direct radiometric dates for this stage were missing when that time scale was compiled. Recently, Upper Carnian beds in southern Italy yielded an age of 230.91 ± 0.33 Ma. The age and duration of the Carnian need thus to be reconsidered.

Biostratigraphy

In the Tethys domain, the Carnian stage contains six ammonite biozones:

- zone of *Anatropites spinosus*
- zone of *Tropites subbullatus*
- zone of *Tropites dilleri*
- zone of *Austrotrachyceras austriacum*
- zone of *Trachyceras*

Paleogeography and climate

The paleogeography of the Carnian was basically the same as for the rest of the Triassic. Most continents were merged into the supercontinent Pangaea and there was a single global ocean, Panthalassa. The global ocean had a western branch at tropical latitudes called Paleo-Tethys. The sediments of Paleo-Tethys now crop out in southeastern Europe, in the Middle East, in the Himalayas and up to the island of Timor.

The extreme land-sea distribution led to "mega-monsoons", i.e., an atmospheric monsoon regime more intense than the present one.

As for most of the Mesozoic, there were no ice caps. Climate was mostly arid in the tropics, but an episode of wet tropical climate is documented at least in the Paleo-Tethys. This putative climatic event is called the “Carnian Pluvial Event”, its age being between latest early Carnian (Julian) and the beginning of late Carnian (Tuvalian). The nature of this event is still discussed; some scientists believe it is only an artifact, due to the migration of continents of the Tethyan area across the equatorial climatic belt. Following this idea, the apparent shift from arid to humid and then back to arid climate simply testifies the continents going from southern tropical, to equatorial and then to northern tropical latitudes.

Life

In the marine realm, the Carnian saw the first abundant occurrences of calcareous nannoplankton, a morphological group including the Coccolithophores.

Invertebrates

There are a few invertebrates which are typical and characteristic of the Carnian. Among molluscs, the ammonoid genus *Trachyceras* is exclusive to the lower Carnian (i.e., Julian of the two-substages subdivision, see above). The family Tropitidae and the genus *Tropites* appear at the base of the upper Carnian (Tuvalian). The bivalve genus *Halobia*, a bottom-dweller of deep sea environments, differentiated from *Daonella* at the beginning of this age. Scleractinian coral reefs, i.e., reefs with corals of the modern type, became relatively common for the first time in the Carnian.

Vertebrates

The earliest dinosaur *Eoraptor* originated slightly before the Carnian stage began around 230 Ma. The oldest well documented dinosaurian assemblage, in the Ischigualasto Formation of Argentina, is most probably late Carnian in age.

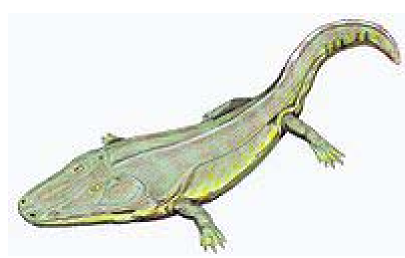
In this stage the archosaurs became the dominant faunas in the world, evolving into groups such as the phytosaurs, rhynchosaurs, aetosaurs and rauisuchians. The first dinosaurs also appeared in this stage and though at the time they were small and insignificant, they diversified rapidly and would dominate the fauna for the rest of the Mesozoic. On the other hand, the therapsids, which included the ancestors of mammals, decreased in both size and diversity and would remain relatively small until the extinction of the dinosaurs.

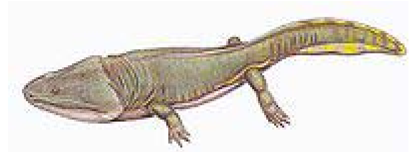
Conodonts were present in Triassic marine sediments. *Paragondolella polygnathiformis* appeared at the base of the Carnian stage and is perhaps the most characteristic species. A partial list of Carnian vertebrates is given below.

Many Carnian vertebrates are found in Santa Maria Formation rocks of the Paleorrota geopark.

†Temnospondyls

Temnospondyls of the Carnian

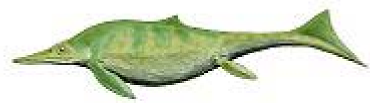
Taxa	Presence	Location	Description	Images
• *Cyclotosaurus*		All Across Europe		 Cyclotosaurus
• *Deltasaurus*		Australia		
• *Metoposaurus*		Europe and North America		



Metoposaurus

†Ichthyosaurs

Ichthyosaurs of the Carnian

Taxa	Presence	Location	Description	Images
• *Californosaurus*				 *Californosaurus*
• *Shastasaurus*				
• *Shonisaurus*				

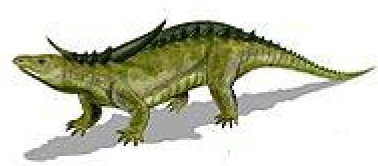
†Archosauromorphs (non-archosaurian)

Non-Archosaurian Archosauromorphs of the Carnian

Taxa	Presence	Location	Description	Images
• *Hyperodapedon*		Paleorrota, Brazil.		 *Hyperodapedon*
• *Trilophosaurus*				

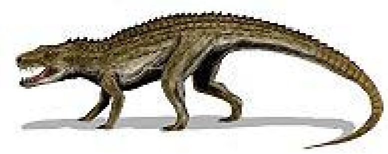
†Crurotarsans (non-crocodylomorph)

†Non-crocodylomorph Crurotarsans of the Carnian

Taxa	Presence	Location	Description	Images
• *Desmatosuchus*				
• *Doswellia*				
• *Ornithosuchus*				

- *Paleorhinus*
- *Postosuchus*
- *Rutiodon*
- *Saurosuchus*
- *Stagonolepis*

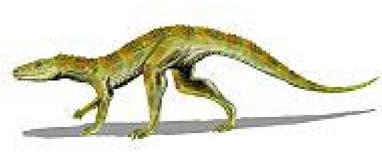
Desmatosuchus



Postosuchus

Crocodylomorphs

Crocodylomorphs of the Carnian

Taxa	Presence	Location	Description	Images
• *Hesperosuchus*				 *Hesperosuchus*

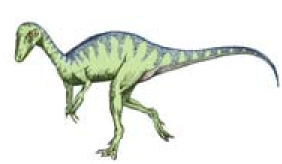
†Non-dinosaur Ornithodira

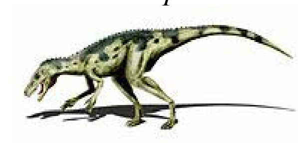
†Ornithodira of the Carnian

Taxa	Presence	Location	Description	Images
• *Silesaurus*		Silesia, Poland		 *Silesaurus*
• *Sacisaurus*		Agudo, Rio Grande do Sul, Brazil		

Dinosaurs

†Dinosaurs of the Carnian

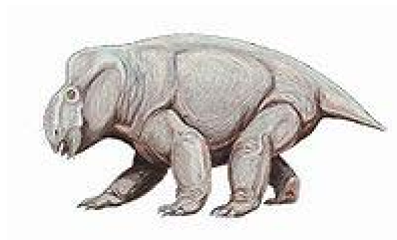
Taxa	Presence	Location	Description	Images
• *Blikanasaurus*	Disputed: considered Norian by some researchers.			

Camposaurus	Chinle Formation, Arizona		Some palaeontologists believe that it's actually a junior synonym of the better known *Coelophysis*.	*Eoraptor* 
Eoraptor				*Herrerasaurus* 
Euskelosaurus	Disputed: considered Norian by some researchers.			
Guaibasaurus		Paleorrota, Brazil.		Staurikosaurus eating a rhynchosaur.
Staurikosaurus		Paleorrota, Rio Grande do Sul, Brazil.		
Saturnalia		Paleorrota, Rio Grande do Sul, Brazil.	May have been a primitive sauropodomorph, probably grew to about 1.5 meters (5 ft) long.	
Unaysaurus		Paleorrota, Rio Grande do Sul, Brazil.		
Herrerasaurus				
Panphagia				
Pisanosaurus		Ischigualasto Formation, San Juan, Argentina	A small, lightly-built dinosaur approximately 1 m (3 ft 3 in) in length and 30 cm (12 in) in height. It was bipedal and, like all ornithischians, was probably exclusively herbivorous.	

- *Teyuwasu*

†Therapsids (non-mammalian)

†Non-mammalian Therapsids of the Carnian

Taxa	Presence	Location	Description	Images
• *Exaeretodon*		Paleorrota, Brazil.		
• *Placerias*				 *Placerias*.

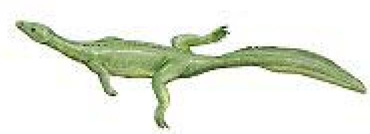
Mammaliaformes

Mammaliaformes of the Carnian

Taxa	Presence	Location	Description	Images
• *Adelobasileus*		Tecovas formation, Texas, USA	Thought to be the common ancestor of all modern mammals or a close relative of the common ancestor	 *Adelobasileus*

†Thalattosaurians

Thalattosauria of the Carnian

Taxa	Presence	Location	Description	Images
• *Miodentosaurus*		Falang Formation, Guizhou, China	A relatively large thalattosaurian, more than 4 meters long.	 *Miodentosaurus*

Classic localities and lagerstätten

The lower Carnian fauna of the San Cassiano Formation (Dolomites, northern Italy) has been studied since the 19th century. Fossiliferous localities are many and are distributed mostly in the surroundings of Cortina d'Ampezzo and in the high Badia Valley, near the village of San Cassiano, after which the formation was named. This fauna is extremely diverse, including ammonoids, gastropods, bivalves, echinoderms, calcareous sponge, corals, brachiopods and a variety of less common fossils. A collection of this fauna is exposed in the “Museo delle Regole”, a museum in Cortina d'Ampezzo.

The Ischigualasto Formation of northwestern Argentina yielded a very important vertebrate association, including the oldest dinosaurian assemblage.

Chapter- 5

Anisian

System	Series	Stage	Age (Ma)
Jurassic	Lower	Hettangian	younger
Triassic	Upper	Rhaetian	199.6–203.6
		Norian	203.6–216.5
		Carnian	216.5–228.0
	Middle	Ladinian	228.0–237.0
		Anisian	237.0–245.0
	Lower	Olenekian	245.0–249.7
		Induan	249.7–251.0
Permian	Lopingian	Changhsingian	older

Subdivision of the Triassic system according to the IUGS, as of July 2009.

In the geologic timescale, the **Anisian** is the lower stage or earliest age of the Middle Triassic series or epoch and lasted from 245 million years ago until 237 million years ago, approximately. The Anisian age succeeds the Olenekian age (part of the Lower Triassic epoch) and precedes the Ladinian age.

Stratigraphic definitions

The stage and its name were established by Austrian geologists Wilhelm Heinrich Waagen and Carl Diener in 1895. The name comes from *Anisus*, the Latin name of the river Enns. The original type locality is at Großreifling in the Austrian state of Styria.

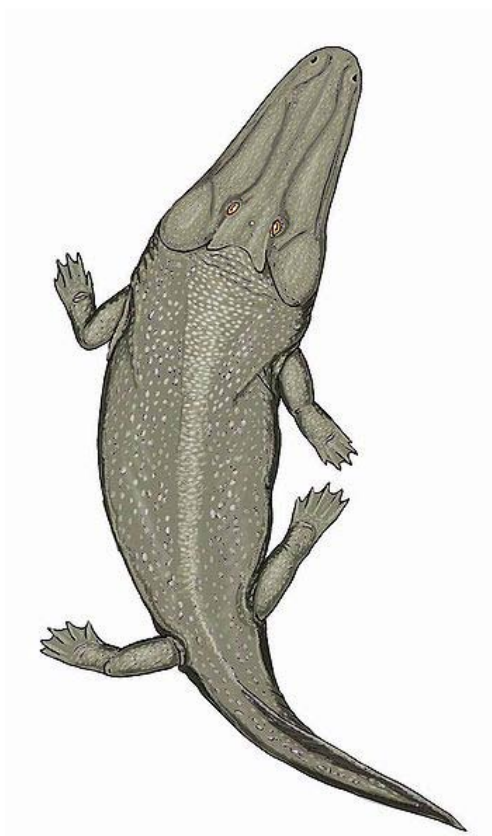
The base of the Anisian stage (also the base of the Middel Triassic series) is sometimes laid at the first appearance of conodont species *Chiosella timorensis* in the stratigraphic record. Other stratigraphers prefer to use the base of magnetic chronozone MT1n. The global reference profile for the base (the GSSP or golden spike) is at a flank of the mountain Deşli Caira in the Romanian Dobruja.

The top of the Anisian (the base of the Ladinian) is at the first appearance of ammonite species *Eoprotrachyceras curionii* and the ammonite family Trachyceratidae. The conodont species *Neogondolella praehungarica* appears at the same level.

Sometimes (especially in Central Europe) the Anisian stage is subdivided into four substages: Aegean, Bythinian, Pelsonian and Illyrian.

The Anisian contains six ammonite biozones:

- zone of *Nevadites*
- zone of *Hungarites*
- zone of *Paraceratites*
- zone of *Balatonites balatonicus*
- zone of *Kocaelia*
- zone of *Acrochordiceras*



Cherninia, giant temnospondyl from India

Palaeontology

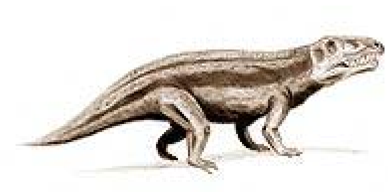
The earliest potential dinosaur fossil to date is a partial pubis from Anisian-age rocks of the Moenkopi Formation, Arizona. It may have come from a herrerasaurid.

Examples of vertebrates from this age are:

- Ichthyosaurs
- Prestosuchids
- Trigoniids

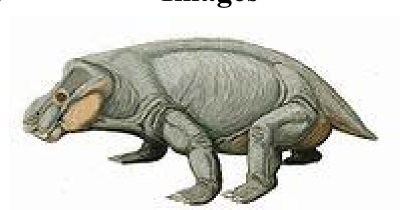
†Archosauromorphs (non-archosaurians)

†Non-archosaurian Archosauromorphs of the Anisian

Taxa	Presence	Location	Description	Images
• *Erythrosuchus*				 *Erythrosuchus*

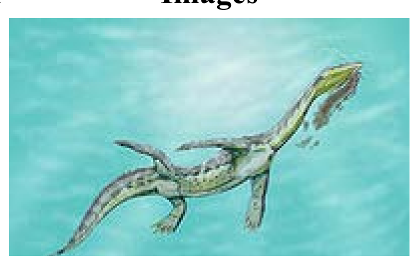
†Therapsids (non-mammalian)

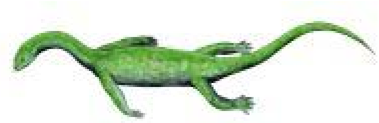
†Non-mammalian Therapsids of the Anisian

Taxa	Presence	Location	Description	Images
• *Kannemeyeria*				 *Kannemeyeria*

†Nothosauroids

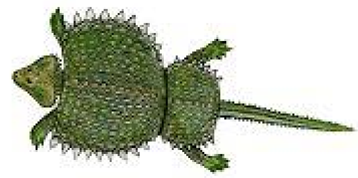
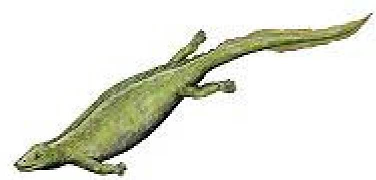
Nothosauroids of the Anisian

Taxa	Presence	Location	Description	Images
• *Anarosaurus*				
• *Ceresiosaurus*				
• *Dactylosaurus*				

			Ceresiosaurus
• *Keichousaurus*	Guizhou and Hubei, China		 *Keichousaurus*

†Placodonts

Placodonts of the Anisian

Taxa	Presence	Location	Description	Images
• *Cyamodus*				 *Cyamodus*
• *Paraplacodus*		Northern Italy		 *Paraplacodus*

†Thalattosaurians

Thalattosauria of the Anisian

Taxa	Presence	Location	Description	Images
• *Askeptosaurus*		Italy	A very thin, elongated creature (about 2 meters long) that probably swam like an eel, that was probably a fish eater and hunted in deep waters, based on its	 *Askeptosaurus*

large eyes (which would allow it to see better in dark water) and the protective bony ring around them (also seen in ichthyosaurs), which prevented them from getting squashed in by the immense water pressure at great depths.

