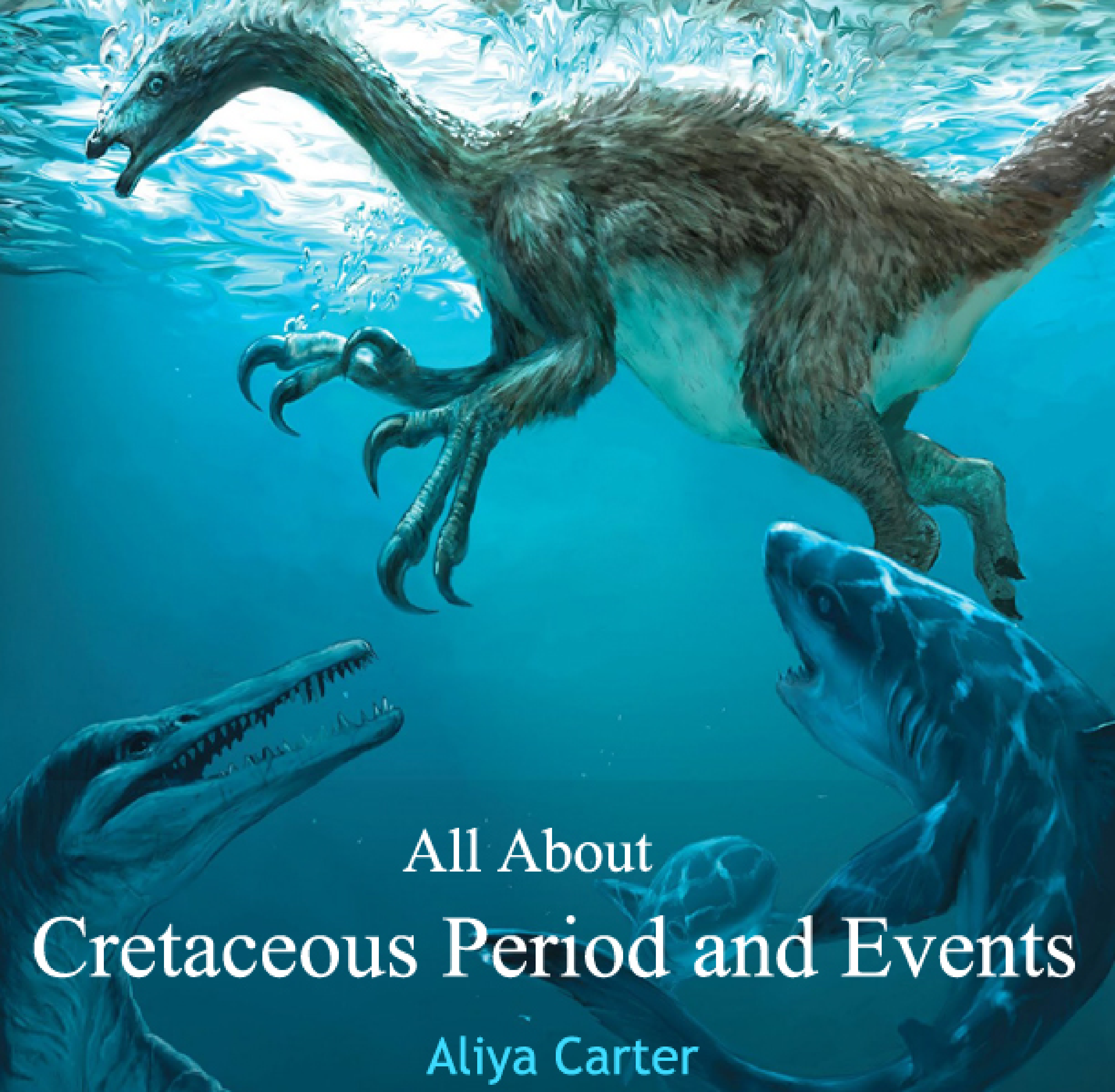

All About

Cretaceous Period and Events

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Chapter- 1

Cretaceous

The **Cretaceous**, Latin for "chalky", usually abbreviated **K** for its German translation *Kreide* (chalk), is a geologic period and system from circa 145.5 ± 4 to 65.5 ± 0.3 million years (Ma) ago. In the geologic timescale, the Cretaceous follows on the Jurassic Period and is followed by the Paleogene Period of the Cenozoic Era. It is the youngest period of the Mesozoic Era, and at 80 million years long, the longest period of the Phanerozoic Eon. The end of the Cretaceous defines the boundary between the Mesozoic and Cenozoic eras. In many languages this period is known as "chalk period".

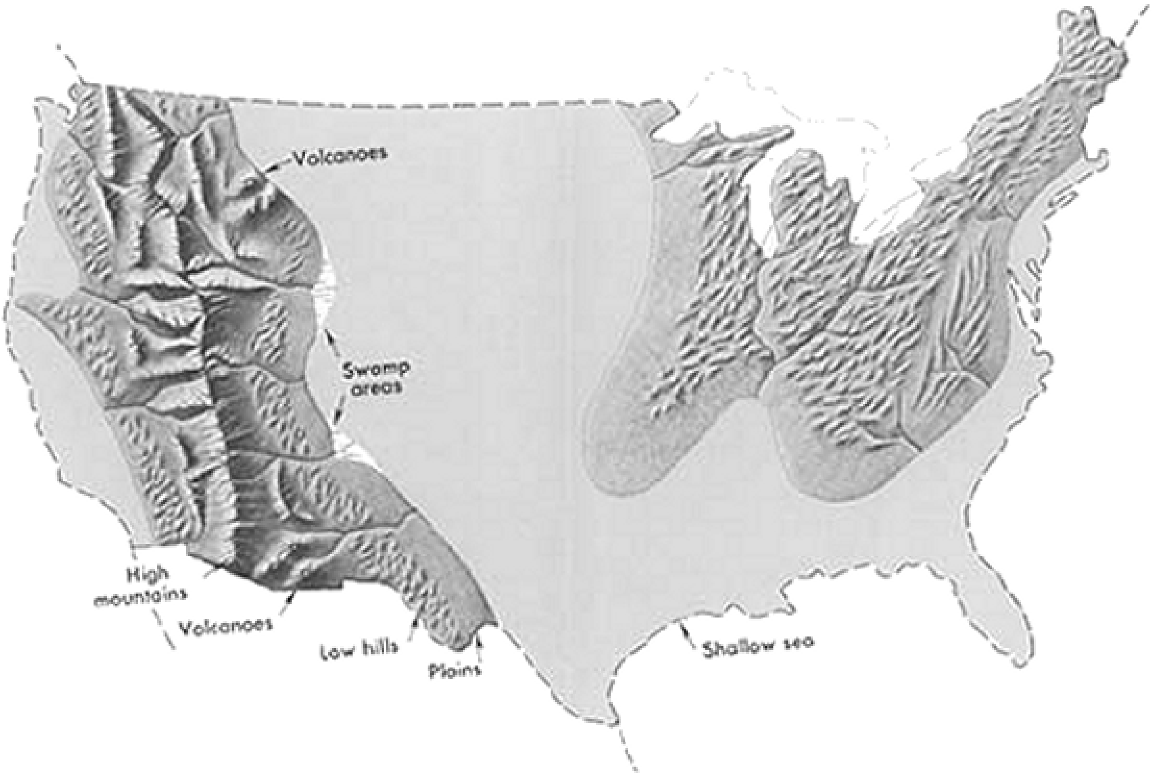
The Cretaceous was a period with a relatively warm climate and high eustatic sea level. The oceans and seas were populated with now extinct marine reptiles, ammonites and rudists; and the land by dinosaurs. At the same time, new groups of mammals and birds as well as flowering plants appeared. The Cretaceous ended with one of the largest mass extinctions in Earth history, the K-T extinction, when many species, including non-avian dinosaurs, pterosaurs, and large marine reptiles, disappeared.

A plate with *Nematonotus sp.* , *Pseudostacus sp.*, and a partial *Dercetis triqueter* from Cretaceous found in Hakel, Lebanon

The Cretaceous world

Paleogeography

During the Cretaceous, the late-Paleozoic-to-early-Mesozoic supercontinent of Pangaea completed its tectonic breakup into present day continents, although their positions were substantially different at the time. As the Atlantic Ocean widened, the convergent-margin orogenies that had begun during the Jurassic continued in the North American Cordillera, as the Nevadan orogeny was followed by the Sevier and Laramide orogenies.



Geography of the US in the Late Cretaceous Period

Though Gondwana was still intact in the beginning of the Cretaceous, it broke up as South America, Antarctica and Australia rifted away from Africa (though India and Madagascar remained attached to each other); thus, the South Atlantic and Indian Oceans were newly formed. Such active rifting lifted great undersea mountain chains along the welts, raising eustatic sea levels worldwide. To the north of Africa the Tethys Sea continued to narrow. Broad shallow seas advanced across central North America (the Western Interior Seaway) and Europe, then receded late in the period, leaving thick marine deposits sandwiched between coal beds. At the peak of the Cretaceous transgression, one-third of Earth's present land area was submerged.

The Cretaceous is justly famous for its chalk; indeed, more chalk formed in the Cretaceous than in any other period in the Phanerozoic. Mid-ocean ridge activity—or rather, the circulation of seawater through the enlarged ridges—enriched the oceans in calcium; this made the oceans more saturated, as well as increased the bioavailability of the element for calcareous nanoplankton. These widespread carbonates and other sedimentary deposits make the Cretaceous rock record especially fine. Famous formations from North America include the rich marine fossils of Kansas's Smoky Hill Chalk Member and the terrestrial fauna of the late Cretaceous Hell Creek Formation. Other important Cretaceous exposures occur in Europe (e.g., the Weald) and China (the Yixian Formation). In the area that is now India, massive lava beds called the Deccan Traps were erupted in the very late Cretaceous and early Paleocene.

Climate

The Berriasian epoch showed a cooling trend that had been seen in the last epoch of the Jurassic. There is evidence that snowfalls were common in the higher latitudes and the tropics became wetter than during the Triassic and Jurassic. Glaciation was however restricted to alpine glaciers on some high-latitude mountains, though seasonal snow may have existed farther south. Rafting by ice of stones into marine environments occurred during much of the Cretaceous but evidence of deposition directly from glaciers is limited to the Early Cretaceous of the Eromanga Basin in southern Australia.

After the end of the Berriasian, however, temperatures increased again, and these conditions were almost constant until the end of the period. This trend was due to intense volcanic activity which produced large quantities of carbon dioxide. The development of a number of mantle plumes across the widening mid-ocean ridges further pushed sea levels up, so that large areas of the continental crust were covered with shallow seas. The Tethys Sea connecting the tropical oceans east to west also helped in warming the global climate. Warm-adapted plant fossils are known from localities as far north as Alaska and Greenland, while dinosaur fossils have been found within 15 degrees of the Cretaceous south pole.

A very gentle temperature gradient from the equator to the poles meant weaker global winds, contributing to less upwelling and more stagnant oceans than today. This is evidenced by widespread black shale deposition and frequent anoxic events. Sediment cores show that tropical sea surface temperatures may have briefly been as warm as 42 °C (107 °F), 17 °C (31 °F) warmer than at present, and that they averaged around 37 °C (99 °F). Meanwhile deep ocean temperatures were as much as 15 to 20 °C (27 to 36 °F) higher than today's.

Geology

Research history

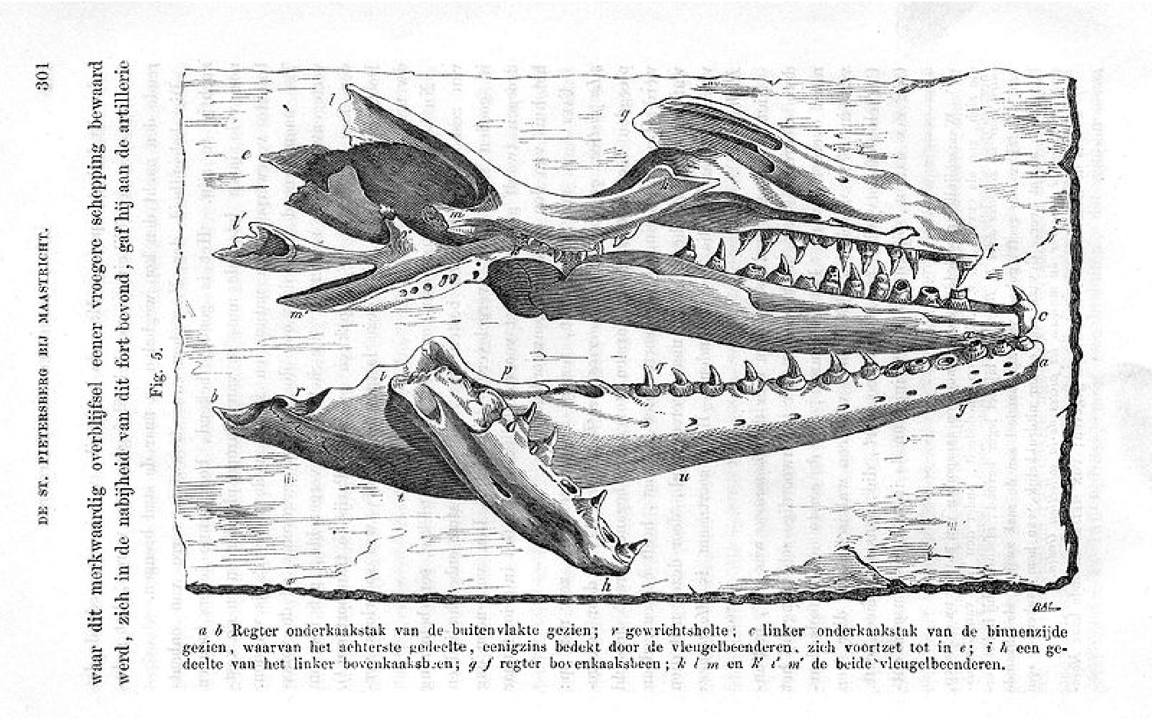
The Cretaceous as a separate period was first defined by a Belgian geologist Jean d'Omalius d'Halloy in 1822, using strata in the Paris Basin and named for the extensive beds of chalk (calcium carbonate deposited by the shells of marine invertebrates, principally coccoliths), found in the upper Cretaceous of western Europe. The name Cretaceous was derived from Latin *creta*, meaning *chalk*. The name of the island Crete has the same origin.

Stratigraphic subdivisions

The Cretaceous is divided into Early and Late Cretaceous epochs or Lower and Upper Cretaceous series. In older literature the Cretaceous is sometimes divided into three series: Neocomian (lower/early), Gallic (middle) and Senonian (upper/late). A subdivision in eleven stages, all origining from European stratigraphy, is now used worldwide. In many parts of the world, alternative local subdivisions are still in use.

As with other older geologic periods, the rock beds of the Cretaceous are well identified but the exact ages of the system's top and base are uncertain by a few million years. No great extinction or burst of diversity separates the Cretaceous from the Jurassic. However, the top of the system is sharply defined, being placed at an iridium-rich layer found worldwide that is believed to be associated with the Chicxulub impact crater in Yucatan and the Gulf of Mexico. This layer has been tightly dated at 65.5 Ma.

Rock formations



Drawing of fossil jaws of *Mosasaurus hoffmanni*, from the Maastrichtian of Dutch Limburg, by Dutch geologist Pieter Harting (1866).

The high eustatic sea level and warm climate of the Cretaceous meant a large area of the continents was covered by warm shallow seas. The Cretaceous was named for the extensive chalk deposits of this age in Europe, but in many parts of the world, the Cretaceous system consists for a major part of marine limestone, a rock type that is formed under warm, shallow marine circumstances. Due to the high sea level there was extensive accommodation space for sedimentation so that thick deposits could form. Because of the relatively young age and great thickness of the system, Cretaceous rocks crop out in many areas worldwide.

Chalk is a rock type characteristic for (but not restricted to) the Cretaceous. It consists of coccoliths, microscopically small calcite skeletons of coccolithophores, a type of algae that prospered in the Cretaceous seas.

In northwestern Europe, chalk deposits from the Upper Cretaceous are characteristic for the Chalk Group, which forms the white cliffs of Dover on the south coast of England and similar cliffs on the French Normandian coast. The group is found in England, northern France, the low countries, northern Germany, Denmark and in the subsurface of the southern part of the North Sea. Chalk is not easily consolidated and the Chalk Group still consists of loose sediments in many places. The group also has other limestones and arenites. Among the fossils it contains are sea urchins, belemnites, ammonites and sea reptiles such as *Mosasaurus*.

In southern Europe, the Cretaceous is usually a marine system consisting of competent limestone beds or incompetent marls. Because the Alpine mountain chains did not yet exist in the Cretaceous, these deposits formed on the southern edge of the European continental shelf, at the margin of the Tethys Ocean.

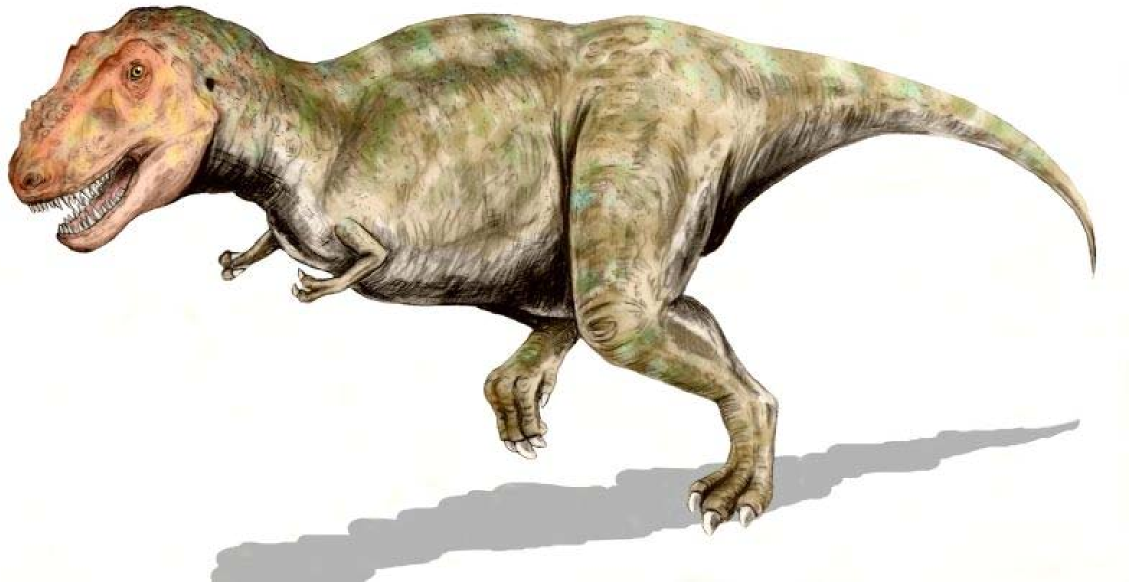
Stagnation of deep sea currents in middle Cretaceous times caused anoxic circumstances in the sea water. In many places around the world, dark anoxic shales were formed during this interval. These shales are an important source rock for oil and gas, for example in the subsurface of the North Sea.

Life

Plants

Flowering plants (angiosperms) spread during this period, although they did not become predominant until the Campanian stage near the end of the epoch. Their evolution was aided by the appearance of bees; in fact angiosperms and insects are a good example of coevolution. The first representatives of many leafy trees, including figs, planes and magnolias, appeared in the Cretaceous. At the same time, some earlier Mesozoic gymnosperms like Conifers continued to thrive; pehuéns (Monkey Puzzle trees, *Araucaria*) and other conifers being notably plentiful and widespread. Some fern orders such as Gleicheniales appeared as early in the fossil record as the Cretaceous, and achieved an early broad distribution. Gymnosperm taxa like Bennettitales died out before the end of the period.

Terrestrial fauna



Tyrannosaurus rex, one of the largest land predators of all time, lived during the late Cretaceous.

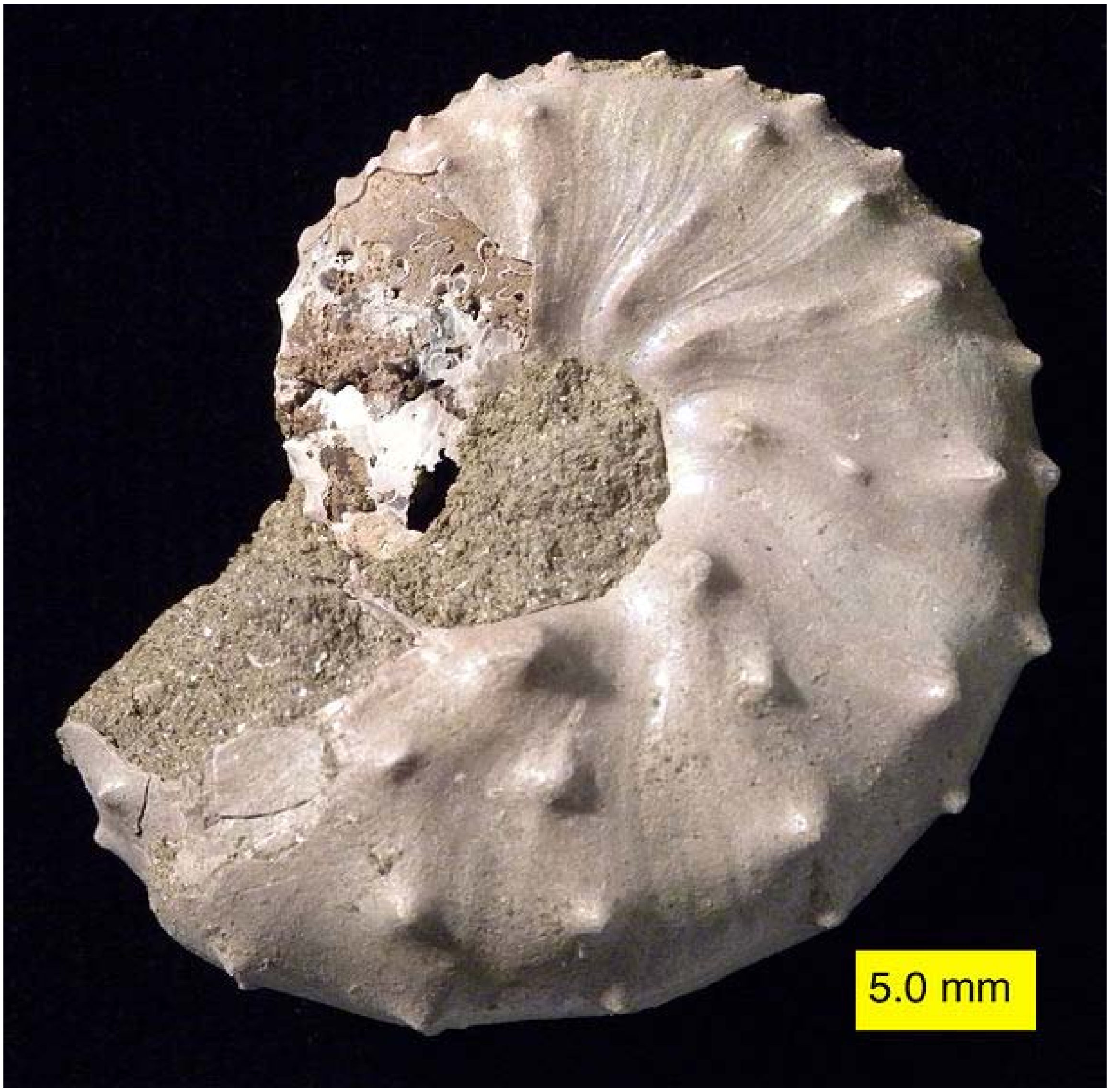
A pterosaur, *Anhanguera piscator*

On land, mammals were a small and still relatively minor component of the fauna. Early marsupial mammals evolved in the Early Cretaceous, with true placentals emerging in the Late Cretaceous period. The fauna was dominated by archosaurian reptiles, especially dinosaurs, which were at their most diverse stage. Pterosaurs were common in the early and middle Cretaceous, but as the Cretaceous proceeded they faced growing competition from the adaptive radiation of birds, and by the end of the period only two highly specialized families remained.

The Liaoning lagerstätte (Chaomidianzi formation) in China provides a glimpse of life in the Early Cretaceous, where preserved remains of numerous types of small dinosaurs, birds, and mammals have been found. The coelurosaur dinosaurs found there represent types of the group Maniraptora, which is transitional between dinosaurs and birds, and are notable for the presence of hair-like feathers.

During the Cretaceous, insects began to diversify, and the oldest known ants, termites and some lepidopterans, akin to butterflies and moths, appeared. Aphids, grasshoppers, and gall wasps appeared.

Marine fauna



Discoscaphites iris, Owl Creek Formation (Upper Cretaceous), Ripley, Mississippi.

In the seas, rays, modern sharks and teleosts became common. Marine reptiles included ichthyosaurs in the early and middle of the Cretaceous, becoming extinct during the late Cretaceous, plesiosaurs throughout the entire period, and mosasaurs appearing in the Late Cretaceous.

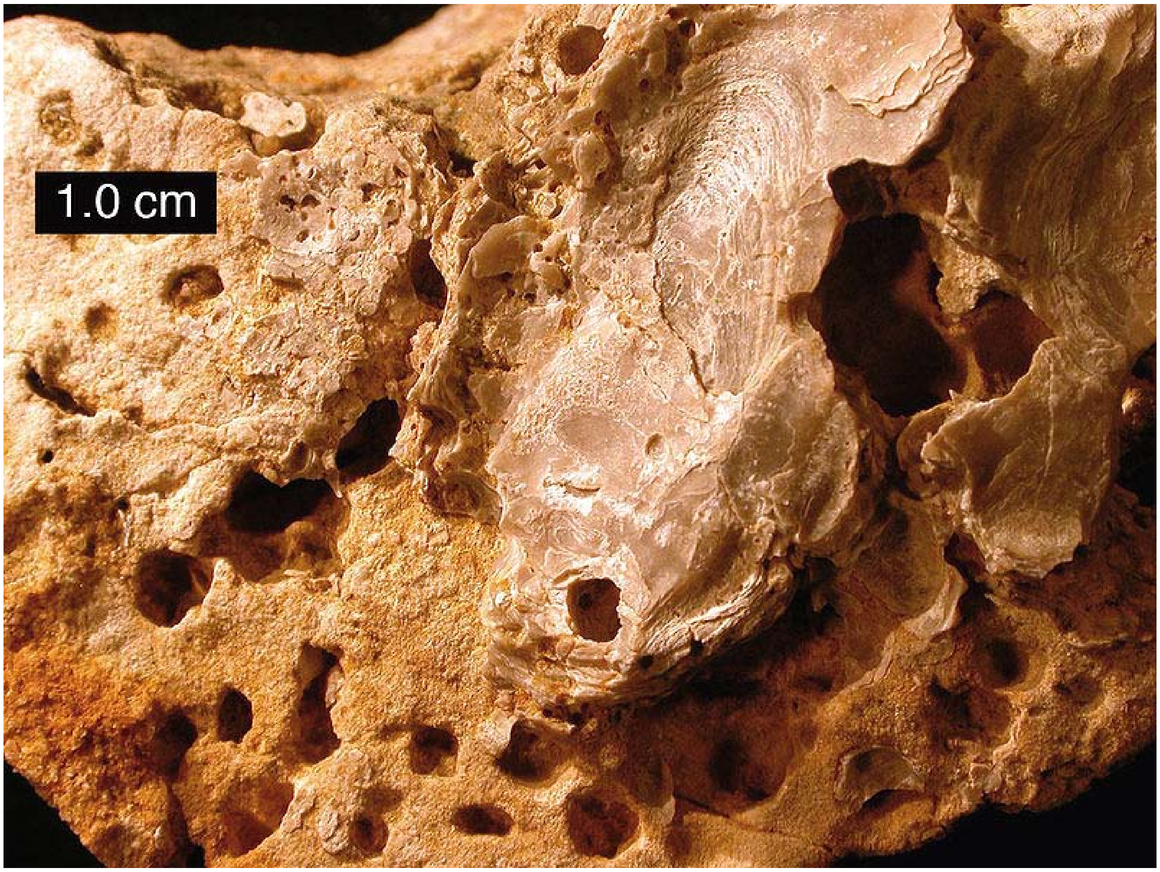
Baculites, an ammonite genus with a straight shell, flourished in the seas along with reef-building rudist clams. The Hesperornithiformes were flightless, marine diving birds that swam like grebes. Globotruncanid Foraminifera and echinoderms such as sea urchins and starfish (sea stars) thrived. The first radiation of the diatoms (generally siliceous, rather than calcareous) in the oceans occurred during the Cretaceous; freshwater diatoms did not appear until the Miocene. The Cretaceous was also an important interval in the evolution of bioerosion, the production of borings and scrapings in rocks, hardgrounds and shells (Taylor and Wilson, 2003).

Extinction

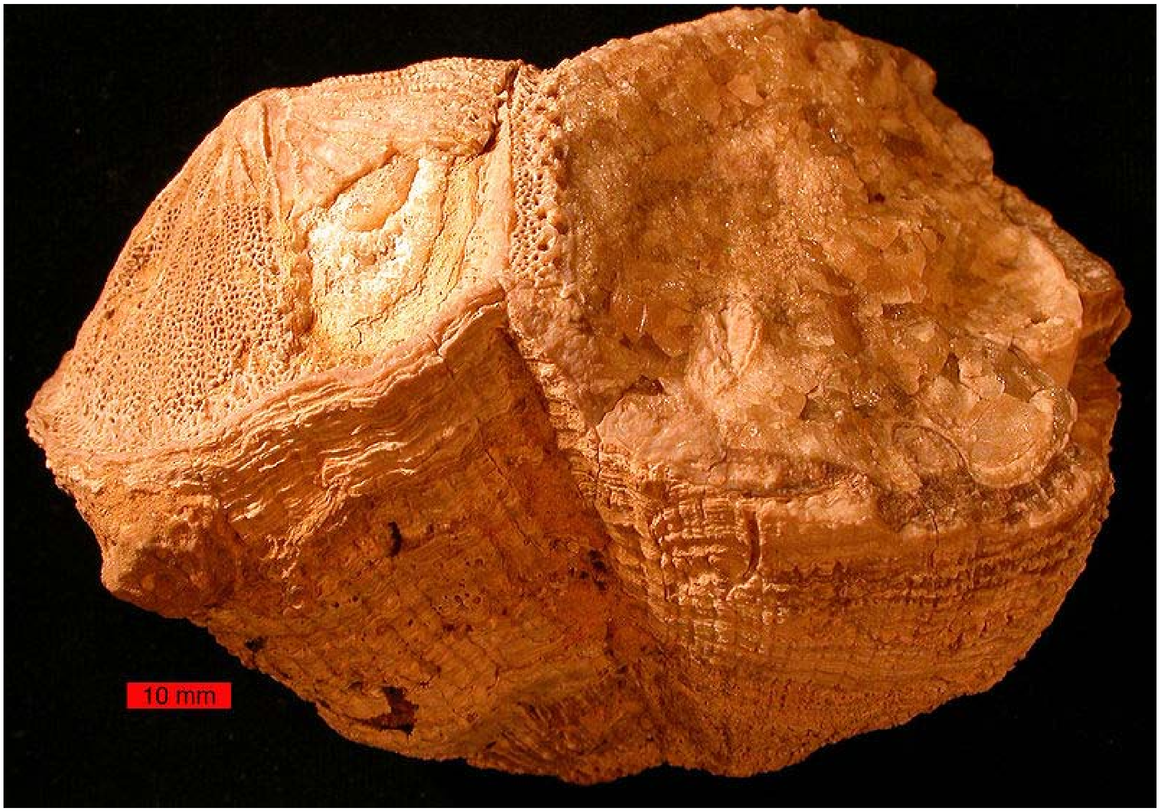
There was a progressive decline in biodiversity during the Maastrichtian stage of the Cretaceous Period prior to the suggested ecological crisis induced by events at the K-T boundary. Furthermore, biodiversity required a substantial amount of time to recover from the K-T event, despite the probable existence of an abundance of vacant ecological niches.

Despite the severity of this boundary event, there was significant variability in the rate of extinction between and within different clades. Species which depended on photosynthesis declined or became extinct because of the reduction in solar energy reaching the Earth's surface due to atmospheric particles blocking the sunlight. As is the case today, photosynthesizing organisms, such as phytoplankton and land plants, formed the primary part of the food chain in the late Cretaceous. Evidence suggests that herbivorous animals, which depended on plants and plankton as their food, died out as their food sources became scarce; consequently, top predators such as *Tyrannosaurus rex* also perished.

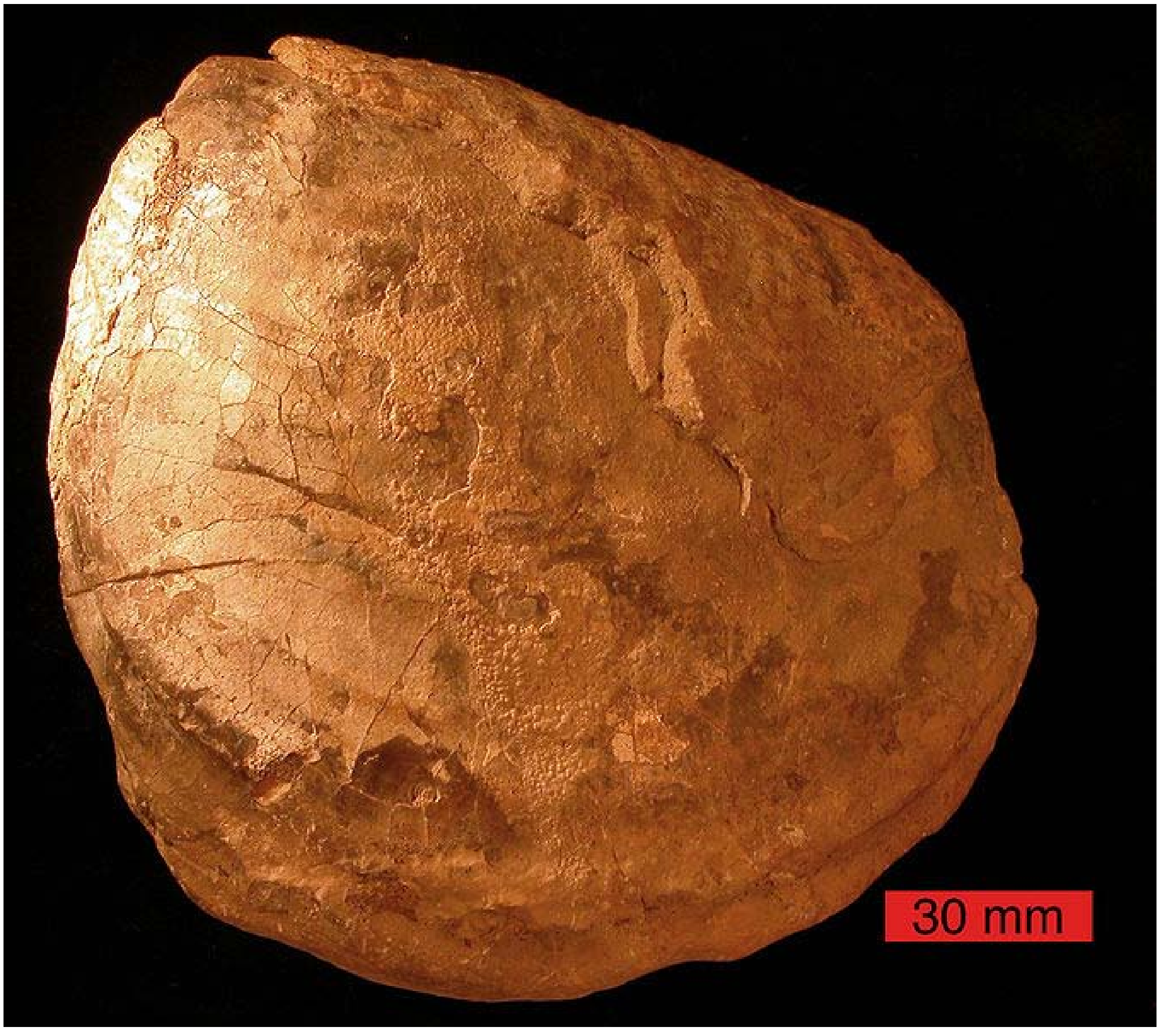
Numerous borings in a Cretaceous cobble, Faringdon, England; these are excellent examples of fossil bioerosion.



Cretaceous hardground from Texas with encrusting oysters and borings. The scale bar is 10 mm.



Rudist bivalves from the Cretaceous of the Omani Mountains, United Arab Emirates. Scale bar is 10 mm.



Inoceramus from the Cretaceous of South Dakota.

Coccolithophorids and molluscs, including ammonites, rudists, freshwater snails and mussels, as well as organisms whose food chain included these shell builders, became extinct or suffered heavy losses. For example, it is thought that ammonites were the principal food of mosasaurs, a group of giant marine reptiles that became extinct at the boundary.

Omnivores, insectivores and carrion-eaters survived the extinction event, perhaps because of the increased availability of their food sources. At the end of the Cretaceous there seem to have been no purely herbivorous or carnivorous mammals. Mammals and birds which survived the extinction fed on insects, larvae, worms, and snails, which in turn fed on dead plant and animal matter. Scientists theorise that these organisms survived the collapse of plant-based food chains because they fed on detritus.

In stream communities, few groups of animals became extinct. Stream communities rely less on food from living plants and more on detritus that washes in from land. This particular ecological niche buffered them from extinction. Similar, but more complex patterns have been found in the oceans. Extinction was more severe among animals living in the water column, than among animals living on or in the sea floor. Animals in the water column are almost entirely dependent on primary production from living phytoplankton, while animals living on or in the ocean floor feed on detritus or can switch to detritus feeding.

The largest air-breathing survivors of the event, crocodilians and champsosaurs, were semi-aquatic and had access to detritus. Modern crocodilians can live as scavengers and can survive for months without food, and their young are small, grow slowly, and feed largely on invertebrates and dead organisms or fragments of organisms for their first few years. These characteristics have been linked to crocodilian survival at the end of the Cretaceous.

Chapter- 2

Cretaceous–Tertiary Extinction Event

Artist's rendering of bolide impact

Badlands near Drumheller, Alberta, where erosion has exposed the K–T boundary

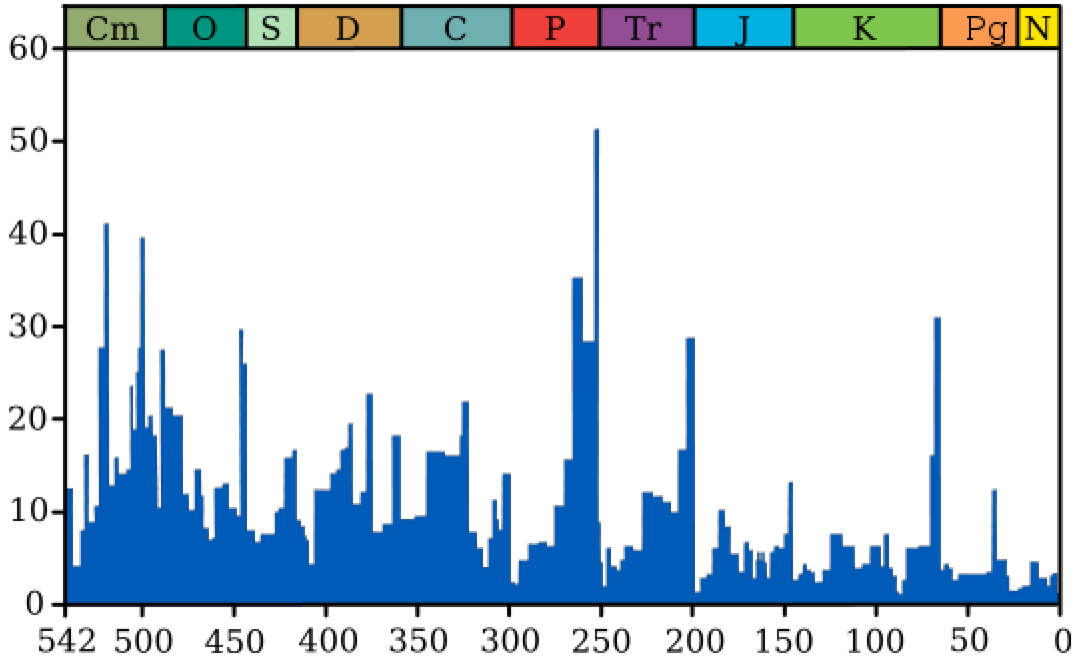
A Wyoming (US) rock with an intermediate claystone layer that contains 1000 times more iridium than the upper and lower layers. Picture taken at the San Diego Natural History Museum

The **Cretaceous–Tertiary extinction event**, which occurred approximately 65.5 million years ago (Ma), was a large-scale mass extinction of animal and plant species in a geologically short period of time. Widely known as the **K–T extinction event**, it is associated with a geological signature known as the K–T boundary, usually a thin band of sedimentation found in various parts of the world. *K* is the traditional abbreviation for the Cretaceous Period derived from the German name *Kreidezeit*, and *T* is the abbreviation for the Tertiary Period (a historical term for the period of time now covered by the Paleogene and Neogene periods). The event marks the end of the Mesozoic Era and the beginning of the Cenozoic Era. With "Tertiary" being discouraged as a formal time or rock unit by the International Commission on Stratigraphy, the K–T event is now called the **Cretaceous–Paleogene** (or **K–Pg**) **extinction event** by many researchers.

