A Comprehensive Introduction to
The Oligocene Epoch and Events

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Introduction to Oligocene

System	Series	Stage	Age (Ma)
Neogene	Miocene	Aquitanian	**younger**
Paleogene	**Oligocene**	Chattian	23.03–28.4
		Rupelian	28.4–33.9
	Eocene	Priabonian	33.9–37.2
		Bartonian	37.2–40.4
		Lutetian	40.4–48.6
		Ypresian	48.6–55.8
	Paleocene	Thanetian	55.8–58.7
		Selandian	58.7–61.7
		Danian	61.7–65.5
Cretaceous	Upper	Maastrichtian	**older**

Subdivision of the Paleogene Period according to the IUGS, as of July 2009.

The **Oligocene** is a geologic epoch of the Paleogene Period and extends from about 34 million to 23 million years before the present (33.9 ± 0.1 to 23.03 ± 0.05 Ma). As with other older geologic periods, the rock beds that define the period are well identified but the exact dates of the start and end of the period are slightly uncertain. The name Oligocene comes from the Greek ὀλίγος (*oligos*, few) and καινός (*kainos*, new) and refers to the sparsity of additional modern mammalian faunas after a burst of evolution during the Eocene. The Oligocene follows the Eocene Epoch and is followed by the Miocene Epoch. The Oligocene is the third and final epoch of the Paleogene Period.

The Oligocene is often considered an important time of transition, a link between "[the] archaic world of the tropical Eocene and the more modern-looking ecosystems of the Miocene." Major changes during the Oligocene included a global expansion of grasslands and a regression of tropical broad leaf forests to the equatorial belt.

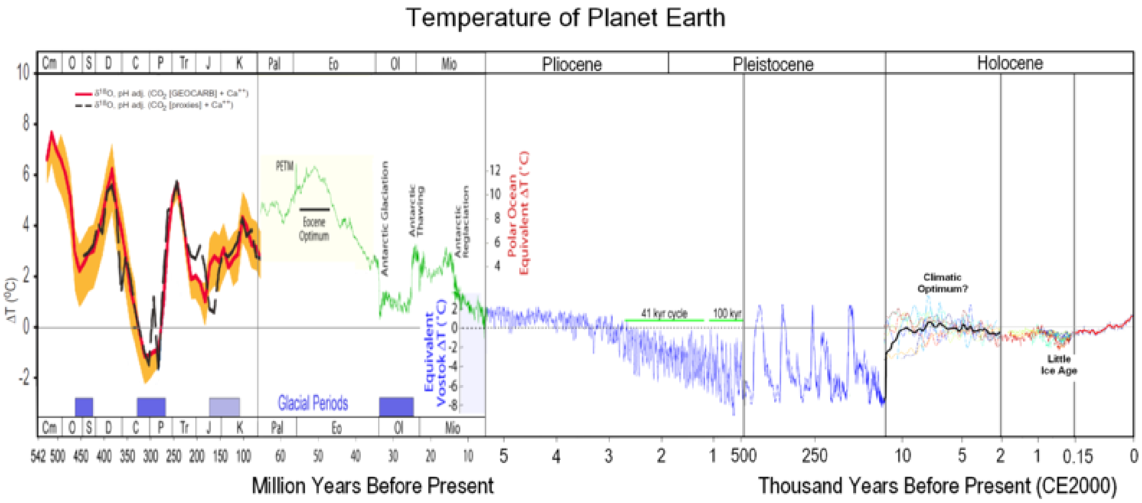
The start of the Oligocene is marked by a major extinction event, a faunal replacement of European with Asian fauna except for the endemic rodent and marsupial families called the Grande Coupure. The Oligocene-Miocene boundary is not set at an easily identified worldwide event but rather at regional boundaries between the warmer late Oligocene and the relatively cooler Miocene.

Subdivisions

Oligocene faunal stages from youngest to oldest are:

Chattian or Late Oligocene (28.4 ± 0.1 – 23.03 mya)
Rupelian or Early Oligocene (33.9 ± 0.1 – 28.4 ± 0.1 mya)

Climate



The Paleogene Period general temperature decline is interrupted by an Oligocene 7M-year stepwise climate change. A deeper 8.2°C 0.4M-year temperature depression leads the 2°C 7M-year stepwise climate change 33.5Ma. The stepwise climate spanned 7M-years 25.5Ma through 32.5Ma as depicted in the PaleoTemps chart. The Oligocene climate change was a global increase in ice volume and a 55m decrease in sea level (35.7-33.5Ma) with a closely related (25.5-32.5Ma) temperature depression. The 7M-year depression abruptly terminated within 1-2M-year of the La Garita Caldera volcanism event 28-26 Ma. A deep 400 k-year glaciating Oligocene Miocene boundary event is recorded at the McMurdo Sound and King George Island.

Paleogeography

During this period, the continents continued to drift toward their present positions. Antarctica continued to become more isolated and finally developed a permanent ice cap. (Haines)

Mountain building in western North America continued and the Alps started to rise in Europe as the African plate continued to push north into the Eurasian plate, isolating the remnants of the Tethys Sea. A brief marine incursion marks the early Oligocene in Europe. Oligocene marine exposures are rare in North America. There appears to have been a land bridge in the early Oligocene between North America and Europe since the faunas of the two regions are very similar. During sometime in the Oligocene, South America was finally detached from Antarctica and drifted north towards North America. It also allowed the Antarctic Circumpolar Current to flow, rapidly cooling the continent.

Flora

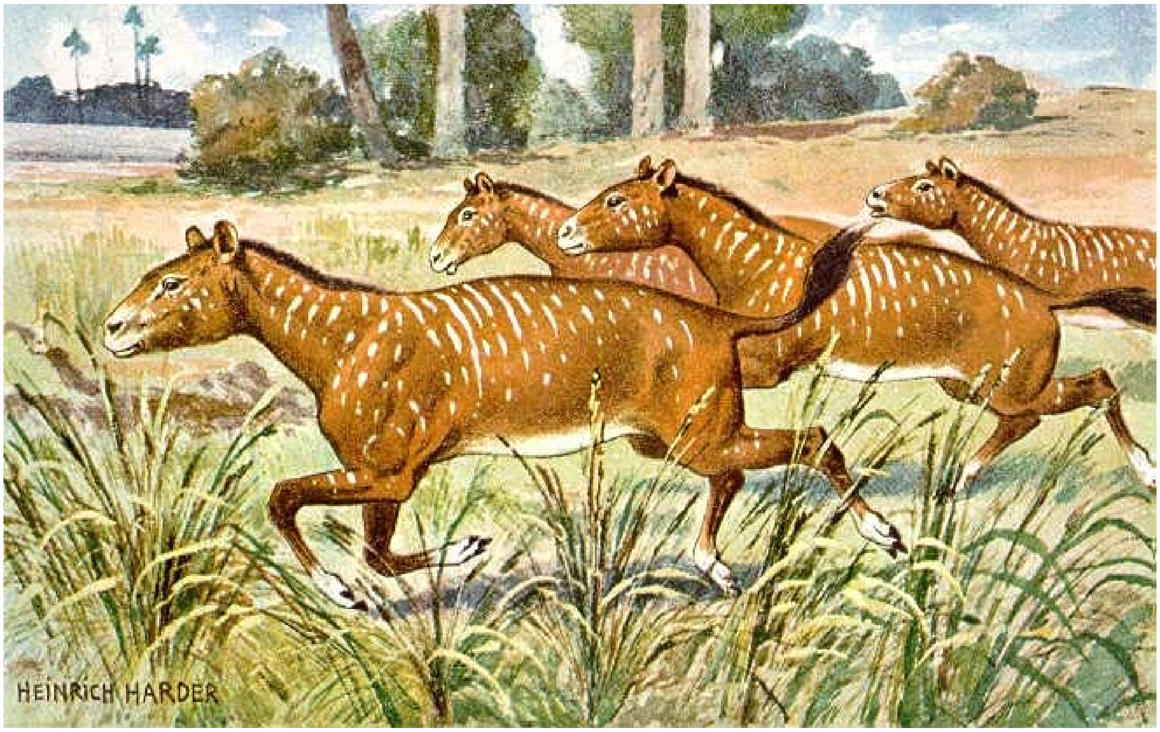
Angiosperms continued their expansion throughout the world; tropical and sub-tropical forests were replaced by temperate deciduous woodlands. Open plains and deserts became more common. Grasses expanded from the water-bank habitat in the Eocene and moved out into open tracts; however even at the end of the period it was not quite common enough for modern savanna.(Haines)

In North America, subtropical species dominated with cashews and lychee trees present and temperate trees such as roses, beech and pine were common. The legumes of the pea and bean family spread and sedges, bulrushes and ferns continued their ascent.

Fauna

Hyaenodon

Important Oligocene land faunas are found on all continents at this time. Even more open landscapes allowed animals to grow to larger sizes than they had earlier in the Paleogene. Marine faunas became fairly modern, as did terrestrial vertebrate faunas in the northern continents. This was probably more as a result of older forms dying out than as a result of more modern forms evolving. Many groups during this time, such as horses, entelodonts, rhinoceroses, oreodonts and camels, became more cursorial during this time, adapting to the plains that were spreading as the Eocene rainforests receded.



Mesohippus

South America was isolated from the other continents and evolved a quite distinct fauna during the Oligocene, home to strange animals such as pyrotheres and astrapotheres, as well as litopterns and notoungulates. Sebecosuchian crocodiles, terror birds and carnivorous marsupials like the borhyaenids remained the dominant predators. Brontotheres died out in the Earliest Oligocene and creodonts died out outside Africa and the Middle East at the end of the period. Multituberculates, an ancient lineage of primitive mammals, also went extinct in the Oligocene. The Oligocene was home to a wide variety of strange mammals. A good example of this would be in the White River Badlands of the United States, which were formerly a semi-arid prairie home to many different types of endemic mammals, including entelodonts like *Archaeotherium*, camels (such as *Poebrotherium*), running rhinos, three-toed horses (such as *Mesohippus*), nimravids, protoceratids and early dogs like *Hesperocyon*. Oreodonts, an endemic American group, were very diverse during this time. In Asia during the Oligocene, a group of running rhinos gave rise to the indricotheres, like *Indricotherium*, which were the largest land mammals ever to walk the Earth.

The marine animals of Oligocene oceans resembled today's fauna, such as the bivalves. The fossil record of marine mammals is a little spotty during this time and not as well known as the Eocene or Miocene, but some fossils have been found. The baleen and toothed cetaceans (whales) just appeared and their ancestors, the archaeocete cetaceans began to decrease in diversity due to their lack of echolocation, which was very useful as the water became colder and cloudier. Other factors to their decline could include climate changes and competition with today's modern cetaceans and the carcharhinid sharks, which also appeared in this epoch. Early desmostylians, like *Behemotops*, are known from the Oligocene. Pinnipeds probably appeared near the end of the epoch from a bear-like or otter-like ancestor.

Chapter- 2

Chattian and Rupelian

Chattian

The **Chattian** is, in the geologic timescale, the youngest of two ages or upper of two stages of the Oligocene epoch/series. It spans the time between 28.4 ± 0.1 Ma and 23.03 ± 0.05 Ma (million years ago). The Chattian is preceded by the Rupelian and is followed by the Aquitanian (the lowest stage of the Miocene).

Stratigraphic definition

The Chattian was introduced by Austrian palaeontologist Theodor Fuchs in 1894. Fuchs named the stage after the Chatti, a Germanic tribe. The original type locality was near the German city of Kassel.

The base of the Chattian is at the extinction of the foram genus *Chiloguembelina* (which is also the base of foram biozone P21b). An official GSSP for the Chattian stage had not been established yet in 2009.

The top of the Chattian stage (which is the base of the Aquitanian stage, Miocene series and Neogene system) is at the first appearance of foram species *Paragloborotalia kugleri*, the extinction of calcareous nannoplankton species *Reticulofenestra bisecta* (which forms the base of nannoplankton biozone NN1) and the base of magnetic chronozone C6Cn.2n.

The Chattian is coeval with regionally used stages or zones like the upper Avernian European mammal zone (it spans the Mammal Paleogene zones 30 through 26 and part of 25.), the upper Geringian and lower Arikareean mammal zones of North America, most of the Deseadan mammal zone of South America, the upper Hsandgolian and whole Tabenbulakian mammal zone of Asia, the upper Kiscellian and lower Egerian Paratethys stages of Central and eastern Europe, the upper Janjukian and lower Longfordian Australian regional stages, part of the Zemorrian Californian stage and Chickasawhayan regional stage of the eastern US.

Volcanic event

During the Chattian the largest known single-event volcanic eruption occurred: the Fish Canyon eruption of La Garita with a magnitude of 9.2. It has been dated to 27.51 Ma ago.

Rupelian

The **Rupelian** is, in the geologic timescale, the older of two ages or the lower of two stages of the Oligocene epoch/series. It spans the time between 33.9 ± 0.1 Ma and 28.4 ± 0.1 Ma (million years ago). It is preceded by the Priabonian stage (part of the Eocene) and is followed by the Chattian stage.

Name

The stage is named after the small river Rupel in Belgium, a tributary to the Scheldt. The Belgian Rupel Group derives its name from the same source. The name Rupelian was introduced in scientific literature by Belgian geologist André Hubert Dumont in 1850. The separation between the group and the stage was made in the second half of the 20th century, when stratigraphers saw the need to distinguish between lithostratigraphic and chronostratigraphic names.

Stratigraphic definition

The base of the Rupelian stage (which is also the base of the Oligocene series) is at the extinction of foram genus *Hantkenina*. An official GSSP had not yet been assigned to the Rupelian in 2009.

The top of the Rupelian stage (the base of the Chattian) is at the extinction of the foram genus *Chiloguembelina* (which is also the base of foram biozone P21b).

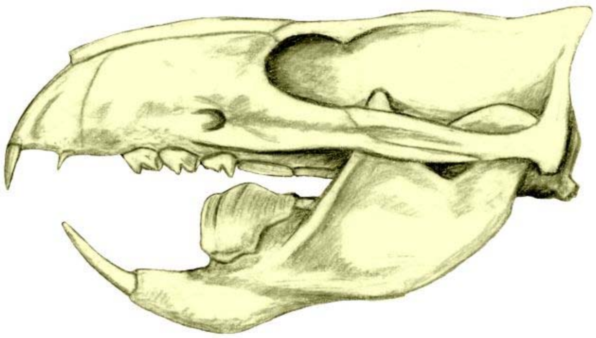
The Rupelian overlaps the Orellan, Whitneyan and lower Arikareean North American Land Mammal Ages, the upper Mustersan and Tinguiririan South American Land Mammal Ages, the uppermost Headonian, Suevian and lower Arvernian European Land Mammal Mega Zones (the Rupelian spans the Mammal Paleogene zones 21 through 24 and part of 25) and the lower Hsandgolian Asian Land Mammal Age. It is also coeval with the only regionally used upper Aldingan and lower Janjukian stages of Australia), the upper Refugian and lower Zemorrian stages of California and the lower Kiscellian Paratethys stage of Central and eastern Europe. Other regionally used alternatives include the Stampian, Tongrian, Latdorfian and Vicksburgian.

Chapter- 3

Multituberculata and Archaeotherium (Extinct during Oligocene Epoch)

Multituberculata

Multituberculates
Fossil range: Middle Jurassic-Oligocene, 160–35 Ma



Skull of *Ptilodus*

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Subclass:	Allotheria
Order:	**†Multituberculata** Cope, 1884

Suborders

- †Cimolodonta
- †Plagiaulacida

The **Multituberculata** were a group of rodent-like mammals that existed for approximately one hundred million years—the longest fossil history of any mammal lineage—but were eventually outcompeted by rodents, becoming extinct during the early Oligocene. At least 200 species are known, ranging from mouse-sized to beaver-sized. These species occupied a diversity of ecological niches, ranging from burrow-dwelling to squirrel-like arborealism. Multituberculates are usually placed outside either of the two main groups of living mammals—Theria, including placentals and marsupials and Monotremata—but some cladistic analyses put them closer to Theria than to monotremes.

History

The multituberculates existed for over 100 million years and are often considered the most successful, diversified and long-lasting mammals in natural history. They first appeared in the early Jurassic, or perhaps even the Triassic, survived the mass extinction in the Cretaceous and became extinct in the early Oligocene epoch, some 35 million years ago.

Geographic distribution

With the possible exception of some poorly preserved South American material, multituberculates are only known from the northern hemisphere. A southern grouping, Gondwanatheria, has in the past been referred to the order, though this placement currently has little support.

In the late Cretaceous multituberculates were widespread and diverse in the northern hemisphere, making up more than half of the mammal species of typical faunas. Although some lineages became extinct during the faunal turnover at the end of the Cretaceous, multituberculates managed very successfully to cross the K/T boundary and reached their peak of diversity during the Paleocene. They were an important component of nearly all Paleocene faunas of Europe and North America and of some late Paleocene faunas of Asia. Multituberculates also were most diverse in size during the Paleocene, ranging from the size of a very small mouse to that of a beaver.

Biology

The multituberculates had a cranial and dental anatomy similar to rodents with cheek-teeth separated from the chisel-like front teeth by a wide tooth-less gap (the diasteme). Each cheek-tooth displayed several rows of small cusps (or tubercles, hence the name) that operated against similar rows in the teeth of the jaw. Like in modern rodents, this masticatory apparatus formed an efficient chopping device.

During the Cretaceous and Paleocene the multituberculates radiated into a wide variety of morphotypes, including the squirrel-like arboreal ptilodonts. The peculiar shape of their last lower premolar is their most outstanding feature. These teeth were larger and more elongated than the other cheek-teeth and had an occlusive surface forming a serrated slicing blade. Though it can be assumed that this was used for crushing seeds and nuts, it is believed that most small multituberculates also supplemented their diet with insects, worms and fruits.

