CRETACEOUS

N. MacLeod, Department of Palaeontology, The Natural History Museum, London, UK

Introduction

The Cretaceous System/Period is that last major subdivision of Mesozoic time. It was established by J. J. d”Omalius in 1822 and divided into an upper and lower series/epochs by W. D. Conybeare and William Phillips that same year. Cretaceous rocks are currently assigned to 12 stage/age-level subdivisions, the combination of which represent an interval estimated to lie between 145.5 and 65.5 Ma. This is the longest single system/period of the Phanerozoic and Cretaceous rocks are found on all continents. The Cretaceous is also the first system/period to be entirely represented in the ocean basins. Palaeogeographically, the Cretaceous represents the time during which Pangea continued to fragment and continental plates began to move into their current positions. Prominent tectonic features of Cretaceous time include the rifting of Laurasia to form the northern and southern embayments of the proto-Atlantic Ocean, the joining of these embayments into a single north-south trending Atlantic Ocean basin, and the rifting of southern supercontinent of Gondwana into South America, Antarctica, India, and Australia. During the Cretaceous sea-level stood high flooding the interiors of most continental platforms and resulting in the establishment of marine chemical conditions that favored the deposition of calcite. This, in turn, led to the widespread deposition, and subsequent preservation, of the rock type uniquely associated with the Cretaceous: chalk. As a result of this high sea-level, the Cretaceous was characterized by warm, equable, greenhouse-type climates over most areas with temperatures that both exceeded and were more stable than those at present. There was very little or no ice at the Cretaceous poles and reefs, swamps, crocodiles, and even dinosaurs reached latitudes in the vicinity of—and, at times even greater than—60° latitude. Cretaceous atmospheric composition also differed from that of today with higher levels of oxygen and carbon dioxide. The Cretaceous was a quiet time for magnetic reversals, but also a time of widespread volcanism. Biotically, the Cretaceous represents the culmination of many evolutionary-ecological trends begun in the Jurassic, including the diversification of many plant and animal lineages (e.g., diatoms, coccoliths, gymnosperms, angiosperms, foraminifera, ammonoids, molluscs, insects, dinosaurs, ichthyosaurs, plesiosaurs, mosasaurs, pterosaurs, mammals). Finally, the Cretaceous includes two extinction events: an ‘Aptian’ event (which may be an analytic artifact), and the Cenomanian-Turonian event, in which ~ 27 percent of all marine genera disappeared as a result of the coincidental juxtaposition of sea-level rise, the (possibly volcanically accentuated) upwelling of oxygen-poor waters into the shallow chalk seas, and the effects of global cooling induced by more efficient marine circulation patterns. This period was also ended by a very large extinction event which is the subject of a separate article in this volume.

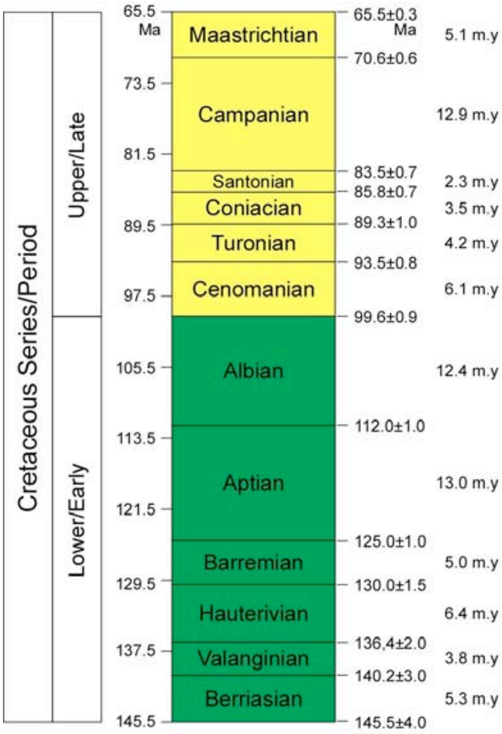


Figure 1. Chronostratigraphy and geochronometry of Cretaceous system/stages. Time scale based on Gradstein and Ogg (this volume). Stage thicknesses scaled to reflect relative durations. Interpolated duration estimates given in far right column.

Stratigraphy

Terrain Cretacé was the name originally given by the French geologist J. J. d”Omalius d’Halloy in 1822 to a sequence of chalk beds underlain by tufas, sands, and marls that crop out in the structural basis of southern England, northern France, and Belgium. d”Omalius d’Halloy’s usage followed that of William Smith’s map that identified four sequences of strata between the Tertiary ‘lower clay’ and the (Jurassic) Portland Stone. These were (from oldest to youngest) micaceous clay, also known as ‘brick earth’, Greensand, brown or grey chalk, and White Chalk. Later that same year the English geologists W. D. Conybeare and William Phillips gathered these four units into two groups—the upper chalk facies and the lower, predominately clastic facies—and first used the term ‘Cretaceous’ to describe the entire stratigraphic package. Conybeare and

Phillips' subdivision is reflected today in the fact that most time scales recognize only two Cretaceous epochs (upper and lower) instead of the more typical three-fold subdivision of upper, middle, and lower.

From 1840 to 1871 each Cretaceous epoch was further subdivided into six stages (**Figure 1**) based on rocks cropping out in France, Switzerland, and southern Holland. Cretaceous chronostratigraphy was originally based on molluscan biostratigraphy; especially the biostratigraphy of ammonites. These fossils were used to subdivide each stage into either three-fold or two-fold substage intervals. Beginning in the 1950's, however, Cretaceous biostratigraphic zonations were further refined through the use of microfossils, chiefly planktonic foraminifera (28 biozones) and calcareous nannoplankton (26 biozones). At least seven key radioisotopic tie points have been identified in Cretaceous sediments, providing good geochronometric control, especially for Upper Cretaceous stage boundaries.