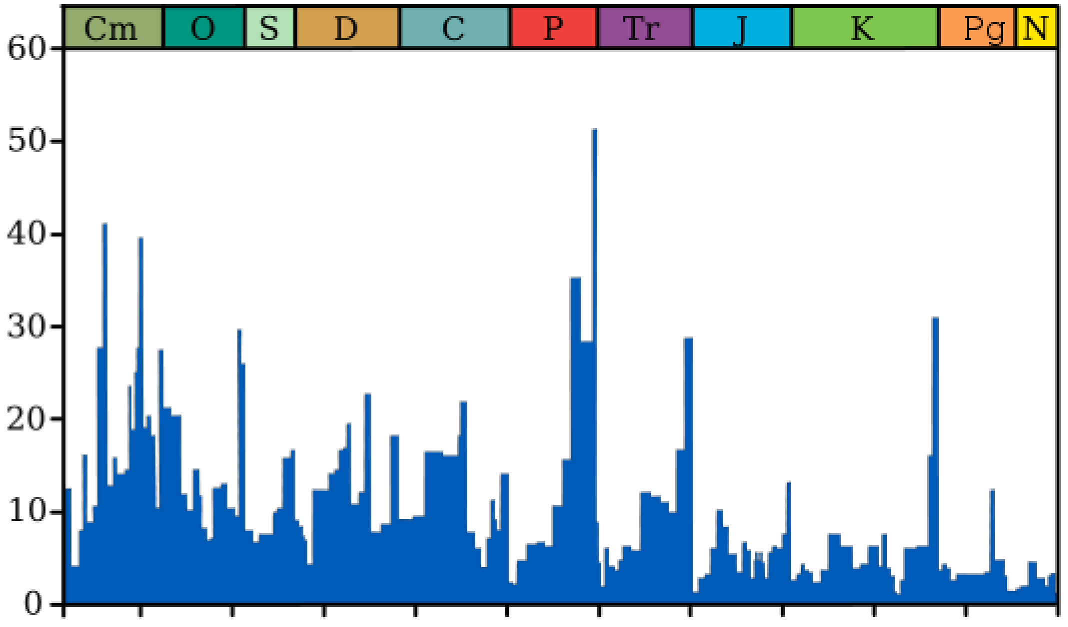
Non-avian dinosaur fossils are found only below the K–T boundary, indicating that non-avian dinosaurs became extinct immediately before, or during the event. A very small number of dinosaur fossils have been found above the K–T boundary, but they have been explained as *reworked*, that is, fossils that have been eroded from their original locations then preserved in later sedimentary layers. Mosasaurs, plesiosaurs, pterosaurs and many species of plants and invertebrates also became extinct. Mammalian and bird clades passed through the boundary with few extinctions, and evolutionary radiation from those Maastrichtian clades occurred well past the boundary. Rates of extinction and radiation varied across different clades of organisms.

Scientists theorize that the K–T extinctions were caused by one or more catastrophic events, such as massive asteroid impacts (like the Chicxulub impact), or increased volcanic activity. Several impact craters and massive volcanic activity, such as that in the Deccan traps, have been dated to the approximate time of the extinction event. These geological events may have reduced sunlight and hindered photosynthesis, leading to a massive disruption in Earth's ecology. Other researchers believe the extinction was more gradual, resulting from slower changes in sea level or climate. On March 4, 2010, a panel of 41 scientists agreed that the Chicxulub asteroid impact triggered the mass extinction.

Extinction patterns



K–T
Tr–J
P–Tr
Late D
O–S
Millions of years ago



Marine extinction intensity through time. The blue graph shows the apparent *percentage* (not the absolute number) of marine animal genera becoming extinct during any given time interval. It does not represent all marine species, just those that are readily fossilized.

Even though the boundary event was severe, there was significant variability in the rate of extinction between and within different clades. Species that depended on photosynthesis declined or became extinct as atmospheric particles blocked sunlight and reduced the solar energy reaching the Earth's surface. This plant extinction caused a major reshuffling of the dominant plant groups. Photosynthesizing organisms, including phytoplankton and land plants, formed the foundation of the food chain in the late Cretaceous as they do today. Evidence suggests that herbivorous animals died out when the plants on which they depended for food became scarce. Consequently, top predators such as *Tyrannosaurus rex* also perished.

Coccolithophorids and molluscs (including ammonites, rudists, freshwater snails and mussels, and those organisms whose food chain included these shell builders) became extinct or suffered heavy losses. For example, it is thought that ammonites were the principal food of mosasaurs, a group of giant marine reptiles that became extinct at the boundary.

Omnivores, insectivores and carrion-eaters survived the extinction event, perhaps because of the increased availability of their food sources. At the end of the Cretaceous there seem to have been no purely herbivorous or carnivorous mammals. Mammals and birds that survived the extinction fed on insects, worms, and snails, which in turn fed on dead plant and animal matter. Scientists hypothesize that these organisms survived the collapse of plant-based food chains because they fed on detritus (non-living organic material).

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After the K–T event, biodiversity required substantial time to recover, despite the existence of abundant vacant ecological niches.

Microbiota

The K–T boundary represents one of the most dramatic turnovers in the fossil record for various calcareous nanoplankton that formed the calcium deposits that gave the Cretaceous its name. The turnover in this group is clearly marked at the species level. Statistical analysis of marine losses at this time suggests that the decrease in diversity was caused more by a sharp increase in extinctions than by a decrease in speciation. The K–T boundary record of dinoflagellates is not as well-understood, mainly because only microbial cysts provide a fossil record, and not all dinoflagellate species have cyst-forming stages, thereby likely causing diversity to be underestimated. Recent studies indicate that there were no major shifts in dinoflagellates through the boundary layer.

Radiolaria have left a geological record since at least the Ordovician times, and their mineral fossil skeletons can be tracked across the K–T boundary. There is no evidence of mass extinction of these organisms, and there is support for high productivity of these species in Southern high latitudes as a result of cooling temperatures in the early Paleocene. Approximately 46% of diatom species survived the transition from the Cretaceous to the Upper Paleocene. This suggests a significant turnover in species, but not a catastrophic extinction of diatoms, across the K–T boundary.

The occurrence of planktonic foraminifera across the K–T boundary has been studied since the 1930s. Research spurred by the possibility of an impact event at the K–T boundary resulted in numerous publications detailing planktonic foraminiferal extinction at the boundary. However, there is debate ongoing between groups that believe the evidence indicates substantial extinction of these species at the K–T boundary, and those who believe the evidence supports multiple extinctions and expansions through the boundary.

Numerous species of benthic foraminifera became extinct during the K–T event, presumably because they depend on organic debris for nutrients, since the biomass in the ocean is thought to have decreased. However, as the marine microbiota recovered, it is thought that increased speciation of benthic foraminifera resulted from the increase in food sources. Phytoplankton recovery in the early Paleocene provided the food source to support large benthic foraminiferal assemblages, which are mainly detritus-feeding. Ultimate recovery of the benthic populations occurred over several stages lasting several hundred thousand years into the early Paleocene.

Marine invertebrates

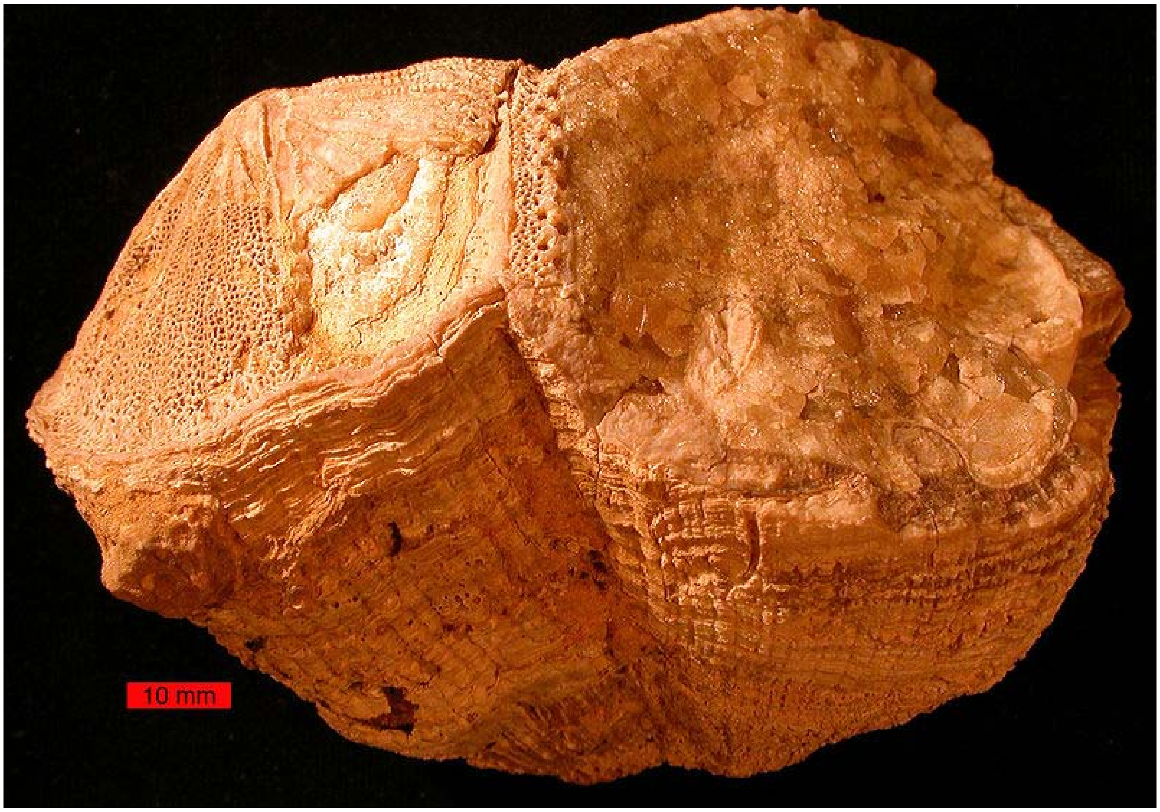
An ammonite fossil

There is variability in the fossil record as to the extinction rate of marine invertebrates across the K–T boundary. The apparent rate is influenced by the lack of fossil records rather than actual extinction.

Ostracodes, a class of small crustaceans that were prevalent in the upper Maastrichtian, left fossil deposits in a variety of locations. A review of these fossils shows that ostracode diversity was lower in the Paleocene than any other time in the Tertiary. However, current research cannot ascertain whether the extinctions occurred prior to or during the boundary interval itself.

Approximately 60% of late-Cretaceous Scleractinia coral genera failed to cross the K–T boundary into the Paleocene. Further analysis of the coral extinctions shows that approximately 98% of colonial species, ones that inhabit warm, shallow tropical waters, became extinct. The solitary corals, which generally do not form reefs and inhabit colder and deeper (below the photic zone) areas of the ocean were less impacted by the K–T boundary. Colonial coral species rely upon symbiosis with photosynthetic algae, which collapsed due to the events surrounding the K–T boundary. However, the use of data from coral fossils to support K–T extinction and subsequent Paleocene recovery must be weighed against the changes that occurred in coral ecosystems through the K–T boundary.

The numbers of cephalopod, echinoderm, and bivalve genera exhibited significant diminution after the K–T boundary. Most species of brachiopods, a small phylum of marine invertebrates, survived the K–T event and diversified during the early Paleocene.



Rudist bivalves from the Late Cretaceous of the Omani Mountains, United Arab Emirates. Scale bar is 10 mm.

Except for nautiloids (represented by the modern order Nautilida) and coleoids (which had already diverged into modern octopodes, squids, and cuttlefish) all other species of the molluscan class Cephalopoda became extinct at the K–T boundary. These included the ecologically significant belemnoids, as well as the ammonoids, a group of highly diverse, numerous, and widely distributed shelled cephalopods. Researchers have pointed out that the reproductive strategy of the surviving nautiloids, which rely upon few and larger eggs, played a role in outsurviving their ammonoid counterparts through the extinction event. The ammonoids utilized a planktonic strategy of reproduction (numerous eggs and planktonic larvae), which would have been devastated by the K–T boundary event. Additional research has shown that subsequent to this elimination of ammonoids from the global biota, nautiloids began an evolutionary radiation into shell shapes and complexities theretofore known only from ammonoids.

Approximately 35% of echinoderm genera became extinct at the K–T boundary, although taxa that thrived in low-latitude, shallow-water environments during late Cretaceous had the highest extinction rate. Mid-latitude, deep-water echinoderms were much less affected at the K–T boundary. The pattern of extinction points to habitat loss, specifically the drowning of carbonate platforms, the shallow-water reefs in existence at that time, by the extinction event.

Other invertebrate groups, including rudists (reef-building clams) and inoceramids (giant relatives of modern scallops), also became extinct at the K–T boundary.

Fish

There are substantial fossil records of jawed fishes across the K–T boundary, which provides good evidence of extinction patterns of these classes of marine vertebrates. Within cartilaginous fish, approximately 80% of the sharks, rays, and skates families survived the extinction event, and more than 90% of teleost fish (bony fish) families survived. There is evidence of a mass kill of bony fishes at a fossil site immediately above the K–T boundary layer on Seymour Island near Antarctica, apparently precipitated by the K–T boundary event. However, the marine and freshwater environments of fishes mitigated environmental effects of the extinction event.

Terrestrial invertebrates

Insect damage to the fossilized leaves of flowering plants from fourteen sites in North America were used as a proxy for insect diversity across the K–T boundary and analyzed to determine the rate of extinction. Researchers found that Cretaceous sites, prior to the extinction event, had rich plant and insect-feeding diversity. However, during the early Paleocene, flora were relatively diverse with little predation from insects, even 1.7 million years after the extinction event.

Terrestrial plants

There is overwhelming evidence of global disruption of plant communities at the K–T boundary. However, there were important regional differences in plant succession. In North America, the data suggest massive devastation and mass extinction of plants at the K–T boundary sections, although there were substantial megafloral changes before the boundary.

In high southern hemisphere latitudes, such as New Zealand and Antarctica the mass die-off of flora caused no significant turnover in species, but dramatic and short-term changes in the relative abundance of plant groups. In North America, approximately 57% of plant species became extinct. The Paleocene recovery of plants began with recolonizations by fern species, represented as a fern spike in the geologic record; this same type of fern recolonization was observed after the 1980 Mount St. Helens eruption.

Due to the wholesale destruction of plants at the K–T boundary there was a proliferation of saprotrophic organisms such as fungi that do not require photosynthesis and use nutrients from decaying vegetation. The dominance of fungal species lasted only a few years while the atmosphere cleared and there was plenty of organic matter to feed on. Once the atmosphere cleared, photosynthetic organisms like ferns and other plants returned. Polyploidy appears to have enhanced the ability of flowering plants to survive the extinction, probably because the additional copies of the genome such plants possessed allowed them to more readily adapt to the rapidly changing environmental conditions which followed the impact.

Amphibians

There is no evidence of K–T boundary mass extinctions of amphibians, and there is strong evidence that most amphibians survived the event relatively unscathed. Several in-depth studies of salamander genera in fossil beds in Montana show that six of seven genera were unchanged after the event.

Frog species appear to have survived into the Paleocene with few species becoming extinct. However, the fossil record for frog families and genera is uneven. An extensive survey of three genera of frogs in Montana show that they were unaffected by the K–T event and survived apparently unchanged. The data show little or no evidence for extinction of amphibian families that bracket the K–T event. Amphibian survival resulted from the clade's ability to seek shelter in water or to build burrows in sediments, soil, wood, or beneath rocks.

Non-archosaur reptiles

The two living non-archosaurian reptile taxa, testudines (turtles) and lepidosaurs (snakes, lizards, and worm lizards), along with choristoderes (semi-aquatic archosauromorphs which died out in the early Miocene), survived through the K–T boundary. Over 80% of Cretaceous turtle species passed through the K–T boundary. Additionally, all six turtle families in existence at the end of the Cretaceous survived into the Tertiary and are represented by current species.

Living lepidosaurs include Rhynchocephalia (tuataras) and Squamata. The Rhynchocephalia were a widespread and relatively successful group of lepidosaurs in the early Mesozoic, but began to decline by the mid-Cretaceous. They are represented today by a single genus located exclusively in New Zealand.

The order Squamata, which is represented today by lizards, snakes, and amphisbaenia, radiated into various ecological niches during the Jurassic and were successful throughout the Cretaceous. They survived through the K–T boundary and are currently the most successful and diverse group of living reptiles with more than 6,000 extant species. No known family of terrestrial squamates became extinct at the boundary, and fossil evidence indicates they did not suffer any significant decline in numbers. Their small size, adaptable metabolism, and ability to move to more favorable habitats were key factors in their survivability during the late Cretaceous and early Paleocene.

Non-archosaurian marine reptiles including mosasaurs and plesiosaurs, giant aquatic reptiles that were the top marine predators, became extinct by the end of the Cretaceous.

Archosaurs

The archosaur clade includes two living orders, crocodilians (of which Alligatoridae, Crocodylidae and Gavialidae are the only surviving families) and dinosaurs (of which birds are the sole surviving members), along with the extinct non-avian dinosaurs and pterosaurs.

Crocodyliforms

Ten families of crocodilians or their close relatives are represented in the Maastrichtian fossil records, of which five died out prior to the K–T boundary. Five families have both Maastrichtian and Paleocene fossil representatives. All of the surviving families of crocodyliforms inhabited freshwater and terrestrial environments, except for the Dyrosauridae which lived in freshwater and marine locations. Approximately 50% of crocodyliform representatives survived across the K–T boundary, the only apparent trend being that no large crocodiles survived. Crocodyliform survivability across the boundary may have resulted from their aquatic niche and ability to burrow, which reduced susceptibility to negative environmental effects at the boundary. Jouve and colleagues suggested in 2008 that juvenile marine crocodyliforms lived in freshwater environments like modern marine crocodile juveniles, which would have helped them survive where other marine reptiles became extinct; freshwater environments were not as strongly affected by the K–T event as marine environments.

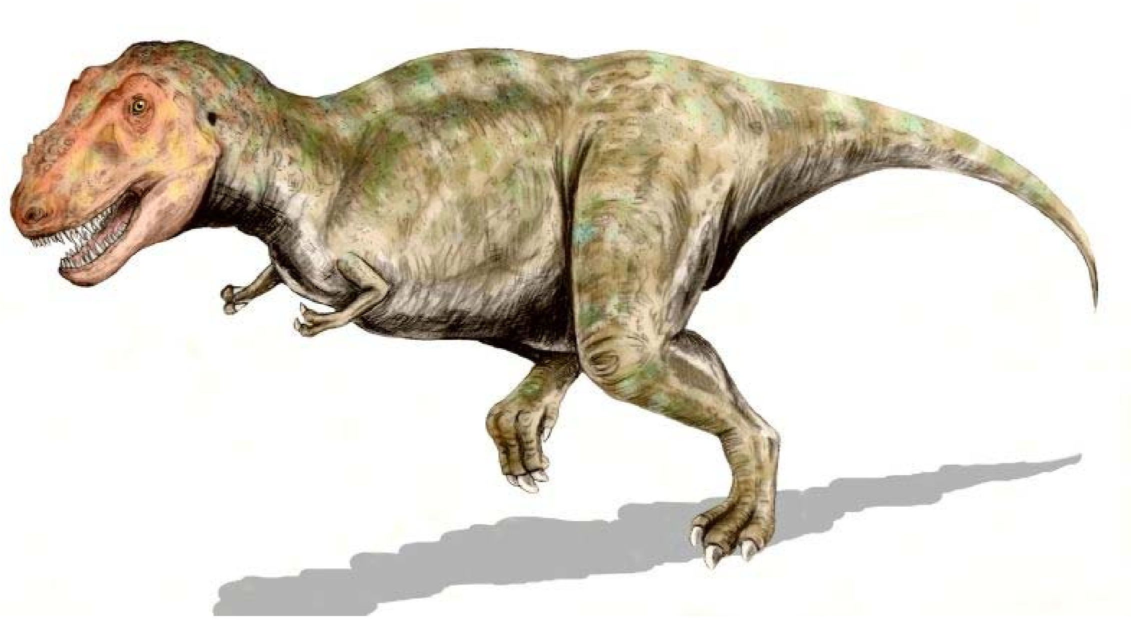
Pterosaurs

Only one family of pterosaurs, Azhdarchidae, was definitely present in the Maastrichtian, and it became extinct at the K–T boundary. These large pterosaurs were the last representatives of a declining group that contained 10 families during the mid-Cretaceous. Smaller pterosaurs became extinct prior to the Maastrichtian during a period that saw a decline in smaller animal species while larger species became more prevalent. While this was occurring, modern birds were undergoing diversification and replacing archaic birds and pterosaur groups, possibly due to direct competition, or they simply filled empty niches.

Avian dinosaurs (birds)

Most paleontologists regard birds as the only surviving dinosaurs. However, all non-neornithean birds became extinct, including flourishing groups like enantiornithines and hesperornithiforms. Several analyses of bird fossils show divergence of species prior to the K–T boundary, and that duck, chicken and ratite bird relatives coexisted with non-avian dinosaurs. Neornithine birds survived the K–T boundary as a result of their abilities to dive, swim, or seek shelter in water and marshlands. Many species of birds can build burrows, or nest in tree holes or termite nests, all of which provided shelter from the environmental effects at the K–T boundary. Long-term survival past the boundary was assured as a result of filling ecological niches left empty by extinction of non-avian dinosaurs.

Non-avian dinosaurs

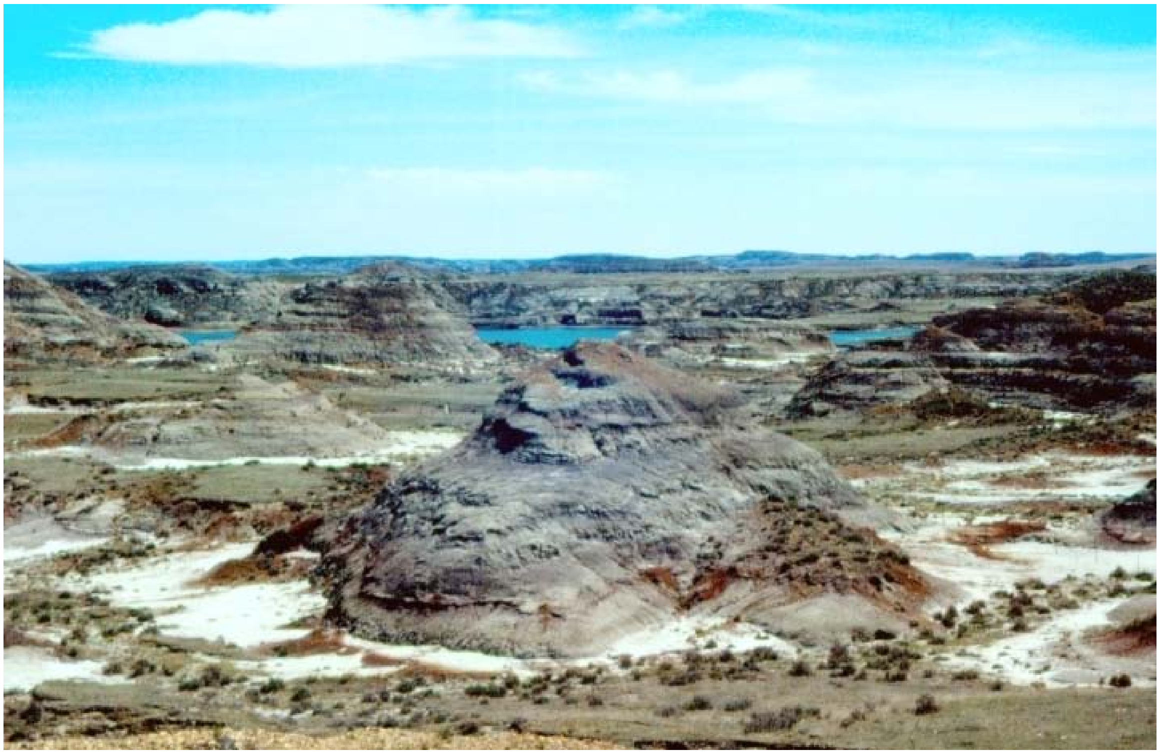


Tyrannosaurus was one of the last dinosaurs to thrive on Earth before the extinction

Excluding a few controversial claims, scientists agree that all non-avian dinosaurs became extinct at the K–T boundary. The dinosaur fossil record has been interpreted to show both a decline in diversity and no decline in diversity during the last few million years of the Cretaceous, and it may be that the quality of the dinosaur fossil record is simply not good enough to permit researchers to distinguish between the options. Since there is no evidence that late Maastrichtian nonavian dinosaurs could burrow, swim or dive, they were unable to shelter themselves from the worst parts of any environmental stress that occurred at the K–T boundary. It is possible that small dinosaurs (other than birds) did survive, but they would have been deprived of food as both herbivorous dinosaurs would have found plant material scarce, and carnivores would have quickly found prey to be in short supply. The growing consensus about the endothermy of dinosaurs helps to understand their full extinction in contrast with their close relatives, the crocodilians. Ectothermic ("cold-blooded") crocodiles have very limited needs for food (they can survive several months without eating) while endothermic ("warm-blooded") animals of similar size need much more food in order to sustain their faster metabolism. Thus, under the circumstances of food chain disruption previously mentioned, non-avian dinosaurs died while some crocodiles survived. In this context, the survival of other endothermic animals, such as some birds and mammals, could be due, among other reasons, to their smaller needs for food, related to their small size at the extinction epoch.

Whether the extinction occurred gradually or very suddenly is debatable, as both views have support in the fossil record. A study of 29 fossil sites in Catalan Pyrenees of Europe in 2010 support that dinosaurs there had great diversity until the proposed asteroid impact. Others have interpreted the fossil bearing rocks along Red Deer River in Alberta, Canada, as supporting a gradual extinction of non-avian dinosaurs; during the last 10 million years of the Cretaceous layers there, the number of dinosaur species seems to have decreased from about 45 to about 12. Other scientists have pointed out the same.

Several researchers have argued for Paleocene dinosaurs. These arguments are based on the discovery of dinosaur remains in the Hell Creek Formation up to 1.3 metres (4 ft 3 in) above and 40,000 years later than the K–T boundary. Pollen samples recovered near a fossilized hadrosaur femur recovered in the Ojo Alamo Sandstone at the San Juan River indicate that the animal lived during the Tertiary, approximately 64.5 Ma (about 1 million years after the K–T event). If their existence past the K–T boundary can be confirmed, these hadrosaurids would be considered a Dead Clade Walking. Current research indicates that these fossils were eroded from their original locations and then re-buried in much later sediments (reworked).



Hell Creek formation

Mammals

All major Cretaceous mammalian lineages, including monotremes (egg-laying mammals), multituberculates, marsupials and placentals, dryolestoideans, and gondwanatheres survived the K–T event, although they suffered losses. In particular, marsupials largely disappeared from North America, and the Asian deltatheroidans, primitive relatives of extant marsupials, became extinct. In the Hell Creek beds of North America, at least half of the ten known multituberculate species and all eleven marsupial species are not found above the boundary.

Mammalian species began diversifying approximately 30 million years prior to the K–T boundary. Diversification of mammals stalled across the boundary. Current research indicates that mammals did not explosively diversify across the K–T boundary, despite the environment niches made available by the extinction of dinosaurs. Several mammalian orders have been interpreted as diversifying immediately after the K–T boundary, including Chiroptera (bats) and Cetartiodactyla (a diverse group that today includes whales and dolphins and even-toed ungulates), although recent research concludes that only marsupial orders diversified after the K–T boundary.

K–T boundary mammalian species were generally small, comparable in size to rats; this small size would have helped them to find shelter in protected environments. In addition, it is postulated that some early monotremes, marsupials, and placentals were semiaquatic or burrowing, as there are multiple mammalian lineages with such habits today. Any burrowing or semiaquatic mammal would have had additional protection from K–T boundary environmental stresses.

Evidence

North American fossils

In North American terrestrial sequences, the extinction event is best represented by the marked discrepancy between the rich and relatively abundant late-Maastrichtian palynomorph record and the post-boundary fern spike.

At present the most informative sequence of dinosaur-bearing rocks in the world from the K–T boundary is found in western North America, particularly the late Maastrichtian-age Hell Creek Formation of Montana, US. This formation, when compared with the older (approximately 75 Ma) Judith River/Dinosaur Park Formations (from Montana and Alberta, Canada, respectively) provides information on the changes in dinosaur populations over the last 10 million years of the Cretaceous. These fossil beds are geographically limited, covering only part of one continent.

The middle–late Campanian formations show a greater diversity of dinosaurs than any other single group of rocks. The late Maastrichtian rocks contain the largest members of several major clades: *Tyrannosaurus*, *Ankylosaurus*, *Pachycephalosaurus*, *Triceratops* and *Torosaurus*, which suggests food was plentiful immediately prior to the extinction.

In addition to rich dinosaur fossils, there are also plant fossils that illustrate the reduction in plant species across the K–T boundary. In the sediments below the K–T boundary the dominant plant remains are angiosperm pollen grains, but the actual boundary layer contains little pollen and is dominated by fern spores. Normal pollen levels gradually resume above the boundary layer. This is reminiscent of areas blighted by modern volcanic eruptions, where the recovery is led by ferns which are later replaced by larger angiosperm plants.

Marine fossils

The mass extinction of marine plankton appears to have been abrupt and right at the K–T boundary.¯ Ammonite genera became extinct at or near the K–T boundary; however, there was a smaller and slower extinction of ammonite genera prior to the boundary that was associated with a late Cretaceous marine regression. The gradual extinction of most inoceramid bivalves began well before the K–T boundary, and a small, gradual reduction in ammonite diversity occurred throughout the very late Cretaceous. Further analysis shows that several processes were in progress in the late Cretaceous seas and partially overlapped in time, then ended with the abrupt mass extinction.

Duration

The length of time taken for the extinction to occur is a controversial issue, because some theories about the extinction's causes require a rapid extinction over a relatively short period (from a few years to a few thousand years) while others require longer periods. The issue is difficult to resolve because of the Signor-Lipps effect; that is, the fossil record is so incomplete that most extinct species probably died out long after the most recent fossil that has been found. Scientists have also found very few continuous beds of fossil-bearing rock which cover a time range from several million years before the K–T extinction to a few million years after it.

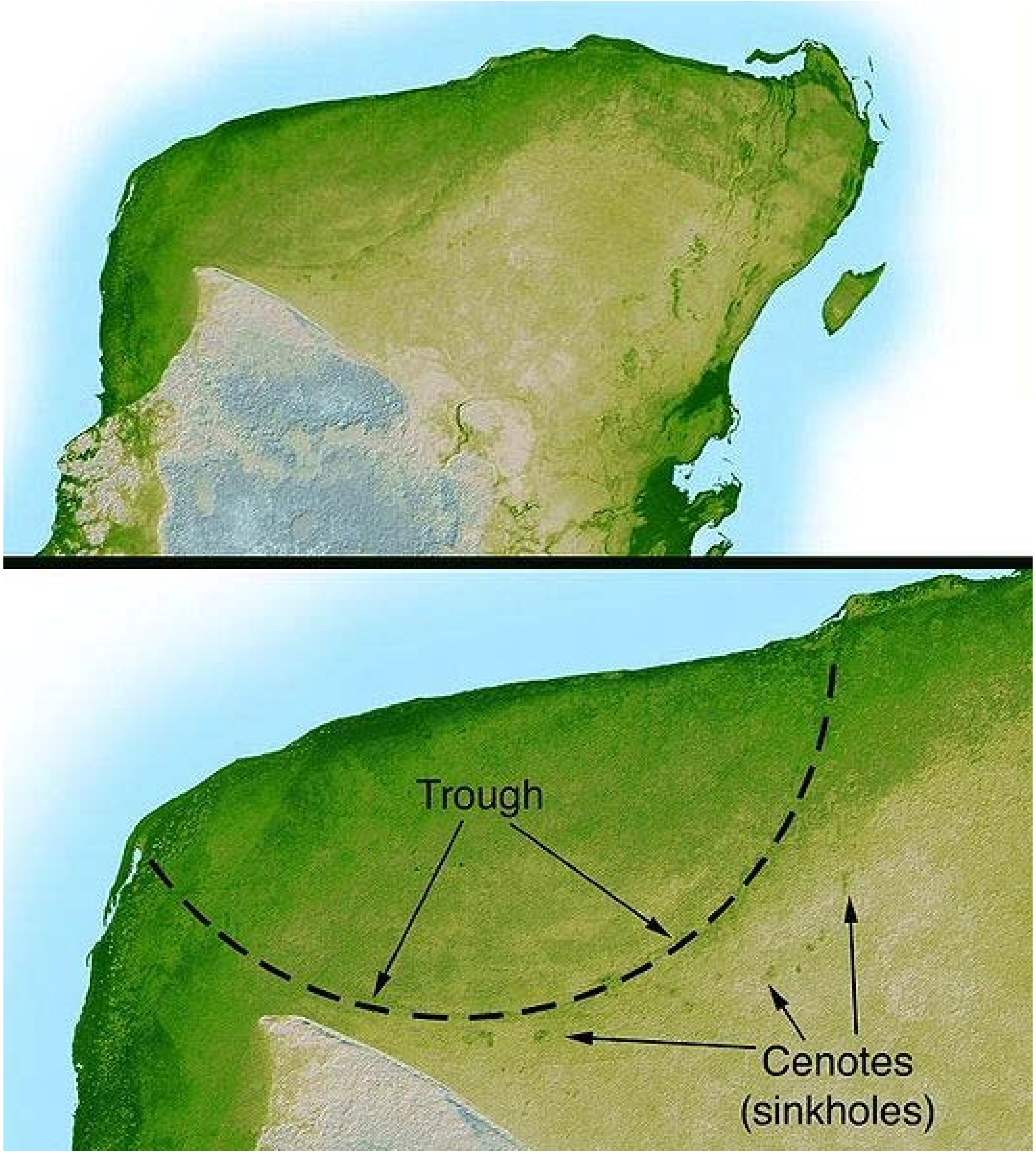
Causes of extinctions

There have been several theories on the cause of the K–T boundary which led to the massive extinction. These theories have centered on either impact events or increased volcanism; some include elements of both.

Impact event

The K–T boundary exposure in Trinidad Lake State Park, in the Raton Basin of Colorado, shows an abrupt change from dark- to light-colored rock.

White line added to mark the transition.



Radar topography reveals the 180 km (112 mi) wide ring of the Chicxulub Crater.

In 1980, a team of researchers consisting of Nobel prize-winning physicist Luis Alvarez, his son geologist Walter Alvarez, and chemists Frank Asaro and Helen Michel discovered that sedimentary layers found all over the world at the Cretaceous–Tertiary boundary contain a concentration of iridium many times greater than normal (30 times and 130 times background in the two sections originally studied). Iridium is extremely rare in the earth's crust because it is a siderophile, and therefore most of it travelled with the iron as it sank into the earth's core during planetary differentiation. As iridium remains abundant in most asteroids and comets, the Alvarez team suggested that an asteroid struck the earth at the time of the K–T boundary. There were other earlier speculations on the possibility of an impact event, but this was the first evidence uncovered.

Such an impact would have inhibited photosynthesis by generating a dust cloud, which would block sunlight for a year or less, and by injecting sulfuric acid aerosols into the stratosphere, which would reduce sunlight reaching the Earth's surface by 10–20%. It would take at least ten years for those aerosols to dissipate, which would account for the extinction of plants and phytoplankton, and of organisms dependent on them (including predatory animals as well as herbivores). Small creatures whose food chains were based on detritus would have a reasonable chance of survival.‐ The consequences of reentry of ejecta into Earth's atmosphere would include a brief (hours long) but intense pulse of infrared radiation, killing exposed organisms. Global firestorms may have resulted from the heat pulse and the fall back to Earth of incendiary fragments from the blast. High O_2 levels during the late Cretaceous would have supported intense combustion. The level of atmospheric O_2 plummeted in the early Tertiary Period. If widespread fires occurred, they would have increased the CO_2 content of the atmosphere and caused a temporary greenhouse effect once the dust cloud settled, and this would have exterminated the most vulnerable organisms that survived the period immediately after the impact.

The impact may also have produced acid rain, depending on what type of rock the asteroid struck. However, recent research suggests this effect was relatively minor, lasting for approximately 12 years.‐ The acidity was neutralized by the environment, and the survival of animals vulnerable to acid rain effects (such as frogs) indicate this was not a major contributor to extinction. Impact theories can only explain very rapid extinctions, since the dust clouds and possible sulfuric aerosols would wash out of the atmosphere in a fairly short time—possibly under ten years.

Subsequent research identified the Chicxulub Crater buried under Chicxulub on the coast of Yucatán, Mexico as the impact crater which matched the Alvarez hypothesis dating. Identified in 1990 based on the work of Glen Penfield done in 1978, this crater is oval, with an average diameter of about 180 kilometers (112 mi), about the size calculated by the Alvarez team. The shape and location of the crater indicate further causes of devastation in addition to the dust cloud. The asteroid landed in the ocean and would have caused megatsunamis, for which evidence has been found in several locations in the Caribbean and eastern United States—marine sand in locations which were then inland, and vegetation debris and terrestrial rocks in marine sediments dated to the time of the impact. The asteroid landed in a bed of gypsum (calcium sulfate), which would have produced a vast sulfur dioxide aerosol. This would have further reduced the sunlight reaching the Earth's surface and then precipitated as acid rain, killing vegetation, plankton and organisms which build shells from calcium carbonate (coccolithophores and molluscs). In February 2008, a team of researchers used seismic images of the crater to determine that the impactor landed in deeper water than was previously assumed. They argued that this would have resulted in increased sulfate aerosols in the atmosphere, which could have made the impact deadlier by altering climate and by generating acid rain.

Most paleontologists now agree that an asteroid did hit the Earth about 65 Ma ago, but there is an ongoing dispute whether the impact was the sole cause of the extinctions. There is evidence that there was an interval of about 300 ka from the impact to the mass extinction. In 1997, paleontologist Sankar Chatterjee drew attention to the proposed and much larger 600 km (373 mi) Shiva crater and the possibility of a multiple-impact scenario.

In 2007, a hypothesis was put forth that argued the impactor that killed the dinosaurs 65 Ma ago belonged to the Baptistina family of asteroids. Concerns have been raised regarding the reputed link, in part because very few solid observational constraints exist of the asteroid or family. Indeed, it was recently discovered that 298 Baptistina does not share the same chemical signature as the source of the K–T impact. Although this finding may make the link between the Baptistina family and K–T impactor more difficult to substantiate, it does not preclude the possibility.

