Encyclopedia of

Megafauna and Dinosaurs

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Chapter 1

Megafauna

The African bush elephant, Earth's largest living land animal

In terrestrial zoology, **megafauna** are "giant", "very large" or "large" animals. Their original and most common definition is 100 lb, often rounded in the metric system to 40 or 45 kg. This thus includes many species not popularly thought of as overly large, such as white-tailed deer and red kangaroo, as well as humans.

In practice the most common usage encountered in academic and popular writing describes land animals roughly larger than a human which are not (solely) domesticated. The term is especially associated with the Pleistocene megafauna — the giant and very large land animals considered archetypical of the last ice age such as mammoths. It is also commonly used for the largest extant wild land animals, especially elephants, giraffes, hippopotamuses, rhinoceroses, elk, condors, etc. Megafauna may be subcategorized by their trophic position into megaherbivores (e.g. elk), megacarnivores (e.g. lions), and more rarely, megaomnivores (e.g. bears).

Other common uses are for giant aquatic species, especially whales, any larger wild or domesticated land animals such as larger antelope and cattle, and dinosaurs and other extinct giant reptilians.

The term is also sometimes applied to animals (usually extinct) of great size *relative to* a more common or surviving type of the animal, for example the 1 m (3 ft) dragonflies of the Carboniferous period.

Ecological strategy

Megafauna — in the sense of the largest mammals and birds — are generally K-strategists, with great longevity, slow population growth rates, low death rates, and few or no natural predators capable of killing adults. These characteristics, although not exclusive to such megafauna, make them highly vulnerable to human over-exploitation.

Mass extinctions

A well-known mass extinction of megafauna, the Holocene extinction occurred at the end of the last ice age glacial period (a.k.a. the Würm glaciation) and wiped out many giant ice age animals, such as woolly mammoths, in the Americas and northern Eurasia. Various theories have attributed the wave of extinctions to human hunting, climate change, disease, a putative extraterrestrial impact, or other causes. However, this extinction pulse near the end of the Pleistocene was just one of a series of megafaunal extinction pulses that have occurred during the last 50,000 years over much of the Earth's surface, with Africa and southern Asia being largely spared. (The latter areas did suffer a gradual attrition of megafauna, particularly of the slower-moving species, over the last several million years.) Outside of Eurasia, these megafaunal extinctions followed a distinctive landmass-by-landmass pattern that closely parallels the spread of humans into previously uninhabited regions of the world, and which shows no correlation with climate. Australia was struck first around 50,000 years ago, followed by the Solomon Islands 30,000 years ago, the Americas 13,000 years ago, Cyprus 9000 years ago, the Antilles 6000 years ago, New Caledonia 3000 years ago, Madagascar 2000 years ago, New Zealand 800 years ago, the Mascarenes 400 years ago, and the Commander Islands 250 years ago. Nearly all of the world's isolated islands could furnish examples of extinctions occurring shortly after the arrival of *Homo sapiens*, though most of these islands, such as the Hawaiian Islands, never had terrestrial megafauna, so their extinct fauna were smaller.

Continuing human hunting and environmental disturbance has led to additional megafaunal extinctions in the recent past, and has created a serious danger of further extinctions in the near future.

A number of other mass extinctions occurred earlier in Earth's geologic history, in which some or all of the megafauna of the time also died out. Famously, in the Cretaceous–Tertiary extinction event the dinosaurs and most other giant reptilians were eliminated. However, the earlier mass extinctions were more global and not so selective for megafauna; i.e., many species of other types, including plants, marine invertebrates and plankton, went extinct as well. Thus, the earlier events must have been caused by more generalized types of disturbances to the biosphere.

Effect of megafaunal extinctions on methane emissions

Many herbivores produce methane as a byproduct of foregut fermentation in digestion, and release it through belching. Large populations of herbivore megafauna have the potential to contribute greatly to the atmospheric concentration of methane, which is an important greenhouse gas. Today, around 20% of annual methane emissions come from livestock methane release. Recent studies have indicated that the extinction of megafaunal herbivores may have caused a reduction in atmospheric methane. This hypothesis is relatively new.

Several studies have examined the effect of elimination of megaherbivorous mammals on methane emissions. One study examined the methane emissions from the bison that occupied the Great Plains of North America before contact with European settlers. The study estimated that the removal of the bison caused a decrease of 2.2 Tg/yr. This is a proportionally large change for the time period.

Another study examined the change of methane concentration in the atmosphere at the end of the Pleistocene epoch after the extinction of megafauna in the Americas. After early humans migrated to the Americas ~13,000 BP, their hunting and other associated ecological impacts led to the extinction of many megafaunal species in the region. Calculations suggest that this extinction decreased methane production by ~9.6 Tg/yr. Ice core records support this hypothesis of rapid methane decrease during the time period. This suggests that the absence of megafaunal methane emissions may have contributed to the abrupt climatic cooling at the onset of the Younger Dryas.

Examples

The following are some notable examples of animals often considered as megafauna (in the sense of the "large animal" definition). This list is not intended to be exhaustive:

class Mammalia

- infraclass Metatheria
    - order Diprotodontia
        - The red kangaroo (*Macropus rufus*) is the largest living Australian mammal and marsupial at a weight of up to 85 kg (187 lb). However, its extinct relative, the giant short-faced kangaroo *Procoptodon goliah* reached 230 kg (510 lb), while extinct diprotodonts attained the largest size of any marsupial in history, up to an estimated 2,750 kg (6,060 lb). The extinct marsupial lion (*Thylacleo carnifex*), at up to 160 kg (350 lb) was much larger than any extant carnivorous marsupial.
- infraclass Eutheria
    - superorder Afrotheria
        - order Proboscidea
            - Elephants are the largest living land animals. They and their relatives arose in Africa, but until recently had a nearly worldwide distribution. The African bush elephant (*Loxodonta africana*) has a shoulder height of up to 4.3 m (14 ft) and weighs up to 13 tons. Among recently extinct proboscideans, mammoths (*Mammuthus*) were close relatives of elephants, while mastodons (*Mammut*) were much more distantly related. The Songhua River mammoth (*M. sungari*) is estimated to have weighed 17 tonnes, making it the largest proboscid and second largest land mammal after indricotherines.

order Sirenia

- The largest sirenian at up to 1500 kg is the West Indian manatee (*Trichechus manatus*). Steller's sea cow (*Hydrodamalis gigas*) was probably around five times as massive, but unfortunately was exterminated by humans within 27 years of its discovery off the remote Commander Islands in 1741. In prehistoric times this sea cow also lived along the coasts of northeastern Asia and northwestern North America; it was apparently eliminated from these more accessible locations by aboriginal hunters.

superorder Xenarthra

- order Cingulata

    - The glyptodonts were a group of large, heavily armored ankylosaur-like xenarthrans related to living armadillos. They originated in South America, invaded North America during the Great American Interchange, and went extinct at the end of the Pleistocene epoch.
- order Pilosa
    - Ground sloths were another group of slow, terrestrial xenarthrans, related to modern tree sloths. They had a similar history, although they reached North America earlier, and spread farther north. The largest genera, *Megatherium* and *Eremotherium*, reached sizes comparable to elephants.
        - superorder Euarchontoglires
            - order Primates
            - The largest living primate, at up to 266 kg (586 lb), is the gorilla (*Gorilla beringei* and *Gorilla gorilla*, with three of four subspecies being critically endangered). The extinct Malagasy sloth lemur *Archaeoindris* reached a similar size, while the extinct *Gigantopithecus blacki* of Southeast Asia is believed to have been several times larger. Some populations of archaic *Homo* were significantly larger than recent *Homo sapiens*; for example, *Homo heidelbergensis* in southern Africa may have commonly reached 7 feet in height, while Neanderthals were about 30% more massive.

order Rodentia

- The extant capybara (*Hydrochoerus hydrochaeris*) of South America, the largest living rodent, weighs up to 65 kg (140 lb). Several recently extinct North American forms were larger: the capybara *Neochoerus pinckneyi* (another neotropic migrant) was about 40% heavier; the giant beaver (*Castoroides ohioensis*) was similar. The extinct blunt-toothed giant hutia (*Amblyrhiza inundata*) of several Caribbean islands may have been larger still. However, several million years ago South America harbored much more massive rodents. *Phoberomys pattersoni*, known from a nearly full skeleton, probably reached 700 kg (1,543 lb). Fragmentary remains suggest that *Josephoartigasia monesi* grew to upwards of 1,000 kg (2,200 lb).

superorder Laurasiatheria

- order Carnivora
    - Big cats include the tiger (*Panthera tigris*) and lion (*Panthera leo*). The largest subspecies, at up to 306 kg, is the Siberian tiger (*P. tigris altaica*), in accord with Bergmann's rule. Members of *Panthera* are distinguished by morphological features which enable them to roar. Larger extinct felids include the American lion (*Panthera leo atrox*) and the South American saber-toothed cat *Smilodon populator*.

- Bears are large carnivorans of the caniform suborder. The largest living forms are the polar bear (*Ursus maritimus*), with a body weight of up to 680 kg (1,500 lb), and the similarly sized Kodiak bear (*Ursus arctos middendorffi*), again consistent with Bergmann's rule. The extinct giant short-faced bear of North America (*Arctodus simus*) was the largest fully terrestrial mammalian carnivore of the late Pleistocene, reaching 1,136 kg (2,504 lb). *Ursus maritimus tyrannus*, a very large extinct subspecies of polar bear, may have attained comparable average body weights (1200 kg or more).

    - Seals, sea lions, and walruses are amphibious marine carnivorans that evolved from bearlike ancestors. The southern elephant seal (*Mirounga leonina*) of Antarctic and subantarctic waters is the largest carnivoran of all time, with bull males reaching a maximum length of 6–7 m (20–23 ft) and maximum weight of 5,000 kilograms.

- order Perissodactyla

    - Tapirs are browsing animals, with a short prehensile snout and pig-like form that appears to have changed little in 20 million years. They inhabit tropical forests of Southeast Asia and South and Central America, and include the largest surviving land animals of the latter two regions. There are four species.
    - Rhinoceroses are odd-toed ungulates with horns made of keratin, the same type of protein composing hair. They are among the largest living land mammals after elephants (hippos attain a similar size). Three of five extant species are critically endangered. Their extinct central Asian relatives the indricotherines were the largest terrestrial mammals of all time.

- order Artiodactyla (or cladistically, Cetartiodactyla)

    - Giraffes (*Giraffa camelopardalis*) are the tallest living land animals, reaching heights of up to nearly 6 m (20 ft).

- Bovine ungulates include the largest surviving land animals of Europe and North America. The water buffalo (*Bubalis arnee*), bison (*Bison bison* and *B. bonasus*), and gaur (*Bos gaurus*) can all grow to weights of over 900 kg (1,984 lb).

    - The semiaquatic hippopotamus (*Hippopotamus amphibius*) is the heaviest living even-toed ungulate; it and the critically endangered pygmy hippo (*Choeropsis liberiensis*) are believed to be the closest extant relatives of cetaceans.

order Cetacea (or cladistically, Cetartiodactyla)

- Whales, dolphins, and porpoises are marine mammals. The blue whale (*Balaenoptera musculus*) is the largest baleen whale and the largest animal that has ever lived. The sperm whale (*Physeter macrocephalus*) is the largest toothed whale, as well as the planet's loudest and brainiest animal (with a brain about five times as massive as a human's). The killer whale (*Orcinus orca*) is the largest dolphin.

- class Aves (phylogenetically, a clade within Coelurosauria, a taxon within the order Saurischia of the clade Sauropsida; see below)
  - order Struthioniformes
    - The ratites are an ancient and diverse group of flightless birds that are found on fragments of the former supercontinent Gondwana. The largest living bird, the Ostrich (*Struthio camelus*) was surpassed by the extinct *Aepyornis* of Madagascar, the heaviest of the group, and the extinct giant moa (*Dinornis*) of New Zealand, the tallest, growing to heights of 3.4 m (11 ft). The latter two are examples of island gigantism.
  - order Anseriformes
    - Extinct dromornithids of Australia such as *Dromornis* may have exceeded the largest ratites in size. (Due to its small size for a continent and its isolation, Australia is sometimes viewed as the world's largest island; thus, these species could also be considered insular giants.)
- class Reptilia (or cladistically, Sauropsida)
  - order Crocodilia
    - Alligators and crocodiles are large semiaquatic reptiles, the largest of which, the saltwater crocodile (*Crocodylus porosus*), can grow to a weight of 1,360 kg (3,000 lb). Crocodilians' distant ancestors and their kin, the crurotarsans, dominated the world in the late Triassic, until the Triassic–Jurassic extinction event allowed dinosaurs to overtake them. They remained diverse during the later Mesozoic, when crocodyliforms such as *Deinosuchus* and *Sarcosuchus* reached lengths of 12 m. Similarly large crocodilians, such as *Mourasuchus* and *Purussaurus*, were present as recently as the Miocene in South America.
  - order Saurischia
    - Saurischian dinosaurs of the Jurassic and Cretaceous include sauropods, the longest (at up to 40 m or 130 ft) and most massive terrestrial animals known (*Argentinosaurus* reached 80–100 metric tonnes, or 90–110 tons), as well as theropods, the largest terrestrial carnivores (*Spinosaurus* grew to 7–9 tonnes).
  - order Squamata
    - While the largest extant lizard, the Komodo dragon (*Varanus komodoensis*), another island giant, can reach 3 m (10 ft) in length, its extinct Australian relative *Megalania* may have reached more than twice that size. These monitor lizards' marine relatives, the mosasaurs, were apex predators in late Cretaceous seas.
    - The heaviest extant snake is considered to be the green anaconda (*Eunectes murinus*), while the reticulated python (*Python

reticulatus), at up to 8.7 m or more, is considered the longest. An extinct Australian Pliocene species of *Liasis*, the Bluff Downs giant python, reached 10 m, while the Paleocene *Titanoboa* of South America reached lengths of 12–15 m and an estimated weight of about 1135 kilograms (2500 lb).

- order Testudines
  - The largest turtle is the critically endangered marine leatherback turtle (*Dermochelys coriacea*), weighing up to 900 kg (2,000 lb). It is distinguished from other sea turtles by its lack of a bony shell. The most massive terrestrial chelonians are the giant tortoises of the Galápagos Islands (*Chelonoidis nigra*) and Aldabra Atoll (*Aldabrachelys gigantea*), at up to 300 kg (660 lb). These tortoises are the biggest survivors of an assortment of giant tortoise species that were widely present on continental landmasses and additional islands during the Pleistocene.

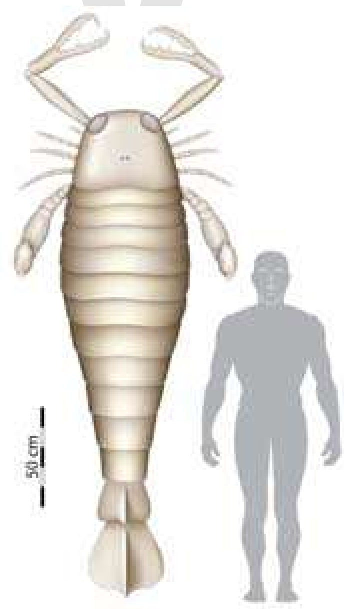
- class Amphibia
  - order Temnospondyli
    - The Permian temnospondyl *Prionosuchus*, the largest amphibian known, reached 9 m in length and was an aquatic predator resembling a crocodilian. After the appearance of real crocodilians, temnospondyls such as *Koolasuchus* (5 m long) had retreated to the Antarctic region by the Cretaceous, before going extinct.
- class Actinopterygii
  - order Tetraodontiformes
    - The largest extant bony fish is the ocean sunfish (*Mola mola*), whose average adult weight is 1,000 kg (2,200 lb). While phylogenetically a "bony fish", its skeleton is primarily cartilage (which is lighter than bone). It has a disk-shaped body, and propels itself with its long, thin dorsal and anal fins; it feeds primarily on jellyfish. In these three respects (as well as in its size and diving habits), it resembles a leatherback turtle.
  - order Acipenseriformes
    - The critically endangered beluga (European sturgeon, *Huso huso*) at up to 1476 kg (3250 lb) is the largest sturgeon (which are also mostly cartilaginous) and is considered the largest anadromous fish.
  - order Siluriformes
    - The critically endangered Mekong giant catfish (*Pangasianodon gigas*), at up to 293 kg (646 lb), is often viewed as the largest freshwater fish.
- class Chondrichthyes
  - order Lamniformes
    - The largest living predatory fish, the great white shark (*Carcharodon carcharias*), reaches weights up to 2,240 kg (4,940 lb). Its extinct relative *C. megalodon* (the disputed genus being either *Carcharodon* or *Carcharocles*) was more than an

order of magnitude larger, and is the largest predatory shark or fish of all time; it preyed on whales and other marine mammals.

- order Orectolobiformes
  - The largest extant shark, cartilaginous fish, and fish overall is the whale shark (*Rhincodon typus*), which reaches weights in excess of 21.5 tonnes (47,000 lb). Like baleen whales, it is a filter feeder and primarily consumes plankton.
- order Rajiformes
  - The manta ray (*Manta birostris*) is another filter feeder and the largest ray, growing to up to 2300 kg.

- class Cephalopoda
  - order Teuthida
    - A number of deep ocean creatures exhibit abyssal gigantism. These include the giant squid (*Architeuthis*) and colossal squid (*Mesonychoteuthis hamiltoni*); both (although rarely seen) are believed to attain lengths of 12 m (39 ft) or more. The latter is the world's largest invertebrate, and has the largest eyes of any animal. Both are preyed upon by sperm whales.

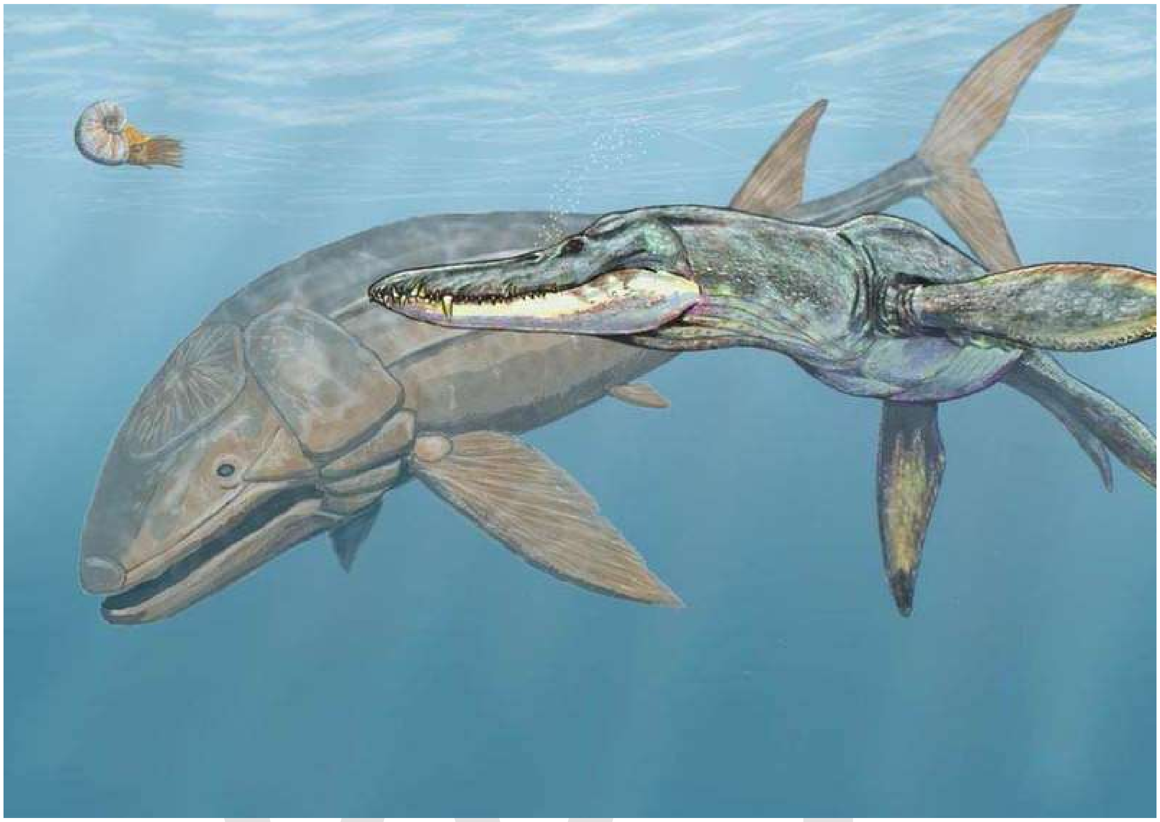
Extinct



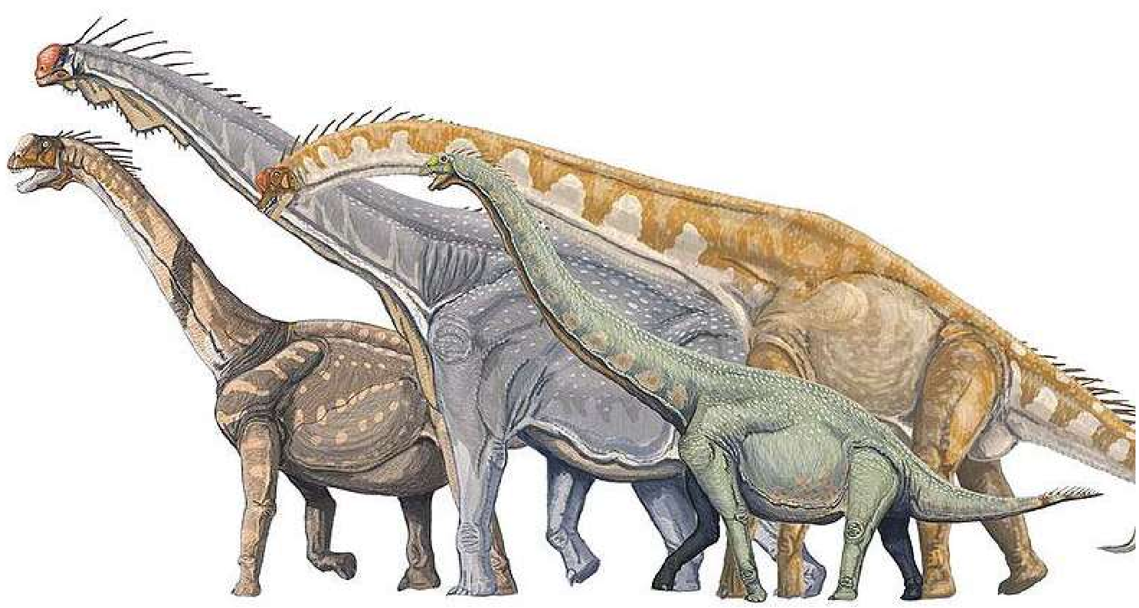
Jaekelopterus was a Devonian sea scorpion and likely an ambush predator.