The current base of the Cretaceous is undefined by a boundary stratotype, but is taken as being near the first occurrence of the ammonite *Berriasella jacobi*. The base of the Cenozoic Danian stage defines the top of the Cretaceous and was established in 1991 at the base of the 'boundary clay layer' associated with a geochemical Ir anomaly and a major extinction of planktonic foraminifer and calcareous nannoplankton in the stratotype section outside the town of El Kef, Tunisia. This stratotype definition is somewhat unusual in that it is not taken at a biostratigraphic datum and coincides with a local extinction horizon rather than a first occurrence horizon. It is also unfortunate that the El Kef stratotype has been destroyed subsequent to 1991 due to local farming practices. Studies are currently underway to re-establish the stratotype in the Tunisian type area at an outcrop less susceptible to such damage.

The Cretaceous System is has the greatest duration of any Phanerozoic stratigraphic system (76.5 m.y.). It's distinctive sediments—especially the characteristic Upper Cretaceous chalk facies—are present on all large continental platforms. The Cretaceous is also the first stratigraphic system to be well represented in the deep-sea, owing to the fact that most pre-Cretaceous sediments deposited in the deep ocean basins have been subducted.

Palaeogeography and tectonics

At the beginning of the Cretaceous (**Figure 2A**) the post-Permian breakup of Pangea had progressed to the point where the northern (Laurasian) continents of North America, North China, Siberia, and Eurasia had rifted away from Gondwana (Africa, South America, India, Antarctica, Australia), though the latter remained coherent. Gondwana was, in turn separated from North America by a narrow Atlantic Seaway, and from North China by a broad Tethys Ocean. Surrounding this region of intense tectonic activity, the Pacific Ocean occupied fully half the surface of the planet.

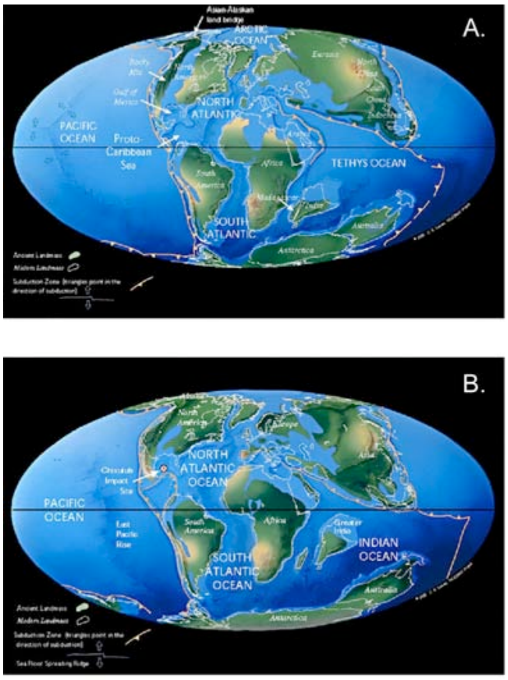


Figure 2. Reconstructions of Cretaceous palaeogeography at (A) 94 Ma (Cenomanian) and (B) 66 Ma (Maastrichtian). See text for discussion. Palaeogeographic maps generated as part of the GeoMap Project and used with permission.

In terms of continental landmasses, the primary Cretaceous event was the rifting of Gondwana. Near the Jurassic Cretaceous boundary (~140 Ma) a large rift between Africa and India formed and propagated south until, by 150 Ma Gondwana has been effectively split in two parts: South America-Africa and India-Antarctica-Australia. Late in the Early Cretaceous (~120 Ma) a rift opened up along the southern coast of South America-Africa and propagated north to form a proto-South Atlantic Seaway. Early in the Late Cretaceous (~110 Ma) southward propagating rifts had opened up between India and Antarctica as well as along the northeastern coast of Australia. Sea-floor spreading took place along all these rifts throughout the Late Cretaceous (**Figure 2B**) causing (1) the South Atlantic Seaway to open northward where, by 100 Ma, it had joined with the Central Atlantic Seaway, (2) India to drift northward along the coast of Africa, and (3) Antarctica-Australia to drift southward. In order to compensate for the northeastern drift of the Tethyan sea floor and the westward drift of the Atlantic sea floor, oceanic subduction systems developed along the northeastern margin of the Tethys and along virtually the entire circumference of the Pacific Plate.

Patterns of marine circulation were also effected substantially by these tectonic reconfigurations. During the Early Cretaceous trade winds blowing westward across the Tethys Ocean would have set up a strong westward

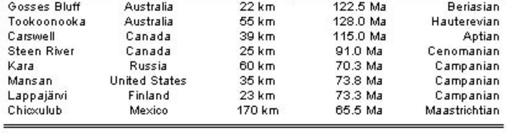
Table 1. Cretaceous large igneous provice eruptions (from Courtillot et al. 1996; Courtillot 1999).