In March 2010 an international panel of scientists endorsed the asteroid hypothesis, specifically the Chicxulub impact, as being the cause of the extinction. A team of 41 scientists reviewed 20 years of scientific literature and in so doing also ruled out other theories such as massive volcanism. They had determined that a 10–15 km (6–9 mi) space rock hurtled into earth at Chicxulub on Mexico's Yucatan Peninsula. The collision would have released the same energy as 100,000 gigatonnes of TNT or 420,000 EJ or over a billion times the energy of the bombs dropped on Nagasaki and Hiroshima.

Deccan Traps

Before 2000, arguments that the Deccan Traps flood basalts caused the extinction were usually linked to the view that the extinction was gradual, as the flood basalt events were thought to have started around 68 Ma and lasted for over 2 million years. The most recent evidence shows that the traps erupted over 800,000 years spanning the K–T boundary, and therefore may be responsible for the extinction and the delayed biotic recovery thereafter.

The Deccan Traps could have caused extinction through several mechanisms, including the release of dust and sulfuric aerosols into the air which might have blocked sunlight and thereby reduced photosynthesis in plants. In addition, Deccan Trap volcanism might have resulted in carbon dioxide emissions which would have increased the greenhouse effect when the dust and aerosols cleared from the atmosphere.

In the years when the Deccan Traps hypothesis was linked to a slower extinction, Luis Alvarez (who died in 1988) replied that paleontologists were being misled by sparse data. While his assertion was not initially well-received, later intensive field studies of fossil beds lent weight to his claim. Eventually, most paleontologists began to accept the idea that the mass extinctions at the end of the Cretaceous were largely or at least partly due to a massive Earth impact. However, even Walter Alvarez has acknowledged that there were other major changes on Earth even before the impact, such as a drop in sea level and massive volcanic eruptions that produced the Indian Deccan Traps, and these may have contributed to the extinctions.

Multiple impact event

Several other craters also appear to have been formed about the time of the K–T boundary. This suggests the possibility of near simultaneous multiple impacts, perhaps from a fragmented asteroidal object, similar to the Shoemaker-Levy 9 cometary impact with Jupiter. In addition to the 180-km (112 mi) Chicxulub Crater, there is the 24-km (15 mi) Boltysh crater in Ukraine (65.17 ± 0.64 Ma), the 20-km (12 mi) Silverpit crater, a suspected impact crater in the North Sea (60–65 Ma), and the controversial and much bigger 600-km (370 mi) Shiva crater. Any other craters that might have formed in the Tethys Ocean would have been obscured by tectonic events like the relentless northward drift of Africa and India.

Maastrichtian sea-level regression

There is clear evidence that sea levels fell in the final stage of the Cretaceous by more than at any other time in the Mesozoic era. In some Maastrichtian stage rock layers from various parts of the world, the later ones are terrestrial; earlier ones represent shorelines and the earliest represent seabeds. These layers do not show the tilting and distortion associated with mountain building, therefore, the likeliest explanation is a "regression", that is, a drop in sea level. There is no direct evidence for the cause of the regression, but the explanation which is currently accepted as the most likely is that the mid-ocean ridges became less active and therefore sank under their own weight.

A severe regression would have greatly reduced the continental shelf area, which is the most species-rich part of the sea, and therefore could have been enough to cause a *marine* mass extinction. However research concludes that this change would have been insufficient to cause the observed level of ammonite extinction. The regression would also have caused climate changes, partly by disrupting winds and ocean currents and partly by reducing the Earth's albedo and therefore increasing global temperatures.

Marine regression also resulted in the loss of epeiric seas, such as the Western Interior Seaway of North America. The loss of these seas greatly altered habitats, removing coastal plains that ten million years before had been host to diverse communities such as are found in rocks of the Dinosaur Park Formation. Another consequence was an expansion of freshwater environments, since continental runoff now had longer distances to travel before reaching oceans. While this change was favorable to freshwater vertebrates, those that prefer marine environments, such as sharks, suffered.

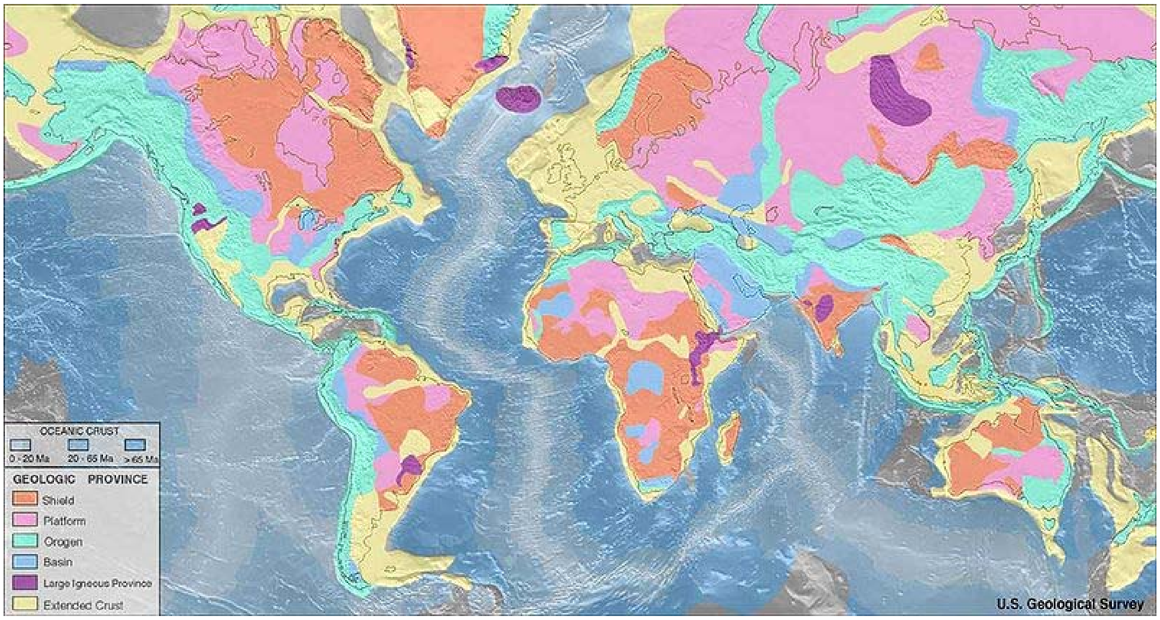
Multiple causes

In a review article, J. David Archibald and David E. Fastovsky discussed a scenario combining three major postulated causes: volcanism, marine regression, and extraterrestrial impact. In this scenario, terrestrial and marine communities were stressed by the changes in and loss of habitats. Dinosaurs, as the largest vertebrates, were the first to be affected by environmental changes, and their diversity declined. At the same time, particulate materials from volcanism cooled and dried areas of the globe. Then, an impact event occurred, causing collapses in photosynthesis-based food chains, both in the already-stressed terrestrial food chains and in the marine food chains. The major difference between this hypothesis and the single-cause hypotheses is that its proponents view the suggested single causes as either not sufficient in strength to cause the extinctions or not likely to produce the taxonomic pattern of the extinction.

Chapter- 3

Deccan Traps

The Deccan Traps as seen from Matheran, MH, India



The Deccan Traps shown as dark purple spot on the geographic map of India

Deccan Traps near Matheran, east of Mumbai

The Deccan Traps near Pune

The **Deccan Traps** are a large igneous province located on the Deccan Plateau of west-central India (between 17–24N, 73–74E) and one of the largest volcanic features on Earth. They consist of multiple layers of solidified flood basalt that together are more than 2,000 m (6,562 ft) thick and cover an area of 500,000 km^2 (193,051 sq mi) and a volume of 512,000 km^3 (123,000 cu mi). The term 'trap', used in geology for such rock formations, is derived from the Dutch word for stairs, referring to the step-like hills forming the landscape of the region.

History

The Deccan Traps formed between 60 and 68 million years ago, at the end of the Cretaceous period. The bulk of the volcanic eruption occurred at the Western Ghats (near Mumbai) some 66 million years ago. This series of eruptions may have lasted less than 30,000 years in total.

The original area covered by the lava flows is estimated to have been as large as 1.5 million km^2, approximately half the size of modern India. The Deccan Traps region was reduced to its current size by erosion and plate tectonics; the present area of directly observable lava flows is around 512,000 km^2 (197,684 sq mi).

Influence

The release of volcanic gases, particularly sulfur dioxide, during the formation of the traps contributed to contemporary climate change. Data point to an average fall in temperature of 2 °C in this period.

Due to the volcanic gases and subsequent temperature drop, the formation of the traps is seen as a major stressor on biodiversity at the time. This is confirmed by a mass extinction topping 17 families per million years (about 15 families per million years above the average). Sudden cooling due to sulfurous volcanic gases released by the formation of the traps and localised gas concentrations may have been enough to drive a less significant mass extinction, but the impact of the meteoroid that formed the Chicxulub Crater (which made a sunlight blocking dust cloud that killed much of the plants, called an impact winter) made this one of the most pronounced mass extinctions in the Phanerozoic.

Because of its magnitude, scientists formerly speculated that the gases released during the formation of the Deccan Traps played a role in the Cretaceous–Tertiary extinction event, which included the extinction of the non-avian dinosaurs. The current consensus among the scientific community is that the extinction was triggered by the Chicxulub impact event in Central America.

Chemical composition

Within the Deccan Traps at least 95% of the lavas are tholeiitic basalts, however other rock types occur:

- Alkali basalts
- Nephelinites
- Lamprophyre
- Carbonatites

Mantle xenoliths have been described from Kachchh (northwestern India) and elsewhere in the western Deccan.

Fossils

The Deccan Traps are famous for the beds of fossils that have been found between layers of traps lava. Particularly well known species include the frog *Oxyglossus pusillus* (Owen) of the Eocene of India and the toothed bufonid toad *Indobatrachus*, similar to Australian forms.

Theories of formation

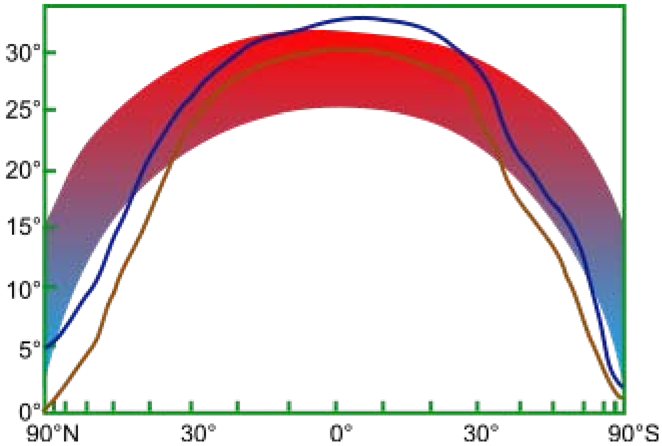
It is postulated that the Deccan Traps eruption was associated with a deep mantle plume. The area of long-term eruption (the hotspot), known as the Réunion hotspot, is suspected of both causing the Deccan Traps eruption and opening the rift that once separated the Seychelles plateau from India. Seafloor spreading at the boundary between the Indian and African Plates subsequently pushed India north over the plume, which now lies under Réunion island in the Indian Ocean, southwest of India. The mantle plume model has, however, been challenged.

Link to Shiva Crater

A large impact crater has been claimed to exist in the sea floor off the west coast of India. Called the Shiva crater, it has also been dated at sixty-five million years, right at the K–T boundary. The researchers suggest that the impact may have been the triggering event for the Deccan Traps as well as contributing to the acceleration of the Indian plate in the early Tertiary. However, opinion in the geologic community is not unanimous that this feature is actually an impact crater. Also, the reported age is in the middle of the ages given for the Deccan rocks.

Chapter- 4

Cool Tropics Paradox



The cool tropics paradox. The geological evidence appeared to constrain temperatures to the red/blue band, whereas models produced the brown line taking just continental configuration into account, and the blue line when they included increased atmospheric CO_2. Vertical axis: Temperature; horizontal:latitude.

The **cool tropics paradox** refers to an apparent difference between modelled estimates of tropical temperatures during warm, ice-free periods of the Cretaceous and Eocene, and the colder temperatures which proxies suggested were present. The long-standing paradox was resolved when it became clear that the proxies were misleading, meaning that tropics were warmer than previously believed.

Origin of the paradox

Proxy-based reconstructions of paleotemperature appeared to predict a low temperature gradient between the tropics and poles. Data from surface-dwelling foramanifera suggested that during the late Cretaceous, an unusually warm period, sea surface temperatures were cooler than today's. The term was later applied to similar situations, for example during the Eocene.

Climate models which worked during the Tertiary failed to produce this low temperature gradient; in order to match the observed data, they predicted that the tropics should be

40°C or more - much hotter than the proxies said they were. To attempt to match the data, bizarre models involving unreasonable eddies were required.

Models

Models were developed to predict and explain the lack of ice during the warm periods of the Cretaceous and Eocene. Models are developed according to the fundamental principle that they should be kept as simple as possible. Consequently, the first models attempted to explain the lack of ice using solely the different continental configuration. These could not produce an ice-free state without using an increased atmospheric concentration of CO_2; this assumption was checked against the evidence and found to be valid. This introduced a new difficulty: more CO_2 would produce warmer tropical sea temperatures, and the evidence suggested they were the same or even colder than today's.

Data supporting cool tropical oceans

Foramaniferal data, suggesting tropical temperatures cooler than today's, disagreed with terrestrial proxies, which spoke of warmer temperatures - although most of the terrestrial figures are based on extrapolation of data from outside the tropics.

Sources of error

Analytical error is around 2-3°C for individual specimens, but this drops to 0.5-1.0°C when a sample is analysed - not enough to explain the discrepancy. Other factors mean that any pristine sample can be considered to have an associated error of up to 3°C. Changes in salinity, kinetic and diagenesis, can also confound analysis: the latter two are each estimated to reduce estimated temperatures by 1-2°C, and are difficult to quantify.

Reconciling the data with the model

Taking the data to be true, how could they be reconciled with the predictions of the model? The only way the model could be "tweaked" was by fiddling with the parameterisation of clouds, one of the most unpredictable aspects of any model. The model was adjusted to assume that the higher CO_2 levels produced more tropical cloud, shielding these regions from the sun's heat. However, there was no evidence for this behaviour, and still left problems. The poles were still *warmer* than the models predicted. Further feedbacks, including increased poleward heat transport by the oceans, and vegetational responses at high latitudes, were proposed, but these didn't fully explain behaviour in the southern hemisphere, and winter, respectively.

Unravelling the paradox

Hints of warmth - terrestrial proxies

Data from terrestrial proxies suggested that the equator may have reached 30°C - however, this figure is based upon extrapolation of data found outside the tropics. This would imply that the foramaniferal proxies were wrong - the tests may perhaps have been overprinted by diagenesis. Researchers turned to shallow marine molluscs as it is easy to determine whether their shells had been altered by diagenesis.

Detecting diagenesis in molluscs

Many mollusc shells are constructed from aragonite, a mineral that is quickly replaced by calcite by diagenetic alteration. Also, near-shore molluscs preserve seasonal variability in their shells, a feature that would be lost in the presence of a diagenetic signal. This removes ambiguity about whether or not a shell has been affected by post-deposition processes.

Data from molluscs

Evidence from the molluscs suggested a cooling between the Eocene and Oligocene. Taken from the Mississippi embayment, they recorded temperatures of around 26°C in the Eocene, and 22°C in the Oligocene; this cooling was markedly seasonal, with reconstructed water temperatures being 5° cooler in the summer, but just 3° cooler in winter. This trend fits best if CO_2 was the dominant force for cooling.

The winter temperatures of molluscs match well with the foramaniferal temperatures, suggesting that foramanifera predominantly grew during the winter months. The overall temperatures corresponded well with terrestrial and modelled estimates of a sea surface temperature around 4-5° warmer than today's.

Reassessment of the foramaniferal record

The magnesium/calcium paleothermometer is a recently developed alternative to the $\delta^{18}O$ method, and avoids many of the uncertainties inherent in the latter method. Use of this technique generates results more consistent with those expected, in contrast to the original $\delta^{18}O$ records from the same sites. Further painstaking studies targeted solely those foramanifera which could be demonstrated not to have undergone any diagenesis in fact give a $\delta^{18}O$ signature similar to that expected, suggesting that poor preservation was responsible for the original confusion.

Chapter- 5

Cretaceous Geologic Formations

Cedar Mountain Formation

The **Cedar Mountain Formation** is the name given to distinctive sedimentary rocks in eastern Utah that occur between the underlying Morrison Formation and overlying Naturita Formation (sometimes incorrectly called the Dakota Formation). It is composed of non-marine sediments, that is, sediments deposited in rivers, lakes and on flood plains. Based on various fossils and radiometric dates, the Cedar Mountain Formation was deposited during the last half of the Early Cretaceous, about 127 - 98 million years ago (mya).

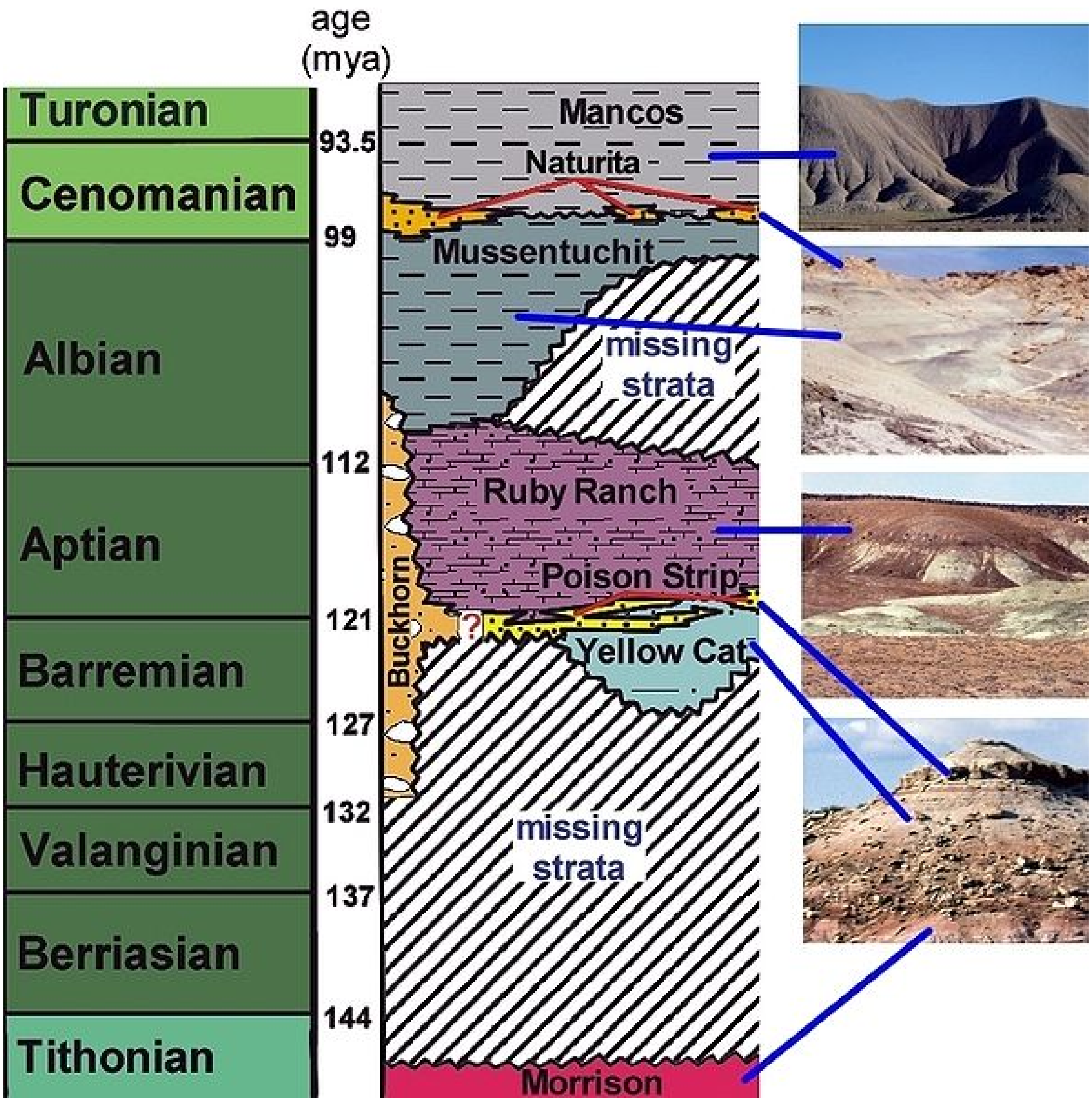
Dinosaurs occur throughout the formation, but their study has only occurred since the early 1990s. The dinosaurs in the lower part of the formation differ from those in the upper part. These two dinosaur assemblages, characterized by distinct dinosaurs, show the replacement of older, European-like dinosaurs with younger, Asian-like dinosaurs as the North American Continental Plate drifted westward. A middle dinosaur assemblage may be present, but the fossil record is not clear.

The formation was named for Cedar Mountain in northern Emery County, Utah, where William Lee Stokes first studied the exposures in 1944. Only recently did the 125 m (410 ft) thick formation get subdivided into smaller, distinctive beds called members. There is a debate as to whether there are five members or four depending whether the Buckhorn Conglomerate is considered to be at the top of the Morrison Formation or at the base of the Cedar Mountain Formation; most geologists and paleontologist consider it part of the Cedar Mountain Formation. In ascending order the remaining members are the Yellow Cat Member, Poison Strip Sandstone, Ruby Ranch Member, and the Mussentuchit Member. Each of these members are named after a geographic area where they were first studied.

The drab-colored lower portion of the Cedar Mountain Formation overlying the brighter Morrison Formation.

Stratigraphy

The Cedar Mountain Formation is sandwiched between the Morrison Formation below and the Naturita Formation and Mancos Shale above. The youngest date for Morrison just below the Cedar Mountain Formation is 148.1 ± 0.5 Ma . or lower Tithonian. Typically, the Jurassic-Cretaceous boundary in western North America is marked by an unconformity of variable length, and typically signifies 10-49 million years of missing geologic time. This boundary between the Morrison and Cedar Mountain is commonly marked by a horizon of carbonate nodules or by highly polished pebbles that are allegedly gastroliths.



Stratigraphic column showing the various members that make up the Cedar Mountain Formation and their approximate geologic age. Missing strata either were not deposited or were deposited, but later eroded

- The **Buckhorn Conglomerate** is considered the lowermost member of the Cedar Mountain Formation in the region of the San Raphael Swell by Stokes. It is named for exposures near Buckhorn Reservoir near Cedar Mountain. Its position immediately below the Ruby Ranch Member suggests that it may be equivalent to the channel sandstones in the Yellow Cat Member and the Poison Strip Sandstone farther to the east. This idea is strengthened by the similar composition of the gravels in these members, but a direct correlation has not yet been established.

- The **Yellow Cat Member** is named for exposures near the Yellow Cat mining area north of Arches National Park. It is limited to the eastern portions of the formation and is thickest near Arches National Monument. The member is composed of drab greyish mudstones and some lenses of sandstone. The mudstones were deposited on flood plains, and show evidence of ancient soil development called paleosols. The mudstones originated as flood deposits from river channels that are marked by the sandstone lenses. A recent radiometric date of 126 ± 2.5 Ma places Yellow Cat Member in the Barremian, which verifies previous estimates based on fossil evidence

- The **Poison Strip Sandstone** was named for prominent, cliff-forming sandstones in the Poison Strip uranium district north of Arches National Monument. It is actually a series of sandstones that were deposited in river channels, and lesser amounts of mudstones and limestones that were deposited on the flood plain and small ponds. Based on the position of the Poison Strip between the Yellow Cat and Ruby Ranch members, it probably was latest Barremian to earliest Aptian.

- The **Ruby Ranch Member** is the most widespread and distinctive member of the Cedar Mountain. It was named for exposures on the Ruby Ranch located southeast of Green River, Utah. The member is composed of maroon mudstones with irregular spheres of carbonate nodules. The nodules formed in ancient soils that developed in the mud deposited on the flood plain in a strongly seasonal, semiarid climate. Evaporation of groundwater during the dry season concentrated calcium carbonate and other minerals in the upper parts of the soil horizon. Radiometric dates place the upper portions of the Ruby Ranch in the late Aptian. Exhumed river channels in the Ruby Ranch indicate that stream flow during the Aptian was towards the northeast, the direction of the encrouching Western Interior Seaway.

- The **Mussentuchit Member** is the uppermost member of the Cedar Mountain Formation. It was named for exposures along Mussentuchit Wash southwest of the San Rafael Swell. It is predominantly composed of grey mudstones high in organic carbon from fossil plant material, as well as volcanic ash. The mudstones were originally deposited on a broad coastal plain with a high water table or with abundant rainfall. Thus, carbonate nodules are rare. A radiometric date of 98.37 ± 0.07 Ma places the upper part of the member in the Lower Cenomanian, while lower portions of the member have been dated to 104.46 ± 0.95 Ma, in the Albian stage.

- Although not part of the Cedar Mountain Formation, the **Naturita Formation** immediately overlies the Cedar Mountain and marks the encroaching Western Interior Seaway. The Naturita is not uniformly distributed and was eroded away in places by the advancing Seaway so that the marine shales of the Mancos Formation lay directly on the Mussentuchit or its equivalent. The name Dakota Formation has been improperly used for these strata.

Dinosaurs

The Cedar Mountain Formation is one of the last major dinosaur-bearing formations to be studied in the United States. Although sporadic bone fragments were known prior to 1990, serious research did not begin until that year. Since then, several organizations have conducted field work collecting dinosaurs, chiefly the Oklahoma Museum of Natural History, the Denver Museum of Nature & Science, the College of Eastern Utah, the Utah Geological Survey, Brigham Young University, and Dinosaur National Monument staff. This research indicates that at least two, possibly three dinosaur assemblages are contained within the formation.

Example of dinosaurs from the Cedar Mountain Formation include the polacanthid ankylosaur *Gastonia* from the Yellow Cat Member (upper left), *Utahraptor* from the Yellow Cat Member (upper right), a large theropod represented by a tooth from the Ruby Ranch Member (lower left), and *Tenontosaurus* from the base of the Mussentuchit (lower right).

The oldest of these assemblages is from the Yellow Cat, Poison Strip and basal Ruby Ranch members. The small, *Ornitholestes*-like theropod *Nedcolbertia* and the brachiosaurid sauropod *Cedarosaurus* may be considered as relics, with their closest relatives in the Morrison Formation. In contrast, the polacanthid ankylosaur *Gastonia* and a yet unnamed iguanodontid are similar to related forms from the Lower Cretaceous of southern England. These dinosaurs show that the connection between North America and Europe still existed during the Barremian. All of this changes, however, with the upper dinosaur assemblage from the top of the Ruby Ranch and Mussentuchit members. This upper assemblage shows greater similarities with Asian dinosaur assemblages from the same time. For example, the primitive ankylosaurid *Cedarpelta* is related to *Gobisaurus* and *Shamosaurus* from Mongolia, but is more primitive than either because it has teeth in the premaxilla. The upper assemblage also has a tyrannosaurid, a ceratopsian, and a pachycephalosaur. Although not a dinosaur, the primitive mammal *Gobiconodon* is known from both Mongolia and the Mussentuchit Member. Evidence for a middle dinosaur assemblage between the older and younger ones is controversial because the evidence mostly depends on a single specimen of the ornithopod *Tenontosaurus* from high in the Ruby Ranch Member and the sauropod *Astrodon* from low in the Ruby Ranch. Regardless, the upper and lower dinosaur assemblages in the Cedar Mountain Formation document the separation of North America and Europe, the westward drift of North America, and its connection with Asia 10 to 15 million years later.

Data from Carpenter (2006), Cifelli et al. (1999), Kirkland and Madsen (2007), and The Paleobiology Database.

Ornithischians

New genus and species of iguanodont present in the Ruby Ranch and Yellow Cat members. Indeterminate neoceratopsian present in the Mussentuchit Member. Indeterminate pachycephalosaurid present in the Mussentuchit Member.

Cloverly Formation

The **Cloverly Formation** are Lower Cretaceous strata located in Montana and Wyoming, in the western United States. The term now includes strata that had formerly been called the Dakota Formation in central and southern Wyoming.

Members

In the Bighorn Basin region along the Montana - Wyoming border, the Cloverly is divided into several members.

Brightly colored Himes Member of the Cloverly Formation near Shell, Wyoming. These Lower Cretaceous rocks have produced numerous dinosaurs.

- **Pryor Conglomerate** lies at the base and contains abundant black chert. It is named from thick beds exposed on the west side of the Pryor Mountains.
- The **Little Sheep Member** lies in the middle and is composed of pale-purple, gray to almost white, bentonitic mudstone. A radiometric date of 115 +/- 10 MA has been obtained from low in the member (Chen and Lubin 1997), and other near the top at 108.5 +/- 0.2 MA (Burton et al. 2006). These dates confirm that the Cloverly is Aptian-Albian in age.
- The uppermost member is the **Himes Member** contains some coarse grained channel deposits, but is primarily brightly, multicolored (variegated) mudstones.

Vertebrate fauna

Animals recovered include the dinosaurs *Deinonychus*, *Microvenator Tenontosaurus*, *Zephyrosaurus* and *Sauropelta* as well as fragmentary remains of Titanosaurs and Ornithomimids. As well, two genera of turtle *Naomichelys* and *Glyptops* and the lungfish *Ceratodus*.

Dinosaur eggs have been found in Montana.

References for data: Ostrom 1970; Cifelli et al. 1998; Cifelli 1999; Nydam and Cifelli 2002. Possible goniopholidid remains are known from the formation.

Fruitland Formation

The **Fruitland Formation** is a sedimentary geological formation containing layers of sandstone, shale, and coal. It was laid down in marshy delta conditions, with poor drainage and frequent flooding, under a warm, humid and seasonal climate. It is dated from the late Campanian (part of the Cretaceous period), and is found in the San Juan Basin in the states of New Mexico and Colorado, in the United States of America.

The Fruitland is underlain by the Pictured Cliffs Sandstone, and overlain by the more recent Kirtland Formation. The sequence of rocks represents the final filling of the Cretaceous seaway. The underlying Pictured Cliffs is a marginal marine sandstone, deposited in an environment similar to offshore barrier islands of the southeast United States. As the seaway retreated, the Pictured Cliffs was covered by the Fruitland Formation, which was deposited in near-shore swampy lowlands.

The Fruitland Formation contains beds of bituminous coal that are mined in places along the outcrop.

Since the 1980s, the coal beds of the Fruitland Formation have yielded large quantities of coalbed methane. The productive area for coalbed methane straddles the Colorado-New Mexico state line, and is one of the most productive areas for coalbed methane in the United States.

Laramie Formation

Typical exposure of the Laramie Formation in northeastern Colorado. Dinosaur bones have been found in the area.

The **Laramie Formation** is a geologic formation of Cretaceous age, named by Clarence King in 1876 for exposures in northeastern Colorado, in the United States.

The formation is exposed around the edges of the Denver Basin and ranges from 400–500 feet on the western side of the basin and 200–300 feet thick on the eastern side. The Laramie conformably overlies the Fox Hills Sandstone and unconformably underlies the Arapahoe Conglomerate. The formation can be divided into a lower unnamed member containing bedded sandstone, clay, and coal and an upper unnamed member composed predominately of 90 to 190 m of drab-colored mudstone, some sandstone, and thin coal beds. Nodular ironstone concretions occur in the mudstones that contain plant remains. The coal and clay were once economically important. The Laramie Formation was deposited on a coastal plain containing coastal swamp. Some of the material in the sandstones originated from silicic volcanoes far to the west.

Paleofauna

Skull of *Triceratops* from the Laramie Formation. This skull may be the oldest known for the genus. Currently on display at the courthouse in Greeley, Colorado

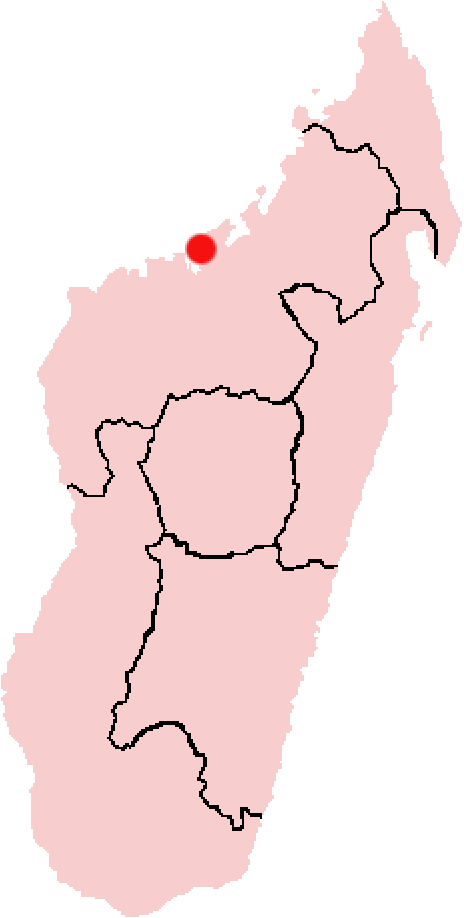
Fossil vertebrates from the Laramie Formation were among the first dinosaurs to be discovered in the American West (Carpenter and Young 2003). In 1873, Edward D. Cope accompanied Ferdinand V. Hayden, who was leader of the U.S. Geological and Geographical Survey of the Territories. The route of the expedition included eastern Colorado where Cope collected specimens in what is now the Laramie Formation along Bijou Creek on the east side of the Denver Basin (Cope, 1874).

Cope named three species of dinosaurs without description: *Cinodon arctatus* (later changed to *Cionodon arctatus*), *Polyonax mortuarius* and *Agathaumas milo* (later renamed *Hadrosaurus occidentalis*). These specimens are currently in the American Museum of Natural History. These specimens are very scrappy and the names no longer considered valid. Subsequent discoveries of dinosaurs occur through the formation, and include a nearly complete skull of *Triceratops*. Non-dinosaur vertebrates also occur (Carpenter 1979) .

Maevarano Formation

The **Maevarano Formation** is an Upper Cretaceous sedimentary rock formation found in the Mahajanga Province of northwestern Madagascar. It is most likely Maastrichtian in age, and records a seasonal, semiarid environment with rivers that had greatly varying discharges. Notable animal fossils recovered include the theropod dinosaur *Majungasaurus* and the early birds *Rahonavis* and *Vorona*, the titanosaurian sauropod *Rapetosaurus*, and the giant frog *Beelzebufo*.

Description



The Maevarano Formation outcrops in the Mahajanga Province of Madagascar, particularly within 50 kilometers (30 miles) southeast of the provincial capital, Mahajanga (marked with a red dot on the map).

The Maevarano Formation is well-exposed in the Mahajanga Basin, in particular near the village of Berivotra near the northwestern coast of the island where its outcrops have been heavily dissected by erosion. At the time it was being deposited, its latitude was between 30°S and 25°S as Madagascar drifted northward after splitting from India about 88 million years ago. It is composed of three smaller units or members. The lowest is the Masorobe Member, which is usually reddish and is at least 80 meters thick (262 ft). Its rocks are mostly poorly-sorted coarse-grained sandstones with some finer-grained beds. It is separated by an erosional disconformity from the next member, the Anembalemba Member. The lower portion of the Anembalemba Member is fine to coarse clay-rich sandstone, whitish or light grey in color, with cross-bedding. The upper portion of this member is made of poorly-sorted clay-rich sandstone, light olive-grey in color, that lacks cross-bedding. Most vertebrate fossils come from the Anembalemba Member, especially from the upper portion. The Miadana Member, the third and uppermost member, is not always present, and is up to 25 meters thick (82 ft); in some places. Elsewhere, it is replaced by the marine Berivotra Formation. The Miadana Member is made up of claystone, siltstone, and sandstone, lacks cross-bedding, and has several colors of rock. The Maevarano Formation as a whole is underlain by the Marovoay beds and capped by the Berivotra Formation.

The age of the Maevarano Formation has been debated; the Berivotra Formation, which is partially contemporaneous with the upper portions of the formation, shows that at least the upper part of the Maevarano is Maastrichtian in age. There is no evidence that it is Campanian, despite previous reports to that effect. The Berivotra Formation appears to include near its top a magnetic reversal, interpreted as the shift from Chron 30N to Chron 29R, which occurred approximately 65.8 million years ago (about 300 000 years before the K–T boundary and associated Cretaceous–Tertiary extinction event. This suggests that Maevarano organisms also lived shortly before (geologically speaking) the extinction event.

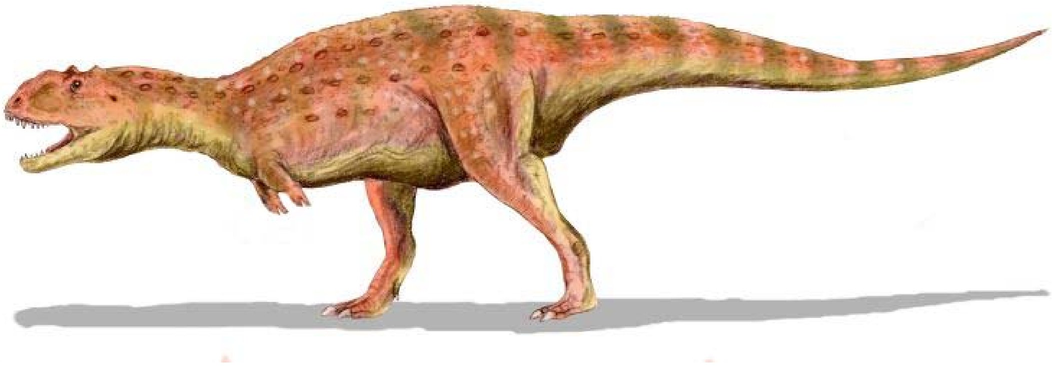
History of exploration

The Maevarano Formation was first explored by French military physician Dr. Félix Salètes and his staff officer Landillon in 1895, and fossils and geologic data were sent to paleontologist Charles Depéret. He briefly described the formation and named two dinosaurs from the remains (*Titanosaurus madagascariensis* and *Megalosaurus crenatissimus*, now *Majungasaurus*). Similar collections were made throughout the 20th century, yielding mostly fragmentary fossils; one such specimen, a rough partial skull roof, became the holotype of supposed pachycephalosaur (bonehead dinosaur) *Majungatholus* in 1979. (This specimen was later shown to be part of the skull ornamentation of a *Majungasaurus*.) Large scale expeditions (seven to date), under the banner of the Mahajanga Basin Project, began in 1993. These expeditions, conducted jointly by Stony Brook University and the University of Antananarivo, have greatly expanded knowledge of this formation and the organisms that lived while it was being deposited.

Paleoenvironment

The Maevarano Formation is interpreted as a low-relief alluvial plain that over time was covered by a marine transgression. Broad, shallow rivers flowed to the northwest from central highlands; evidence for debris flows suggests that the discharges of the rivers varied greatly, with periods of dilute water flow, and periods of rapid erosion dumping sediment into the channels. Paleosols are reddish and include root casts. The paleosols and other sedimentologic evidence indicate well-drained floodplains with abundant vegetation adapted to a relatively dry climate, strongly seasonal (rainy and dry seasons) and at times semiarid (not unlike the present climate of the area).

Vertebrate paleofauna



Majungasaurus crenatissimus, top land predator of the Maevarano Formation.

Animals found in the formation include frogs (including *Beelzebufo ampinga*), turtles, snakes, lizards, at least seven species of crocodyliforms (including species of *Mahajangasuchus* and *Trematochampsa*), abelisaurid theropod *Majungasaurus*, noasaurid *Masiakosaurus*, two types of titanosaurian sauropods (*Rapetosaurus* and an unnamed second form), and at least five species of birds or very bird-like dinosaurs, including *Rahonavis*. The 6 to 7 meter long (20 to 23 ft) *Majungasaurus* was likely the apex predator in the terrestrial environment. Crocodyliforms were very diverse and abundant.