Restoration of *Saurornitholestes* digging a multituberculate out of a burrow

A ptilodont that successfully strived in North America was *Ptilodus*. Thanks to the well-preserved *Ptilodus* specimens found in the Bighorn Basin, Wyoming, we know that these multituberculates were able to abduct and adduct their big toes and thus that their foot mobility was similar to that of modern squirrels which descend trees head first.

In Europe another family of multituberculates were equally successful—the Kogaionidae, first discovered in Hațeg, Romania. They also developed an enlarged blade-like lower premolar and the *Hainina*, the most successful genus, was originally believed to be a ptilodont. However, more detailed analysis of this genus reviled a smaller number of dental cusps and a retained fifth premolar—a unique combination of primitive and advanced features indicating that *Hainina* were related to some Jurassic genera and that enlarged, blade-like premolar were acquired independently in Europe and North America.

Another group of multituberculates, the taeniolabids, were heavier and more massively built and could reach the size of a modern beaver; indicating they lived a fully terrestrial life. They reached their highest diversity in Asia during the late Cretaceous and Paleocene, which suggests they originated from there.

The structure of the pelvis in the Multituberculata suggests that they gave birth to tiny helpless young, similar to modern marsupials.

About 80 genera of Multituberculata are known, including *Lambdopsalis*, *Ptilodus* and *Meniscoessus*. In the northern hemisphere during the late Cretaceous, more than half of typical land mammalian species were multituberculates.

Groups within Multituberculata

In their 2001 study, Kielan-Jaworowska and Hurum found that most multituberculates could be referred to two suborders: Plagiaulacida and Cimolodonta. The exception is the genus *Arginbaatar*, which shares characteristics with both groups.

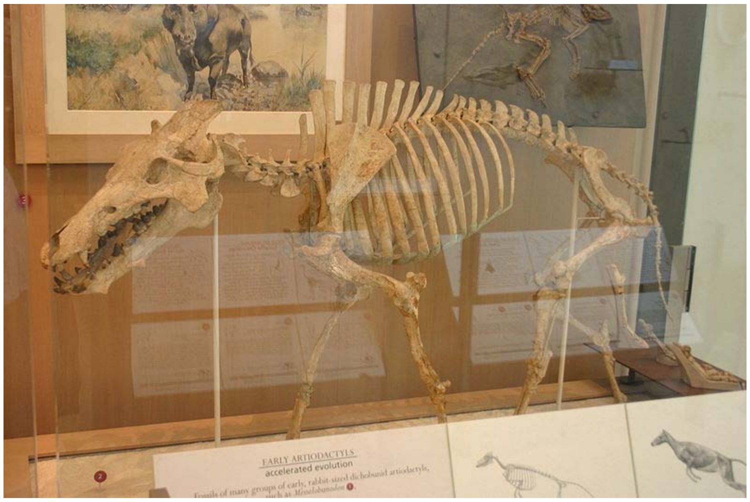
"Plagiaulacida" is paraphyletic; it is an informal suborder which does not satisfy the cladistic criterion of consisting of an ancestor and all of its descendants. Its members are the more basal Multituberculata. Chronologically, they ranged from perhaps the middle Jurassic (unnamed material), until the lower Cretaceous. This group is further subdivided into three informal groupings: the Allodontid line, the Paulchoffatiid line and the Plagiaulacid line.

Cimolodonta is apparently a natural (monophyletic) suborder. This includes the more derived Multituberculata, which have been identified from the lower Cretaceous to the Eocene. Recognized are the superfamilies Djadochtatherioidea, Taeniolabidoidea, Ptilodontoidea and the Paracimexomys group.

Additionally, there are the families Cimolomyidae, Boffiidae, Eucosmodontidae, Kogaionidae, Microcosmodontidae and the two genera *Uzbekbaatar* and *Viridomys*. More precise placement of these types awaits further discoveries and analysis.

Archaeotherium

Archaeotherium
Fossil range: Early Oligocene



Archaeotherium mortoni skeleton

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Artiodactyla
Family:	†Entelodontidae
Genus:	†***Archaeotherium***

Archaeotherium (Greek, "Ancient Beast") is an extinct artiodactyl genus of the family *Entelodontidae*, endemic to North America during the Oligocene epoch (38—24.8 mya), existing for approximately 6 million years.

It was a relative of javelinas and pigs. Evidence from the Wyoming Dinosaur Center suggests that *Archaeotherium*, like modern carnivores, kept caches of food when their hunting was unsuccessful. These bones were mainly those of *Poebrotherium*.

Taxonomy

Archaeotherium was named by Leidy (1850). Its type is *Archaeotherium mortoni.* It was synonymized subjectively with *Entelodon* by Joseph Leidy (1853) and synonymized subjectively with *Elotherium* by Leidy (1857). It was assigned to *Entelodontidae* by Leidy (1850), Peterson (1909), Scott (1940), Galbreath (1953), Russell (1980), Carroll (1988) and Effinger (1998).

Morphology

Archaeotherium mortoni restoration

Archaeotherium mortoni skull

In life, *Archaeotherium* probably resembled a large, fanged, peccary with bumps projecting from the side of its head. It had high shoulders, presumably to carry strong neck muscles to support the heavy head. The brain was tiny, but had relatively large olfactory lobes, suggesting that the animal had a keen sense of smell.

The largest (and type) species, *A. mortoni* was an aggressive, cow-sized apex predator. Rhino jaws and other mammal bones have been found with bite marks on them that match the large canines of *A. mortoni*. A fossil trackway in Toadstool Park depicts the path of a *Subhyracodon* walking forward, stopping to see an *Archaeotherium* approach, then breaking into a gallop with the entelodont chasing after it. In leaner times, it is suggested that *Archaeotherium* dug for roots and tubers, as with other pig-like mammals.

Body mass

A single specimen was examined by M. Mendoza, C. M. Janis and P. Palmqvist for body mass and was estimated to have a weight of 1,091.8 kg (2,400 lb). The second was estimated to have a weight of 129.1 kg (280 lb).

Chapter- 4

Oligocene Birds

Anthropornis

Anthropornis
Fossil range: Eocene–Oligocene, 45–37 Ma

Scientific classification

Kingdom:	Animalia

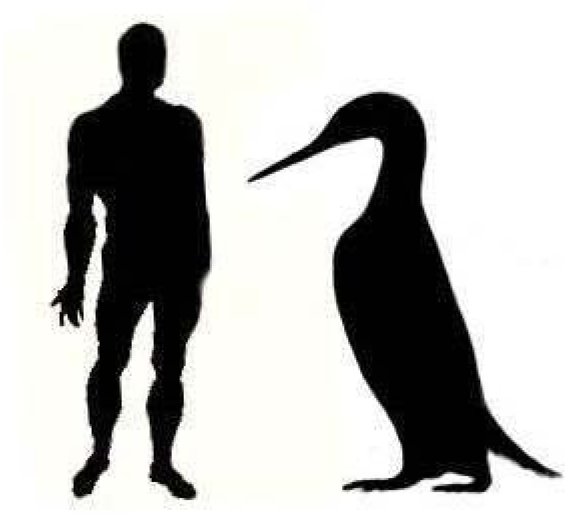
Phylum:	Chordata
Class:	Aves
Order:	Sphenisciformes
Family:	Spheniscidae
Genus:	*Anthropornis* Wiman, 1905

Species

- ***A. nordenskjoldi*** Wiman, 1905 (type)
- ***A. grandis*** (Wiman, 1905)

Anthropornis is a genus of giant penguin that lived 45–37 million years ago, during the Late Eocene and the earliest part of the Oligocene. It reached 1.7 m (5 ft 7 in) in height and 90 kg (200 lb) in weight. Fossils of it have been found on Seymour Island off the coast of Antarctica and in New Zealand. By comparison, the largest modern penguin species, the Emperor Penguin, is just 1.2 m (3 ft 11 in) tall.

The type species, *Anthropornis nordenskjoldi*, had a bent joint in the wing, probably a carryover from flying ancestors.



Human and A.nordenskjoldi size comparison

In literature

The enormous six-foot and blind albino penguins in H. P. Lovecraft's 1931 novel *At the Mountains of Madness* were fictional cave-dwelling descendants of this bird. They used their large beaks to prey on small dinosaurs.

Archaeospheniscus lopdelli

Lopdell's Penguin **Fossil range: late Eocene - Late Oligocene**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Class:	Aves
Order:	Sphenisciformes
Family:	Spheniscidae
Genus:	*Archaeospheniscus*
Species:	***A. lopdelli***
Binomial name	
Archaeospheniscus lopdelli Marples, 1952	

Lopdell's Penguin (*Archaeospheniscus lopdelli*) was the largest species of the extinct penguin genus *Archaeospheniscus*, standing about 90-120 cm high, or somewhat less than the extant Emperor Penguin. It is only known from bones of a single individual (Otago Museum C.47.21) which was found in the Late Oligocene Kokoamu Greensand Formation (27-28 MYA) at Duntroon, New Zealand. Bones apparently belonging to this species are now also known from the Late Eocene La Meseta Formation (34-37 MYA) on Seymour Island, Antarctica (Tambussi *et al.*, 2006).

As the bird is not very well distinguished except in size from its contemporary congener *Archaeospheniscus lowei* and the size range, an estimated 85-120 cm, is in the upper range of the variation found in modern penguins, it is probable that *A. lopdelli* is a synonym of *A. lowelli*. As the recent finds in Antarctica suggest, this is far from certain, however and there remains much to be learned about the systematics and biogeography of the two larger *Archaeospheniscus* species.

The species' binomen honors J. C. Lopdell, who assisted Marples in recovering the fossils of this bird and others found in the Duntroon excavations.

Copepteryx

Copepteryx
Fossil range: Late Oligocene

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Aves
Order:	Pelecaniformes
Family:	Plotopteridae
Genus:	***Copepteryx***

Copepteryx is an extinct genus of flightless bird of the family *Plotopteridae* endemic to Japan during the Oligocene living from 28.4—23 mya, existing for approximately 5.4 million years.

Copepteryx is a plotopterid bird.

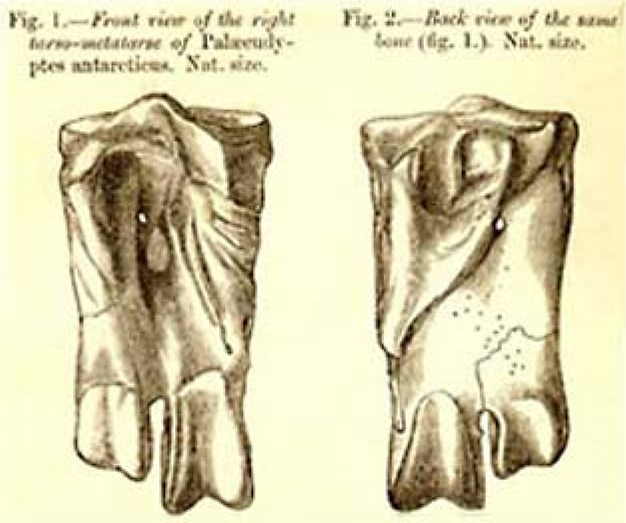
Taxonomy

Copepteryx was named by Olson and Hasegawa (1996). Its type is *Copepteryx hexeris*. It was assigned to *Plotopteridae* by Olson and Hasegawa (1996).

Palaeeudyptes antarcticus

Palaeeudyptes antarcticus

Fossil range: Late Oligocene - Late Eocene



Huxley's original illustration of the fossil of an ankle bone from *Palaeeudyptes antarcticus* described in 1859.

Conservation status

Fossil

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Class:	Aves
Order:	Sphenisciformes

Family:	Spheniscidae
Genus:	*Palaeeudyptes*
Species:	***P. antarcticus***

Binomial name

Palaeeudyptes antarcticus
Huxley, 1859

Synonyms

Palaeeudyptes antarctica (*lapsus*) Lowe, 1933

Palaeeudyptes antarcticus, rarely called the **Narrow-flippered Penguin** is the type species of the extinct penguin genus *Palaeeudyptes*. It was a huge species, albeit probably with a large size variation. Although the size range can only be loosely estimated, the birds seem to have stood between 110 and 140 cm high in life (*i.e.* somewhat larger than an Emperor Penguin), placing this species and its congener *Palaeeudyptes marplesi* among the largest penguin species known. It was the last known *Palaeeudyptes* species and although the exact time when it lived is not precisely determined, it may have evolved from *P. marplesi*, or they might even have been a single species which slightly decreased in size over time.

P. antarcticus was the first fossil penguin to become known to science. It was described from a single, slightly damaged, tarsometatarsus (BM A.1084) found in the Late Oligocene Otekaike Limestone (23-28, possibly up to 34 MYA) at Kakanui, New Zealand. An older date seems quite possible in fact as other bones have now been recovered from the Late Eocene (34-37 MYA) of the La Meseta Formation on Seymour Island, Antarctica (Tambussi *et al.*, 2006), but given the considerable distances in age and range involved, it is not completely certain that the bones belong to a single species.

This remains the only fossil unequivocally assigned to this species, but numerous other bones have been found that may belong to it too. These fossils were once uncritically considered as being from *P. antarcticus*, merely because other large penguins were not known at that time, but have not been subject to scientific review according to modern standards. While some of these bones are now known to belong to other species, a large number are not unequivocally assignable to either *P. antarcticus* or *P. marplesi*, being intermediate in size (Simpson, 1971), lending support to the theory that these taxa were in reality a single species.

Psilopterus

Psilopterus
Fossil range: Middle Oligocene to Late Miocene

Psilopterus australis

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Aves
Order:	Cariamae
Family:	Phorusrhacidae
Genus:	***Psilopterus*** Moreno & Mercerat, 1891

Species

- *P. bachmani* (Moreno & Mercerat, 1891) (type)
- *P. lemoinei* (Moreno & Mercerat, 1891)
- *P. affinis* (Ameghino, 1899)
- *P. colzecus* Tonni & Tambussi, 1988

Synonyms

- *Pelecyornis* Ameghino, 1891
- *Staphylornis* Mercerat, 1897

Psilopterus (Greek for "bare wing") is an extinct genus of phorusrhacid ("terror bird") from the Middle Oligocene to Late Miocene of Argentina. Compared to other phorusrhacids, members of the genus are both relatively gracile and diminutive and include the smallest known species of terror bird: with the head raised *P. bachmanni* was 70–80 centimeters (2.3–2.6 ft) in height and weighed about 5 kilograms (11 lb), while the largest members of the genus were only about 7 kilograms (15 lb). The birds resemble the modern cariama (*Cariama cristata*), except with a heavier build and considerably smaller wings. The strong morphological similarity between the claws of the predatory cariama and *Psilopterus*, both of which are sharp, curved and laterally compressed, may indicate they were used to strike prey. In contrast to the other, larger terror birds, Tonni and Tambussi also suggested *Psilopterus* could use their claws to climb trees and could even fly, but this has been rejected in more recent literature.

Description and taxonomy

The most recent systematic revision of Phorusrhacidae placed *Psilopterus* within the Psilopterinae subfamily, along with the *Procariama* and *Paleopsilopterus* genera and divided *Psilopterus* into four species.

P. bachmanni

Psilopterus bachmanni (Moreno & Mercerat, 1891) is the smallest species of phorusrhacid, rivaled only by *P. affinis*. The species (and genera) is defined by the upper portion of a fused ankle and leg bone (the lectotype MLP-168 is a tarsometatarsus). Other material assigned the species includes additional leg bones that are probably from the same bird and an almost complete skeleton (PUM-15.904) The material is from several sites in the Santa Cruz Province of Argentina dating to the Middle Miocene (Santacrucian). The most important diagnostic characteristics are a low skull and upper jaw (or maxilla; similar to the mesembriornithine phorusrhacids) and the extreme slant of the front edge of the hole just before the eye (rostal portion of the antorbital fenestra), though there are also differences in the rest of the skeleton.

Synonyms:

- *Psilopterus bachmanni* (Moreno & Mercerat, 1891)
- *Patagornis bachmanni* Moreno & Mercerat, 1891
- *Psilopterus communis* Moreno & Mercerat, 1891
- *Psilopterus intermedius* Moreno & Mercerat, 1891
- *Phororhacos delicatus* Amegino, 1891

Brodkorb considered *Psilopterus minutus* Amerghino, 1981 a separate species, but the incomplete foot bone (tarsometatarsus) is indistinguishable from *P. bachmanni*.

P. lemoinei

Psilopterus lemoinei (Moreno & Mercerat, 1891) is contemporaneous with *P. bachmanni* and likely filled a very similar ecological niche, though *P. lemoinei* is slightly larger, with an estimated weigh approaching 7 kilograms (15 lb). The species is defined by part of a lower leg bone (the lectotype, MLP-162, is the distal end of a tibiotarsus), but a wide variety of material has been referred to the taxon. This material has been found at a number of sites in the Santa Cruz Province of Argentina that are dated to the Middle Miocene (Santacrucian). Diagnostic characteristics include a higher skull and upper jaw (maxilla) and the front portion of the hole in front of the eyes (rostral edge of the antorbital fenestra) is less slanted. Additional differences in the remainder of the skeleton are noted in Sinclair and Farr (1932). A number of discrepancies between various specimens have been attributed to differences in age or sex, but material currently assigned to *P. lemonei* and *P. bachmanni* may be reclassified at the species level if reexamined in depth.