Dunkleosteus was a gigantic, 10 m (33 ft) long predatory Devonian placoderm fish.

Sail-backed pelycosaur *Dimetrodon* and temnospondyl *Eryops* from North America's Permian.



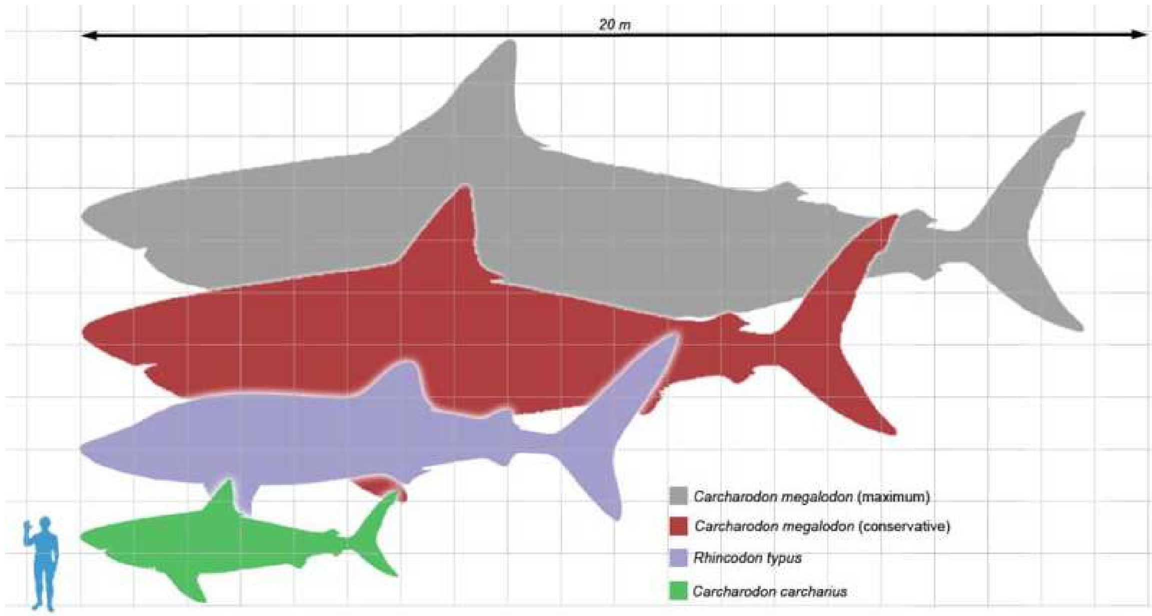
Pliosaur *Liopleurodon* (right) harassing the filter feeder fish *Leedsichthys* during the Jurassic.



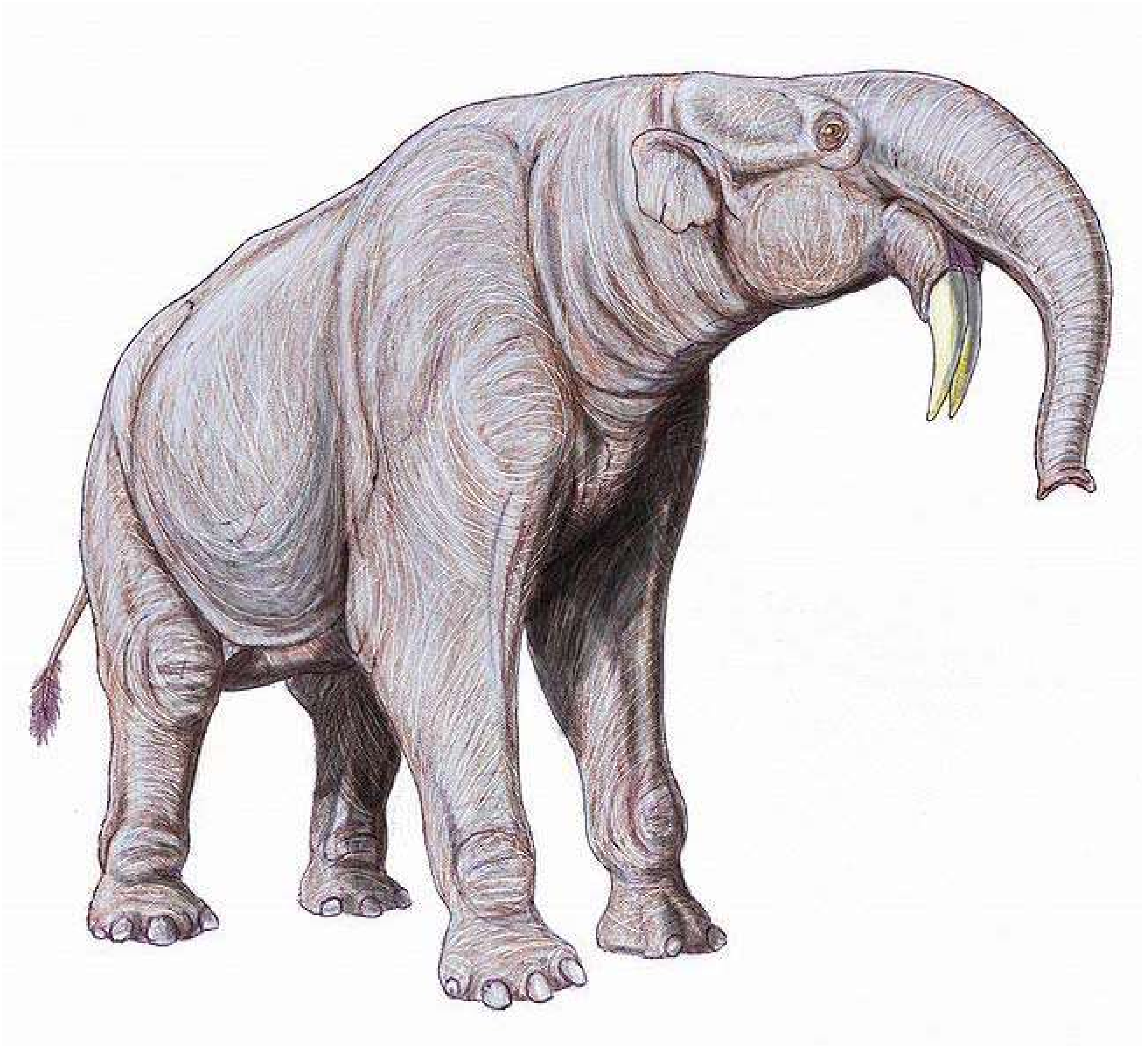
Macronarian sauropods; from left, *Camarasaurus*, *Brachiosaurus*, *Giraffatitan*, *Euhelopus*.

Indricotheres, the land mammals closest to sauropods in size and lifestyle, were rhinos.

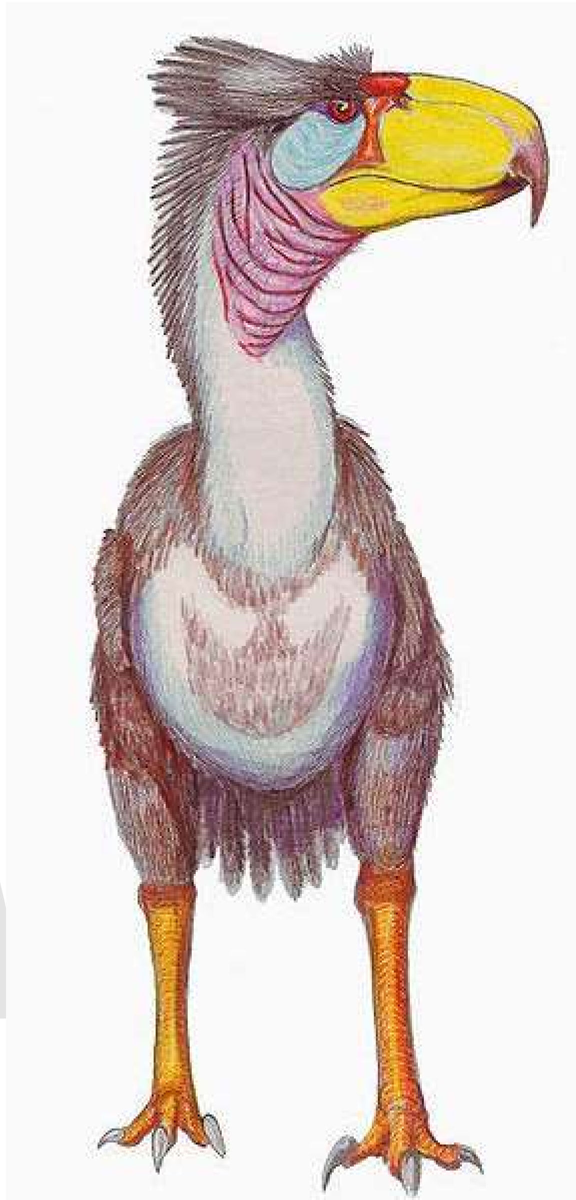
The Late Miocene teratorn *Argentavis* of South America had an 8 m (26 ft) wingspan.



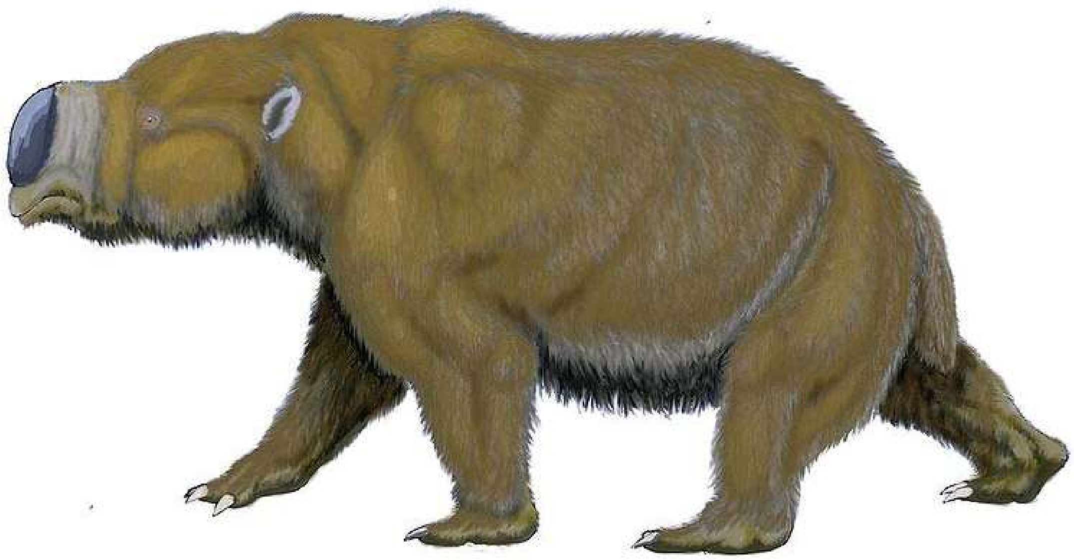
C. megalodon with a whale shark, great white shark and a human for scale.



Deinotherium had downward-curving tusks and ranged widely over Afro-Eurasia.



Titanis walleri, the most recent terror bird and the only one known to have invaded North America.



Hippo-sized *Diprotodon* of Australia, the largest marsupial of all time, went extinct 40,000 years ago.

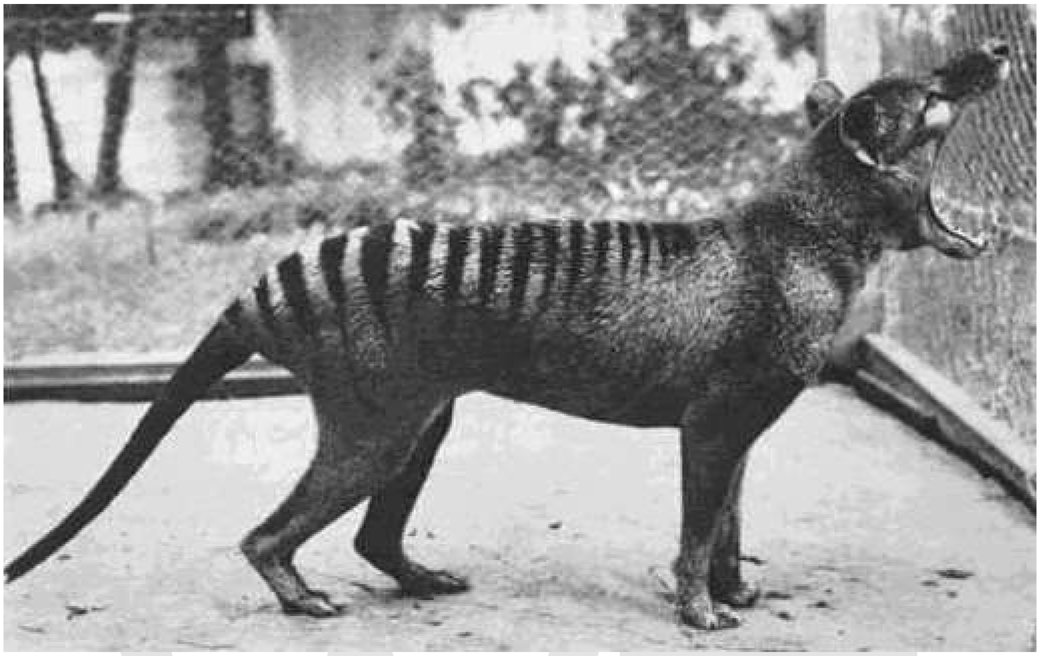
Elephant-sized *Megatherium*, from South America's Pleistocene, was the largest sloth.

Toxodon, one of South America's largest and last notoungulates. It had a relative in Mexico.

American lions exceeded extant lions in size and ranged over two continents until 10,000 BP.

Woolly mammoths vanished shortly after *Homo sapiens* invaded their habitat.

Haast's Eagle, the largest eagle known, attacking moa (which included the tallest bird known).



The Tasmanian thylacine was the largest carnivorous marsupial of modern times.

Living

The gorilla is the largest and one of the most endangered primates on the planet.

Siberian tigers are the biggest living cats, exemplifying Bergmann's rule.

Polar bears, the largest bears and semi-aquatic carnivores, are vulnerable to global warming.

The critically endangered black rhinoceros, up to 14 feet long, is threatened by poaching.

Wild Bactrian camels are critically endangered. Their ancestors originated in North America.

Unlike woolly rhinos and mammoths, muskoxen narrowly survived the Holocene extinction.

Hippos, the heaviest and most aquatic even-toed ungulates, are whales' closest living relatives.

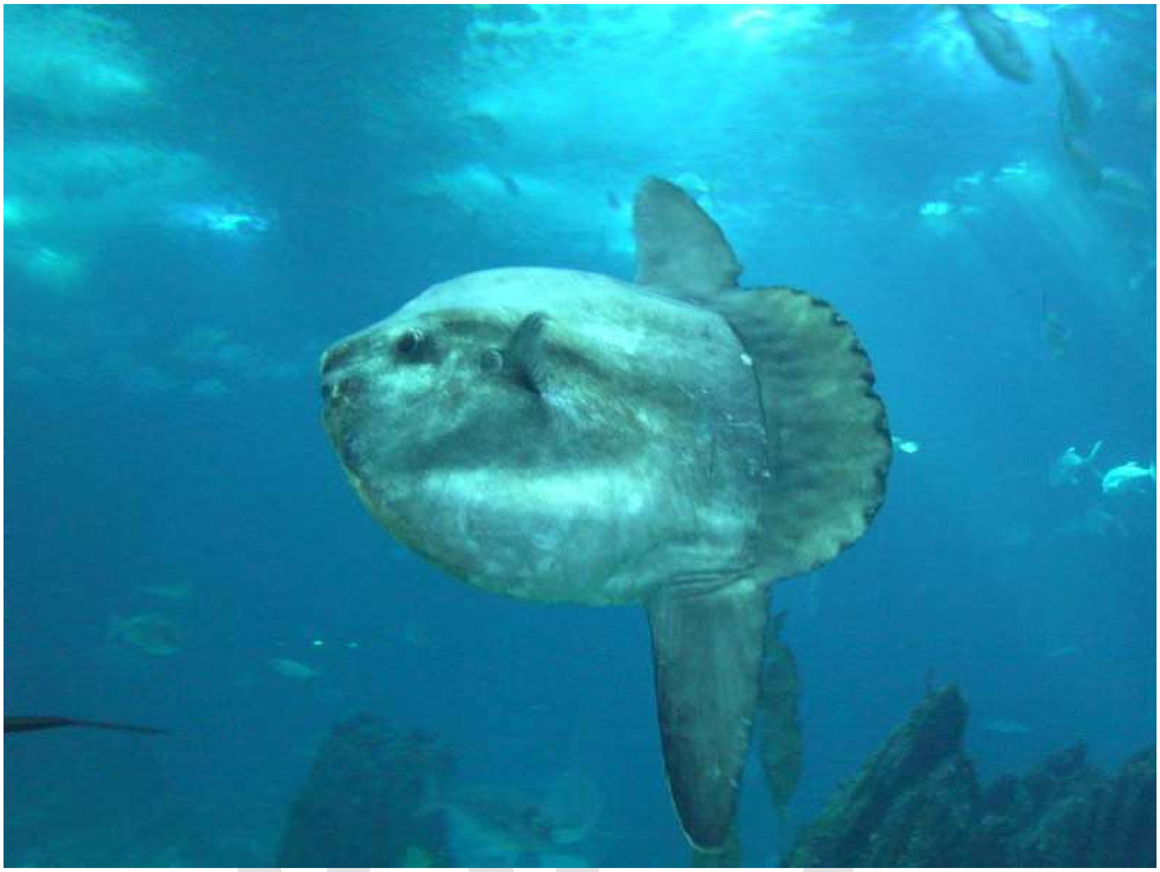
The orca, the largest dolphin and pack predator, is highly intelligent and lives in complex societies.

The Ostrich is the largest ratite, the heaviest living bird, and, at 70 km/h, the fastest running bird.

The saltwater crocodile is the largest living reptile and a dangerous predator of humans.

The Komodo dragon, an insular giant, is the largest lizard and has infectious and venomous saliva.

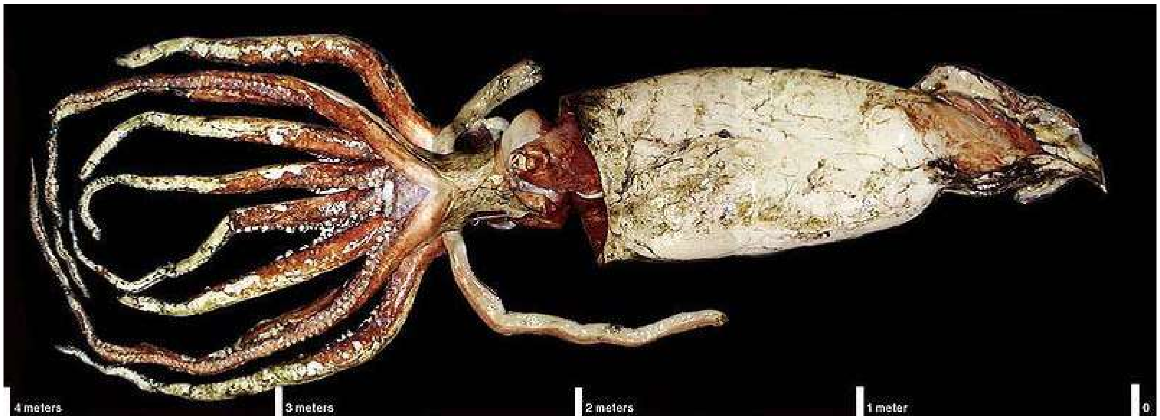
The green anaconda, an aquatic constrictor, is the heaviest snake, weighing up to 97.5 kg (215 lb).