Naturita Formation

The **Naturita Formation** was named by Robert G. Young (1960, 1965) for Cretaceous sedimentary rocks exposed near Naturita, Colorado.

Naturita Formation exposed above the town of Naturita Colorado.

The formation lies between the Cedar Mountain Formation (sometimes called the Burro Canyon Formation in Colorado) and Mancos Shale, thus occupies the position for sedimentary strata that have historically been called the Dakota Formation. However, as Witzke and Ludvigson (1994) noted, the term cannot be used for Cretaceous strata that were deposited on the western side of the Cretaceous Seaway.

Naturita Formation exposed in a roadcut in eastern Utah. A coal seam is visible below the sandstone bed. A thin volcanic ash (white layer) occurs in the upper portion of the coal.

In most areas, the Naturita Formation is composed of a lower unit of conglomeratic sandstone, a middle part of lignitic mudstones and coal, and fine- to medium-grained sandstones in the upper part. The Naturita is not uniform in thickness and in many places is very thin or missing so that the Mancos Formation is in direct contact with the Cedar Mountain Formation. Where missing, a lag of conglomerate may be present to indicate winnowing of sediments, which occurred by advancing Cretaceous sea. In other places, deposition of Naturita sediments did not occur, and these areas may have been quiet lagoons. Coastal coal swamps also formed in low areas as the encroaching sea raised the base level of rivers and the water table.

Fossils from the Naturita including dinosaur bone fragments of ceratopsians, a possible primitive tyrannosaurid, nodosaurid ankylosaurs, and a brachiosaurid sauropod (Carpenter 2006). Abundant fossil plants are also known from the coal-rich layers (Rushforth 1971)

Raton Formation

The **Raton Formation** is a geological formation of Upper Cretaceous and Paleocene age which outcrops in the Raton Basin of northeast New Mexico and southeast Colorado.

The Raton Formation was originally named "Raton Hills Group" by Hayden in 1869 for coal beds in the Raton Hills in Colfax County, New Mexico. In 1913, Lee changed the name to Raton Formation. Lee described the formation as a coal with carbonaceous shale with brown to buff sandstone and conglomerate (usually at the base). The Raton Formation is about 1140 feet thick at the type locality. The formation unconformably overlies the Vermejo Formation, and unconformably (?) underlies the Poison Canyon Formation.

In 1954, Brown determined that the Raton Formation was of Late Cretaceous and Paleocene age.

Pillmore measured the formation thickness as 2000 feet, and divided the Raton Formation into three divisions. The lowest division is a basal sandstone and conglomerate of quartzite, chert and gneiss pebbles and cobbles in a coarse-grained quartzose to arkosi sandstone matrix. The middle division is fine to coarse grained sandstone, with some siltstone, mudstone, and coal. The upper division is coal-bearing and contains sandstone, siltstone, mudstone, shale, and mineable coal.

Because the Raton Formation is a well-preserved sequence of rocks spanning the Cretaceous-Tertiary boundary, it has been studied for evidence of a large meteor impact at the end of the Cretaceous that is thought to have caused the Cretaceous–Tertiary extinction event. The boundary is represented by a 1-cm thick tonstein clay layer which has been found to contain anomalously high concentrations of iridium. The boundary clay layer is accessible to the public at Trinidad Lake State Park, among other places in the Raton Basin.

Santa Marta Formation

The **Santa Marta Formation** is a geologic formation in Antarctica. It, along with the Mount Kirkpatrick Formation and the Snow Hill Island Formation, are the only formations yet known on the continent where dinosaur fossils have been found. The formation outcrops on James Ross Island off the coast of the northern tip of the Antarctic Peninsula. In its entirety, the Santa Marta Formation is on average one kilometer thick.

Stratigraphy

The Santa Marta Formation was deposited during the Santonian and Campanian ages of the Late Cretaceous. It overlies the Gustav Group laid down during the Barremian and Santonian ages and is succeeded by the Snow Hill Island Formation of late Campanian age. Together, the Santa Marta Formation, Snow Hill Island Formation, the overlying López de Bertodano Formation (deposited from the late Campanian age of the Late Cretaceous to the early Paleocene epoch of the early Paleogene), and the Sobral Formation (deposited during the early Paleocene) form the Marambio Group.

Originally the formation was subdivided into three informal members termed the Alpha, Beta, and Gamma members. The names were later changed to the Lachman Crags, Herbert Sound, and Rabot members. The Lachman Crags and Herbert Sound members, named after the areas in which they outcrop, are found in the northern part of James Ross Island. Both members are late Campanian in age. The Lachman Crags Member, the older of the two, is around 500 meters thick. The lower section of the member consists of tuffaceous mudstone while the upper section consists of tuffaceous turbidites formed by underwater avalanches. Bioturbation is evident in tuff beds throughout the member due to the disruption of sediments by benthic life during the time of deposition. The Herbert Sound member is also around 500 meters thick and also can be divided into two distinct sections. Channeled debris flows interbedded with turbides make up the lower portion of the member and are overlain by fine sandstones (followed by coarser sandstones and coquinas) that make up the upper portion of the member.

The depositional environment is thought to have been a system of abyssal fans radiating out from a large river delta. The rapid aggradation of sediments from the delta produced a steep delta slope, which may have resulted in occasional debris flows that formed the turbides. A high degree of tectonic activity in the region at the time may explain the intermittent tuff beds throughout the formation.

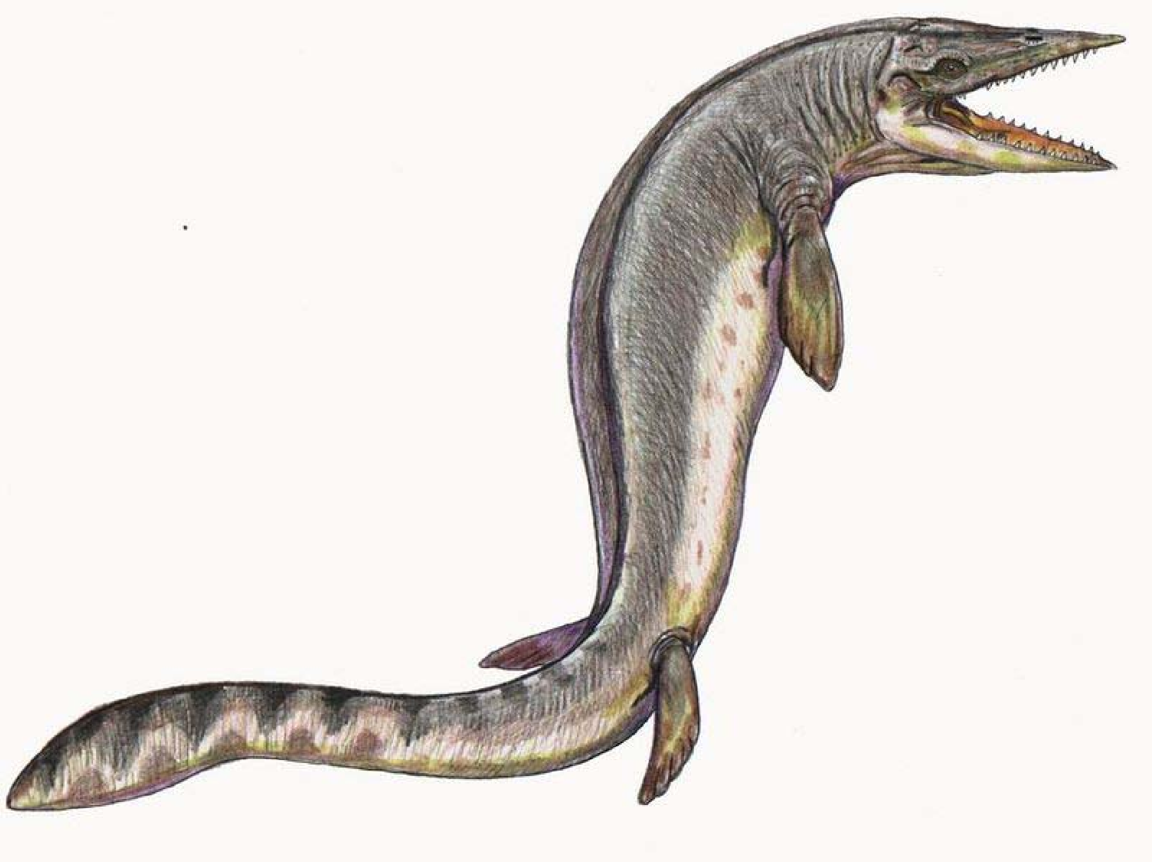
The Rabot Member of the Santa Marta Formation is confined to the southeastern part of James Ross Island and dates back to the early to late Campanian. Outcroppings of the member are separated from those of other members in the northern part of the island. Originally the member was regarded as its own formation, and now it is considered to be the lateral equivalent of both the Lachman Crags and Herbert Sound members. Like the Lachman Crags and Herbert Sound members, the Rabot member consists of mudstones and beds of tuff that are often highly bioturbated, and also consists of rare conglomerates. Recently a fourth member has been assigned to the formation called the Hamilton Point Member. The beds of this member used to be considered part of the upper portion of the Rabot member, but now are considered to be their own distinct member.

Flora and fauna

A wide variety of microorganisms inhabited the coastal waters at the time of the deposition of the Santa Marta Formation. Microfossils include ostracods and dinoflagellates.

Invertebrates were also common. Fossils of ammonites can be found in the formation, often embedded vertically in the bedding plane. Originally it was thought that dead ammonites could only be oriented this way in sediment if they were in shallow waters below a certain pressure, but there is evidence to support that due to specific conditions during burial, it was possible for these ammonites to be vertically oriented at greater depths. Ammonite genera present in the formation include *Anagaudryceras*, *Anapachydiscus*, *Eupachydiscus*, *Gaudryceras*, *Maorites*, *Natalites*, *Parasolenoceras*, *Yezoites*, and the heteromorph ammonites *Ainoceras*, *Eubostrychoceras*, *Ryugasella* and *Baculites*. Many bivalve fossils have been found such as *Cucullaea*, *Panopea*, *Pinna*, and *Pterotrigonia*. Polychaete annelid worms such as *Rotularia* and gastropods such as the cerithiid sea snail *Cerithium* have also been discovered in beds within the formation.

Numerous ichnofossils provide evidence of benthic activity, along with the bioturbated sediments previously mentioned. Vertical spreite trace fossils have been found as part of fodinichnia dominated ichnocoenosis and were assigned to ichnogenre such as *Paradictyodora*. Trackways thought to belong to decapods have also been found.



Taniwhasaurus

Fish were present, including one of the first frilled sharks, *Chlamydoselachus thomsoni*. Other marine vertebrates included the small mosasaur *Taniwhasaurus antarcticus*, previously known as *Lakumasaurus antarcticus*. The close relation of *T. antarcticus* to other species of *Taniwhasaurus* found in New Zealand and Patagonia provides evidence for a Gondwanan endemism.

Antarctopelta oliveroi, an ankylosaur, was discovered in 1986 on the northern part of James Ross Island about 2 kilometers south of Santa Marta Cove in beds that were part of the Santa Marta Formation. It was the first dinosaur found in Antarctica. It may be a possible nodosaur but there has been no formal phylogenic analysis to prove its relationship with other ankylosaurs. Although the formation is made up of only marine deposits, the bodies of these animals along with other debris may have frequently been washed out to sea to later sink to the bottom and be buried by sediment.

Leaves and fragments of plants are commonly found as fossils throughout the formation as well as large tree trunks in the lower members. This is evidence of the forested environment that covered Antarctica during the Late Cretaceous due to the overall warmer global temperature and milder climate. At that time the river delta had much vegetation, and was able to support large herbivores such as *Antarctopelta*.

Chapter- 6

Cretaceous Impact Craters

Avak crater

Avak is an impact crater centered approximately 12 km (7.5 mi) southeast of Barrow, Alaska, United States.

Avak is a subcircular structure about 8 km (5.0 mi) in diameter and 1 km (0.62 mi) deep. In the structure, metamorphic basement rocks and regionally flat lying sedimentary rocks are uplifted and intensely deformed. The Avak structure has no surface expression in the swampy, lake-dotted tundra of the Arctic coastal plain. The structure is covered by a thin veneer or permanently frozen Pliocene and Pleistocene rock. This means that the age of the impact took place anywhere between 95 million and 3 million years ago.

History

The Avak structure was first recognized from seismic and gravity surveys in the National Petroleum Reserve No. 4 (NPR4) by the U.S. Navy during the period from 1943 to 1953. The Navy drilled the Avak 1 well in 1951, and encountered deformed rocks from near the surface to a total depth of 1,225 m (4,019 ft). This led to the suggestion that Avak might be an impact structure.

The Avak structure provides the structural trap for the natural gas in the adjacent South Barrow and East Barrow gas fields. These fields have accumulated about 37 bcf of natural gas in Jurassic sandstones.

In 1996, geologists from the U.S. Geological Survey found geologic evidence that indicated that the Avak structure was a meteorite impact structure. The presence of planar deformation features (PDFs) was reported in 1995, so Avak is considered to a "confirmed" impact structure

Boltysh crater

Crater characteristics

Planet	Earth
Coordinates	48°54′N 32°15′E / 48.9°N 32.25°ECoordinates: 48°54′N 32°15′E / 48.9°N 32.25°E
Diameter	24 km
Depth	550 m

Location of the Boltysh Crater

The **Boltysh Crater** is an impact crater in the Kirovohrad Oblast province of Ukraine. The crater is 24 km in diameter and its age of 65.17 ± 0.64 million years, based on argon dating techniques, is within error of that of Chicxulub Crater in Mexico, and the KT boundary. The Chicxulub impact is believed to have caused the mass extinction at the end of the Cretaceous era, which included the extinction of the dinosaurs. The Boltysh impact likely occurred several thousand years before Chicxulub, suggesting the extinction event may have been driven by multiple meteor strikes over an extended period of time about 65 million years ago.

Overview

Boltysh Crater is located in central Ukraine, in the basin of the Tiasmyn River, a tributary of the Dnieper River. It is 24 km in diameter, and is surrounded by an ejecta blanket of breccia preserved over an area of 6500 km². It is estimated that immediately after the impact, ejecta covered an area of 25,000 km² to a depth of 1 m or greater, and was some 600 m deep at the crater rim.

The crater contains a central uplift about 6 km in diameter, rising about 550 m above the base level of the crater. This uplift currently lies beneath about 500 m of sediment deposited since the impact, and was discovered in the 1960s during oil exploration.

Age

When first identified, the age of the crater could only be roughly constrained between the age of the impacted rocks (the target) and the age of overlying sediments. The target rocks date from the Cenomanian (98.9 to 93.5 million years ago) and Turonian (93.5 to 89 million years ago) epochs. Bore samples of sediments overlying the crater contain fossils dating from the Paleocene epoch, 65 to 54.8 million years ago. The age of the crater was thus constrained to between 54.8 and 98.9 million years.

Subsequent radiometric dating reduced the uncertainty. The concentration of uranium-238 decay products in impact glasses from the crater were used to derive an age of 65.04 ± 1.10 million years. Analysis of argon radioactive decay products yielded an age of 65.17 ± 0.64 million years. These ages are similar to that of Chicxulub Crater. An August 2010 study of ancient fern spikes suggests the Boltysh impact likely occurred several thousand years before Chicxulub.

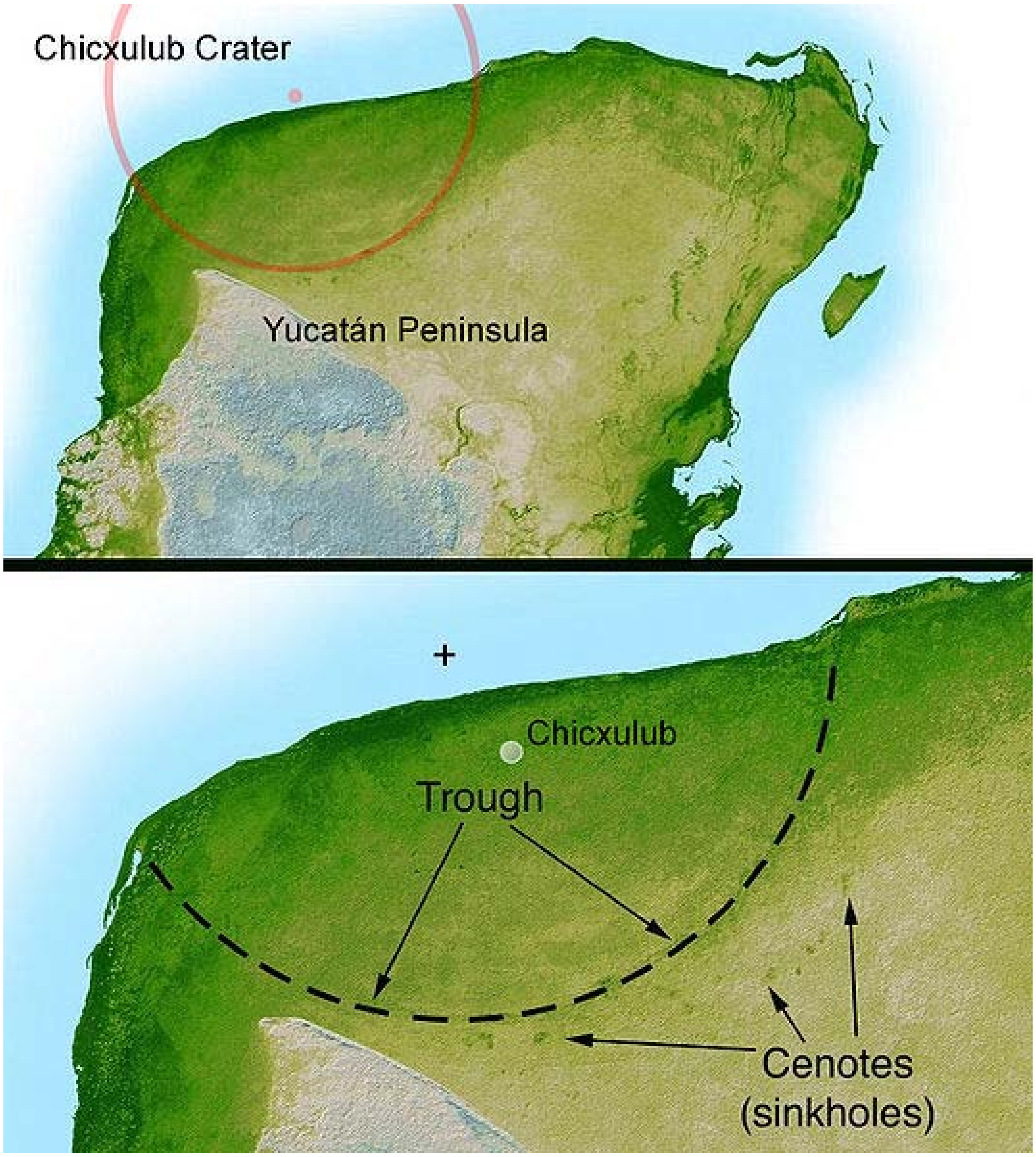
Likelihood of multiple impact

Although the ages derived for Chicxulub and Boltysh are the same to within their statistical errors, it does not necessarily follow that they formed at exactly the same time. At the estimated rate of impacts on the Earth, it would not be extremely unusual for a Boltysh-sized crater to be formed within half a million years of Chicxulub. The dating of these impact craters is not yet accurate enough to establish whether the impactors arrived thousands of years apart, perhaps as part of a generally elevated rate of impacts at that time, or were almost simultaneous, like the impacts of the fragments of Comet Shoemaker-Levy 9 on Jupiter in 1994.

The discovery of the unconfirmed Silverpit crater and the early report of its age as 65 – 60 million years initially gave greater weight to the hypothesis that the Earth was struck by multiple impactors at this time, however, the age estimate has now been broadened to 74 – 45 million years.

The controversial Shiva crater is claimed to have formed around the same time, but its status as an impact crater is disputed.

Chicxulub crater



Radar topography from NASA reveals part of the 180 kilometer (112 mi) diameter ring of the crater; clustered around the crater's trough are numerous sinkholes, suggesting a prehistoric oceanic basin in the depression left by the impact.

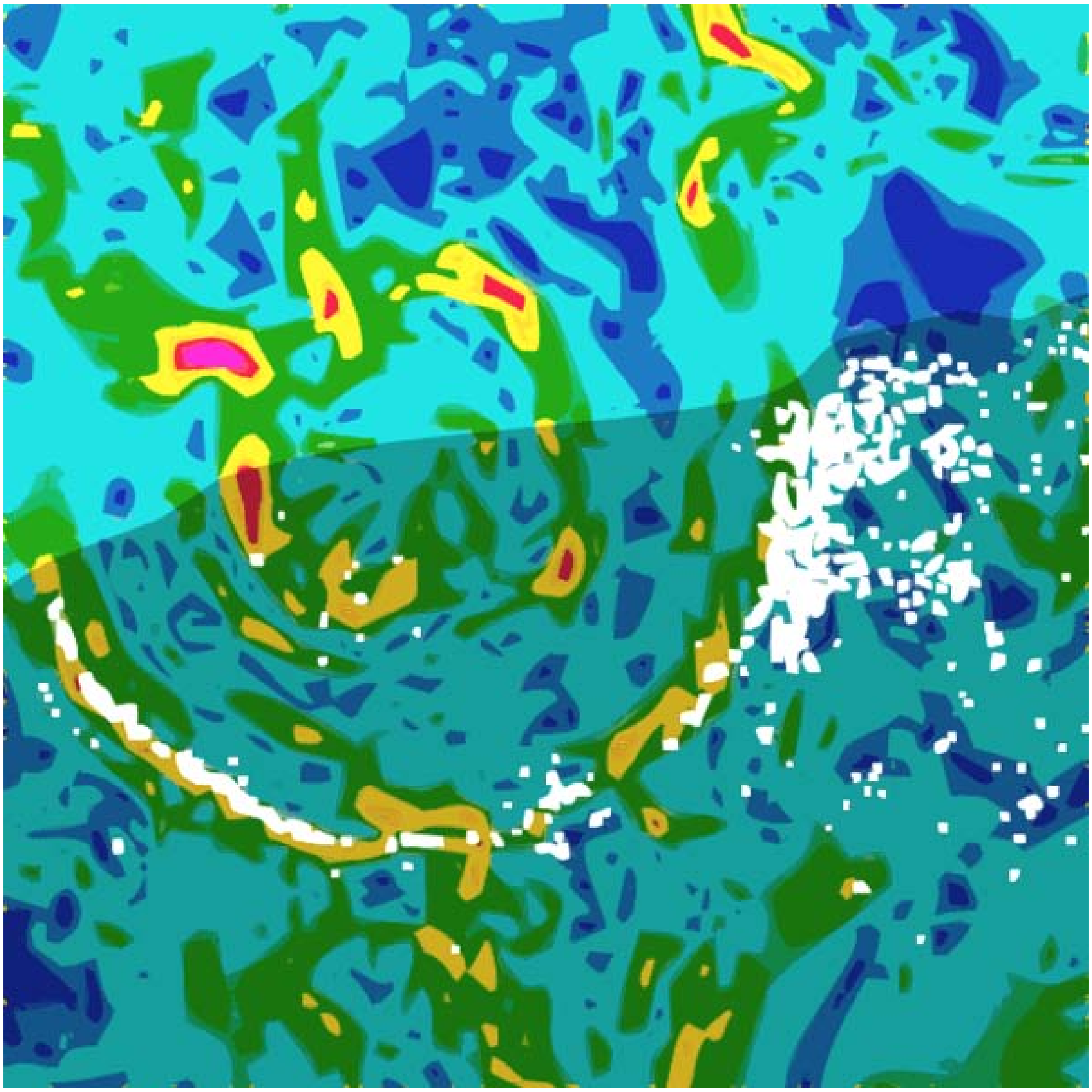
The **Chicxulub crater** is an ancient impact crater buried underneath the Yucatán Peninsula in Mexico. Its center is located near the town of Chicxulub, after which the crater is named. The crater is more than 180 km (110 mi) in diameter, making the feature one of the largest confirmed impact structures on Earth; the impacting bolide that formed the crater was at least 10 km (6 mi) in diameter.

The crater was discovered by Glen Penfield, a geophysicist who had been working in the Yucatán while looking for oil during the late 1970s. Penfield was initially unable to obtain evidence that the unique geological feature was in fact a crater, and gave up his search. Through contact with Alan Hildebrand, Penfield was able to obtain samples that suggested it was an impact feature. Evidence for the impact origin of the crater includes shocked quartz, a gravity anomaly, and tektites in surrounding areas.

The age of the rocks and isotope analysis show that this impact structure dates from the end of the Cretaceous Period, roughly 65 million years ago. The impact associated with the crater is implicated in causing the extinction of the dinosaurs as suggested by the K–T boundary, the geological boundary between the Cretaceous and Tertiary periods, although some critics argue that the impact was not the sole reason and others debate whether there was a single impact or whether the Chicxulub impactor was one of several that may have struck the Earth at around the same time. Recent evidence suggests that the impactor may have been a piece of a much larger asteroid that broke up in a collision in distant space more than 160 million years ago.

In March 2010, following extensive analysis of the available evidence covering 20 years' worth of data spanning the fields of palaeontology, geochemistry, climate modelling, geophysics and sedimentology, 41 international experts from 33 institutions reviewed available evidence and concluded that the impact at Chicxulub triggered the mass extinctions during K-T boundary including those of dinosaurs.

Discovery



Artist's rendering of the gravity anomaly map of the Chicxulub Crater area. Red and yellow are gravity highs; green and blue are gravity lows. White areas indicate multiple sinkholes, "cenotes". The shaded area is the Yucatan Peninsula.

In 1978, geophysicists Antonio Camargo and Glen Penfield were working for the Mexican state-owned oil company Petróleos Mexicanos, or Pemex, as part of an airborne magnetic survey of the Gulf of Mexico north of the Yucatán peninsula. Penfield's job was to use geophysical data to scout possible locations for oil drilling. Within the data, Penfield found a huge underwater arc with 'extraordinary symmetry' in a ring 70 km (40 mi) across. He then obtained a gravity map of the Yucatán made in the 1960s. A decade earlier, the same map suggested an impact feature to contractor Robert Baltosser, but he was forbidden to publicize his conclusion by Pemex corporate policy of the time. Penfield found another arc on the peninsula itself whose ends pointed northward. Comparing the two maps, he found the separate arcs formed a circle, 180 km (111 mi) wide, centered near the Yucatán village Chicxulub; he felt certain the shape had been created by a cataclysmic event in geologic history.

Pemex disallowed release of specific data but let Penfield and company official Antonio Camargo present their results at the 1981 Society of Exploration Geophysicists conference. That year's conference was underattended and their report attracted scant attention. Ironically, many experts in impact craters and the K-T boundary were attending a separate conference on Earth impacts. Although Penfield had plenty of geophysical data sets, he had no rock cores or other physical evidence of an impact.

He knew Pemex had drilled exploratory wells in the region in 1951; one bored into what was described as a thick layer of andesite about 1.3 km (4,200 ft) down. This layer could have resulted from the intense heat and pressure of an Earth impact, but at the time of the borings it was dismissed as a lava dome -- a feature uncharacteristic of the region's geology. Penfield tried to secure site samples but was told such samples had been lost or destroyed. When attempts at returning to the drill sites and looking for rocks proved fruitless, Penfield abandoned his search, published his findings and returned to his Pemex work.

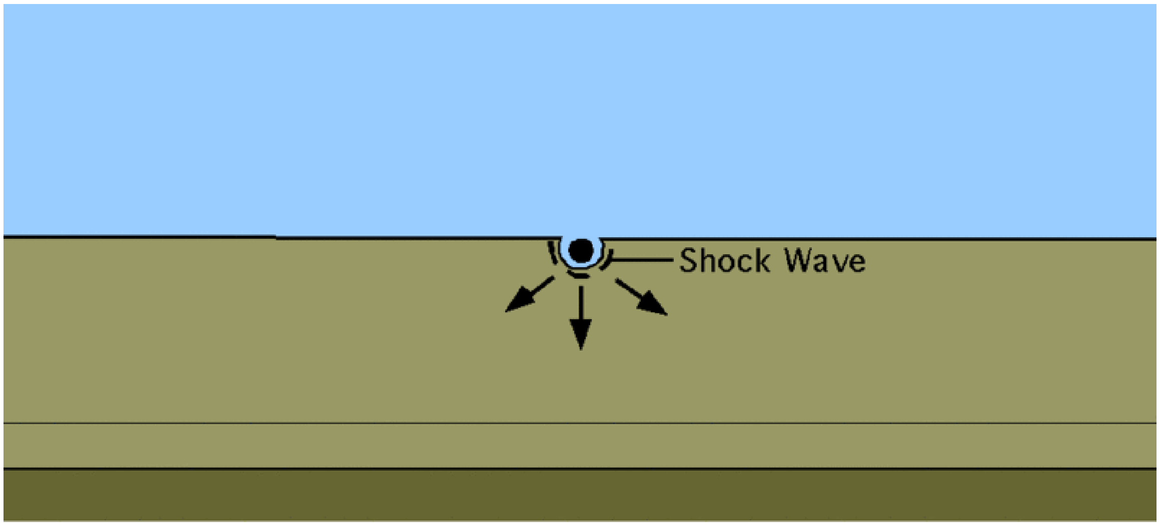
Penfield with the sample of shocked quartz found at Well #2, Chicxulub.

At the same time, scientist Luis Walter Alvarez put forth his hypothesis that a large extraterrestrial body had struck Earth; and in 1981, oblivious to Penfield's discovery, University of Arizona grad student Alan R Hildebrand and faculty adviser William V Boynton published a draft Earth-impact theory and were seeking a candidate crater. Their evidence included greenish-brown clay with surplus iridium containing shocked quartz grains and small weathered glass beads that looked to be tektites. Thick, jumbled deposits of coarse rock fragments were also present, thought to have been scoured from one place and deposited elsewhere by a kilometres-high tsunami likely resulting from an Earth impact. Such deposits occur in many locations but seem concentrated in the Caribbean basin at the K–T boundary. So when Haitian professor Florentine Morás discovered what he thought to be evidence of an ancient volcano on Haiti, Hildebrand suggested it could be a telltale feature of a nearby impact. Tests on samples retrieved from the K–T boundary revealed more tektite glass, formed only in the heat of asteroid impacts and high-yield nuclear detonations.

In 1990, *Houston Chronicle* reporter Carlos Byars told Hildebrand of Penfield's earlier discovery of a possible impact crater. Hildebrand contacted Penfield in April 1990 and the pair soon secured two drill samples from the Pemex wells, stored in New Orleans. Hildebrand's team tested the samples, which clearly showed shock-metamorphic materials.

A team of California researchers including Kevin Pope, Adriana Ocampo, and Charles Duller, surveying regional satellite images in 1996, found a sinkhole (cenote) ring centered on Chicxulub that matched the one Penfield saw earlier; the sinkholes were thought to be caused by subsidence of the impact crater wall. More recent evidence suggests the actual crater is 300 km (190 mi) wide, and the 180 km ring an inner wall of it.

Impact specifics



An image showing the impact, and subsequent crater formation (University of Arizona, Space Imagery Center)

The impactor's estimated size was about 10 km (6 mi) in diameter and is estimated to have released 4×10^{23} joules of energy, equivalent to 100,000,000 megatons of TNT on impact. By contrast, the most powerful man-made explosive device ever detonated, the Tsar Bomba, had a yield of only 50 megatons, making the Chicxulub impact 2 million times more powerful. Even the largest known explosive volcanic eruption, which released approximately 10^{21} joules and created La Garita Caldera, was substantially less powerful than the Chicxulub impact.

Effects

The impact would have caused some of the largest megatsunamis in Earth's history, reaching thousands of feet high. A cloud of super-heated dust, ash and steam would have spread from the crater, as the impactor burrowed underground in less than a second. Excavated material along with pieces of the impactor, ejected out of the atmosphere by the blast, would have been heated to incandescence upon re-entry, broiling the Earth's surface and possibly igniting global wildfires; meanwhile, colossal shock waves spawned global earthquakes and volcanic eruptions. The emission of dust and particles could have covered the entire surface of the Earth for several years, possibly a decade, creating a harsh environment for living things. The shock production of carbon dioxide caused by the destruction of carbonate rocks would have led to a sudden greenhouse effect. Over a longer period of time, sunlight would have been blocked from reaching the surface of the earth by the dust particles in the atmosphere, cooling the surface dramatically. Photosynthesis by plants would also have been interrupted, affecting the entire food chain. A model of the event developed by Lomax et al. (2001) suggests that net primary productivity (NPP) rates may have increased to higher than pre-impact levels over the long term because of the high carbon dioxide concentrations.

In February 2008, a team of researchers led by Sean Gulick at the University of Texas at Austin’s Jackson School of Geosciences used seismic images of the crater to determine that the impactor landed in deeper water than was previously assumed. They argued that this would have resulted in increased sulfate aerosols in the atmosphere. According to the press release, that "could have made the impact deadlier in two ways: by altering climate (sulfate aerosols in the upper atmosphere can have a cooling effect) and by generating acid rain (water vapor can help to flush the lower atmosphere of sulfate aerosols, causing acid rain)."

Geology and morphology

In their 1991 paper, Hildebrand, Penfield, and company described the geology and composition of the impact feature. The rocks above the impact feature are layers of marl and limestone reaching to almost 1,000 metres (3,300 ft) in depth. These rocks date back as far as the Paleocene. Below these layers lie more than 500 m (1,600 ft) of andesite glass and breccia. These andesitic igneous rocks were found only within the supposed impact feature; similarly, quantities of feldspar and augite, normally only found in impact-melt rocks, are present, as is shocked quartz. The K–T boundary inside the feature is depressed between 600 and 1,100 m (2,000–3,600 ft) compared to the normal depth of about 500 m (1,600 ft) depth 5 km (3 mi) away from the impact feature. Along the edge of the crater are clusters of cenotes or sinkholes, which suggest that there was a water basin inside the feature during the Tertiary period, after the impact. Such a basin's groundwater dissolved the limestone and created the caves and cenotes beneath the surface. The paper also noted that the crater seemed to be a good candidate source for the tektites reported at Haiti.

Astronomical origin of asteroid

On September 5, 2007 a report published in *Nature* proposed an origin for the asteroid that created Chicxulub Crater. The authors, William F. Bottke, David Vokrouhlický, and David Nesvorný, argued that a collision in the asteroid belt 160 million years ago resulted in the creation of the Baptistina family of asteroids, the largest surviving member of which is 298 Baptistina. They proposed that the "Chicxulub asteroid" was also a member of this group. The connection between Chicxulub and Baptistina is supported by the large amount of carbonaceous material present in microscopic fragments of the impactor, suggesting the impactor was a member of a rare class of asteroids called carbonaceous chondrites, like Baptistina. According to Bottke, the Chicxulub impactor was a fragment of a much larger parent body about 170 km (105 mi) across, with the other impacting body being around 60 km (40 mi) in diameter.

In 2010, another hypothesis was offered which implicated the newly-discovered asteroid P/2010 A2, a member of the Flora family of asteroids, as a possible remnant cohort of the K/T impactor.

Chicxulub and mass extinction

The piece of clay, held by Walter Alvarez, which sparked research into the impact theory. The greenish-brown band in the center is extremely rich in iridium.

The Chicxulub Crater lends support to the theory postulated by the late physicist Luis Alvarez and his son, geologist Walter Alvarez, that the extinction of numerous animal and plant groups, including dinosaurs, (the Cretaceous-Tertiary extinction event), may have resulted from a bolide impact. Luis and Walter Alvarez, at the time both faculty members at the University of California, Berkeley, postulated that this enormous extinction event, which was roughly contemporaneous with the postulated date of formation for the Chicxulub crater, could have been caused by just such a large impact. This theory is now widely accepted by the scientific community. Some critics, including paleontologist Robert Bakker, argue that such an impact would have killed frogs as well as dinosaurs, yet the frogs survived the extinction event. Gerta Keller of Princeton University argues that recent core samples from Chicxulub prove the impact occurred about 300,000 years *before* the mass extinction, and thus could not have been the causal factor.

The main evidence of such an impact, besides the crater itself, is contained in a thin layer of clay present in the K–T boundary across the world. In the late 1970s, the Alvarezes and colleagues reported that it contained an abnormally high concentration of iridium. Iridium levels in this layer reached 6 parts per billion by weight or more compared to 0.4 for the Earth's crust as a whole; in comparison, meteorites can contain around 470 parts per billion of this element. It was hypothesised that the iridium was spread into the atmosphere when the impactor was vaporized and settled across the Earth's surface amongst other material thrown up by the impact, producing the layer of iridium-enriched clay.

Multiple impact theory

In recent years, several other craters of around the same age as Chicxulub have been discovered, all between latitudes 20°N and 70°N. Examples include the Silverpit crater in the North Sea and the Boltysh crater in Ukraine. Both are much smaller than Chicxulub, but likely to have been caused by objects many tens of metres across striking the Earth. This has led to the hypothesis that the Chicxulub impact may have been only one of several impacts that happened nearly at the same time. Another possible crater thought to have been formed at the same time is the Shiva crater, though the structure's status as a crater is contested.

The collision of Comet Shoemaker-Levy 9 with Jupiter in 1994 demonstrated that gravitational interactions can fragment a comet, giving rise to many impacts over a period of a few days if the comet should collide with a planet. Comets undergo gravitational interactions with the gas giants, and similar disruptions and collisions are very likely to have occurred in the past. This scenario may have occurred on Earth 65 million years ago, though Shiva and the Chicxulub craters might have been formed 300,000 years apart.

In late 2006, Ken MacLeod, a geology professor from the University of Missouri, completed an analysis of sediment below the ocean's surface, bolstering the single-impact theory. MacLeod conducted his analysis approximately 4,500 km (2,800 mi) from the Chicxulub Crater to control for possible changes in soil composition at the impact site, while still close enough to be affected by the impact. The analysis revealed there was only one layer of impact debris in the sediment, which indicated there was only one impact. Multiple-impact proponents such as Gerta Keller regard the results as "rather hyper-inflated" and do not agree with the conclusion of MacLeod's analysis.

Gosses Bluff crater

Gosse Bluff from the north, approximately 30 kilometres away

Gosses Bluff crater photographed from the ISS.

Gosses Bluff (Gosse's Bluff) is thought to be an impact crater. It is located in the southern Northern Territory, near the centre of Australia, about 175 km (109 mi) west of Alice Springs., It is thought to have been formed by the impact of an asteroid or comet approximately 142.5 ± 0.8 million years ago, in the earliest Cretaceous, very close to the Jurassic - Cretaceous boundary. The original crater rim has been estimated at about 22 km (13.7 Mi) in diameter, but this has been eroded away. The 5 km (3 mi) diameter, 150 m (500 ft) high crater-like feature, now exposed, is interpreted as the eroded relic of the crater's central uplift. The impact origin of this topographic feature was first proposed in the 1960s, the strongest evidence coming from the abundance of shatter cones.