†Ceratitida

Ananorites Arthaberites Beyrichites Bosnites Buddhaites Bukowskiites Caucasites Danubites Gangadharites Japonites Laboceras Longobarditoides Mesocladiscites Noetlingites Parapinacoceras Parasageceras Phyllocladiscites Proavites Pseudodanubites Psilocladiscites Salterites Tropigymnites Xiphogymnites Pararcestes Sageceras

Lower

Alloptychites Anagymnites Grambergia Groenlandites Gymnites Lenotropites Pearylandites Silberlingites Isculites Stenopopanoceras

Middle

Acrochordiceras Alanites Anagymnotoceras Arctohungarites Balatonites Bulogites Cuccoceras Czekanowskites Epacrochordiceras Hollandites Huishuites Inaigymnites Ismidites Kiparisovia Malletophychites Nicomedites Phillipites Platycuccoceras Pronoetlingites Reiflingites Discoptychites Intornites Nevadisculites Paraceratites Parapopanoceras Proarcestes Longobardites Ptychites

Upper

Amphipopanoceras Aplococeras Arctogymnites Eudiscoceras Eutomoceras Gymnotoceras Halilucites Judicarites Kellnerites Metadinarites Nevadites Parakellnerites Proteusites Repossia Semiornites Serpianites Stoppaniceras Ticinites Tozerites Tropigastrites Joannites Epigymnites Ceratites Flexoptychites Frechites Norites Gevanites Hungarites

†Phylloceratida

Spinoleiophyllites Ussurites Monophyllites

Nautilida

Trachynautilus Thuringionautilus Styrionautilus

Lower

Indonautilus Sibyllonautilus

Middle

Paranautilus

Upper

Holconautilus Proclydonautilus

†Aulacocerida

Crassiatractites Breviatractites

Lower

Mojsisovicsteuthis

Pterioida

Ramonalinidae

Chapter- 6

Triassic Extinctions

1. Bellerophon

Bellerophon **Fossil range: Silurian–Early Triassic**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Gastropoda or Monoplacophora
Superfamily:	Bellerophontoidea
Family:	Bellerophontidae
Subfamily:	Bellerophontinae
Genus:	***Bellerophon*** Montfort, 1808

Bellerophon is a genus of extinct paleozoic marine molluscs of uncertain position (Gastropoda or Monoplacophora) in the family Bellerophontidae.

The genus was named after Bellerophon, the ancient Greek hero.

Bellerophon is the type genus of the family Bellerophontidae.

Shell description

The genus is characterised by a shell which is globose, convolute and planispiral (symmetrically coiled). The shell of *Bellerophon* superficially resembles that of a miniature cephalopod (e.g. *Nautilus* or an ammonite), except that septa are lacking.

The shell of *Bellerophon* is often a couple of centimeters in maximum dimension. The external surface is smooth, ornamented only by growth lines. There is a low crest or ridge running along the midline of the shell.

Many specimens of *Bellerophon* show something resembling a "waterline" about half-way up the shell, suggesting that a large amount of the mantle and foot were exposed and covered the outside of the shell, as in the extant Cypraeidae and Naticidae.

Possible life habits

These animals were probably quick moving, relying on speed to avoid predators and, when this was not possible, withdrawing deeply into the shell.

Range of distribution

The genus occurs worldwide and is known from the Silurian to the Early Triassic periods.

Discussion of the taxonomy

Although usually classified as a primitive gastropod, there is a minority view that the Bellerophontida actually represented a more primitive, untorted type of mollusk, which evolved a spiral shell independently. Another view is that some Bellerophontids, including *Bellerophon*, were torted gastropods, but that others were untorted forms.

Species

Species within the genus *Bellerophon* include:

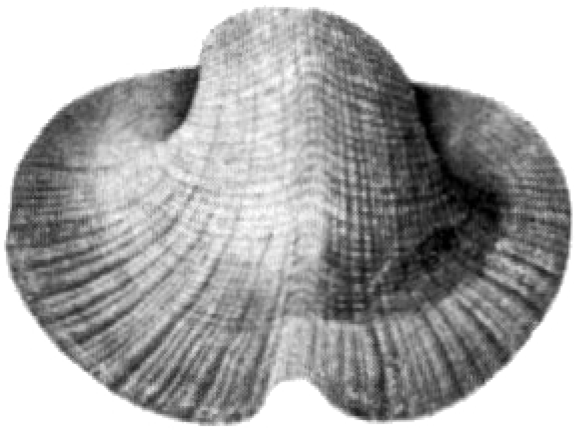
subgenus *Bellerophon*

- *Bellerophon needlensis* - from Late Mississippian from Utah
- *Bellerophon welshi* - from Late Mississippian from Utah

subgenus ?

- *Bellerophon bicarenus* Lévillé from early Carboniferous
- *Bellerophon graphicus* Moore from the late Pennsylvanian (Virgilian) of Kansas
- *Bellerophon regularis* (Waagen) from the Permian of India
- *Bellerophon vasulites* Montfort - the type species, from the Middle Devonian of Germany
- and others

2. Bellerophontidae

Bellerophontidae	
	
Bucanopsis leda (subfamily Bucanopsinae)	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Gastropoda or ? Monoplacophora
Superfamily:	Bellerophontoidea
Family:	**Bellerophontidae** McCoy, 1852

The **Bellerophontidae** is an extinct family of specialized globose bellerophontids; Paleozoic and Early Triassic mollusks of uncertain position (Gastropoda or Monoplacophora).

Geological range

These mollusks appeared in the Late Cambrian and continued until the Early Triassic.

Shell description

The shell resembles a miniature *Nautilus*, with greatly overlapping, rounded whorls, in which the last whorl completely encompasses the others, leaving either a very narrow umbilicus on either side, or none at all. At the aperture of the shell is a slit, which results in a sort of low ridge that runs along the length of shell. The shell has a low profile and it is possible that these were active, fast-moving molluscs.

Taxonomy

1960 taxonomy

Knight et al. 1960 in the Treatise on Invertebrate Paleontology consider the Bellerophontidae a very large family made up of a number of subfamilies and tribes.

The 1960 classification places the family Bellerophontidae in the order Bellerophontida Ulrich & Scofield, 1897.

The classification presented is as follows:

ordo Bellerophontida Ulrich & Scofield, 1897

- **Family Bellerophontidae** McCoy, 1851
    - Subfamily Tropidodiscinae Knight, 1956
    - Subfamily Bucaniinae Ulrich & Scofield, 1897
        - Tribe Bucaniides Ulrich & Scofield, 1897
        - Tribe Salpingostomatides Koken, 1925
    - Subfamily Carinaropsinae Ulrich & Scofield, 1897
    - Subfamily Pterothecinae Wenz, 1938
    - Subfamily Bellerophontinae McCoy, 1851
    - Subfamily Knightitinae Knight, 1956

2001 taxonomy

Recently Peter J. Wagner presented cladograms which divide this assemblage into a number of different groups, as well as combining the Bellerophontidae with the family Sinuitidae. while Bouchet & Rocroi (2005) places Sinuitidae as a family in superfamily Bellerophontoidea.

2005 taxonomy

The taxonomy of the Gastropoda by Bouchet & Rocroi, 2005 categorizes Bellerophontidae like this:

- Paleozoic molluscs of uncertain systematic position
    - Paleozoic molluscs with isostrophically coiled shells of uncertain position within Mollusca (Gastropoda or Monoplacophora)
        - superfamily Bellerophontoidea McCoy, 1852 - Bellerophontoidea is the only superfamily in this taxon.
            - family Bellerophontidae McCoy, 1852

        - subfamily Bellerophontinae McCoy, 1852 - synonym: Liljevallospiridae Golikov & Starobogatov, 1889
        - subfamily Bucanopsinae Wahlman, 1992
        - subfamily Cymbulariinae Horný, 1963
        - subfamily Knightitinae Knight, 1956

Bouchet & Rocroi, on page 271 (2005), also state that the assignation of "*symmetrical univalved mollusks "bellerophonts" either to Gastropoda or to Monoplacophora or Tergomya is controversial."* In other words, it is not yet certain whether bellerophonts are in fact real gastropods, they might be monoplacophorans or they might belong to a group (Tergomya) that is closely related to the gastropods, but not actually gastropods.

Genera

Genera in the family Bellerophontidae include:

- subfamily Bellerophontinae
    - genus *Bellerophon* Montfort, 1808 - type genus of the subfamily Bellerophontinae

- subfamily Bucanopsinae
    - genus *Bucanopsis* Ulrich, 1897 - type genus of the subfamily Bucanopsinae

- subfamily Cymbulariinae
    - genus *Cymbularia* Koken, 1896 - type genus of the subfamily Cymbulariinae

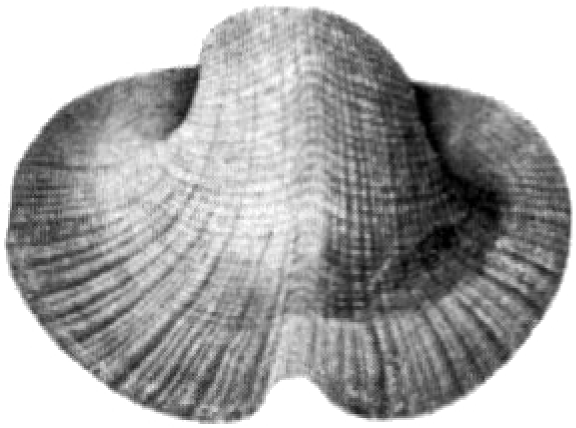
- subfamily Knightitinae
    - genus *Knightites* Moore, 1941 - type genus of the subfamily Knightitinae

other genera include:

- *Aglaoglypta*
- *Liljevallospira*
- *Pharkidonotus*
- *Prosoptychus*
- *Ptychobellerophon*
- *Ptychosphaera*

3. Bellerophontoidea

Bellerophontoidea **Fossil range: Late Cambrian–Triassic**	



Bucanopsis leda (family Bellerophontidae, subfamily Bucanopsinae)

Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Gastropoda or Monoplacophora
(unranked):	"*Paleozoic uncertain* ..."
Superfamily:	**Bellerophontoidea** (=Bellerophontaceae) McCoy, 1852

The **Bellerophontoidea**, (Bellerophontaceae Ulrich & Schofield, 1897, ex Bellerophontidae McCoy 1951), common name "**bellerophonts**", is a superfamily of extinct planospirally coiled globose molluscs, generally included in the Gastropoda that first appeared late in the Cambrian and continued until late in the Triassic.

Biology

Unlike normal gastropods, the shells of Bellerophonts are characterised by a completely planispiral pattern of coiling, such as one finds in shelled cephalopods. Experts disagree whether Bellerophontids should be classified as torted gastropods or as untorted Tergomya, or whether the group Bellerophontida is perhaps an artificial construct, consisting of a number of distinct groups of Palaeozoic molluscs which evolved the same type of spiral shell independently.

Taxonomy

Historical Background

The taxomony of the Bellerophontoidea (renamed from the original Bellerophontacea) has gone through a number of revisions since M'Coy established the Bellerophontaceae in 1851 for planospiral archeogastropods. The naming followed the convention for superfamilies that prevailed until at least 1992 with Wahlman

The Bellerophontacea were placed in the order Bellerophontida established by Ulrich and Scofield in 1897 and included the families Bellerophontidae, Bucaniidae, Cyrtolitidae and Protowarthiidae.

Knight, et al. 1960 (Treatise Part I reprinted 1989) discuss the Superfamily Bellerophontacea at some length and include within it the Bellerophontidae, Cyrtolitidae, Sinuopeidae and Tropidodiscidae.

2005 Bellerophontid taxonomy

Bouchet et al. (2005) leaves the higher taxonomic position of the Bellerophontoidea as uncertain (Gastropoda or Monoplacophora) and divides the group into 8 families as listed:

- Bellerophontoidea
    - † Bellerophontidae
    - † Bucanellidae
    - † Bucaniidae
    - † Euphemitidae
    - † Pterothecidae
    - † Sinuitidae
    - † Tremanotidae
    - † Tropidodiscidae

The **Bellerophontidae**, **Bucanitidae**, **Pterothacidae** and **Tropododiscidae** compare with the subfamilies Bellerophontinae, Bucanitinae, Pterothacinae and Tropododiscinae included in the Bellerophontidae and the **Bucanellidae**, **Euphemitidae** and **Sinuitidae** compare with the subfamilies Bucanellinae, Euphemitinae and Sinuitinae included in the Sinuitidae, as found in the Treatise. The **Tremanitiae** is based on the genus *Tremanotus* which was included in the Bucanitinae in the Treatise.

Bouchet & Rocroi (2005) points out (page 271) that assignment of "*symetrical univalved mollusks "bellerophonts" either to Gastropoda or to Monoplacophora or Tergomya is controversial."*

Note on Nomenclature

Until recently with the ruling of the ICZN, -ACEA, or -ACEAE, was pretty much the standard ending for superfamilies in invertebrate paleontology and zoology. -OIDEA used now as the ending on superfamily names was generally reserved for subclasses and superorders

4. Gnathorhizidae

Gnathorhizidae **Fossil range: Late Carboniferous - Middle Triassic**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Class:	Sarcopterygii
Subclass:	**Dipnoi** Müller, 1844
Family:	**†Gnathorhizidae**
Genera	

- †*Gnathorhiza*
- †*Monongahela*
- †*Beltanodus*
- ? †*Microceratodus*
- †*Namatozodia*

The **Gnanthorhizidae** are an extinct family of lungfish that lived from the late Carboniferous until the middle Triassic. Gnathorhizid fossils have been found in North America, Madagascar, Australia and possibly Eastern Europe and South Africa. They are characterized by high-ridged toothplates that form cutting blades and a reduction in cranial bones.

Distribution

Gnathorhizids are found in North America, Eastern Europe, Australia and Africa. Gnathorhizids from North America range from the Gzhelian through the Roadian. In Africa, gnathorhizids are found in Olenekian of Madagascar and possibly South Africa. Lungfish teeth attributed to gnathorhizids have been reported from the Lopingian to the

Olenekian in Poland and Western Russia. It is likely, then, that gnathorhizids had a Pangean distribution throughout the late Paleozoic and early Mesozoic.

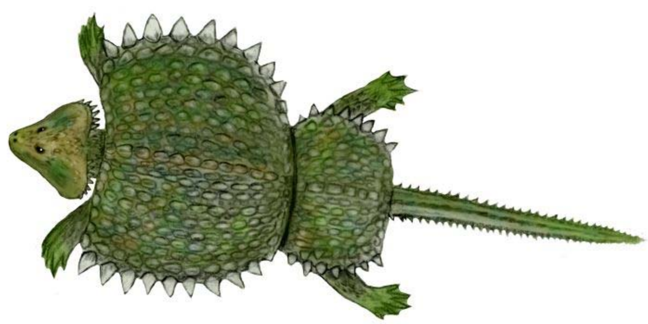
Paleoecology and behavior

Gnathorhizids are found primarily in paleosols representing ephemeral wetlands. Additionally, gnathorhizids, unlike most groups of fossil lungfish, are often found in association with regular burrow structures, suggesting that this group of lungfish may have estivated during the dry season, much like modern African and South American lungfish.