The deep-diving ocean sunfish is the largest bony fish, but its skeleton is mostly cartilaginous.

The manta ray, a filter feeder, is the largest ray at up to 7.6 m across, yet can breach clear of the water.

The Nile perch is one of the largest freshwater fish, as well as a damaging invasive species.



The giant squid is an abyssal giant and the second largest cephalopod.

Chapter 2

Basking Shark

Basking shark
Temporal range: Early Oligocene–Present

Conservation status

Vulnerable (IUCN 3.1)

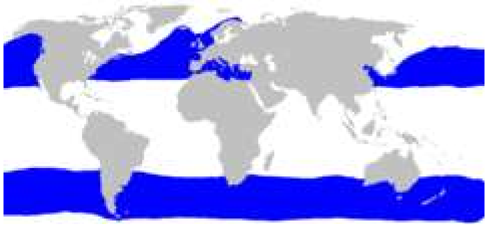
Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Chondrichthyes
Subclass:	Elasmobranchii
Order:	Lamniformes
Family:	**Cetorhinidae** Gill, 1862

Genus:	***Cetorhinus*** Blainville, 1816
Species:	***C. maximus***

Binomial name

Cetorhinus maximus
(Gunnerus, 1765)



Range of the basking shark

Synonyms

Cetorhinus blainvillei Capello, 1869
Cetorhinus maximus infanuncula Deinse & Adriani, 1953
Cetorhinus normani Siccardi, 1961
Hannovera aurata van Beneden, 1871
*Halsydrus pontoppidiani** Neill, 1809
Polyprosopus macer Couch, 1862
*Scoliophis atlanticus** Anonymous, 1817
Selachus pennantii Cornish, 1885
*Squalis gunneri** Blainville, 1816
*Squalis shavianus** Blainville, 1816
Squalus cetaceus Gronow, 1854
Squalus elephas Lesueur, 1822
Squalus gunnerianus Blainville, 1810
Squalus homianus Blainville, 1810
Squalus isodus Macri, 1819
Squalus maximus Gunnerus, 1765
Squalus pelegrinus Blainville, 1810
Squalus rashleighanus Couch, 1838
*Squalus rhinoceros** DeKay, 1842
Squalus rostratus Macri, 1819
*Tetraoras angiova** Rafinesque, 1810
*Tetroras angiova** Rafinesque, 1810
Tetroras maccoyi Barrett, 1933

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* ambiguous synonym

The **basking shark** (*Cetorhinus maximus*) is the second largest living shark, after the whale shark. It is a cosmopolitan species, found in all the world's temperate oceans. It is a slow moving and generally harmless filter feeder.

Taxonomy

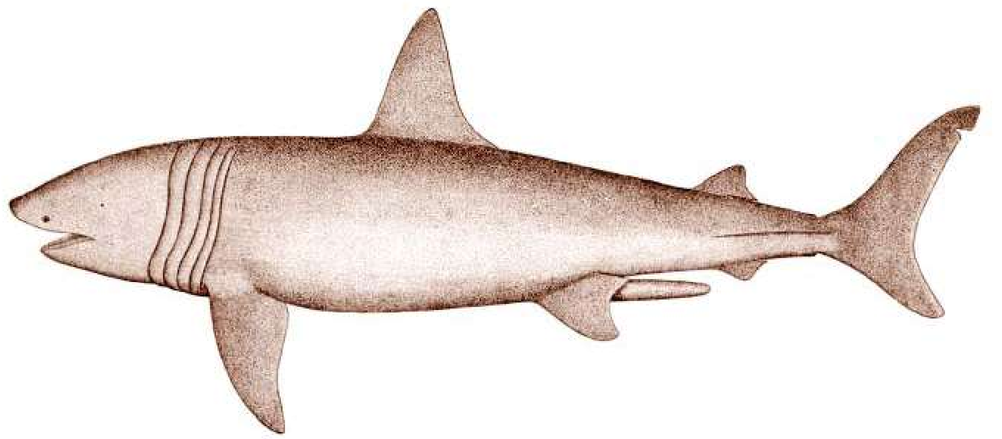
This shark is called the *basking* shark because it is most often observed when feeding at the surface and appears to be basking in the warmer water there. It is the only member of the family Cetorhinidae, part of the mackerel shark order Lamniformes. Gunnerus was the first to describe and name the species *Cetorhinus maximus* from a specimen found in Norway. The genus name *Cetorhinus* comes from the Greek, *ketos* which means marine monster or whale and *rhinos* meaning nose, the species name *maximus* is from Latin and means "greatest". The following centuries featured more attempts at naming: *Squalus isodus*, in 1819 by Macri; *Squalus elephas*, by Lesueur in 1822; *Squalus rashleighanus*, by Couch in 1838; *Squalus cetaceus*, by Gronow in 1854; *Cetorhinus blainvillei* by Capello in 1869; *Selachus pennantii*, by Cornish in 1885; *Cetorhinus maximus infanuncula*, by Deinse & Adriani 1953; and finally *Cetorhinus maximus normani*, by Siccardi 1961.

Range and habitat

The basking shark is a coastal-pelagic shark found worldwide in boreal to warm-temperate waters around the continental shelves. It prefers 8 to 14.5 °C (46 to 58 °F) temperatures, but recently has been confirmed to cross the much-warmer waters at the equator. It is often seen close to land, including bays with narrow openings. The shark follows plankton concentrations in the water column and is therefore often visible at the surface. They characteristically migrate with the seasons. The basking shark is found from the surface down to at least 910 metres (2,990 ft).

Anatomy and appearance

The largest accurately-measured specimen was trapped in a herring net in the Bay of Fundy, Canada in 1851. Its total length was 12.27 metres (40.3 ft), and it weighed an estimated 19 short tons (17 t). There are dubious reports from Norway of three basking sharks over 12 metres (39 ft), the largest at 13.7 metres (45 ft), dubious because few anywhere near that size have been caught in the area since. Normally the basking shark reaches a length of between 6 metres (20 ft) and a little over 8 metres (26 ft). Some specimens surpass 9–10 metres (30–33 ft), but after years of large-scale fishing, specimens of this size have become rare.



Male basking shark

They possess the typical shark lamniform body plan and have been mistaken for great white sharks. The two species can be easily distinguished, however, by the basking shark's cavernous jaw, up to 1 metre (3 ft 3 in) in width, longer and more obvious gill slits that nearly encircle the head and are accompanied by well-developed gill rakers, smaller eyes, and smaller average girth. Great whites possess large, dagger-like teeth, basking shark teeth are much smaller 5–6 millimetres (0.20–0.24 in) and hooked; only the first 3 or 4 rows of the upper jaw and 6 or 7 rows of the lower jaw function. There are also several behavioral differences between the two.

Other distinctive characteristics include a strongly keeled caudal peduncle, highly textured skin covered in placoid scales and a mucus layer, a pointed snout—distinctly hooked in younger specimens—and a lunate caudal fin. In large individuals the dorsal fin may flop to one side when above the surface. Coloration is highly variable (and likely dependent on observation conditions and the individual's condition: commonly, the coloring is dark brown to black or blue dorsally fading to a dull white ventrally. The sharks are often noticeably scarred, possibly through encounters with lampreys or cookiecutter sharks. The basking shark's liver, which may account for 25% of its body weight, runs the entire length of the abdominal cavity and is thought to play a role in buoyancy regulation and long-term energy storage.

Life history

Head of a basking shark

Studies in 2003 proved that basking sharks do not hibernate, showing that they are active year-round. In winter, basking sharks move to depths of up to 900 metres (3,000 ft) to feed on deep water plankton.

Migration

Satellite tagging confirms that basking sharks move thousands of kilometres during the winter months, seeking plankton blooms. It also found that basking sharks shed and renew their gill rakers in an ongoing process, rather than over one short period.

A 2009 study tagged 25 sharks off the coast of Cape Cod, Massachusetts, and indicated that at least some individuals migrate south in the winter. Remaining at depths between 200 metres (660 ft) and 1,000 metres (3,300 ft) for many weeks, the tagged sharks crossed the equator to reach Brazil. One individual spent a month near the mouth of the Amazon River. It is unknown why they undertake this journey. Lead author Gregory Skomal of the Massachusetts Division of Marine Fisheries, suspects it may be related to reproduction.

They are slow-moving sharks (feeding at about 2 knots (3.7 km/h; 2.3 mph) and do not evade approaching boats (unlike great white sharks). They are harmless to humans if left alone and are not attracted to chum.

Even though the basking shark is large and slow, it can breach, jumping entirely out of the water. This behavior could be an attempt to dislodge parasites or commensals.

Interactions

A basking shark filter feeding.

Basking sharks are social animals and form sex-segregated schools, usually in small numbers (3 or 4) but reportedly up to 100 individuals. Their social behavior is thought to follow visual cues. Although the basking shark's eyes are small, they are fully developed. They may visually inspect boats, possibly mistaking them for conspecifics. Females are thought to seek shallow water to give birth.

Predators

While basking sharks have few if any predators, white sharks have been reported to scavenge on the remains of these sharks. Observers have long suspected that killer whales, also known as orcas, actively pursue and feed on basking sharks; yet, this is based upon the account of only one person, a West Cornwall fisherman who claims to have witnessed a frenzied attack by a killer whale on a large basking shark off Porthcurno more than 50 years ago.

Lampreys are often seen attached to them, although it is unlikely that they are able to cut through the shark's thick skin.

Diet

Basking Shark filter feeding at Dursey Sound

The basking shark is a passive filter feeder, filtering zooplankton, small fish and invertebrates from up to 2,000 short tons (1,800 t) of water per hour. They feed at or close to the surface with their mouths wide open and gill rakers erect. Unlike the megamouth shark and whale shark, the basking shark does not appear to actively seek quarry, but it does possess large olfactory bulbs that may guide it. It relies only on the water that it pushes through its gills by swimming; the megamouth shark and whale shark can suck or pump water through their gills.

Reproduction

Basking sharks are ovoviviparous: the developing embryos first rely on a yolk sac, and there is no placental connection. Their seemingly useless teeth may play a role before birth in helping them feed on the mother's unfertilized ova (a behaviour known as oophagy).

In females, only the right ovary appears to function.

Gestation is thought to span over a year (perhaps 2 or 3 years), with a small though unknown number of young born fully developed at 1.5–2 metres (4 ft 10 in–6 ft 7 in). Only one pregnant female is known to have been caught; she was carrying 6 unborn young. Mating is thought to occur in early summer and birthing in late summer, following the female's movement into shallow waters.

The age of maturity is not known but is thought to be between the ages of 6 and 13 and at a length of 4.6–6 metres (15–20 ft). Breeding frequency is also unknown, but is thought to be 2 to 4 years.

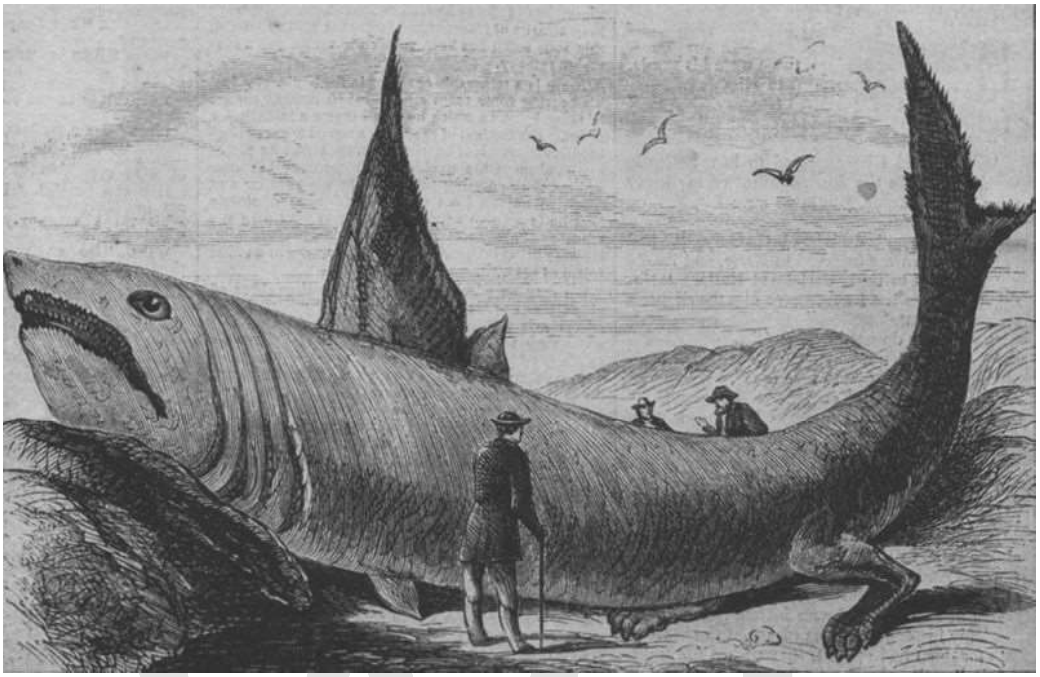
Importance to humans

Historically, the basking shark has been a staple of fisheries because of its slow swimming speed, unaggressive nature and previously abundant numbers. Commercially it was put to many uses: the flesh for food and fishmeal, the hide for leather, and its large liver (which has a high squalene content) for oil. It is currently fished mainly for its fins (for shark fin soup). Parts (such as cartilage) are also used in traditional Chinese medicine and as an aphrodisiac in Japan, further adding to demand.

As a result of rapidly declining numbers, the basking shark has been protected and trade in its products restricted in many countries. It is fully protected in the UK, Ireland, Malta, Florida and US Gulf and Atlantic waters. Targeted fishing for basking sharks is illegal in New Zealand. Once considered a nuisance along the Canadian Pacific coast, basking sharks were the target of a government eradication program there from 1945 to 1970. As of 2008, efforts are underway to determine if any sharks still live in the area and monitor their potential recovery.

It is tolerant of boats and divers approaching it and may even circle divers, making it an important draw for dive tourism in areas where it is common.

Basking sharks and cryptozoology



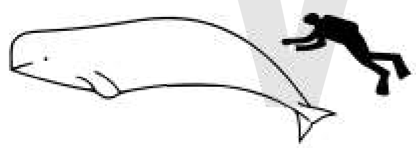
The "wonderful fish" described in *Harper's Weekly* on October 24, 1868, was likely the remains of a basking shark.

On several occasions, "globster" corpses initially thought to be sea serpents or plesiosaurs have later been identified as likely to be the decomposing carcasses of basking sharks, as in the Stronsay beast and the *Zuiyo Maru* cases.

Chapter 3

Beluga Whale

Beluga



Size compared to an average human

Conservation status

Near Threatened (IUCN 3.1)

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Cetacea
Family:	Monodontidae
Genus:	***Delphinapterus***
Species:	***D. leucas***

Binomial name

Delphinapterus leucas
(Pallas, 1776)

Beluga range

The **beluga** or **white whale**, ***Delphinapterus leucas***, is an Arctic and sub-Arctic species of cetacean. It is one of two members of the family Monodontidae, along with the narwhal. This marine mammal is commonly referred to simply as the **beluga** or **sea canary** due to its high-pitched twitter. It is up to 5 m (16 ft) in length and an unmistakable all-white color with a distinctive protuberance on the head. From a conservation perspective, the beluga is considered "near threatened" by the International Union for Conservation of Nature; however the subpopulation from the Cook Inlet in Alaska is considered critically endangered and is under the protection of the United States' Endangered Species Act. Of seven Canadian beluga populations, two are listed as endangered, inhabiting eastern Hudson Bay, and Ungava Bay.

Taxonomy

In 1776 Peter Simon Pallas first described the beluga. It is a member of the Monodontidae family, which is in turn part of the toothed whale suborder. The Irrawaddy dolphin was once placed in the same family; however, recent genetic evidence suggests otherwise. The narwhal is the only other species within the Monodontidae family besides the beluga.

The Red List of Threatened Species gives both beluga and white whale as common names, though the former is now more popular. The English name comes from the Russian белуга (*beluga*) or белуха (*belukha*), which derives from the word белый (*belyy*), meaning "white". It is sometimes referred to by scientists as the belukha whale in order to avoid confusion with the beluga sturgeon.

The whale is also colloquially known as the Sea Canary on account of its high-pitched squeaks, squeals, clucks and whistles. A Japanese researcher says he taught a beluga to "talk" by using these sounds to identify three different objects, offering hope that humans may one day be able to communicate effectively with sea mammals.

Description

A beluga in the shallow waters of the Vancouver Aquarium

Male belugas are larger than females. Males can reach 5.5 metres (18 ft) long, while females grow to 4.1 metres (13 ft). Males weigh between 1,100 and 1,600 kilograms (2,400 and 3,500 lb) while females weigh between 700 and 1,200 kilograms (1,500 and 2,600 lb). This is larger than most dolphins, but is smaller than most other toothed whales.

The adult beluga is rarely mistaken for another species, because it is completely white or whitish-gray in color. Calves, however, are usually gray. Its head is unlike that of any other cetacean. Like most toothed whales it has a melon—an oily, fatty tissue lump found at the center of the forehead. The beluga's melon is extremely bulbous and even malleable. The beluga is able to change the shape of its head by blowing air around its sinuses. Unlike many dolphins and whales, the vertebrae in the neck are not fused together, allowing the animal to turn its head laterally. The rostrum has about 8 to 10 teeth on each side of the jaw and a total of 34 to 40 teeth.

Belugas have a dorsal ridge, rather than a dorsal fin. The absence of the dorsal fin is reflected in the genus name of the species—*apterus* the Greek word for "wingless." The evolutionary preference for a dorsal ridge rather than a fin is believed to be an adaptation to under-ice conditions, or possibly as a way of preserving heat. As in other cetaceans, the thyroid gland is relatively large compared to terrestrial mammals (proportionally three times as large as a horse's thyroid) and may help to sustain higher metabolism during the summer estuarine occupations.

Its body is round, particularly when well-fed, and tapers less smoothly to the head than the tail. The sudden tapering to the base of its neck gives it the appearance of shoulders, unique among cetaceans. The tail fin grows and becomes increasingly and ornately curved as the animal ages. The flippers are broad and short—making them almost square-shaped.

Range and habitat

Beluga at the mouth of Churchill River into Hudson Bay, Canada

The beluga inhabits a discontinuous circumpolar distribution in Arctic and sub-Arctic waters ranging from 50° N to 80° N, particularly along the coasts of Alaska, Canada, Greenland, and Russia. The southernmost extent of their range includes isolated populations in the St. Lawrence River estuary and the Saguenay fjord, around the village of Tadoussac, Quebec, in the Atlantic and the Amur River delta, the Shantar Islands and the waters surrounding Sakhalin Island in the Sea of Okhotsk.

In the spring, the beluga moves to its summer grounds: bays, estuaries and other shallow inlets. These summer sites are discontinuous. A mother usually returns to the same site year after year. As its summer homes clog with ice during autumn, the beluga moves away for winter. Most travel in the direction of the advancing icepack and stay close its edge for the winter months. Others stay under the icepack—surviving by finding ice leads and polynyas (patches of open water in the ice) in which they can surface to breathe. Beluga may also find air pockets trapped under the ice. The beluga's ability to find the thin slivers of open water within a dense ice pack that may cover more than 96% of the surface mystifies scientists. Its echo-location capabilities are highly adapted to the sub-ice sea's peculiar acoustics and it has been suggested that belugas can sense open water through echo-location.

In 1849, while constructing the first railroad between Rutland and Burlington in Vermont, workers unearthed the bones of a mysterious animal in the town of Charlotte. Buried nearly 10 feet (3.0 m) below the surface in a thick blue clay, these bones were unlike those of any animal previously discovered in Vermont. Experts identified the bones as those of a beluga. Because Charlotte is over 150 miles (241 km) from the nearest ocean, early naturalists were at a loss to explain the bones of a marine mammal buried beneath the fields of rural Vermont. Today, the Charlotte whale aids in the study of the geology and the history of the Champlain Basin, and this fossil is now the official Vermont State Fossil (making Vermont the only state whose official fossil is that of a still extant animal).

On June 9, 2006, a young beluga carcass was found in the Tanana River near Fairbanks in central Alaska, nearly 1,700 kilometers (1,056 mi) from the nearest ocean habitat. Belugas sometimes follow migrating fish, leading Alaska state biologist Tom Seaton to speculate that it had followed migrating salmon up the river at some point in the prior fall.

Life history

Pod of belugas swimming

Belugas are highly sociable. Groups of males may number in the hundreds, while mothers with calves generally mix in slightly smaller groups. When pods aggregate in estuaries, they may number in the thousands. This can represent a significant proportion of the entire population and is when they are most vulnerable to hunting.