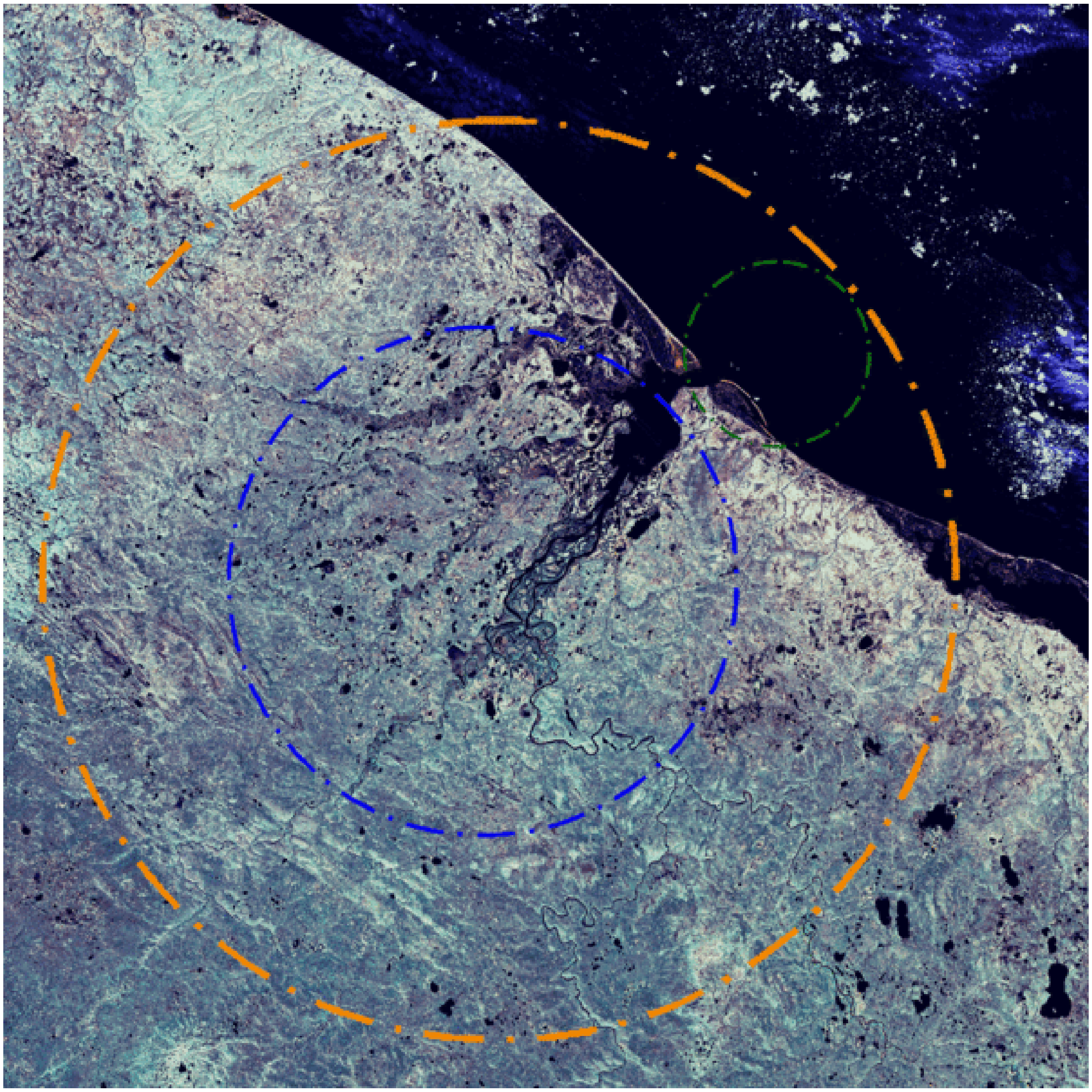
Another possible explanation is that Gosses Bluff could have been formed by an underwater, volcanic eruption.

Uluru (Ayers Rock) is about 132 miles to the southwest. In the past the crater has been the target of petroleum exploration, and two abandoned exploration wells lie near its centre.

Aboriginal Significance

The site is known as **Tnorala** to the Western Arrernte Aboriginal people, and is a sacred place. It is now located in the Tnorala Conservation Reserve. A Western Arrernte story attributes its origins to a cosmic impact: in the Dreaming, a group of celestial women were dancing as stars in the Milky Way. One of the women grew tired and placed her baby in a wooden basket. As the women continued dancing, the basket fell and plunged into the earth. The baby fell to the earth and forced the rocks upward, forming the circular mountain range. The baby's parents, the evening and morning star (Venus), continue to search for their baby.

Kara crater



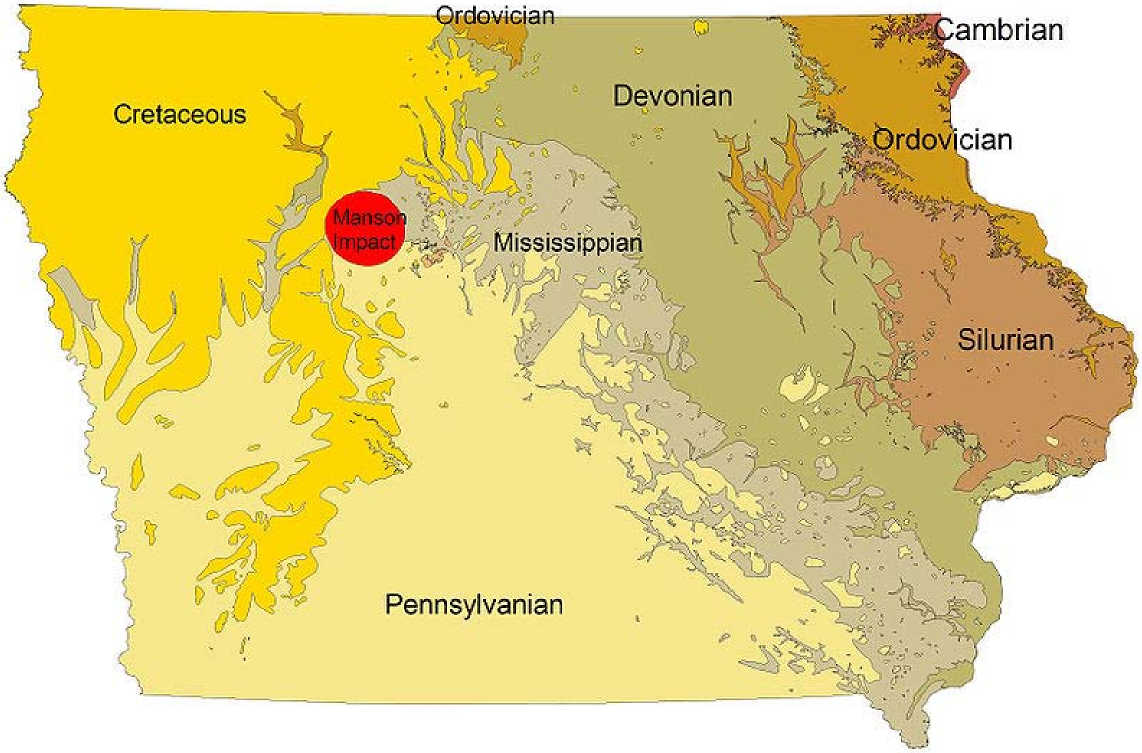
Kara crater

Kara is a meteor crater in the Yugorsky Peninsula, Nenetsia, Russia.

It is 65 km in diameter and the age is estimated to be 70.3 ± 2.2 million years old (Upper Cretaceous). Impactite outcrops located on the Baydarata Gulf shore north-east of the crater imply that the original size of the crater, now greatly eroded, was 120 km in diameter . The crater is not exposed to the surface.

The Kara crater lies in the southeastern end of the Yugorsky Peninsula, while the **Ust-Kara** site lies offshore, 15 km east of the small Kara or Karskaya Guba inlet. It was formerly believed that these two sites were two separate craters and that they formed a twin impact structure from a large-scale meteorite hit in the late Cretaceous. However, it seems that the Ust-Kara site does not exist as a separate site. Apparently, the Suevite outcrops of the Ust-Kara impact structure are only a part of the Kara impact structure. (Hodge 1994 and NASA 1988)

Manson crater



Manson impact location shown in red on bedrock map of Iowa.

The **Manson impact crater** is near the site of Manson, Iowa where an asteroid or comet nucleus struck the Earth during the Cretaceous Period, 74 million years ago. It was one of the largest impacts by an object from outer space to have happened in North America and was previously thought to have led to the extinction of the dinosaurs until isotopic ages proved that it was too old.

No surface evidence exists due to coverage by glacial till and the site where the crater lies buried is now a flat landscape. But, hidden about 20 to 90 metres below the surface is a buried structure about 38 km in diameter. It lies under the southeast corner of Pocahontas County and extends under portions of three adjoining counties. That an anomalous structure underlaid the area was known from the early 1900s from unusual water well drill cuttings. A research investigation was started in 1955 and it was labeled a "cryptovolcanic structure" (volcanic - steam explosion). Further investigation was undertaken by Robert S. Dietz who proposed an impact origin in 1959 and by Nicholas Short in 1966 who produced evidence of shocked quartz grains which confirmed the impact origin of the structure. In 1991 and 1992 the U.S. Geological Survey along with others including the Iowa Geological Survey conducted detailed research in part to test the possible connection of the Manson Crater with the K-T boundary extinction event. 40Ar/39Ar isotopic dating of core from the impact structure by Izett et al. (1993), however, gave an age of about 74 Ma, or about 10 Ma older than the K-T boundary. The impactor is considered to have been a stoney meteorite about two kilometres in diameter. The impact disrupted granite, gneiss, and shales of the Precambrian basement as well as sedimentary formations of Paleozoic age, Devonian through Cretaceous.

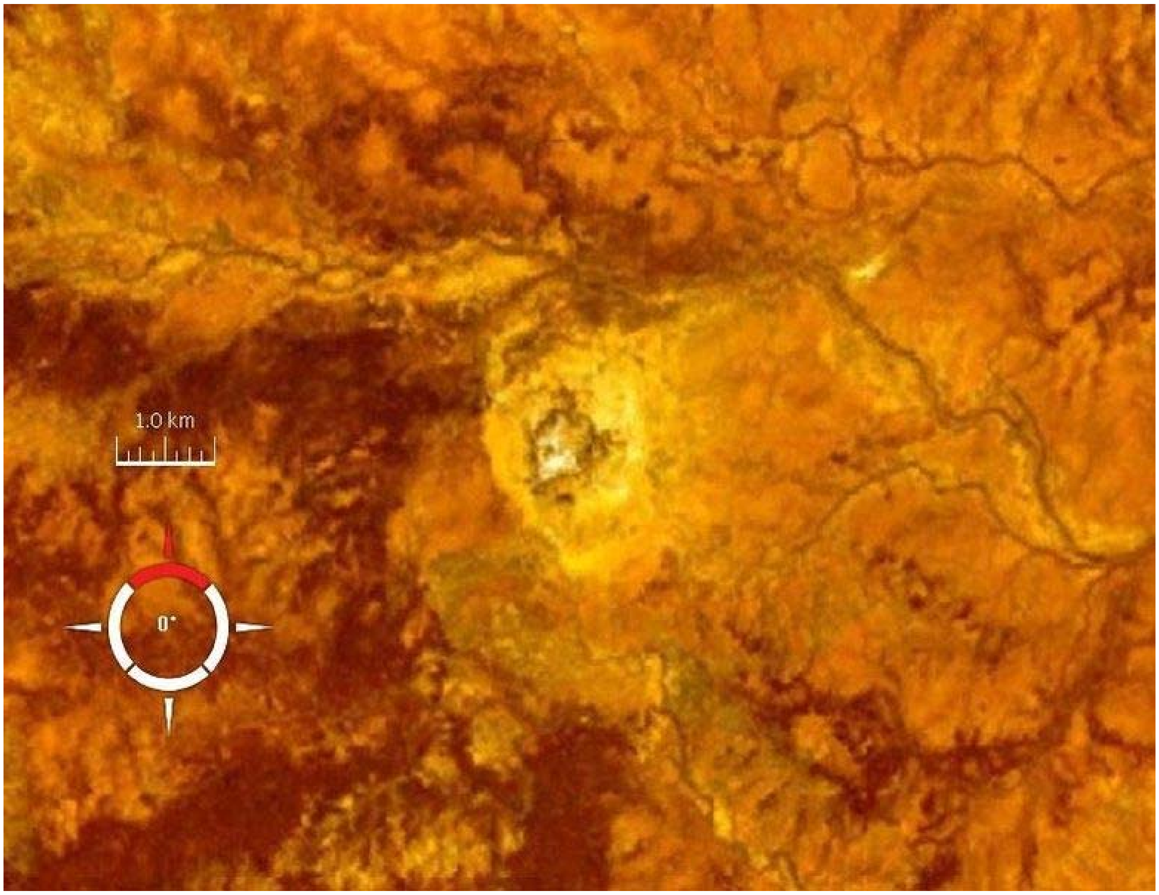
Morokweng crater

The **Morokweng crater** (or **Morokweng impact structure**) is an impact crater buried beneath the Kalahari Desert near the town of Morokweng in the Northwest Province of South Africa, close to the border with Botswana.

The crater, formed by an asteroid 5-10 km (3-6 miles) in diameter, is at least about 160 km (100 miles)in diameter and the age is estimated to be 145.0 ± 0.8 million years, placing it on the Jurassic-Cretaceous boundary. Discovered in 1994, it is not exposed at the surface but has been mapped by magnetic and gravimetric surveys. Core samples have shown it to have been formed by the impact of an L chondrite asteroid.

In May, 2006, a group of scientists drilling into the site announced the discovery of a 25-centimetre (9.8 in) diameter fragment of the original asteroid at a depth of 770 metres (2,500 ft) below the surface, along with several much smaller pieces a few millimetres across at other depths. This discovery was unexpected since previous drillings on large impact craters had not produced such fragments, and it was thought that the asteroid had been almost entirely vaporised. Some of the fragments can be seen in the Antenna Wing of London's Science Museum.

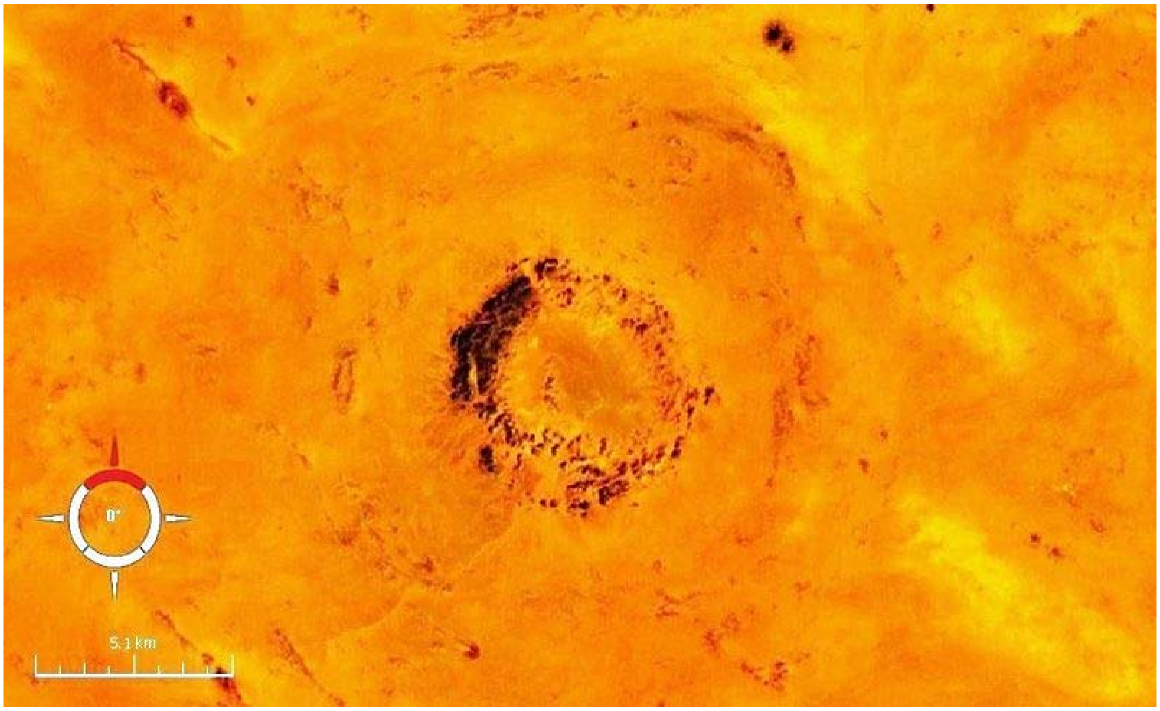
Mount Toondina crater



Landsat image of Mount Toondina crater; screen capture from the NASA World Wind

Mount Toondina crater is an impact structure (or astrobleme), the eroded remnant of a former impact crater, situated in northern South Australia 45 km south of the township of Oodnadatta. Mount Toondina is the high point of a circular topographic feature rising out of an otherwise relatively flat desert area of the Eromanga Basin. An impact origin was first suggested in 1976, challenging the earlier diapir (salt dome) hypothesis, and strongly supported by subsequent studies. A geophysical survey using gravity methods indicates an internal structure typical of complex impact craters, including an uplifted centre, and suggests that the original crater was about 3–4 km in diameter., The crater must be younger than the Early Cretaceous age of the rocks in which it is situated, but otherwise is not well dated. It has clearly undergone significant erosion since the impact event.

Oasis crater

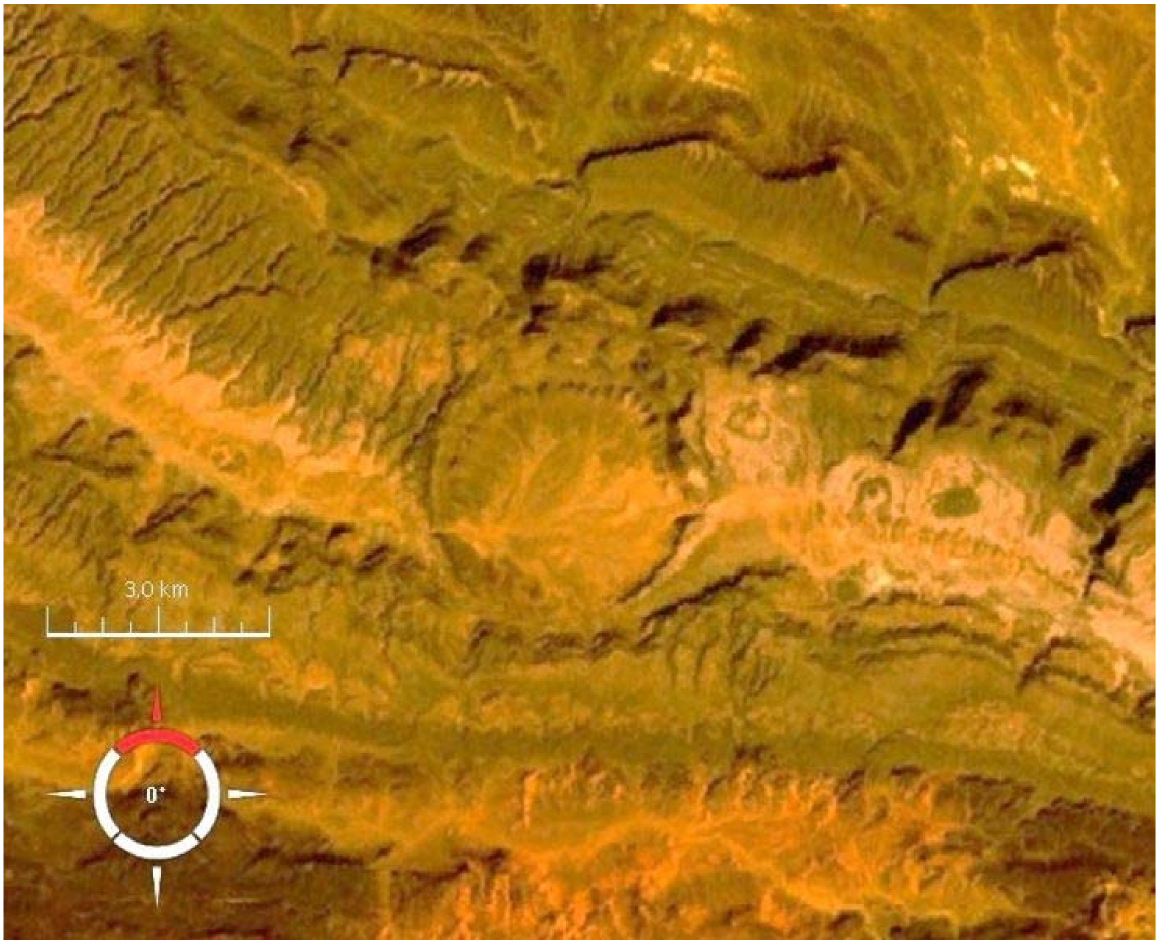


Landsat image of the Oasis crater; screen capture from NASA World Wind

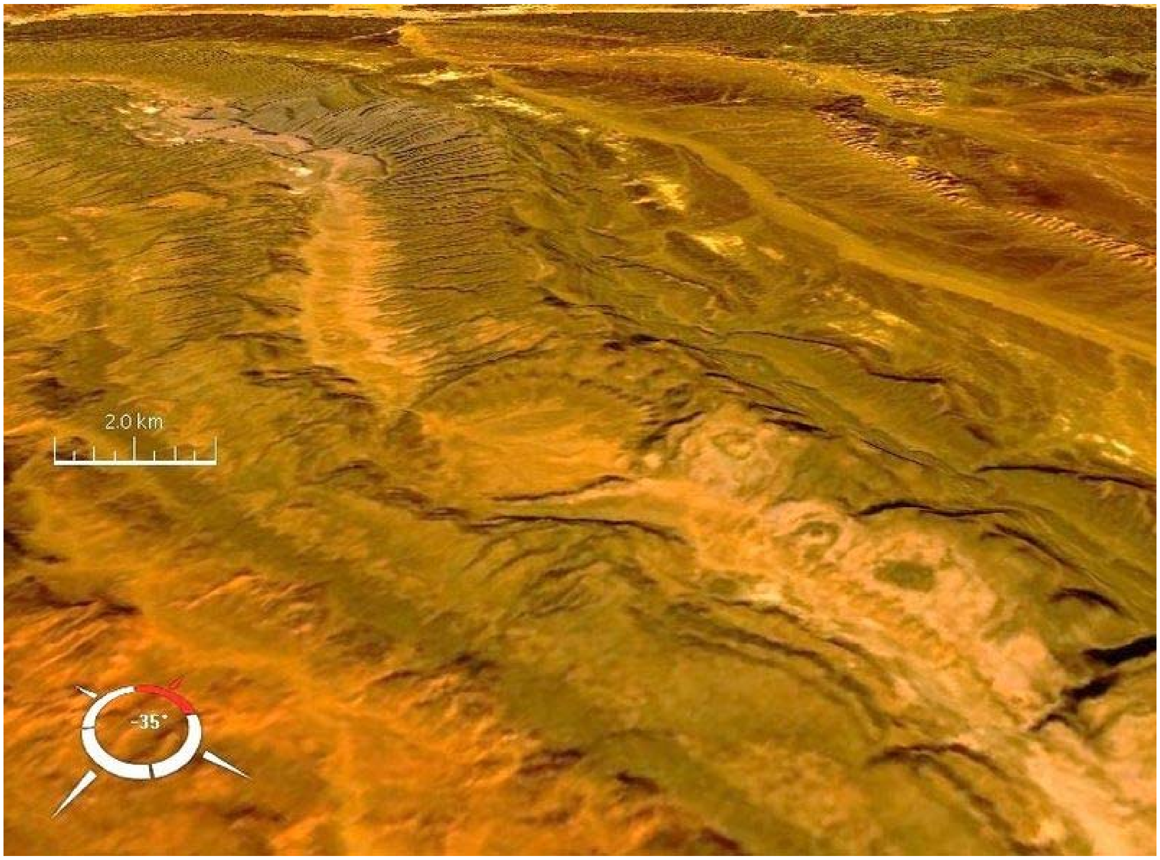
Oblique Landsat image of Oasis crater draped over digital elevation model (x5 vertical exaggeration); screen capture from NASA World Wind

Oasis is a meteorite crater in Libya. The crater is exposed at the surface, but has been significantly eroded. The prominent topographic ring is only the central uplift, while the original crater rim is estimated to have been 18 km in diameter. The age is estimated to be less than 120 million years (Lower Cretaceous).

Ouarkziz crater



Landsat image of the Ouarkziz crater; screen capture from NASA World Wind



Oblique Landsat image of Ouarkziz crater draped over digital elevation model (x2 vertical exaggeration); screen capture from NASA World Wind

Ouarkziz (Arabic: أوركزيز) is a meteorite impact crater in Algeria. It is 3.5 kilometers in diameter and the age is estimated to be less than 70 million years (Cretaceous or younger). The crater is exposed at the surface.

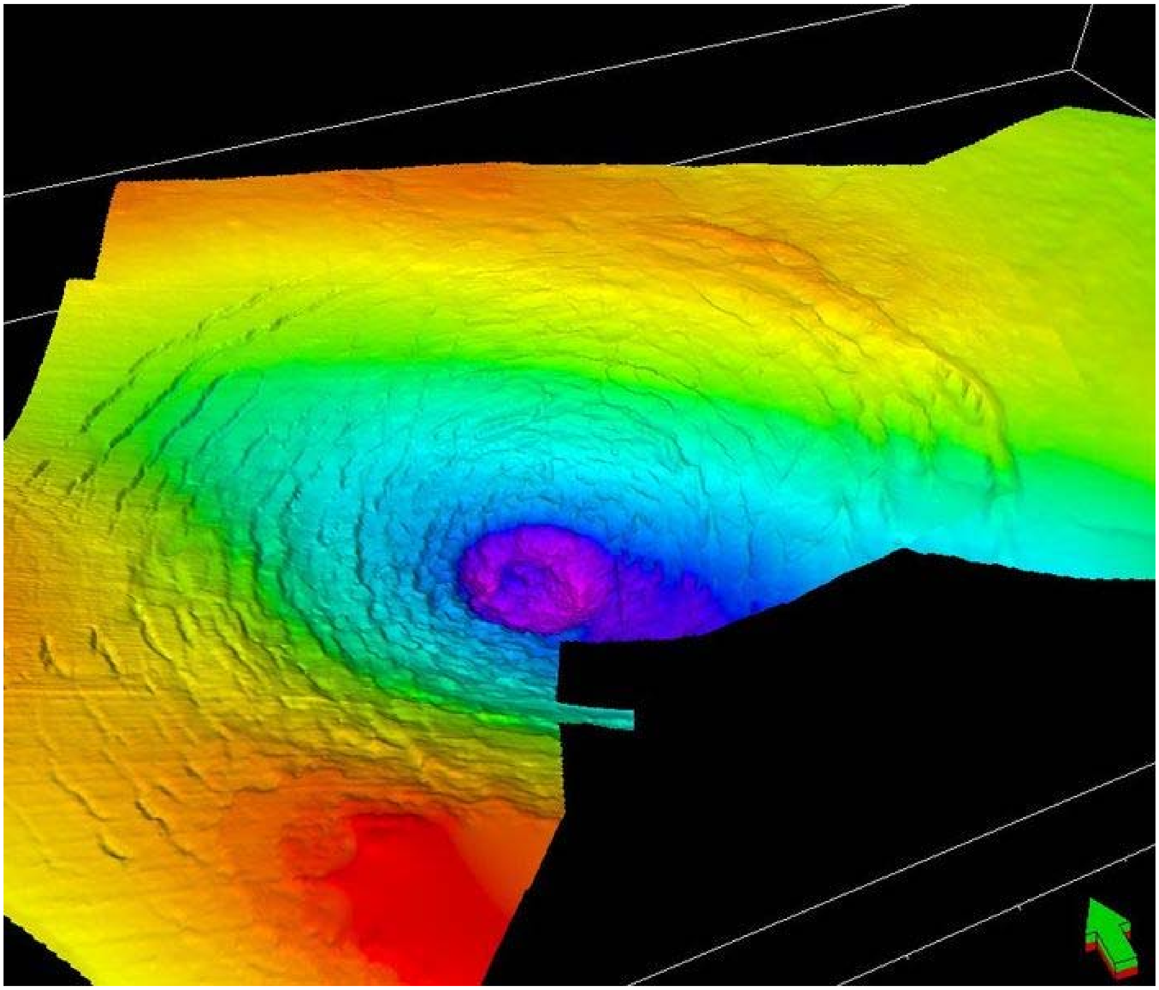
Silverpit crater

Approximate location of the Silverpit crater

Silverpit crater is a buried sub-sea structure under the North Sea off the coast of the United Kingdom. The crater-like form, named after the Silver Pit — a nearby sea-floor valley recognized by generations of fishermen — was discovered during the routine analysis of seismic data collected during exploration for gas in the Southern North Sea Sedimentary Basin. Its meteor impact origin was first proposed and widely reported in 2002. If correct, it would be the first impact crater identified in or near the United Kingdom. Its age was proposed to lie somewhere in a 29-million year interval between 74 – 45 million years (Late Cretaceous – Eocene).

However, the interpretation is controversial and other authors have disputed its extraterrestrial origin. An alternative origin has been proposed in which the feature was created by withdrawal of rock support by salt mobility.

Discovery



A perspective view of the top chalk surface, looking north-east, showing the central crater and its surrounding rings. False colours indicate depth (red/yellow=shallow; blue/purple=deep).

The crater-like structure was discovered by petroleum geoscientists Simon Stewart of BP and Philip Allen, then of Production Geoscience Ltd, during routine analysis of seismic data while exploring for natural gas deposits in a region 130 km off the Humber estuary. Allen noticed an unusual set of concentric rings. Although they looked like they may have been caused by a meteor, he had no experience of impact structures. So he hung an image of them on the wall of his office, hoping someone else might be able to shed light on the mystery. Stewart, visiting Production Geoscience on an unrelated matter, had long predicted that a crater would be found on 3D seismic data, saw the image and suggested it might be an impact feature. The discovery of the crater and the impact hypothesis were reported in the journal *Nature* in 2002.

Silverpit crater is named after the Silver Pit fishing grounds in which it is located. The name is given by fishermen to a large elongated depression in the bed of the North Sea, which is thought to be an old river valley formed while the sea level was lower during the Ice Age. The structure currently lies below a layer of sediment up to 1,500 m thick, which forms the bed of the North Sea at a depth of about 40 m. Stewart and Allen's studies suggest that at the time of its formation, the area was under 50 to 300 m of water.

Only three years before the announcement of the discovery of the Silverpit crater, it had been suggested that seismic data from the North Sea would have a good chance of containing evidence of an impact crater: given the rate of crater formation on the Earth and the size of the North Sea, the expected number of impact craters would be one. Finding the crater form at Silverpit was serendipity.

Origin

The origin of the crater is currently being hotly debated by the Geoscience community with alternate theories of salt withdrawal and pull-apart basin proposed, raising doubts as to Silverpit's categorization as an impact structure.

Evidence in favour of impact origin

Other mechanisms for producing a crater were considered and rejected by Allen and Stewart when they discovered the crater. Volcanism was excluded because there were no magnetic anomalies in the crater, which would be expected if eruptions had occurred there. Withdrawal of salt deposits below the crater, known to be a mechanism for the formation of some craters, was ruled out because the Triassic and Permian layers of rock beneath the crater appeared to be undisturbed. Another strong indication that an impact had created the crater was the presence of a central peak - something that Stewart & Allen contend is difficult to form except through a meteorite impact.

Evidence for alternative interpretations

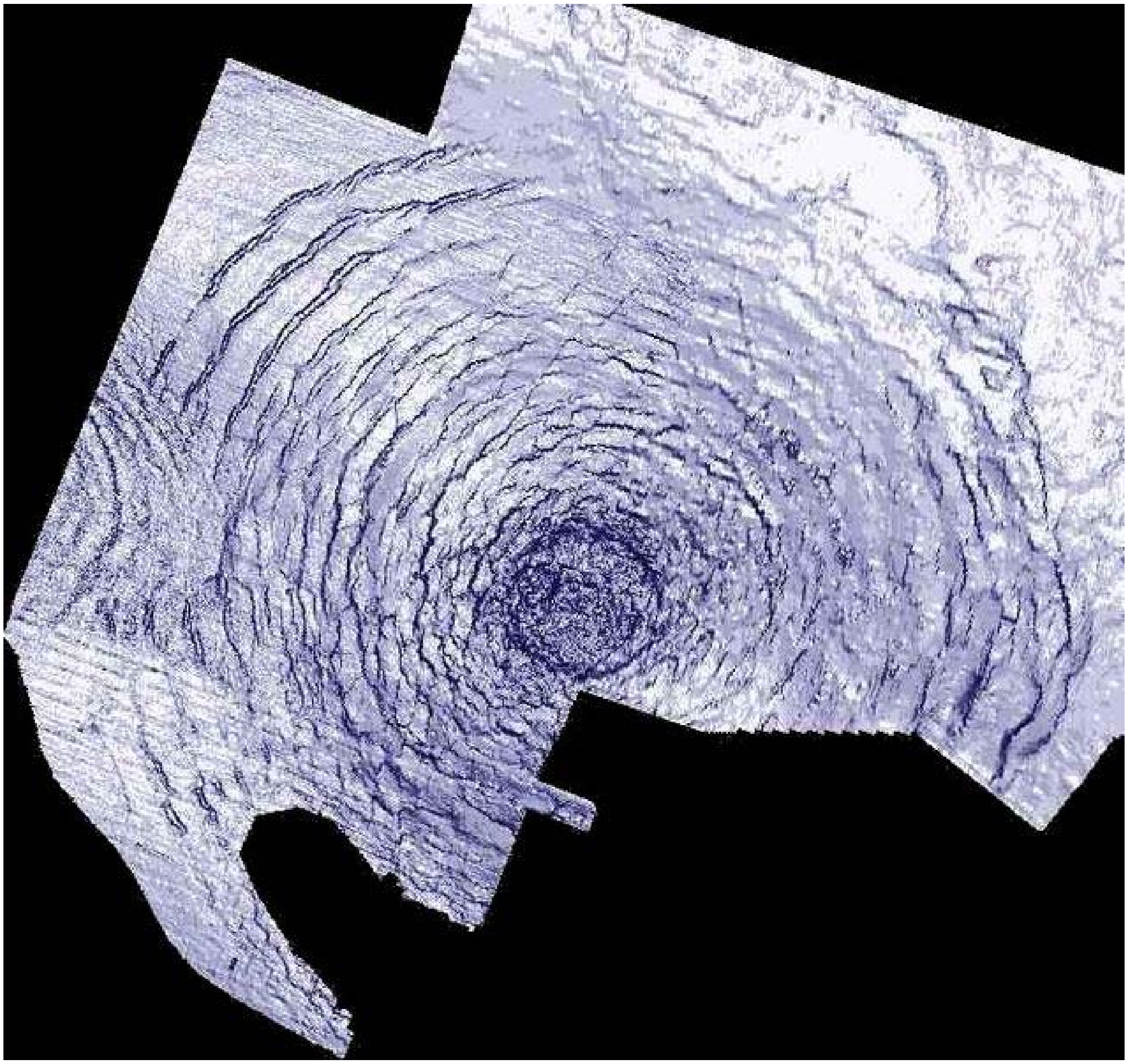
Analysis of regional 2D seismic lines and 3D seismic volumes by John Underhill, a geologist at the University of Edinburgh, led to the counterproposal that withdrawal of Upper Permian (Zechstein Supergroup) salt at depth was in fact a better explanation. Underhill found that all layers of rock down to the Permian (with an age of about 250 million years) are synclinically folded, and that sediments of Tertiary age at the crater onlap its sides and thicken into its axis, suggesting that the salt was moving (a process called halokinesis) while Tertiary sediments were being laid down.

In 2007, Underhill continued to present evidence that he argues does not support the impact hypothesis. After analyzing seismic data over a wide region, he proposed that Silverpit was just one of many similar features related to the withdrawal of the Permian-age Zechstein salt. This result was presented at the April 2007 annual meeting of the American Association of Petroleum Geologists

Underhill then focused his research attention upon understanding why the salt moves where it does when it does and why the so-called crater took the form that it did. This led him to publish a peer-review article in the journal, *Petroleum Geoscience* in August 2009 in which he outlined the evidence for an intrusion-related salt withdrawal cause for the feature's formation.

In October 2009, an open debate of the motion that "the Silverpit Crater was formed by meteor impact" was held at the Geological Society of London. Simon Stewart gave the case for the motion and John Underhill presented the case against. The outcome was overwhelming support for Underhill's alternative genesis through melt-induced salt withdrawal.

Structure



Seismic data showing the crater and its concentric ring structure

Silverpit crater is about 3 km wide at the top Cretaceous level. Unusually for a terrestrial crater, it is surrounded by a set of concentric rings, which extend to about 10 km radius from the centre. These rings give the crater a somewhat similar appearance to Valhalla crater on Jupiter's moon Callisto, and other craters on Europa. Normally, multi-ringed craters tend to be much larger than Silverpit, and so, if the impact hypothesis is correct, the origin of Silverpit's rings is subject to debate. A complicating factor is that almost all known impact craters are on land, despite the fact that two-thirds of impacting objects will land in oceans and seas, so the results of impacts on water are much less well established than those of impacts on land. Compare the Chesapeake Bay impact crater, probably the most thoroughly studied marine impact zone.

One possibility is that after the impact excavated a bowl-shaped depression, soft material surrounding it slumped towards the centre, leaving the concentric rings. It is thought that for this to happen, the soft material would have to be quite a thin layer, with more brittle material on top. A thin layer of mobile material beneath a solid crust is easy to understand in the context of icy moons, but is not a common occurrence on the rocky bodies of the solar system. One suggestion is that overpressured chalk below the surface may have acted as the soft mobile layer.

The impact

If one assumes the meteor impact theory is right, the size of the crater can be combined with assumptions about the speed of an impacting object to estimate the size of the impactor itself. Impacting objects are generally moving at speeds of the order of 20–50 km/s, and at these speeds an object about 120 m across and with a mass of 2.0×10^9 kg would be required to form a Silverpit-sized crater, if the object was rocky. If it had been a comet, the crater would have been larger.

For comparison, the object which struck the Earth at Chicxulub is estimated to have measured approximately 9.6 km across, while the object responsible for the Tunguska event in 1908 is thought to have been a comet or asteroid about 60 m across, with a mass of about 4×10^8 kg.

An object 120 m across smashing into the sea at many kilometres per second would generate enormous tsunamis. Scientists are currently searching for any evidence of large tsunamis in the surrounding areas dating from around that time, but no such evidence has been uncovered yet.

Age

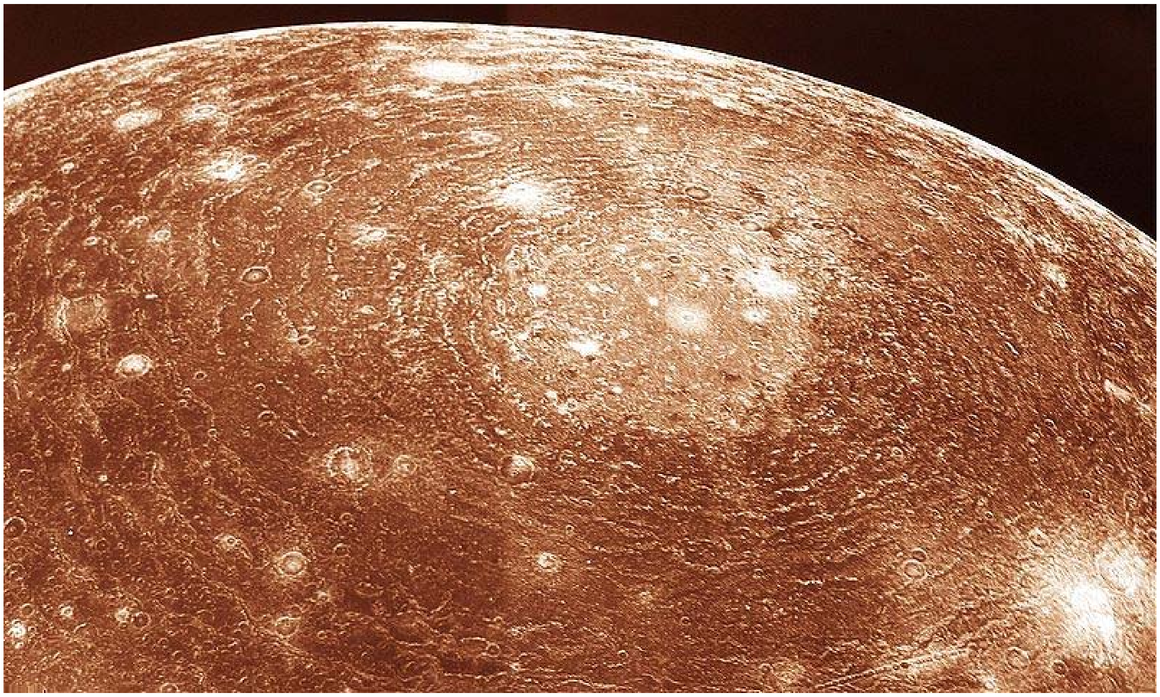
The position of the crater within the layers of rock and sediment on the sea floor could in theory be used to constrain its age: sediments laid down before the crater's formation might conceivably be disturbed by the impact, while those laid down afterwards will not. In their discovery paper, Allen and Stewart stated that Silverpit was formed in Cretaceous chalk and Jurassic shale, but is covered by an undisturbed layer of Tertiary sediment. The

Cretaceous Period ended about 65 million years ago, but, on the evidence of nearby boreholes, the lowermost Tertiary sediments appear to be absent. Thus the age of the Silverpit event was initially stated to lie somewhere between 65 and 60 million years before present. However, after a more detailed apprasial of the seismic data, Allen and Stewart gave a more cautious estimate of the age as between 74 – 45 million years (Late Cretaceous – Eocene).