Synonyms:

- *Patagornis lemoinei* Moreno & Mercerat, 1891
- *Psilopterus australis* Moreno & Mercerat, 1891
- *Pelecyornis tubulatus* Ameghino, 1895 (synonym of *Psilopterus australis*)
- *Phororhacos modicus* Ameghino, 1895
- *Staphylornis gallardoi* Mercerat, 1897 (possible synonym of *Psilopterus australis*)
- *Staphylornis erythacus* Mercerat, 1897 (possible synonym of *Psilopterus australis*)
- *Pelecyornis tenuirostris* Sinclair & Farr, 1932 (synonym of *Psilopterus australis*)

P. affinus

Psilopterus affinus (Ameghino, 1899) is the most poorly known species of terror bird, represented only by part of a leg bone (tarsometatarsus, MACN-A-52-184) which indicates the bird was very close to *P. bachmanni* in size. *P. affinus* is one of several species known from fragmentary material found in 1899 in the Chubut Province of Argentina (Patagonia), in rocks which dated to the Middle to Late Oligocene (Deseadan). Additional specimens might help clarify the taxonomy of the four apparently unrelated species. *P. affinus* was originally assigned to the *Phororhacos* genus despite the difference in size and is distinguished from *P. bachmanni* by a groove on the leg bone. Brodkorb assigned the species to *Andrewsornis* in 1967, but this is no longer considered accurate.

P. colzecus

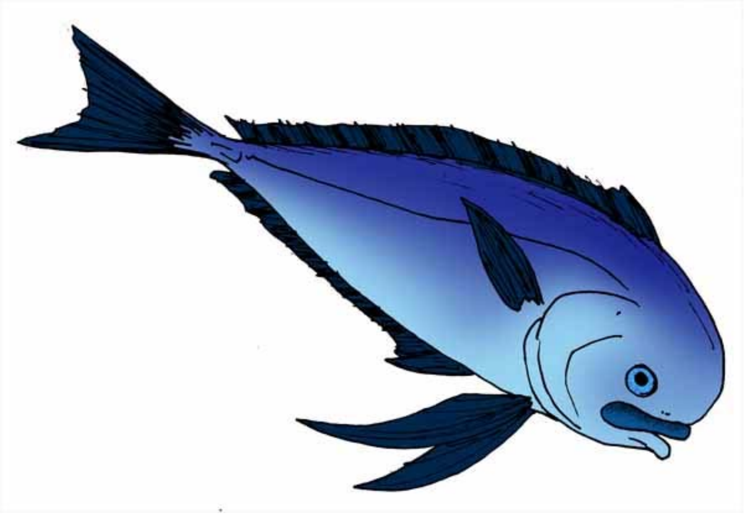
The most recently discovered species in the genus, *Psilopterus colzecus* Tonni & Tambussi, 1988, is similar to *P. lemoinei* in size. Known only from a single incomplete skeleton that includes parts of the jaw, arm and leg (holotype MLP-76-VI-12-2), the species is defined by a groove in the front of the thigh bone (trochlea). The elements were found in the Buenos Aires Province of Argentina and are dated to the Late Miocene (Chasicóan).

Chapter- 5

Oligocene Fish

Aluvarus

Aluvarus praeimperialis
Fossil range: Rupelian



Artist's reconstruction

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Infraphylum:	Gnathostomata
Superclass:	Osteichthyes
Class:	Actinopterygii
Order:	?Perciformes
Suborder:	?Acanthuroidei
Family:	*incertae sedis*
Genus:	***Aluvarus***
Species:	*A. praeimperialis*

Binomial name
Aluvarus praeimperialis (Arambourg), 1967
Synonyms
Luvarus praeimperialis (Arambourg), 1967

Aluvarus praeimperialis is an extinct bony fish, known from two headless fossil specimens found in the Elam Formation, a Lower Oligocene stratum from the Rupelian epoch, of what is now Iran. *A. praeimperialis* was originally thought to be a luvar, described as "*Luvarus praeimperialis*," as it was thought to be a predecessor to the modern luvar. A later reexamination of the specimens showed that they were too incomplete to demonstrate such a conclusion and were renamed "*Aluvarus*," meaning "Not" or "Different than Luvar."

Carcharocles angustidens

Angustidens **Fossil range: Oligocene - Miocene**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Chondrichthyes
Subclass:	Elasmobranchii
Order:	Lamniformes
Family:	Disputed; either Lamnidae or **Otodontidae**
Genus:	Disputed; either *Carcharodon* or ***Carcharocles***
Binomial name	
Disputed; either *Carcharodon angustidens* or *Carcharocles angustidens* For *Carcharodon angustidens,* Agassiz, 1843	

Carcharocles angustidens is a prehistoric megatoothed shark, which lived during the Oligocene and Miocene epochs approximately about 35 to 22 million years ago. This shark is believed to be closely related to another extinct megatoothed shark, *C. megalodon*. However, just as in the case of *C. megalodon*, the classification of this species is also under dispute.

Fossil record

As is the case with most extinct sharks, this species is also known from fossil teeth and some fossilized vertebral centra. Shark skeleton is composed of cartilage and not bone and cartilage rarely gets fossilized. Hence, fossils of *C. angustidens* are generally poorly preserved. To date, the best preserved specimen of this species have been excavated from New Zealand, which comprises 165 associated teeth and about 35 associated vertebral centrum. This specimen is around 26 million years old. *C. angustidens* teeth are noted for their triangular crowns and small side cusps that are fully serrated. The serrations are very sharp and very well pronounced. *C. angustidens* was a widely distributed species with fossils found in North America, South America, Europe, Africa, New Zealand, Japan, Australia and Malta.

Size estimation

Like other known megatooth sharks, the fossils of *C. angustidens* indicate that it was considerably larger than the extant great white shark, *Carcharodon carcharias*. The well preserved specimen from New Zealand is estimated at 9.3 metres (31 ft) in length. This specimen had teeth measuring up to 9.87 cm (3.9 inch) in diagonal length and vertebral centra of around 1.10 cm (4.33 inch) in diameter. However, there are reports of larger *C. angustidens* fossils.

Dentition

The dental formula for *C. angustidens* is:

Dentition

2.1.5.4
3.0.6.3

Diet

C. angustidens was an apex predator and likely preyed upon penguins, fish, dolphins and baleen whales.

Classification dispute

Even after decades of scrutinizing fossils, *C. angustidens* remains a disputed genus. A Swiss naturalist, Louis Agassiz, first identified this shark as a species of *Carcharodon* genus, in 1835.

In 1964, shark expert, L. S. Glikman recognized the transition of *Otodus obliquus* to *C. auriculatus* and moved *C. angustidens* to genus *Otodus*.

However, in 1987, shark expert, H. Cappetta realized the *C. auriculatus* - *C. megalodon* lineage and placed all related megatooth sharks along with these species in the genus, *Carcharocles*. For the first time, the complete *Otodus obliquus* to *C. megalodon* transition became clear and since have gained acceptance of many other experts with passage of time.

Within the *Carcharocles* lineage; *C. angustidens* is the succeeding species of *C. sokolovi* and is exceeded by *C. chubutensis*.

However, in 2001, a discovery of a best preserved *C. angustidens* specimen to date by two scientists, M. D. Gottfried and R. Ewan Fordyce, have been presented by the team as an evidence for its close morphological ties with the extant great white shark and the team argued that *C. angustidens* along with all other related megatooth sharks (including *C. megalodon*) deserve to be assigned to *Carch' genus as done before by Louis Agassiz.*

Carcharocles chubutensis

Chubutensis

Fossil range: Oligocene - Pliocene

Partially preserved *C. chubutensis* tooth with a slant height of 129 mm.

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Chondrichthyes
Subclass:	Elasmobranchii
Order:	Lamniformes
Family:	Disputed; either Lamnidae or **Otodontidae**
Genus:	Disputed; either *Carcharodon* or ***Carcharocles***

Binomial name

Disputed; either *Carcharodon subauriculatus* or *Carcharocles chubutensis*

For *Carcharodon subauriculatus,* Agassiz, 1843

Synonyms

- *Carcharodon mexicanus*
- *Carcharodon productus*
- *Megaselachus chubutensis* Glikman, 1964

Carcharocles chubutensis is a prehistoric megatoothed shark that lived during Oligocene, Miocene and Pliocene epochs, approximately about 28 - 5 million years ago. This shark is considered to be a close relative of another prehistoric megatoothed shark, *C. megalodon*. However, as is the case with *C. megalodon*, the classification of this species is disputed.

Fossil record

This species is also known from fossil teeth and some fossilized vertebral centra. Shark skeleton is composed of cartilage and not bone and cartilage rarely gets fossilized. Hence, fossils of *C. chubutensis* are generally poorly preserved. Although the teeth of *C. chubutensis* are morphologically similar to teeth of *C. megalodon*, they are comparatively slender with curved crown and with presence of lateral heels feebly serrated. Fossils of this species have been found in North America, South America, Cuba, Puerto Rico, Africa and Europe.

Size

C. chubutensis was larger than *C. angustidens*. Teeth of *C. chubutensis* can approach 130 mm in slant height (diagonal length), which according to size estimation method proposed by Gottfried at al, in 1996, indicate 12.2 m (40 ft) long specimen.

Paleoecology

Paleontological research suggests that this species may have changed habitat preferences through time, or it may have had enough behavioral flexibility to occupy different environments at different times.

Diet

C. chubutensis was likely an apex predator and commonly preyed upon fish, sea turtles, cetaceans (e.g. whales) and sirenids.

Phylogeny

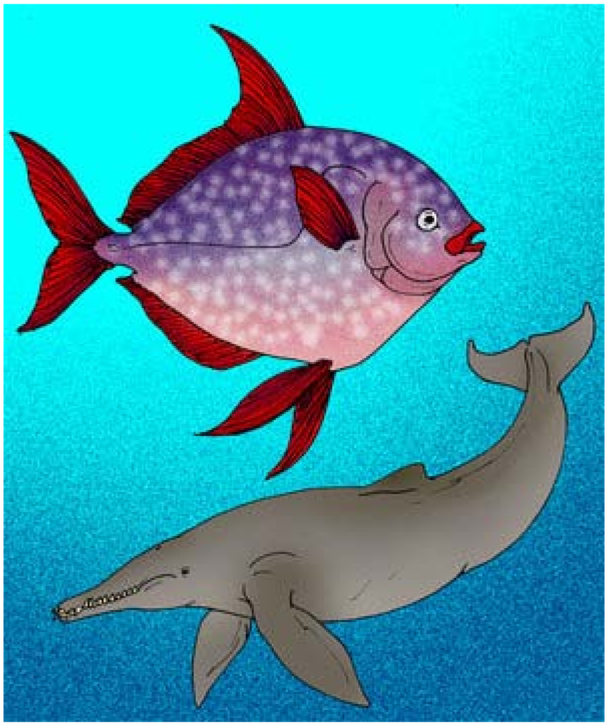
As is the case with other known megatoothed sharks, the genus of *C. chubutensis* remains in dispute. The Swiss naturalist Louis Agassiz first identified this shark as a species of *Carcharodon* in 1843. In 1906, Ameghino renamed this shark as *C. chubutensis*. In 1964, shark researcher, L. S. Glikman recognized the transition of *Otodus obliquus* to *C. auriculatus*. In 1987, shark researcher, H. Cappetta reorganized the *C. auriculatus* - *C. megalodon* lineage and placed all related megatoothed sharks along with this species in the genus *Carcharocles*. Finally, the complete *Otodus obliquus* to *C. megalodon* progression became clear and has since gained the acceptance of many shark researchers.

Within the *Carcharocles* lineage; *C. chubutensis* is the succeeding species of *C. angustidens* and is succeeded by *C. megalodon*. In short, *C. chubutensis* is considered to be the ancestor of *C. megalodon*. However, due to its co-existence with *C. megalodon* during the Miocene and Pliocene epochs, it is regarded as a morpho-species.

Megalampris

Megalampris

Fossil range: Late Oligocene



M. keyesi and *Waipatia maerewhenua*

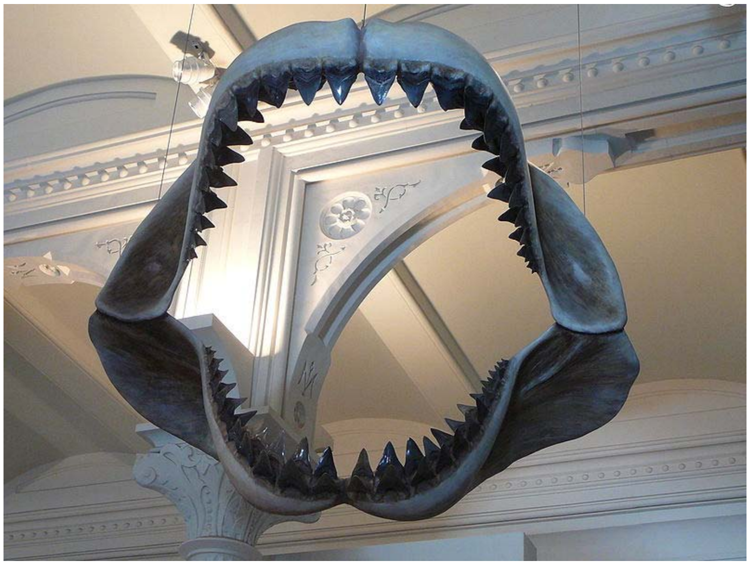
Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Actinopterygii
Order:	Lampriformes
Family:	Lampridae
Genus:	***Megalampris***
Species:	***M. keyesi*** Gottfried, Fordyce & Rust, 2006

Megalampris keyesi is an extinct Opah from the late Oligocene of New Zealand about 26 million years ago. It was recovered from the Otekaike Limestone in North Otago, by a team from the University of Otago. Its spectacular remains, mostly caudal skeleton, are on display in the Otago Museum, Dunedin, New Zealand. Comparison with the skeleton of living Lampris species suggest that it was around 4 meters in length.

Megalodon

Megalodon
Fossil range: Late Oligocene-Early Pleistocene 25–1.5 Ma



Model of the jaws of the megalodon at the American Museum of Natural History.

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Class:	Chondrichthyes
Subclass:	Elasmobranchii
Order:	Lamniformes
Family:	Disputed; Lamnidae or †Otodontidae
Genus:	Disputed; *Carcharodon* or †*Carcharocles*
Species:	***†C. megalodon***

Binomial name

Disputed; *Carcharodon megalodon* or *Carcharocles megalodon*
For *Carcharodon megalodon,* Agassiz, 1843

Synonyms

- *Procarcharodon megalodon* Casier, 1960
- *Megaselachus megalodon* Glikman, 1964

The **megalodon**, *Carcharodon* or *Carcharocles megalodon* is an extinct megatoothed shark that existed in prehistoric times, from the Oligocene to Pleistocene epochs, approximately 25 to 1.5 million years ago.

C. megalodon was an apex predator of its time and possibly the largest and most powerful macro-predatory fish that ever lived. Fossil remains of *C. megalodon* indicate that it may have approached a maximum of around 20.3 metres (67 ft) in length. *C. megalodon* has been assigned to the order Lamniformes but its phylogeny is disputed. Scientists suggest that *C. megalodon* looked like a stockier version of the great white shark, *Carcharodon carcharias*, in life. Fossil evidence confirms that *C. megalodon* had a cosmopolitan distribution.

Discovery

Glossopetrae

The depiction of a shark's head by Nicolaus Steno in his work, *The Head of a Shark Dissected*.

According to Renaissance accounts, gigantic, triangular fossil teeth often found embedded in rocky formations were once believed to be petrified tongues, or glossopetrae, of the dragons and snakes. This interpretation was corrected in 1667 by a Danish naturalist, Nicolaus Steno, who recognized them as ancient shark teeth (and famously produced a depiction of a shark's head bearing such teeth). He mentioned his findings in a book, *The Head of a Shark Dissected*, which also contained an illustration of a *C. megalodon* tooth, previously considered to be a tongue stone.

Identification

A Swiss naturalist, Louis Agassiz, gave this shark its scientific name, *Carcharodon megalodon*, in 1835, in his research work *Recherches sur les poissons fossiles* (*Research on fossil fish*), which he completed in 1843. The teeth of the *C. megalodon* are morphologically similar to the teeth of the great white shark. On the basis of this observation, Agassiz assigned the genus *Carcharodon* to the *megalodon*. While the scientific name is *C. megalodon*, it is often informally dubbed the *megatooth shark* or *giant white shark* or even *monster shark*.

Fossils

As with all other sharks, the megalodon skeleton was formed of cartilage rather than bone; this results in mostly poorly preserved fossil specimens.

Fossil teeth

Megalodon tooth with slant height (diagonal length) of over 170 mm.

The most common fossils of *C. megalodon* are its teeth, which are morphologically similar to the teeth of great white shark but are more robust and more regularly serrated. The teeth of *C. megalodon* can measure over 180 millimetres (7.1 in) in slant height or diagonal length and are the largest in size of any known shark species.