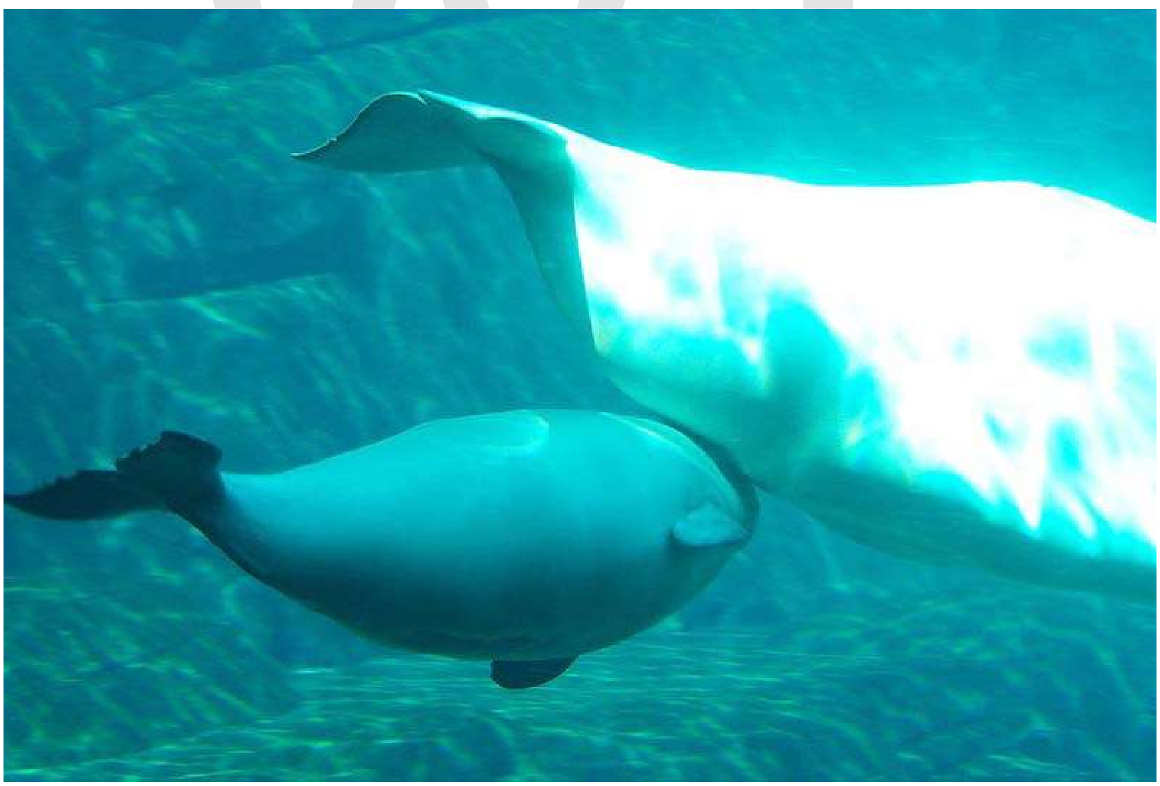
Pods tend to be unstable, meaning that they tend to move from pod to pod. Radio tracking has shown that belugas can start out in a pod and within a few days be hundreds of miles away from that pod. Mothers and calves form the beluga's closest social relationship. Nursing times of two years have been observed and lactational anestrus may not occur. Calves often return to the same estuary as their mother in the summer, meeting her sometimes even after becoming fully mature.

Belugas can be playful—they may spit at humans or other whales. It is not unusual for an aquarium handler to be drenched by one of his charges. Some researchers believe that spitting originated with blowing sand away from crustaceans at the sea bottom.

Unlike most whales, it is capable of swimming backwards.

Males reach sexual maturity between four and seven years, while females mature at between six and nine years. The beluga can live more than 50 years.

Reproduction



Female and calf

Female belugas typically give birth to one calf every three years. Most mating occurs between February and May, but some mating occurs at other times of year. It is questionable whether the beluga has delayed implantation. Gestation last 12 to 14.5 months.

Calves are born over a protracted period that varies by location. In the Canadian Arctic, calves are born between March and September, while in Hudson Bay the peak calving period is in late June and in Cumberland Sound most calves are born from late July to early August.

Newborns are about 1.5 metres (4.9 ft) long, weigh about 80 kilograms (180 lb), and are grey in color. The calves remain dependent on their mothers for at least two years.

Ecology

Feeding

The beluga is a slow swimmer that feeds mainly on fish. It also eats cephalopods (squid and octopus) and crustaceans (crab and shrimp). Foraging on the seabed typically takes place at depths of up to 1,000 feet (300 m) but they can dive at least twice this depth. A typical feeding dive lasts 3–5 minutes, but belugas submerge for up to 20 minutes at a time.

Predation

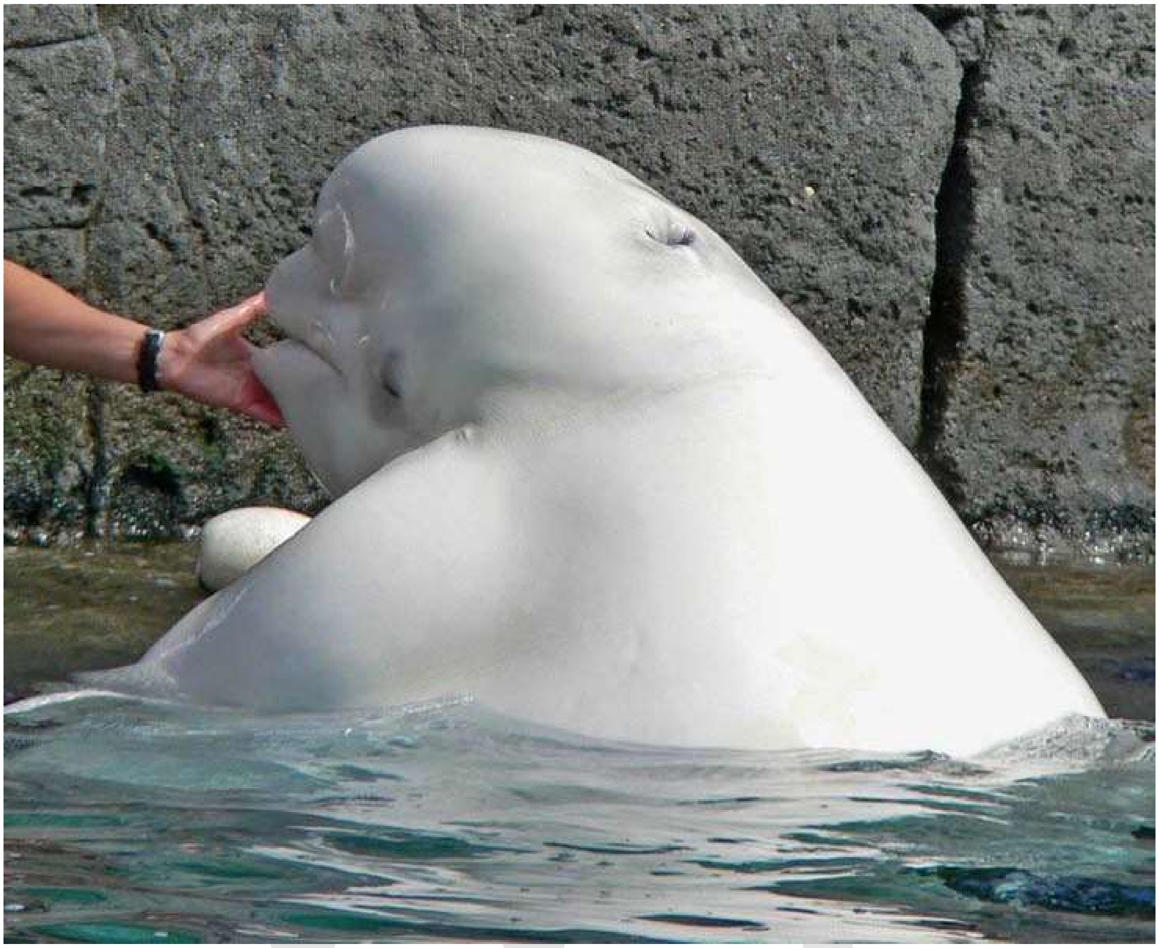
Polar bears take particular advantage of situations when belugas become trapped by ice and are thus unable to reach the ocean. The bears swipe at the belugas and drag them onto the ice. The orca is its other significant natural predator.

Relation to humans

Belugas were among the first whale species in captivity. The first beluga was shown at Barnum's Museum in New York City in 1861. Today it remains one of the few whale species kept at aquaria and sea life parks across North America, Europe, and Asia. Its popularity there with visitors reflects its attractive color, and its range of facial expressions. While most cetacean "smiles" are fixed, the extra movement afforded by the beluga's unfused cervical vertebrae allows a greater range of apparent expression. Most belugas found in aquariums are caught in the wild, though captive breeding programs enjoy some success.

Both the United States Navy and the Russian Navy have used belugas in anti-mining operations in Arctic waters. In one instance, a captive beluga helped bring a distressed diver who was performing a stunt in his pool up to the surface, possibly saving the diver's life. Another time, a captive beluga brought a cramp-paralized diver from the bottom of the pool up to the surface by holding her foot in its mouth, certainly saving the female diver's life.

Population and threats



A beluga whale in an aquarium with a trainer

The global population of belugas today stands at about 100,000. Although this number is much greater than that of many other cetaceans, it is much smaller than pre-hunting populations. There are estimated to be 40,000 individuals in the Beaufort Sea, 25,045 in Hudson Bay, 18,500 in the Bering Sea, and 28,008 in the Canadian Low Arctic. The population in the St. Lawrence estuary is estimated to be around 1,000. It is considered an excellent sentinel species (indicator of environment health and changes). This is because it is long-lived, on top of the food web, bearing large amounts of fat and blubber, relatively well-studied for a cetacean, and still somewhat common.

Because the beluga congregates in river estuaries, pollution is proving to be a significant health danger. Incidents of cancer have been reported to be rising as a result of St. Lawrence River pollution. Local beluga carcasses contain so many contaminants that they are treated as toxic waste. Reproductive pathology has been discovered here, possibly caused by organochlorines. Levels between 240 ppm and 800 ppm of PCBs have been found, with males typically having higher levels. The long-term effects of this pollution on the affected populations is not known.

A beluga resurfaces

Indirect human disturbance may also be a threat. While some populations tolerate small boats, others actively try to avoid ships. Whale-watching has become a booming activity in the St. Lawrence and Churchill River areas.

Because of its predictable migration pattern and high concentrations, the beluga has been hunted by indigenous Arctic peoples for centuries. In many areas, hunting continues, and is believed to be sustainable. However, in other areas, such as the Cook Inlet, Ungava Bay, and off western Greenland, previous commercial operations left the populations in great peril. Indigenous whaling continues in these areas, and some populations continue to decline. These areas are the subject of intensive dialogue between Inuit communities and national governments aiming to create a sustainable hunt.

Pathogens

Papillomaviruses have been found in the gastric compartments of belugas in the St. Lawerence River. Herpesvirus as well has been detected on occasion in belugas. Encephalitis has sometimes been observed and the protozoa *Sarcocystis* can infect the animals. Ciliates have been observed to colonize the blowhole yet may not be pathogenic or especially harmful.

Erysipelothrix rhusiopathiae bacilli, likely from contaminated fish in the diet, can endanger captive belugas, causing anorexia, dermal plaques, and lesions. This may lead to death if not diagnosed early and treated with antibiotics.

Conservation status

Pictured on Faroe Islands stamp

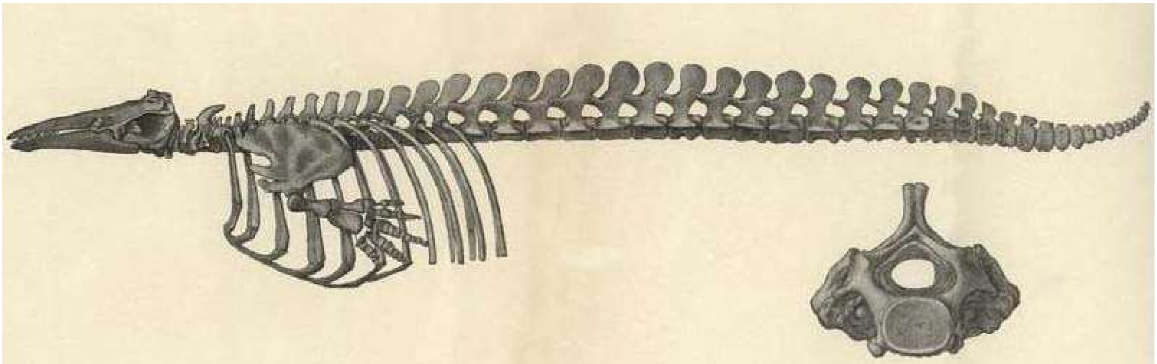
As of 2008, the beluga is listed as "near threatened" by the IUCN. This is due to uncertainty about the number of belugas over parts of its range (especially the Russian Arctic) and the expectation that if current conservation efforts cease, especially hunting management, the beluga population is likely to qualify for "threatened" status within five years. Prior to 2008, the beluga was listed as "vulnerable", a higher level of concern. IUCN cited the stability of the largest subpopulations and improved census methods that indicate a larger population than previously estimated.

To prevent hunting, belugas are protected under the International Moratorium on Commercial Whaling; however, small amounts of beluga whaling are still allowed. Since it is very difficult to know the exact population of belugas because their habitats include inland waters away from the ocean, it is easy for them to come in contact with oil and gas development centers. To prevent whales from coming in contact with industrial waste, the Alaskan and Canadian governments are relocating sites where whales and waste come in contact.

To prevent captive whales from dying, researchers from the Vancouver Aquarium Marine Science Centre are finding ways to prevent fungi from entering the habitats and to constantly check their health. Healthy captive belugas are important because they are one of the only whales found in many marine aquariums. The high numbers of captives adds to the threat to the beluga population, while their carcasses contribute to scientific research.

Subpopulations are subject to differing levels of threat and warrant individual assessment. The Cook Inlet subpopulation is listed as "Critically Endangered" by the IUCN as of 2006. The Cook Inlet beluga population is listed as Endangered under the Endangered Species Act as of October 2008. This was due to overharvesting of belugas prior to 1998. The population has failed to recover even though the reported harvest has been small. The most recent published estimate as of May 2008 was 302 (CV=0.16) in 2006. In addition, the National Marine Fisheries Service indicated that the 2007 aerial survey's point estimate was 375.

Evolution



Skeleton of D. leucas

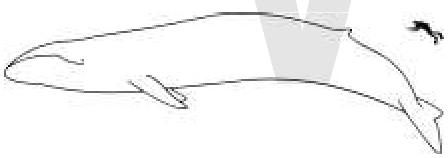
The beluga's earliest known ancestor is the prehistoric *Denebola brachycephala* from the late Miocene period. A single fossil from the Baja California peninsula, indicates that the family once inhabited warmer waters. The fossil record also indicates that in comparatively recent times the beluga's range varied with that of the polar ice packs—expanding during ice ages and contracting when the ice retreats.

Chapter 4

Blue Whale

Blue whale

Adult blue whale from the eastern Pacific Ocean



Size compared to an average human

Conservation status

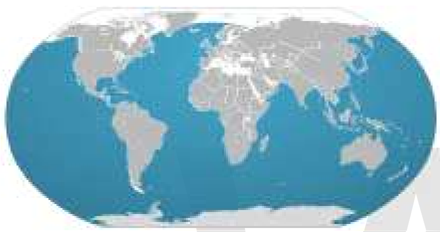
Endangered (IUCN 3.1)

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Cetacea
Suborder:	Mysticeti
Family:	Balaenopteridae
Genus:	*Balaenoptera*

Species:	***B. musculus***

Binomial name
Balaenoptera musculus   (Linnaeus, 1758)
Subspecies
• *B. m. brevicauda* Ichihara, 1966   • ?*B. m. indica* Blyth, 1859   • *B. m. intermedia* Burmeister, 1871   • *B. m. musculus* Linnaeus, 1758



Blue whale range (in blue)

The **blue whale** (***Balaenoptera musculus***) is a marine mammal belonging to the suborder of baleen whales (called Mysticeti). At perhaps over 33 metres (108 ft) in length and 180 metric tons (200 short tons) or more in weight, it is the largest animal ever known to have existed.

Long and slender, the blue whale's body can be various shades of bluish-grey dorsally and somewhat lighter underneath. There are at least three distinct subspecies: *B. m. musculus* of the North Atlantic and North Pacific, *B. m. intermedia* of the Southern Ocean and *B. m. brevicauda* (also known as the pygmy blue whale) found in the Indian Ocean and South Pacific Ocean. *B. m. indica*, found in the Indian Ocean, may be another subspecies. As with other baleen whales, its diet consists almost exclusively of small crustaceans known as krill.

Blue whales were abundant in nearly all the oceans on Earth until the beginning of the twentieth century. For over a century, they were hunted almost to extinction by whalers until protected by the international community in 1966. A 2002 report estimated there were 5,000 to 12,000 blue whales worldwide, located in at least five groups. More recent research into the Pygmy subspecies suggests this may be an underestimate. Before whaling, the largest population was in the Antarctic, numbering approximately 239,000 (range 202,000 to 311,000). There remain only much smaller (around 2,000) concentrations in each of the North-East Pacific, Antarctic, and Indian Ocean groups. There are two more groups in the North Atlantic, and at least two in the Southern Hemisphere.

Taxonomy

Blue whales are rorquals (family Balaenopteridae), a family that includes the humpback whale, the fin whale, Bryde's whale, the sei whale and the minke whale. The family Balaenopteridae is believed to have diverged from the other families of the suborder Mysticeti as long ago as the middle Oligocene. However, it is not known when the members of those families diverged from each other.

The blue whale is usually classified as one of eight species in the genus *Balaenoptera*; one authority places it in a separate monotypic genus, *Sibbaldus*, but this is not accepted elsewhere. DNA sequencing analysis indicates that the blue whale is phylogenetically closer to the sei whale (*Balaenoptera borealis*) and Bryde's whale (*Balaenoptera brydei*) than to other *Balaenoptera* species, and closer to the humpback whale (*Megaptera*) and the gray whale (*Eschrichtius*) than to the minke whales (*Balaenoptera acutorostrata* and *Balaenoptera bonaerensis*). If further research confirms these relationships, it will be necessary to reclassify the rorquals.

There have been at least 11 documented cases of blue/fin hybrid adults in the wild. Arnason and Gullberg describe the genetic distance between a blue and a fin as about the same as that between a human and a gorilla. Researchers working off of Fiji believe they photographed a hybrid humpback/blue whale.

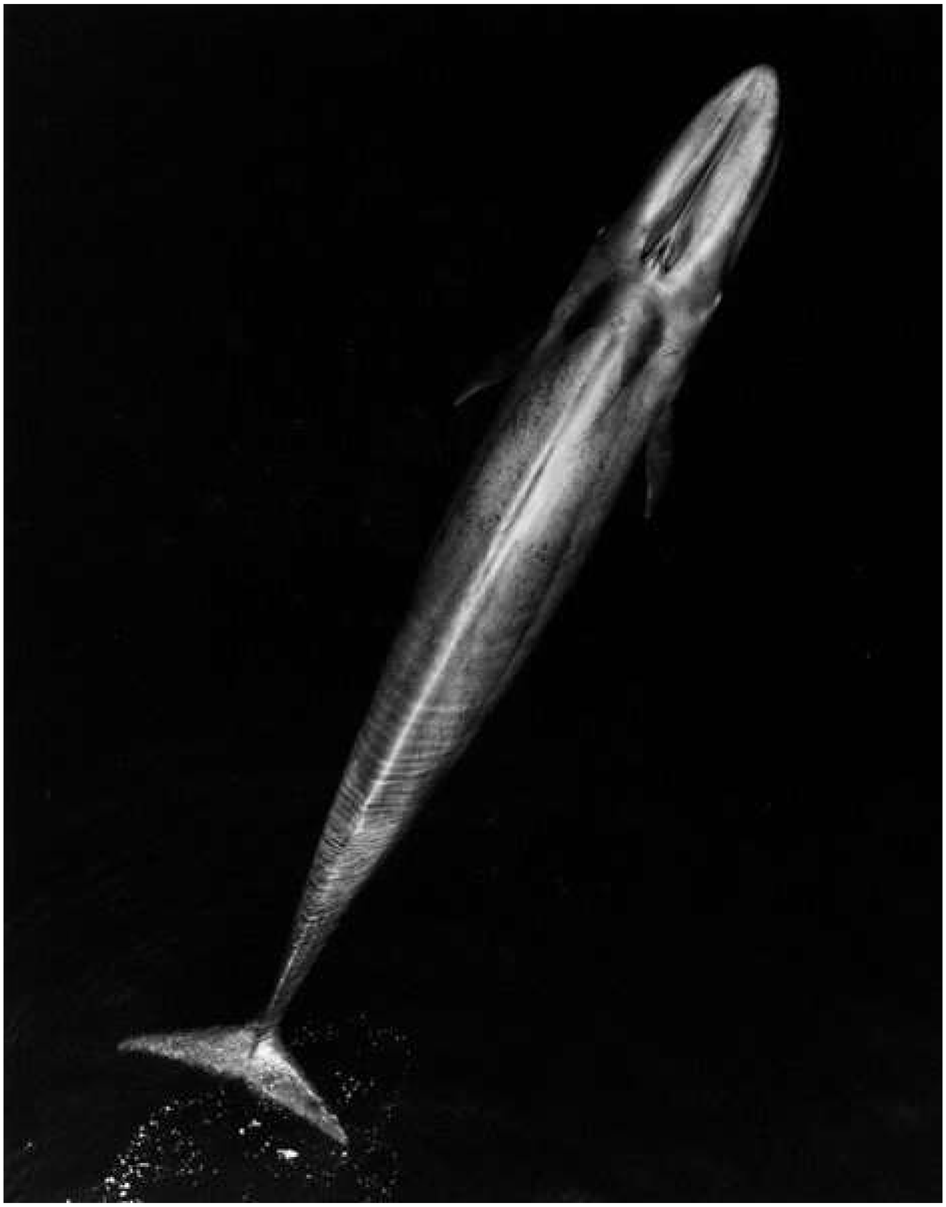
The first published description of the blue whale comes from Robert Sibbald's *Phalainologia Nova* (1694). In September 1692, Sibbald found a blue whale that had stranded in the Firth of Forth—a male 78-feet-long—which had "black, horny plates" and "two large apertures approaching a pyramid in shape".