Unlike most fossil lungfish, but again, like modern South American and African lungfish, gnathorhizids have bladelike toothplates. This suggests that gnathorhizids were active predators unlike most lungfish, which feed primarily on benthic invertebrates.

5. Placodont

Placodonts
Fossil range: 235–200 Ma
Triassic



Cyamodus, a member of the superfamily Cyamodontoidea.

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Sauropsida
Superorder:	Sauropterygia
Order:	**Placodontia** Cope, 1871

Families

Cyamodontidae

Henodontidae
Paraplacodontidae
Placochelyidae
Placodontidae

Placodonts ("Tablet teeth") were a group of marine reptiles that lived during the Triassic period, becoming extinct at the end of the period. It is believed that they were part of Sauropterygia, the group that includes Plesiosaurs. Placodonts were generally between 1 to 2 metres (3 to 7 ft) in length, with some of the largest measuring 3 metres (10 ft) long.

The first specimen was discovered in 1830 and they have since been discovered throughout central Europe, North Africa, the Middle East and China.

Palaeobiology

Macroplacus raeticus

The earliest forms like *Placodus*, which lived in the early to middle Triassic, resembled barrel-bodied lizards somewhat similar to the marine iguana of today, but larger. But unlike the marine iguana, which feeds on algae, the placodonts ate molluscs and so their teeth were flat and tough to crush their shells. In the earliest periods their size was probably enough to take away the top sea predators of the time: the sharks. However, as time passed other kinds of carnivore reptiles began to colonize the seas, such as ichthyosaurs and nothosaurs and later placodonts developed bony plates on their backs to protect their bodies while feeding. By the Late Triassic, these plates had grown so much that placodonts of the time such as *Henodus* and *Placochelys* resembled the sea turtles of modern day more than their ancestors without bony plates. Other placodonts like *Psephoderma* developed plates as well, but in a different articulated manner that resembled the shells of horseshoe crabs and trilobites more than those of sea turtles. All these adaptations can be counted as perfect examples of convergent evolution, as placodonts were not related to any of these animals.

Because of their dense bone and heavy armour plating, these creatures would have been too heavy to float in the ocean and would have used a lot of energy to reach the water surface. For this reason and because of the type of sediment found accompanying fossils it is suggested they lived in shallow waters and not in deep oceans.

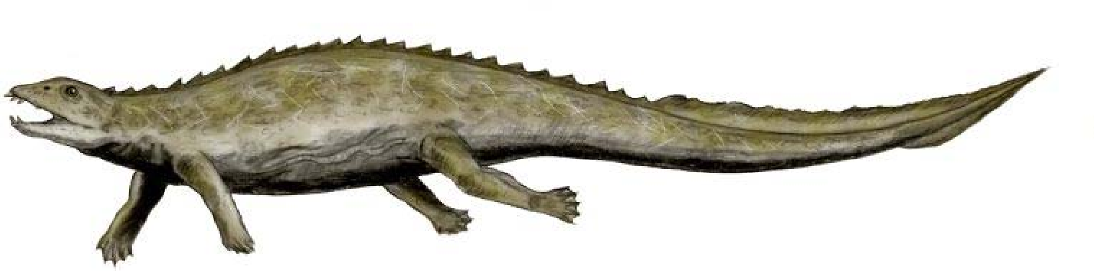
Their diet consisted of marine bivalves, brachiopods and other invertebrates. They were notable for their large, flat, often protruding teeth which they used to crush molluscs and brachiopods, which they hunted on the sea bed (another way in which they were similar to walruses). The palate teeth were adapted for this durophagous diet, being extremely thick and large enough to crush thick shell.

Classification

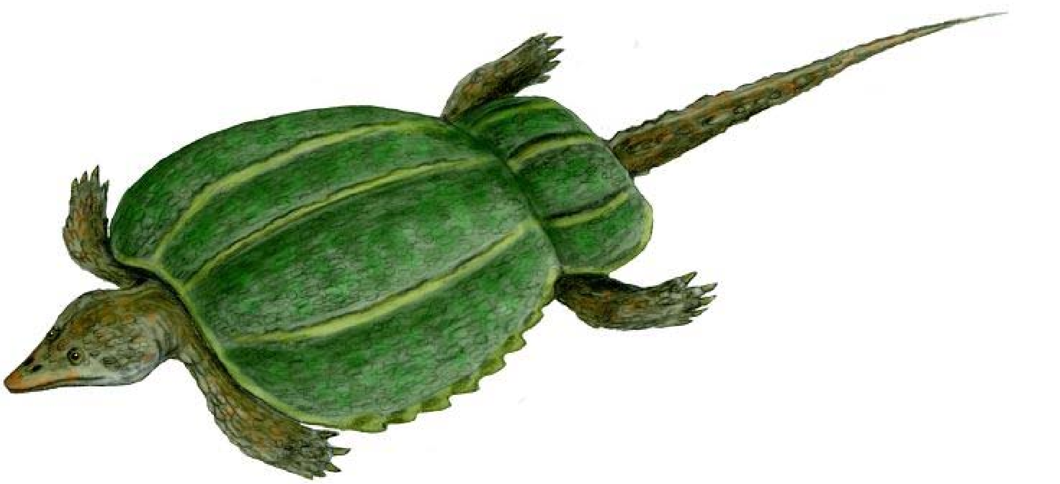
- **Class Sauropsida**
  - **Superorder Sauropterygia**
    - **Order Placodontia**
      - **Superfamily Placodontoidea**
        - Family Paraplacodontidae
          - Genus *Paraplacodus*
        - Family Placodontidae
          - Genus *Placodus*
      - **Superfamily Cyamodontoidea**
        - Family Henodontidae
          - Genus *Henodus*
        - Family Cyamodontidae
          - Genus *Cyamodus*
          - Genus *Protenodontosaurus*
        - Family Placochelyidae
          - Genus *Placochelys*
          - Genus *Psephoderma*
      - *incertae sedis*
        - Genus *Saurosphargis*

The clade **Helveticosauroidea** was previously considered to be a basal superfamily of placodonts with the sole member *Helveticosaurus*. However, it is now thought that

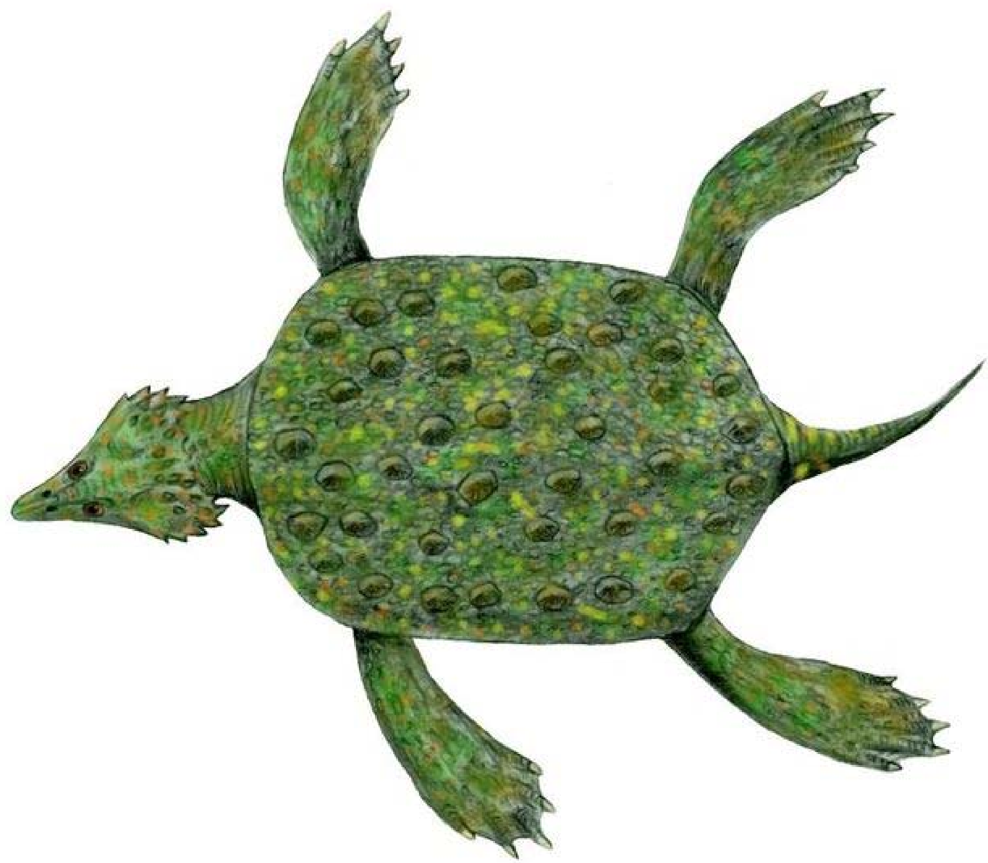
Helveticosaurus was not a placodont but possibly an unusual member of the Archosauromorpha.



Placodus



Psephoderma



Placochelys

6. Pseudotemperoceras

Pseudotemperoceras **Fossil range: Triassic**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Nautiloidea
Superorder:	Orthoceratoidea
Order:	Orthocerida

Family:	incertae sedis
Genus:	***Pseudotemperoceras*** Schastlivtseva, 1986

Pseudotemperoceras is an extinct nautiloid cephalapod belonging to the Orthocerida from the far eastern part of the Russian Federation that lived during the Triassic from 249.7—245 mya, existing for approximately 4.7 million years.

Taxonomy

Pseudotemperoceras was named by Schastlivtseva (1986) and is listed in the Orthocerida in Sepkoski (2002)

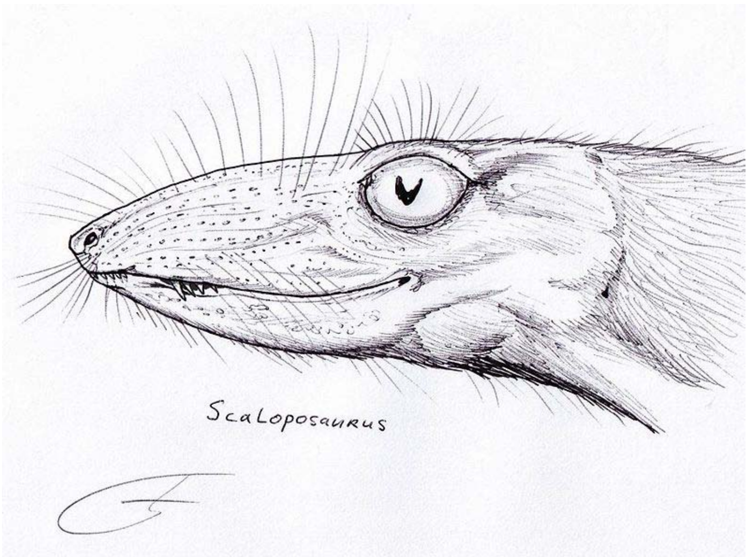
Morphology

Pseudotemperoceras has a slender, orthoconic shell that resembles that of the earlier, Paleozoic, *Temperoceras* from which it gets its name, although *Temperoceras* is a geisonoceratid rather than an orthoceratid

Fossil distribution

So far *Pseudotemperoceras* is known only from the western Verkhoyansk Range, Kharaulakhsk Mountains, in the Russian state of Yakutia in eastern Siberia, where it is associated with species of *Trematoceras*.

7. Scaloposaurus

Scaloposaurus **Fossil range: Early Triassic**	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Synapsida
Order:	Therapsida
Suborder:	Therocephalia
Genus:	***Scaloposaurus***

Scaloposaurus is an extinct carnivorous genus of therocephalian living during the Triassic 251.0—245.0 Ma existing for approximately 5 million years.

Taxonomy

Scaloposaurus was named by Owen (1876). It is not extant. It was assigned to Therocephalia by Broom (1913); and to Scaloposauridae by Carroll (1988).

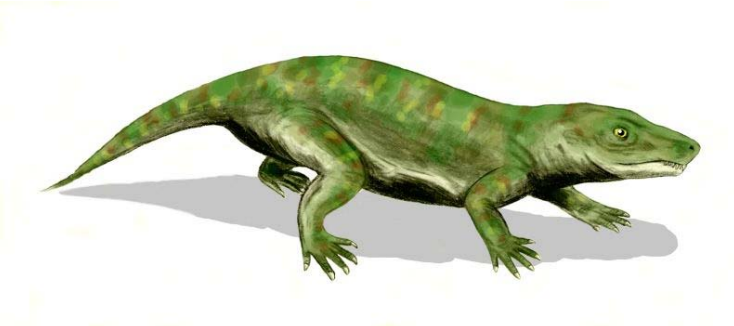
8. Smilosuchus

Smilosuchus **Fossil range: Late Triassic**	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Sauropsida
(unranked):	Archosauria
Order:	Phytosauria
Family:	Phytosauridae
Genus:	***Smilosuchus***

Smilosuchus is an extinct genus of phytosaur from the Late Triassic of North America. It was first described in 1995 as a replacement generic name for *Leptosuchus gregorii*. Because of the large rostral crest it possessed, it was considered to be distinct enough from other species of *Leptosuchus* (all of which had smaller and more restricted crests) to be within its own genus. Despite this, recent studies seem to suggest that *Smilosuchus* is congeneric with *Leptosuchus*, as the enlarged crest could have been independently developed in *Leptosuchus*.

9. Therocephalia

Therocephalia Fossil range: Middle Permian–Middle Triassic	



Bauria, an advanced therocephalian from the Early Triassic of South Africa

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Class:	Synapsida
Order:	Therapsida
(unranked)	Theriodontia
Suborder:	**†Therocephalia** Broom, 1905

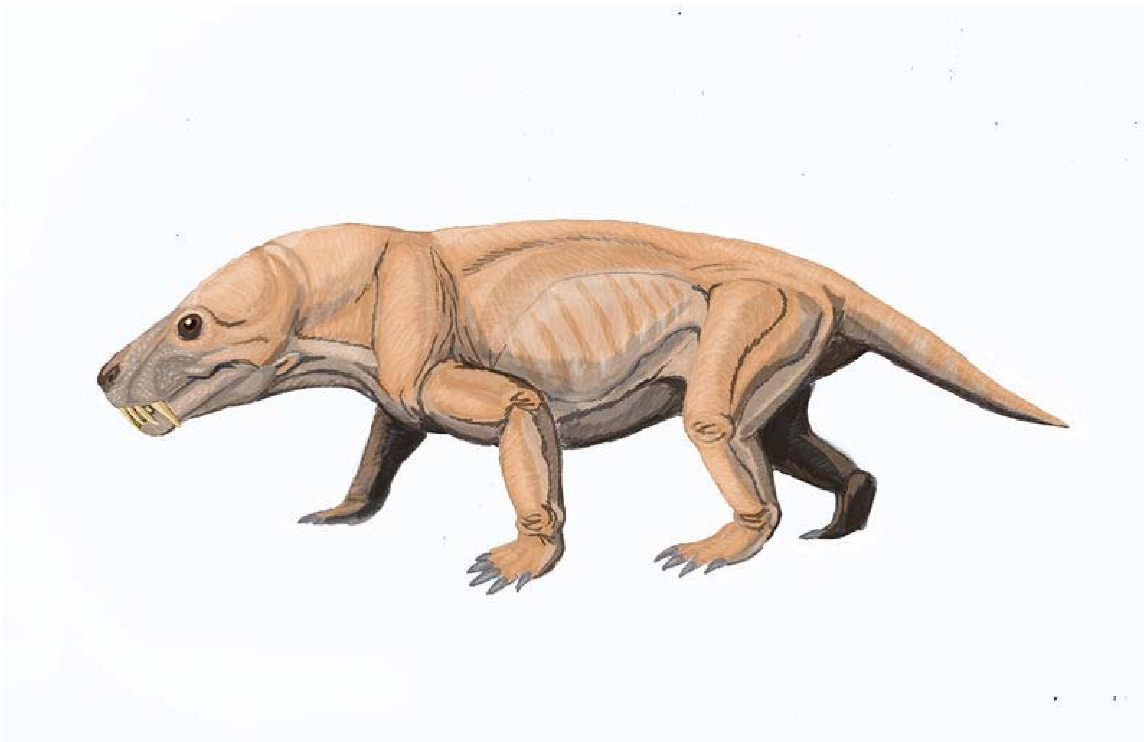
Therocephalians are an extinct suborder of carnivorous eutheriodont therapsids that lived from the middle and late Permian into the Triassic 265.0—245.0 Ma existing for approximately 20 million years.