Fossil vertebrae

Some partially preserved fossil vertebrae of *C. megalodon* have also been found. The most notable example is a partially preserved but associated vertebral column of a single

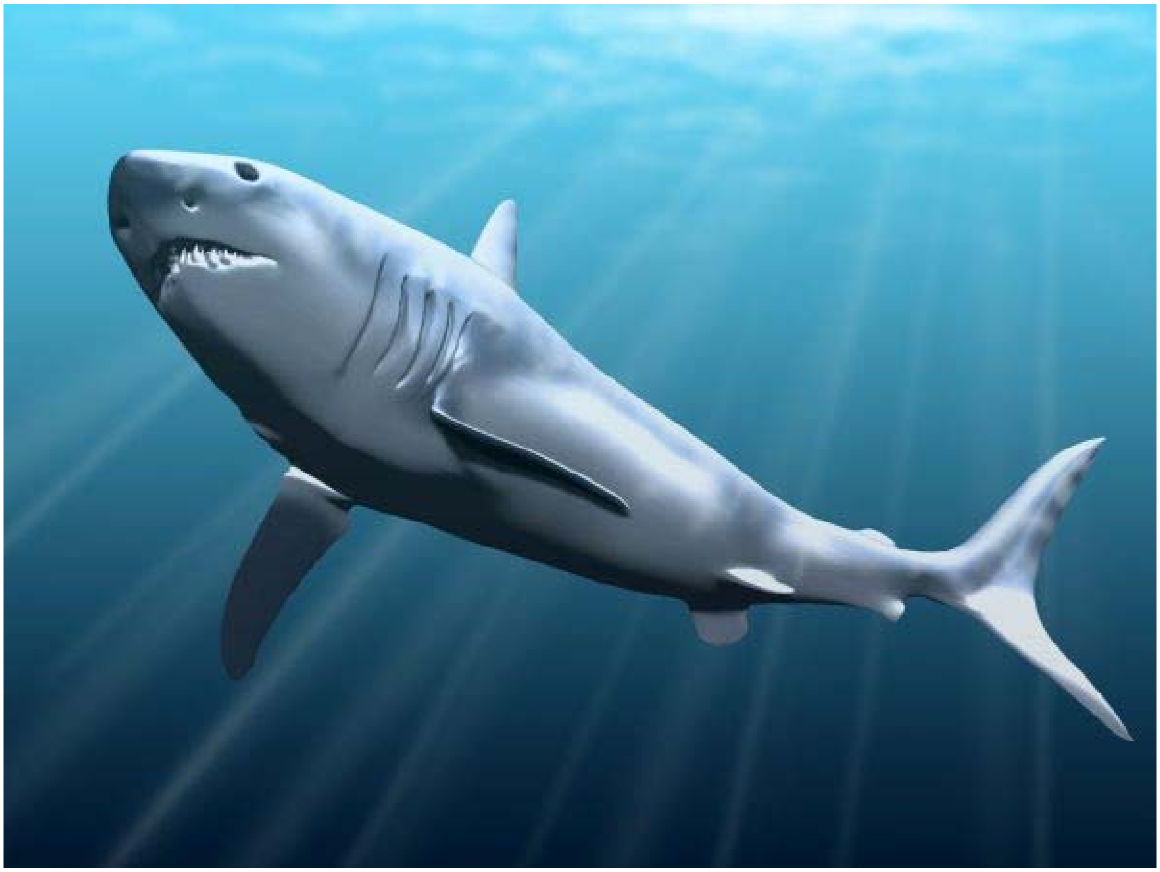
C. megalodon specimen excavated from Belgium in 1926. This specimen comprises 150 vertebral centra, with the largest centra being 155 mm in diameter. However, the vertebral centra of *C. megalodon* can be over 225 mm in diameter and are likely the largest in size of any known shark species.

Fossil distribution and range

The fossils of *C. megalodon* have been excavated from many parts of the world, including Europe, North America, South America, Puerto Rico, Cuba, Jamaica, Australia, New Zealand, Japan, Africa, Malta, Grenadines and India. *C. megalodon* teeth have also been excavated from regions far away from continental lands (i.e. Mariana Trench in the Pacific).

The earliest remains of *C. megalodon* have been reported from late Oligocene strata, circa 25 million years old. Although fossils of *C. megalodon* are predominantely absent in strata extending beyond the Tertiary boundary, they have been reported from subsequent Pleistocene strata. It is believed that *C. megalodon* became extinct in the Pleistocene, probably about 1.5 million years ago.

Physical anatomy



Life restoration

Among extant species, the great white shark is regarded as the best analogue to *C. megalodon*. The lack of well preserved fossil skeletons of *C. megalodon* have forced scientists to rely on the morphology of the great white shark for the basis of its reconstruction and size estimation.

Size estimation

Estimating the maximum size of *C. megalodon* is a highly controversial and difficult subject. However, the scientific community acknowledges that *C. megalodon* was larger than the whale shark, *Rhincodon typus*. The first attempt on reconstructing the jaw of this shark was made by Professor Bashford Dean in 1909. From the dimensions of this jaw reconstruction, the size of *C. megalodon* was theorized to be around 30 metres (98 ft), but in the light of new fossil discoveries and advances in vertebrate sciences, this jaw reconstruction is now considered to be inaccurate. Major reasons cited for this inaccuracy are; (1) relatively poor knowledge of *C. megalodon's* dentition in Dean's time; and (2) inaccurate muscle structures. Experts suggest that a rectified version of *C. megalodon'*s jaw model by Bashford Dean would be about 70 percent of its original size and would lead to a shark size consistent with modern findings. Hence, to resolve such errors, scientists, aided by new fossil discoveries of *C. megalodon* and improved knowledge of its closest living analogue's anatomy, introduced more quantitative methods for estimating its size based on the statistical relationships between the tooth sizes and body lengths in the great white shark.

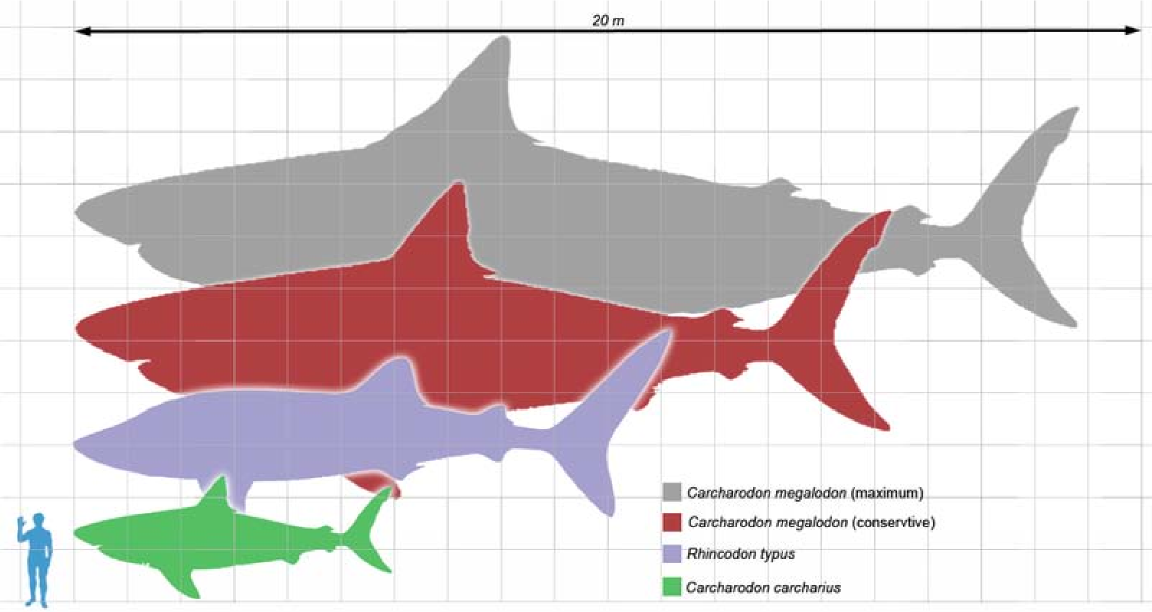
Method proposed by John E. Randall

In 1973, the ichthyologist John E. Randall introduced a method to determine the size of the great white shark and extrapolated it to estimate the size of *C. megalodon*. The proposed method is: "Megatooth's" Total Length in meters = [(0.096) × (enamel height of tooth in mm)]. The logic behind this method is that the enamel height (the vertical distance of the blade from the base of the enamel portion of the tooth to its tip) of the largest upper anterior tooth in the jaw of the shark can be used to determine its total length. The largest *C. megalodon* tooth in his possession at that time had an enamel height of around 120 mm, which yielded 13 metres (43 ft) length. However, two shark experts, Richard Ellis and John E. McCosker, pointed out a flaw in Randall's method in 1991. According to them, shark's tooth enamel height does not necessarily increase in proportion to the animal's total length. This observation led to proposals for new, more accurate methods to determine the size of the *great white shark* and similar sharks.

Method proposed by Gottfried *et al.*

Three scientists, Michael D. Gottfried, Leonard J. V. Compagno and S. Curtis Bowman, after thorough research and scrutiny of many great white shark specimens, proposed a conservative but more accurate method for measuring the size of *C. carcharias* and *C. megalodon* that was published in 1996. The proposed method is: "Megatooth's" Total Length in meters = − (0.22) + (0.096) × [(Tooth maximum height in mm)]. The biggest *C. megalodon* tooth in the possession of this team was an upper anterior specimen, which had a maximum height of 168 mm (6.61 inch). This tooth was discovered by L. J. V. Compagno in 1993 and it yielded a length of 15.9 metres (52 ft). However, rumors of larger *C. megalodon* teeth persisted at that time. The maximum tooth height for this method is measured as a vertical line from the tip of the crown to the bottom of the lobes of the root, parallel to the long axis of the tooth. In short words, the maximum height of the tooth is its slant height.

Body mass estimation



Megalodon (gray and red) with the whale shark (violet), great white shark (green) and a human (blue) for scale. **Note:** The maximum size attained by *C. megalodon* is indicated by the 20 m scale.

Gottfried et al., also introduced a method to determine the body mass of the great white shark after studying the length – mass relationship data of 175 specimens at various growth stages and extrapolated it to estimate the body mass of *C. megalodon*. The proposed method is: Weight in kilogram = $3.29E^{-06}$[TL in $(\text{meters})^{3.174}$]. And according to this method, a 15.9 metres (52 ft) long specimen would have a body mass of about 47 metric tons (52 short tons).

Method proposed by Clifford Jeremiah

In 2002, shark researcher Dr. Clifford Jeremiah also proposed a method to determine the size of great white shark and similar sharks (i.e., *C. megalodon*). which is believed to be based on a sound principle that works well with most large sharks. The proposed method is: "Shark's" Total Length in feet = [(Root width of an upper anterior tooth in cm) x (4.5)]. It translates as for every centimeter of root width of an upper anterior tooth, there is approximately 4.5 feet of the shark. Dr. C. Jeremiah asserts that the jaw perimeter of a shark is directly proportional to its total length, with the width of the roots of the largest teeth being a proxy for estimating jaw perimeter. The largest tooth in the possession of Dr. C. Jeremiah had a root width of nearly 12 cm, which yielded 15.5 metres (51 ft) length.

Maximum size and verdict

The existing fossil evidence indicates that *C. megalodon* likely exceeded 18 metres (59 ft) in total length. In 1994, a marine biologist Patrick J. Schembri claimed that *C. megalodon* may have approached a maximum length of 25 metres (82 ft). The early size estimation of *C. megalodon* was perhaps not far fetched. However, Gottfried et al., in 1996, proposed that *C. megalodon* could likely approach a maxima of 20.3 metres (67 ft) in total length. The shark weight measuring technique suggested by the same team indicates that *C. megalodon* at this length would have a body mass of 103 metric tons (114 short tons).

Hence, scientific research makes it clear that *C. megalodon* is the largest shark that has ever lived and is among the largest fish known to have lived.

Dentition and jaw mechanics

Reconstruction showing the position of the replacement teeth

A team of Japanese scientists, T. Uyeno, O. Sakamoto and H. Sekine, discovered and excavated partial remains of a *C. megalodon*, with nearly complete associated set of its teeth, from Saitama, Japan in 1989. Another nearly complete associated *C. megalodon* dentition was excavated from Yorktown Formations of Lee Creek, North Carolina in USA and served as the basis of a jaw reconstruction of *C. megalodon* in the American Museum of Natural History in NYC. These associated tooth sets solved the mystery of how many teeth would be in the jaws of the *C. megalodon* in each row in life. Hence, highly accurate jaw reconstructions were now possible. More associated dentitions of *C. megalodon* have also been found in later years. Based upon these discoveries, two scientists, S. Applegate and L. Espinosa, published an artificial dental formula (representation of dentition of an animal with respect to types of teeth and their arrangement within the animal's jaw) for *C. megalodon* in 1996. Most accurate modern *C. megalodon* jaw reconstructions are based on this dental formula.

The dental formula of *C. megalodon* is: $\frac{2.1.5.4}{3.0.5.3}$.

As evident from the dental formula, *C. megalodon* had four kinds of teeth in its jaws.

- *Anterior* - A
- *Intermediate* - I (In the case of *C. megalodon*, this tooth technically appears to be an upper anterior and is termed as "A3" because it is fairly symmetrical and does not points mesially (side of the tooth toward the midline of the jaws where left and right jaws meet), but this tooth is still designated as an intermediate tooth. However, in the case of the great white shark, the intermediate tooth does point mesially. This point has often been raised in the *Carcharodon* vs. *Carcharocles* debate regarding the megalodon and favors the case of *Carcharocles* proponents.)
- *Lateral* - L
- *Posterior* - P

Reconstructed jaws on display at the National Aquarium in Baltimore

C. megalodon had a very robust dentition and it had a total of about 276 teeth in its jaws, spanning in 5 rows.

Paleontologists suggest that a very large *C. megalodon* had jaws over 2 metres (7 ft) across.

Bite force

In 2008, a team of scientists led by Stephen Wroe conducted an experiment to determine the bite force of *C. megalodon*; results indicate that it had one of the most powerful bites in history. At 15.9 metres (52 ft) long, *C. megalodon* was capable of exerting a bite force estimated at 108,514 newtons (N) or 24,000 pound-force and at 20.3 metres (67 ft) long, *C. megalodon* was capable of exerting a bite force estimated at 182,201 newtons (N) or 41,000 pound-force.

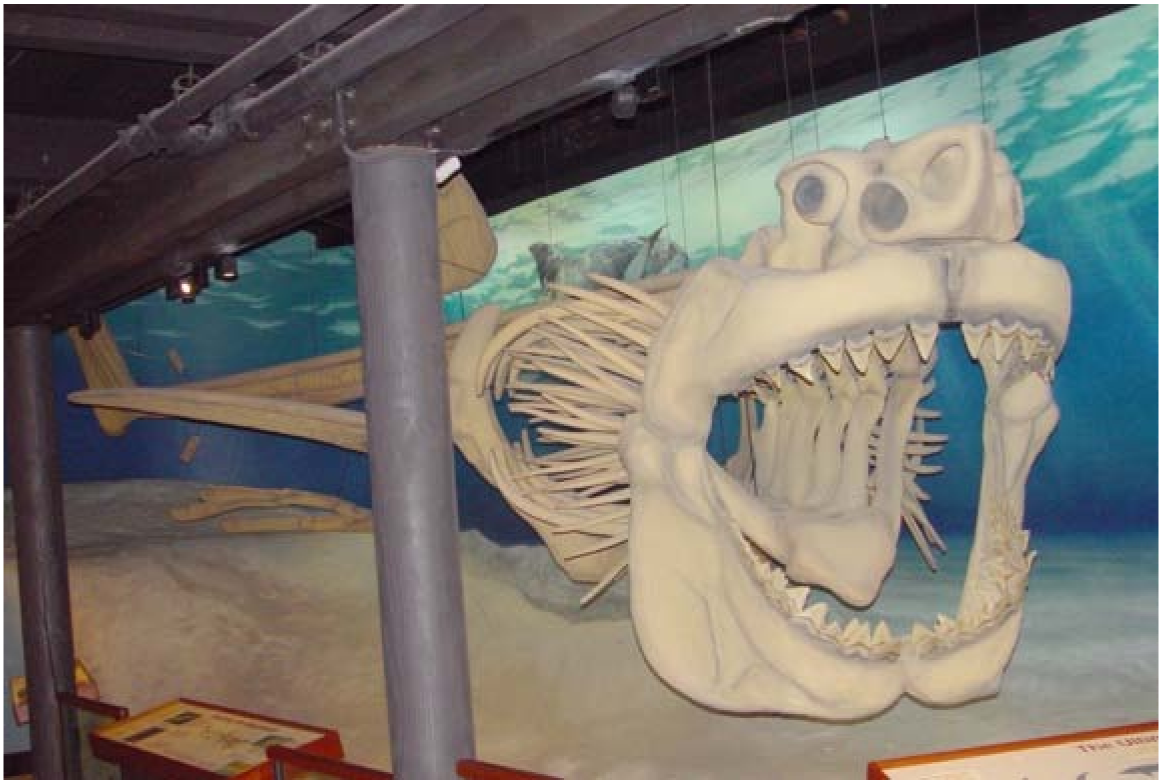
C. megalodon's bite force, at maximum estimated size, is over 28 times greater than that of *Dunkleosteus* at 5.3 kN (1,100 lbf), over 10 times greater than that of the great white shark at 18 kN (4,100 lbf), over 5 times greater than that of *T. rex* at 31 kN (7,000 lbf) and also greater than that of *Predator X* at 150 kN (33,000 lbf).

In addition, Wroe *et al.* pointed out that sharks also shake sideways while feeding, amplifying the postcranial generated forces. Therefore the total forces experienced by prey are likely higher than the forces estimated through the experiment. The extraordinary bite forces in *C. megalodon* must be considered in the context of the great size of this fossil predator and of paleontological evidence suggesting that *C. megalodon* was an active predator of large whales.

Functional parameters of teeth

The exceptionally robust teeth of *C. megalodon* are serrated, which would have improved efficiency in slicing the flesh of prey items. Paleontologist Dr. Bretton Kent suggests that these teeth are comparatively thicker for their size with much lower slenderness and bending strength ratios. They also have roots that are substantially larger relative to total tooth heights and so have a greater mechanical advantage. Teeth with these traits are not just good cutting tools but also are well suited for grasping powerful prey and would seldom crack even when slicing through bones.