The specific name *musculus* is Latin and could mean "muscle", but it can also be interpreted as "little mouse". Linnaeus, who named the species in his seminal *Systema Naturae* of 1758, would have known this and may have intended the ironic double meaning. Herman Melville called this species **sulphur-bottom** in his novel *Moby-Dick* due to an orange-brown or yellow tinge on the underparts from diatom films on the skin. Other common names for the blue whale have included **Sibbald's rorqual** (after Sibbald, who first described the species), the **great blue whale** and the **great northern rorqual**. These names have now fallen into disuse. The first known usage of the term **blue whale** was in Melville's *Moby-Dick*, which only mentions it in passing and doesn't specifically attribute it to the species in question. The name was really derived from the Norwegian **blåhval**, coined by Svend Foyn shortly after he had perfected the harpoon gun; the Norwegian scientist G.O. Sars adopted it as the Norwegian common name in 1874.

Authorities classify the species into three or four subspecies: *B. m. musculus*, the northern blue whale consisting of the North Atlantic and North Pacific populations, *B. m. intermedia*, the southern blue whale of the Southern Ocean, *B. m. brevicauda*, the pygmy blue whale found in the Indian Ocean and South Pacific, and the more problematic *B. m. indica*, the great Indian rorqual, which is also found in the Indian Ocean and, although described earlier, may be the same subspecies as *B. m. brevicauda*.

Description and behaviour

A blue whale lifting its tail flukes.



Adult blue whale

Aerial view of a blue whale showing both pectoral fins

The blow of a blue whale

The small dorsal fin of this blue whale is just visible on the far left.

The blue whale has a long tapering body that appears stretched in comparison with the stockier build of other whales. The head is flat and *U*-shaped and has a prominent ridge running from the blowhole to the top of the upper lip. The front part of the mouth is thick with baleen plates; around 300 plates (each around one metre (3.2 ft) long) hang from the upper jaw, running 0.5 m (1.6 ft) back into the mouth. Between 60 and 90 grooves (called ventral pleats) run along the throat parallel to the body length. These pleats assist with evacuating water from the mouth after lunge feeding.

The dorsal fin is small, visible only briefly during the dive sequence. Located around three-quarters of the way along the length of the body, it varies in shape from one individual to another; some only have a barely perceptible lump, but others may have prominent and falcate (sickle-shaped) dorsals. When surfacing to breathe, the blue whale raises its shoulder and blowhole out of the water to a greater extent than other large whales, such as the fin or sei whales. Observers can use this trait to differentiate between species at sea. Some blue whales in the North Atlantic and North Pacific raise their tail fluke when diving. When breathing, the whale emits a spectacular vertical single-column spout up to 12 metres (39 ft), typically 9 metres (30 ft). Its lung capacity is 5,000 litres (1320 U.S. gallons). Blue whales have twin blowholes shielded by a large splashguard.

The flippers are 3–4 metres (9.8–13 ft) long. The upper sides are grey with a thin white border; the lower sides are white. The head and tail fluke are generally uniformly grey. The whale's upper parts, and sometimes the flippers, are usually mottled. The degree of mottling varies substantially from individual to individual. Some may have a uniform slate-grey color, but others demonstrate a considerable variation of dark blues, greys and blacks, all tightly mottled.

Blue whales can reach speeds of 50 kilometres per hour (31 mph) over short bursts, usually when interacting with other whales, but 20 kilometres per hour (12 mph) is a more typical traveling speed. When feeding, they slow down to 5 kilometres per hour (3.1 mph).

Blue whales most commonly live alone or with one other individual. It is not known how long traveling pairs stay together. In locations where there is a high concentration of food, as many as 50 blue whales have been seen scattered over a small area. However, they do not form the large, close-knit groups seen in other baleen species.

Size

A 19-foot-long blue whale skull in the collections of the Smithsonian Museum of Natural History.

Blue whales are difficult to weigh because of their size. Most blue whales killed by whalers were not weighed whole, but cut up into manageable pieces first. This caused an underestimate of the total weight of the whale, due to the loss of blood and other fluids.

Nevertheless, measurements between 150–170 metric tons (170–190 short tons) were recorded of animals up to 27 metres (89 ft) in length. The weight of an individual 30 metres (98 ft) long is believed by the American National Marine Mammal Laboratory (NMML) to be in excess of 180 metric tons (200 short tons). The largest blue whale accurately weighed by NMML scientists to date was a female that weighed 177 metric tons (195 short tons).

The blue whale is the largest animal ever known to have lived. The largest known dinosaur of the Mesozoic Era was the *Argentinosaurus*, which is estimated to have weighed up to 90 metric tons (99 short tons), though a controversial vertebra of *Amphicoelias fragillimus* may indicate an animal of up to 122 metric tons (134 short tons) and 40–60 metres (130–200 ft). Furthermore, there are weight estimates for the very poorly known *Bruhathkayosaurus* ranging from 140–220 metric tons (150–240 short tons), besides length estimates up to about 45 metres (148 ft). The extinct fish *Leedsichthys* may have approached its size. However, complete fossils are difficult to come by, making size comparisons difficult. All these animals are considered to be smaller than the blue whale.

There is some uncertainty about the biggest blue whale ever found, as most data come from blue whales killed in Antarctic waters during the first half of the twentieth century, and was collected by whalers not well-versed in standard zoological measurement techniques. The longest whales ever recorded were two females measuring 33.6–33.3 metres (110–109 ft) respectively. The longest whale measured by scientists at the NMML was 29.9 metres (98 ft).

A blue whale's tongue weighs around 2.7 metric tons (3.0 short tons) and, when fully expanded, its mouth is large enough to hold up to 90 metric tons (99 short tons) of food and water. Despite the size of its mouth, the dimensions of its throat are such that a blue whale cannot swallow an object wider than a beach ball. Its heart weighs 600 kilograms (1,300 lb) and is the largest known in any animal. A blue whale's aorta is about 23 centimetres (9.1 in) in diameter. During the first seven months of its life, a blue whale calf drinks approximately 400 litres (100 U.S. gallons) of milk every day. Blue whale calves gain weight quickly, as much as 90 kilograms (200 lb) every 24 hours. Even at birth, they weigh up to 2,700 kilograms (6,000 lb)—the same as a fully grown hippopotamus.

Feeding

Blue whales feed almost exclusively on krill, though they also take small numbers of copepods. The species of this zooplankton eaten by blue whales varies from ocean to ocean. In the North Atlantic, *Meganyctiphanes norvegica*, *Thysanoessa raschii*, *Thysanoessa inermis* and *Thysanoessa longicaudata* are the usual food; in the North Pacific, *Euphausia pacifica*, *Thysanoessa inermis*, *Thysanoessa longipes*, *Thysanoessa spinifera*, *Nyctiphanes symplex* and *Nematoscelis megalops*; and in the Antarctic, *Euphausia superba*, *Euphausia crystallorophias* and *Euphausia valentin*.

An adult blue whale can eat up to 40 million krill in a day. The whales always feed in the areas with the highest concentration of krill, sometimes eating up to 3,600 kilograms (7,900 lb) of krill in a single day. This daily requirement of an adult blue whale is in the region of 1.5 million kilocalories.

Because krill move, blue whales typically feed at depths of more than 100 metres (330 ft) during the day and only surface-feed at night. Dive times are typically 10 minutes when feeding, though dives of up to 20 minutes are common. The longest recorded dive is 36 minutes. The whale feeds by lunging forward at groups of krill, taking the animals and a large quantity of water into its mouth. The water is then squeezed out through the baleen plates by pressure from the ventral pouch and tongue. Once the mouth is clear of water, the remaining krill, unable to pass through the plates, are swallowed. The blue whale also incidentally consumes small fish, crustaceans and squid caught up with krill.

Life history

A juvenile blue whale with its mother

Mating starts in late autumn and continues to the end of winter. Little is known about mating behaviour or breeding grounds. Females typically give birth once every two to three years at the start of the winter after a gestation period of ten to twelve months. The calf weighs about 2.5 metric tons (2.8 short tons) and is around 7 metres (23 ft) in length. Blue whale calves drink 380–570 litres (100–150 U.S. gallons) of milk a day. Weaning takes place for about six months, by which time the calf has doubled in length. Sexual maturity is typically reached at eight to ten years, by which time males are at least 20 metres (66 ft) long (or more in the Southern Hemisphere). Females are larger still, reaching sexual maturity at around the age of five, by which they are about 21 metres (69 ft) long.

Scientists estimate that blue whales can live for at least 80 years; however, since individual records do not date back into the whaling era, this will not be known with certainty for many years. The longest recorded study of a single individual is 34 years, in the northeast Pacific. The whales' only natural predator is the orca. Studies report that as many as 25% of mature blue whales have scars resulting from orca attacks. The mortality rate of such attacks is unknown.

Blue whale strandings are extremely uncommon, and, because of the species' social structure, mass strandings are unheard of. However, when strandings do occur, they can become the focus of public interest. In 1920, a blue whale washed up near Bragar on the Isle of Lewis in the Outer Hebrides of Scotland. It had been shot by whalers, but the harpoon had failed to explode. As with other mammals, the fundamental instinct of the whale was to try to carry on breathing at all costs, even though this meant beaching to prevent itself from drowning. Two of the whale's bones were erected just off a main road on Lewis and remain a tourist attraction.

Vocalizations

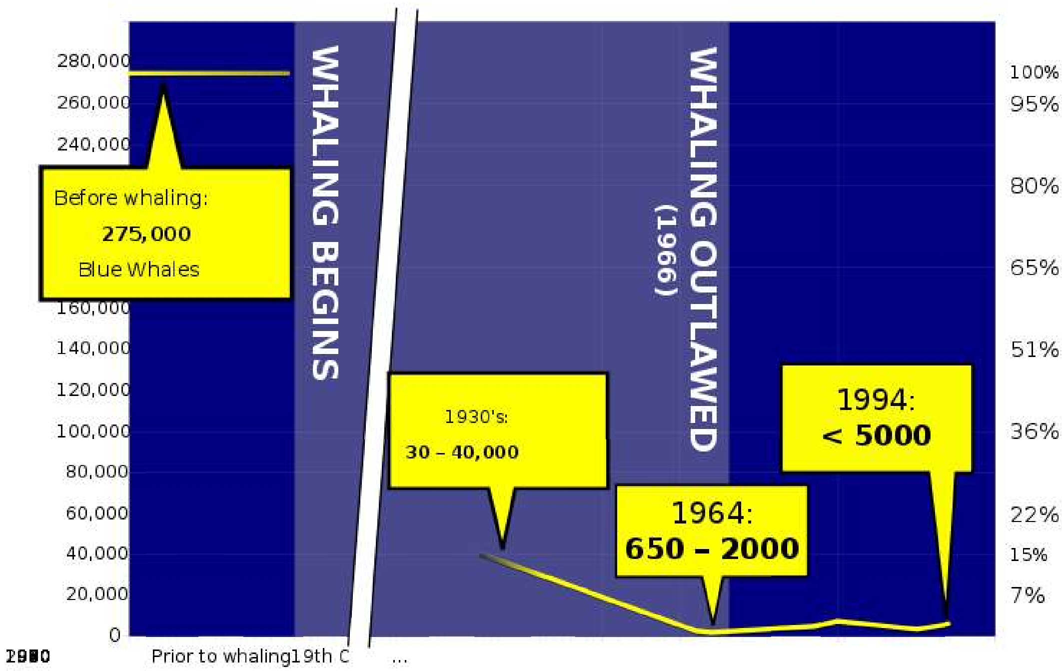
Estimates made by Cummings and Thompson (1971) suggest the source level of sounds made by blue whales are between 155 and 188 decibels when measured relative to a reference pressure of one micropascal at one metre. All blue whale groups make calls at a fundamental frequency between 10 and 40 Hz; the lowest frequency sound a human can typically perceive is 20 Hz. Blue whale calls last between ten and thirty seconds. Blue whales off the coast of Sri Lanka have been repeatedly recorded making "songs" of four notes, lasting about two minutes each, reminiscent of the well-known humpback whale songs. As this phenomenon has not been seen in any other populations, researchers believe it may be unique to the *B. m. brevicauda* (pygmy) subspecies.

The reason for vocalization is unknown. Richardson *et al.* (1995) discuss six possible reasons:

1. Maintenance of inter-individual distance
2. Species and individual recognition
3. Contextual information transmission (e.g., feeding, alarm, courtship)
4. Maintenance of social organization (e.g., contact calls between females and males)
5. Location of topographic features
6. Location of prey resources

Population and whaling

Hunting era



Blue whale populations have declined dramatically due to commercial whaling.

Blue whales are not easy to catch or kill. Their speed and power meant that they were rarely pursued by early whalers, who instead targeted sperm and right whales. In 1864, the Norwegian Svend Foyn equipped a steamboat with harpoons specifically designed for catching large whales. Although initially cumbersome and with a low success rate, Foyn perfected the harpoon gun, and soon several whaling stations were established on the coast of Finnmark in northern Norway. Because of disputes with the local fishermen, the last whaling station in Finnmark was closed down in 1904.

Soon, blue whales were being hunted in Iceland (1883), the Faroe Islands (1894), Newfoundland (1898), and Spitsbergen (1903). In 1904-05 the first blue whales were taken off South Georgia. By 1925, with the advent of the stern slipway in factory ships and the use of steam-driven whale catchers, the catch of blue whales, and baleen whales as a whole, in the Antarctic and sub-Antarctic began to increase dramatically. In the 1930-31 season, these ships caught 29,400 blue whales in the Antarctic alone. By the end of World War II, populations had been significantly depleted, and, in 1946, the first quotas restricting international trade in whales were introduced, but they were ineffective because of the lack of differentiation between species. Rare species could be hunted on an equal footing with those found in relative abundance.

Arthur C. Clarke, in his 1962 book *Profiles of the Future*, was the first prominent intellectual to call attention to the plight of the blue whale. He mentioned its large brain and said, "we do not know the true nature of the entity we are destroying."

Blue whale hunting was banned in 1966 by the International Whaling Commission, and illegal whaling by the USSR finally halted in the 1970s, by which time 330,000 blue whales had been caught in the Antarctic, 33,000 in the rest of the Southern Hemisphere, 8,200 in the North Pacific, and 7,000 in the North Atlantic. The largest original population, in the Antarctic, had been reduced to 0.15% of their initial numbers.

Population and distribution today

A blue whale set against the backdrop of the Azores

Image of a blue whale's tail fluke with the Santa Barbara Channel Islands in the background, August 2007

Since the introduction of the whaling ban, studies have failed to ascertain whether the conservation reliant global blue whale population is increasing or remaining stable. In the Antarctic, best estimates show a significant increase at 7.3% per year since the end of illegal Soviet whaling, but numbers remain at under 1% of their original levels. It has also been suggested that Icelandic and Californian populations are increasing but these increases are not statistically significant. The total world population was estimated to be between 5,000 and 12,000 in 2002, although there are high levels of uncertainty in available estimates for many areas.

The IUCN Red List counts the blue whale as "endangered" as it has since the list's inception. In the United States, the National Marine Fisheries Service lists them as endangered under the Endangered Species Act. The largest known concentration, consisting of about 2,800 individuals, is the northeast Pacific population of the northern blue whale (*B. m. musculus*) subspecies that ranges from Alaska to Costa Rica, but is most commonly seen from California in summer. Infrequently, this population visits the northwest Pacific between Kamchatka and the northern tip of Japan.

In the North Atlantic, two stocks of *B. m. musculus* are recognised. The first is found off Greenland, Newfoundland, Nova Scotia and the Gulf of Saint Lawrence. This group is estimated to total about 500. The second, more easterly group is spotted from the Azores in spring to Iceland in July and August; it is presumed the whales follow the Mid-Atlantic Ridge between the two volcanic islands. Beyond Iceland, blue whales have been spotted as far north as Spitsbergen and Jan Mayen, though such sightings are rare. Scientists do not know where these whales spend their winters. The total North Atlantic population is estimated to be between 600 and 1,500.

In the Southern Hemisphere, there appear to be two distinct subspecies, *B. m. intermedia*, the Antarctic blue whale, and the little-studied pygmy blue whale, *B. m. brevicauda*, found in Indian Ocean waters. The most recent surveys (midpoint 1998) provided an estimate of 2,280 blue whales in the Antarctic., of which fewer than 1% are likely to be pygmy blue whales Estimates from a 1996 survey were that 424 pygmy blue whales were in a small area south of Madagascar alone, thus it is likely that numbers in the entire Indian Ocean are in the thousands. If this is true, the global numbers would be much higher than estimates predict.

A fourth subspecies, *B. m. indica*, was identified by Blyth in 1859 in the northern Indian Ocean, but difficulties in identifying distinguishing features for this subspecies led to it being used a synonym for *B. m. brevicauda*, the pygmy blue whale. Records for Soviet catches seem to indicate that the female adult size is closer to that of the Pygmy Blue than *B. m. musculus*, although the populations of *B. m. indica* and *B. m. brevicauda* appear to be discrete, and the breeding seasons differ by almost six months.

Migratory patterns of these subspecies are not well known. For example, pygmy blue whales have been recorded in the northern Indian Ocean (Oman, Maldives and Sri Lanka), where they may form a distinct resident population. In addition, the population of blue whales occurring off Chile and Peru may also be a distinct population. Some Antarctic blue whales approach the eastern South Atlantic coast in winter, and occasionally, their vocalizations are heard off Peru, Western Australia, and in the northern Indian Ocean. In Chile, the Cetacean Conservation Center, with support from the Chilean Navy, is undertaking extensive research and conservation work on a recently discovered feeding aggregation of the species off the coast of Chiloe Island in the Gulf of Corcovado, where 326 blue whales were spotted in the summer of 2007.

Efforts to calculate the blue whale population more accurately are supported by marine mammologists at Duke University, who maintain the Ocean Biogeographic Information System—Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP), a collation of marine mammal sighting data from around 130 sources.

Threats other than hunting

A blue whale surfaces off Santa Cruz Island in the Channel Islands, near Santa Barbara, CA

Due to their enormous size, power and speed, adult blue whales have virtually no natural predators. There is, however, one documented case in *National Geographic Magazine* of a blue whale being attacked by orcas off the Baja California Peninsula; although the orcas were unable to kill the animal outright during their attack, the blue whale sustained massive wounds and probably died as a result of them shortly after the attack. Up to a quarter of the blue whales identified in Baja bear scars from orca attacks.

Blue whales may be wounded, sometimes fatally, after colliding with ocean vessels, as well as becoming trapped or entangled in fishing gear. The ever-increasing amount of ocean noise, including sonar, drowns out the vocalizations produced by whales, which may make it harder for them to communicate. Human threats to the potential recovery of blue whale populations also include accumulation of polychlorinated biphenyl (PCB) chemicals within the whale's body.

With global warming causing glaciers and permafrost to melt rapidly and allowing a large amount of fresh water to flow into the oceans, there are concerns that if the amount of fresh water in the oceans reaches a critical point, there will be a disruption in the thermohaline circulation. Considering the blue whale's migratory patterns are based on ocean temperature, a disruption in this circulation, which moves warm and cold water around the world, would be likely to have an effect on their migration. The whales summer in the cool, high latitudes, where they feed in krill-abundant waters; they winter in warmer, low latitudes, where they mate and give birth.

The change in ocean temperature would also affect the blue whale's food supply. The warming trend and decreased salinity levels would cause a significant shift in krill location and abundance.

Museums

Blue whale skeleton, outside the Long Marine Laboratory at the University of California, Santa Cruz

The Natural History Museum in London contains a famous mounted skeleton and life-size model of a blue whale, which were both the first of their kind in the world, but have since been replicated at the University of California, Santa Cruz. Similarly, the American Museum of Natural History in New York City has a full-size model in its Milstein Family Hall of Ocean Life. A juvenile blue whale skeleton is installed at the New Bedford Whaling Museum in New Bedford, Massachusetts.