Name	Location	Assoc. Mantle Plume	Age	Stage
Deccan Traps	India	Reunion	65 Ma	Maastrichtian-Danian
Madagascar Traps	Madagascar	Crozet(?)	88 Ma	Turonian
Ontong Java Plateau	SE Asia	Ontong-Java	122 Ma	Aptian
Rajmahal-Tasman Traps	India	Kerguelen	115 Ma	Aptian
Etendeka-Parana Traps	Brazil-Namibia	Tristan da Cunha	133 Ma	Valanginian

equatorial current that circled the globe owing to its passage between North America and the northern part of Gondwana down the Central Atlantic Seaway. Direct evidence for the existence of this current comes from the similarity of shallow marine faunas from submerged parts of the Europe and southern Asia through to (now) submerged seamounts—island systems in the Cretaceous—over 1000 miles west of Hawaii. Aside from this circum-equatorial current, paired cyclonic gyres would have been present in the Pacific Ocean leading to the evolution of distinctive northern and southern hemisphere marine invertebrate faunas. With continued continental fragmentation and northern drift through the Cretaceous, this very simple, Early Cretaceous, marine circulation pattern would have grown more complex, especially once the South Atlantic Seaway opened up between South America and Africa.

In terms of physio-chemical characteristics, the Cretaceous in noteworthy for the number of large igneous province eruptions (**Table 1**) the number of large bolide impact craters (**Table 2**) that occurred during its span, as well as its large number of major marine anoxic events (Aptian, Albian, Cenomanian, Turonian, Coniacian, Santonian, Campanian), and very small number of magnetic polarity reversal events (the Long Cretaceous Normal interval stretches from the Aptian to the Santonian, some 40 million years). Cretaceous rates of weathering are inferred to have been relatively low, partly as a result of relatively high sea-levels and partly because of a relative lack of mountain building, especially during the Early Cretaceous. These, along with the proliferation of phytoplankton (see below), are thought to have been responsible for elevated levels of both carbon dioxide and free oxygen in the Cretaceous atmosphere, relative to modern concentrations

Table 2. Large Cretaceous bolide impact craters.



Name	Location	Size (diam.)	Age	Stage
Gosses Bluff	Australia	22 km	122.5 Ma	Beriasian
Tookoonooka	Australia	55 km	128.0 Ma	Hauterevian
Carswell	Canada	39 km	115.0 Ma	Aptian
Steen River	Canada	25 km	91.0 Ma	Cenomanian
Kara	Russia	60 km	70.3 Ma	Campanian
Mansan	United States	35 km	73.8 Ma	Campanian
Lappajärvi	Finland	23 km	73.3 Ma	Campanian
Chicxulub	Mexico	170 km	65.5 Ma	Maastrichtian

Sea level and sedimentation patterns

As with other intervals of Phanerozoic history, the determination of Cretaceous sea-level history is necessarily tied to analyses of sedimentation patterns and complicated by the fact that regional tectonic factors can modify, or in some cases even obscure, the global or eustatic signal. The first-order trend toward rising sea-level in the Jurassic culminated in the Tithonian and was followed by a eustatic sea-level fall of ~ 50 m into the Berriasian (**Figure 3**). The nadir of late Hauterevian sea level represents the lowest sea level documented for the entire system. Major sea-level rises take place in the early Barremian, Albian, and early Campanian. with the Turonian transgression achieving the highest global sea-level stand—some 250 m above present sea-level—not only for the Cretaceous System, but also for the entire Mesozoic-Cenozoic interval. Global sea-level remained high throughout the Upper Cretaceous, but suffered quite a sudden (tens off thousands of years) and deep (50-100 m) sea-level fall more-or-less coincident with the Cretaceous-Tertiary (K-T) boundary. Owing of the lack of evidence for widespread glaciation in the Cretaceous rocks of Gondwana, it is presumed that these sea-level fluctuations were largely driven by changes in the heat-flow surrounding mid-ocean ridge systems, causing the ridge systems to swell and contract with consequent effects of the volume of the deep-ocean basins.

The very high sea levels achieved throughout the Late Cretaceous meant that large portions of the continental platforms were flooded to form very broad, but shallow, epicontinental seas (**Figure 2**). The sediments that accumulated in these seas are largely responsible for the excellent Cretaceous geological and biological record. In North America and South America, collisions between the western margins of those plate and the eastern Pacific subduction centers resulted in the fold-thrust uplift of the Cordilleran mountain ranges (e.g., Sevier Orogeny), along with associated volcanic and plutonic activity. Sediments from these mountains were shed to the east and west. In North America this erosion led to deposition of the predominately clastic Great Valley sequence in California which were subsequently deformed and uplifted themselves during the Cretaceous accretion of microcontinental fragments (e.g., Wrangalia).

To the east of the Sevier-Laramide mountains a large epicontinjental sea (the Mowry Sea) encroached form the north and south as a result of the late Early Cretaceous sea-level rise. During its initial transgression (Albian) this sea was characterized by dysareobic to anoxic conditions as evidenced by the abundant oil shales and black shales of this age. Clastic deposition characterized the northern part of the Mowry Sea during the Early Cretaceous whereas carbonate-evaporite deposition char-

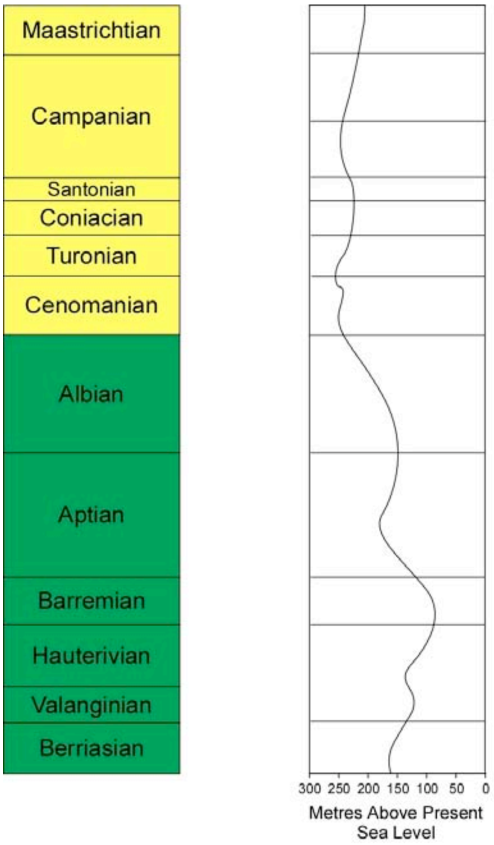


Figure 3. Global variation in sea level throughout the Cretaceous. Sea-level curve redrawn from Haq et al. 1988.