The therocephalians ("beast-heads") are named after their large skulls, which, along with the structure of their teeth, suggest that they were successful carnivores. Like other non-mammalian synapsids, therocephalians are described as mammal-like reptiles, although in fact, Therocephalia is the group most closely related to the cynodonts, which gave rise to the mammals. This relationship takes evidence in a variety of anatomical features, possibly including whiskers and hair. There remain many unanswered questions about the phylogeny, anatomy and physiology of therocephalians.

The fossils of therocephalians are numerous in the Karoo of South Africa, but have also been found in Russia, China and Antarctica. Early therocephalian fossils discovered in Middle Permian deposits of South Africa support a Gondwanan origin for the group, which seems to have spread quickly throughout the world. Although almost every therocephalian lineage ended during the great Permian–Triassic extinction event, a few representatives of the subgroup called Eutherocephalia survived into the Early Triassic and continued to diversify. However, the last therocephalians became extinct by the early

Middle Triassic, possibly due to climate change and competition with cynodonts and various groups of reptiles.

Classification

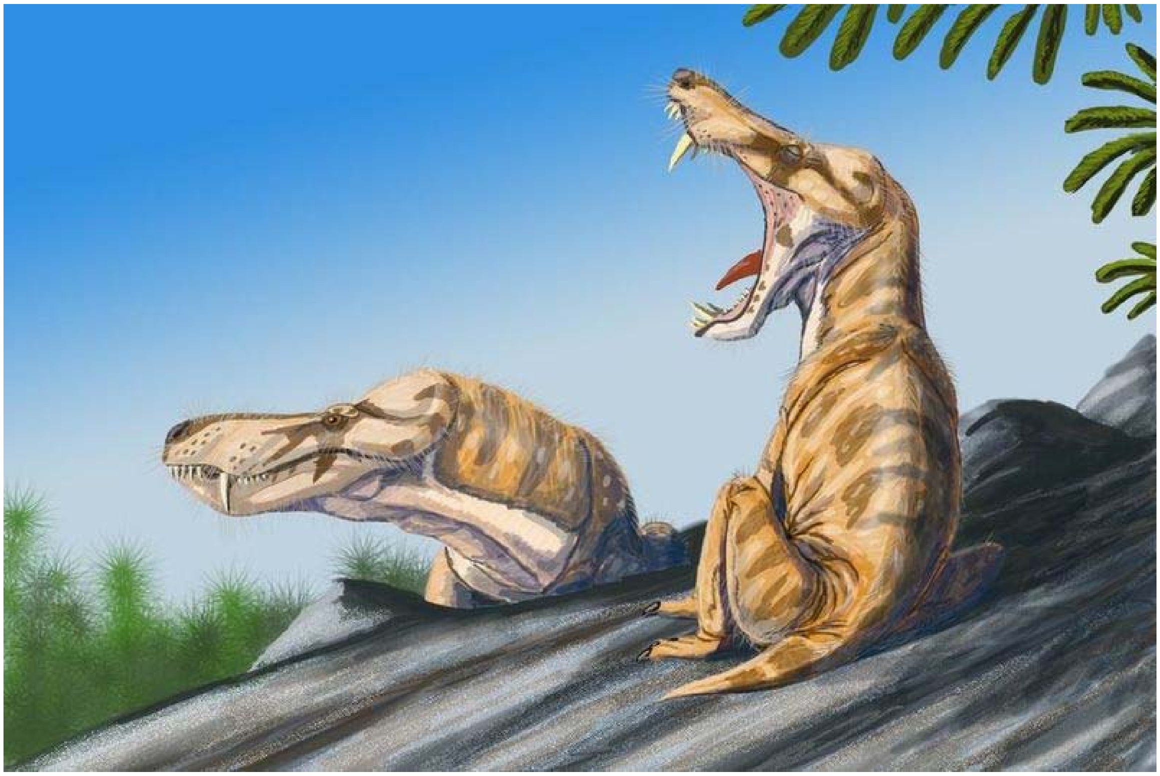


Moschorhinus

The therocephalians evolved from an early line of pre-mammalian therapsids called 'theriodonts' and are a sister group to the cynodonts which include mammals and their ancestors. Therocephalians are at least as ancient as a third large branch of theraspids, the gorgonopsids (also 'theriodonts'), which they resemble in many primitive features. The therocephalians, however, outlasted the gorgonopsians, persisting into the early-Middle Triassic period.

While common ancestry with cynodonts (and, thus, mammals) accounts for many similarities among these groups, some scientists believe that other similarities may be better attributed to convergent evolution, such as the loss of the postorbital bar in some forms, a mammalian phalangeal formula and some form of a secondary palate in most taxa (see below). A current consensus of the taxonomic framework of therocephalians is provided at the bottom of the page.

Anatomy and physiology



Pristerognathus

Like the gorgonopsids and many cynodonts, many therocephalians were presumably carnivores. The earlier therocephalians were in many respects as primitive as the gorgonopsids, but they did show certain advanced features such as

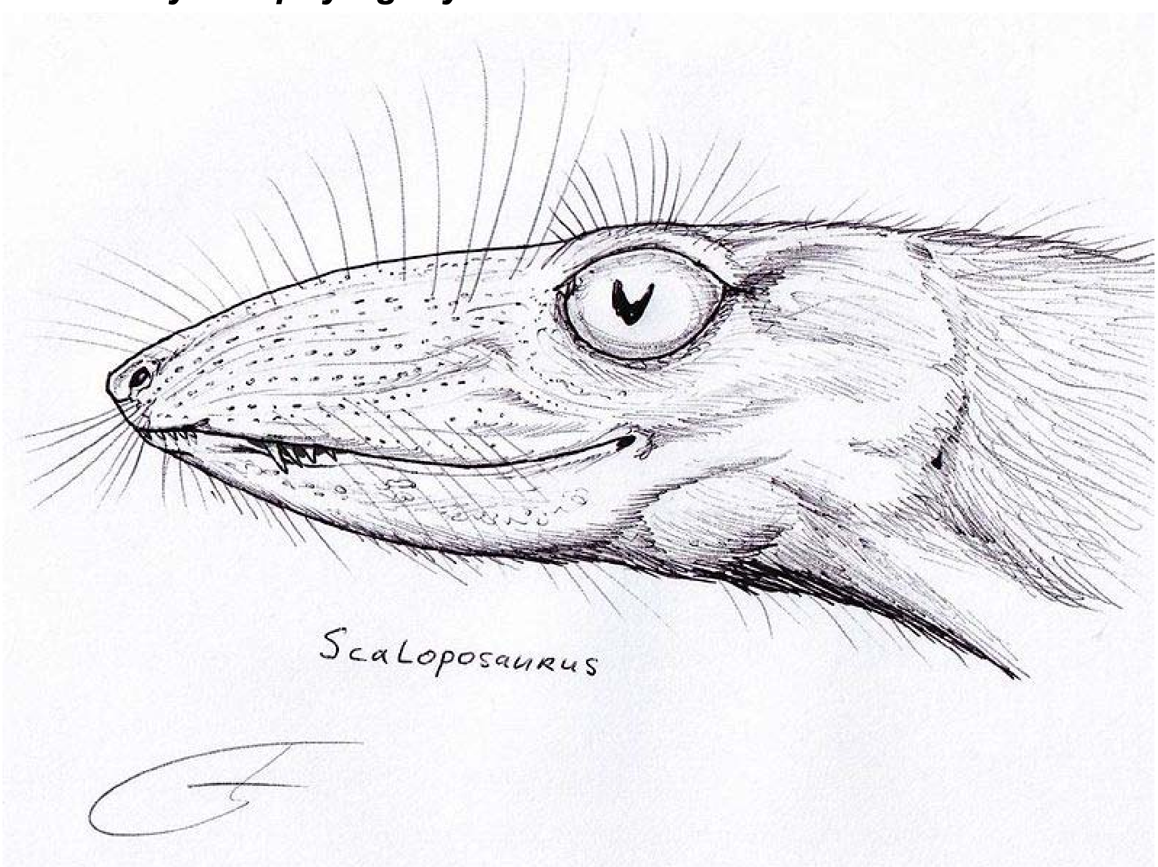
- enlargement of the temporal opening for broader jaw adductor muscle attachment
- reduction of the phalanges (finger and toe bones) to the mammalian phalangeal formula.
- the presence of an incipient secondary palate

The discovery of maxilloturbinal ridges in some specimens, such as the primitive therocephalian *Glanosuchus*, suggests that at least some therocephalians may have been warm-blooded.

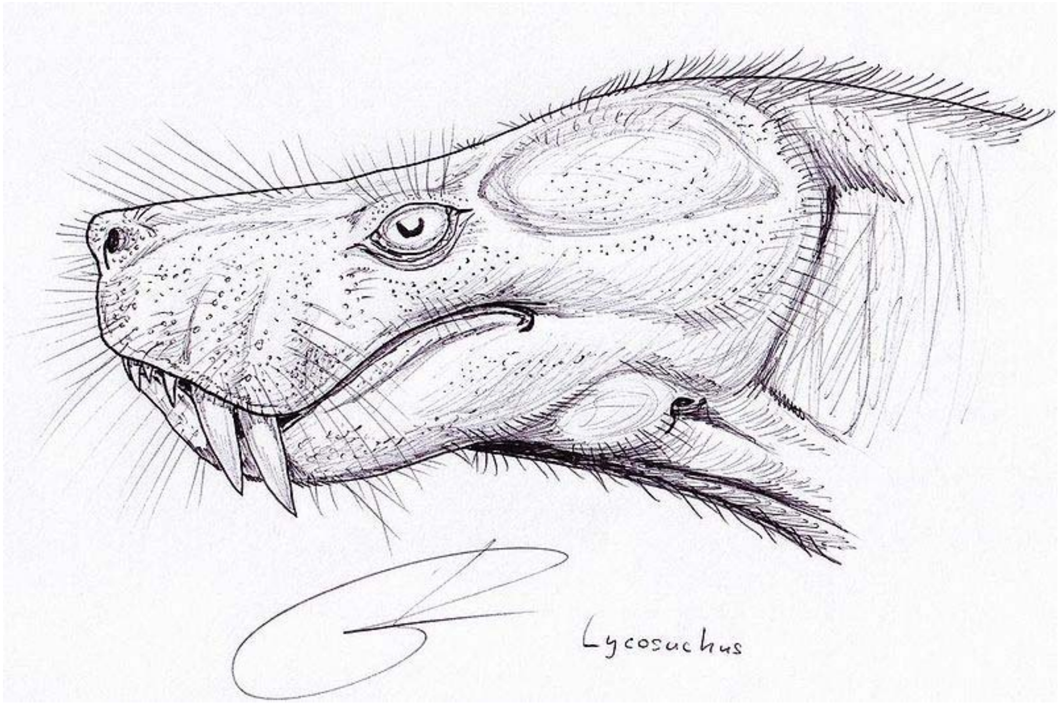
The later therocephalians included the advanced Baurioidea, which carried some theriodont characteristics to a high degree of specialization. For instance, small baurioids and the herbivorous *Bauria* did not have an ossified postorbital bar separating the orbit from the temporal opening — a condition typical of primitive mammals. These and other advanced features led to the long-held opinion, now rejected, that the ictidosaurs and even some early mammals arose from a baurioid therocephalian stem. Mammalian characteristics such as this seem to have evolved in parallel among a number of different therapsid groups, even within Therocephalia.

Lycosuchus reconstruction, with hypothetical fur

Taxonomy and phylogeny



Scaloposaurus



Lycosuchus head reconstruction

Head of unnamed East European moschorhinid

Some previously recognized therocephalian clades have turned out to be artificial. For example, the Scaloposauridae were classified based on fossils with mostly juvenile characteristics, but probably represent immature specimens from other known therocephalian families.

On the other hand, the aberrant therocephalian family Lycosuchidae, once identified by the presence of multiple caniniform teeth, was thought to represent an unnatural group based on a study of canine replacement in that group (van den Heever, 1980). However, subsequent analysis has exposed additional synapomorphies supporting the monophyly of this group and Lycosuchidae is currently considered the most basal clade within a monophyletic Therocephalia (van den Heever, 1994).

- Order **Therapsida**
    - Suborder **Therocephalia**
        - Family Lycosuchidae
    - (unranked) Scylacosauria van den Heever, 1994
        - Family Scylacosauridae
        - Infraorder **Eutherocephalia Hopson & Barghusen, 1986**
            - Family Hofmeyriidae
            - Family Moschorhinidae (=Akidnognathidae, Annatherapsididae, Euchambersiidae)
            - Family Whaitsiidae
        - Superfamily Baurioidea
            - Family Bauriidae
                - Subfamily Nothogomphodontinae
                - Subfamily Bauriinae
            - Family Ericiolacertidae
            - Family Ictidosuchidae
            - Family Ictidosuchopsidae
            - Family Lycideopsidae
            - Family Regisauridae

Chapter- 7

Dinosaur (Triassic Animal)

Dinosaurs **Fossil range:** **Late Triassic-Late Cretaceous, 231.4–65.5 Ma** **Descendant taxon Aves survives to present**	

Mounted skeletons of *Tyrannosaurus* (left) and *Apatosaurus* (right) at the American Museum of Natural History

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
(unranked):	Ornithodira
(unranked):	Dinosauromorpha
(unranked):	Dinosauriformes
Superorder:	**Dinosauria** Owen, 1842

Orders and suborders

- **†Ornithischia**
    - †Cerapoda
    - †Thyreophora
- **Saurischia**

- †Sauropodomorpha
- Theropoda

Dinosaurs are a diverse group of animals that were the dominant terrestrial vertebrates for over 160 million years, from the late Triassic period (about 230 million years ago) until the end of the Cretaceous (about 65 million years ago). The extinction of most dinosaur species occurred during the Cretaceous–Tertiary extinction event. The fossil record indicates that birds evolved from theropod dinosaurs during the Jurassic period. Some of them survived the Cretaceous–Tertiary extinction event, including the ancestors of all modern birds. Consequently, in modern classification systems, birds are considered a type of dinosaur — the only group of which that has survived to the present day.

Dinosaurs are a diverse and varied group of animals; birds, at over 9,000 species, are the most diverse group of vertebrate besides perciform fish. Paleontologists have identified over 500 distinct genera and more than 1,000 different species of non-avian dinosaurs. Dinosaurs are represented on every continent by both extant species and fossil remains. Some dinosaurs are or were herbivorous, others carnivorous. Some have been bipedal, others quadrupedal and others have been able to shift between these body postures. Many non-avian species developed elaborate skeletal modifications such as bony armor, horns or crests. Avian dinosaurs have been the planet's dominant flying vertebrate since the extinction of the pterosaurs. Although generally known for the large size of some species, most dinosaurs were human-sized or even smaller. Most groups of dinosaurs are known to have built nests and laid eggs.