The Aquarium of the Pacific in Long Beach, California features a life-size model of a mother blue whale with her calf suspended from the ceiling of its main hall. The Beaty Biodiversity Museum at the University of British Columbia, Canada, houses a display of a blue whale skeleton directly on the main campus boulevard. A real skeleton of a blue whale at the Canadian Museum of Nature in Ottawa, Canada was also unveiled in May 2010

The Museum of Natural History in Gothenburg, Sweden contains the only stuffed blue whale in the world. There one can also find the skeleton of the whale mounted beside the whale.

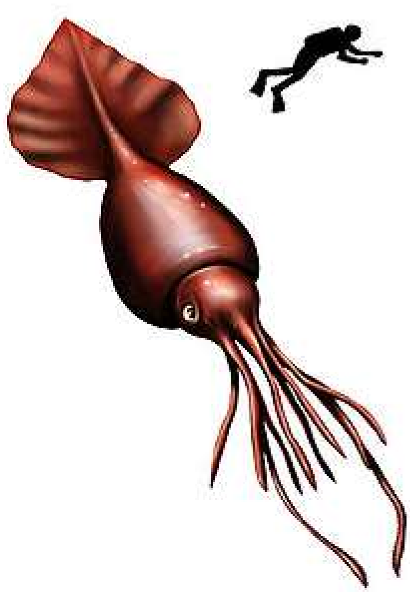
The Melbourne Museum features a skeleton of the pygmy blue whale.

Whale-watching

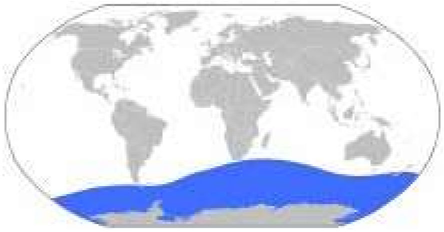
Living blue whales may be encountered on whale-watching cruises in the Gulf of Maine and are the main attractions along the north shore of the Gulf of Saint Lawrence and in the Saint Lawrence estuary.

Chapter 5

Colossal Squid

Colossal Squid	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Order:	Teuthida
Family:	Cranchiidae
Subfamily:	Taoniinae
Genus:	***Mesonychoteuthis*** Robson, 1925
Species:	***M. hamiltoni***
Binomial name	

Mesonychoteuthis hamiltoni
Robson, 1925



Global range of *M. hamiltoni*

The **Colossal Squid** (*Mesonychoteuthis hamiltoni*, from Greek *mesos* (middle), *nychus* (claw), and *teuthis* (squid)), sometimes called the **Antarctic** or **Giant Cranch Squid**, is believed to be the largest squid species in terms of mass. It is the only known member of the genus ***Mesonychoteuthis***. Though it is known from only a few specimens, current estimates put its maximum size at 12–14 metres (39–46 feet) long, based on analysis of smaller and immature specimens, making it the largest known invertebrate.

Morphology

Unlike the giant squid, whose arms and tentacles only have suckers lined with small teeth, the Colossal Squid's limbs are also equipped with sharp hooks: some swiveling, others three-pointed. Its body is wider and stouter, and therefore heavier, than that of the giant squid. Colossal Squids are believed to have a longer mantle than giant squids, although their tentacles are shorter.

The squid exhibits abyssal gigantism. The beak of *Mesonychoteuthis hamiltoni* is the largest known of any squid, exceeding that of *Architeuthis* (giant squid) in size and in robustness. The Colossal Squid also has the largest eyes documented in the animal kingdom.

Distribution

The squid's known range extends thousands of miles northward from Antarctica to southern South America, southern South Africa, and the southern tip of New Zealand, making it primarily an inhabitant of the entire circumantarctic Southern Ocean.

Ecology and life history

While little is known about the life of this creature, it is believed to feed on prey such as chaetognatha, large fish like the Patagonian toothfish and other squid in the deep ocean using bioluminescence. The Colossal Squid is thought to have a slow metabolic rate, requiring only around 30 g of prey daily. Estimates of its energetic demands suggest that it is a slow-moving ambush predator, using its large eyes primarily for predator detection rather than active hunting.

Based on capture depths of a few specimens, as well as beaks found in sperm whale stomachs, the adult squid ranges at least to a depth of 2200 metres, while juveniles can go as deep as 1000 metres. It is believed to be sexually dimorphic, with mature females generally being much larger than mature males, as is common in many species of invertebrates.

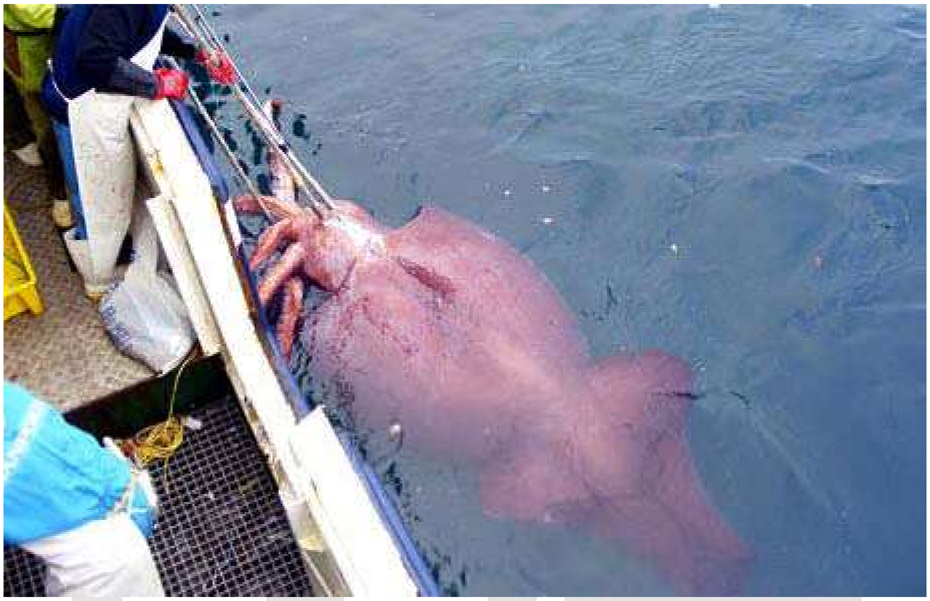
The squid's method of reproduction has not been observed, although some data on their reproduction can be inferred from anatomy. Since males lack an organ called a hectocotylus (a tentacle used in other cephalopods to transfer a spermatophore to the female), they probably use a penis instead, which would be used to directly implant sperm into females.

Many sperm whales carry scars on their backs believed to be caused by the hooks of Colossal Squid. Colossal Squid are a major prey item for Antarctic sperm whales feeding in the Southern Ocean; 14% of the squid beaks found in the stomachs of these sperm whales are those of the Colossal Squid, which indicates that Colossal Squid make up 77% of the biomass consumed by these whales. Many other animals also feed on this squid, including beaked whales (such as the bottlenose whales), pilot whales, southern elephant seals, Patagonian toothfish, sleeper sharks (*Somniosus* cf. *microcephalus*), and albatrosses (e.g., the Wandering and Sooty albatrosses). However, beaks from mature adults have only been recovered from those animals large enough to take such prey (i.e., sperm whales and sleeper sharks), while the remaining predators are limited to eating juveniles or young adults.

Timeline

- 1925 – Species was first discovered in the form of two tentacles found in the stomach of a sperm whale.
- 1981 – A Russian trawler in the Ross Sea, off the coast of Antarctica, caught a large squid with a total length of 4 metres (13 ft), which was later identified as an immature female of *Mesonychoteuthis hamiltoni*.
- 2003 – A complete specimen of a subadult female was found near the surface with a total length of 6 m (20 ft) and a mantle length of 2.5 m (8 ft).
- 2005 – A specimen was captured at a depth of 1625 m while taking a toothfish from a longline off South Georgia Island. Although the mantle was not brought aboard, the mantle length was estimated at over 2.5 m, and the tentacles measured 230 cm. The animal is thought to have weighed between 150 and 200 kg.
- 2007 – The largest recorded specimen was captured by a New Zealand fishing boat off Antarctica. It was initially estimated to measure 10 m (33 ft) in length and weigh 450 kg (992 lb). The squid was taken back to New Zealand for scientific study. A study on the specimen later showed that its actual weight was 495 kg (1,091 lb), but that it only measured 4.2 m (14 ft) in total length as a result of the tentacles shrinking *post mortem*.

Largest known specimen



This specimen, caught in early 2007, is the largest cephalopod ever recorded. Here it is shown in its live state during capture, with the delicate red skin still intact and the mantle characteristically inflated.

On February 22, 2007, it was announced by authorities in New Zealand that the largest known Colossal Squid had been captured. The specimen weighed 495 kg (1,091 lb) and was initially estimated to measure 10 m (33 ft) in total length. Fishermen on the vessel *San Aspiring*, owned by the Sanford seafood company, caught the animal in the freezing Antarctic waters of the Ross Sea. It was brought to the surface as it fed on an Antarctic toothfish that had been caught off a long line. It would not let go of its prey and could not be removed from the line by the fishermen, so they decided to catch it instead. They managed to envelop it in a net, hauled it aboard and froze it. The specimen eclipsed the previous largest find in 2003 by about 195 kilograms (430 lb), although it is still considerably smaller than some estimates have predicted. The specimen was frozen in a cubic metre of water and transported to the Museum of New Zealand Te Papa Tongarewa, New Zealand's national museum. Media reports suggested that scientists at the museum were considering using a giant microwave to defrost the squid because defrosting the squid at room temperatures would take days and it would be likely for the outside to rot while the core remained frozen. However, they later opted for the more conventional approach of thawing the specimen in a bath of salt water. After thawing, the squid measured only 4.2 m (14 ft) in total length, with the tentacles having shrunk significantly. Although initially thought to be a male, closer inspection of the specimen showed it to be a female.

Defrosting and dissection, April-May 2008

Thawing and dissection of the specimen took place at the Museum of New Zealand Te Papa Tongarewa under the direction of senior biologist Chris Paulin, with technician Mark Fenwick, Dutch marine biologist and toxicologist Olaf Blaauw, AUT biologist Dr Steve O'Shea, Dr Tsunemi Kubodera, and AUT biologist Kat Bolstad.

Parts of the specimen have been examined:

- The beak is considerably smaller than some found in the stomachs of sperm whales, suggesting there are Colossal Squid much larger than this one.
- The eye is 27 cm (10.63 in) wide, with a lens 12 cm across. This is the largest eye of any known animal. These measurements are of the partly collapsed specimen: when living the eye was probably 30 to 40 cm (12 to 16 in) across.
- Inspection of the specimen with an endoscope revealed ovaries containing thousands of eggs.

Exhibition

The specimen on display at the Museum of New Zealand Te Papa Tongarewa

The Museum of New Zealand Te Papa Tongarewa is displaying this specimen in an exhibition which opened on December 13, 2008. A website on the squid specimen is also available.

Chapter 6

Giant Clam

Giant Clam	
	
Conservation status	
	
Vulnerable (IUCN 2.3)	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Bivalvia
Subclass:	Heterodonta
Infraclass:	Euheterodonta
Order:	Euheterodonta *incertae sedis*
Superfamily:	Cardioidea
Subfamily:	Tridacninae
Genus:	*Tridacna*
Subgenus:	*Tridacna (Tridacna)*
Species:	***T. gigas***
Binomial name	
Tridacna (Tridacna) gigas	

(Linnaeus, 1758)

Synonyms

Chama gigantea Perry, 1811

The **giant clam**, *Tridacna gigas* (known as *pā'ua* in Cook Islands Māori), is the largest living bivalve mollusc. *T. gigas* is one of the most endangered clam species. It was mentioned as early as 1825 in scientific reports. One of a number of large clam species native to the shallow coral reefs of the South Pacific and Indian oceans, they can weigh more than 200 kilograms (441 lb) measure as much as 120 cm (47.2 in) across, and have an average lifespan in the wild of 100 years or more. They are also found off the shores of the Philippines, where they are called **taklobo**. *T. gigas* lives in flat coral sand or broken coral and can be found at depth of as much as 20 m (66 ft). Its range covers the Indo-Pacific, but populations are diminishing quickly and the giant clam has become extinct in many areas where it was once common. *T. maxima* has the largest geographical distribution among giant clam species; it can be found in high- or low-islands, lagoons, or fringeing reefs. Its rapid growth rate is likely due to its ability to cultivate plants in its body tissue.

Although larval clams are planktonic, they become sessile in adulthood. The creature's mantle tissues act as a habitat for the symbiotic single-celled dinoflagellate algae (zooxanthellae) from which it gets nutrition. By day, the clam opens its shell and extends its mantle tissue so that the algae receive the sunlight they need to photosynthesize.

Anatomy

Young *T. gigas* are difficult to distinguish from other species of Tridacnidae. Adult *T. gigas* are the only giant clams unable to close their shells completely. Even when closed, part of the mantle is visible, unlike the very similar *T. derasa*. However, this can only be recognized with increasing age and growth. Small gaps always remain between shells through which retracted brownish-yellow mantle can be seen.

T. gigas has four or five vertical folds in its shell; this is the main characteristic that separates it from the very similar shell of *T. derasa*, which has six or seven vertical folds. As with massive deposition of coral matrices composed of calcium carbonate, the bivalves containing zooxanthellae have a tendency to grow massive calcium carbonate shells. The mantle's edges are packed with symbiotic zooxanthellae that presumably utilize carbon dioxide, phosphates, and nitrates supplied by the clam.

Largest Specimens

The largest known *T. gigas* specimen measured 137 cm. It was discovered around 1817 on north western coast of Sumatra. The weight of the two shells was 230 kilograms (507 lb). This suggests that the live weight of the animal would have been roughly 250 kilograms (551 lb). Today these shells are on display in a museum in Northern Ireland.

Another unusually large giant clam was found in 1956 off the Japanese island of Ishigaki. However, it was not examined scientifically before 1984. The shell's length was 115 cm and the weight of the shells and soft parts was 333 kilograms (734 lb). Scientists estimated the live weight to be around 340 kilograms (750 lb).

Ecology

Feeding

Algae provide giant clams with a supplementary source of nutrition. These plants consist of unicellular algae, whose metabolic products add to the clam's filter food. As a result, they are able to grow as large as100 cm length even in nutrient-poor coral-reef waters. The clams cultivate algae in a special circulatory system which enables them to keep a substantially higher number of symbionts per unit of volume.

In small clams—10 milligrams (0.010 g) dry tissue weight—filter feeding provides about 65% of total carbon needed for respiration and growth; large clams (10 g) acquire only 34% of carbon from this source. A single species of zooxenthellae may be symbionts of both giant clams and nearby reef–building (hermatypic) corals.

Reproduction

T. gigas reproduce sexually, and are hermaphrodites (producing both eggs and sperm). Self-fertilization is not possible but, this characteristic does allow them to reproduce with any other member of the species. This reduces the burden of finding a compatible mate, while simultaneously doubling the number of offspring produced by the process. As with all other forms of sexual reproduction, hermaphroditism ensures that new gene combinations are passed to further generations.

Since giant clams cannot move themselves, they adopt broadcast spawning. They release sperm and eggs into the water. A transmitter substance called Spawning Induced Substance (SIS) helps synchronize the release of sperm and eggs to ensure fertilization. The substance is released through a syphonal outlet. Other clams can detect SIS immediately. Incoming water passes chemoreceptors situated close to the inccurent syphon, which transmit the information directly to the cerebral ganglia, a simple form of brain.

Detection of SIS stimulates the giant clam to swell its mantle in the central region and to contract its adductor muscle. Each clam then fills its water chambers and closes the incurrent syphon. The shell contracts vigorously with the adductor's help, so the excurrent chamber's contents flows through the excurrent syphon. After a few contractions containing only water, eggs and sperm appear in the excurrent chamber and then pass through the excurrent syphon into the water. Female eggs have a diameter of 100 micrometres (0.0039 in). Egg release initiates the reproductive process. An adult *T. gigas* can release more than 500 million eggs at a time.

Richard D. Braley of the University of New South Wales School of Zoology observed that spawning seems to coincide with incoming tides near the second (full), third, and fourth (new) quarters of the moon phase. Spawning contractions occurred every 2–3 minutes, with intense spawning ranging from thirty minutes to two and a half hours. Braley also hypothesized that clams that do not respond to the spawning of neighbor clams may be reproductively inactive.

Development

The fertilized egg floats in the sea for about 12 hours until eventually a larva (trocophore) hatches. It then starts to produce a chalk shell. Two days after fertilization it measures 160 micrometres (0.0063 in). Soon it develops a "foot," which is used to move on the ground; it can also swim to search for appropriate habitat.

At roughly one week of age, the clam settles on the ground, although it changes location frequently within the first few weeks. The larva does not yet have symbiotic algae, so it depends completely on plankton. Free floating zooxanthellae are also captured while filtering food. Eventually the front adductor muscle disappears and the rear muscle moves into the clam's center. Many small clams die at this stage. The clam is considered a juvenile when it reaches a length of 20 cm . It is difficult to observe the growth rate of *T. gigas* in the wild, but laboratory-reared giant clams have been observed to grow 12 cm a year.

Relation to People

The main reason that giant clams are becoming endangered is likely to be intensive exploitation by mussel-catching vessels. Mainly large adults are killed since they are the most profitable.

The giant clam is considered a delicacy in Japan (known as *Himejako*), France, South East Asia and many Pacific Islands. Some Asian foods include the meat from the muscles of clam. On the black market, giant clam shells are sold as decorative accouterments. At times large amounts of money were paid for the adductor muscle, which Chinese people believed have aphrodisiac powers.

Legend

As is often the case with uncharacteristically large species, the giant clam has been historically misunderstood. It was known in times past as the *killer clam* or *man-eating clam*, and reputable scientific and technical manuals once claimed that the great mollusc had caused deaths; versions of the *U.S. Navy Diving Manual* even gave detailed instructions for releasing oneself from its grasp by severing the adductor muscles used to close its shell.

In a colorful account of the discovery of the Pearl of Lao Tzu, Wilburn Cobb said he was told that a Dyak diver was drowned when the *Tridacna* closed its shell on his arm.

Today the giant clam is considered neither aggressive nor particularly dangerous. While it is certainly capable of gripping a person, the shell's closing action is defensive, not aggressive and the shell valves close too slowly to pose a serious threat. Furthermore, many large individuals are unable to completely close their shells.

Aquaculture

Mass culture of giant clams began at the Micronesian Mariculture Demonstration Center in Palau (belau). A large Australian government-funded project from 1985-1992 mass cultured giant clams, particularly T. gigas at James Cook University's Orpheus Island Research Station, and supported the development of hatcheries in the Pacific Islands and the Philippines. Recent developments in aquaculture, specifically at Harbor Branch Oceanographic Institute in Ft. Pierce, Florida, and in the Marshall Islands, have succeeded in tank-raising *T. gigas* both for use in home aquariums and for release into the wild.

Conservation status

The IUCN lists the giant clams as vulnerable. There is concern among conservationists about whether those who use the species as a source of livelihood are overexploiting it. The numbers in the wild have been greatly reduced by extensive harvesting for food and the aquarium trade.