Skeletal anatomy



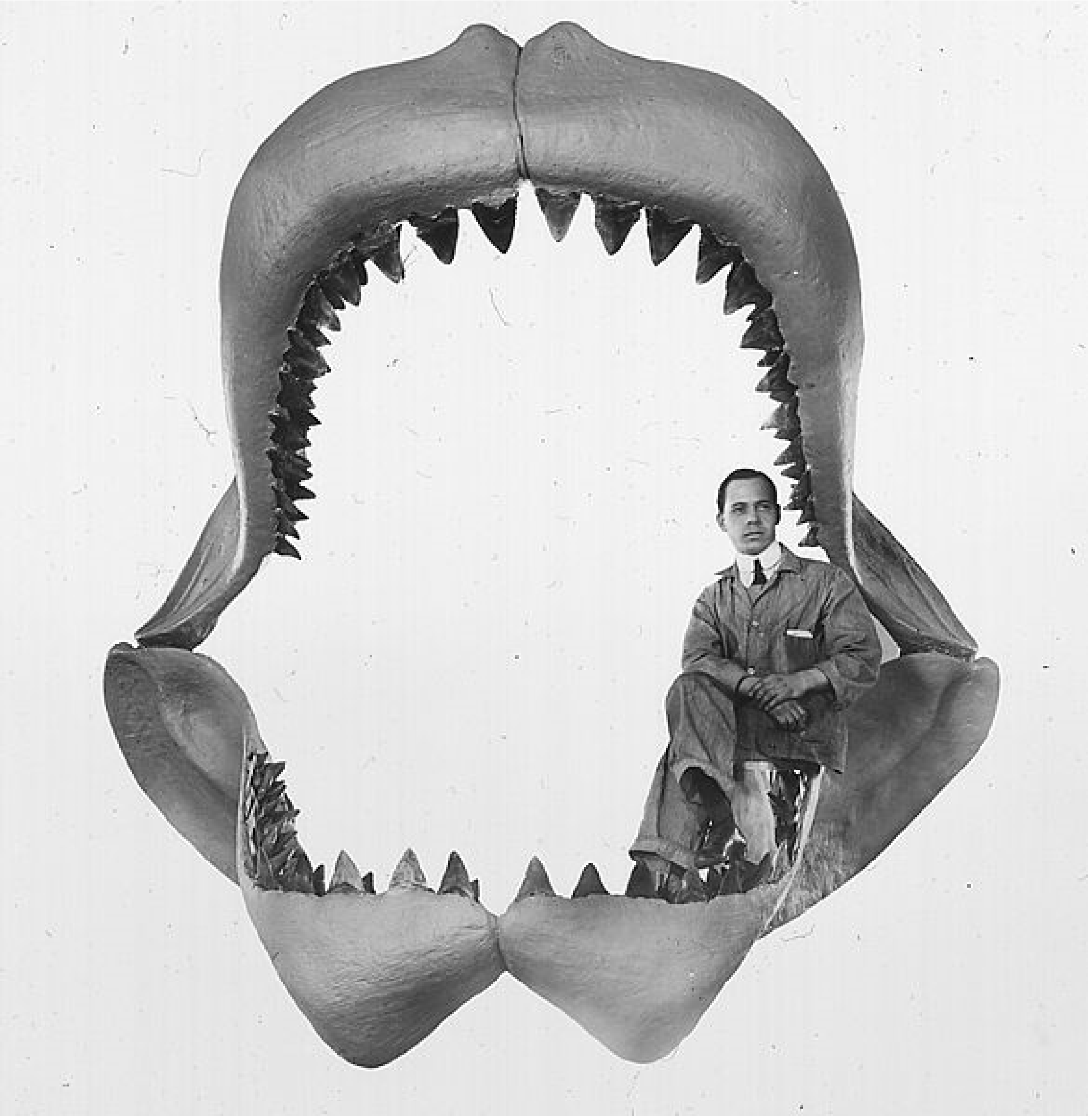
Reconstructed Megalodon skeleton on display at the Calvert Marine Museum

Aside from estimating the size of *C. megalodon*, Gottfried et al., also have tried to determine the schematics of the entire skeleton of *C. megalodon*.

Jaw structure

To functionally support the very large and robust dentition, the jaws of the *C. megalodon* would have been massive, stouter and more strongly developed than that of the great white shark, which possesses a somewhat gracile dentition in comparison. The strongly developed jaws would have somewhat of a pig-eyed appearance.

Chondrocranium



Reconstruction by Bashford Dean in 1909

The chondrocranium of *C. megalodon* would have a blockier and more robust appearance than that of the great white shark, in order to functionally reflect its more massive jaws and dentition in comparison.

Fins

The fins of *C. megalodon* would have been most likely proportionally larger and thicker in comparison to the fins of great white sharks because relatively larger fins are a necessity for propulsion and control of movements of a shark of greater size.

Axial skeleton

Through thorough scrutiny of the partially preserved vertebral *C. megalodon* specimen from Belgium, it became apparent that *C. megalodon* had a higher vertebral count than found in large specimens of any known shark. Only the vertebral count in great white shark came close in quantity, symbolizing close anatomical ties between the two species.

The complete skeleton

On the basis of the characteristics mentioned above, Gottfried and his colleagues eventually managed to reconstruct the entire skeleton of *C. megalodon*, which has been put on display in Calvert Marine Museum at Solomons island, Maryland in USA. This *C. megalodon* skeletal reconstruction is 11.5 metres (38 ft) long and represents a young individual. The team stresses that relative and proportional changes in the skeletal features of *C. megalodon* are ontogenetic in nature in comparison to that of great white shark, as they occur in great white sharks while growing larger. In addition, the fossil remains of *C. megalodon* confirm that it had a heavily calcified skeleton in life.

Paleoecological considerations

Range and habitat

C. megalodon was a pelagic fish that predominantly inhabited temperate and warm water environments. The fossil records of *C. megalodon* confirm that it was a cosmopolitan species. Prior to the formation of the Isthmus of Panama, the oceans were relatively warmer. This would have made it possible for the species to thrive in all the oceans of the world.

C. megalodon had enough behavioral flexibility to inhabit wide range of marine environments (i.e. coastal shallow waters, coastal upwelling, swampy coastal lagoons, sandy littorals and offshore deep water environments) and exhibited a transient life-style. The adult *C. megalodon* were not abundant in shallow water environments and mostly lurked offshore.

Nursery areas

Collection of teeth of juvenile Megalodon from a probable nursery area in the Gatun Formation of Panama.

Fossil evidence suggests that the preferred nursery sites of *C. megalodon* were likely to have been warm water coastal environments, where potential threats were minor and food sources were plentiful. As is the case with most sharks, *C. megalodon* also likely gave birth to live young. The size of the neonate *C. megalodon* teeth indicate that *C. megalodon* pups were around 2–3 metres (7–10 ft) in length at birth. The young *C. megalodon* commonly preyed upon fish, giant sea turtles, dugongs and small cetaceans. Upon approaching maturity, *C. megalodon* predominantly preferred off-shore cetacean high-use areas and preyed upon large cetaceans, depicting an ontogenetic shift in diet. At present, nursery sites of *C. megalodon* have been identified in the Gatun Formation of Panama, the Calvert Formation of Maryland and the Bone Valley Formation of Florida.

Prey relationships

Sharks are generally opportunistic predators. However, scientists propose that *C. megalodon* was "arguably the most formidable carnivore ever to have existed." The factors — great size, high-speed swimming capability and powerful jaws coupled with formidable killing apparatus, ensured a super-predator with the capability to consume a broad spectrum of fauna.

Fossil evidence indicates that *C. megalodon* preyed upon cetaceans (i.e., whales, including sperm whales, bowhead whales, cetotherrids, squalodontids, rorquals and *Odobenocetops*, dolphins and porpoises), sirenians, pinnipeds and giant sea turtles. Due to its size, *C. megalodon* would have fed primarily on large animals and whales were likely important prey–many whale bones have been found with clear signs of large bite marks (deep gashes) made by teeth that match those of *C. megalodon* and various excavations have revealed *C. megalodon* teeth lying close to the chewed remains of whales and sometimes in direct association with them. Like other sharks, *C. megalodon* also would have been piscivorous. *C. megalodon* likely also had a tendency for cannibalism.

Hunting behavior

Sharks often employ complex hunting strategies to engage large prey animals. Some paleontologists suggest that the hunting strategies of the great white shark may offer clues as to how *C. megalodon* might have hunted its unusually large prey (i.e., whales). However, fossil evidence suggests that *C. megalodon* employed more effective hunting strategies against large prey compared to the strategies employed by the great white shark.

Paleontologists have conducted a survey of fossils to determine attacking patterns of *C. megalodon* on prey. The findings suggest that the attack patterns could differ against prey with respect to its size. Fossil remains of some small cetaceans suggest that they were likely rammed with great force from below before being killed and eaten. One particular specimen — remains of a 9 metres (30 ft) long prehistoric baleen whale (unknown taxon from Miocene) provided the first opportunity to quantitatively analyze the attacking behavior of *C. megalodon*. The predator primarily focused its attack on the tough bony portions (i.e. bony shoulders, flippers, rib cage and upper spine) of the prey, which great white sharks generally avoid. Dr. Bretton Kent elaborated that *C. megalodon* attempted to crush the bones and damage delicate organs (i.e. heart and lungs) harbored within the rib cage of the prey. Such an attack would have immobilized the prey, which would have died quickly due to injuries to these vital organs. These findings also clarify why the ancient shark needed more robust dentition than the great white shark's.

During the Pliocene, larger and more advanced cetaceans appeared. *C. megalodon* apparently further refined its hunting strategies to cope with these larger animals. Numerous fossilized flipper bones (i.e., segments of the pectoral fins) and caudal vertebrae of large whales from the Pliocene have been found with bite marks that were caused by attacks of *C. megalodon*. This paleontological evidence suggests that *C. megalodon* would attempt to immobilize a large whale by ripping apart or biting off its propulsive structures before killing and feeding on it.

Interactions with cetaceans and other sharks

Artistic impression of a Megalodon pursuing two *Eobalaenoptera* whales

C. megalodon faced a highly competitive environment during its time of existence. However, *C. megalodon* was likely one of the most powerful and dominant predators in vertebrate history and probably had a profound impact on the structuring of marine communities. Fossil evidence indicates a correlation between the emergence of *C. megalodon* and extensive diversification of cetaceans around the world. Juvenile *C. megalodon* preferred regions where small cetaceans were abundant and adult *C. megalodon* preferred regions where large cetaceans were abundant. Such preferences may have developed in ages prior to Miocene. In addition, *C. megalodon* was contemporaneous with macro-predatory odontocetes (particularly raptorial sperm whales and squalodontids), such as *Livyatan melvillei*, which were also likely among the apex predators of that time and provided competition. In response to the threat of attack by *C. megalodon*, odontocetes may have generally functioned in pods for increased safety and some species evolved gigantic sizes. In addition, some species employed co-ordinated hunting behaviour for greater competitive effectiveness. However, bite marks on the fossil remains of odontocetes indicate that they were preyed on by giant macro-predatory sharks. Furthermore, fossil evidence indicates that *C. megalodon* developed the capability to tackle gigantic whales. By the end of Miocene, raptorial sperm whales vanished from the fossil record and left an ecological void.

Fossil evidence also indicates that other notable species of macro-predatory sharks (e.g. great white sharks) responded to competitive pressure from *C. megalodon* by avoiding regions it inhabited.

Extinction

It is not yet clear why *C. megalodon* became extinct after millions of years of dominance; however, several factors may have been involved.

Climatic cooling and ice ages

A major reason cited behind the extinction of *C. megalodon* is the decline in ocean temperatures at global scale. The Isthmus of Panama closed around 5 million years ago and fundamentally changed global ocean circulation. This geological event initially set the stage for glaciation in the northern hemisphere and later on, also facilitated cooling of the entire planet. Consequently, during the late Pliocene and Pleistocene, there were ice ages, which cooled the oceans significantly. The cooling trend adversely impacted *C. megalodon*, as it preferred warmer waters. Fossil evidence confirms the absence of *C. megalodon* in regions where water temperatures had significantly declined during the Pliocene.

In addition, wide-scale glaciation during the Pliocene and Pleistocene tied up huge volumes of water in continental ice sheets, resulting in significant sea level drops. Lower sea levels may have restricted many of the suitable warm water nursery sites for *C. megalodon*, hindering population maintenance. Nursery areas are pivotal for the survival of a species.

Decline in food supply

Cetaceans attained their greatest diversity during the Miocene, with over 20 recognized genera in comparison to only six living genera. Such diversity presented an ideal setting to support a giant predator like *C. megalodon*. However, the dependency of *C. megalodon* on large prey made it over-specialized. In addition, during the Pliocene, many species of cetaceans became extinct and most surviving species disappeared from the tropics. Whale migratory patterns during the Pliocene have been reconstructed from the fossil record, suggesting that most surviving species showed a trend towards polar regions. The cooler water temperatures during the Pliocene cut *C. megalodon* off from polar regions and large prey was effectively "no longer within the range" of *C. megalodon* after the migrations. These developments diminished the food supply for *C. megalodon* in warm waters. Paleontologist Albert Sanders suggests that *C. megalodon* had become too large to sustain itself on the available food supply in the tropics. In addition, the shortage of food sources in warm waters during the Pliocene and Pleistocene might have fueled cannibalism within *C. megalodon*. The juvenile individuals were at increased risk from attacks by adult individuals during times of starvation.

Evolution of the orca

The ancient relatives of the orca evolved during the Pliocene and likely filled the ecological void left by raptorial sperm whales by the end of Miocene. Some paleontologists have speculated that orcas may also have contributed to the extinction of *C. megalodon*. However, paleontologist Robert Purdy pointed out that there is not much fossil evidence for the history of marine vertebrates for the last three million years to support this hypothesis. In addition, *C. megalodon* was already absent in high latitudes since the early Pliocene due to cooling trends in the oceans, where ancient relatives of the orca commonly occurred. Competition may have occurred in other regions — bite marks on the fossil remains of delphinids indicate that *C. megalodon* preyed on them. However, the relatively common occurrence of the ancient relatives of the orca in high latitudes during the Pliocene indicates the potential of orcas to cope with cold water temperatures and this trend continues with modern orca. This capability would have helped ancient relatives of the orca cope with ice ages, while *C. megalodon* disappeared.

Taxonomy

Even after decades of research and scrutiny, the controversy on phylogeny of *C. megalodon* still persists. Several shark researchers (e.g. J. E. Randall, A. P. Klimley, D. G. Ainley, M. D. Gottfried, L. J. V. Compagno, S. C. Bowman and R. W. Purdy) insist that *C. megalodon* is a close relative of the great white shark. However, several other shark researchers (e.g. D. S. Jordan, H. Hannibal, E. Casier, C. DeMuizon, T. J. DeVries, D. Ward and H. Cappetta) dismiss the proposal that *C. megalodon* is a close relative of the great white shark and cite convergent evolution as the reasons for the dental similarity. The arguments of the supporters of the *Carcharocles* genus for *C. megalodon* seem to have gained noticeable support. However, the original taxonomic assignment still has wide-scale acceptance.

Megalodon within *Carcharodon*

The traditional view is that *C. megalodon* should be classified within the genus *Carcharodon* along with the great white shark. Main reasons cited for this phylogeny are; (1) an ontogenetic gradation, whereby the teeth of *C. carcharias* shift from having coarse serrations as a juvenile to fine serrations as an adult, the latter resemble those of *C. megalodon*; (2) morphological similarity of teeth of young *C. megalodon* to those of *C.*

carcharias; (3) a symmetrical second anterior tooth; (4) large intermediate tooth that is inclined mesially; and (5) upper anterior teeth that have a chevron-shaped neck area on the lingual surface. The supporters of classification as *Carcharodon* for *C. megalodon* suggest that *C. megalodon* and *C. carcharias* share a common ancestor, *Palaeocarcharodon orientalis*.

Megalodon within *Carcharocles*

Around 1923, the genus ***Carcharocles*** was proposed by two shark researchers, D. S. Jordan and H. Hannibal, to classify a shark *C. auriculatus*. Later on, *Carcharocles* proponents assigned *C. megalodon* to *Carcharocles* genus. *Carcharocles* proponents also suggest that the direct ancestor of the sharks belonging to the *Carcharocles* genus, is an ancient giant shark called *Otodus obliquus*, which lived during the Paleocene and Eocene epochs. According to supporters of classification as *Carcharocles* for *C. megalodon*; *Otodus obliquus* evolved in to *Carcharocles aksuaticus*, which evolved in to *Carcharocles auriculatus*, which evolved into *Carcharocles angustidens*, which evolved into *Carcharocles chubutensis*, which eventually evolved into megalodon. Hence, the immediate ancestor of *C. megalodon* is *Carcharocles chubutensis*, because it serves as the missing link between *Carcharocles augustidens* and *C. megalodon* and it bridges the loss of the "lateral cusps" that characterize *C. megalodon*.

Megalodon as chronospecies?

Shark researcher David Ward has further elaborated on the *Carcharocles* evolutionary process by implying that this lineage, stretching from the Paleocene to the Pliocene, is of a **single giant shark** which gradually changed through time, suggesting a case of chronospecies.

New evolutionary position for great white shark

Carcharocles proponents point out that the great white shark is closely related to an ancient shark *Isurus hastalis*, the "broad tooth mako", rather than to *C. megalodon*. One reason cited by paleontologist Dr. Chuck Ciampaglio is that the dental morphometrics (variations and changes in the physical form of objects) of *I. hastalis* and *C. carcharias* are remarkably similar. Another reason cited is that *C. megalodon* teeth have much finer serrations than in *C. carcharias* teeth. Further evidence linking the great white shark more closely to ancient mako sharks, rather than to *C. megalodon*, has been provided in 2009 — The fossilized remains of an ancient form of the great white shark were excavated from southwestern Peru in 1988, which are about 4 million years old. These fossilized remains demonstrate a likely shared ancestor of modern mako and great white sharks.