The term "dinosaur" was coined in 1842 by the English paleontologist Richard Owen and derives from Greek *δεινός* (*deinos*) "terrible, powerful, wondrous" + *σαῦρος* (*sauros*) "lizard". Through the first half of the twentieth century, most of the scientific community believed dinosaurs to have been sluggish, unintelligent cold-blooded animals. Most research conducted since the 1970s, however, has indicated that dinosaurs were active animals with elevated metabolisms and numerous adaptations for social interaction.

Since the first dinosaur fossils were recognized in the early nineteenth century, mounted dinosaur skeletons have been major attractions at museums around the world and dinosaurs have become a part of world culture. They have been featured in best-selling books and films such as *Jurassic Park* and new discoveries are regularly covered by the media. In informal speech, the word "dinosaur" is used to describe things that are impractically large, slow-moving, obsolete, or bound for extinction, reflecting the outdated view that dinosaurs were maladapted monsters of the ancient world.

Etymology

The taxon **Dinosauria** was formally named in 1842 by Sir Richard Owen, who used it to refer to the "distinct tribe or sub-order of Saurian Reptiles" that were then being recognized in England and around the world. The term is derived from the Greek words δεινός (*deinos* meaning "terrible", "powerful", or "wondrous") and σαῦρος (*sauros* meaning "lizard" or "reptile").[:103] Though the taxonomic name has often been interpreted as a reference to dinosaurs' teeth, claws and other fearsome characteristics, Owen intended it merely to evoke their size and majesty. In colloquial English "dinosaur" is sometimes used to describe an obsolete or unsuccessful thing or person, despite the dinosaurs' 160 million year reign and the global abundance and diversity of their avian descendants: modern-day birds.

Modern definition

Triceratops skeleton at the American Museum of Natural History in New York City

Under phylogenetic taxonomy, dinosaurs are usually defined as the group consisting of "*Triceratops*, Neornithes [modern birds], their most recent common ancestor and all descendants." It has also been suggested that Dinosauria be defined with respect to the most recent common ancestor of *Megalosaurus* and *Iguanodon*, because these were two of the three genera cited by Richard Owen when he recognized the Dinosauria. Both definitions result in the same set of animals being defined as dinosaurs, including theropods (mostly bipedal carnivores), sauropodomorphs (mostly large herbivorous quadrupeds with long necks and tails), ankylosaurians (armored herbivorous quadrupeds), stegosaurians (plated herbivorous quadrupeds), ceratopsians (herbivorous quadrupeds with horns and frills) and ornithopods (bipedal or quadrupedal herbivores including "duck-bills"). These definitions are written to correspond with scientific conceptions of dinosaurs that predate the modern use of phylogenetics. The continuity of meaning is intended to prevent confusion about what the term "dinosaur" means.

There is a wide consensus among paleontologists that birds are the descendants of theropod dinosaurs. Using the strict cladistical definition that all descendants of a single common ancestor must be included in a group for that group to be natural, birds would thus *be* dinosaurs and dinosaurs are, therefore, not extinct. Birds are classified by most paleontologists as belonging to the subgroup Maniraptora, which are coelurosaurs, which are theropods, which are saurischians, which are dinosaurs.

From the point of view of cladistics, birds are dinosaurs, but in ordinary speech the word "dinosaur" does not include birds. Additionally, referring to dinosaurs that are not birds as "non-avian dinosaurs" is cumbersome. For clarity, here we will use "dinosaur" as a synonym for "non-avian dinosaur". The term "non-avian dinosaur" will be used for emphasis as needed.

General description

Stegosaurus skeleton, Field Museum, Chicago

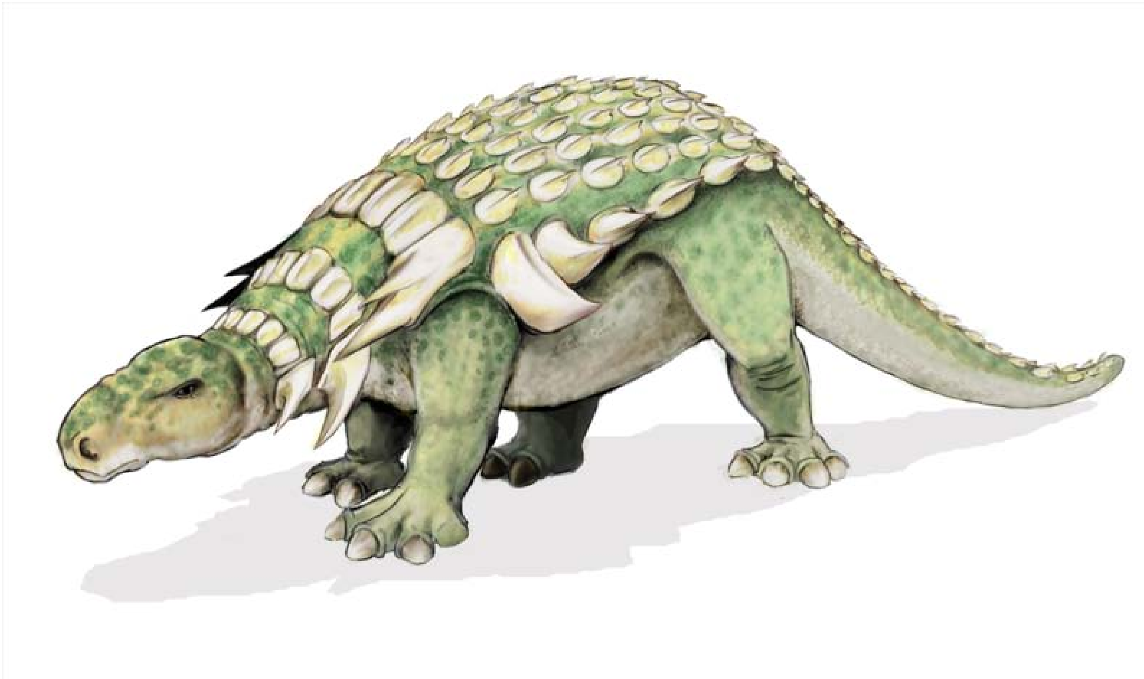
Using one of the above definitions, dinosaurs (aside from birds) can be generally described as terrestrial archosaurian reptiles with limbs held erect beneath the body, that existed from the Late Triassic (first appearing in the Carnian faunal stage) to the Late Cretaceous (going extinct at the end of the Maastrichtian). Many prehistoric animals are popularly conceived of as dinosaurs, such as ichthyosaurs, mosasaurs, plesiosaurs, pterosaurs and *Dimetrodon*, but are not classified scientifically as dinosaurs. Marine reptiles like ichthyosaurs, mosasaurs and plesiosaurs were neither terrestrial nor archosaurs; pterosaurs were archosaurs but not terrestrial; and *Dimetrodon* was a Permian animal more closely related to mammals. Dinosaurs were the dominant terrestrial vertebrates of the Mesozoic, especially the Jurassic and Cretaceous. Other groups of animals were restricted in size and niches; mammals, for example, rarely exceeded the size of a cat and were generally rodent-sized carnivores of small prey. One notable exception is *Repenomamus giganticus*, a triconodont weighing between 12 kilograms (26 lb) and 14 kilograms (31 lb) that is known to have eaten small dinosaurs like young *Psittacosaurus*.

Dinosaurs were an extremely varied group of animals; according to a 2006 study, over 500 dinosaur genera have been identified with certainty so far and the total number of genera preserved in the fossil record has been estimated at around 1850, nearly 75% of which remain to be discovered. An earlier study predicted that about 3400 dinosaur genera existed, including many which would not have been preserved in the fossil record. As of September 17, 2008, 1047 different species of dinosaurs have been named. Some were herbivorous, others carnivorous. Some dinosaurs were bipeds, some were quadrupeds and others, such as *Ammosaurus* and *Iguanodon*, could walk just as easily on two or four legs. Many had bony armor, or cranial modifications like horns and crests. Although known for large size, many dinosaurs were human-sized or smaller. Dinosaur remains have been found on every continent on Earth, including Antarctica. No dinosaurs are known to have lived in marine or aerial habitats, although it is possible some feathered theropods were flyers. There is also evidence that some spinosaurids had semi-aquatic habits.

Distinguishing anatomical features

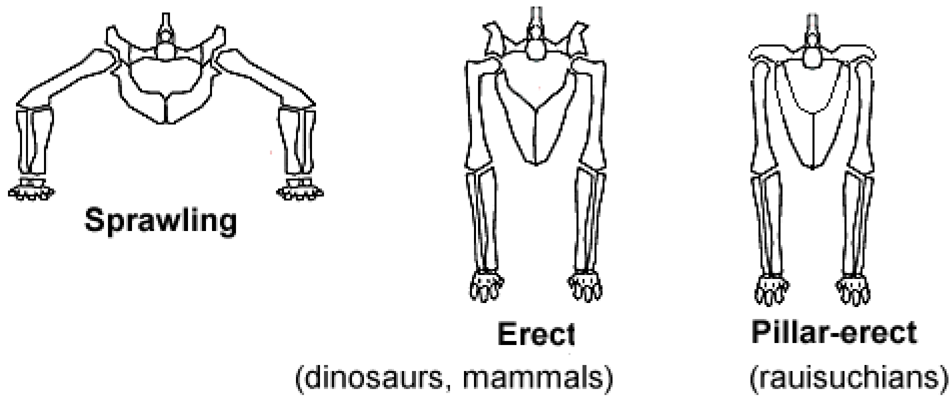
While recent discoveries have made it more difficult to present a universally agreed-upon list of dinosaurs' distinguishing features, nearly all dinosaurs discovered so far share certain modifications to the ancestral archosaurian skeleton. Although some later groups of dinosaurs featured further modified versions of these traits, they are considered typical across Dinosauria; the earliest dinosaurs had them and passed them on to all their descendants. Such common features across a taxonomic group are called synapomorphies.

Dinosaur synapomorphies include an elongated crest on the humerus, or upper arm bone, to accommodate the attachment of deltopectoral muscles; a shelf at the rear of the ilium, or main hip bone; a tibia, or shin bone, featuring a broad lower edge and a flange pointing out and to the rear; and an ascending projection on the astragalus, one of the ankle bones, which secures it to the tibia.



Edmontonia was an armored dinosaur of the group Ankylosauria

A variety of other skeletal features were shared by many dinosaurs. However, because they were either common to other groups of archosaurs or were not present in all early dinosaurs, these features are not considered to be synapomorphies. For example, as diapsid reptiles, dinosaurs ancestrally had two pairs of temporal fenestrae (openings in the skull behind the eyes) and as members of the diapsid group Archosauria, had additional openings in the snout and lower jaw. Additionally, several characteristics once thought to be synapomorphies are now known to have appeared before dinosaurs, or were absent in the earliest dinosaurs and independently evolved by different dinosaur groups. These include an elongated scapula, or shoulder blade; a sacrum composed of three or more fused vertebrae (three are found in some other archosaurs, but only two are found in *Herrerasaurus*); and an acetabulum, or hip socket, with a hole at the center of its inside surface (closed in *Saturnalia*, for example). Another difficulty of determining distinctly dinosaurian features is that early dinosaurs and other archosaurs from the Late Triassic are often poorly known and were similar in many ways; these animals have sometimes been misidentified in the literature.



Hip joints and hindlimb postures

Dinosaurs stood erect in a manner similar to most modern mammals, but distinct from most other reptiles, whose limbs sprawl out to either side. Their posture was due to the development of a laterally facing recess in the pelvis (usually an open socket) and a corresponding inwardly facing distinct head on the femur. Their erect posture enabled dinosaurs to breathe easily while moving, which likely permitted stamina and activity levels that surpassed those of "sprawling" reptiles. Erect limbs probably also helped support the evolution of large size by reducing bending stresses on limbs. Some non-dinosaurian archosaurs, including rauisuchians, also had erect limbs but achieved this by a "pillar erect" configuration of the hip joint, where instead of having a projection from the femur insert on a socket on the hip, the upper pelvic bone was rotated to form an overhanging shelf.

Natural history

Origins and early evolution

Marasuchus, a dinosaur-like ornithodiran

For a long time many scientists thought dinosaurs were polyphyletic with multiple groups of unrelated "dinosaurs" evolving due to similar pressures, but dinosaurs are now known to have formed a single group.

Dinosaurs diverged from their archosaur ancestors approximately 230 million years ago during the Middle to Late Triassic period, roughly 20 million years after the Permian–Triassic extinction event wiped out an estimated 95% of all life on Earth. Radiometric dating of the rock formation that contained fossils from the early dinosaur genus *Eoraptor* establishes its presence in the fossil record at this time. Paleontologists believe *Eoraptor* resembles the common ancestor of all dinosaurs; if this is true, its traits suggest that the first dinosaurs were small, bipedal predators. The discovery of primitive, dinosaur-like ornithodirans such as *Marasuchus* and *Lagerpeton* in Argentinian Middle Triassic strata supports this view; analysis of recovered fossils suggests that these animals were indeed small, bipedal predators.

When dinosaurs appeared, terrestrial habitats were occupied by various types of basal archosaurs and therapsids, such as aetosaurs, cynodonts, dicynodonts, ornithosuchids, rauisuchias and rhynchosaurs. Most of these other animals became extinct in the Triassic, in one of two events. First, at about the boundary between the Carnian and Norian faunal stages (about 215 million years ago), dicynodonts and a variety of basal archosauromorphs, including the prolacertiforms and rhynchosaurs, became extinct. This was followed by the Triassic–Jurassic extinction event (about 200 million years ago), that saw the end of most of the other groups of early archosaurs, like aetosaurs, ornithosuchids, phytosaurs and rauisuchians. These losses left behind a land fauna of crocodylomorphs, dinosaurs, mammals, pterosaurians and turtles.

The early forms *Herrerasaurus* (large), *Eoraptor* (small) and a *Plateosaurus* skull

The first few lines of primitive dinosaurs diversified through the Carnian and Norian stages of the Triassic, most likely by occupying the niches of groups that became extinct. Traditionally, dinosaurs were thought to have replaced the variety of other Triassic land animals by proving superior through a long period of competition. This now appears unlikely, for several reasons. Dinosaurs do not show a pattern of steadily increasing in diversity and numbers, as would be predicted if they were competitively replacing other groups; instead, they were very rare through the Carnian, making up only 1–2% of individuals present in faunas. In the Norian, however, after the extinction of several other groups, they became significant components of faunas, representing 50–90% of individuals. Also, what had been viewed as a key adaptation of dinosaurs, their erect stance, is now known to have been present in several contemporaneous groups that were not as successful (aetosaurs, ornithosuchids, rauisuchians and some groups of crocodylomorphs). Finally, the Late Triassic itself was a time of great upheaval in life, with shifts in plant life, marine life and climate. Crurotarsans, today represented only by crocodilians but in the Late Triassic also encompassing such now-extinct groups as aetosaurs, phytosaurs, ornithosuchians and rauisuchians, were actually more diverse in the Late Triassic than dinosaurs, indicating that the survival of dinosaurs had more to do with luck than superiority.