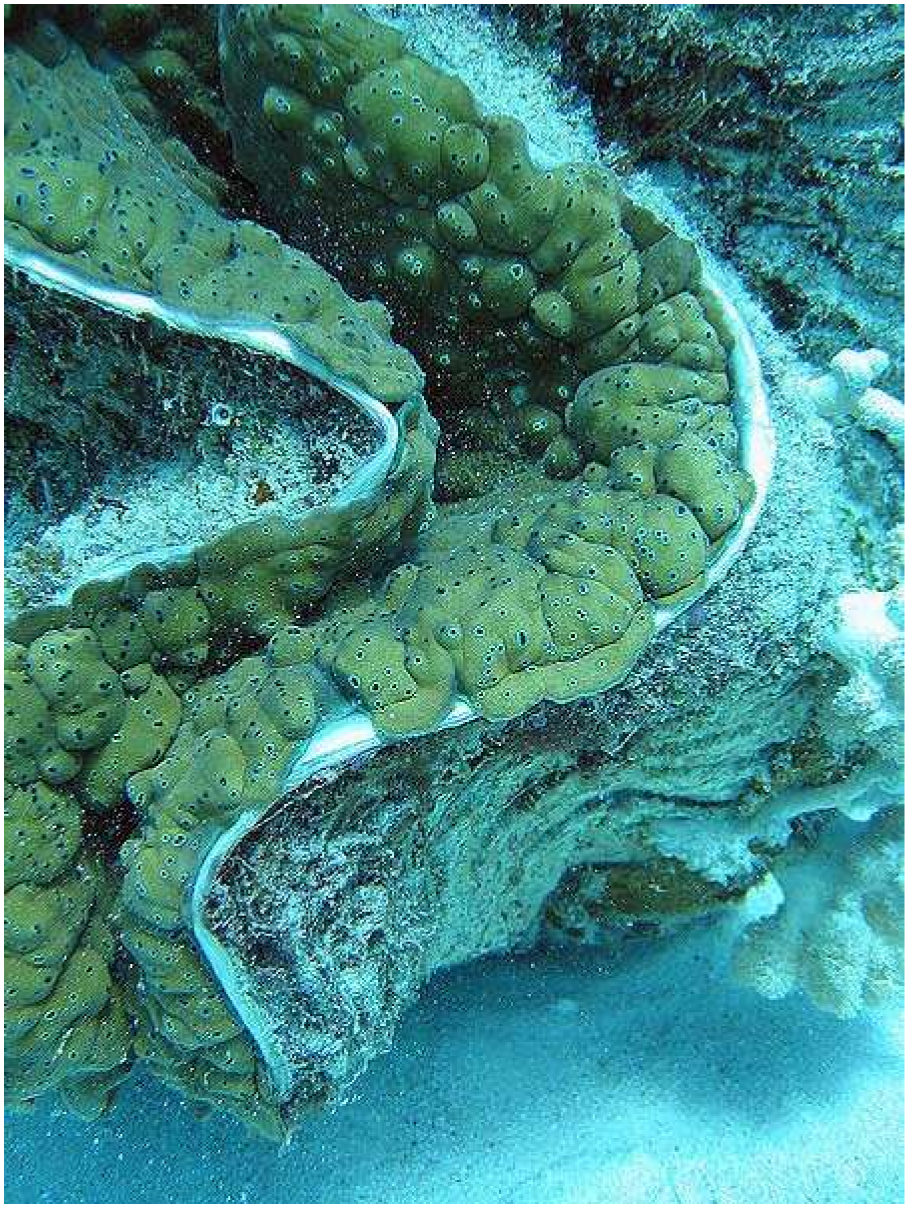
Green and blue giant clam from East Timor

Camouflaged giant clam

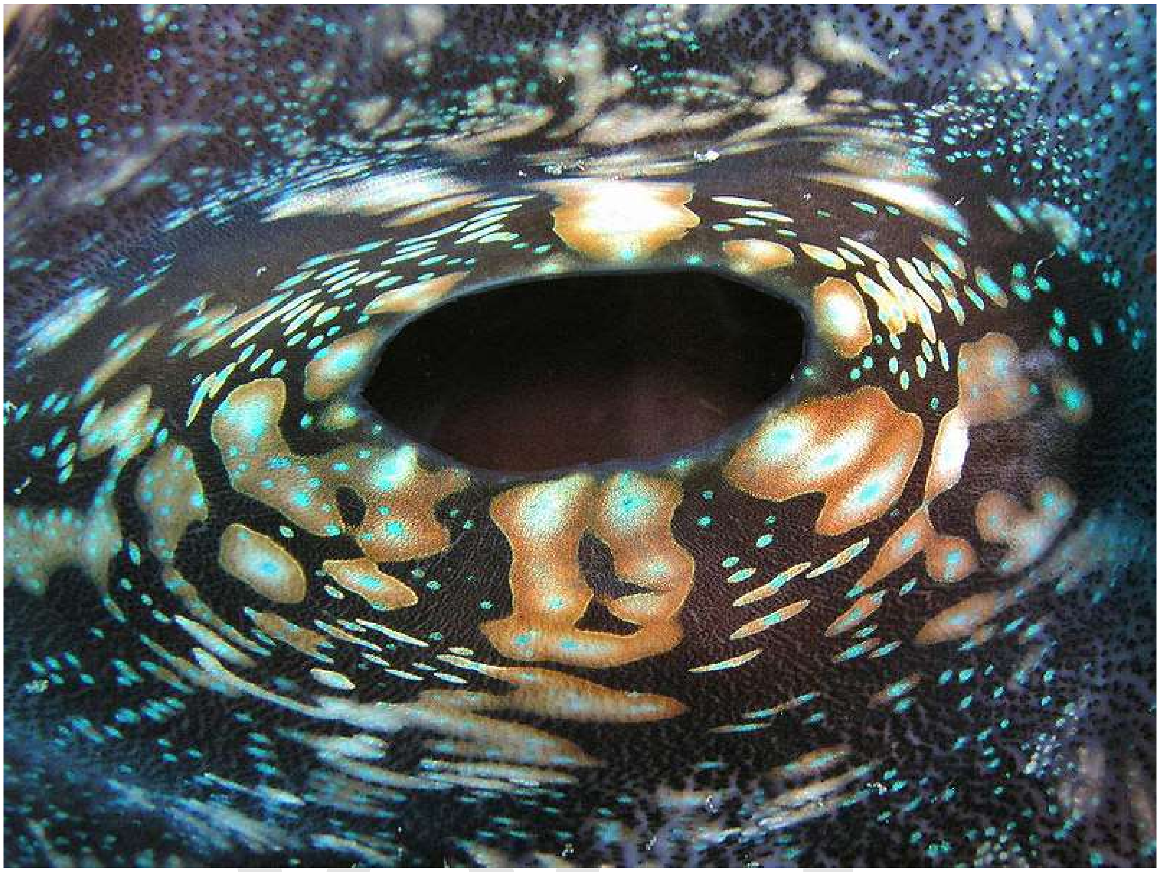
Colorful giant clam from Komodo National Park

Fully opened giant clam from Komodo National Park

The largest of all clam species



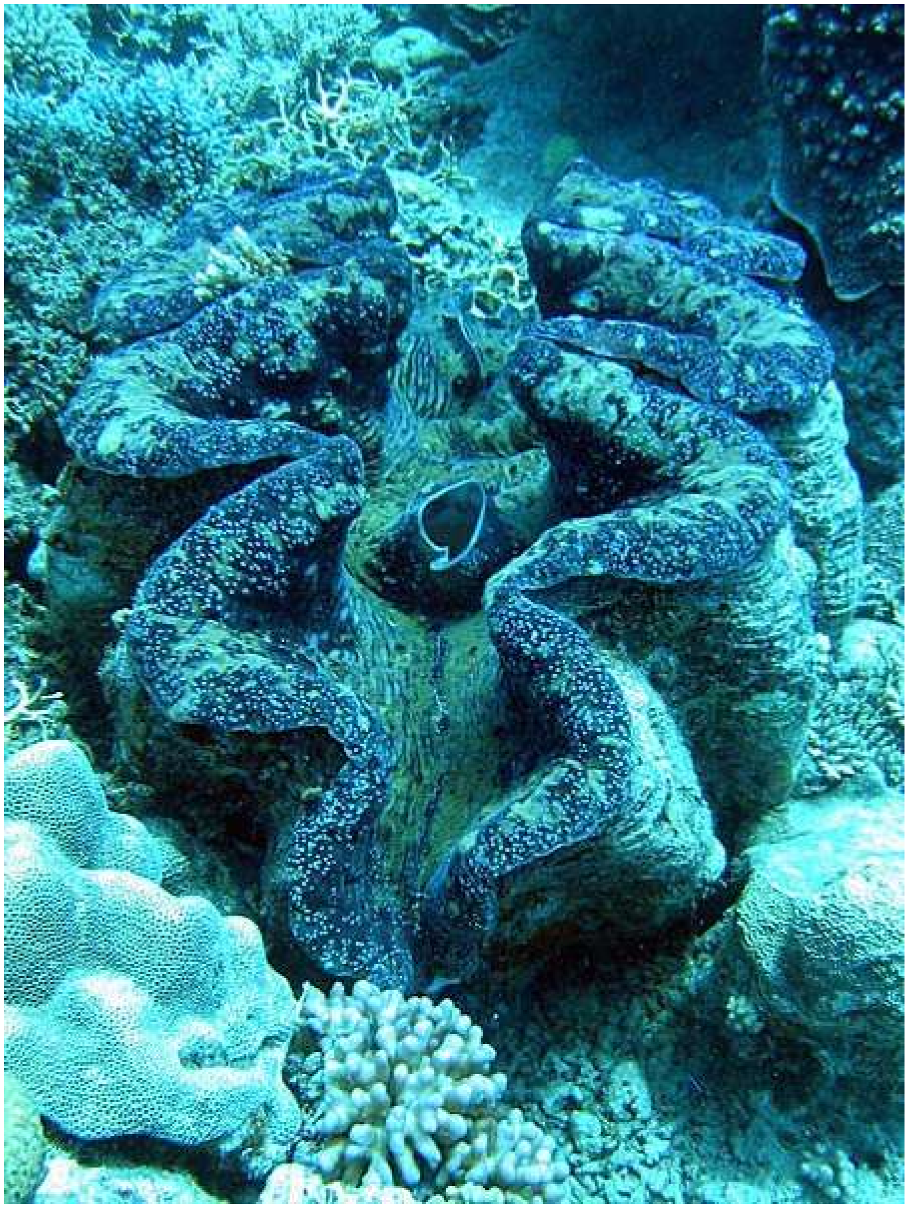
Mantle detail 1



Giant clam siphon

Crocus giant clam

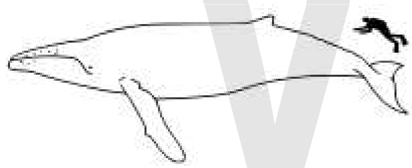
A giant clam from East Timor of over 1 meter in length.



Chapter 7

Humpback Whale

Humpback whale	



Size comparison against an average human

Conservation status

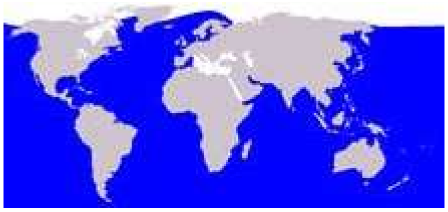
Least Concern (IUCN 3.1)

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Subclass:	Eutheria
Order:	Cetacea
Suborder:	Mysticeti
Family:	Balaenopteridae
Genus:	***Megaptera*** Gray, 1846

Species: ***M. novaeangliae***

Binomial name
Megaptera novaeangliae Borowski, 1781



Humpback whale range

The **humpback whale** (*Megaptera novaeangliae*) is a species of baleen whale. One of the larger rorqual species, adults range in length from 12–16 metres (39–52 ft) and weigh approximately 36,000 kilograms (79,000 lb). The humpback has a distinctive body shape, with unusually long pectoral fins and a knobbly head. It is an acrobatic animal, often breaching and slapping the water. Males produce a complex whale song, which lasts for 10 to 20 minutes and is repeated for hours at a time. The purpose of the song is not yet clear, although it appears to have a role in mating.

Found in oceans and seas around the world, humpback whales typically migrate up to 25,000 kilometres (16,000 mi) each year. Humpbacks feed only in summer, in polar waters, and migrate to tropical or sub-tropical waters to breed and give birth in the winter. During the winter, humpbacks fast and live off their fat reserves. The species' diet consists mostly of krill and small fish. Humpbacks have a diverse repertoire of feeding methods, including the bubble net feeding technique.

Like other large whales, the humpback was and is a target for the whaling industry. Due to over-hunting, its population fell by an estimated 90% before a whaling moratorium was introduced in 1966. Stocks have since partially recovered; however, entanglement in fishing gear, collisions with ships, and noise pollution also remain concerns. There are at least 80,000 humpback whales worldwide. Once hunted to the brink of extinction, humpbacks are now sought by whale-watchers, particularly off parts of Australia, New Zealand, South America, Canada, and the United States.

Taxonomy

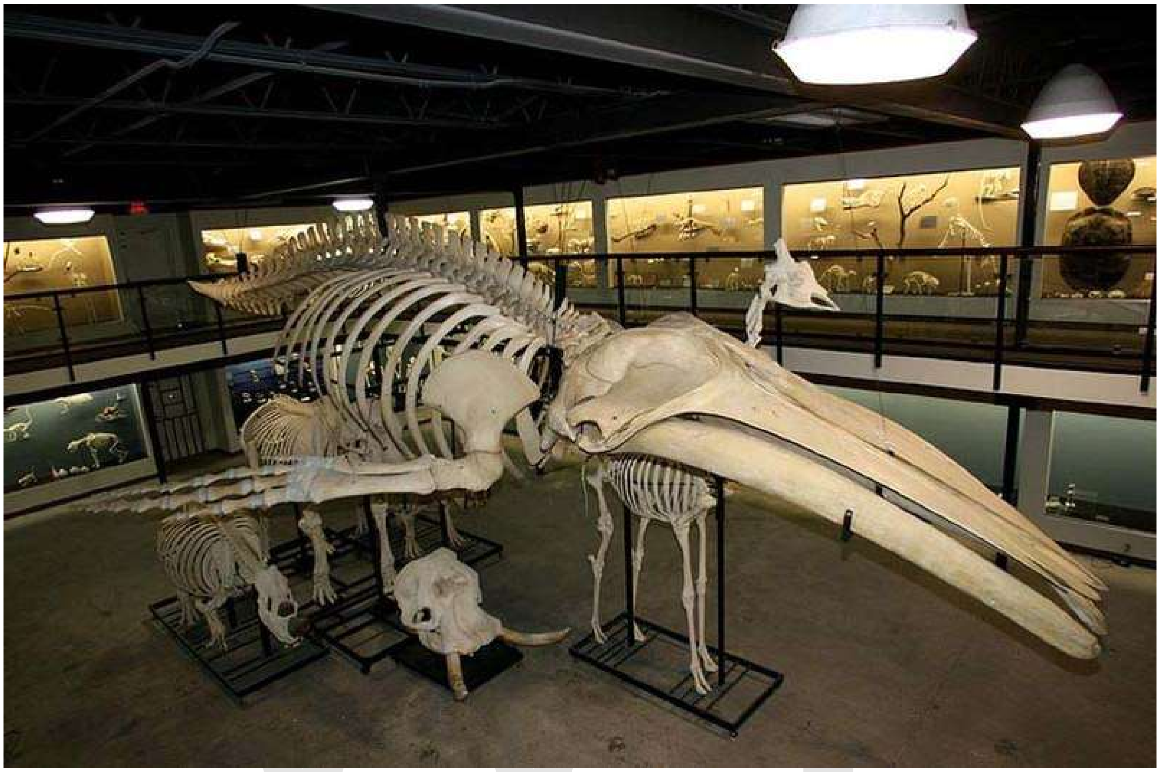
Young whale with blowholes clearly visible

Humpback whales are rorquals (family Balaenopteridae), a family that includes the blue whale, the fin whale, the Bryde's whale, the sei whale and the minke whale. The rorquals are believed to have diverged from the other families of the suborder Mysticeti as long ago as the middle Miocene. However, it is not known when the members of these families diverged from each other.

Though clearly related to the giant whales of the genus *Balaenoptera*, the humpback has been the sole member of its genus since Gray's work in 1846. More recently though, DNA sequencing analysis has indicated the Humpback is more closely related to the gray whale (*Eschrichtius robustus*) and to certain rorquals, such as the fin whale (*Balaenoptera physalus*) than it is to other rorquals such as the minke whales. If further research confirms these relationships, it will be necessary to reclassify the rorquals.

The humpback whale was first identified as "*baleine de la Nouvelle Angleterre*" by Mathurin Jacques Brisson in his *Regnum Animale* of 1756. In 1781, Georg Heinrich Borowski described the species, converting Brisson's name to its Latin equivalent, *Balaena novaeangliae*. Early in the 19th century Lacépède shifted the humpback from the Balaenidae family, renaming it *Balaenoptera jubartes*. In 1846, John Edward Gray created the genus *Megaptera*, classifying the humpback as *Megaptera longpinna*, but in 1932, Remington Kellogg reverted the species names to use Borowski's *novaeangliae*. The common name is derived from the curving of their back when diving. The generic name *Megaptera* from the Greek *mega-*/μεγα- "giant" and *ptera*/πτερα "wing", refers to their large front flippers. The specific name means "New Englander" and was probably given by Brisson due the regular sightings of humpbacks off the coast of New England.

Description



Humpback Whale Skeleton on Display at The Museum of Osteology, Oklahoma City, Oklahoma

A diving humpback whale, showing hump and tail fins

Humpback whales can easily be identified by their stocky bodies with obvious humps and black dorsal coloring. The head and lower jaw are covered with knobs called tubercles, which are actually hair follicles and are characteristic of the species. The fluked tail, which it lifts above the surface in some dive sequences, has wavy trailing edges. There are four global populations, all under study. North Pacific, Atlantic, and Southern Ocean humpbacks have distinct populations which complete a migratory roundtrip each year. The Indian Ocean population does not migrate, prevented by that ocean's northern coastline.

The long black and white tail fin, which can be up to a third of body length, and the pectoral fins have unique patterns, which make individual whales identifiable. Several hypotheses attempt to explain the humpback's pectoral fins, which are proportionally the longest fins of any cetacean. The two most enduring mention the higher maneuverability afforded by long fins, and the usefulness of the increased surface area for temperature control when migrating between warm and cold climates. Humpbacks also have 'rete mirable', a heat exchanging system, which works similarly in humpbacks, sharks and other fish.

A humpback whale tail displaying wavy rear edges

A tail from a different individual - the tail of each humpback whale is visibly unique.

Humpbacks have 270 to 400 darkly coloured baleen plates on each side of the mouth. The plates measure from a mere 18 inches (46 cm) in the front to approximately 3 feet (0.91 m) long in the back, behind the hinge. Ventral grooves run from the lower jaw to the umbilicus about halfway along the underside of the whale. These grooves are less numerous (usually 16–20) and consequently more prominent than in other rorquals.

The stubby dorsal fin is visible soon after the blow when the whale surfaces, but disappears by the time the flukes emerge. Humpbacks have a 3 metres (9.8 ft) heart-shaped to bushy blow, or exhalation of water through the blowholes. Because Humpback Whales breathe voluntarily, researchers have said that it is possible that the whales shut off only half of the brain when sleeping. Early whalers also noted blows from humpback adults to be 10–20 feet (3.0–6.1 m) high.

Newborn calves are roughly the length of their mother's head. At birth, calves measure 20-foot (6.1 m) at 2 short tons (1.8 t) The mother, by comparison, is about 50-foot (15 m). They nurse for approximately six months, then mix nursing and independent feeding for possibly six months more. Humpback milk is 50% fat and pink in color. Some calves have been observed alone after arrival in Alaskan waters.

Females reach sexual maturity at the age of five, achieving full adult size a little later. Males reach sexual maturity at approximately 7 years of age. The humpback whale lifespan ranges from 45-100 years.

Fully grown, the males average 15–16 metres (49–52 ft). Females are slightly larger at 16–17 metres (52–56 ft), and 40,000 kilograms (44 short tons); the largest recorded specimen was 19 metres (62 ft) long and had pectoral fins measuring 6 metres (20 ft) each.

Females have a *hemispherical lobe* about 15 centimetres (5.9 in) in diameter in their genital region. This visually distinguishes males and females. The male's penis usually remains hidden in the genital slit. Male whales have distinctive scars on heads and bodies, some resulting from battles over females.

Identifying individuals

The varying patterns on the tail flukes are sufficient to identify individuals. Unique visual identification is not currently possible in most cetacean species (other exceptions include orcas and right whales), making the humpback a popular study species. A study using data from 1973 to 1998 on whales in the North Atlantic gave researchers detailed information on gestation times, growth rates, and calving periods, as well as allowing more accurate population predictions by simulating the mark-release-recapture technique (Katona and Beard 1982). A photographic catalogue of all known North Atlantic whales was developed over this period and is currently maintained by College of the Atlantic. Similar photographic identification projects have begun in the North Pacific by SPLASH (Structure of Populations, Levels of Abundance and Status of Humpbacks), and around the world.

Life history

Reproduction

Females typically breed every two or three years. The gestation period is 11.5 months, yet some individuals have been known to breed in two consecutive years. The peak months for birth are January, February, July, and August. There is usually a 1-2 year period between humpback births. Humpback whales were thought to live 50–60 years, but new studies using the changes in amino acids behind eye lenses proved another baleen whale, the bowhead, to be 211 years old. This animal was taken by the Inuit off Alaska.

Recent research on humpback mitochondrial DNA reveals that groups that live in proximity to each other may represent distinct breeding pools.

Social structure

Humpbacks frequently breach, throwing two thirds or more of their bodies out of the water and splashing down on their backs.

The humpback social structure is loose-knit. Typically, individuals live alone or in small, transient groups that disband after a few hours. These whales are not excessively social in most cases. Groups may stay together a little longer in summer to forage and feed cooperatively. Longer-term relationships between pairs or small groups, lasting months or even years, have rarely been observed. It is possible that some females retain bonds created via cooperative feeding for a lifetime. The humpback's range overlaps considerably with other whale and dolphin species — for instance, the minke whale. However, humpbacks rarely interact socially with them, though humpback calves in Hawaiian waters sometimes play with bottlenose dolphin calves.

Courtship

Courtship rituals take place during the winter months, following migration toward the equator from summer feeding grounds closer to the poles. Competition is usually fierce, and unrelated males dubbed *escorts* by researcher Louis Herman frequently trail females as well as mother-calf dyads. Groups of two to twenty males gather around a single female and exhibit a variety of behaviors over several hours to establish dominance of what is known as a *competitive group*. Group size ebbs and flows as unsuccessful males retreat and others arrive to try their luck. Behaviors include breaching, spy-hopping, lob-tailing, tail-slapping, fin-slapping, peduncle throws, charging and parrying. Less common "super pods" may number more than 40 males, all vying for the same female. (M. Ferrari et al.)

Whale song is assumed to have an important role in mate selection; however, scientists remain unsure whether song is used between males to establish identity and dominance, between a male and a female as a mating call, or both.