Additional controversy and considerations

Two teeth of great white shark (white) compared to a single tooth of Megalodon (black). A coin 23 mm in width shows the scale.

Paleontologist Dr. C. Ciampaglio asserts that similarities between the teeth of *C. megalodon* and the great white shark are superficial and there are noticeable morphometric differences between them and that these findings are sufficient to warrant a separate genus for *C. megalodon*. However, some proponents of the *Carcharodon* genus for *C. megalodon* (i.e. M. D. Gottfried and R. E. Fordyce) have provided more arguments for a close relationship between the extinct megatooth sharks and the great white shark. With respect to the recent controversy regarding fossil lamnid shark relationships, the overall morphology – particularly the internal calcification patterns – of the great white shark vertebral centra have been compared to well-preserved fossil centra from the megatooth sharks, including *C. megalodon* and *C. angustidens*. The morphological similarity apparent from these comparisons supports a close relationship of the giant fossil megatooth species to living white sharks.

With respect to the origins of the great white shark, M. D. Gottfried and R. E. Fordyce have pointed out that some great white shark fossils are about 16 million years old and predate the transitional Pliocene fossils. In addition, the Oligocene records of *C. megalodon*, contradict the suggestion that *Carcharocles chubutensis* is the immediate ancestor of *C. megalodon*. These records also indicate that *C. megalodon* actually co-existed with *Carcharocles angustidens*. Hence, proponents for the *Carcharodon* genus for *C. megalodon* argue that extinct megatoothed sharks should be placed within the genus *Carcharodon*.

Some paleontologists argue that the genus *Otodus* should be used for sharks within the *Carcharocles* lineage and the genus *Carcharocles* should be discarded.

At present, *Carcharocles* proponents accept that both species belong to the order *Lamniformes* and in the absence of living members of the family *Otodontidae*, great white sharks should be regarded as ecologically analogous to *C. megalodon*.

In fiction

Ever since the remains of *C. megalodon* were discovered, it has been an object of fascination. It has been portrayed in several works of fiction, including films and novels and continues to hold its place among the most popular subjects for fiction involving sea monsters. Many of these works of fiction posit that at least a relict population of *C. megalodon* survived extinction and lurk in the depths of the ocean and that individuals may manage to surface from the vast depths, either by human intervention or by natural means. Jim Shepard's story "*Tedford and the Megalodon*" is a good example of this. Such beliefs are usually inspired by the discovery and excavation of a *C. megalodon* tooth by HMS Challenger in 1872, a tooth which some believed to be only 10,000 years old. However, this tooth has been re-examined and findings indicate that it is untestable for age.

Some works of fiction (such as *Shark Attack 3: Megalodon* and Steve Alten's *Meg* series) incorrectly depict the megalodon as being a species over 70 million years old and to have been alive during the time of dinosaurs. The writers of the movie *Shark Attack 3: Megalodon* depicted this assumption by including an altered copy of a book by the shark researcher, Richard Ellis, called "Great White Shark". The copy shown in the film had several pages that do not exist in the real book. The author of the real book sued the film's distributor Lions Gate Entertainment, asking for a halt to the film's distribution along with $150,000 in damages. Steve Alten's *Meg: A Novel of Deep Terror* is probably best known for portraying this inaccuracy with its prologue and cover artworks depicting *C. megalodon* killing a tyrannosaur in the sea.

Mega Shark Versus Giant Octopus (2009) and its sequel *Mega Shark Versus Crocosaurus* (2010) are parodies of disaster films with a giant shark similar to a megalodon in the title role.

Chapter- 6

Oligocene Mammals

Aeluroidea

Aeluroidea **Fossil range: Oligocene**	
Conservation status	
Fossil	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Carnivora
Suborder:	Feliformia
Superfamily:	**Aeluroidea**

Aeluroidea is an extant and extinct superfamily of feline-like carnivores which are or were endemic to North America, South America, Africa and Asia. They appeared during the Oligocene about 33.3 million years ago.

This superfamily includes extant families of: Felidae (cats), Herpestidae (mongoose), Hyaenidae, Nandinia (civet) and the extinct *Africanictis*, *Anictis*, *Asiavorator*, *Haplogale*, *Herpestides*, *Mioprionodon*, *Moghradictis*, *Palaeoprionodon*, *Proailurus*, *Shandgolictis*, *Stenogale* and *Stenoplesictis*.

Taxonomy

Aeluroidea was named by Flower (1869). It is extant. It was assigned to Carnivora by Flower (1883) and Carroll (1988); and to Feliformia by Bryant (1991).

Amphicynodon

Amphicynodon **Fossil range: Oligocene**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Carnivora
Suborder:	Caniformia
Superfamily:	Arctoidea
Family:	Ursoidae
Genus:	***Amphicynodon***
Species:	Filhol (1881)

Amphicynodon is an extinct genus of mammal of the superfamily Ursoidae, endemic to Europe and Asia during the Oligocene, living from ~33.9—28.4 Mya, existing for approximately 5.5 million years.

Amphicynodon is a small basal member of Ursoidae similar to early Mustelids in both size and existence.

Taxonomy

Amphicynodon was named by Filhol (1881). It was assigned to Phocoidea by McKenna and Bell (1997) then to Ursidae by Filhol (1881) and Hunt (1998); and to Ursoidea by Wang et al. (2005).

Fossil distribution

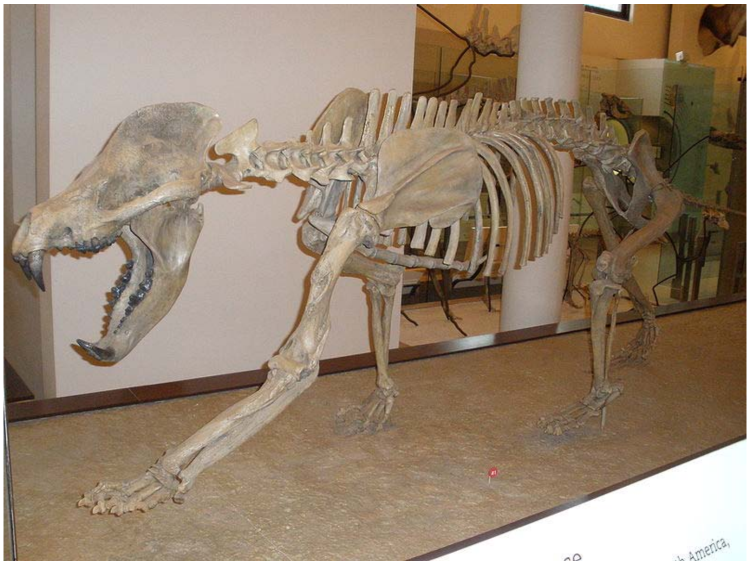
Sites and specimen ages:

- Ulaan Khongil, Mongolia ~33.9—28.4 Mya.
- Ronzon site, Auvergne France ~33.9—28.4 Mya.

Amphicyon

Amphicyon

Fossil range: Early Oligocene–Early Miocene



A. ingens, American Museum of Natural History

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Carnivora
Family:	†Amphicyonidae
Subfamily:	†Amphicyoninae
Genus:	†***Amphicyon***

Species

- *A. intermedius* (type)
- *A. frendens*
- *A. frendes*
- *A. galushai*
- *A. giganteus*
- *A. ingens*
- *A. laugnacensis*
- *A. longiramus*
- *A. major*
- *A. pontoni*
- *A. reinheimeri*
- *A. riggsi*

Range of Amphicyon based on fossil evidence

Amphicyon ("ambiguous dog") is an extinct genus of large carnivorous bone-crushing mammals, known as bear-dogs, of the family Amphicyonidae, subfamily Amphicyoninae, from the middle Oligocene and early Miocene. They ranged over North America, Europe, Asia and Africa from 20—1.810 Ma ago, existing approximately 18.19 million years.

Morphology

Jaws, Paläontologische Museum München

Amphicyon was the typical bear-dog amphicyonid with morphology similar to both bears and dogs. With its robust build and maximum length of 2.5 m (8 ft), the largest species looked more like a bear than a dog. It had a large heavy tail, thick neck, robust limbs and teeth like a wolf. It was probably an omnivore with a lifestyle comparable to that of the brown bear.

Body mass

A single specimen was examined by Legendre and Roth and estimated to have a body mass of 84.2 kg (190 lb), roughly half that of *Ischyrocyon* and twice that of *Epicyon* which shared its time period and habitat. *A. ingens* was much bigger: Sorkin (2008) estimated the largest known specimen (AM 68108) to weigh 600 kg, making it the largest amphicyonid and one of the largest known carnivorous land mammals.

Fossil distribution

The earliest occurrences of *Amphicyon* in North America are from the early to mid-Miocene, found in the Runningwater Formation in Sioux County, Nebraska and from the lower part of the Troublesome Formation, Colorado (*A. galushai, A. frendens* and *A. ingens*). Although other large amphicyonids from the Miocene of North America have been placed in *Amphicyon*, many of these carnivores are now placed in other amphicyonid genera. The *Amphicyon* lineage in the New World is restricted to the above three species (18.8–14.2 Ma). Particularly rich samples of the large North American species of *Amphicyon* have been found in the Sheep Creek Formation (*A. frendens*) and Olcott Formation (*A. ingens*) of central Sioux County, northwest Nebraska. *Amphicyon* has also been found in France, Spain and Germany in Europe.

Species

Amphicyon frendens lived from 20.16–13.6 Ma, approximately 6.56 million years. The species was originally described by W. Matthew in 1924 from specimens found in the middle member of the Sheep Creek Formation, Sioux County, Nebraska. *A. frendens* specimens have since been found at sites in Harney and Malheur Counties, Oregon. A specimen examined by S. Legendre and C. Roth in 1988 yielded an estimated body mass of 135.6 kg (300 lb), similar to that of *Ischyrocyon*, *Amphicyon galushai* and its borophagine competitor *Epicyon*, which it coexisted with.

Amphicyon galushai lived from 20.6–16.3 Ma, approximately 4.3 million years. *A. galushai* was described by R. Hunt in 2003 based on the type specimen F:AM 25406, found in the Dunlap Camel Quarry, Runningwater Formation, Dawes County, Nebraska Specimens assigned to this species have since been found at several sites in Nebraska and one site in Colorado.

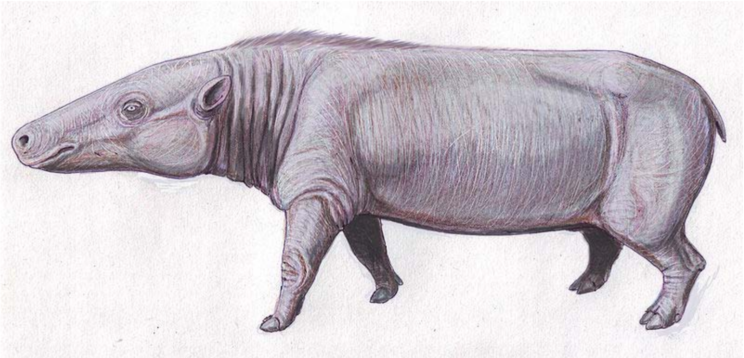
Amphicyon giganteus lived from 16.8–7.2 Ma, approximately 9.7 million years, in what is now Europe and Namibia. The species was first described in 1884 by Kaup. A specimen of *Iberotherium rexmanueli zbyszewskii* with teeth marks from *A. giganteus* was found in Portugal. It is unknown if he young *Iberotherium* was attacked or the carcass found and scavenged. The find was described by paleontologists Antunesa et al. in 2006.

Amphicyon ingens lived from 20.06–13.6 Ma, approximately 6.46 million years. The species was originally described by W. Matthew in 1924 from specimens found in the Olcott Formation, Sioux County, Nebraska. Specimens attributed to this species have since been found in California, Colorado and New Mexico.

Amphicyon major lived from 16.9–9.0 Ma, approximately 7.9 million years. Specimens have been found in across Europe and in western Turkey. The species was named by De Blainville in 1841.

Anthracotherium

Anthracotherium
Fossil range: Oligocene to Mid Miocene



Anthracotherium magnum

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Artiodactyla
Family:	†Anthracotheriidae
Subfamily:	†Anthracotheriinae
Genus:	†***Anthracotherium***

Species

- †*A. sminthos* (Forster-Cooper, 1913)
- †*A. magnum*
- †*A. pangan*

- †*A. monsvialense*
- †*A. minus*
- †*A. minimum*
- †*A. bumbachense*
- †*A. meneghinii*

Synonyms

- ***Anthracohyus*** Pilgrim and Cotter, 1916
- ***Anthracokeryx*** Pilgrim and Cotter, 1916
- ***Anthracothema*** Pilgrim, 1928

Anthracotherium ("Coal Beast") was a genus of extinct artiodactyl ungulate mammals, characterized by having 44 teeth, with five semi-crescentic cusps on the crowns of the upper molars. The genus ranged throughout the Oligocene period, having a distribution throughout Europe, Asia and North America. They died out during the mid to late Miocene, possibly due to a combination of climatic change and competition from other artiodactyls, including pigs and hippopotami (such may have been the case in Europe).

The genus typifies the family Anthracotheriidae, if only because it is the most thoroughly studied. In many respects, especially the anatomy of the lower jaw, *Anthracotherium*, as with the other members of the family, is allied to the hippopotamus, of which it is probably an ancestral form. Recent evidence further suggests that anthracotheres, together with hippos, may be close to the ancestry of the whales.

The genus name stems from the fact that the remains first described having been obtained from the Tertiary lignite-beds of Europe.

The European *Anthracotherium magnum* was approximately as large as a hippo, but there were several smaller species and the genus also occurs in Egypt, India and North America. Members of the genus *Anthracotherium*, as well as other members of the family Anthracotheriidae, are known colloquially as anthracotheres.

Anthracotherium monsvialense mandible

Anthracotherium sp. coprolite at the Museum für Naturkunde, Berlin

Apidium

Apidium Fossil range: 36–32 Ma Late Eocene-Early Oligocene	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Primates
Family:	†Parapithecidae
Genus:	***†Apidium*** Osborn, 1908
Paleospecies	
†Apidium phiomense *†Apidium moustafai* *†Apidium bowni*	

The genus ***Apidium*** (from Latin for "small bull", as the first fossils were thought to be from a type of a cow) is that of at least three extinct primates living in the early Oligocene, roughly 36 to 32 millions years ago. *Apidium* fossils are common in the Fayoum deposits of Egypt. Fossils of the earlier species, *Apidium moustafai*, are rare; fossils of the later species *Apidium phiomense* are fairly common.

Apidium and its fellow members of the Parapithecidae family are stem anthropoids that possess all the hallmarks of modern Anthropoidea. Their ancestry is closely tied to the Eocene Asian group Eosimiidae.

Behaviour

The *Apidium* species were well adapted to life in what once were the tropical forests of North Africa. They lived in trees and apparently moved on top of tree limbs by a combination of quadrupedalism and leaping, much as do living squirrel monkeys of the genus *Saimiri*. These primates appear to have been frugivorous and diurnal, with keen eyesight.

Male *Apidium* were bigger than the females, which, by comparing them with living primates, suggests that they probably lived in groups, where a small number of males would have had control over several females. The males had large canine teeth

Archaelurus

Nimravus is an extinct genus of the family *Nimravidae*, subfamily *Nimravinae* (false saber-toothed cat) endemic to North America during the Oligocene epoch (33.3—26.3 mya), existing for approximately 7 million years.

Taxonomy

Nimravus was named by Cope (1879) [status called into question by Bryant 1996]. It is the type genus of *Nimravidae, Nimravinae*. It was assigned to *Nimravidae* by Cope (1879) and Martin (1998); and to *Nimravinae* by Flynn and Galiano (1982), Bryant (1991) and Hunt (1998).

Unrealated to saber-toothed cats, they evolved a similar form through parallel evolution.

Morphology

Nimravus was around 1.2 metres (4 ft) in body length. With its sleek body, it may have resembled the modern caracal, although it had a longer back and more dog-like feet with partially retractile claws. It probably hunted birds and small mammals, ambushing them like modern cats, rather than chasing them down. *Nimravus* competed with other false sabre-tooths such as *Eusmilus*.

A *Nimravus* skull, found in North America, had been pierced in the forehead region, the hole exactly matching the dimensions of the sabre-like canine of *Eusmilus*. This particular individual of *Nimravus* apparently survived this encounter, as the wound showed signs of healing.

A single specimen was examined by M. Mendoza for body mass and was estimated to have a weight of 29.5 kg (65 lbs).

Fossil distribution

Fossils were uncovered in the western U.S. from Oregon to southern California to Nebraska.

Species

N. brachyops (syn. Archaelurus debilis, Dinictis major, N. altidens, N. bumpensis, N. confertus, N. gomphodus, N. meridianus), N. sectator.