Low diversification in the Cretaceous

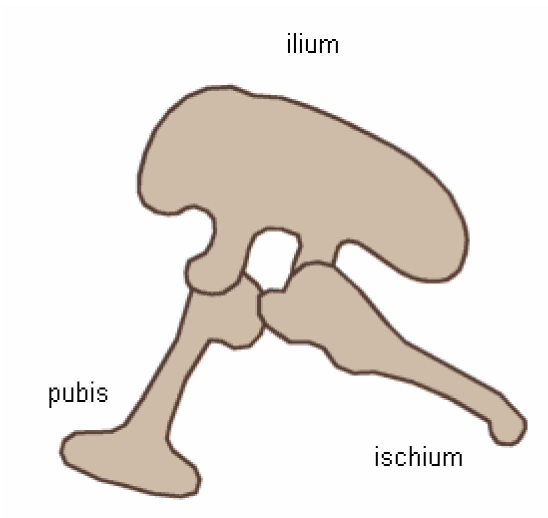
Statistical analyses based on raw data suggest that dinosaurs diversified, i.e. the number of species increased, in the Late Cretaceous. However in July 2008 Graeme T. Lloyd *et al.* argued that this apparent diversification was an illusion caused by sampling bias, because Late Cretaceous rocks have been very heavily studied. Instead, they wrote, dinosaurs underwent only two significant diversifications in the Late Cretaceous, the initial radiations of the euhadrosaurs and ceratopsians. In the Mid Cretaceous, the flowering angiosperm plants became a major part of terrestrial ecosystems, which had previous been dominated by gymnosperms such as conifers. Dinosaur coprolites (fossilized dung) indicate that, while some ate angiosperms, most herbivorous dinosaurs mainly ate gymnosperms. Meanwhile herbivorous insects and mammals diversified rapidly to take advantage of the new type of plant food, while lizards, snakes, crocodilians and birds also diversified at the same time. Lloyd *et al.* suggest that dinosaurs' failure to diversify as ecosystems were changing doomed them to extinction.

Classification

Dinosaurs (including birds) are archosaurs, like modern crocodilians. Archosaurs' diapsid skulls have two holes, called temporal fenestrae, located where the jaw muscles attach and an additional antorbital fenestra in front of the eyes. Most reptiles (including birds) are diapsids; mammals, with only one temporal fenestra, are called synapsids; and turtles, with no temporal fenestra, are anapsids. Anatomically, dinosaurs share many other archosaur characteristics, including teeth that grow from sockets rather than as direct extensions of the jawbones. Within the archosaur group, dinosaurs are differentiated most noticeably by their gait. Dinosaur legs extend directly beneath the body, whereas the legs of lizards and crocodilians sprawl out to either side.

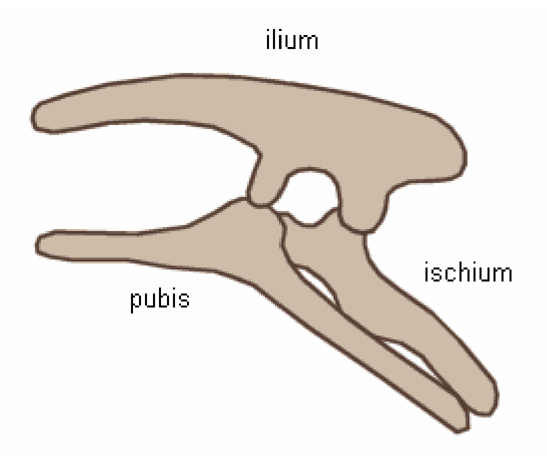
Collectively, dinosaurs are usually regarded as a superorder or an unranked clade. They are divided into two orders, Saurischia and Ornithischia, depending upon pelvic structure. Saurischia includes those taxa sharing a more recent common ancestor with birds than with Ornithischia, while Ornithischia includes all taxa sharing a more recent common ancestor with *Triceratops* than with Saurischia. Saurischians ("lizard-hipped", from the Greek *sauros* (*σαυρος*) meaning "lizard" and *ischion* (*ισχιον*) meaning "hip joint") retained the hip structure of their ancestors, with a pubis bone directed cranially, or forward. This basic form was modified by rotating the pubis backward to varying degrees in several groups (*Herrerasaurus*, therizinosauroids, dromaeosaurids and birds). Saurischia includes the theropods (bipedal and mostly carnivores, except for birds) and sauropodomorphs (long-necked quadrupedal herbivores).

By contrast, ornithischians ("bird-hipped", from the Greek *ornitheios* (*ορνιθειος*) meaning "of a bird" and *ischion* (*ισχιον*) meaning "hip joint") had a pelvis that superficially resembled a bird's pelvis: the pubis bone was oriented caudally (rear-pointing) Unlike birds, the ornithischian pubis also usually had an additional forward-pointing process. Ornithischia includes a variety of herbivores. (**NB:** the terms "lizard hip" and "bird hip" are misnomers – birds evolved from dinosaurs with "lizard hips".)



Saurischian pelvis structure (left side)

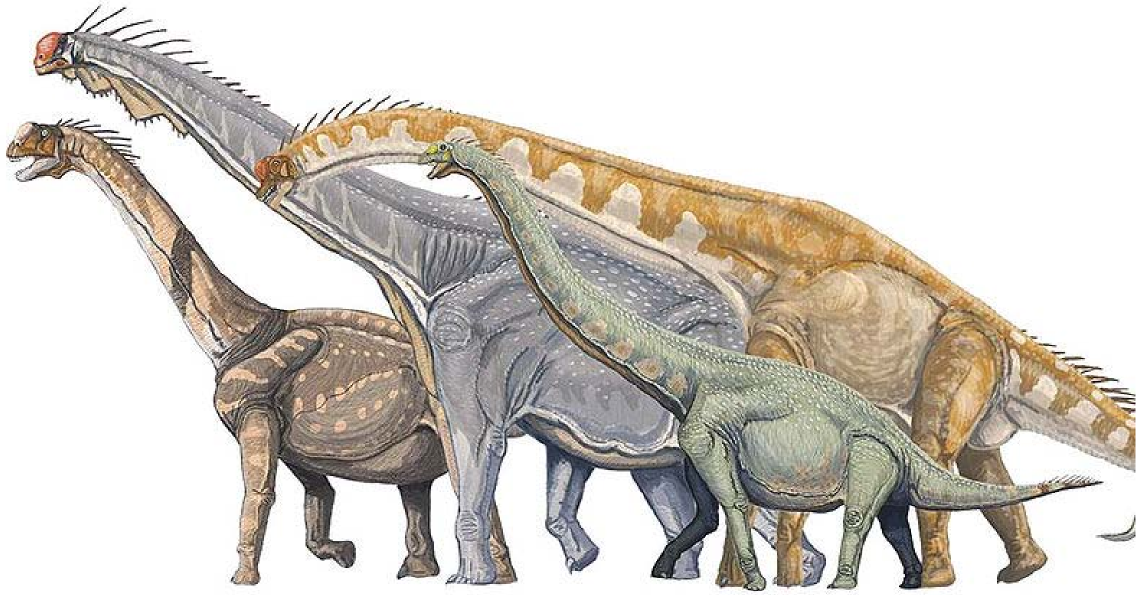
Tyrannosaurus pelvis (showing saurischian structure – left side)



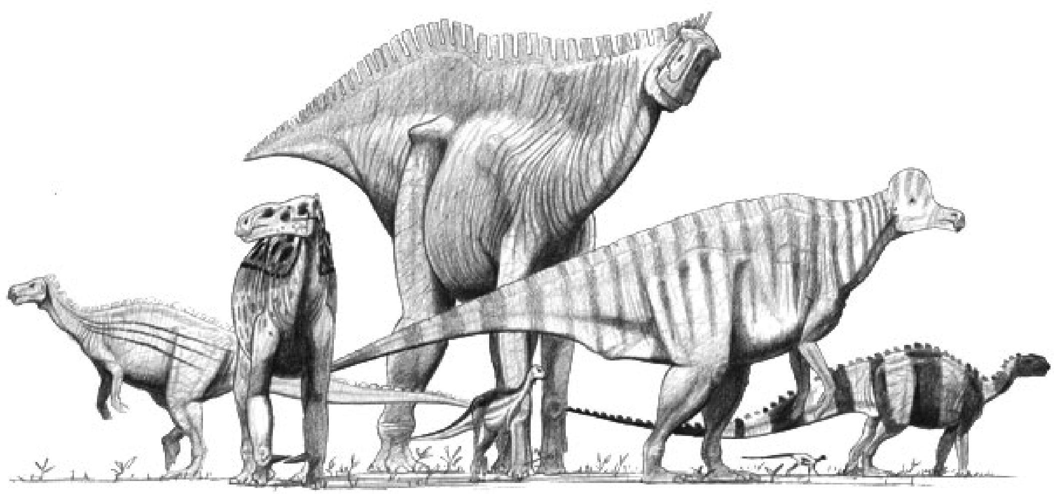
Ornithischian pelvis structure (left side)

Edmontosaurus pelvis (showing ornithischian structure – left side)

The following is a simplified classification of dinosaur families. A more detailed version can be found at List of dinosaur classifications.



Several macronarian Sauropods: from left to right *Camarasaurus*, *Brachiosaurus*, *Giraffatitan* and *Euhelopus*



Various ornithopod dinosaurs and one heterodontosaurid. Far left: *Camptosaurus*, left: *Iguanodon*, center background: *Shantungosaurus*, center foreground: *Dryosaurus*, right: *Corythosaurus*, far right (small): *Heterodontosaurus*, far right (large) *Tenontosaurus*.

- Dinosauria
  - Saurischia (theropods and sauropods)

- †Herrerasaurians (early bipedal predators)
- Theropods (all bipedal; most were carnivores)

- †Coelophysoids (*Coelophysis* and close relatives)
- †Ceratosaurians (*Ceratosaurus* and abelisaurids – the latter were important Late Cretaceous predators in southern continents)
- †Spinosauroids (long bodies; short arms; some with crocodile-like skulls and bony "sails" on their backs)
- †Carnosaurians (*Allosaurus* and close relatives, like *Carcharodontosaurus*)
- Coelurosaurians (diverse, with a range of body sizes and niches)

- †Tyrannosauroids (small to gigantic, often with reduced forelimbs)
- †Ornithomimosaurians ("ostrich-mimics"; mostly toothless; carnivores to possible herbivores)
- †Therizinosauroids (bipedal herbivores with large hand claws and small heads)
- †Oviraptorosaurians (mostly toothless; their diet and lifestyle are uncertain)
- †Dromaeosaurids (popularly known as "raptors"; bird-like carnivores)
- †Troodontids (similar to dromaeosaurids, but more lightly built)
- Avialans (flying dinosaurs, including modern birds: the only living dinosaurs)

- †Sauropodomorphs (quadrupedal herbivores with small heads, long necks and tails and elephant-like bodies)

- †"Prosauropods" (early relatives of sauropods; small to quite large; some possibly omnivorous; bipeds and quadrupeds)
- †Sauropods (very large, usually over 15 meters long [49 ft])

- †Diplodocoids (skulls and tails elongated; teeth typically narrow and pencil-like)
- †Macronarians (boxy skulls; spoon-shaped or pencil-shaped teeth)

- †Brachiosaurids (very long necks; forelimbs longer than hindlimbs)
- †Titanosaurians (diverse; stocky, with wide hips; most common in the Late Cretaceous of southern continents)

- †Ornithischians (diverse bipedal and quadrupedal herbivores)

- †Heterodontosaurids (meter- or yard-scale herbivores or omnivores with prominent canine teeth)
- †Thyreophorans (armored dinosaurs; mostly quadrupeds)

- †Ankylosaurians (scutes as primary armor; some had club-like tails)

- †Stegosaurians (spikes and plates as primary armor)
- †Ornithopods (diverse, from meter- or yard-scale bipeds to 12-meter (39 ft) animals that could move as both bipeds and quadrupeds; evolved a method of chewing using skull flexibility and large numbers of teeth)
- †Hadrosaurids ("duckbilled dinosaurs")
- †Pachycephalosaurians ("bone-heads"; bipeds with domed or knobby growth on skulls)
- †Ceratopsians (dinosaurs with horns and frills, although most early forms had only the beginnings of these features)

Evolution and paleobiogeography

Dinosaur evolution after the Triassic follows changes in vegetation and the location of continents. In the Late Triassic and Early Jurassic, the continents were connected as the single landmass Pangaea and there was a worldwide dinosaur fauna mostly composed of coelophysoid carnivores and prosauropod herbivores. Gymnosperm plants (particularly conifers), a potential food source, radiated in the Late Triassic. Prosauropods did not have sophisticated mechanisms for processing food in the mouth and so must have employed other means of breaking down food farther along the digestive tract. The general homogeneity of dinosaurian faunas continued into the Middle and Late Jurassic, where most localities had predators consisting of ceratosaurians, spinosauroids and carnosaurians and herbivores consisting of stegosaurian ornithischians and large sauropods. Examples of this include the Morrison Formation of North America and Tendaguru Beds of Tanzania. Dinosaurs in China show some differences, with specialized sinraptorid theropods and unusual, long-necked sauropods like *Mamenchisaurus*. Ankylosaurians and ornithopods were also becoming more common, but prosauropods had become extinct. Conifers and pteridophytes were the most common plants. Sauropods, like the earlier prosauropods, were not oral processors, but ornithischians were evolving various means of dealing with food in the mouth, including potential cheek-like organs to keep food in the mouth and jaw motions to grind food. Another notable evolutionary event of the Jurassic was the appearance of true birds, descended from maniraptoran coelurosaurians.

By the Early Cretaceous and the ongoing breakup of Pangaea, dinosaurs were becoming strongly differentiated by landmass. The earliest part of this time saw the spread of ankylosaurians, iguanodontians and brachiosaurids through Europe, North America and northern Africa. These were later supplemented or replaced in Africa by large spinosaurid and carcharodontosaurid theropods and rebbachisaurid and titanosaurian sauropods, also found in South America. In Asia, maniraptoran coelurosaurians like dromaeosaurids, troodontids and oviraptorosaurians became the common theropods and ankylosaurids and early ceratopsians like *Psittacosaurus* became important herbivores. Meanwhile, Australia was home to a fauna of basal ankylosaurians, hypsilophodonts and iguanodontians. The stegosaurians appear to have gone extinct at some point in the late

Early Cretaceous or early Late Cretaceous. A major change in the Early Cretaceous, which would be amplified in the Late Cretaceous, was the evolution of flowering plants. At the same time, several groups of dinosaurian herbivores evolved more sophisticated ways to orally process food. Ceratopsians developed a method of slicing with teeth stacked on each other in batteries and iguanodontians refined a method of grinding with tooth batteries, taken to its extreme in hadrosaurids. Some sauropods also evolved tooth batteries, best exemplified by the rebbachisaurid *Nigersaurus*.

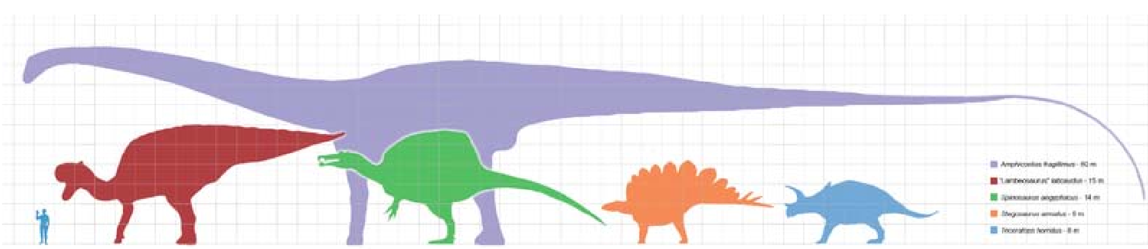
There were three general dinosaur faunas in the Late Cretaceous. In the northern continents of North America and Asia, the major theropods were tyrannosaurids and various types of smaller maniraptoran theropods, with a predominantly ornithischian herbivore assemblage of hadrosaurids, ceratopsians, ankylosaurids and pachycephalosaurians. In the southern continents that had made up the now-splitting Gondwana, abelisaurids were the common theropods and titanosaurian sauropods the common herbivores. Finally, in Europe, dromaeosaurids, rhabdodontid iguanodontians, nodosaurid ankylosaurians and titanosaurian sauropods were prevalent. Flowering plants were greatly radiating, with the first grasses appearing by the end of the Cretaceous. Grinding hadrosaurids and shearing ceratopsians became extremely diverse across North America and Asia. Theropods were also radiating as herbivores or omnivores, with therizinosaurians and ornithomimosaurians becoming common.