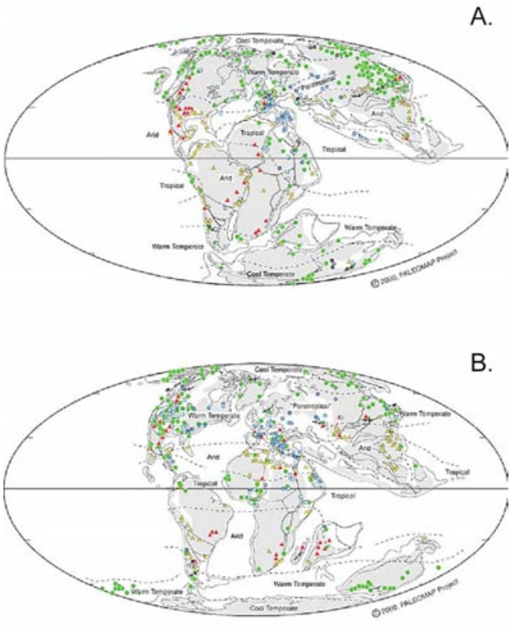


Figure 4. Environmental zones and climate variation (as inferred from sediments and biotas) at (A) 120 Ma (Aptian) and (B) 80 Ma (Campanian). Palaeogeographic maps and environmental data generated as part of the GeoMap Project and used with permission.

acterized its southern arm. These two arms coalesced in the early Late Cretaceous (during the sea-level maximum) and a single interior seaway occupied the central portion of North America through to the Maastrichtian, during which time a more typical basinal carbonate-clastic depositional pattern become dominant. This same pattern of Early Cretaceous drowning of continental platforms also took place in South America, Europe, southern Asia, and Australia.

During the Upper Cretaceous the characteristic chalk lithofacies developed in most large, epicontinental, marine, ocean basins. These enormous chalk seas represented a singular environment that had no equivalent prior to the Late Cretaceous nor in all but the earliest part of the subsequent Cenozoic. Chalk is predominately an epipelagic sedimentary deposit composed of astronomical numbers of calcareous microfossil skeletons, chiefly nannoplankton and planktonic foraminifera. These organisms are present in the world's oceans today, but large areas of modern chalk deposits are not being created because the steady rain of calcareous from the water column is diluted by clastic sediments and by the dissolution of calcareous materials in deeper water. The shallow Late Cretaceous epicontinental seas, however, combined shallow depths with high productivity (because of their chemistry, see below) and low clastic input (because of their size) to produce near ideal conditions for the development and preservation of plankton tests. Moreover, these planktonic groups served as the basis for a highly productive and stable Late Cretaceous marine food chain, fostering the diversification of both marine invertebrate and vertebrate groups (see below). With the late Maastrichtian sea-level regression, though, these chalk seas retreated from the continental interiors although a few regional centers of chalk deposition continued into the Paleocene.

Climate

Continuing on from the Jurassic greenhouse, world climates in the Cretaceous were, if anything, even more stable, uniform, and equable, even at very high latitudes (**Figure 4A**). During the Early Cretaceous, climate bands with essentially modern latitude limits were found in both the northern and southern hemispheres. Exceptions include a tropical zone largely confined to the western Tethys (as evidenced by widespread reef facies), a paratropical embayment reaching across southern Europe and into Eurasia (as evidenced by high-latitude bauxite deposits) and a very large arid region (as evidenced by widespread evaporite and calcrete deposits) in southern North America and northern South America. The overall equability of the Early Cretaceous climate is supported by the observation of coal deposits throughout Pangea and Laurasia—even in areas reconstructed as being near the Early

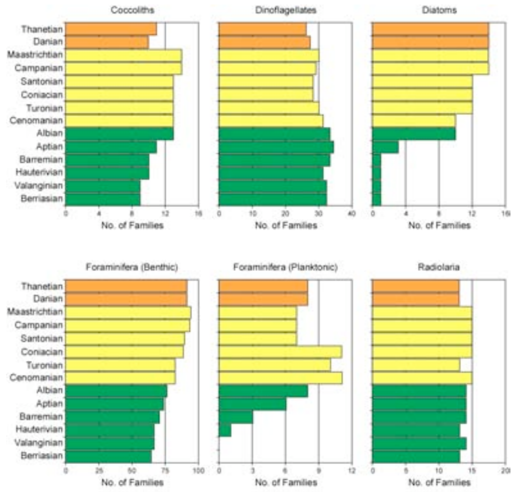


Figure 5. Fossil protist family-richness patterns through the Cretaceous and first two stages of the Paleocene. Data summarized from Benton (1993). Note different scales on each graph.

Cretaceous poles—along with crocodile fossils above 30°N latitude and, amazingly, above 60°S latitude!