The stratigraphic method of estimating the age of a crater is somewhat crude and imprecise, and the result is questioned by Underhill's non-impact hypothesis. Assuming an impact origin, other possible ways of dating the event include looking for evidence of ejecta material such as tektites, and deposits from the hypothesised tsunami, which might be found anywhere around the North Sea basin. As well as allowing a more accurate age determination, finding such evidence would also strengthen the impact hypothesis. Two nearby oil exploration wells penetrate the ring system, yet cutting samples from these fail to provide any independent support for the meteor theory, thus weakening the case for it being due to an extraterrestrial body.

Analysis of samples taken directly from the central crater would also assist age determination as well as confirm one or other of the proposed theories; until this has occurred Silverpit cannot be confirmed as an impact structure.

Part of a multiple impact?



Silverpit bears a stronger resemblance to Valhalla crater on Jupiter's moon Callisto than it does to other terrestrial craters

The early estimate of the age of the Silverpit event, stated as 65 – 60 million years before present, overlaps with the age of the Chicxulub impact, which occurred 65 million years ago and probably played a major role in the extinction of the dinosaurs. Several other large impact craters of around the same age have been discovered, all between latitudes 20°N and 70°N, leading to the speculative hypothesis that the Chicxulub impact may have been only one of several impacts that happened all at the same time.

The collision of Comet Shoemaker-Levy 9 with Jupiter in 1994 proved that gravitational interactions can fragment a comet, giving rise to many impacts over a period of a few days if the comet fragments should collide with a planet. Comets frequently undergo gravitational interactions with the gas giants, and similar disruptions and collisions are very likely to have occurred in the past.

While this scenario may have occurred on Earth 65 million years ago, evidence for this hypothesis is not strong. In particular, the ages of some of the possibly related craters are only known to an accuracy of a few million years. Also, the now widely held previously stated belief that Silverpit was not formed by bolide impact eliminates the possibility of it being involved in this hypothesis. Even if it were formed by bolide impact, the increased uncertainty in the age estimate for Silverpit to 74 – 45 million years further weakens the hypothesis.

Chapter- 7

Tyrannosaurus (Dinosaurs of Cretaceous Period)

Tyrannosaurus
Fossil range: Late Cretaceous, 67–65.5 Ma

Cast of a specimen nicknamed "Stan" (specimen BHI 3033), at Manchester Museum

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia

Superorder:	Dinosauria
Order:	Saurischia
Suborder:	Theropoda
Family:	†Tyrannosauridae
Subfamily:	†Tyrannosaurinae
Tribe:	†**Tyrannosaurini** Osborn, 1906
Genus:	†***Tyrannosaurus*** Osborn, 1905
Species:	†***T. rex*** Osborn, 1905

Synonyms

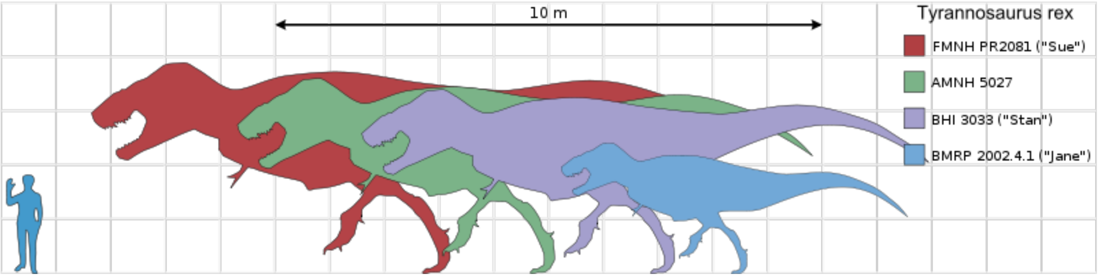
- *Manospondylus gigas* Cope, 1892
- *Dynamosaurus imperiosus* Osborn, 1905
- *Nanotyrannus lancensis*? (Gilmore, 1946) Bakker, Williams & Currie, 1988 [originally *Gorgosaurus*]
- *Aublysodon molnari* Paul, 1988
- *Dinotyrannus megagracilis* Olshevsky, 1995
- *Stygivenator molnari* (Paul, 1988) Olshevsky, 1995

Tyrannosaurus meaning "tyrant lizard", from Greek τυράννος (*tyrannos*, "tyrant") and σαύρος' (*sauros*, "lizard")), is a genus of theropod dinosaur. The species ***Tyrannosaurus rex*** (*rex* meaning "king" in Latin), commonly abbreviated to ***T. rex***, is a fixture in popular culture. It lived throughout what is now western North America, with a much wider range than other tyrannosaurids. Fossils are found in a variety of rock formations dating to the last two million years of the Cretaceous Period, 67 to 65.5 million years ago. It was among the last non-avian dinosaurs to exist prior to the Cretaceous–Tertiary extinction event.

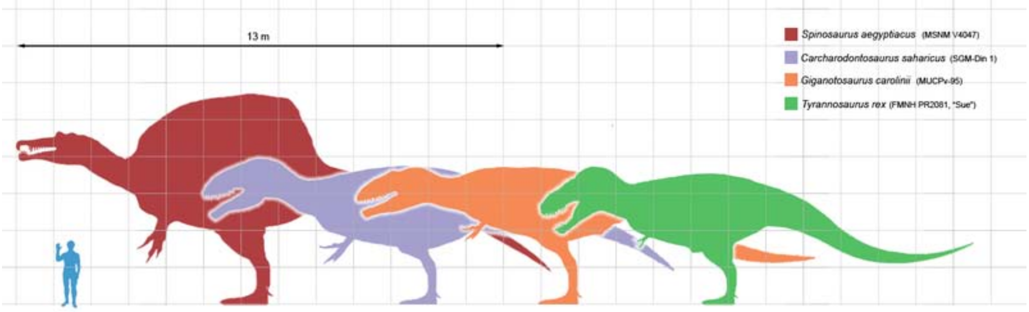
Like other tyrannosaurids, *Tyrannosaurus* was a bipedal carnivore with a massive skull balanced by a long, heavy tail. Relative to the large and powerful hindlimbs, *Tyrannosaurus* forelimbs were small, though unusually powerful for their size, and bore two clawed digits. Although other theropods rivaled or exceeded *Tyrannosaurus rex* in size, it was the largest known tyrannosaurid and one of the largest known land predators, measuring up to 12.8 m (42 ft) in length, up to 4 metres (13 ft) tall at the hips, and up to 6.8 metric tons (7.5 short tons) in weight. By far the largest carnivore in its environment, *Tyrannosaurus rex* may have been an apex predator, preying upon hadrosaurs and ceratopsians, although some experts have suggested it was primarily a scavenger. The debate over *Tyrannosaurus* as apex predator or scavenger is among the longest running debates in paleontology.

More than 30 specimens of *Tyrannosaurus rex* have been identified, some of which are nearly complete skeletons. Soft tissue and proteins have been reported in at least one of these specimens. The abundance of fossil material has allowed significant research into many aspects of its biology, including life history and biomechanics. The feeding habits, physiology and potential speed of *Tyrannosaurus rex* are a few subjects of debate. Its taxonomy is also controversial, with some scientists considering *Tarbosaurus bataar* from Asia to represent a second species of *Tyrannosaurus* and others maintaining *Tarbosaurus* as a separate genus. Several other genera of North American tyrannosaurids have also been synonymized with *Tyrannosaurus*.

Description



Size of various specimens compared with a human

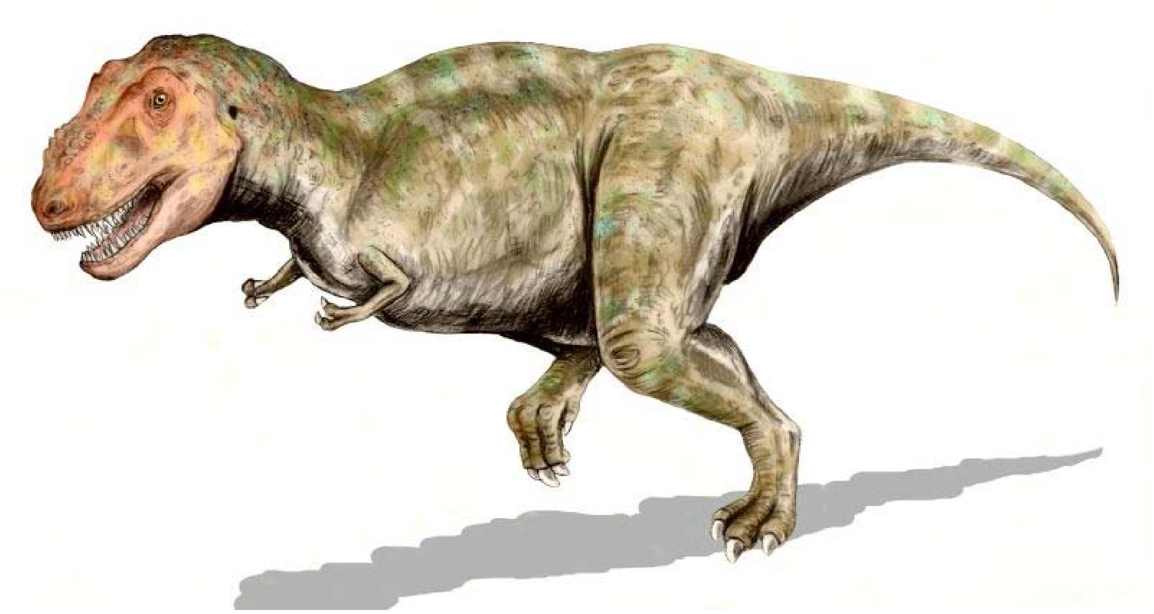


Size (in green) compared with selected giant theropods

Tyrannosaurus rex was one of the largest land carnivores of all time; the largest complete specimen, FMNH PR2081 ("Sue"), measured 12.8 metres (42 ft) long, and was 4.0 metres (13.1 ft) tall at the hips. Mass estimates have varied widely over the years, from more than 7.2 metric tons (7.9 short tons), to less than 4.5 metric tons (5.0 short tons), with most modern estimates ranging between 5.4 and 6.8 metric tons (6.0 and 7.5 short tons). Packard *et al.* (2009) tested dinosaur mass estimation procedures on elephants and concluded that dinosaur estimations are flawed and produce over-estimations; thus, the weight of *Tyrannosaurus* could be much less than usually estimated.

Although *Tyrannosaurus rex* was larger than the well known Jurassic theropod *Allosaurus*, it was slightly smaller than some other Cretaceous carnivores, such as *Spinosaurus* and *Giganotosaurus*.

The neck of *Tyrannosaurus rex* formed a natural S-shaped curve like that of other theropods, but was short and muscular to support the massive head. The forelimbs had only two clawed fingers, along with an additional small metacarpal representing the remnant of a third digit. In contrast the hind limbs were among the longest in proportion to body size of any theropod. The tail was heavy and long, sometimes containing over forty vertebrae, in order to balance the massive head and torso. To compensate for the immense bulk of the animal, many bones throughout the skeleton were hollow, reducing its weight without significant loss of strength.

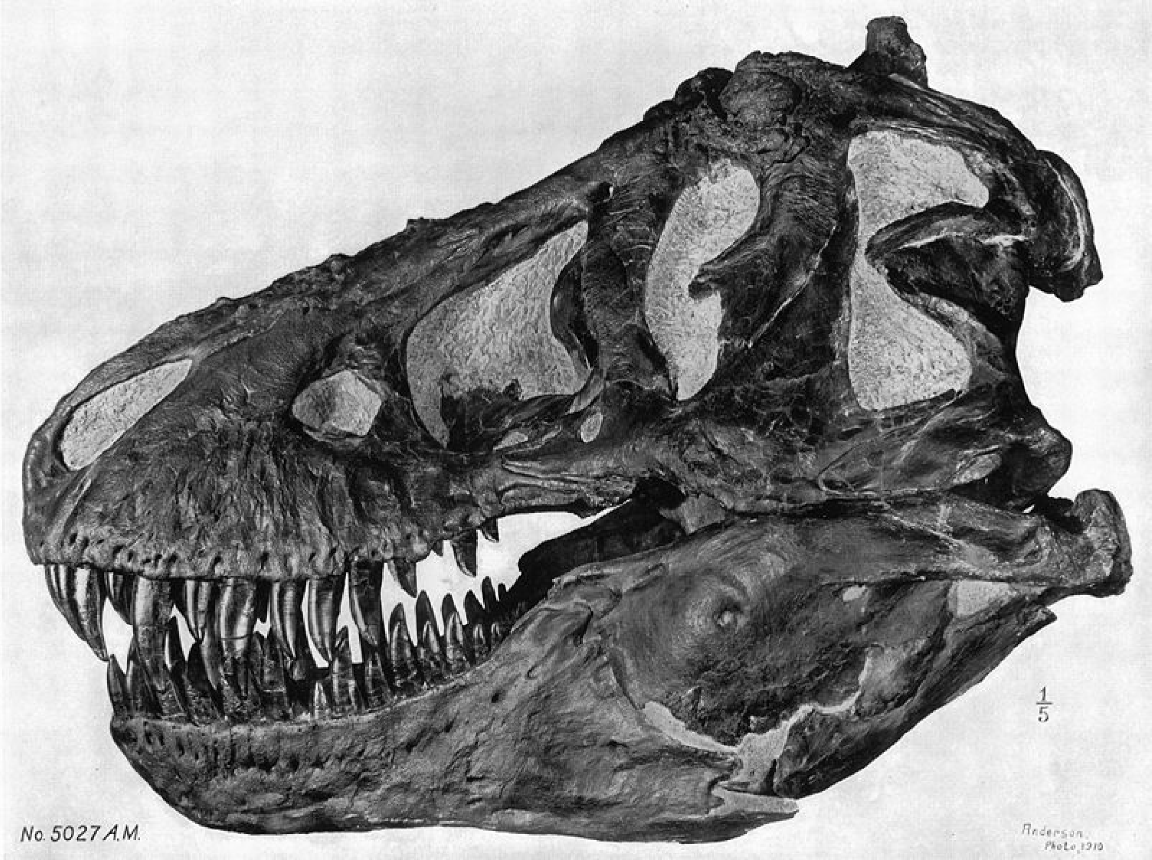


Restoration

The largest known *Tyrannosaurus rex* skulls measure up to 5 feet (1.5 m) in length. Large *fenestrae* (openings) in the skull reduced weight and provided areas for muscle attachment, as in all carnivorous theropods. But in other respects *Tyrannosaurus*' skull was significantly different from those of large non-tyrannosauroid theropods. It was extremely wide at the rear but had a narrow snout, allowing unusually good binocular vision. The skull bones were massive and the nasals and some other bones were fused, preventing movement between them; but many were pneumatized (contained a "honeycomb" of tiny air spaces) which may have made the bones more flexible as well as lighter. These and other skull-strengthening features are part of the tyrannosaurid trend towards an increasingly powerful bite, which easily surpassed that of all non-tyrannosaurids. The tip of the upper jaw was U-shaped (most non-tyrannosauroid carnivores had V-shaped upper jaws), which increased the amount of tissue and bone a tyrannosaur could rip out with one bite, although it also increased the stresses on the front teeth.

The teeth of *Tyrannosaurus rex* displayed marked heterodonty (differences in shape). The premaxillary teeth at the front of the upper jaw were closely packed, D-shaped in cross-section, had reinforcing ridges on the rear surface, were incisiform (their tips were chisel-like blades) and curved backwards. The D-shaped cross-section, reinforcing ridges and backwards curve reduced the risk that the teeth would snap when *Tyrannosaurus* bit and pulled. The remaining teeth were robust, like "lethal bananas" rather than daggers; more widely spaced and also had reinforcing ridges. Those in the upper jaw were larger than those in all but the rear of the lower jaw. The largest found so far is estimated to have been 30 centimetres (12 in) long including the root when the animal was alive, making it the largest tooth of any carnivorous dinosaur yet found.

Classification



Profile view of a skull (AMNH 5027)

Tyrannosaurus is the type genus of the superfamily Tyrannosauroidea, the family Tyrannosauridae, and the subfamily Tyrannosaurinae; in other words it is the standard by which paleontologists decide whether to include other species in the same group. Other members of the tyrannosaurine subfamily include the North American *Daspletosaurus* and the Asian *Tarbosaurus*, both of which have occasionally been synonymized with *Tyrannosaurus*. Tyrannosaurids were once commonly thought to be descendants of earlier large theropods such as megalosaurs and carnosaurs, although more recently they were reclassified with the generally smaller coelurosaurs.

In 1955, Soviet paleontologist Evgeny Maleev named a new species, *Tyrannosaurus bataar*, from Mongolia. By 1965, this species had been renamed *Tarbosaurus bataar*. Despite the renaming, many phylogenetic analyses have found *Tarbosaurus bataar* to be the sister taxon of *Tyrannosaurus rex*, and it has often been considered an Asian species of *Tyrannosaurus*. A recent redescription of the skull of *Tarbosaurus bataar* has shown that it was much narrower than that of *Tyrannosaurus rex* and that during a bite, the distribution of stress in the skull would have been very different, closer to that of *Alioramus*, another Asian tyrannosaur. A related cladistic analysis found that *Alioramus*, not *Tyrannosaurus*, was the sister taxon of *Tarbosaurus*, which, if true, would suggest that *Tarbosaurus* and *Tyrannosaurus* should remain separate.

Reconstructed head and neck in the Naturhistorisches Museum in Vienna

Other tyrannosaurid fossils found in the same formations as *Tyrannosaurus rex* were originally classified as separate taxa, including *Aublysodon* and *Albertosaurus megagracilis*, the latter being named *Dinotyrannus megagracilis* in 1995. However, these fossils are now universally considered to belong to juvenile *Tyrannosaurus rex*. A small but nearly complete skull from Montana, 60 centimetres (2.0 ft) long, may be an exception. This skull was originally classified as a species of *Gorgosaurus* (*G. lancensis*) by Charles W. Gilmore in 1946, but was later referred to a new genus, *Nanotyrannus*. Opinions remain divided on the validity of *N. lancensis*. Many paleontologists consider the skull to belong to a juvenile *Tyrannosaurus rex*. There are minor differences between the two species, including the higher number of teeth in *N. lancensis*, which lead some scientists to recommend keeping the two genera separate until further research or discoveries clarify the situation.

Manospondylus

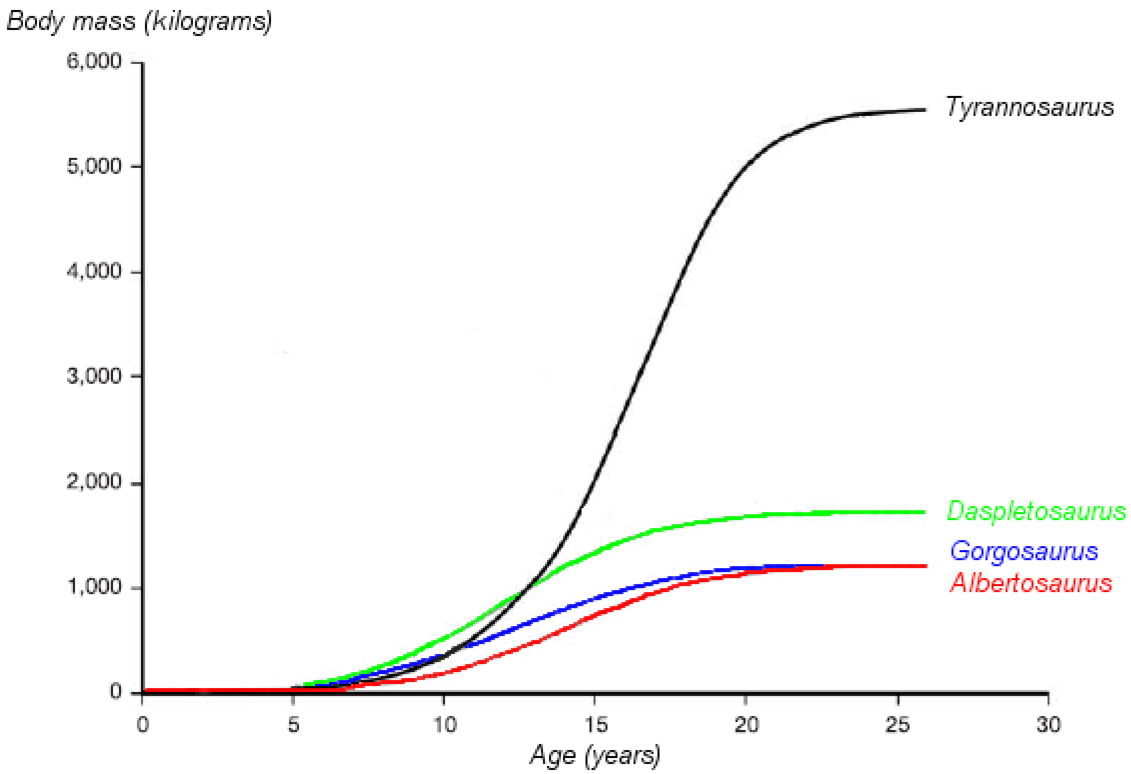
Skull of the type specimen (CM 9380) at the Carnegie Museum of Natural History. This was heavily and inaccurately restored with plaster using *Allosaurus* as a model

The first named fossil specimen which can be attributed to *Tyrannosaurus rex* consists of two partial vertebrae (one of which has been lost) found by Edward Drinker Cope in 1892. Cope believed that they belonged to an "agathaumid" (ceratopsid) dinosaur, and named them *Manospondylus gigas*, meaning "giant porous vertebra" in reverence to the numerous openings for blood vessels he found in the bone. The *M. gigas* remains were later identified as those of a theropod rather than a ceratopsid, and H.F. Osborn recognized the similarity between *M. gigas* and *Tyrannosaurus rex* as early as 1917. however, due to the fragmentary nature of the *Manospondylus* vertebrae, Osborn did not synonymize the two genera.

In June 2000, the Black Hills Institute located the type locality of *M. gigas* in South Dakota and unearthed more tyrannosaur bones there. These were judged to represent further remains of the same individual, and to be identical to those of *Tyrannosaurus rex*. According to the rules of the International Code of Zoological Nomenclature (ICZN), the system that governs the scientific naming of animals, *Manospondylus gigas* should therefore have priority over *Tyrannosaurus rex*, because it was named first. However, the Fourth Edition of the ICZN, which took effect on 1 January 2000, states that "the prevailing usage must be maintained" when "the senior synonym or homonym has not been used as a valid name after 1899" and "the junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years ..." *Tyrannosaurus rex* may qualify as the valid name under these conditions and would most likely be considered a *nomen protectum* ("protected name") under the ICZN if it is ever formally published on, which it has not yet been. *Manospondylus gigas* could then be deemed a *nomen oblitum* ("forgotten name").

Paleobiology

Life history



A graph showing the hypothesized growth curve, body mass versus age (drawn in black, with other tyrannosaurids for comparison).

The identification of several specimens as juvenile *Tyrannosaurus rex* has allowed scientists to document ontogenetic changes in the species, estimate the lifespan, and determine how quickly the animals would have grown. The smallest known individual (LACM 28471, the "Jordan theropod") is estimated to have weighed only 30 kg (66 lb), while the largest, such as FMNH PR2081 ("Sue") most likely weighed over 5,400 kg (12,000 lb). Histologic analysis of *Tyrannosaurus rex* bones showed LACM 28471 had aged only 2 years when it died, while "Sue" was 28 years old, an age which may have been close to the maximum for the species.

Histology has also allowed the age of other specimens to be determined. Growth curves can be developed when the ages of different specimens are plotted on a graph along with their mass. A *Tyrannosaurus rex* growth curve is S-shaped, with juveniles remaining under 1,800 kg (4,000 lb) until approximately 14 years of age, when body size began to increase dramatically. During this rapid growth phase, a young *Tyrannosaurus rex* would gain an average of 600 kg (1,300 lb) a year for the next four years. At 18 years of age, the curve plateaus again, indicating that growth slowed dramatically. For example, only 600 kg (1,300 lb) separated the 28-year-old "Sue" from a 22-year-old Canadian specimen (RTMP 81.12.1). Another recent histological study performed by different workers corroborates these results, finding that rapid growth began to slow at around 16 years of age. This sudden change in growth rate may indicate physical maturity, a hypothesis which is supported by the discovery of medullary tissue in the femur of a 16 to 20-year-old *Tyrannosaurus rex* from Montana (MOR 1125, also known as "B-rex"). Medullary tissue is found only in female birds during ovulation, indicating that "B-rex" was of reproductive age. Further study indicates an age of 18 for this specimen. Other tyrannosaurids exhibit extremely similar growth curves, although with lower growth rates corresponding to their lower adult sizes.

Over half of the known *Tyrannosaurus rex* specimens appear to have died within six years of reaching sexual maturity, a pattern which is also seen in other tyrannosaurs and in some large, long-lived birds and mammals today. These species are characterized by high infant mortality rates, followed by relatively low mortality among juveniles. Mortality increases again following sexual maturity, partly due to the stresses of reproduction. One study suggests that the rarity of juvenile *Tyrannosaurus rex* fossils is due in part to low juvenile mortality rates; the animals were not dying in large numbers at these ages, and so were not often fossilized. However, this rarity may also be due to the incompleteness of the fossil record or to the bias of fossil collectors towards larger, more spectacular specimens.

Sexual dimorphism

Skeleton casts mounted in a mating position, Jurassic Museum of Asturias.

As the number of specimens increased, scientists began to analyze the variation between individuals and discovered what appeared to be two distinct body types, or *morphs*, similar to some other theropod species. As one of these morphs was more solidly built, it was termed the 'robust' morph while the other was termed 'gracile.' Several morphological differences associated with the two morphs were used to analyze sexual dimorphism in *Tyrannosaurus rex*, with the 'robust' morph usually suggested to be female. For example, the pelvis of several 'robust' specimens seemed to be wider, perhaps to allow the passage of eggs. It was also thought that the 'robust' morphology correlated with a reduced chevron on the first tail vertebra, also ostensibly to allow eggs to pass out of the reproductive tract, as had been erroneously reported for crocodiles.

In recent years, evidence for sexual dimorphism has been weakened. A 2005 study reported that previous claims of sexual dimorphism in crocodile chevron anatomy were in error, casting doubt on the existence of similar dimorphism between *Tyrannosaurus rex* genders. A full-sized chevron was discovered on the first tail vertebra of "Sue," an extremely robust individual, indicating that this feature could not be used to differentiate the two morphs anyway. As *Tyrannosaurus rex* specimens have been found from Saskatchewan to New Mexico, differences between individuals may be indicative of geographic variation rather than sexual dimorphism. The differences could also be age-related, with 'robust' individuals being older animals.

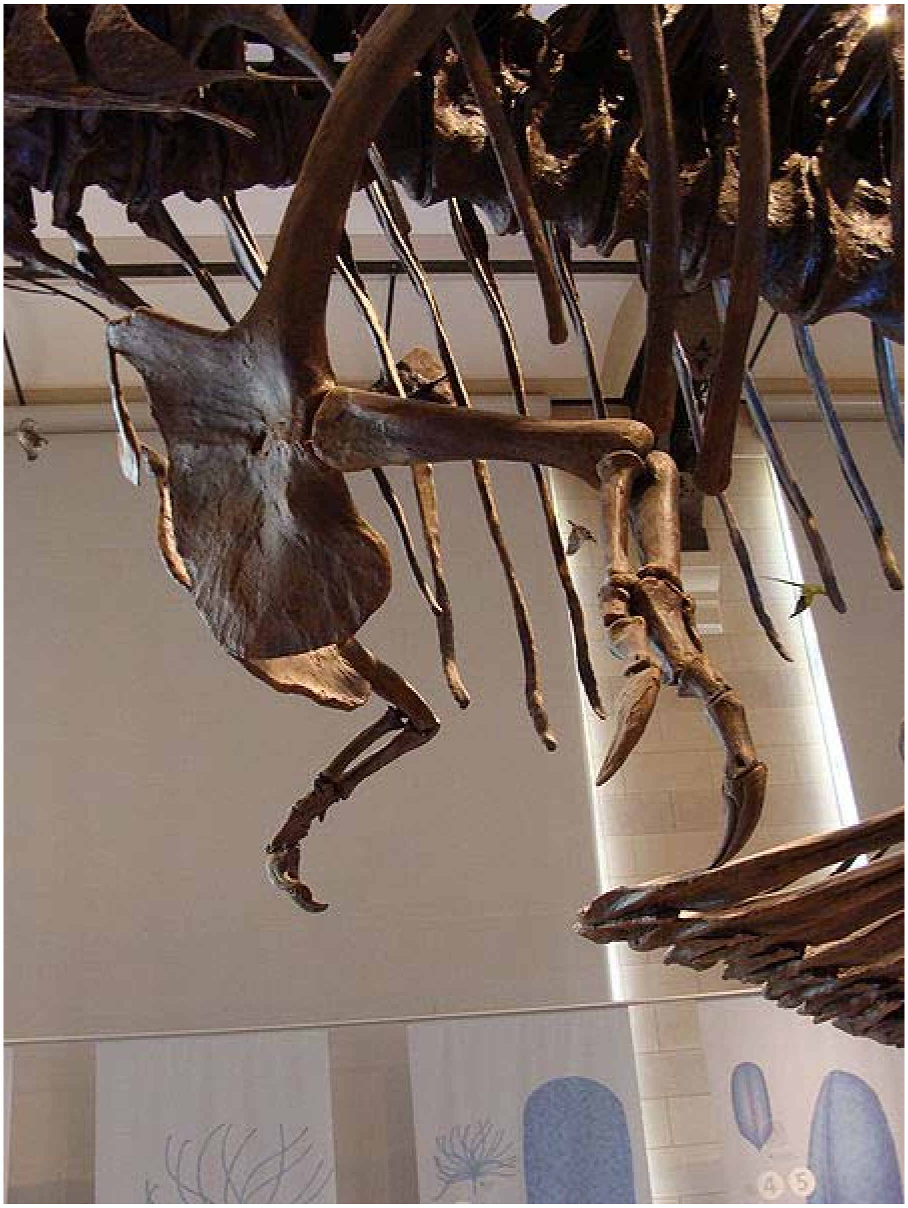
Only a single *Tyrannosaurus rex* specimen has been conclusively shown to belong to a specific gender. Examination of "B-rex" demonstrated the preservation of soft tissue within several bones. Some of this tissue has been identified as a medullary tissue, a specialized tissue grown only in modern birds as a source of calcium for the production of eggshell during ovulation. As only female birds lay eggs, medullary tissue is only found naturally in females, although males are capable of producing it when injected with female reproductive hormones like estrogen. This strongly suggests that "B-rex" was female, and that she died during ovulation. Recent research has shown that medullary tissue is never found in crocodiles, which are thought to be the closest living relatives of dinosaurs, aside from birds. The shared presence of medullary tissue in birds and theropod dinosaurs is further evidence of the close evolutionary relationship between the two.

Posture

Outdated reconstruction (by Charles R. Knight), showing upright pose

Like many bipedal dinosaurs, *Tyrannosaurus rex* was historically depicted as a 'living tripod', with the body at 45 degrees or less from the vertical and the tail dragging along the ground, similar to a kangaroo. This concept dates from Joseph Leidy's 1865 reconstruction of *Hadrosaurus*, the first to depict a dinosaur in a bipedal posture. Henry Fairfield Osborn, former president of the American Museum of Natural History (AMNH) in New York City, who believed the creature stood upright, further reinforced the notion after unveiling the first complete *Tyrannosaurus rex* skeleton in 1915. It stood in this upright pose for nearly a century, until it was dismantled in 1992. By 1970, scientists realized this pose was incorrect and could not have been maintained by a living animal, as it would have resulted in the dislocation or weakening of several joints, including the hips and the articulation between the head and the spinal column. The inaccurate AMNH mount inspired similar depictions in many films and paintings (such as Rudolph Zallinger's famous mural *The Age Of Reptiles* in Yale University's Peabody Museum of Natural History) until the 1990s, when films such as *Jurassic Park* introduced a more accurate posture to the general public. Modern representations in museums, art, and film show *Tyrannosaurus rex* with its body approximately parallel to the ground and tail extended behind the body to balance the head.

Arms



Closeup of forelimb

When *Tyrannosaurus rex* was first discovered, the humerus was the only element of the forelimb known. For the initial mounted skeleton as seen by the public in 1915, Osborn substituted longer, three-fingered forelimbs like those of *Allosaurus*. However, a year earlier, Lawrence Lambe described the short, two-fingered forelimbs of the closely related *Gorgosaurus*. This strongly suggested that *Tyrannosaurus rex* had similar forelimbs, but this hypothesis was not confirmed until the first complete *Tyrannosaurus rex* forelimbs were identified in 1989, belonging to MOR 555 (the "Wankel rex"). The remains of "Sue" also include complete forelimbs. *Tyrannosaurus rex* arms are very small relative to overall body size, measuring only 1 metre (3.3 ft) long. However, they are not vestigial but instead show large areas for muscle attachment, indicating considerable strength. This was recognized as early as 1906 by Osborn, who speculated that the forelimbs may have been used to grasp a mate during copulation. It has also been suggested that the forelimbs were used to assist the animal in rising from a prone position. Another possibility is that the forelimbs held struggling prey while it was dispatched by the tyrannosaur's enormous jaws. This hypothesis may be supported by biomechanical analysis.

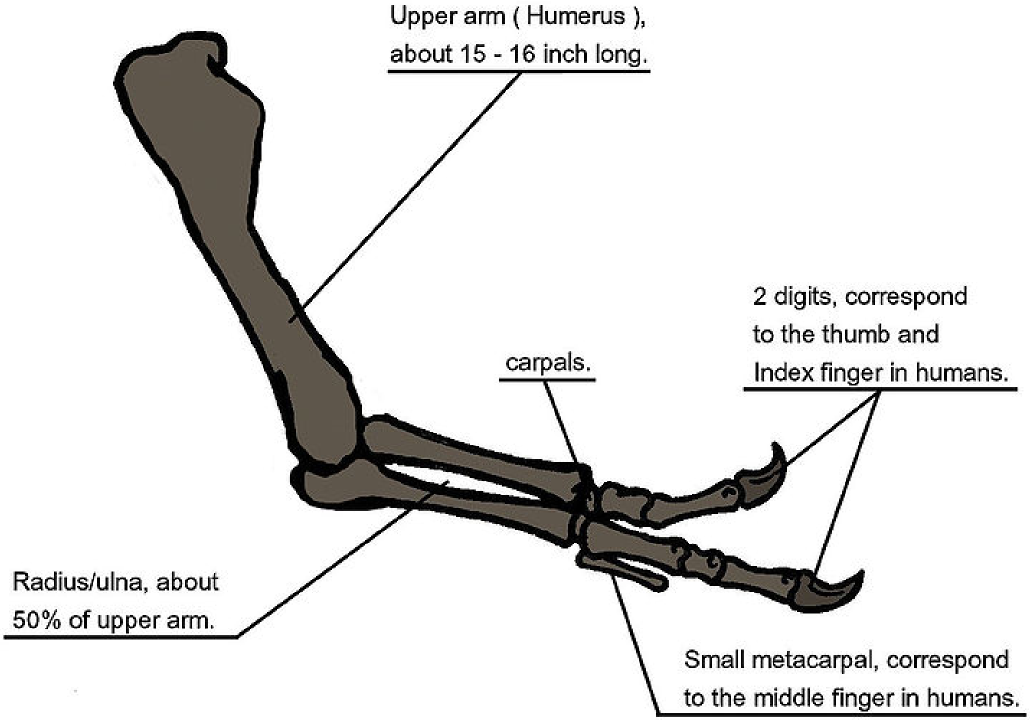


Diagram illustrating arm anatomy

Tyrannosaurus rex forelimb bones exhibit extremely thick cortical bone, indicating that they were developed to withstand heavy loads. The biceps brachii muscle of a full-grown

Tyrannosaurus rex was capable of lifting 199 kilograms (439 lb) by itself; this number would only increase with other muscles (like the brachialis) acting in concert with the biceps. A *Tyrannosaurus rex* forearm also had a reduced range of motion, with the shoulder and elbow joints allowing only 40 and 45 degrees of motion, respectively. In contrast, the same two joints in *Deinonychus* allow up to 88 and 130 degrees of motion, respectively, while a human arm can rotate 360 degrees at the shoulder and move through 165 degrees at the elbow. The heavy build of the arm bones, extreme strength of the muscles, and limited range of motion may indicate a system evolved to hold fast despite the stresses of a struggling prey animal.

Soft tissue

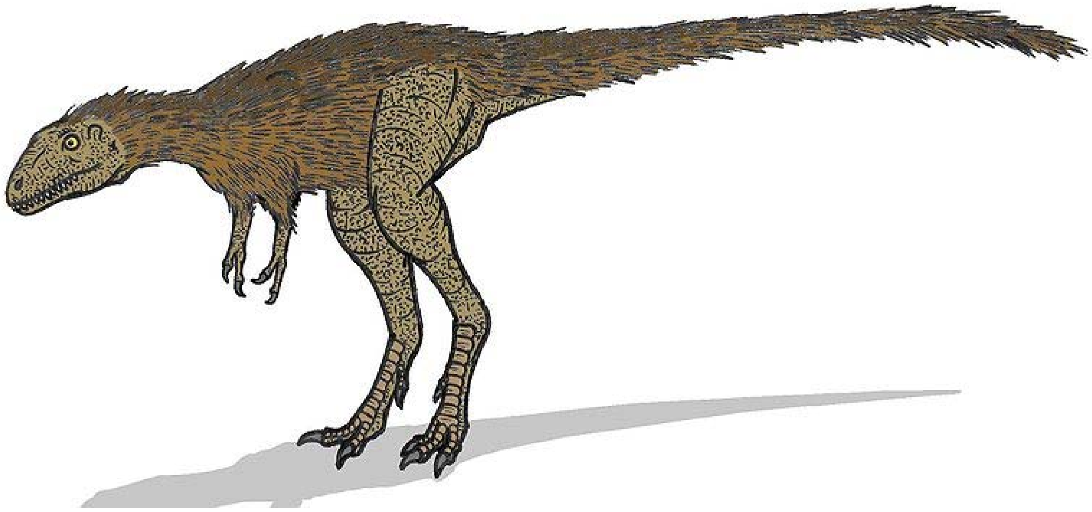
In the March 2005 issue of *Science*, Mary Higby Schweitzer of North Carolina State University and colleagues announced the recovery of soft tissue from the marrow cavity of a fossilized leg bone, from a *Tyrannosaurus rex*. The bone had been intentionally, though reluctantly, broken for shipping and then not preserved in the normal manner, specifically because Schweitzer was hoping to test it for soft tissue. Designated as the Museum of the Rockies specimen 1125, or MOR 1125, the dinosaur was previously excavated from the Hell Creek Formation. Flexible, bifurcating blood vessels and fibrous but elastic bone matrix tissue were recognized. In addition, microstructures resembling blood cells were found inside the matrix and vessels. The structures bear resemblance to ostrich blood cells and vessels. Whether an unknown process, distinct from normal fossilization, preserved the material, or the material is original, the researchers do not know, and they are careful not to make any claims about preservation. If it is found to be original material, any surviving proteins may be used as a means of indirectly guessing some of the DNA content of the dinosaurs involved, because each protein is typically created by a specific gene. The absence of previous finds may merely be the result of people assuming preserved tissue was impossible, therefore simply not looking. Since the first, two more tyrannosaurs and a hadrosaur have also been found to have such tissue-like structures. Research on some of the tissues involved has suggested that birds are closer relatives to tyrannosaurs than other modern animals.