The Cretaceous–Tertiary extinction event, which occurred approximately 65 million years ago at the end of the Cretaceous period, caused the extinction of all dinosaurs except for the birds. Some other diapsid groups, such as crocodilians, lizards, snakes, sphenodontians and choristoderans, also survived the event.

Paleobiology

Knowledge about dinosaurs is derived from a variety of fossil and non-fossil records, including fossilized bones, feces, trackways, gastroliths, feathers, impressions of skin, internal organs and soft tissues. Many fields of study contribute to our understanding of dinosaurs, including physics (especially biomechanics), chemistry, biology and the earth sciences (of which paleontology is a sub-discipline). Two topics of particular interest and study have been dinosaur size and behavior.

Size



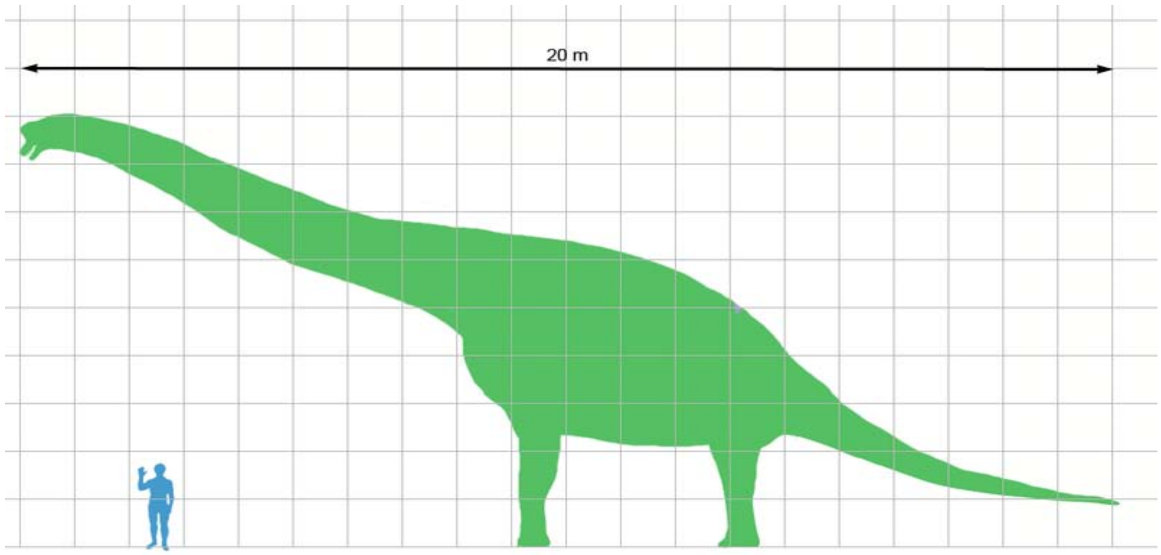
Scale diagram comparing the largest known dinosaurs in five major clades and a human

While the evidence is incomplete, it is clear that, as a group, dinosaurs were large. Even by dinosaur standards, the sauropods were gigantic. For much of the dinosaur era, the smallest sauropods were larger than anything else in their habitat and the largest were an order of magnitude more massive than anything else that has since walked the Earth. Giant prehistoric mammals such as the *Indricotherium* and the Columbian mammoth were dwarfed by the giant sauropods and only a handful of modern aquatic animals approach or surpass them in size – most notably the blue whale, which reaches up to 173000 kg (381000 lb) and over 30 meters (100 ft) in length. There are several proposed advantages for the large size of sauropods, including protection from predation, reduction of energy use and longevity, but it may be that the most important advantage was dietary. Large animals are more efficient at digestion than small animals, because food spends more time in their digestive systems. This also permits them to subsist on food with lower nutritive value than smaller animals. Sauropod remains are mostly found in rock formations interpreted as dry or seasonally dry and the ability to eat large quantities of low-nutrient browse would have been advantageous in such environments.

Most dinosaurs, however, were much smaller than the giant sauropods. Current evidence suggests that dinosaur average size varied through the Triassic, early Jurassic, late Jurassic and Cretaceous periods. Theropod dinosaurs, when sorted by estimated weight into categories based on order of magnitude, most often fall into the 100 to 1000 kilogram (220 to 2200 lb) category, whereas recent predatory carnivorans peak in the 10 to 100 kilogram (22 to 220 lb) category. The mode of dinosaur body masses is between one and ten metric tonnes. This contrasts sharply with the size of Cenozoic mammals, estimated by the National Museum of Natural History as about 2 to 5 kilograms (5 to 10 lb).

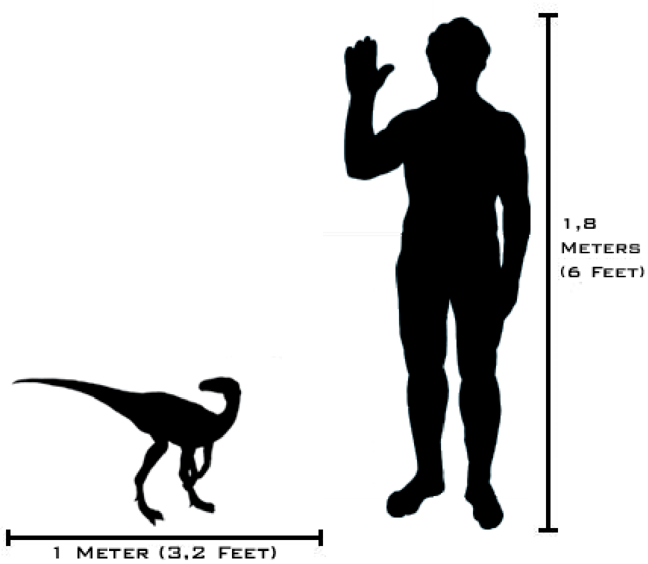
Largest and smallest

Only a tiny percentage of animals ever fossilize and most of these remain buried in the earth. Few of the specimens that are recovered are complete skeletons and impressions of skin and other soft tissues are rare. Rebuilding a complete skeleton by comparing the size and morphology of bones to those of similar, better-known species is an inexact art and reconstructing the muscles and other organs of the living animal is, at best, a process of educated guesswork. As a result, scientists will probably never be certain of the largest and smallest dinosaurs.



Comparative size of *Giraffatitan*

The tallest and heaviest dinosaur known from good skeletons is *Giraffatitan brancai* (previously classified as a species of *Brachiosaurus*). Its remains were discovered in Tanzania between 1907–12. Bones from multiple similar-sized individuals were incorporated into the skeleton now mounted and on display at the Humboldt Museum of Berlin; this mount is 12 meters (39 ft) tall and 22.5 meters (74 ft) long and would have belonged to an animal that weighed between 30000 and 60000 kilograms (70000 and 130000 lb). The longest complete dinosaur is the 27-meter (89 ft) long *Diplodocus*, which was discovered in Wyoming in the United States and displayed in Pittsburgh's Carnegie Natural History Museum in 1907.



Comparative size of *Eoraptor*

There were larger dinosaurs, but knowledge of them is based entirely on a small number of fragmentary fossils. Most of the largest herbivorous specimens on record were all discovered in the 1970s or later and include the massive *Argentinosaurus*, which may have weighed 80000 to 100000 kilograms (90 to 110 short tons); some of the longest were the 33.5 meters (110 ft) long *Diplodocus hallorum* (formerly *Seismosaurus*) and the 33 meters (110 ft) long *Supersaurus*; and the tallest, the 18 meters (59 ft) tall *Sauroposeidon*, which could have reached a sixth-floor window. The longest of them all may have been *Amphicoelias fragillimus*, known only from a now lost partial vertebral neural arch described in 1878. Extrapolating from the illustration of this bone, the animal may have been 58 meters (190 ft) long and weighed over 120000 kg (260000 lb). The largest known carnivorous dinosaur was *Spinosaurus*, reaching a length of 16 to 18 meters (50 to 60 ft) and weighing in at 8150 kg (18000 lb). Other large meat-eaters included *Giganotosaurus*, *Carcharodontosaurus* and *Tyrannosaurus*.

Not including modern birds, the smallest dinosaurs known were about the size of a pigeon. The theropods *Anchiornis* and *Epidexipteryx* both had a total skeletal length of under 35 centimeters (1.1 ft). *Anchiornis* is currently the smallest dinosaur described from an adult specimen, with an estimated weight of 110 grams. The smallest herbivorous dinosaurs included *Microceratus* and *Wannanosaurus*, at about 60 cm (2 ft) long each.

Behavior

A nesting ground of *Maiasaura* was discovered in 1978

Interpretations of dinosaur behavior are generally based on the pose of body fossils and their habitat, computer simulations of their biomechanics and comparisons with modern animals in similar ecological niches. As such, the current understanding of dinosaur behavior relies on speculation and will likely remain controversial for the foreseeable future. However, there is general agreement that some behaviors which are common in crocodiles and birds, dinosaurs' closest living relatives, were also common among dinosaurs.

The first potential evidence of herding behavior was the 1878 discovery of 31 *Iguanodon* dinosaurs which were then thought to have perished together in Bernissart, Belgium, after they fell into a deep, flooded sinkhole and drowned. Other mass-death sites have been subsequently discovered. Those, along with multiple trackways, suggest that gregarious behavior was common in many dinosaur species. Trackways of hundreds or even thousands of herbivores indicate that duck-bills (hadrosaurids) may have moved in great herds, like the American Bison or the African Springbok. Sauropod tracks document that these animals traveled in groups composed of several different species, at least in Oxfordshire, England, although there is not evidence for specific herd structures. Dinosaurs may have congregated in herds for defense, for migratory purposes, or to provide protection for their young. There is evidence that many types of dinosaurs, including various theropods, sauropods, ankylosaurians, ornithopods and ceratopsians, formed aggregations of immature individuals. One example is a site in Inner Mongolia that has yielded the remains of over twenty *Sinornithomimus*, from one to seven years old. This assemblage is interpreted as a social group that was trapped in mud. The interpretation of dinosaurs as gregarious has also extended to depicting carnivorous theropods as pack hunters working together to bring down large prey. However, this lifestyle is uncommon among the modern relatives of dinosaurs (crocodiles and other reptiles and birds – Harris's Hawk is a well-documented exception) and the taphonomic evidence suggesting pack hunting in such theropods as *Deinonychus* and *Allosaurus* can also be interpreted as the results of fatal disputes between feeding animals, as is seen in many modern diapsid predators.

Fossilized egg of the oviraptorid *Citipati*, American Museum of Natural History

Jack Horner's 1978 discovery of a *Maiasaura* ("good mother dinosaur") nesting ground in Montana demonstrated that parental care continued long after birth among the ornithopods. There is also evidence that other Cretaceous-era dinosaurs, like Patagonian titanosaurian sauropods (1997 discovery), also nested in large groups. The Mongolian oviraptorid *Citipati* was discovered in a chicken-like brooding position in 1993, which may mean it was covered with an insulating layer of feathers that kept the eggs warm. Parental care is also implied by other finds. For example, the fossilized remains of a grouping of *Psittacosaurus* has been found, consisting of one adult and 34 juveniles; in this case, the large number of juveniles may be due to communal nesting. Additionally, a dinosaur embryo (pertaining to the prosauropod *Massospondylus*) was found without teeth, indicating that some parental care was required to feed the young dinosaur. Trackways have also confirmed parental behavior among ornithopods from the Isle of Skye in northwestern Scotland. Nests and eggs have been found for most major groups of dinosaurs and it appears likely that dinosaurs communicated with their young, in a manner similar to modern birds and crocodiles.

Artist's rendering of two *Centrosaurus*, herbivorous ceratopsid dinosaurs from the late Cretaceous fauna of North America

The crests and frills of some dinosaurs, like the marginocephalians, theropods and lambeosaurines, may have been too fragile to be used for active defense and so they were likely used for sexual or aggressive displays, though little is known about dinosaur mating and territorialism. Head wounds from bites suggest that theropods, at least, engaged in active aggressive confrontations.

From a behavioral standpoint, one of the most valuable dinosaur fossils was discovered in the Gobi Desert in 1971. It included a *Velociraptor* attacking a *Protoceratops*, providing evidence that dinosaurs did indeed attack each other. Additional evidence for attacking live prey is the partially healed tail of an *Edmontosaurus*, a hadrosaurid dinosaur; the tail is damaged in such a way that shows the animal was bitten by a tyrannosaur but survived. Cannibalism amongst some species of dinosaurs was confirmed by tooth marks found in Madagascar in 2003, involving the theropod *Majungasaurus*.

Based on current fossil evidence from dinosaurs such as *Oryctodromeus*, some herbivorous species seem to have led a partially fossorial (burrowing) lifestyle and some bird-like species may have been arboreal (tree-climbing), most notably primitive dromaeosaurids such as *Microraptor* and the enigmatic scansoriopterygids. However, most dinosaurs seem to have relied on land-based locomotion. A good understanding of how dinosaurs moved on the ground is key to models of dinosaur behavior; the science of biomechanics, in particular, has provided significant insight in this area. For example, studies of the forces exerted by muscles and gravity on dinosaurs' skeletal structure have investigated how fast dinosaurs could run, whether diplodocids could create sonic booms via whip-like tail snapping and whether sauropods could float.

Communication and vocalization

The nature of dinosaur communication remains enigmatic and is an active area of research. In 2008, paleontologist Phil Senter examined the evidence for vocalization in Mesozoic animal life, including dinosaurs. Senter found that, contrary to popular depictions of roaring dinosaurs in motion pictures, it is likely that most dinosaurs were not capable of creating any vocalizations. To draw this conclusion, Senter studied the distribution of vocal organs in reptiles and birds. He found that vocal chords in the larynx probably evolved multiple times among reptiles, including crocodilians, which are able to produce guttural roars. Birds, on the other hand, lack a larynx. Instead, bird calls are produced by the syrinx, a vocal organ found only in birds and which is not related to the larynx, meaning it evolved independently from the vocal organs in reptiles. The syrinx depends on the air sac system in birds to function; specifically, it requires the presence of a *clavicular air sac* near the wishbone or collar bone. This air sac leaves distinctive marks or opening on the bones, including a distinct opening in the upper arm bone (*humerus*). While many dinosaurs show evidence of extensive air sac systems, almost none possess the clavicular air sac necessary to vocalize (one exception, *Aerosteon*, probably evolved its clavicular air sac independently of birds for reasons other than vocalization).

The most primitive animals with evidence of a vocalizing syrinx are the enantironithine birds. Any bird-line archosaurs more primitive than this probably did not make vocal calls. Rather, several lines of evidence suggest that dinosaurs used primarily visual communication, in the form of distinctive-looking (and possibly brightly colored) horns, frills, crests, sails and feathers. This is similar to some modern reptile groups such as lizards, in which many forms are largely silent (though like dinosaurs they possess well-developed senses of hearing) but use complex coloration and display behaviors to communicate.

Also, though they may not have been able to vocalize, some dinosaurs may have used other methods of producing sound for communication. Modern animals, including reptiles and birds, use a wide variety of non-vocal sound communication, including hissing, jaw grinding or clapping, use of environment (such as splashing) and wing beating (which would have been possible in winged maniraptoran dinosaurs).

Some studies have suggested that the hollow crests of the lambeosaurines may have functioned as resonance chambers used for a wide range of vocalizations. However, Senter (2008) noted that such chambers are also used in modern non-vocal animals to accentuate or deepen non-vocal sounds like hissing. For example, many snakes, which lack vocal chords, have resonating chambers in the skull.