The Late Cretaceous sea-level rise further intensified these climatic gradients (**Figure 4B**) by creating arid belts both north and south of the tropical equatorial zone and pushing the paratropical embayment well into Asia. An asymmetry developed between the north and south polar areas in the Late Cretaceous though, with the northern polar region containing coal deposits, crocodile fossils, and even dinosaur fossils well above the Arctic Circle, while these deposits stop at or near the 60°S latitude. No doubt the fact that Antarctica had drifted to occupy a position at the Late Cretaceous South Pole was a significant factor in the development of this climatic contrast between the hemispheres.

In the sea $\delta^{18}O$ analyses of planktonic foraminifera indicate that both surface and bottom-water temperatures rose steadily through the Lower Cretaceous with a single, strong, high temperature anomaly in the upper Berriasian-lower Aptian. Cretaceous marine temperatures peaked in the Turonian (average surface temperatures of ~ 18°C) and then went into a rapid decline to the Campanian. The Campanian-Maastrichtian interval was characterized by strong marine surface-water temperature instabilities with several strong reversals between warm and cool phases that varied by as much as 4°C continuing to the K-T boundary. In contrast, marine bottom-water temperatures do not appear to have been subject to these strong variations.

Biota

Fossil Protists

The Cretaceous is, in many ways, the acme of the microfossil record. Two of the three modern phytoplankton groups—calcareous nannoplankton and diatoms (**Figure 5**) underwent major family-level diversifications during this period with diatoms a particularly rapid family-level diversification in the late Lower Cretaceous. Dinoflagellates maintained their very high diversities throughout the interval albeit with a long-term drift to slightly lower family-richness values through the Late Cretaceous that continued into the Paleocene. Foraminifera responded to this change in the marine environment by maintaining a steady diversification of benthic forms through the Late Cretaceous (likely a response to enhanced carbon deposition to the sea floor by plankivorous zooplankton and nekton). Planktonic foraminifer first appear in the Hauterevian and, after an initial radiation that extended into the early part of the Upper Cretaceous (e.g., appearance of the first hedbergellids, heterohelicids, guembelitrids), appear to settle back to a steady-state family-level diversity in the upper part of the Late Cretaceous. Radiolaria appear to maintain a more-or-less steady state family-level diversity throughout the interval.

As a result of these radiations the Cretaceous sea beds were, for the first time, blanketed with calcareous oozes. Of course, the most dramatic example of this was the extensive—and economically important—chalk deposits of North America and Europe. Massive Cretaceous chalk production appears to have occurred because of the very low Mg/Ca ratio of Cretaceous seawater. This chemical environment favors the production of calcite which is then preserved because the small size of the nannoplankton-produced grains makes the (later uplifted) chalk deposit nearly impenetrable to groundwater. Widespread chalk deposition ended in the middle Paleocene when the seawater Mg/Ca ratio began to rise from its all-Phanerozoic Cretaceous low.

Marine Invertebrates

Like the most marine protist groups, corals, marine molluscs (chiefly gastropods, cephalopods and bivalves), as well as marine arthropods (chiefly crustaceans and ostracods) underwent long-term family-level radiations through the Cretaceous and extending into the overlying Paleocene (**Figure 6**). Corals diversified strongly throughout the interval, but declined in abundance in the Late Cretaceous, presumably because the low Mg/Ca ratio made it more difficult to secrete their aragonite skeletons. The total mollusc patterns shown in **Figure 6** masks strongly differing patterns among the constituent groups. For example, cehalopods exhibit a particularly impressive diversification un the latter half of the Early Cretaceous and across into the earlier part of the Late Cretaceous, whereas gastropods and bivalves exhibit the greater part of their family-level diversification histories in the Late Cretaceous. Burrowing bivalves and gastropods of modern aspect (neogastropods) diversified strongly throughout the period. The Cretaceous

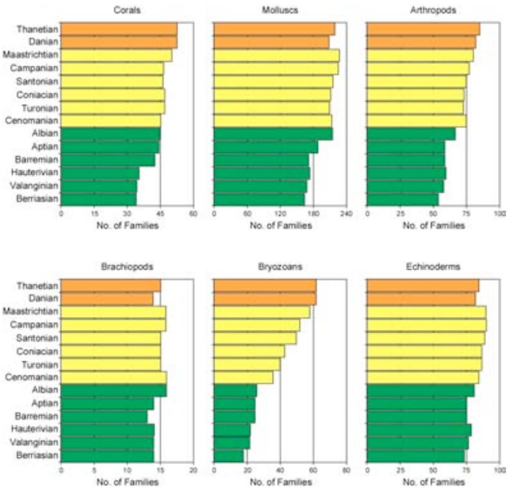


Figure 6. Fossil marine, invertebrate, family-richness patterns through the Cretaceous and first two stages of the Paleocene. Data summarized from Benton (1993). Note different scales on each graph.