Archaeocyon

Archaeocyon
Fossil range: Early Oligocene–Late Oligocene

Skull of *Archaeocyon leptodus*

Scientific classification

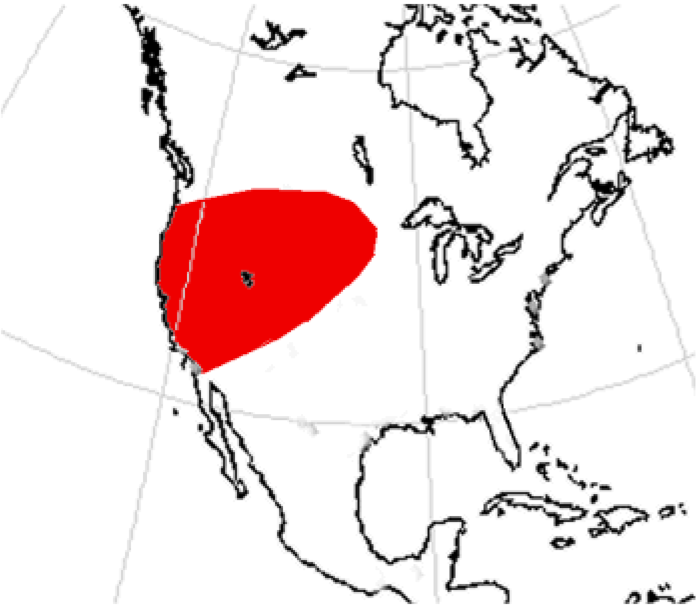
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Carnivora
Family:	Canidae
Subfamily:	†Borophaginae
Genus:	†***Archaeocyon*** Wang, Tedford, & Taylor, 1999

Type species

†*Pseudocynodictis pavidus*

Species

- †*A. falkenbachi*
- †*A. leptodus*
- †*A. pavidus*



Range of Archaeocyon based on fossil distribution

Archaeocyon ("beginning dog") is a small extinct genus of the *Borophaginae* within the family *Canidae* (terrestrial canine) which inhabited most of North America during the Whitneyan stage through Geringian stage of the Oligocene epoch 33.3—26.3 Ma *Archaeocyon* existed for approximately 7.3 million years.

Species of *Archaeocyon* are among the earliest known borophagines, although a species of *Otarocyon* has a slightly earlier first appearance.

Taxonomy

Archaeocyon was a comparatively small and unspecialized dog. Its dentition (teeth) suggests a slightly more hypocarnivorous (omnivorous) diet than the otherwise similar *Hesperocyon*. The skeleton is also generalized, lacking specializations for running and retaining a plantigrade foot posture.

A few derived features of the dentition support a relationship to Borophaginae and Caninae (the subfamily that includes living canids), rather than to the basal canid subfamily Hesperocyoninae. The temporal position of *Archaeocyon* suggests an affinity to borophagines because the first members of Caninae appear substantially earlier.

Morphology

Fossil specimens of two individuals' body mass were examined by Legendre and Roth. The first specimen was estimated to weigh 1.43 kg (3.15 lbs). The second specimen was estimated to weigh 1.49 kg (3.28 lbs).

Species

Three species of *Archaeocyon* have been described. The two earlier species, *A. pavidus* and *A. leptodus*, differ primarily in size, with *A. leptodus* being larger. The third species, *A. falkenbachi*, is the size of *A. leptodus* and differs from other *Archaeocyon* species in having a shorter, broader skull.

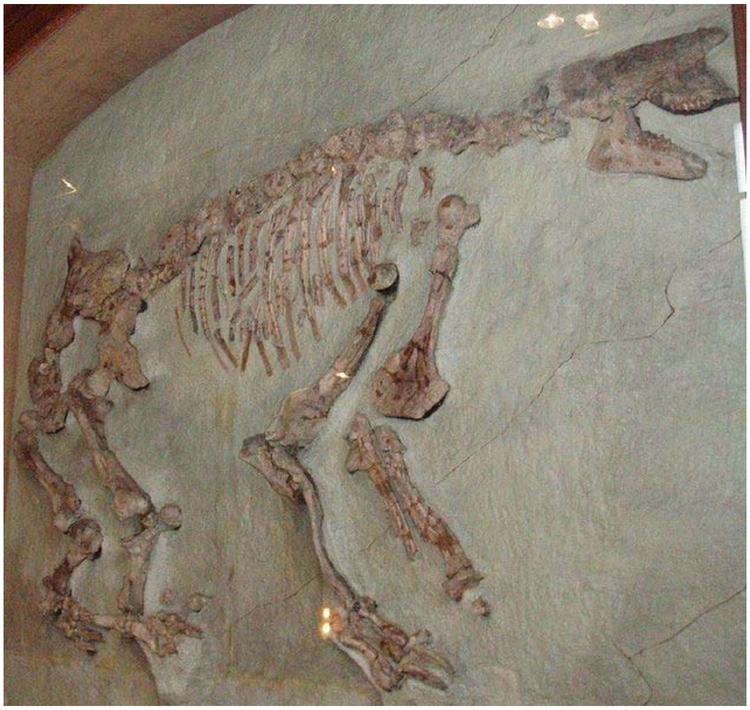
Barytherium

Barytherium (meaning *heavy beast*) is a genus of an extinct family (**Barytheriidae**) of primitive proboscidean that lived during the late Eocene and early Oligocene in North Africa. The Barytheriidae were the first large size proboscideans to appear in the fossil records and were characterized by a strong sexual dimorphism.

The only known species within this family is *Barytherium grave*, found at the beginning of the 20th century in the Fayum, Egypt. More complete specimens have been found since then, at Dor el Talha Libya. In some respects, these animals would have looked similar to a modern Asian Elephant, but with a more slender build. The most visible difference, however, would have been the tusks. *Barytherium* had eight very short tusks, four each in the upper and lower jaws, which resembled those of a modern hippopotamus more than those of an elephant. The upper pairs were vertical, while the lower pairs projected forwards from the mouth horizontally. Together, these would have created a shearing action for cropping plants.

Chalicotherium

Chalicotherium
Fossil range: Late Oligocene–Early Pliocene



Fossil remains of a *Chalicotherium*

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Perissodactyla
Family:	†Chalicotheriidae
Genus:	†***Chalicotherium*** J. J. Kaup, 1833

Synonyms

- *Macrotherium* Lartet, 1837
- *Butleria*

Chalicotherium (Ancient Greek χαλιξ/*khalix*, *khalik*-: pebble/gravel + θηρίον/*thērion*, diminutive of θηρ/*thēr*: beast) is a genus of extinct grazing odd-toed ungulates of the order Perissodactyla and family Chalicotheriidae, endemic to Europe, Africa and Asia during the Late Oligocene to Lower Pliocene, living from 16—7.75 mya, existing for approximately 8.25 million years.

This animal would look much like other chalicotheriid species: an odd looking herbivore with long clawed forelimbs and stouter weight bearing hindlimbs.

The type species, *Chalicotherium goldfussi*, from Miocene and Pliocene Europe, was described by J. J. Kaup in 1833 and since then 7 other species have been confidently assigned to this genus. According to current phylogenetic analyses *Chalicotherium* has two daughter genera nested within in, *Anisodon* Lartet, 1851 and *Nestoritherium* J. J. Kaup, 1859, thus rendering it paraphyletic.

Description

Foot bones of Chalicotherium grande

Chalicotherium, like many members of Perissodactyla, was adapted to browsing, though uniquely adapted to do so among its ungulate relatives. Its arms were long and heavily clawed, allowing them to walk on their knuckles only. The arms were used to reach for high branches and bring them close to its short-faced head to strip them clean of leaves. The horse-like head itself shows adaptation to a diet of soft vegetation, since, as the animal reached sexual maturity, the incisors and upper canines were shed, suggesting that its muscular lips and the resulting gum pads were enough to crop fodder which was then processed by squarish, low-crowned molars.

Callosities on the ischium imply that these animals would sit on their haunches for extended periods of time, probably while feeding. Pad-supporting bony growth on the dorsal side of the manual phalanges is interpreted as evidence of knuckle-walking, which would probably be useful to avoid wearing down the claws, preserving them for use either as a forage collecting rake or as a formidable defensive weapon.

All of these characteristics show some convergence with the unrelated ground sloths, gorillas and giant pandas.

Classification

Taxonomic history

The type specimens for *Chalicotherium goldfussi* were found in the Upper Miocene strata of the *Dinotherien-sande* beds near Eppelsheim, in the Grand Duchy of Hesse, Germany. Kaup, when describing this new animal in 1833, found the teeth to be pebble-like and named the creature accordingly. Later on, limbs found in strata located at Sansan in the department of Gers, Southwestern France, were first described as *Macrotherium* by Lartet in 1837. Further study of these fossil remains and subsequent finds by Filhol warranted a referral of the material described as *Macrotherium* to *Chalicotherium*. A more recently synonymized genus is *Butleria*, preoccupied by a butterfly genus.

Referral history for each species is detailed in the species list below along with morphological and geographical data where available.

Species

Valid:

- *Chalicotherium goldfussi* J. J. Kaup, 1833.

  The type species, it was found in Upper Miocene beds located in Germany. It weighed around 1500 kg and was 2.6 m high at the shoulder.

- *Chalicotherium giganteum* Pictet, 1844.

  First described as *Macrotherium giganteum* Gervais, later sunk into the type species for lack of distinguishing skeletal morphology, it was found in the Upper Miocene strata located at Sansan, France.

- *Chalicotherium brevirostris*

First described as *Macrotherium brevirostris* Colbert 1934, this species hails from the Upper Miocene Tung Gur Formation, Inner Mongolia, China.

- *Chalicotherium rusingense* Butler, 1962.

  This species hails from the Lower Miocene strata located in Kenya and Uganda.

- *Chalicotherium pilgrimi*

  Formerly known as *Schizotherium pilgrimi* Forster Cooper, then referred to *Macrotherium*, this species hails from the Lower Miocene Bugti beds of Pakistan.

- *Chalicotherium wetzleri*

  Formerly named as *Schizotherium wetzleri* this species hails from Oligocene beds located in France and Germany, leading scientists to believe it was widespread in Western Europe.

- *Chalicotherium salinum*

  First described as *Macrotherium salinum* Forster Cooper, this species was first discovered at the Lower Pliocene Lower Siwaliks beds in India; its chronological and geographic range was later extended to the Middle and Upper Miocene and to Pakistan and China, respectively.

- *Chalicotherium wuduensis*

  This species hails from Upper Miocene strata located in Gansu, China.

Invalid:

- *Chalicotherium antiquum* J. J. Kaup, 1833.

  Found at the same locality as the type species, it was later found wanting of diagnostic features and sunk into the type species.

- *Chalicotherium baltavarense*

  This name pertains to a specimen found in Slovakia that was later lumped into *Chalicotherium pentelicum*.

- *Chalicotherium minus*

  For sometime considered a species of *Anisodon*, it was later sunk into the type species.

- *Chalicotherium posterigenium*

  Junior synonym of *Chalicotherium sivalense*

- *Chalicotherium sindiense*

  Junior synonym of *Chalicotherium sivalense*

- *Chalicotherium sinense*

  This species hailing from Lower Pliocene beds found in China is now assigned to the genus *Nestoritherium*.

- *Chalicotherium sivalense*

  Erected from specimens found in Upper Miocene beds located in India it is now assigned to the genus *Nestoritherium*.

- *Chalicotherium pentelicum* (*pentelici* in some older publications)

  Hailing from Upper Miocene strata of Slovakia and Greece, being Samos Island a notable locality of the latter, the species named *Colodus pachygnathum* was later subsumed with it. Further study referred this species to the genus *Ancylotherium*.

- *Chalicotherium grande* Blainville, 1849.

  Further study after this species' first description as *Macrotherium grande* Lartet, 1837 and subsequent referral to *Chalicotherium* by Blainville and later on of *M. rhodanicum*, *M. magnum* and *M. sansaniense*, warranted all the pertaining specimens to be clustered under the revived genus *Anisodon* Lartet, 1851, by Geraads *et al.* in 1995, as *Anisodon grande*.

Attributed specimens:

- *Chalicotherium* cf. *C. brevirostris* Wang *et al.*, 2001.

  Hailing for the Tsaidam Basin, northern Qinghai-Tibetan Plateau, China.

- "Chalicotherium modicum" Stehlin, 1905.

  A *nomen nudum*, actually a *Schizotherium priscum* tooth.

- "*Chalicotherium*" *bilobatum* Cope.

  Hailing from the Oligocene of Saskatchewan, this very fragmentary specimen was the type on which Russel erected the genus *Oreinotherium*.

- *Chalicotherium* spp.

  Specimens found in two Tajikistan localities, thought to pertain to at least two different species.

Cynodesmus

Cynodesmus **Fossil range: Late Oligocene–Early Miocene**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Carnivora
Family:	Canidae
Subfamily:	†Hesperocyoninae
Genus:	†***Cynodesmus*** Scott, 1895
Type species	
†*Cynodesmus thooides*	
Species	
†*C. martini* †*C. thooides*	

Cynodesmus is an extinct genus of omnivorous canine which inhabited North America during the Oligocene living from 33.3—-26.3 Ma and existed for approximately 7 million years.

Cynodemus was one of the first canids to truly look dog-like. At around 1 metre (3.3 ft) in length, it was about the same size as a modern coyote, but had a shorter skull, heavier tail and longer rump. The shape of its limbs suggests that *Cynodesmus* was not a very good runner compared to most other canids; it probably attacked prey from an ambush. Unlike modern dogs, it had five toes on each foot, bearing partially retractable claws.

Taxonomy

Cynodesmus once included numerous species of Oligocene and Miocene canid with highly carnivorous (hypercarnivorous) dentitions. A revision of the genus by Wang

(1994) indicates that most species previously placed in *Cynodesmus* are unrelated to the type species, *C. thooides*. These other species have been placed the genera *Carpocyon*, *Desmocyon*, *Leptocyon*, *Metatomarctus*, *Osbornodon*, *Otarocyon*, *Paracynarctus*, *Paratomarctus* and *Phlaocyon* (Wang, 1994; Wang et al., 1999). Of these, only *Osbornodon* belongs in the same subfamily as *Cynodesmus*, Hesperocyoninae. The remaining genera are placed in the subfamilies Borophaginae and Caninae.

With unrelated species removed, *Cynodesmus* is currently restricted to the type species and the closely related *C. martini* (Wang, 1994).

Studies using the old conception of *Cynodesmus* considered it to be the ancestor of *Tomarctus* (16-23 Ma) from which wolves, dogs, foxes and fennecs developed. The *Cynodesmus* is a good example of convergent evolution because of other species such as the *Borophagus*, the largest and most dominant canids of this Pliocene epoch, both of which evolved from it.

Desmatochoerus

Desmatochoerus
Fossil range: Late Oligocene

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Artiodactyla
Family:	†Merycoidodontidae
Subfamily:	†Desmatochoerinae
Tribe:	**†Sespiini**
Genus:	**†*Desmatochoerus*** (Schultz and Falkenbach, 1968

Type species

†*Desmatochoeru*

Species

- †*D. hesperus*
- †*D. megalodon*

Desmatochoerus is a large extinct genus of terrestrial herbivore of the family *Merycoidodontidae*, subfamily *Merycoidodontinae* (an oreodont), endemic to North America during the middle Oligocene-Late Oligocene epochs (30.8—20.6 mya) existing for approximately 10.2 million years.

Taxonomy

Desmatochoerus was named by Schultz and Falkenbach (1954) [named as a subgenus of *Promerycohoerus* by Thorpe 1921 and treated as such by Thorpe 1937; raised to genus level]. It was synonymized subjectively with *Eporeodon* by Lander (1998). It was assigned to *Merycoidodontidae* by Schultz and Falkenbach (1954) and Stevens and Stevens (1996).

Morphology

A single specimen was examined by M. Mendoza for body mass and estimated to have a weight of 342.4 kg (754.8 lbs).

Fossil distribution

Fossils have been uncovered in several locations in the western U.S.

Species

D. hesperus, D. megalodon (syn. *Promerycochoerus curvidens, Promerycochoerus gregoryi*)

Sister genera

Aclistomycter, *Bathygenys*, *Brachycrus* (syn. *Pronomotherium*), *Eporeodon* (syn. *Hypselochoerus, Pseudodesmatochoerus*), *Hypsiops* (syn. *Pseudomesoreodon, Submerycochoerus*), *Leptauchenia* (syn. *Brachymeryx, Cyclopidius, Hadroleptauchenia, Pithecistes, Pseudocyclopidius*), *Limnenetes, Mediochoerus, Merycoides* (syn. *Paramerychyus*), *Merycochoerus*, *Merycoidodon* (syn. *Blickohyus, Genetochoerus, Oreodon, Otionohyus, Paramerycoidodon, Prodesmatochoerus, Promesoreodon, Subdesmatochoerus*), *Mesoreodon, Miniochoerus* (syn. *Parastenopsochoerus, Platyochoerus, Stenopsochoerus*), *Oreodontoides, Oreonetes, Paroreodon*, *Sespia*, (syn. *Epigenetochoerus*), *Phenacocoelus*, *Ticholeptus* (syn. *Poatrephes*).

Ectopocynus

Ectopocynus **Fossil range: Early Oligocene–Early Miocene**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Carnivora
Family:	Canidae
Subfamily:	†Hesperocyoninae
Genus:	†***Ectopocynus*** Wang, 1994
Type species	
†*Ectopocynus simplicidens*	
Species	
†*E. antiquus* †*E. intermedius* †*E. simplicidens*	

Ectopocynus ("strange dog") is an extinct genus of small bone crushing carnivorous mammal similar to a dog of the family Canidae) which inhabited North America during the Oligocene living from 33.3—16.0 Ma and existed for approximately 17.3 million years.

Though a carnivore, dentition suggests this animal was a hypercarnivore or mesocarnivore.

Taxonomy

Ectopocynus was named by Wang (1994). Its type is Ectopocynus simplicidens. It was assigned to Canidae by Wang (1994) and Munthe (1998). This is kinnndaaa gayy...