Physiology

Tyrannosaurus rex skull and upper vertebral column, Palais de la Découverte, Paris

A vigorous debate on the subject of temperature regulation in dinosaurs has been ongoing since the 1960s. Originally, scientists broadly disagreed as to whether dinosaurs were capable of regulating their body temperatures at all. More recently, dinosaur endothermy has become the consensus view and debate has focused on the mechanisms of temperature regulation.

After dinosaurs were discovered, paleontologists first posited that they were ectothermic creatures: "terrible lizards" as their name suggests. This supposed cold-bloodedness implied that dinosaurs were relatively slow, sluggish organisms, comparable to modern reptiles, which need external sources of heat in order to regulate their body temperature. Dinosaur ectothermy remained a prevalent view until Robert T. "Bob" Bakker, an early proponent of dinosaur endothermy, published an influential paper on the topic in 1968.

Modern evidence indicates that dinosaurs thrived in cooler temperate climates and that at least some dinosaur species must have regulated their body temperature by internal biological means (perhaps aided by the animals' bulk). Evidence of endothermy in dinosaurs includes the discovery of polar dinosaurs in Australia and Antarctica (where they would have experienced a cold, dark six-month winter), the discovery of dinosaurs whose feathers may have provided regulatory insulation and analysis of blood-vessel structures within dinosaur bone that are typical of endotherms. Skeletal structures suggest that theropods and other dinosaurs had active lifestyles better suited to an endothermic cardiovascular system, while sauropods exhibit fewer endothermic characteristics. It is certainly possible that some dinosaurs were endothermic while others were not. Scientific debate over the specifics continues.

Eubrontes, a dinosaur footprint in the Lower Jurassic Moenave Formation at the St. George Dinosaur Discovery Site at Johnson Farm, southwestern Utah

Complicating the debate is the fact that warm-bloodedness can emerge based on more than one mechanism. Most discussions of dinosaur endothermy tend to compare them with average-sized birds or mammals, which expend energy to elevate body temperature above that of the environment. Small birds and mammals also possess insulation, such as fat, fur, or feathers, which slows down heat loss. However, large mammals, such as elephants, face a different problem because of their relatively small ratio of surface area to volume (Haldane's principle). This ratio compares the volume of an animal with the area of its skin: as an animal gets bigger, its surface area increases more slowly than its volume. At a certain point, the amount of heat radiated away through the skin drops below the amount of heat produced inside the body, forcing animals to use additional methods to avoid overheating. In the case of elephants, they have little hair as adults, have large ears which increase their surface area and have behavioral adaptations as well (such as using the trunk to spray water on themselves and mud-wallowing). These behaviors increase cooling through evaporation.

Large dinosaurs would presumably have had to deal with similar issues; their body size suggest they lost heat relatively slowly to the surrounding air and so could have been what are called inertial homeotherms, animals that are warmer than their environments through sheer size rather than through special adaptations like those of birds or mammals. However, so far this theory fails to account for the numerous dog- and goat-sized dinosaur species, or the young of larger species.

Modern computerized tomography (CT) scans of a dinosaur's chest cavity (conducted in 2000) found the apparent remnants of a four-chambered heart, much like those found in today's mammals and birds. The idea is controversial within the scientific community, coming under fire for bad anatomical science or simply wishful thinking. The question of how this find reflects on metabolic rate and dinosaur internal anatomy may be moot, though, regardless of the object's identity: both modern crocodilians and birds, the closest living relatives of dinosaurs, have four-chambered hearts (albeit modified in crocodilians) and so dinosaurs probably had them as well.

Soft tissue and DNA

One of the best examples of soft-tissue impressions in a fossil dinosaur was discovered in Petraroia, Italy. The discovery was reported in 1998 and described the specimen of a small, very young coelurosaur, *Scipionyx samniticus*. The fossil includes portions of the intestines, colon, liver, muscles and windpipe of this immature dinosaur.

In the March 2005 issue of *Science*, the paleontologist Mary Higby Schweitzer and her team announced the discovery of flexible material resembling actual soft tissue inside a 68-million-year-old *Tyrannosaurus rex* leg bone from the Hell Creek Formation in Montana. After recovery, the tissue was rehydrated by the science team.

When the fossilized bone was treated over several weeks to remove mineral content from the fossilized bone-marrow cavity (a process called demineralization), Schweitzer found evidence of intact structures such as blood vessels, bone matrix and connective tissue (bone fibers). Scrutiny under the microscope further revealed that the putative dinosaur soft tissue had retained fine structures (microstructures) even at the cellular level. The exact nature and composition of this material and the implications of Schweitzer's discovery, are not yet clear; study and interpretation of the material is ongoing.

Newer research, published in PloS One (30 July 2008), has challenged the claims that the material found is the soft tissue of *Tyrannosaurus*. Thomas Kaye of the University of

Washington and his co-authors contend that what was really inside the tyrannosaur bone was slimy biofilm created by bacteria that coated the voids once occupied by blood vessels and cells. The researchers found that what previously had been identified as remnants of blood cells, because of the presence of iron, were actually framboids, microscopic mineral spheres bearing iron. They found similar spheres in a variety of other fossils from various periods, including an ammonite. In the ammonite they found the spheres in a place where the iron they contain could not have had any relationship to the presence of blood.

The successful extraction of ancient DNA from dinosaur fossils has been reported on two separate occasions, but, upon further inspection and peer review, neither of these reports could be confirmed. However, a functional visual peptide of a theoretical dinosaur has been inferred using analytical phylogenetic reconstruction methods on gene sequences of related modern species such as reptiles and birds. In addition, several proteins, including hemoglobin, have putatively been detected in dinosaur fossils.

Feathers and the origin of birds

The possibility that dinosaurs were the ancestors of birds was first suggested in 1868 by Thomas Henry Huxley. After the work of Gerhard Heilmann in the early 20th century, the theory of birds as dinosaur descendants was abandoned in favor of the idea of their being descendants of generalized thecodonts, with the key piece of evidence being the supposed lack of clavicles in dinosaurs. However, as later discoveries showed, clavicles (or a single fused wishbone, which derived from separate clavicles) were not actually absent; they had been found as early as 1924 in *Oviraptor*, but misidentified as an interclavicle. In the 1970s, John Ostrom revived the dinosaur–bird theory, which gained momentum in the coming decades with the advent of cladistic analysis and a great increase in the discovery of small theropods and early birds. Of particular note have been the fossils of the Yixian Formation, where a variety of theropods and early birds have been found, often with feathers of some type. Birds share over a hundred distinct anatomical features with theropod dinosaurs, which are now generally accepted to have been their closest ancient relatives. They are most closely allied with maniraptoran coelurosaurs. A minority of scientists, most notably Alan Feduccia and Larry Martin, have proposed other evolutionary paths, including revised versions of Heilmann's basal archosaur proposal, or that maniraptoran theropods are the ancestors of birds but themselves are not dinosaurs, only convergent with dinosaurs.

Feathers

The famous Berlin Specimen of *Archaeopteryx lithographica*

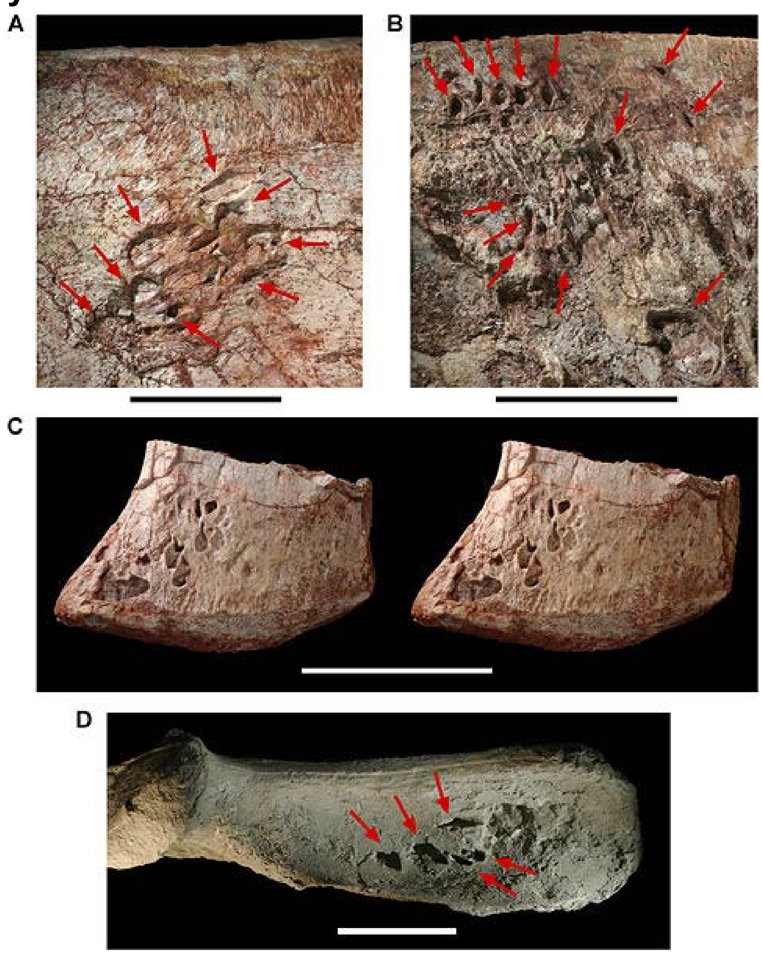
Archaeopteryx, the first good example of a "feathered dinosaur", was discovered in 1861. The initial specimen was found in the Solnhofen limestone in southern Germany, which is a *lagerstätte*, a rare and remarkable geological formation known for its superbly detailed fossils. *Archaeopteryx* is a transitional fossil, with features clearly intermediate between those of modern reptiles and birds. Brought to light just two years after Darwin's seminal *The Origin of Species*, its discovery spurred the nascent debate between proponents of evolutionary biology and creationism. This early bird is so dinosaur-like that, without a clear impression of feathers in the surrounding rock, at least one specimen was mistaken for *Compsognathus*.

Since the 1990s, a number of additional feathered dinosaurs have been found, providing even stronger evidence of the close relationship between dinosaurs and modern birds. Most of these specimens were unearthed in the lagerstätte of the Yixian Formation, Liaoning, northeastern China, which was part of an island continent during the Cretaceous. Though feathers have been found in only a few locations, it is possible that non-avian dinosaurs elsewhere in the world were also feathered. The lack of widespread fossil evidence for feathered non-avian dinosaurs may be because delicate features like skin and feathers are not often preserved by fossilization and thus are absent from the fossil record. To this point, protofeathers (thin, filament-like structures) are known from dinosaurs at the base of Coelurosauria, such as compsognathids like *Sinosauropteryx* and tyrannosauroids (*Dilong*), but barbed feathers are known only among the coelurosaur subgroup Maniraptora, which includes oviraptorosaurs, troodontids, dromaeosaurids and birds. The description of feathered dinosaurs has not been without controversy; perhaps the most vocal critics have been Alan Feduccia and Theagarten Lingham-Soliar, who have proposed that protofeathers are the result of the decomposition of collagenous fiber that underlaid the dinosaurs' integument and that maniraptoran dinosaurs with barbed feathers were not actually dinosaurs, but convergent with dinosaurs. However, their views have for the most part not been accepted by other researchers, to the point that the question of the scientific nature of Feduccia's proposals has been raised.

Skeleton

Because feathers are often associated with birds, feathered dinosaurs are often touted as the missing link between birds and dinosaurs. However, the multiple skeletal features also shared by the two groups represent another important line of evidence for paleontologists. Areas of the skeleton with important similarities include the neck, pubis, wrist (semi-lunate carpal), arm and pectoral girdle, furcula (wishbone) and breast bone. Comparison of bird and dinosaur skeletons through cladistic analysis strengthens the case for the link.

Soft anatomy



Pneumatopores on the left ilium of *Aerosteon riocoloradensis*

Large meat-eating dinosaurs had a complex system of air sacs similar to those found in modern birds, according to an investigation which was led by Patrick O'Connor of Ohio University. The lungs of theropod dinosaurs (carnivores that walked on two legs and had bird-like feet) likely pumped air into hollow sacs in their skeletons, as is the case in birds. "What was once formally considered unique to birds was present in some form in the ancestors of birds", O'Connor said. In a 2008 paper published in the online journal *PLoS ONE*, scientists described *Aerosteon riocoloradensis*, the skeleton of which supplies the strongest evidence to date of a dinosaur with a bird-like breathing system. CT-scanning revealed the evidence of air sacs within the body cavity of the *Aerosteon* skeleton.

Another piece of evidence that birds and dinosaurs are closely related is the use by both of gizzard stones. These stones are swallowed by animals to aid digestion and break down food and hard fibers once they enter the stomach. When found in association with fossils, gizzard stones are called gastroliths.

Reproductive biology

A discovery of features in a *Tyrannosaurus rex* skeleton recently provided more evidence that dinosaurs and birds evolved from a common ancestor and, for the first time, allowed paleontologists to establish the sex of a dinosaur. When laying eggs, female birds grow a special type of bone between the hard outer bone and the marrow of their limbs. This *medullary* bone, which is rich in calcium, is used to make eggshells. The presence of endosteally derived bone tissues lining the interior marrow cavities of portions of the *Tyrannosaurus rex* specimen's hind limb suggested that *T. rex* used similar reproductive strategies and revealed the specimen to be female. Further research has found medullary bone in the theropod *Allosaurus* and the ornithopod *Tenontosaurus*. Because the line of dinosaurs that includes *Allosaurus* and *Tyrannosaurus* diverged from the line that led to *Tenontosaurus* very early in the evolution of dinosaurs, this suggests that dinosaurs in general produced medullary tissue. Medullary bone has been found in specimens of sub-adult size, which suggests that dinosaurs reached sexual maturity rather quickly for such large animals.

Behavioral evidence

A recently discovered troodont fossil demonstrates that some dinosaurs slept with their heads tucked under their arms. This behavior, which may have helped to keep the head warm, is also characteristic of modern birds.

Extinction

Non-avian dinosaurs suddenly became extinct approximately 65 million years ago. Many other groups of animals also became extinct at this time, including ammonites (nautilus-like mollusks), mosasaurs, plesiosaurs, pterosaurs, most birds and many groups of mammals. This mass extinction is known as the Cretaceous–Tertiary extinction event. The nature of the event that caused this mass extinction has been extensively studied since the 1970s; at present, several related theories are supported by paleontologists.

Though the consensus is that an impact event was the primary cause of dinosaur extinction, some scientists cite other possible causes, or support the idea that a confluence of several factors was responsible for the sudden disappearance of dinosaurs from the fossil record.

At the peak of the Mesozoic, there were no polar ice caps and sea levels are estimated to have been from 100 to 250 meters (300 to 800 ft) higher than they are today. The planet's temperature was also much more uniform, with only 25 °C (45 °F) separating average polar temperatures from those at the equator. On average, atmospheric temperatures were also much higher; the poles, for example, were 50 °C (90 °F) warmer than today.

The atmosphere's composition during the Mesozoic was vastly different as well. Carbon dioxide levels were up to 12 times higher than today's levels and oxygen formed 32 to 35% of the atmosphere, as compared to 21% today. However, by the late Cretaceous, the environment was changing dramatically. Volcanic activity was decreasing, which led to a cooling trend as levels of atmospheric carbon dioxide dropped. Oxygen levels in the atmosphere also started to fluctuate and would ultimately fall considerably. Some scientists hypothesize that climate change, combined with lower oxygen levels, might have led directly to the demise of many species. If the dinosaurs had respiratory systems similar to those commonly found in modern birds, it may have been particularly difficult for them to cope with reduced respiratory efficiency, given the enormous oxygen demands of their very large bodies.