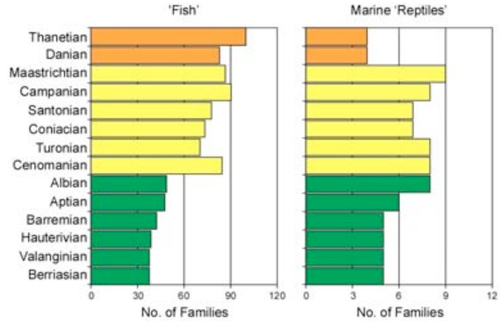


Figure 7. Fossil marine, vertebrate, family-richness patterns through the Cretaceous and first two stages of the Paleocene. Data summarized from Benton (1993). Note different scales on each graph.

is also a time of gigantism among several surface-dwelling bivalve lineages such as the genus *Inoceramus* that could be as much as a meter across (natural inoceramid casts are often mistaken by amateur geologists for 'dinosaur footprints'). One oddly-shaped bivalve group—the rudists—even managed to replace corals as the principal reef builders of the shallow Late Cretaceous seas owing to their superior chemical control of skeleton-secretion processes. The Cretaceous arthropod radiation was driven largely by crustaceans presumably in response to the diversification of neogastropods, their principal prey item. During this time, gastropods and crabs continued their 'arms race' with gastropods developing ever more elaborate predator deterrent mechanisms (e.g., reinforced apertures, shell ribbing, spines) and crabs responding through the development of improved claw designs (e.g., strength, shape). This crustacean diversification was particularly pronounced in the Albian and Campanian. Brachiopod family richness values fell slightly in the Barremian, but recovered quickly and were maintained throughout the Late Cretaceous. Bryozoans exhibit perhaps the most striking richness-change pattern with a strong and sustained diversification throughout the entire Late Cretaceous. This trend is driven by cheilostome bryozoans which almost trebled their number of families through the course of the Late Cretaceous, though ctenstomes and cyclostomes also undergo modest diversifications through this interval as well. Echinoderms appear to have the most conservative diversification history of any major marine invertebrate clade with the slight drift to higher Late Cretaceous values bring driven primarily by an asteroid (starfish) radiation.

Marine Vertebrates

The Cretaceous marine vertebrate faunas (**Figure 7**) exhibit surprising similarities (and differences) between the richness histories of 'fish' (including sharks, rays and bony fish) and marine 'reptiles' (including marine turtles, ichthyosaurs, plesiosaurs, and mosasaurs). Both groups exhibit low, steady-state Early Cretaceous values and both exhibit much higher Late Cretaceous values. Moreover, both group undergo the transition from low Early Cretaceous values to higher Late Cretaceous values, within a stage of one another. This similarity is all the more remarkable when the difference between the sizes of these faunas is taken into consideration. The Late Cretaceous richness increase is primarily driven by diversification within fish clades while the driver of the marine 'reptile' pattern is chiefly a turtle-mosasaur diversification.

Terrestrial Invertebrates

There were several groups of terrestrial and freshwater molluscs (e.g., pulmonate gastopods, unionid bivalves) as well as freshwater arthropods (e.g., curstacea and ostracodes) in addition to the ubiquitous Cretaceous Insects. Among these only the molluscs exhibit a sustained diversification trend (**Figure 8**). This pattern is driven primarily by the Late Cretaceous proliferation of both terrestrial and freshwater gastropods. Both non-insect arthropods and insects exhibit more-or-less steady-state diversification histories throughout this interval, with perhaps some suggestion of a Late Cretaceous increase in the former, driven primarily by a proliferation of Late Cretaceous chelicerate families (e.g., scorpions). Here it is interesting to note the very high richness values for Cretaceous insects, a group many would assume to have a 'poor' fossil record.

Terrestrial Vertebrates

While dinosaurs understandably get most of the attention when it comes to Cretaceous terrestrial vertebrate faunas, it is important to note that essentially all modern terrestrial vertebrate groups had representatives in the Cretaceous. Although not as well-known to the popular audience, salamanders, frogs, lizards, snakes, turtles, crocodiles, birds, and mammals all shared the Cretaceous landscapes along with

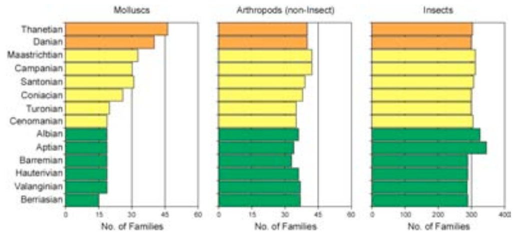


Figure 8. Fossil terrestrial, invertebrate, family-richness patterns through the Cretaceous and first two stages of the Paleocene. Data summarized from Benton (1993). Note different scales on each graph.

the non-avian dinosaurs, non-dinosaur archosaurs (e.g., crocodiles, champosaurs), and pterosaurs (**Figure 9**).

Perhaps the most unusual Cretaceous diversification history is that of freshwater 'fish' (including sharks and rays as well as bony fish). This group begins the Cretaceous with a healthy 20 or so families and undergoes a modest diversification event in the latter part of the Early Cretaceous. The subsequent early part of the Late Cretaceous—when many other groups are diversifying—is a time of progressive diversity reduction in the freshwater fish fauna. This pattern is driven largely by reductions in the number of teleost and sarcopterygian clades. However, this declining pattern reverses dramatically in the Campanian (driven by a Late Cretaceous radiation in teleost clades) and continues unbroken across the K-T boundary and into the Paleocene.

Both amphibians and non-dinosaurian reptiles (e.g., turtles, snakes, lizards) exhibit similar progressive patterns throughout the Cretaceous that also extend into the Paleocene. Dinosaurs exhibit a strong diversification throughout the Late Cretaceous to their Campanian peak from which there is a marked retreat (involving both theropod and sauropodomorph forms) in the Maastrichtian. All non-avian dinosaurs became extinct by the end of the Maastrichtian and the Danian values in **Figure 9** all represent bird families. This having been said, there are persistent reports of dinosaur remains and signs (e.g., nests, trackways) in Danian strata and it would not be surprising if these reports were confirmed and accepted by most vertebrate paleontologists in the near future.