In studies reported in the journal *Science* in April 2007, Asara and colleagues concluded that seven traces of collagen proteins detected in purified *Tyrannosaurus rex* bone most closely match those reported in chickens, followed by frogs and newts. The discovery of proteins from a creature tens of millions of years old, along with similar traces the team found in a mastodon bone at least 160,000 years old, upends the conventional view of fossils and may shift paleontologists' focus from bone hunting to biochemistry. Until these finds, most scientists presumed that fossilization replaced all living tissue with inert minerals. Paleontologist Hans Larsson of McGill University in Montreal, who was not part of the studies, called the finds "a milestone", and suggested that dinosaurs could "enter the field of molecular biology and really slingshot paleontology into the modern world."

Subsequent studies in April 2008 confirmed the close connection of *Tyrannosaurus rex* to modern birds. Postdoctoral biology researcher Chris Organ at Harvard University announced, "With more data, they would probably be able to place *T. rex* on the evolutionary tree between alligators and chickens and ostriches." Co-author John M. Asara added, "We also show that it groups better with birds than modern reptiles, such as alligators and green anole lizards."

The presumed soft tissue was called into question by Thomas Kaye of the University of Washington and his co-authors in 2008. They 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. However, Schweitzer has strongly criticised Hayes' claims and maintains that she really did find blood cells, and argues that there's no reported evidence that biofilms can produce branching, hollow tubes like those noted in her study.

Skin and feathers



Restoration of a young *Tyrannosaurus*, depicted with filamentous feathers.

In 2004, the scientific journal *Nature* published a report describing an early tyrannosauroid, *Dilong paradoxus*, from the famous Yixian Formation of China. As with many other theropods discovered in the Yixian, the fossil skeleton was preserved with a coat of filamentous structures which are commonly recognized as the precursors of feathers. It has also been proposed that *Tyrannosaurus* and other closely related tyrannosaurids had such protofeathers. However, skin impressions from large tyrannosaurid specimens show mosaic scales. While it is possible that protofeathers existed on parts of the body which have not been preserved, a lack of insulatory body covering is consistent with modern multi-ton mammals such as elephants, hippopotamus, and most species of rhinoceros. As an object increases in size, its ability to retain heat increases due to its decreasing surface area-to-volume ratio. Therefore, as large animals evolve in or disperse into warm climates, a coat of fur or feathers loses its selective advantage for thermal insulation and can instead become a disadvantage, as the insulation traps excess heat inside the body, possibly overheating the animal. Protofeathers may also have been secondarily lost during the evolution of large tyrannosaurids like *Tyrannosaurus*, especially in warm Cretaceous climates.

Thermoregulation

Tyrannosaurus, like most dinosaurs, was long thought to have an ectothermic ("cold-blooded") reptilian metabolism. The idea of dinosaur ectothermy was challenged by scientists like Robert T. Bakker and John Ostrom in the early years of the "Dinosaur Renaissance", beginning in the late 1960s. *Tyrannosaurus rex* itself was claimed to have been endothermic ("warm-blooded"), implying a very active lifestyle. Since then, several paleontologists have sought to determine the ability of *Tyrannosaurus* to regulate its body temperature. Histological evidence of high growth rates in young *Tyrannosaurus rex*, comparable to those of mammals and birds, may support the hypothesis of a high metabolism. Growth curves indicate that, as in mammals and birds, *Tyrannosaurus rex* growth was limited mostly to immature animals, rather than the indeterminate growth seen in most other vertebrates.

Oxygen isotope ratios in fossilized bone are sometimes used to determine the temperature at which the bone was deposited, as the ratio between certain isotopes correlates with temperature. In one specimen, the isotope ratios in bones from different parts of the body indicated a temperature difference of no more than 4 to 5 °C (7 to 9 °F) between the vertebrae of the torso and the tibia of the lower leg. This small temperature range between the body core and the extremities was claimed by paleontologist Reese Barrick and geochemist William Showers to indicate that *Tyrannosaurus rex* maintained a constant internal body temperature (homeothermy) and that it enjoyed a metabolism somewhere between ectothermic reptiles and endothermic mammals. Other scientists have pointed out that the ratio of oxygen isotopes in the fossils today does not necessarily represent the same ratio in the distant past, and may have been altered during or after fossilization (diagenesis). Barrick and Showers have defended their conclusions in subsequent papers, finding similar results in another theropod dinosaur from a different continent and tens of millions of years earlier in time (*Giganotosaurus*). Ornithischian dinosaurs also showed evidence of homeothermy, while varanid lizards from the same formation did not. Even if *Tyrannosaurus rex* does exhibit evidence of homeothermy, it does not necessarily mean that it was endothermic. Such thermoregulation may also be explained by gigantothermy, as in some living sea turtles.

Footprints

Probable footprint from New Mexico

Two isolated fossilized footprints have been tentatively assigned to *Tyrannosaurus rex*. The first was discovered at Philmont Scout Ranch, New Mexico, in 1983 by American geologist Charles Pillmore. Originally thought to belong to a hadrosaurid, examination of the footprint revealed a large 'heel' unknown in ornithopod dinosaur tracks, and traces of what may have been a hallux, the dewclaw-like fourth digit of the tyrannosaur foot. The footprint was published as the ichnogenus *Tyrannosauripus pillmorei* in 1994, by Martin Lockley and Adrian Hunt. Lockley and Hunt suggested that it was very likely the track was made by a *Tyrannosaurus rex*, which would make it the first known footprint from this species. The track was made in what was once a vegetated wetland mud flat. It measures 83 centimetres (33 in) long by 71 centimetres (28 in) wide.

A second footprint that may have been made by a *Tyrannosaurus* was first reported in 2007 by British paleontologist Phil Manning, from the Hell Creek Formation of Montana. This second track measures 76 centimetres (30 in) long, shorter than the track described by Lockley and Hunt. Whether or not the track was made by *Tyrannosaurus* is unclear, though *Tyrannosaurus* and *Nanotyrannus* are the only large theropods known to have existed in the Hell Creek Formation. Further study of the track (a full description has not yet been published) will compare the Montana track with the one found in New Mexico.

Locomotion

Replica of a sequence of theropod footprints attributed to *Megalosaurus* at OUMNH. No such sequence has yet been reported for tyrannosaurs, making gait and speed estimates difficult.

There are two main issues concerning the locomotory abilities of *Tyrannosaurus*: how well it could turn; and what its maximum straight-line speed was likely to have been. Both are relevant to the debate about whether it was a hunter or a scavenger (see below).

Tyrannosaurus may have been slow to turn, possibly taking one to two seconds to turn only 45° — an amount that humans, being vertically oriented and tail-less, can spin in a fraction of a second. The cause of the difficulty is rotational inertia, since much of

Tyrannosaurus' mass was some distance from its center of gravity, like a human carrying a heavy timber — although it might have reduced the average distance by arching its back and tail and pulling its head and forelimbs close to its body, rather like the way ice skaters pull their arms closer in order to spin faster.

Scientists have produced a wide range of maximum speed estimates, mostly around 11 metres per second (40 km/h; 25 mph), but a few as low as 5–11 metres per second (18–40 km/h; 11–25 mph), and a few as high as 20 metres per second (72 km/h; 45 mph). Researchers have to rely on various estimating techniques because, while there are many tracks of very large theropods walking, so far none have been found of very large theropods running—and this absence *may* indicate that they did not run. Scientists who think that *Tyrannosaurus* was able to run point out that hollow bones and other features that would have lightened its body may have kept adult weight to a mere 4.5 metric tons (5.0 short tons) or so, or that other animals like ostriches and horses with long, flexible legs are able to achieve high speeds through slower but longer strides. Additionally, some have argued that *Tyrannosaurus* had relatively larger leg muscles than any animal alive today, which could have enabled fast running 40–70 kilometres per hour (25–43 mph).

Jack Horner and Don Lessem argued in 1993 that *Tyrannosaurus* was slow and probably could not run (no airborne phase in mid-stride), because its ratio of femur (thigh bone) to tibia (shin bone) length was greater than 1, as in most large theropods and like a modern elephant. However, Holtz (1998) noted that tyrannosaurids and some closely related groups had significantly longer distal hindlimb components (shin plus foot plus toes) relative to the femur length than most other theropods), and that tyrannosaurids and their close relatives had a tightly interlocked metatarsus that more effectively transmitted locomotory forces from the foot to the lower leg than in earlier theropods ("metatarsus" means the foot bones, which function as part of the leg in digitigrade animals). He therefore concluded that tyrannosaurids and their close relatives were the fastest large theropods.

Femur (thigh bone)
Tibia (shin bone)
Metatarsals (foot bones)
Dewclaw
Phalanges (toe bones)

Skeletal anatomy of a *T. rex* right leg

Christiansen (1998) estimated that the leg bones of *Tyrannosaurus* were not significantly stronger than those of elephants, which are relatively limited in their top speed and never actually run (there is no airborne phase), and hence proposed that the dinosaur's maximum speed would have been about 11 metres per second (40 km/h; 25 mph), which is about the speed of a human sprinter. But he also noted that such estimates depend on many dubious assumptions.

Farlow and colleagues (1995) have argued that a *Tyrannosaurus* weighing 5.4 metric tons (6.0 short tons) to 7.3 metric tons (8.0 short tons) would have been critically or even fatally injured if it had fallen while moving quickly, since its torso would have slammed into the ground at a deceleration of 6 *g* (six times the acceleration due to gravity, or about 60 meters/s^2) and its tiny arms could not have reduced the impact. However, giraffes have been known to gallop at 50 kilometres per hour (31 mph), despite the risk that they might break a leg or worse, which can be fatal even in a "safe" environment such as a zoo. Thus it is quite possible that *Tyrannosaurus* also moved fast when necessary and had to accept such risks.

Most recent research on *Tyrannosaurus* locomotion does not support speeds faster than 40 kilometres per hour (25 mph), i.e. moderate-speed running. For example, a 2002 paper in the journal *Nature* used a mathematical model (validated by applying it to three living animals, alligators, chickens, and humans; additionally later eight more species including emus and ostriches) to gauge the leg muscle mass needed for fast running (over 40 km/h or 25 mph). They found that proposed top speeds in excess of 40 kilometres per hour (25 mph) were unfeasible, because they would require very large leg muscles (more than approximately 40–86% of total body mass). Even moderately fast speeds would have required large leg muscles. This discussion is difficult to resolve, as it is unknown how large the leg muscles actually were in *Tyrannosaurus*. If they were smaller, only 18 kilometres per hour (11 mph) walking/jogging might have been possible.

A 6-tonne chicken would have needed leg muscles making up almost 100% of its body mass for running. Realistically, *T. rex* had the muscles to run at about 5 meters per second (18 km/h, 11 mph)

A study in 2007 used computer models to estimate running speeds, based on data taken directly from fossils, and claimed that *Tyrannosaurus rex* had a top running speed of 8 metres per second (29 km/h; 18 mph). An average professional football (soccer) player would be slightly slower, while a human sprinter can reach 12 metres per second (43 km/h; 27 mph). Note that these computer models predict a top speed of 17.8 metres per second (64 km/h; 40 mph) for a 3-kilogram (6.6 lb) *Compsognathus* (probably a juvenile individual).

Those who argue that *Tyrannosaurus* was incapable of running estimate the top speed of *Tyrannosaurus* at about 17 kilometres per hour (11 mph). This is still faster than its most likely prey species, hadrosaurids and ceratopsians. In addition, some advocates of the idea that *Tyrannosaurus* was a predator claim that tyrannosaur running speed is not important, since it may have been slow but still faster than its probable prey. However, Paul and Christiansen (2000) argued that at least the later ceratopsians had upright forelimbs and the larger species may have been as fast as rhinos. Healed *Tyrannosaurus* bite wounds on ceratopsian fossils are interpreted as evidence of attacks on living ceratopsians (see below). If the ceratopsians that lived alongside *Tyrannosaurus* were fast, that casts doubt on the argument that *Tyrannosaurus* did not have to be fast to catch its prey.

Feeding strategies

The debate about whether *Tyrannosaurus* was a predator or a pure scavenger is as old as the debate about its locomotion. Lambe (1917) described a good skeleton of *Tyrannosaurus*' close relative *Gorgosaurus* and concluded that it and therefore also *Tyrannosaurus* was a pure scavenger, because the *Gorgosaurus*' teeth showed hardly any wear. This argument is no longer taken seriously, because theropods replaced their teeth quite rapidly. Ever since the first discovery of *Tyrannosaurus* most scientists have speculated that it was a predator; like modern large predators it would readily scavenge or steal another predator's kill if it had the opportunity.

Noted hadrosaur expert Jack Horner is currently the major advocate of the idea that *Tyrannosaurus* was exclusively a scavenger and did not engage in active hunting at all. Horner has presented several arguments to support the pure scavenger hypothesis:

Cast of the braincase at the Australian Museum, Sydney

- Tyrannosaur arms are short when compared to other known predators. Horner argues that the arms were too short to make the necessary gripping force to hold on to prey.
- Tyrannosaurs had large olfactory bulbs and olfactory nerves (relative to their brain size). These suggest a highly developed sense of smell which could sniff out carcasses over great distances, as modern vultures do. Research on the olfactory bulbs of dinosaurs has shown that *Tyrannosaurus* had the most highly developed sense of smell of 21 sampled dinosaurs. Opponents of the pure scavenger hypothesis have used the example of vultures in the opposite way, arguing that the scavenger hypothesis is implausible because the only modern pure scavengers are large gliding birds, which use their keen senses and energy-efficient gliding to cover vast areas economically. However, researchers from Glasgow concluded that an ecosystem as productive as the current Serengeti would provide sufficient carrion for a large theropod scavenger, although the theropod might have had to be cold-blooded in order to get more calories from carrion than it spent on foraging. They also suggested that modern ecosystems like Serengeti have no large terrestrial scavengers because gliding birds now do the job much more efficiently, while large theropods did not face competition for the scavenger ecological niche from gliding birds.
- Tyrannosaur teeth could crush bone, and therefore could extract as much food (bone marrow) as possible from carcass remnants, usually the least nutritious parts. Karen Chin and colleagues have found bone fragments in coprolites (fossilized feces) that they attribute to tyrannosaurs, but point out that a

tyrannosaur's teeth were not well adapted to systematically chewing bone like hyenas do to extract marrow.

- Since at least some of *Tyrannosaurus*'s potential prey could move quickly, evidence that it walked instead of ran could indicate that it was a scavenger. On the other hand, recent analyses suggest that *Tyrannosaurus*, while slower than large modern terrestrial predators, may well have been fast enough to prey on large hadrosaurs and ceratopsians.

The eye-sockets faced mainly forwards, giving it good binocular vision

Other evidence suggests hunting behavior in *Tyrannosaurus*. The eye-sockets of tyrannosaurs are positioned so that the eyes would point forward, giving them binocular vision slightly better than that of modern hawks. Horner also pointed out that the tyrannosaur lineage had a history of steadily improving binocular vision. It is not obvious why natural selection would have favored this long-term trend if tyrannosaurs had been pure scavengers, which would not have needed the advanced depth perception that stereoscopic vision provides. In modern animals, binocular vision is found mainly in predators.

Restoration (based on MOR 980) with parasite infections, which might be the cause of scars seen in the skulls of several specimens that were previously explained by intraspecific attacks

A skeleton of the hadrosaurid *Edmontosaurus annectens* has been described from Montana with healed tyrannosaur-inflicted damage on its tail vertebrae. The fact that the damage seems to have healed suggests that the *Edmontosaurus* survived a tyrannosaur's attack on a living target, i.e. the tyrannosaur had attempted active predation. There is also evidence for an aggressive interaction between a *Triceratops* and a *Tyrannosaurus* in the form of partially healed tyrannosaur tooth marks on a *Triceratops* brow horn and squamosal (a bone of the neck frill); the bitten horn is also broken, with new bone growth after the break. It is not known what the exact nature of the interaction was, though: either animal could have been the aggressor. When examining Sue, paleontologist Pete Larson found a broken and healed fibula and tail vertebrae, scarred facial bones and a tooth from another *Tyrannosaurus* embedded in a neck vertebra. If correct, these might be strong evidence for aggressive behavior between tyrannosaurs but whether it would have been competition for food and mates or active cannibalism is unclear. However, further recent investigation of these purported wounds has shown that most are infections rather than injuries (or simply damage to the fossil after death) and the few injuries are too general to be indicative of intraspecific conflict. A 2009 study showed that holes in the skulls of several specimens might have been caused by *Trichomonas*-like parasites that commonly infect avians.

Some researchers argue that if *Tyrannosaurus* were a scavenger, another dinosaur had to be the top predator in the Amerasian Upper Cretaceous. Top prey was the larger marginocephalians and ornithopods. The other tyrannosaurids share so many characteristics that only small dromaeosaurs remain as feasible top predators. In this light, scavenger hypothesis adherents have suggested that the size and power of tyrannosaurs allowed them to steal kills from smaller predators. Most paleontologists accept that *Tyrannosaurus* was both an active predator and a scavenger like most large carnivores.

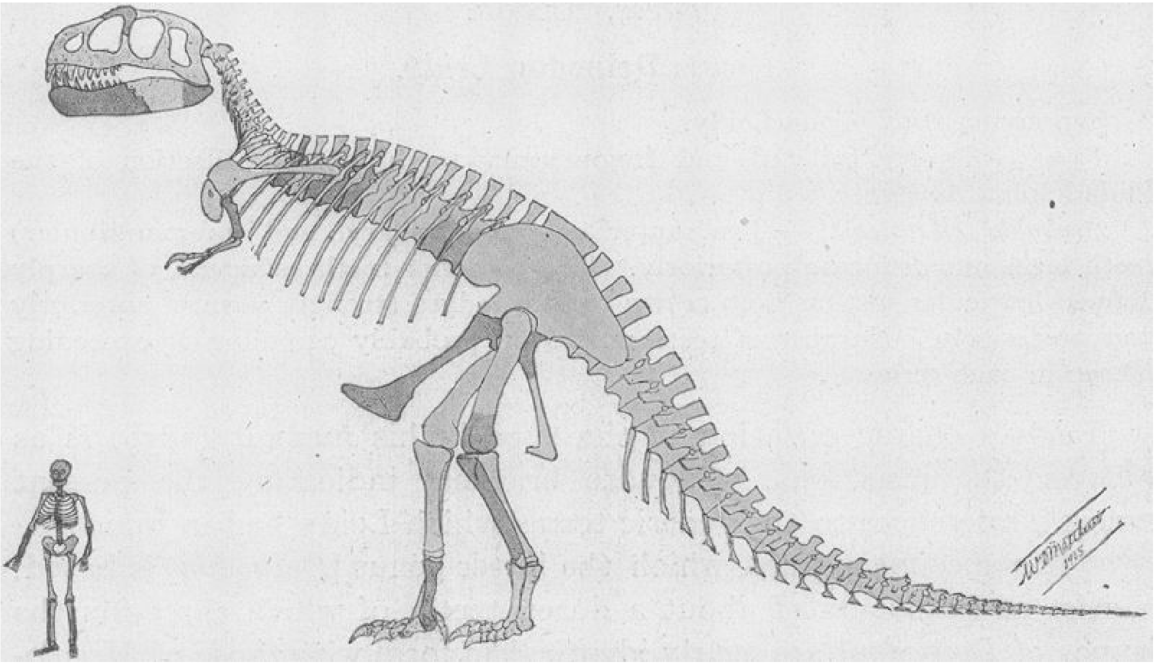
Cannibalism

A study from Currie, Horner, Erickson and Longrich in 2010 has been put forward as evidence of cannibalism in the genus *Tyrannosaurus*. They studied some *Tyrannosaurus* specimens with tooth marks in the bones, attributable to the same genus. The tooth marks were identified in the humerus, foot bones and metatarsals, and this was seen as evidence for opportunistic scavenging, rather than wounds caused by intraspecific combat. In a fight, they proposed it would be difficult to reach down to bite in the feet of a rival, making it more likely that the bitemarks were made in a carcass. As the bitemarks were made in body parts with relatively scantly amounts of flesh, it is suggested that the *Tyrannosaurus* was feeding on a cadaver in which the more fleshy parts already had been eaten up. They were also open to the possibility that other tyrannosaurids practiced cannibalism.

History

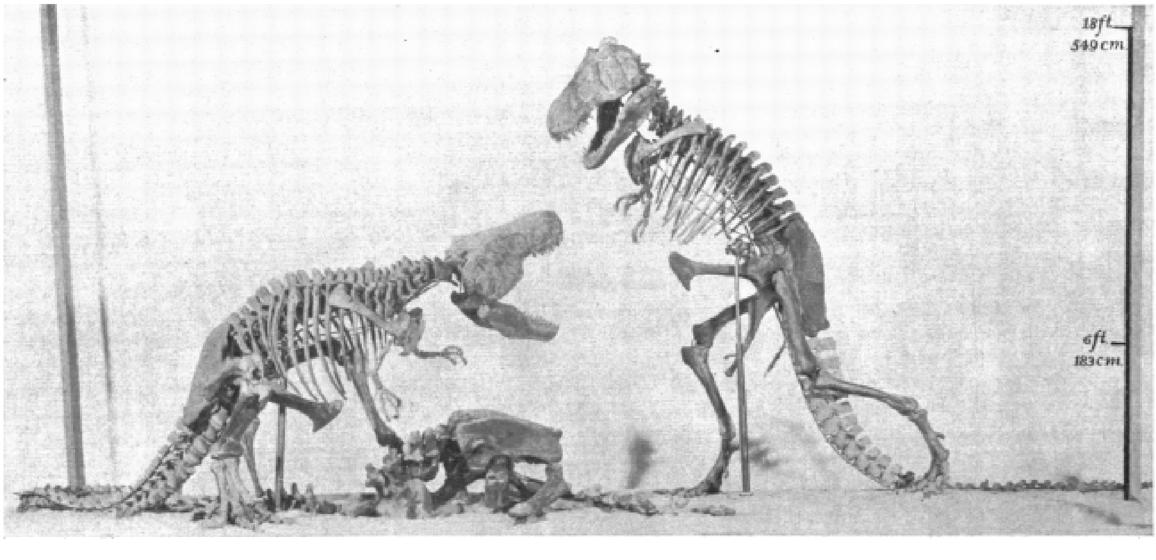
Henry Fairfield Osborn, president of the American Museum of Natural History, named *Tyrannosaurus rex* in 1905. The generic name is derived from the Greek words *τυράννος* (*tyrannos*, meaning "tyrant") and *σαύρος* (*sauros*, meaning "lizard"). Osborn used the Latin word *rex*, meaning "king", for the specific name. The full binomial therefore translates to "tyrant lizard king," emphasizing the animal's size and perceived dominance over other species of the time.

Earliest finds



Skeletal restoration by William D. Matthew from 1905, the first reconstruction of this dinosaur ever published

Teeth from what is now documented as a *Tyrannosaurus rex* were found in 1874 by A. Lakes near Golden, Colorado. In the early 1890s, J. B. Hatcher collected postcranial elements in eastern Wyoming. The fossils were believed to be from a large species of *Ornithomimus* (*O. grandis*) but are now considered *Tyrannosaurus rex*. Vertebral fragments found by E. D. Cope in western South Dakota in 1892 and named as *Manospondylus gigas* have also been recognized as belonging to *Tyrannosaurus rex*.



Scale model of the never-completed exhibit planned for the American Museum of Natural History by H.F. Osborn

Barnum Brown, assistant curator of the American Museum of Natural History, found the first partial skeleton of *Tyrannosaurus rex* in eastern Wyoming in 1900. H. F. Osborn originally named this skeleton *Dynamosaurus imperiosus* in a paper in 1905. Brown found another partial skeleton in the Hell Creek Formation in Montana in 1902. Osborn used this holotype to describe *Tyrannosaurus rex* in the same paper in which *D. imperiosus* was described. In 1906, Osborn recognized the two as synonyms, and acted as first revisor by selecting *Tyrannosaurus* as the valid name. The original *Dynamosaurus* material resides in the collections of the Natural History Museum, London.

In total, Brown found five *Tyrannosaurus* partial skeletons. In 1941, Brown's 1902 find was sold to the Carnegie Museum of Natural History in Pittsburgh, Pennsylvania. Brown's fourth and largest find, also from Hell Creek, is on display in the American Museum of Natural History in New York.

Although there are numerous skeletons in the world, only one track has been documented — at Philmont Scout Ranch in northeast New Mexico. It was discovered in 1983 and identified and documented in 1994.

Notable specimens

"Sue" specimen, Field Museum of Natural History, Chicago

Sue Hendrickson, amateur paleontologist, discovered the most complete (approximately 85%) and, until 2001, the largest, *Tyrannosaurus* fossil skeleton known in the Hell Creek Formation near Faith, South Dakota, on 12 August 1990. This *Tyrannosaurus*, nicknamed "Sue" in her honor, was the object of a legal battle over its ownership. In 1997 this was settled in favor of Maurice Williams, the original land owner. The fossil collection was purchased by the Field Museum of Natural History at auction for USD 7.6

million, making it the most expensive dinosaur skeleton to date. From 1998 to 1999 Field Museum of Natural History preparators spent over 25,000 man-hours taking the rock off each of the bones. The bones were then shipped off to New Jersey where the mount was made. The finished mount was then taken apart, and along with the bones, shipped back to Chicago for the final assembly. The mounted skeleton opened to the public on May 17, 2000 in the great hall (Stanley Field Hall) at the Field Museum of Natural History. A study of this specimen's fossilized bones showed that "Sue" reached full size at age 19 and died at age 28, the longest any tyrannosaur is known to have lived. Early speculation that Sue may have died from a bite to the back of the head was not confirmed. Though subsequent study showed many pathologies in the skeleton, no bite marks were found. Damage to the back of the skull may have been caused by post-mortem trampling. Recent speculation indicates that "Sue" may have died of starvation after contracting a parasitic infection from eating diseased meat; the resulting infection would have caused inflammation in the throat, ultimately leading "Sue" to starve because she could no longer swallow food. This hypothesis is substantiated by smooth-edged holes in her skull which are similar to those caused in modern-day birds that contract the same parasite.

Samson, a *Tyrannosaurus rex* specimen that was put up for auction on eBay in 2000 with an asking price of over USD 8 million

Another *Tyrannosaurus*, nicknamed "Stan", in honor of amateur paleontologist Stan Sacrison, was found in the Hell Creek Formation near Buffalo, South Dakota, in the spring of 1987. It was not collected until 1992, as it was mistakenly thought to be a *Triceratops* skeleton. Stan is 63% complete and is on display in the Black Hills Institute of Geological Research in Hill City, South Dakota, after an extensive world tour during 1995 and 1996. This tyrannosaur, too, was found to have many bone pathologies, including broken and healed ribs, a broken (and healed) neck and a spectacular hole in the back of its head, about the size of a *Tyrannosaurus* tooth.

In the summer of 2000, Jack Horner discovered five *Tyrannosaurus* skeletons near the Fort Peck Reservoir in Montana. One of the specimens, dubbed "C. rex," was reported to be perhaps the largest *Tyrannosaurus* ever found.

"Jane" specimen, Cleveland Museum of Natural History, Cleveland, Ohio

In 2001, a 50% complete skeleton of a juvenile *Tyrannosaurus* was discovered in the Hell Creek Formation in Montana, by a crew from the Burpee Museum of Natural History of Rockford, Illinois. Dubbed "Jane", the find was initially considered the first known skeleton of the pygmy tyrannosaurid *Nanotyrannus* but subsequent research has revealed that it is more likely a juvenile *Tyrannosaurus*. It is the most complete and best preserved juvenile example known to date. Jane has been examined by Jack Horner, Pete Larson, Robert Bakker, Greg Erickson, and several other renowned paleontologists, because of the uniqueness of her age. "Jane" is currently on exhibit at the Burpee Museum of Natural History in Rockford, Illinois.

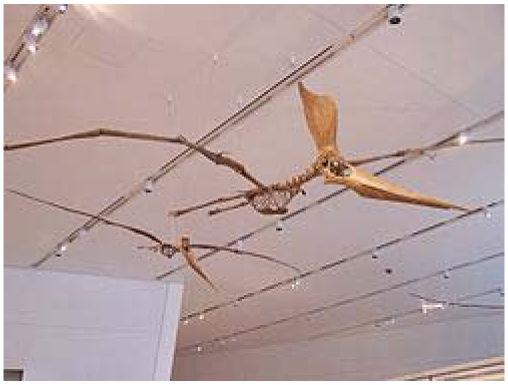
In a press release on 7 April 2006, Montana State University revealed that it possessed the largest *Tyrannosaurus* skull yet discovered. Discovered in the 1960s and only recently reconstructed, the skull measures 59 inches (150 cm) long compared to the 55.4 inches (141 cm) of "Sue's" skull, a difference of 6.5%.

Chapter- 8

Pterosaur (Flying Reptile of Cretaceous Period)

Pterosaurs

Fossil range: Late Triassic–Late Cretaceous, 220–65 Ma



Replica *Pteranodon sternbergi* skeletons, male (right) and female (left)

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Division:	Archosauria
(unranked):	Avemetatarsalia
(unranked):	Ornithodira
Order:	**†Pterosauria** Kaup, 1834

Suborders

†*Pterodactyloidea*
†*Rhamphorhynchoidea* *

Pterosaurs were flying reptiles of the clade or order Pterosauria. They existed from the late Triassic to the end of the Cretaceous Period (220 to 65.5 million years ago).

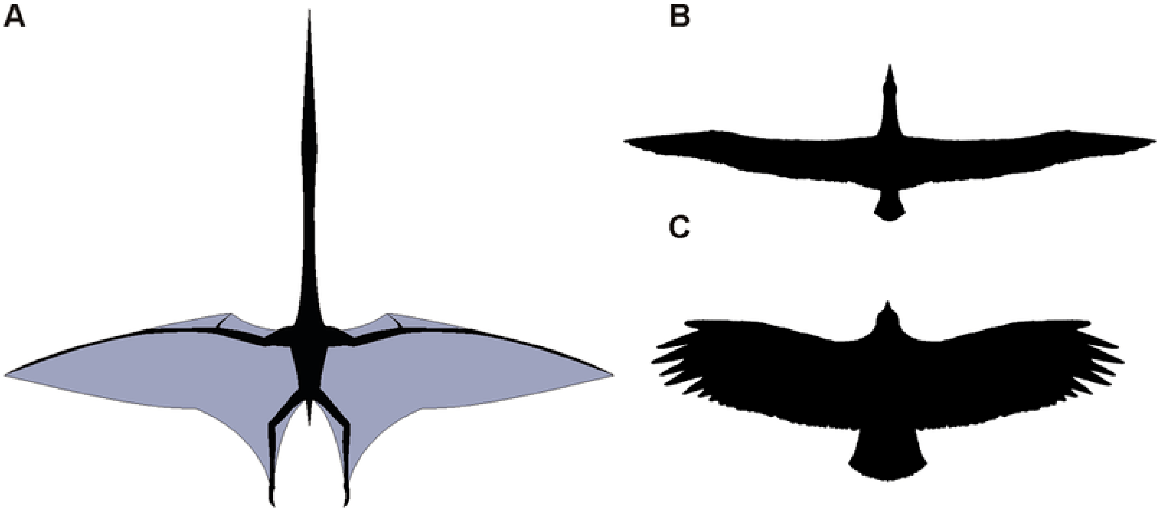
Pterosaurs are the earliest vertebrates known to have evolved powered flight. Their wings were formed by a membrane of skin, muscle, and other tissues stretching from the legs to a dramatically lengthened fourth finger. Early species had long, fully-toothed jaws and long tails, while later forms had a highly reduced tail, and some lacked teeth. Many sported furry coats made up of hair-like filaments known as pycnofibres, which covered their bodies and parts of their wings. Pterosaurs spanned a wide range of adult sizes, from the very small *Nemicolopterus* to the largest known flying creatures of all time, including *Quetzalcoatlus* and *Hatzegopteryx*.

Pterosaurs are sometimes referred to in the popular media as dinosaurs, but this is incorrect. The term "dinosaur" is properly restricted to a certain group of terrestrial reptiles with a unique upright stance (superorder Dinosauria, which includes birds), and therefore excludes the pterosaurs, as well as the various groups of extinct marine reptiles, such as ichthyosaurs, plesiosaurs, and mosasaurs.

Description

The anatomy of pterosaurs was highly modified from their reptilian ancestors for the demands of flight. Pterosaur bones were hollow and air filled, like the bones of birds. They had a keeled breastbone that was developed for the attachment of flight muscles and an enlarged brain that shows specialised features associated with flight. In some later pterosaurs, the backbone over the shoulders fused into a structure known as a notarium, which served to stiffen the torso during flight, and provide a stable support for the scapula (shoulder blade).

Wings



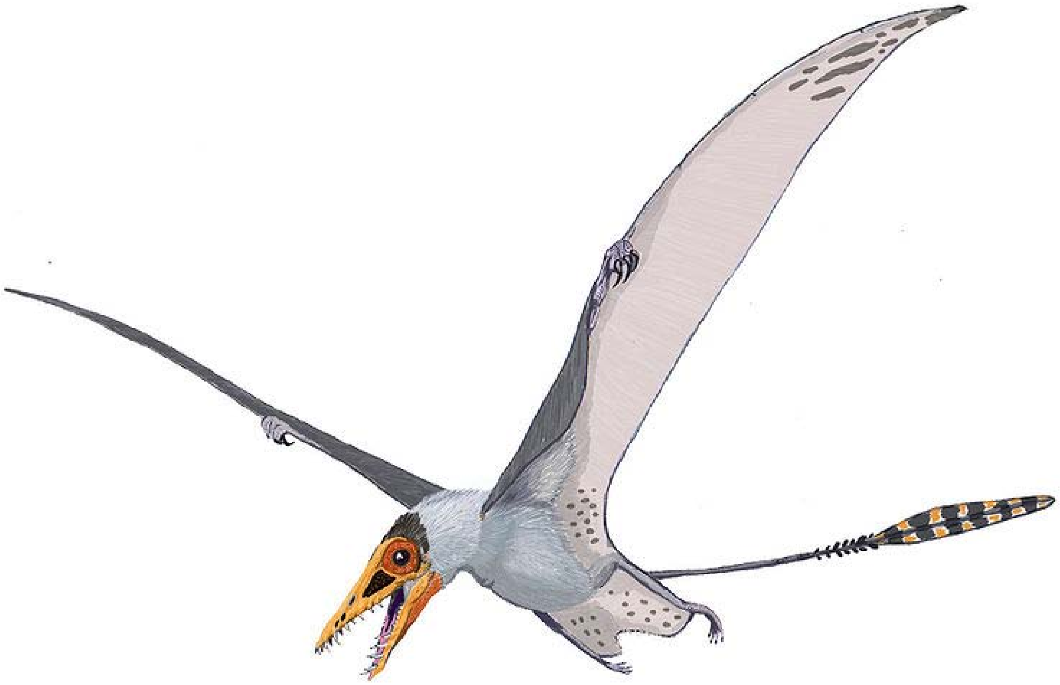
Reconstructed wing planform of *Quetzalcoatlus* compared to the Wandering Albatross and the Andean Condor (not to scale)

Pterosaur wings were formed by membranes of skin and other tissues. The primary membranes attached to the extremely long fourth finger of each arm and extended along the sides of the body to the legs.

While historically thought of as simple, leathery structures composed of skin, research has since shown that the wing membranes of pterosaurs were actually highly complex and dynamic structures suited to an active style of flight. First, the outer wings (from the wing to the elbow) were strengthened by closely spaced fibers called **actinofibrils**. The actinofibrils themselves consisted of three distinct layers in the wing, forming a crisscross pattern when superimposed on one another. The actual function of the actinofibrils is unknown, as is the exact material from which they were made. Depending on their exact composition (keratin, muscle, elastic structures, etc.), they may have been stiffening or strengthening agents in the outer part of the wing. The wing membranes also contained a thin layer of muscle, fibrous tissue, and a unique, complex circulatory system of looping blood vessels.

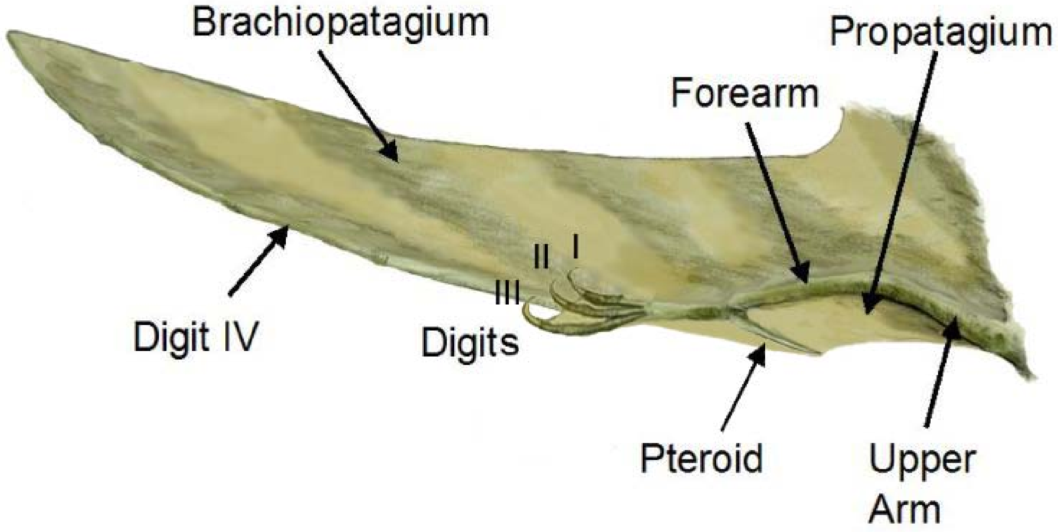
As evidenced by hollow cavities in the wing bones of larger species and soft tissue preserved in at least one specimen, some pterosaurs extended their system of respiratory air sacs into the wing membrane itself.

Parts of the pterosaur wing



Sordes, as depicted here, evidences the possibility that pterosaurs had a cruropatagium (a membrane connecting the legs, but leaving the tail out unlike the chiropteran uropatagium)

The pterosaur wing membrane is divided into three basic units. The first, called the *propatagium* ("first membrane"), was the forward-most part of the wing and attached between the wrist and shoulder, creating the "leading edge" during flight. This membrane may have incorporated the first three fingers of the hand, as evidenced in some specimens. The *brachiopatagium* ("arm membrane") was the primary component of the wing, stretching from the highly elongated fourth finger of the hand to the hind limbs (though where exactly on the hind limbs it anchored is controversial and may have varied between species, see below). Finally, at least some pterosaur groups had a membrane that stretched between the legs, possibly connecting to or incorporating the tail, called the *uropatagium*; the extent of this membrane isn't certain, as studies on *Sordes* seem to suggest that it simply connected the legs but did not involve the tail (rendering it a *cruropatagium*). It is generally agreed though that non-pterodactyloid pterosaurs had a broader uro/cruropatagium, with pterodactyloids only having membranes running along the legs; *Pteranodon* in particular might have developed/redeveloped an uropatagium, given the structure of the tail.