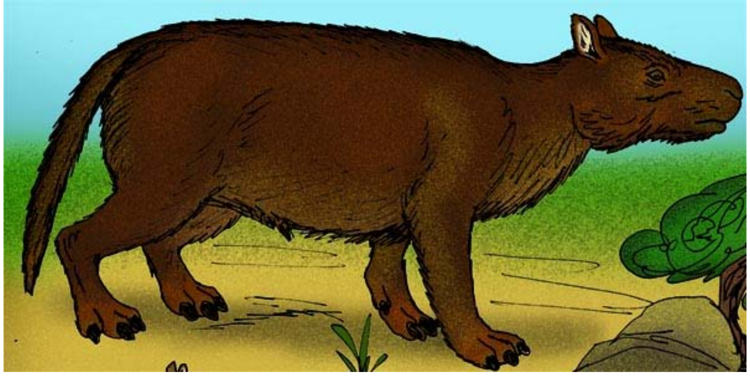
Morphology

Two specimens were examined by Legendre and Roth for body mass. The first specimen was estimated to weigh 16.5 kg (36 lb). The second specimen was estimated to weigh 15.2 kg (34 lb).

Ectopocynus is best described as having simple, robust and blunt yet massive premolars and reduced or lost cusp on lower molars. In this respect, Ectopocynus has many of the characteristics of *Enhydrocyon*. Remains of *Ectopocynus* are limited to mandibles and teeth only.

Eporeodon

Eporeodon
Fossil range: Late Oligocene–Early Miocene



Eporeodon major

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Artiodactyla
Family:	†Merycoidodontidae
Subfamily:	Eporeodontidae
Genus:	***Eporeodon***

Species

- *Eporeodon major*
- *Eporeodon occidentalis*
- *Eporeodon pygmyus*

Eporeodon is an extinct genus of oreodont belonging to the subfamily *Eporeodontidae* during the Oligocene epoch (33.3—20.6 mya) existing for approximately 12.7 million years.

The species of the genus are among the largest members of the family Merycoidontidae. About the size of a cow, its fossils are some of the largest found in the Badlands. It was much larger than *Merycoidodon* and *Miniochoerus*, its contemporaries in the Late

Oligocene. On the other hand, *Eporeodon* was a rare oreodont, as its fossils only make up about one percent of all oreodont fossils found in the Badlands.

Taxonomy

Eporeodon was named by Marsh (1875). It was synonymized subjectively with *Eucrotaphus* by Cope (1884). It was assigned to *Merycoidodontidae* by Marsh (1875), Scott (1890), Thorpe (1921), Thorpe (1937), Stevens and Stevens (1996) and Lander (1998). It's synonymized with *Hypselochoerus* and *Pseudodesmatochoerus*.

Morophólgy

Eporeodon was a tremendous oreodont, growing to be about cow sized. Their skulls were much shorter and squatter than those of *Merycoidodon*, but were longer than those of *Miniochoerus*.

A single specimen was examined by M. Mendoza for body mass and estimated to have a weight of 118.3 kg (260.8 lbs).

Species

E. occidentalis (syn. E. davisi, E. leptacanthus, E. longifrons, E. perbullatus, Eucrotaphus pacificus), *E. pygmyus*.

Eporeodon occidentalis skull

Sister genera

Aclistomycter, *Bathygenys*, *Brachycrus* (syn. *Pronomotherium*), *Desmatochoerus, Hypsiops* (syn. *Pseudomesoreodon, Submerycochoerus*), *Leptauchenia* (syn.

Brachymeryx, Cyclopidius, Hadroleptauchenia, Pithecistes, Pseudocyclopidius), *Limnenetes, Mediochoerus, Merycoides* (syn. *Paramerychyus*), *Merycochoerus*, *Merycoidodon* (syn. *Blickohyus, Genetochoerus, Oreodon, Otionohyus, Paramerycoidodon, Prodesmatochoerus, Promesoreodon, Subdesmatochoerus*), *Mesoreodon, Miniochoerus* (syn. *Parastenopsochoerus, Platyochoerus, Stenopsochoerus*), *Oreodontoides, Oreonetes, Paroreodon* (syn. *Epigenetochoerus*), *Phenacocoelus*, *Sespia*, *Ticholeptus* (syn. *Poatrephes*).

Hemicyonidae

Hemicyonidae
Fossil range: Early Miocene to Pliocene
22–2 Ma

Hemicyon sansaniensis

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Carnivora
Suborder:	Caniformia
Family:	†Hemicyonidae

Genera

- †*Agriotherium*
- †*Dinocyon*
- †*Hemicyon*
- †*Phoberocyon*
- †*Plithocyon*
- †*Zaragocyon*

Hemicyonidae is an extinct family of so-called "dog-bears", literally "Half Dog" (Greek: ἡμικυων/"hemi-kuôn"), bear-like Carnivora living in Europe, North America, Africa and Asia during the Oligocene through Miocene epochs 33.9—5.3 Ma, existing for approximately 28.6 million years.

Morphology

They were about 1.50 m (5 ft) long, 70 centimetres (28 inches) tall, with somewhat tiger-like proportions and dog-like teeth weighing as much as 689.3 kg (1,500 lb).

Hemicyonids are widely accepted to have been hypercarnivorous and highly predaceous. Unlike modern bears, hemicyonids walked on their toes, ie., they were not plantigrade but digitigrade with long metapodials. This suggests that hemicyonids must have been active hunters and a good runners and presumably hunted on the plains, possibly in packs. This also distinguishes them from the plantigrade short metapodials that bears have and gives them a greater affinity to the digitigrade long metapodials like dogs. Note that the hemicyonids are easily confused with the related and often similar-looking "bear-dogs" of the family Amphicyonidae.

Plithocyon armagnacensis skull

Taxonomy

Classification of the hemicyonids has become complicated. Some classifications subdivide the Hemicyonidae into two subfamilies: Phoberocyoninae (including *Phoberocyon* and *Plithocyon*) and Hemicyoninae (including *Zaragocyon*, *Hemicyon* and *Dinocyon*). The earliest known occurrence of the hemicyonids is in Europe from 22.8–20 Ma of Spain: *Phoberocyon hispanicus* from Loranca and *Zaragocyon daamsi* from Cetina de Aragon.

Genus identification

Hemicyonids lived continuously in Europe with the oldest known being Cephalogale existing from ~33.9—20 Ma. In North America specimens have been uncovered which date from ~21.6—21.2 Ma. *Phoberocyon johnhenryi* is yet another old specimen from the large Thomas Farm Site, Florida, (~19–18 Ma). This species of the genus *Phoberocyon* is confirmed by diagnostic features of the lower dentition: posterior accessory cusps in lower premolars and paraconid in m2 and it is a more derived species than *Phoberocyon hispanicus* in that it is larger and has diastemata between the premolars.

All the American hemicyonids are more advanced in character and are assigned to genus *Plithocyon*. They are known from the Barstovian of California, New Mexico, Nebraska, Wyoming and the Love Bone Bed Local Fauna in Florida. In Asia, the earliest hemicyonid is *Phoberocyon youngi* from Shanwang, Shandong (16 Ma) and is very close to the North American *Phoberocyon johnhenry*. The latest occurrence in China is from the Tung-Gur Formation, Nei-Mongol (13 Ma). Dispersal probably occurred from Europe to North America prior to 19 Ma and the American *Plithocyon* is probably a descendant of the *Phoberocyon*.

The genus *Agriotherium* is sometimes considered a member of Hemicyonidae due to the presence of many similar hemicyonine characters (unelongated molars, premasseteric fossa, etc.) and this strongly substantiates its closer affinity with hemicyonines rather than with ursines. *Agriotherium* has its longest history in Asia. The most primitive and earliest form is from a *Hipparion* fauna in Hezheng, Gansu, 9 Ma. All other forms of *Agriotherium* occurred in the Pliocene (5.3 to 2 Ma) in Eurasia and Africa, leaving a hiatus in the record between 9 and 5.3 Ma. In North America, *Agriotherium* appeared suddenly around 7 Ma and probably emigrated from Eurasia. *Agriotherium* fossils have been found at Coffee Ranch, Texas (6.6 Ma); Guymon Local Fauna, Oklahoma; Mount Eden Local Fauna, California; and Old Cabin Quarry, Quiburis Formation (late Hemphillian), Arizona. The occurrence of *Agriotherium* in North and Central America is thus limited to the later half of the Hemphillian (7–5 Ma).

Hemicyonidae fossil evidence may also have been found in the Gaillard Cut Local Fauna, former Panama Canal Zone, Republic of Panama, but it is indeterminant with Amphicyonidae. Despite its close proximity to South America, given the geological context, the Gaillard Cut Local Fauna are distinctly North American fauna and the age of this assemblage is dated between 19.5 and 14 Ma.

Janjucetus

Janjucetus
Fossil range: Late Oligocene

Scientific classification

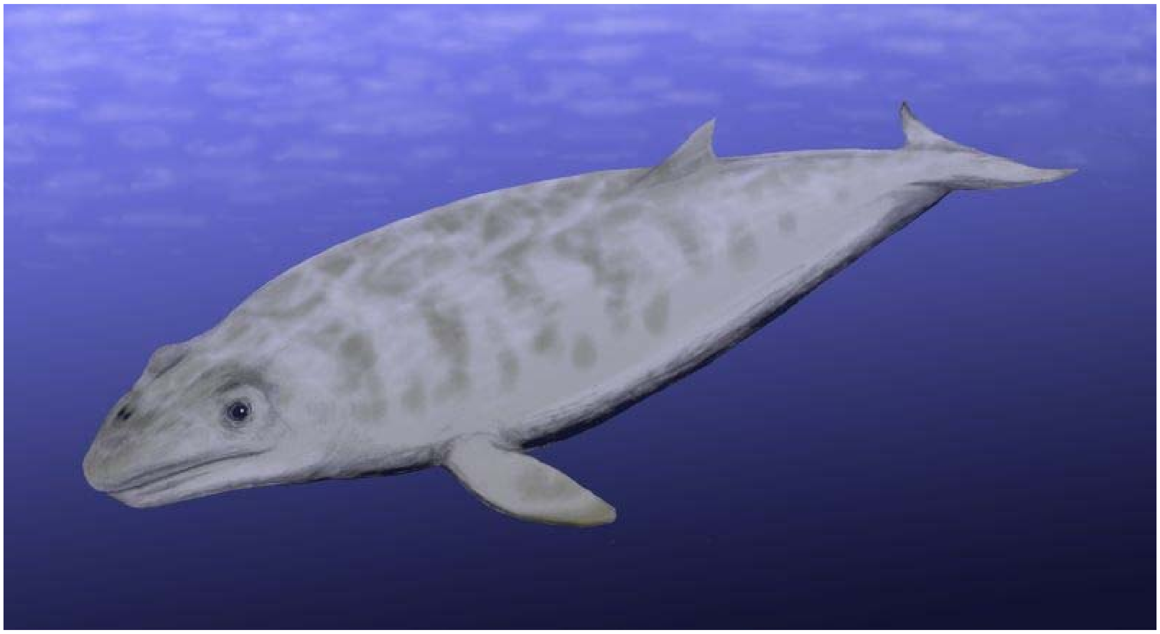
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Cetacea
Suborder:	Mysticeti
Family:	Mammalodontidae
Genus:	***Janjucetus***
Species:	***J. hunderi***

Binomial name

Janjucetus hunderi
Fitzgerald, 2006

Janjucetus is an extinct genus of whale and a basal form of the Mysticeti, a clade which includes the extant baleen whales. The only known species, ***Janjucetus hunderi***, lived during the late Oligocene, about 25 million years ago in coastal seas off southeast Australia. Unlike modern mysticetes, it possessed large teeth for gripping and shredding prey and lacked baleen. *Janjucetus* was likely to have been a raptorial predator that captured large single prey animals rather than bulk-feeding on small organisms in the manner of living baleen whales.

Description



Restoration of *Janjucetus*

Janjucetus is estimated to have been about 3.5 metres (11 ft) in length, about the size of the modern bottlenose dolphin and much smaller than any living baleen whale. It is considered to be a mysticete due to key synapomorphies of the skull anatomy, for example in the way rostral bones meet the bones of the braincase. The relatively short snout tapers anteriorly from a broad base and is triangular in dorsal view. The incisors and canines form a terminal rosette of conical stabbing teeth while the premolars and molars are shaped like serrated blades. The orbits are exceptionally large. There is no evidence *Janjucetus* possessed the ability to echolocate and probably relied on good eyesight to locate its prey.

Janjucetus is considered to be closely related to *Mammalodon*, another genus of toothed mysticete from southeastern Australia. *Janjucetus* was initially assigned to its own monotypic family, Janjucetidae, but a subsequent cladistic analysis by Fitzgerald (2010) transferred it to the Mammalodontidae, making Janjucetidae a jr synonym.

History

The only known fossil of *Janjucetus* was found in the late 1990s by a teenaged surfer named Staumn Hunder, near the Victorian township of Jan Juc. The name *Janjucetus hunderi*, honours both the township and the discoverer. Hunder is said to have seen the brown fossils on a boulder while he surfed. Soon after discovering the site, Hunder and his father removed the boulder and transported it to Monash University for further research. However, until Erich Fitzgerald started long-term research on the fossils in 2003, little had been established about the whale remains. Fitzgerald first published his findings in the journal, *Proceedings of the Royal Society B.*

The well-preserved fossil remains include a nearly complete skull, mandibles, vertebrae, ribs, scapulae and a radius. They are held in the Museum Victoria Palaeontology Collection in Melbourne, Australia. The holotype of *Janjucetus* represents the most complete Paleogene cetacean fossil from Australia.

Leptocyon

Leptocyon **Fossil range: Oligocene–Miocene**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Carnivora
Family:	Canidae
Subfamily:	Caninae
Genus:	†***Leptocyon***
Species	

- †*L. gregorii*
- †*L. vafer*
- †*L. vulpinus*

Fossil range of Leptocyon species.

Leptocyon is a small extinct genus of canidae endemic to North America during the Oligocene through Miocene living from 24.8—10.3 mya, existing for approximately 15.5 million years.

Leptocyon was a small bodied, fox-like animal with a slender jaw.

Taxonomy

Leptocyon was named by Matthew (1918). It was synonymized subjectively with Vulpes by Gregory (1942); it was revalidated by Webb (1969), Carroll (1988) and Munthe (1998). It was assigned to Canidae by Matthew (1918), Webb (1969), Carroll (1988) and Munthe (1998).

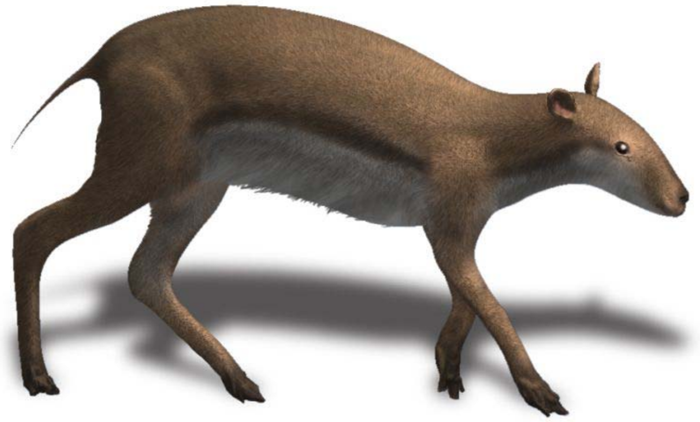
Morphology

Body mass

Two specimens were examined by Legendre and Roth. Estimating the body mass of these two with both weighing an estimated 3.26 kg (7.2 lb)

Leptomeryx

Leptomeryx
Fossil range: middle Eocene to early Miocene



Scientific classification

Kingdom:	Animalia

Phylum:	Chordata
Class:	Mammalia
Order:	Artiodactyla
Family:	†Leptomerycidae
Genus:	†***Leptomeryx*** Leidy, 1853
Type species	
	†*Leptomeryx evansi*
Species	

- †*L. blacki*
- †***L. evansi***
- †*L. mammifer*
- †*L. obliquidens*
- †*L. speciosus*
- †*L. yoderi*

Leptomeryx evansi skull at the Museum für Naturkunde, Berlin

Leptomeryx is an extinct genus of ruminant of the family Leptomerycidae, endemic to North America during the Eocene through Oligocene 38—24.8 Mya, existing for approximately 13.2 million years.

Taxonomy

Leptomeryx was named by Leidy (1853). Its type is *Leptomeryx evansi*. It was assigned to Leptomerycinae by Matthew (1908); to Hypertragulidae by Cook (1934); and to Leptomerycidae by Leidy (1853) and then by Carroll (1988).

Morphology

Leptomeryx was a small deer-like ruminant with somewhat slender body.

Body mass

Four specimens were examined by Legendre and Roth for body mass.

- Specimen 1 weighed an estimated: 7.62 kg (17 lb)
- Specimen 2: 14.7 kg (32 lb)
- Specimen 3: 6.24 kg (14 lb)
- Specimen 4: 5.72 kg (13 lb)

Fossil distribution

Sites and species recovered:

- Titus Canyon, Inyo County, California *(L.blacki)* ~30.6—33.9 Ma.
- UNSM Sx-8 (Orella C), Sioux County, Nebraska *(L. elissae)* ~33.9—24.8 Ma.
- Anxiety Butte, Saskatchewan, Canada *(L. sp., L. evansi)* ~38—24.8 Ma.
- Calf Creek, Saskatchewan, Canada, *(L. mammifer)* ~38—33.3 Ma.
- Toadstool Park, Sioux County, Nebraska *(L. speciosus)* ~37.2—33.3 Ma.
- Medicine Pole Hills, Bowman County, North Dakota *(L. yoderi)* ~38—33.9 Ma