Last, but by no means least, mammals exhibit very low family richness values throughout most of the Early Cretaceous and the lower part of the Late Cretaceous. There is a hint, however, that mammalian diversification started in the Campanian, at about the same time as the final dinosaur diversification. Mammals also underwent a richness reduction in the Maastrichtian coincident with a similar reduction in dinosaur family-richness values. Indeed mammals lost more faamilies in the Maastrichtian than did dinosaurs! The fates of these two clades were decoupled by other events in the Maastrichtian, but it is false to regard their diversity histories as being mirror images of one another—as has been the case in many popular accounts and more than a few scientific treatises. Rather than ships passing in the night, the Cretaceous history of mammals and dinosaurs suggests several striking similarities the interpretation of which would benefit from further investigation.

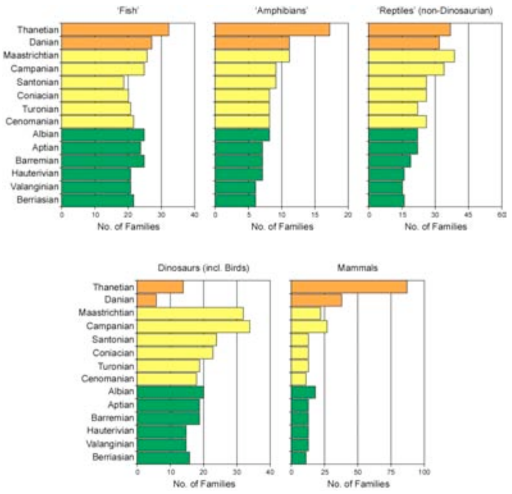


Figure 9. Fossil terrestrial, vertebrate, family-richness patterns through the Cretaceous and first two stages of the Paleocene. Data summarized from Benton (1993). Note different scales on each graph.

Terrestrial Plants

The Cretaceous bore witness to a fundamental transformation of the terrestrial flora with the initial diversification of seed-bearing (angiosperm) plants. While angiosperms first appeared in the Jurassic, 'naked seed' gymnosperms such as conifers, cycads, and ginkos dominated the earliest Cretaceous landscapes. Nevertheless, the strong plant diversification event documented in **Figure 10** is almost entirely the result of family-production within angiosperms. During the Cretaceous over 30 new angiosperm families appear, including beech, birch, fig, holly, magnolia, oak, palm, sycamore, and walnut. Angiosperm seed development is considered superior to that of gymnosperms because the seed is protected from damage inside the plant's ovary. This means that the plant can produce a much larger number of smaller seeds from the same energy investment required to make the less efficient gymnosperm cone. Flowers were another Cretaceous angiosperm development and these literally opened up a host of new possibilities for the attraction of pollinator organisms, effectively co-opting other creatures into the plants' reproductive strategy. Like the first plants, the first angiosperms appear in Early Cretaceous lake and stream habitats where quick-developing, opportunistic, weedy forms have an advantage. However, there were no grasses—and so no grassy plain or savannah habitats—in Cretaceous times.

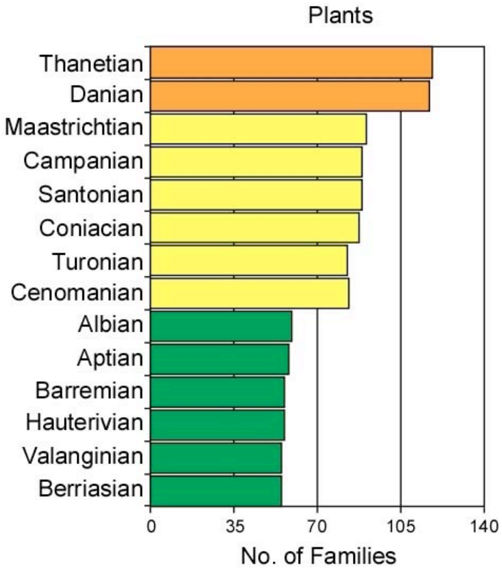


Figure 10. Fossil terrestrial, plant, family-richness patterns through the Cretaceous and first two stages of the Paleocene. Data summarized from Benton (1993).

Extinctions

Two extinction events are widely held to have occurred during the Cretaceous, and Aptian event and a Cenomanian event. [Note: the end-Cretaceous or Cretaceous-Tertiary (K-T) boundary extinction event is the subject of separate article in this volume.] There is considerable debate regarding whether the Aptian event is important, or even recognizable in most palaeontological datasets. In the late J. J. (Jack) Sepkoski's family-level and genus-level compendia an Aptian extinction-intensity peak stands slightly above what he and David Raup regarded as background extinction levels. The extent of this peak's distinctness has changed over successive versions of the Sepkoski dataset and is, to some extent, dependent upon how one 'bins' time across the relatively long Aptian and Albian stages. In addition, an extinction peak in the vicinity of 119 Ma was predicted on the basis of Raup and Sepkoski's extinction-periodicity hypothesis.

Irrespective of these analytic results, specialist biostratigraphers and systematists have been hard pressed to identify which Aptian organismal groups bore the brunt of this putative extinction event. Modest losses among planktonic foraminifera, benthic foraminifera, calcareous algae, and rudustid bivalves have been noted, but none of these appears to have had a dominant effect on the diversity histories of any of these groups, not to mention the biosphere as a whole. Possible extinction mechanisms also abound in the Aptian, including a local seal-level lowstand, an ocean anoxic event, and a large volcanic eruption that emplaced the submarine Ontong-Java Plateau. Nevertheless, the Aptian extinction record appears to have a relatively weak claim on being a major turning point in Earth's biodiversity history.