Wing anatomy

A bone unique to pterosaurs, known as the pteroid, connected to the wrist and helped to support a forward membrane (the propatagium) between the wrist and shoulder. Evidence of webbing between the three free fingers of the pterosaur forelimb suggests that this forward membrane may have been more extensive than the simple pteroid-to-shoulder connection traditionally depicted in life restorations. The position of the pteroid bone itself has been controversial. Some scientists, notably David Unwin, have argued that the pteroid pointed forward, extending the forward membrane. However, this view was strongly refuted in a 2007 paper by Chris Bennett, who showed that the pteroid did not articulate as previously thought and could not have pointed forward, but rather inward toward the body as traditionally thought.

Three lines of evidence, morphological, developmental and histological, indicate that the pteroid is a true bone, rather than ossified cartilage. The origin of the pteroid is unclear: it may be a modified carpal, the first metacarpal, or a neomorph (new bone).

The pterosaur wrist consists of two inner (proximal) and four outer (distal) carpals (wrist bones), excluding the pteroid bone, which may itself be a modified distal carpal. The proximal carpals are fused together into a "syncarpal" in mature specimens, while three of the distal carpals fuse to form a distal syncarpal. The remaining distal carpal, referred to here as the medial carpal, but which has also been termed the distal lateral, or pre-axial carpal, articulates on a vertically elongate biconvex facet on the anterior surface of the distal syncarpal. The medial carpal bears a deep concave fovea that opens anteriorly, ventrally and somewhat medially, within which the pteroid articulates.

There has been considerable argument among paleontologists about whether the main wing membranes (brachiopatagia) attached to the hind limbs, and if so, where. Fossils of the rhamphorhynchoid *Sordes*, the anurognathid *Jeholopterus*, and a pterodactyloid from the Santana Formation seem to demonstrate that the wing membrane did attach to the hindlimbs, at least in some species. However, modern bats and flying squirrels show considerable variation in the extent of their wing membranes and it is possible that, like these groups, different species of pterosaur had different wing designs. Indeed, analysis of pterosaur limb proportions shows that there was considerable variation, possibly reflecting a variety of wing-plans.

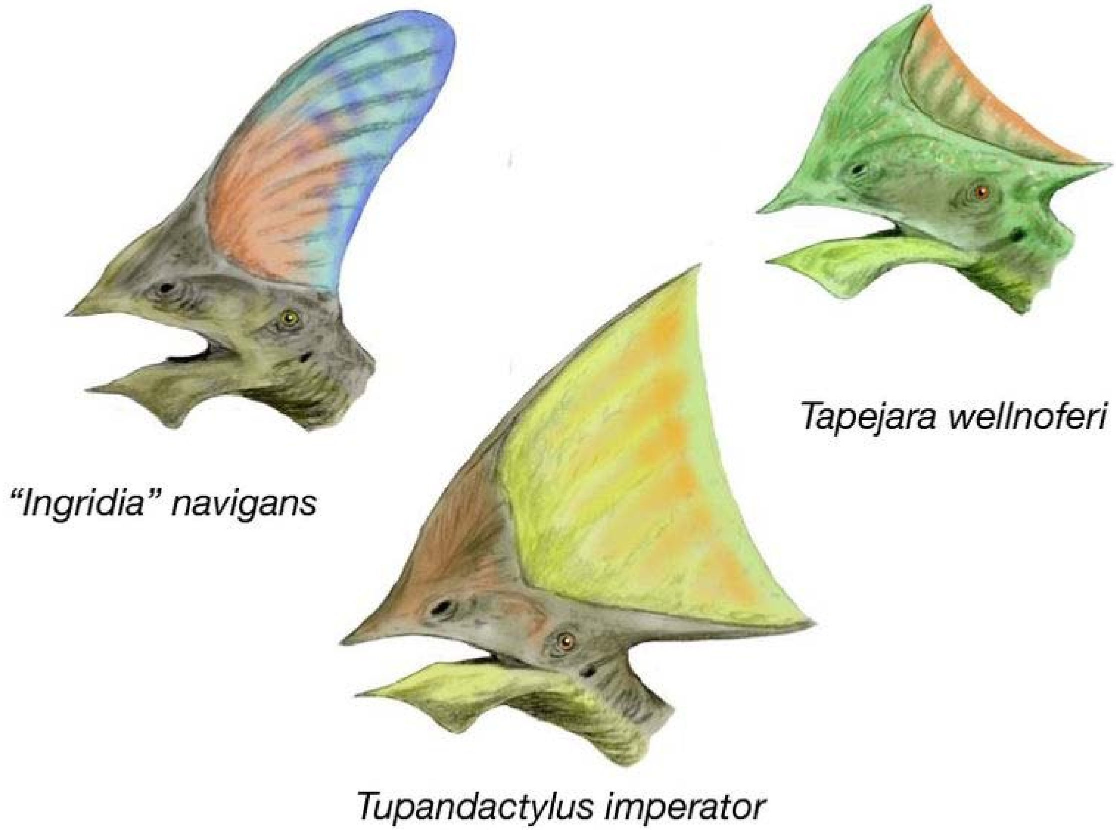
Many if not all pterosaurs also had webbed feet.

Skull, teeth and crests

Tooth, possibly from *Coloborhynchus*

Most pterosaur skulls had elongated, beak-like jaws. Some advanced forms were toothless (such as the pteranodonts and azhdarchids, though most sported a full complement of needle-like teeth. In some cases, actual keratinous beak tissue has been preserved, though in toothed forms, the beak is small and restricted to the jaw tips and does not involve the teeth.

Unlike most archosaurs, which have several openings in the skull in front of the eyes, in pterodactyloid pterosaurs the antorbital opening and the nasal opening was merged into a single large opening, called the *nasoantorbial fenestra*. This likely evolved as a weight-saving feature to lighten the skull for flight.



The crests of three tapejarids. Clockwise from right: *Tapejara*, *Tupandactylus*, and "Tapejara" *navigans* (not to scale)

Pterosaurs are well known for their often elaborate crests. The first and perhaps best known of these is the distinctive backward-pointing crest of some *Pteranodon* species, though a few pterosaurs, such as the tapejarids and *Nyctosaurus* sported incredibly large crests that often incorporated keratinous or other soft tissue extensions of the bony crest base.

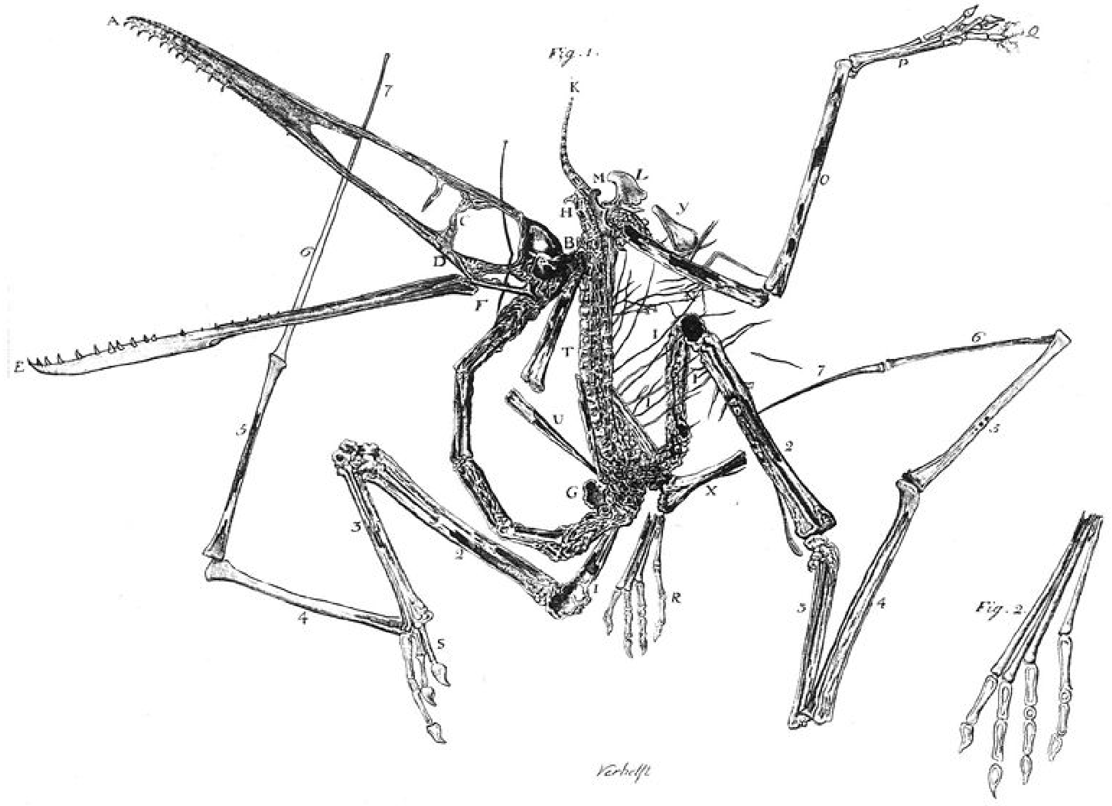
Since the 1990s, new discoveries and more thorough study of old specimens have shown that crests are far more widespread among pterosaurs than previously thought, due mainly to the fact that they were frequently extended by or composed completely of keratin, which does not fossilize as often as bone. In the cases of pterosaurs like *Pterorhynchus* and *Pterodactylus*, the true extent of these crests has only been uncovered using ultraviolet photography. The discovery of *Pterorynchus* and *Austriadactylus*, both crested "rhamphorhynchoids", showed that even primitive pterosaurs had crests (previously, crests were thought to be restricted to the more advanced pterodactyloids).

Pycnofibres

At least some pterosaurs were covered with hair-like filaments known as **pycnofibres**, similar to but not homologous (sharing a common structure) with mammalian hair. Pycnofibres were not true hair as seen in mammals, but a unique structure that developed a similar appearance through convergent evolution. Although in some cases actinofibrils (internal structural fibres) in the wing membrane have been mistaken for pycnofibres or true hair, some fossils such as those of *Sordes pilosus* (which translates as "hairy demon") and *Jeholopterus ninchengensis* do show the unmistakable imprints of pycnofibres on the head and body, not unlike modern-day bats, another example of convergent evolution. The presence of pycnofibres (and the demands of flight) imply that pterosaurs were endothermic (warm-blooded).

The term "pycnofibre", meaning "dense filament", was first coined in a paper on the soft tissue impressions of *Jeholopterus* by palaeontologist Alexander W.A. Kellner and colleagues in 2009.

History of discovery



Engraving of the original *P. antiquus* specimen by Egid Verhelst II, 1784

The first pterosaur fossil was described by the Italian naturalist Cosimo Collini in 1784. Collini misinterpreted his specimen as a seagoing creature that used its long front limbs as paddles. A few scientists continued to support the aquatic interpretation even until 1830, when the German zoologist Johann Georg Wagler suggested that *Pterodactylus* used its wings as flippers. Georges Cuvier first suggested that pterosaurs were flying creatures in 1801, and coined the name "*Ptero-dactyle*" 1809 for the specimen recovered in Germany; however, due to the standardization of scientific names, the official name for this genus became *Pterodactylus*, though the name "pterodactyl" continued to be popularly applied to all members of this first specimen's order.

Since the first pterosaur fossil was discovered in the Late Jurassic Solnhofen limestone in 1784, twenty-nine kinds of pterosaurs have been found in those deposits alone. A famous early UK find was an example of *Dimorphodon* by Mary Anning, at Lyme Regis in 1828. The name Pterosauria was coined by Johann Jakob Kaup in 1834, though the name **Ornithosauria** (or "bird lizards", Bonaparte, 1838) was sometimes used in the early literature.

The three-dimensionally preserved skull of *Anhanguera santanae*, from the Santana Formation, Brazil

Most pterosaur fossils are poorly preserved. Their bones were hollow and, when sediments piled on top of them, the bones were flattened. The best preserved fossils have come from the Araripe Plateau, Brazil. For some reason, when the bones were deposited, the sediments encapsulated the bones, rather than crushing them. This created three-dimensional fossils for paleontologists to study. The first find in the Araripe Plateau was made in 1974.

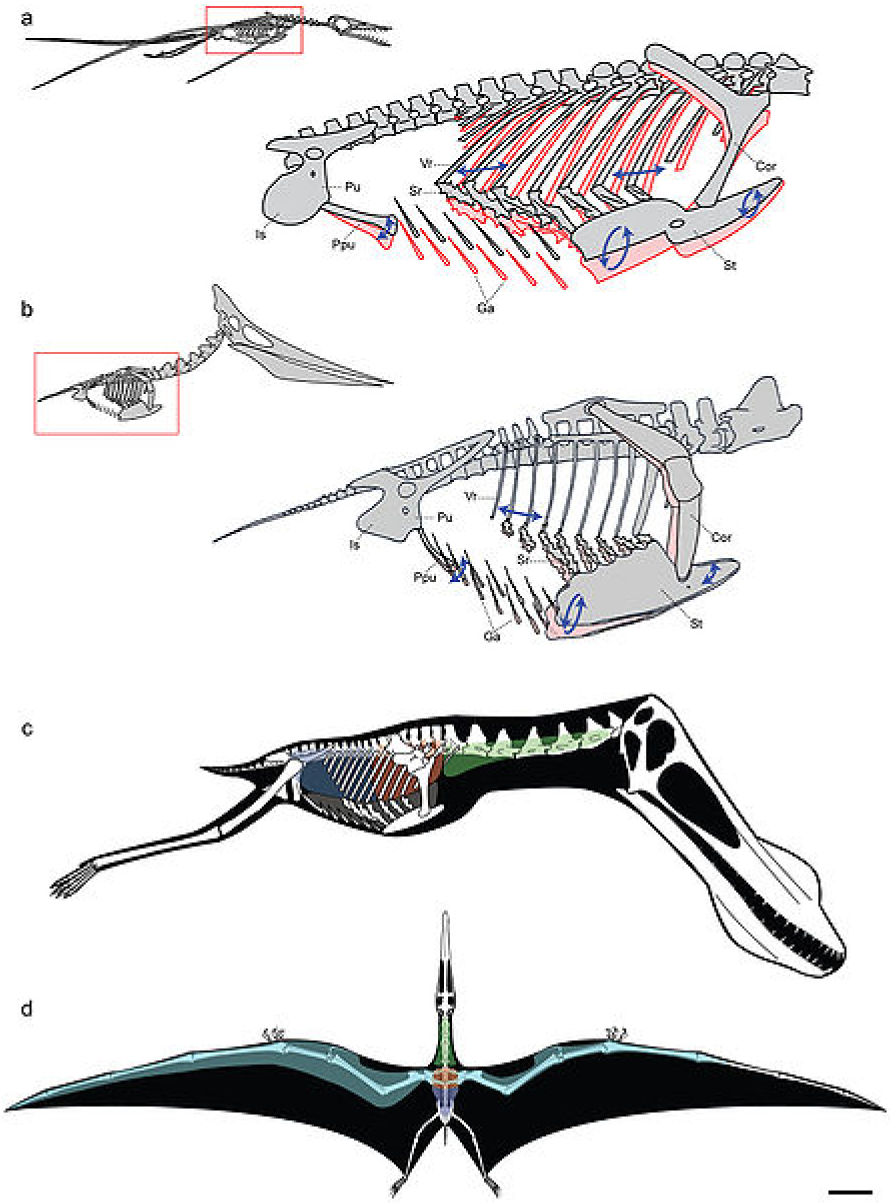
Most paleontologists now believe that pterosaurs were adapted for active flight, not just gliding as was earlier believed. Pterosaur fossils have been found on every continent. At least 60 genera of pterosaurs have been found to date, ranging from the size of a small bird to wingspans in excess of 10 metres (33 ft).

Paleobiology

Flight

Skeletal reconstruction of a quadrupedally launching *Pteranodon longiceps*

The mechanics of pterosaur flight are not completely understood or modeled at this time.



Diagrams showing breathing motion (top two) and internal air sac system (bottom two)

Katsufumi Sato, a Japanese scientist, did calculations using modern birds and decided that it is impossible for a pterosaur to stay aloft. In the book *Posture, Locomotion, and Paleoecology of Pterosaurs* it is theorized that they were able to fly due to the oxygen-rich, dense atmosphere of the Late Cretaceous period. However, one must note both Katsufumi and the authors of *Posture, Locomotion, and Paleoecology of Pterosaurs* based their research on the now outdated theories of pterosaurs being seabird-like, and the size limit doesn't apply to terrestrial pterosaurs like azhdarchids and tapejarids Furthermore, Darren Naish concluded that atmospheric differences between the present and the Mesozoic weren't needed for the giant size of pterosaurs.

However, Mark Witton and Mike Habib, of the University of Portsmouth and John Hopkins University, respectively, argue that pterosaurs used a vaulting mechanism to obtain flight. Once in air, pterosaurs could reach speeds up to 120 kilometres per hour (75 mph) and travel thousands of kilometers.

Air sacs and respiration

A 2009 study showed that pterosaurs had a lung-air sac system and a precisely controlled skeletal breathing pump, which supports a flow-through pulmonary ventilation model in pterosaurs, analogous to that of birds. The presence of a subcutaneous air sac system in at least some pterodactyloids would have further reduced the density of the living animal.

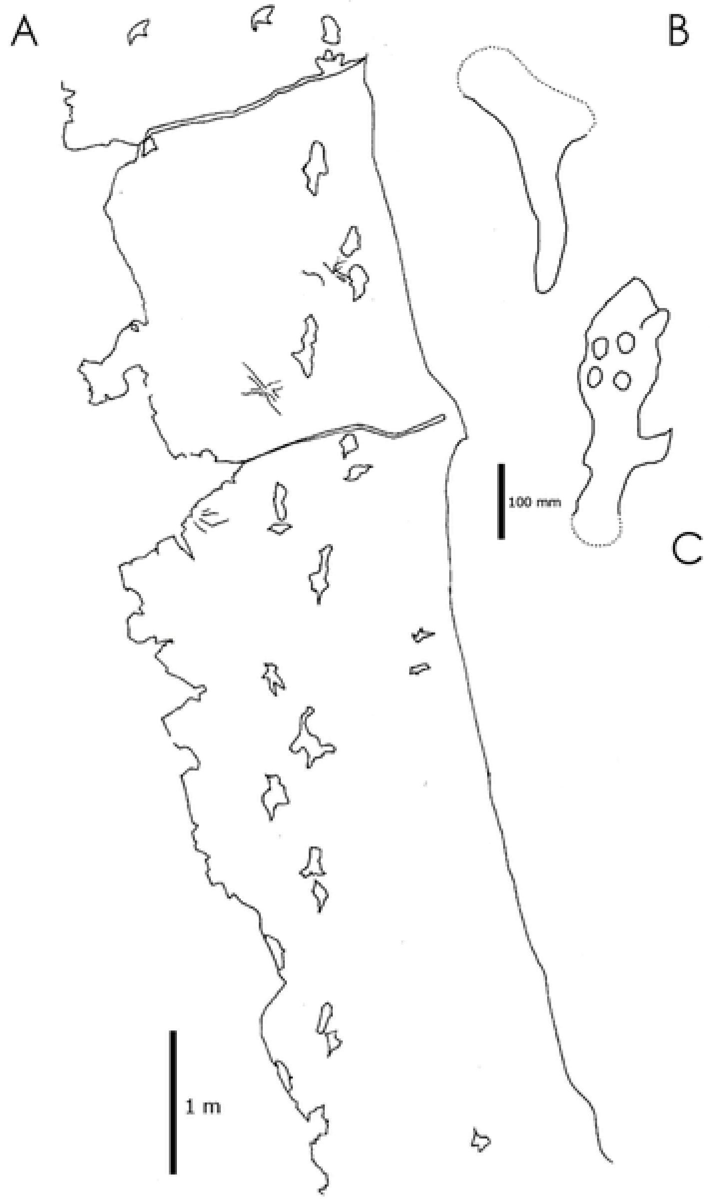
Nervous system

A study of pterosaur brain cavities using X-rays revealed that the animals (*Rhamphorhynchus muensteri* and *Anhanguera santanae*) had massive flocculi. The flocculus is a brain region that integrates signals from joints, muscles, skin and balance organs.

The pterosaurs' flocculi occupied 7.5% of the animals' total brain mass, more than in any other vertebrate. Birds have unusually large flocculi compared with other animals, but these only occupy between 1 and 2% of total brain mass.

The flocculus sends out neural signals that produce small, automatic movements in the eye muscles. These keep the image on an animal's retina steady. Pterosaurs may have had such a large flocculus because of their large wing size, which would mean that there was a great deal more sensory information to process.

Ground movement



The probable azhdarchid trace fossil *Haenamichnus uhangriensis*.

Pterosaur's hip sockets are oriented facing slightly upwards, and the head of the femur (thigh bone) is only moderately inward facing, suggesting that pterosaurs had a semi-erect stance. It would have been possible to lift the thigh into a horizontal position during flight as gliding lizards do.

There was considerable debate whether pterosaurs ambulated as quadrupeds or as bipeds. In the 1980s, paleontologist Kevin Padian suggested that smaller pterosaurs with longer hindlimbs such as *Dimorphodon* might have walked or even run bipedally, in addition to flying, like road runners. However, a large number of pterosaur trackways were later found with a distinctive four-toed hind foot and three-toed front foot; these are the unmistakable prints of pterosaurs walking on all fours.

Unlike most vertebrates, which walk on their toes with ankles held off the ground (digitigrade), fossil footprints show that pterosaurs stood with the entire foot in contact with the ground (plantigrade), in a manner similar to humans and bears. Footprints from azhdarchids show that at least some pterosaurs walked with an erect, rather than sprawling, posture.

Fossil trackways show that pterosaurs like *Quetzalcoatlus northropi* were quadrupeds.

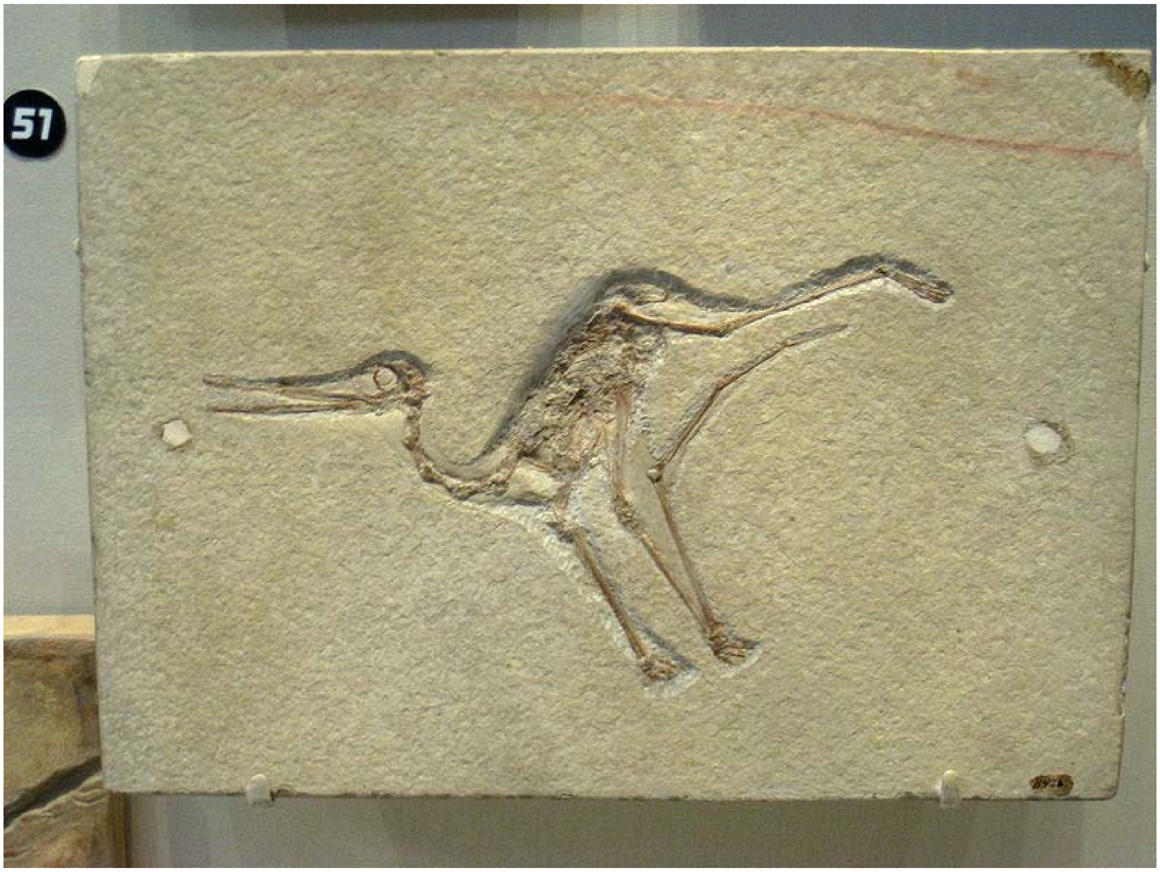
Though traditionally depicted as ungainly and awkward when on the ground, the anatomy of at least some pterosaurs (particularly pterodactyloids) suggests that they were competent walkers and runners. The forelimb bones of azhdarchids and ornithocheirids were unusually long compared to other pterosaurs, and in azhdarchids, the bones of the arm and hand (metacarpals) were particularly elongated. Furthermore, azhdarchid front limbs as a whole were proportioned similarly to fast-running ungulate mammals. Their hind limbs, on the other hand, were not built for speed, but they were long compared with most pterosaurs, and allowed for a long stride length. While azhdarchid pterosaurs probably could not run, they would have been relatively fast and energy efficient.

The relative size of the hands and feet in pterosaurs (by comparison with modern animals such as birds) may indicate what type of lifestyle pterosaurs led on the ground. Azhdarchid pterosaurs had relatively small feet compared to their body size and leg length, with foot length only about 25%-30% the length of the lower leg. This suggests that azhdarchids were better adapted to walking on dry, relatively solid ground. *Pteranodon* had slightly larger feet (47% the length of the tibia), while filter-feeding pterosaurs like the ctenochasmatoids had very large feet (69% of tibial length in *Pterodactylus*, 84% in *Pterodaustro*), adapted to walking in soft muddy soil, similar to modern wading birds.

Natural predators

Pterosaurs are known to have been eaten by spinosaurids. In the 1 July 2004 edition of *Nature*, paleontologist Eric Buffetaut discusses an early Cretaceous fossil of three cervical vertebrae of a pterosaur with the broken tooth of a spinosaur embedded in it. The vertebrae are known not to have been eaten and exposed to digestion, as the joints still articulated.

Reproduction and life history



Fossil pterodactyloid flapling from the Solnhofen Limestone

Very little is known about pterosaur reproduction. A single pterosaur egg has been found in the quarries of Liaoning, the same place that yielded the famous 'feathered' dinosaurs. The egg was squashed flat with no signs of cracking, so evidently the eggs had leathery shells, as in modern lizards. A study of pterosaur eggshell structure and chemistry published in 2007 indicated that it is likely pterosaurs buried their eggs, like modern crocodile and turtles. Egg-burying would have been beneficial to the early evolution of pterosaurs, as it allows for more weight-reducing adaptations, but this method of reproduction also would have put limits on the variety of environments pterosaurs could live in, and may have disadvantaged them when they began to face ecological competition from birds.

Wing membranes preserved in pterosaur embryos are well developed, suggesting pterosaurs were ready to fly soon after birth. Fossils of pterosaurs only a few days to a week old (called **flaplings**) have been found, representing several pterosaur families, including pterodactylids, rhamphorhinchids, ctenochasmatids and azhdarchids. All preserve bones which show a relatively high degree of hardening (*ossification*) for their age, and wing proportions similar to adults. In fact, many pterosaur flaplings have been considered adults and placed in separate species in the past. Additionally, flaplings are normally found in the same sediments as adults and juveniles of the same species, such as the *Pterodactylus* and *Rhamphorhynchus* flaplings found in the Solnhofen limestone of Germany, and *Pterodaustro* flaplings from Brazil. All are found in deep aquatic environment far from shore.

It is not known whether pterosaurs practiced any form of parental care, but their ability to fly as soon as they emerged from the egg and the numerous flaplings found in environments far from nests and alongside adults has led most researchers, including Christopher Bennett and David Unwin, to conclude that the young were only dependent on their parents for a very short period of time, while the wings grew long enough to fly, and left the nest to fend for themselves within days of hatching. Alternately, they may have used stored yolk products for nourishment during their first few days of life, as in modern reptiles, rather than depend on parents for food.

Growth rates of pterosaurs once they hatched varied across different groups. In more primitive, long-tailed pterosaurs ("rhamphorhynchoids") such as *Rhamphorhynchus*, the average growth rate during the first year of life was 130% to 173%, slightly faster than the growth rate of alligators. Growth in these species slowed after sexual maturity, and it would have taken more than three years for *Rhamphorhynchus* to attain maximum size. In contrast, the more advanced, large pterodactyloid pterosaurs such as *Pteranodon* grew to adult size within the first year of life. Additionally, pterodactyloids had *determinate growth*, meaning that the animals reached a fixed maximum adult size and stopped growing.

Evolution and extinction

Origins

Restoration of two *Scleromochlus* on a tree

Because pterosaur anatomy has been so heavily modified for flight, and immediate "missing link" predecessors have not so far been described, the ancestry of pterosaurs is not well understood. Several hypotheses have been advanced, including links to ornithodirans like *Scleromochlus*, an ancestry among the basal archosauriforms like *Euparkeria*, or among the prolacertiformes (which include gliding forms like *Sharovipteryx*).

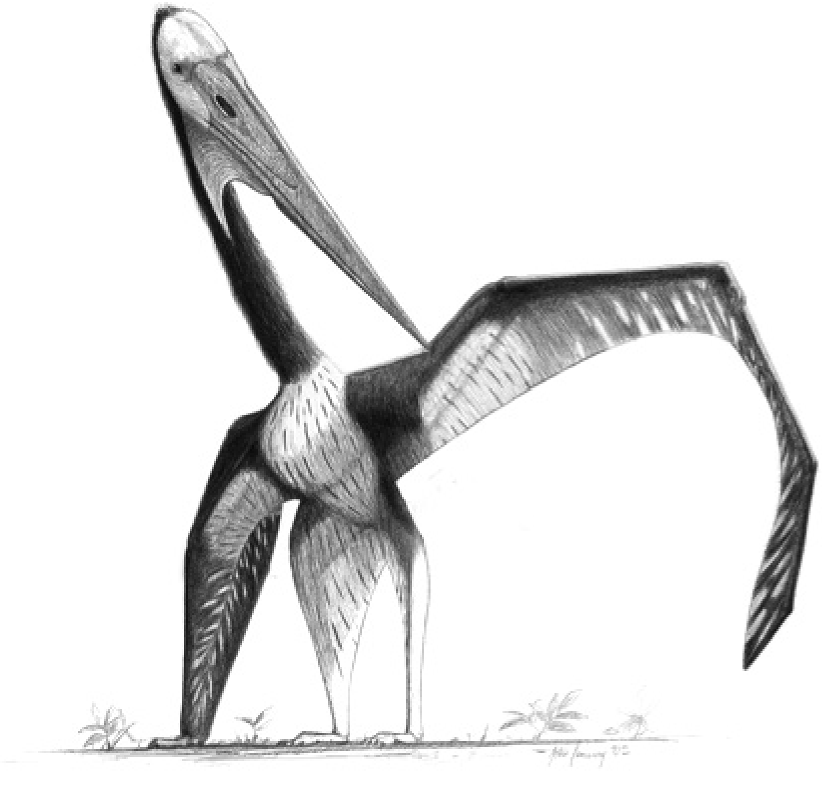
Two researchers, Chris Bennett (1996) and David Peters (2000), have found pterosaurs to be prolacertiformes or closely related to them. Bennett only recovered pterosaurs as close relatives of the prolacertiformes after removing characteristics of the hind limb from his analysis, in an attempt to test the idea that these characters are the result of convergent evolution between pterosaurs and dinosaurs. However, subsequent analysis by Dave Hone and Michael Benton (2007) could not reproduce this result. Hone and Benton found pterosaurs to be closely related to dinosaurs even without hind limb characters. They also criticized previous studies by David Peters, raising "serious questions" about the methods he used to recover pterosaurs among the prolacertiformes. Hone and Benton concluded that although more primitive pterosauromorphs are needed to clarify their relationships, pterosaurs are best considered archosaurs, and specifically ornithodirans, given current evidence. In Hone and Benton's analysis, pterosaurs are either the sister group of *Scleromochlus* or fall between it and *Lagosuchus* on the ornithodiran family tree.

Phylogeny and classification

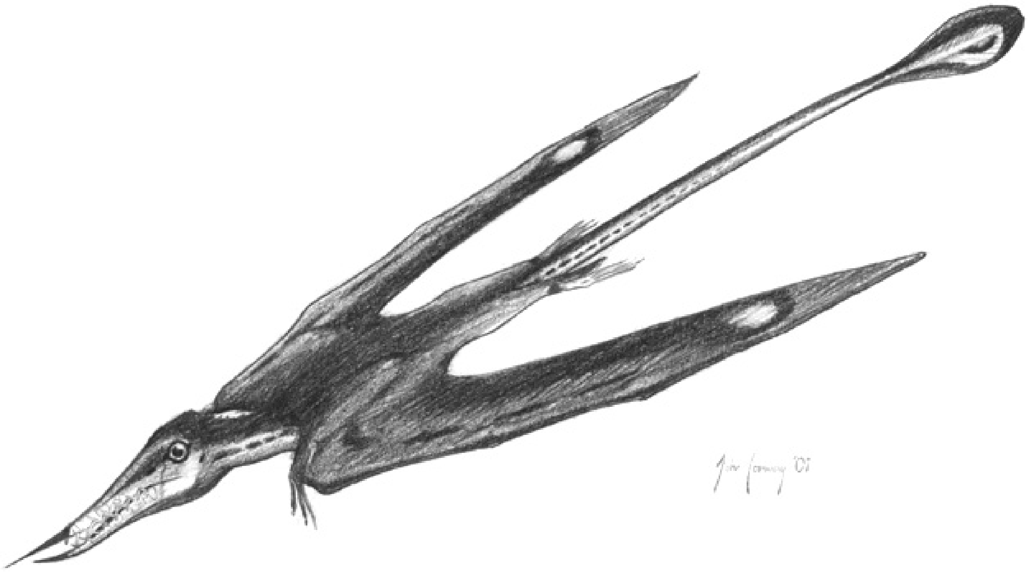
Classification of pterosaurs has historically been difficult, because there were many gaps in the fossil record. Many new discoveries are now filling in these gaps and giving a better picture of the evolution of pterosaurs. Traditionally, they are organized into two suborders:

- Rhamphorhynchoidea (Plieninger, 1901): A group of early, basal ("primitive") pterosaurs, many of which had long tails and short metacarpal bones in the wing. They were small, and their fingers were still adapted to climbing . They appeared in the Late Triassic period, and lasted until the late Jurassic. Rhamphorhynchoidea is a paraphyletic group (since the pterodactyloids evolved directly from them and not from a common ancestor), so with the increasing use of cladistics it has fallen out of favor in most technical literature.

- Pterodactyloidea (Plieninger, 1901): The more derived ("advanced") pterosaurs, with short tails and long wing metacarpals. They appeared in the middle Jurassic period, and lasted until the Cretaceous-Tertiary extinction event wiped them out at the end of the Cretaceous.



Zhejiangopterus, an azhdarchid from the Cretaceous of China



Rhamphorhynchus, a rhamphorhynchid from the Jurassic of Germany

Listing of families and superfamilies within Pterosauria, after Unwin 2006 unless otherwise noted.

- **ORDER PTEROSAURIA** (extinct)
    - **Suborder Rhamphorhynchoidea** *
        - Family Anurognathidae
        - Family Campylognathoididae
        - Family Dimorphodontidae
        - Family Rhamphorhynchidae
    - **Suborder Pterodactyloidea**
        - Superfamily **Ornithocheiroidea**
            - Family Istiodactylidae
            - Family Nyctosauridae
            - Family Ornithocheiridae
            - Family Pteranodontidae
        - Superfamily **Ctenochasmatoidea**
            - Family Ctenochasmatidae
            - Family Gallodactylidae
            - Family Pterodactylidae
        - Superfamily **Dsungaripteroidea**
            - Family Dsungaripteridae
            - Family Germanodactylidae

    - Superfamily **Azhdarchoidea**
        - Family Azhdarchidae
        - Family Chaoyangopteridae
        - Family Lonchodectidae
        - Family Tapejaridae

Extinction

It was once thought that competition with early bird species may have resulted in the extinction of many of the pterosaurs. By the end of the Cretaceous, only large species of pterosaurs are known. The smaller species seem to have become extinct, their niche filled by birds . However, pterosaur decline (if actually present) seems unrelated to bird diversity. At the end of the Cretaceous period, the great extinction which wiped out all non-avian dinosaurs and most avian dinosaurs as well, and many other animals, seemed to also take the pterosaurs. Alternatively, most pterosaurs may have been specialised for an ocean-going lifestyle. Consequently, when the K-T mass-extinction severely affected marine life that most pterosaurs fed on, they went extinct. However, forms like azhdarchids and istiodactylids were not marine in habits.

Well-known genera

Examples of pterosaur genera include:

- *Pteranodon* was 1.8 metres (six ft) long, with a wingspan of 7.5 m (25 ft), and lived during the late Cretaceous period.
- *Pterodactylus* had a wingspan of 50–75 centimetres (20 to –30 inches), and lived during the late Jurassic on lake shores.
- *Pterodaustro* was a Cretaceous pterosaur from South America with a wingspan around 1.33 metres and with over 500 tall, narrow teeth, which were presumably used in filter-feeding, much like modern flamingos. Also like flamingos, this pterosaur's diet may have resulted in the animal having a pink hue. It was South America's first pterosaur find.
- *Quetzalcoatlus* had a wingspan of 10–11 metres (33–36 ft), and was among the largest flying animals ever. It lived during the late Cretaceous period.
- *Rhamphorhynchus* was a Jurassic pterosaur with a vane at the end of its tail, which may have acted to stabilise the tail in flight.

In popular culture

Quetzalcoatlus models in South Bank, created by Mark Witton for the Royal Society's 350th anniversary

Pterosaurs have been a staple of popular culture for as long as their cousins the dinosaurs, though they are usually not featured as prominently in films, literature or other art. Additionally, while the depiction of dinosaurs in popular media has changed radically in response to advances in paleontology, a mainly outdated picture of pterosaurs has persisted since the mid 20th century.

The number and diversity of pterosaurs in the popular consciousness is also not as high as it has been historically for dinosaurs. While the generic term "pterodactyl" is often used to describe these creatures, the animals depicted frequently represent either *Pteranodon* or *Rhamphorhynchus*, or a fictionalized hybrid of the two. Many children's toys and cartoons feature "pterodactyls" with *Pteranodon*-like crests and long, *Rhamphorhynchus*-like tails and teeth, a combination that never existed in nature. However, at least one type of pterosaur *did* have at least the *Pteranodon*-like crest and teeth—for example, the *Ludodactylus*, a name that means "toy finger" for its resemblance to old, inaccurate children's toys.

Pterosaurs were first used in fiction in Arthur Conan Doyle's 1912 novel *The Lost World*, and subsequent 1925 film adaptation. They have been used in a number of films and television programs since, including the 1933 film *King Kong*, and 1966 *One Million*

Years B.C.. In the latter, animator Ray Harryhausen had to add inaccurate bat-like wing fingers to his stop motion models in order to keep the membranes from falling apart, though this particular error was common in art even before the film was made. Pterosaurs were mainly absent from notable film appearances until 2001, with *Jurassic Park III*. However, paleontologist Dave Hone has noted that even after the 40 intervening years, the pterosaurs in this film had not been significantly updated to reflect modern research. Among the errors he noted as persisting from the 1960s to the 2000s were teeth even in toothless species (the *Jurassic Park III* pterosaurs were intended to be *Pteranodon*, which translates as "toothless wing"), nesting behavior that was known to be inaccurate by 2001, and leathery wings, rather than the taut membranes of muscle fiber which was actually present and required for pterosaur flight.