The case for a major extinction event at the Cenomanian-Turonian boundary is much stronger. Beginning in the upper Cenomanian, and continuing into the lower Turonian, marine taxa suffered the lost of ~ 7 percent of all families with fossilizable hard parts and ~ 26 percent of all constituent genera. This event occurred over an interval of from 3-5 m.y. and was complexly structured both temporally and geographically.

Ecologically the extinction appears to exhibit a distinctly 'bottom-up' character with deep-dwelling taxa (e.g., gastropods, bivalves; benthic foraminifera, especially agglutinated-walled forms; deep-dwelling planktonic foraminifera; bottom-feeding ammonoids) being differentially affected. Over a few meters of section species-level extinction rates ranging from 20-50 percent (and occasionally as high as 80%) are commonly reported. At least locally, however, shallower-water taxa (including coccoliths, pelagic ammonites, and rudistid bivalves, as well as sharks, ichthyosaurs, and plesiosaurs) fell victim. Geographically, the extinction appears to have been centered on tropical and temperate biotas with virtually no extinctions being recorded above 60° north or south of the Cretaceous palaeoequator.

Geochemically, the extinction event is correlated with the widespread interruption of chalk formation in epicontinental seaways in favor of clastic deposition; especially in the form of the black shales and limestones that signal low-oxygen or dysaerobic conditions. In addition, this event is associated with pronounced δ^{13}C and δ^{18}O anomalies. a sea-level highstand, and an interval of widespread submarine and subareal volcanism. No convincing or consistent evidence for bolide impact has been recovered from Cenomanian-Turonian boundary sediments to date. Two Ir anomalies are associated with the Cenomanian-Turonian interval, but, owing to similarities between the trace-element signature of these anomalies and the trace-element composition of mid-Atlantic Ridge basalts these anomalies have been interpreted as resulting from volcanic, rather than extraterrestrial, inputs.

Virtually all of the popular extinction mechanisms—including bolide impact—have been advanced to explain the Cenomanian-Turonian extinction. The current geological and palaeontological consensus suggests that this is a multi-causal event that occurred because of a unique juxtaposition of independent factors effecting marine habitats coincided during this interval of Earth history. The most important proximal cause was probably anoxic deep-ocean waters invading middle and, in some cases, shallow shelf habitats as a result of eustatic sea-level rise. The Cenomanian-Turonian interval represents the highest stand of sea-level for the entire Phanerozoic as well as the highest Cretaceous sea-level stand. This primary mechanism was likely intensified by submarine volcanism (which can alter the buoyancy of dysoxic and anoxic deep marine waters casing them to rise further up the continental shelves than would have otherwise been the case) and global cooling resulting from improved marine circulation patterns that were likely a by-product of the sea-level highstand. This improved circulation may have increased the efficiency of heat transfer from tropical to polar regions, thus cooling the topics and (perhaps) exceeding the tolerance of many warm-adapted tropical species, including reef-building rudists and corals. As is the case with most modern extinction events, once a sufficient number of key species had been eliminated other species would become increasingly susceptible to extinction because of complex ecological dependencies rather than physiochemical tolerances per se.

It has recently been suggested that the magnitude of the Cenomanian-Turonian extinction event has been overestimated as a result of the geographic migration of certain types of marine environments in the stratigraphic record and the fact that any single section or core presents a picture of changing local superimposed over changing global conditions. While all fossil record must be examined by biases of this sort, the widespread and, on the whole, consistent nature of the biotic patterns described from the Cenomanian-Turonian interval argues that such biases—though undoubtedly present—can be invoked to discount the entire event. Additional research will be needed in order to test these hypotheses and further sharpen our understanding of this fascinating interval of Earth history.

See Also

Arthropods (crustaceans, ostracodes chelicerates, insects), Atmosphere evolution, Biozones, Brachiopods, Bryozoans, Climate change, Coccoliths (calcareous nannoplankton), Corals (coelenterates), Diatoms, Dinoflegellates, Echinoderms (asteroids, crinoids, echinoids [regular and irrelgular], holothurians), Extinctions (end-Cretaceous [K-T] extinction) 'Fish' (sharks, rays, bony fish), Foraminifera (benthic and planktonic), Molluscs (gastropods, cephalopods, bivalves), Plate tectonics, Principles of Stratigraphy, Radiolaria, Sea-level change, Sequence stratigraphy, Tetrapods ('amphibians', 'reptiles', dinosaurs, mammals), Time scale.

Further Reading

Benton, MJ (1993) *The fossil record 2*. London, Chapman & Hall.

Gould, SJ (ed) (1993) *The book of life*. New York, W. W. Norton and Company.

Hallam, A (1992) *Phanerozoic sea-level changes*. New York, Columbia University Press.

Hallam, A and Wignall, PB (1997) *Mass extinctions and their aftermath*, Oxford, Oxford Science Publications.

Haq, B, Hardenbol, J, and Vail, PR (1987) Chronology and fluctuating sea levels since the Triassic. *Science*, v. 235, p. 1156-1166.

Stanley, S (1989) *Earth and life through time* (second edition). San Francisco, WH Freeman.

Stanley, SM (1999) *Earth system history*. New York, WH Freeman and Company.

Suggested Reference:
MacLeod, N. in press. Cretaceous. *In* **R. C. Selley, L. R. M. Cocks and I. R. Plimer** (eds.), *Encyclopedia of Geology*. Academic Press, London.