Ecology

Humpback swimming on its back in Antarctica

Feeding

A group of 15 whales bubble net fishing near Juneau, Alaska

Aerial view of a bubble net off Cape Fanshaw, Alaska

A whale off Australia on the spring migration, feeding on krill by turning on its side and propelling through the krill.

Humpbacks feed primarily in summer and live off fat reserves during winter. They feed only rarely and opportunistically in their wintering waters. The humpback is an energetic hunter, taking krill and small schooling fish, such as herring *(Clupea harengus)*, salmon *(Salmo salar)*, capelin *(Mallotus villosus)* and sand lance *(Ammodytes americanus)* as well as mackerel *(Scomber scombrus)*, pollock *(Pollachius virens)* and haddock *(Melanogrammus aeglefinus)* in the North Atlantic. Krill and copepods have been recorded from Australian and Antarctic waters. Humpbacks hunt by direct attack or by stunning prey by hitting the water with pectoral fins or flukes.

A pair of humpback whales feeding by lunging

The humpback has the most diverse feeding repertoire of all baleen whales. Its most inventive technique is known as *bubble net feeding*: a group of whales swims in a shrinking circle blowing bubbles below a school of prey. The shrinking ring of bubbles encircles the school and confines it in an ever-smaller cylinder. The whales then suddenly swim upward through the 'net', mouths agape, swallowing thousands of fish in one gulp. The plated grooves in the whales mouth allow the creature to easily drain all the water that was initially taken in.This ring can begin at up to 30 metres (98 ft) in diameter via the cooperation of a dozen animals. Using a crittercam attached to a whale's back it was discovered that some whales blow the bubbles, some dive deeper to drive fish toward the surface, and others herd prey into the net by vocalizing. Humpbacks have been observed bubble net feeding alone as well.

Predation

Given scarring records, killer whales are thought to prey upon juvenile humpbacks, though this has never been witnessed. The result of these attacks is generally nothing more serious than some scarring of the skin, but it is likely that young calves are sometimes killed.

Range and habitat

Humpbacks inhabit all major oceans, in a wide band running from the Antarctic ice edge to 65° N latitude, though not in the eastern Mediterranean or the Baltic Sea.

Humpbacks are migratory, spending summers in cooler, high-latitude waters and mating and calving in tropical and subtropical waters. An exception to this rule is a population in the Arabian Sea, which remains in these tropical waters year-round. Annual migrations of up to 25,000 kilometres (16,000 mi) are typical, making it one of the mammal's best-traveled species.

A large population spreads across the Hawaiian islands every winter, ranging from the island of Hawaii in the south to Kure Atoll in the north. A 2007 study identified seven individuals wintering off the Pacific coast of Costa Rica as having traveled from the Antarctic—around 8,300 kilometres (5,200 mi). Identified by their unique tail patterns, these animals made the longest documented mammalian migration.

In Australia, two main migratory populations have been identified, off the west and east coast respectively. These two populations are distinct, with only a few females in each generation crossing between the two groups.

Whaling

One of the first attempts to hunt humpbacks was made by John Smith in 1614 off the coast of Maine. Opportunistic hunting is likely to have occurred long before. By the 18th century, they had become a common target for whalers.

By the 19th century, many nations (the United States in particular), were hunting the animal heavily in the Atlantic Ocean, and to a lesser extent in the Indian and Pacific Oceans. It was, however, the late 19th century introduction of the explosive harpoon that allowed whalers to accelerate their take. This, along with hunting in the Antarctic Ocean beginning in 1904, sharply reduced whale populations.

It is estimated that during the 20th century, at least 200,000 humpbacks were taken, reducing the global population by over 90%, with North Atlantic populations estimated to have dropped to as low as 700 individuals. In 1946, the International Whaling Commission was founded to oversee the whaling industry. They imposed rules and regulations for hunting whales and set open and closed hunting seasons. To prevent extinction, the International Whaling Commission banned commercial humpback whaling in 1966. By that time the population had been reduced to around 5,000. That ban is still in force.

Prior to commercial whaling, populations could have reached 125,000. North Pacific kills alone are estimated at 28,000. The full toll is much higher. It is now known that the Soviet Union was deliberately under-recording its kills; the Soviet kill was reported at 2,820 whereas the true number is now believed to be over 48,000.

As of 2004, hunting of humpback whales is restricted to a few animals each year off the Caribbean island Bequia in the nation of St. Vincent and the Grenadines. The take is not believed to threaten the local population.

Japan had planned to kill 50 humpbacks in the 2007/08 season under its JARPA II research program, starting in November 2007. The announcement sparked global protests. After a visit to Tokyo by the chairman of the IWC, asking the Japanese for their co-operation in sorting out the differences between pro- and anti-whaling nations on the Commission, the Japanese whaling fleet agreed that no humpback whales would be caught for the two years it would take for the IWC to reach a formal agreement.

Conservation

A dead humpback washed up near Big Sur, California

There are at least 80,000 humpback whales worldwide, with 18,000-20,000 in the North Pacific, about 12,000 in the North Atlantic, and over 50,000 in the Southern Hemisphere, down from a pre-whaling population of 125,000.

This species is considered "least concern" from a conservation standpoint, as of 2008. This is an improvement from vulnerable in the prior assessment. Most monitored stocks of humpback whales have rebounded well since the end of commercial whaling. such as the North Atlantic where stocks are now believed to be approaching pre-hunting levels. However, the species is considered endangered in some countries, including the United States. The United States initiated a status review of the species on August 12, 2009, and is seeking public comment on potential changes to the species listing under the U.S. Endangered Species Act. Areas where population data is limited and the species may be at higher risk include the Arabian Sea, the western North Pacific Ocean, the west coast of Africa and parts of Oceania.

Today, individuals are vulnerable to collisions with ships, entanglement in fishing gear, and noise pollution. Like other cetaceans, humpbacks can be injured by excessive noise. In the 19th century, two humpback whales were found dead near sites of repeated oceanic sub-bottom blasting, with traumatic injuries and fractures in the ears.

Once hunted to the brink of extinction, the humpback has made a dramatic comeback in the North Pacific. A 2008 study estimates that the humpback population that hit a low of 1,500 whales before hunting was banned worldwide, has made a comeback to a population of between 18,000 and 20,000.

Saxitoxin, a paralytic shellfish poisoning (PSP) from contaminated mackerel has been implicated in humpback whale deaths.

The United Kingdom, among other countries, designated the humpback as a priority species under the national Biodiversity Action Plan.

The sanctuary provided by U.S. National Parks such as Glacier Bay National Park and Preserve and Cape Hatteras National Seashore, among others, have also become major factors in sustaining populations.

Although much was learned about humpbacks from whaling, migratory patterns and social interactions were not well understood until two studies by R. Chittleborough and W. H. Dawbin in the 1960s. Roger Payne and Scott McVay made further studies of the species in 1971. Their analysis of whale song led to worldwide media interest and convinced the public mind that whales were highly intelligent, aiding the anti-whaling advocates.

In August 2008, the IUCN changed humpback's status from Vulnerable to Least Concern, although two subpopulations remain endangered.

The United States is considering listing separate humpback populations, so that smaller groups, such as North Pacific humpbacks, which are estimated to number 18,000-20,000 animals, might be delisted. This is made difficult by humpback's extraordinary migrations, which can extend the 5,157 miles (8,299 km) from Antarctica to Costa Rica.

Whale-watching

Humpback near Maui, HI

Humpback whales are generally curious about objects in their environment. Some individuals, referred to as "friendlies", approach whale-watching boats closely, often staying under or near the boat for many minutes. Because humpbacks are often easily approachable, curious, easily identifiable as individuals, and display many behaviors, they have become the mainstay of whale-watching tourism in many locations around the world. Hawaii has used the concept of "eco tourism" to use the species without killing them. This whale watching business attracts 1 million visitors a year, which results in a profit of $80 million.

There are many commercial whale-watching operations on both the humpback's summer and winter ranges:

	North Atlantic	North Pacific	Southern Hemisphere
Summer	New England, Nova Scotia and Newfoundland, the northern St. Lawrence River, the Snaefellsnes peninsula in the west of Iceland	California, Alaska, Oregon, Washington, British Columbia	Antarctica, Bahía Solano and Nuquí in Colombia
Winter	Samaná Province of the Dominican Republic, the Bay of Biscay France,	Hawaii, Baja, the Bahía de Banderas off Puerto Vallarta	Sydney, Byron Bay north of Sydney, Hervey Bay north of Brisbane, North and East of Cape Town, New Zealand,

the Tongan islands,

As with other cetacean species, however, a mother whale is generally extremely protective of her infant, and places herself between any boat and her calf before moving quickly away from the vessel. Skilled tour operators avoid stressing the mother.

Famous humpbacks

Migaloo

A presumably albino humpback whale that travels up and down the east coast of Australia has become famous in the local media, on account of its extremely rare all-white appearance. Migaloo is the only known all-white humpback whale in the world. First sighted in 1991 and believed to be 3–5 years old at that time, Migaloo is a word for "white fella" from one of the languages of the Aboriginals, the Indigenous Australians. Speculation about Migaloo's sex was resolved in October 2004 when researchers from Southern Cross University collected sloughed skin samples from Migaloo as he migrated past Lennox Head, and subsequent genetic analysis of the samples proved he is a male. Because of the intense interest, environmentalists feared that he was becoming distressed by the number of boats following him each day. In response, the Queensland and New South Wales governments introduce legislation each year to create a 500 m (1600 ft) exclusion zone around the whale. Recent close up pictures have shown Migaloo to have skin cancer and/or skin cysts as a result of his lack of protection from the sun.

In 2006, a white calf was spotted with a normal humpback mother in Byron Bay, New South Wales.

This current whale watching season, NSW Parks and Wildlife Services has been monitoring the movement of whales up and down its coastline and while Migaloo is yet to be spotted in warmer waters, an official sighting off Fraser Island has been recorded.

Humphrey

One of the most notable humpback whales is Humphrey the Whale, twice-rescued by The Marine Mammal Center and other concerned groups in California. In 1985, Humphrey swam into San Francisco Bay and then up the Sacramento River towards Rio Vista. Five years later, Humphrey returned and became stuck on a mudflat in San Francisco Bay immediately north of Sierra Point below the view of onlookers from the upper floors of the Dakin Building. He was pulled off the mudflat with a large cargo net and the help of the Coast Guard. Both times he was successfully guided back to the Pacific Ocean using a "sound net" in which people in a flotilla of boats made unpleasant noises behind the whale by banging on steel pipes, a Japanese fishing technique known as "oikami." At the same time, the attractive sounds of humpback whales preparing to feed were broadcast from a boat headed towards the open ocean. Since leaving the San Francisco Bay in 1990 Humphrey has been seen only once, at the Farallon Islands in 1991.

Delta and Dawn

A humpback whale mother and calf captivated the San Francisco Bay Area in May 2007. This pair appeared to have gotten lost on their Northern migration, swam into the bay and up the Sacramento River as far as the Port of Sacramento. First spotted on 13 May, the whales inspired intense news coverage and were named Delta and Dawn. Whale fans became worried as the whales, both injured with what were possibly cuts caused by boat propellers, continued their stay in the brackish waters, despite efforts to get them to return to the sea. Unexpectedly, on 20 May they headed back towards the bay, but they tarried near the Rio Vista bridge for 10 days. Finally, on Memorial Day weekend, they left Rio Vista, California; passing Tuesday night, 29 May, through the Golden Gate out to the Pacific Ocean.

Mister Splashy Pants

Mister Splashy Pants is a humpback in the south Pacific Ocean. It's being tracked with a satellite tag by Greenpeace as a part of its Great Whale Trail Expedition. The whale's name was chosen in an online poll that garnered attention from several websites, including Boing Boing and Reddit. The name "Mister Splashy Pants" received over 78% of the votes.

Colin

Colin was the name given to a presumably abandoned starving humpback calf that was discovered in August 2008 at Pittwater, north of Sydney, Australia. It attempted to suckle from moored boats to obtain food. Despite attempts to reunite the calf with whale pods by luring it out to sea, it returned to Pittwater. Opinion was divided on how best to handle the situation, with some advocating feeding artificial milk formula to the calf, and others advocating euthanasia.

Colin was euthanised on 22 August 2008 due to his deteriorating condition. The calf's plight gained media attention as far afield as the United States, United Kingdom, Italy, Netherlands, Russia, Canada and New Zealand.

A subsequent autopsy found that Colin was terminally ill with an emaciated pancreas, ulcers of the stomach and oesophagus, intestinal erosion and infected shark bites. The calf was estimated to be only 7 to 10 days old and must have been separated from its mother shortly after birth.

Thames beaching

On 12 September 2009, a humpback was seen in the London Thames for the first time ever. The 9.5m young male was found beached and dead near Dartford bridge two days later on 14 September. Initial examination of the body suggested death had been by starvation, without any explanation of why this had occurred. Experts suggested that such events as these indicated the expansion of the areas colonised by humpbacks.

"George & Gracie"

George and Gracie were a pair of fictional humpbacks which featured prominently in *Star Trek IV: The Voyage Home*. In the film, Earth is threatened by large object that transmits a signal disabling the global power system and causing extreme weather patterns to develop. Spock determines the alien signal matches the song of humpback whales, extinct on Earth since the mid-21st century (at least 200 years). The crew devises a plan to go back in time, before the extinction, and return with a whale. Arriving in the late 20th century, Kirk and Spock are able to quickly discover a pair of humpback whales, "George" and "Gracie", at the Cetacean Institute, an aquarium devoted exclusively to whales, and are told by the Institute's whale expert, Dr. Gillian Taylor, that the whales are shortly going to be released into the wild, making the pair ideal for their needs. Despite some upsets and the threat of whalers, the crew is able to return to the future, splashing down into San Francisco Bay, where Kirk releases the whales from the cargo hold. The whales respond to the alien signal, causing the object to restore Earth to its normal condition and to return to the depths of outer space.

Industrial Light & Magic created the visual effects. Most shots of the humpback whales were scale models shot at their studio or life-size animatronics shot at Paramount However, some of the shots, including a scene of a whale breaching are stock footage of actual animals.

Chapter 8

Haast's Eagle

Haast's Eagle

Artist's rendition of a Haast's Eagle attacking moa

Conservation status

Extinct (IUCN 3.1)

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Aves
Order:	Accipitriformes
Family:	Accipitridae
Genus:	†***Harpagornis***
Species:	†***H. moorei***

Binomial name

Harpagornis moorei

Haast, 1872

Haast's Eagle (*Harpagornis moorei*) was a species of massive eagles that once lived on the South Island of New Zealand. The species was the largest eagle known to have existed. Its prey consisted mainly of gigantic flightless birds that were unable to defend themselves from the striking force and speed of these eagles, which at times reached 80 km/h (50 mph). The Haast's Eagle became extinct about 1400 CE, when its major food sources, the moa, were hunted to extinction by humans living on the island and much of its dense-forest habitat was cleared.

Name

A model on display at Te Papa of a Haast's Eagle attacking a moa with its large talons

It is believed that these birds are described in many legends of the Māori, under the names *Pouakai*, *Hokioi*, or *Hakawai*. However, it has been ascertained that the "Hakawai" and "Hokioi" legends refer to the *Coenocorypha* snipe – in particular the extinct South Island subspecies. According to an account given to Sir George Gray, an early governor of New Zealand, Hokioi were huge black-and-white predators with a red crest and yellow-green tinged wingtips. In some Māori legends, Pouakai kill humans, which scientists believe could have been possible if the name relates to the eagle, given the massive size and strength of the bird.

Size and habits

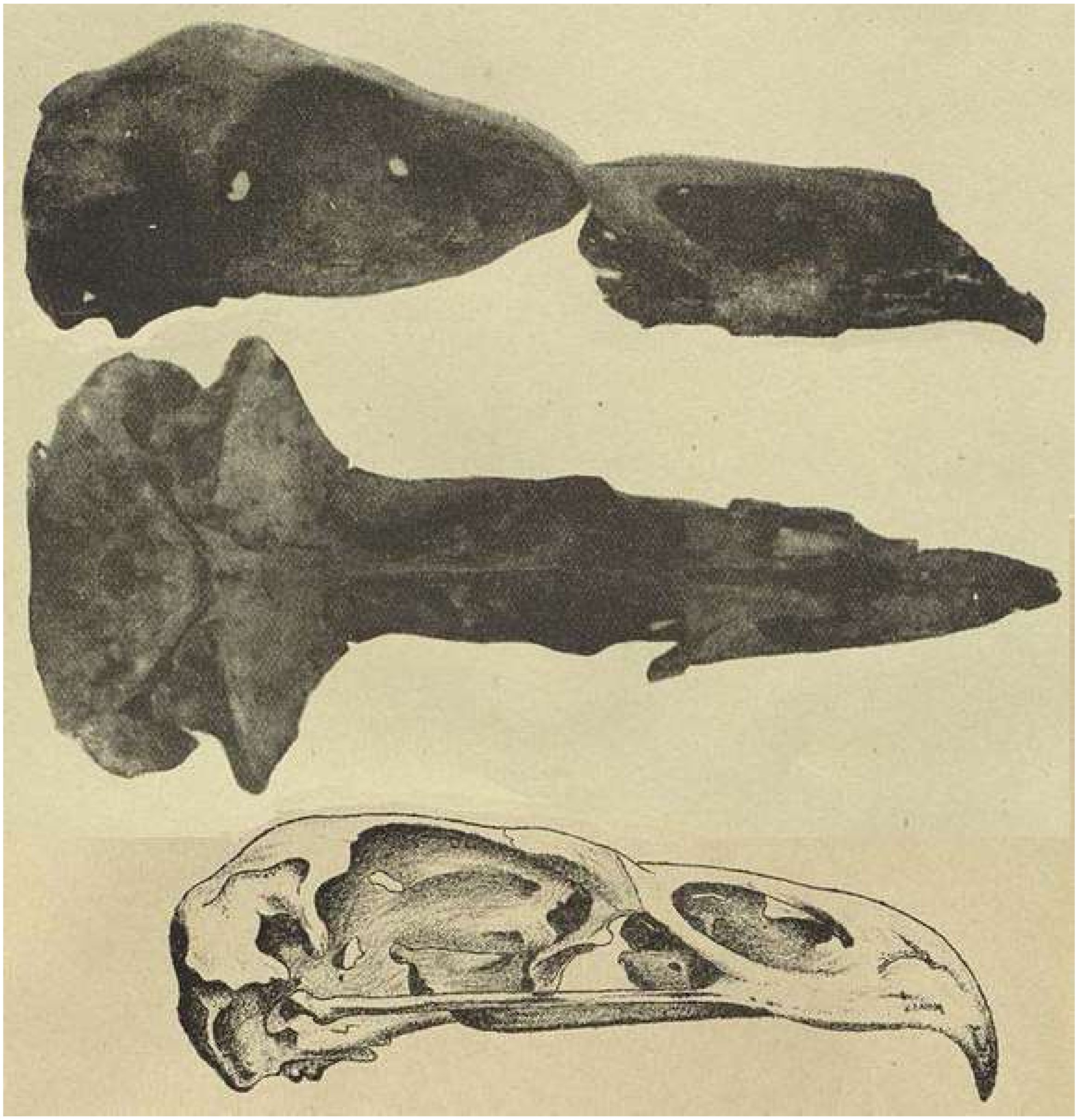
Haast's Eagles were the largest known true raptors, slightly larger even than the largest living vultures. Female eagles are significantly larger than males. Females of the Haast species are believed to have weighed 10–15 kg (22–33 lb) and males 9–12 kg (20–26 lb). They had a relatively short wingspan, measuring roughly 2.6–3 m (8 ft 6 in–9 ft 10 in). This wingspan is similar to that of some extant eagles (the wingspan now reported in large specimens of Golden Eagles and Steller's Sea Eagles). Even the largest extant eagles, however, are about forty percent smaller in body size than the size of Haast's Eagles.

Short wings may have aided Haast's Eagles when hunting in the dense scrubland and forests of New Zealand. Haast's Eagle sometimes is portrayed incorrectly as having evolved toward flightlessness, but this is not so; rather it represents a departure from the mode of its ancestors' soaring flight, toward higher wing loading.

The strong legs and massive flight muscles of these eagles would have enabled the birds to take off with a jumping start from the ground, despite their great weight. The tail was almost certainly long, up to 50 cm (20 inches) in female specimens, and very broad. This characteristic would compensate for the reduction in wing area by providing additional lift. Total length is estimated to have been up to 1.4 m (4 ft 7 in) in females, with a standing height of approximately 90 cm (2 ft 11 in) tall or perhaps slightly greater.

Haast's Eagles preyed on large, flightless bird species, including the moa, which was up to fifteen times the weight of the eagle. It is estimated to have attacked at speeds up to 80 km/h (50 mph), often seizing its prey's pelvis with the talons of one foot and killing with a blow to the head or neck with the other. Its size and weight indicate a bodily striking force equivalent to a cinder block falling from the top of an eight-storey building. Its large beak also could be used to rip into the internal organs of its prey and death then would have been caused by blood loss. In the absence of other large predators or scavengers, a Haast's Eagle easily could have monopolised a single large kill over a number of days.

Extinction



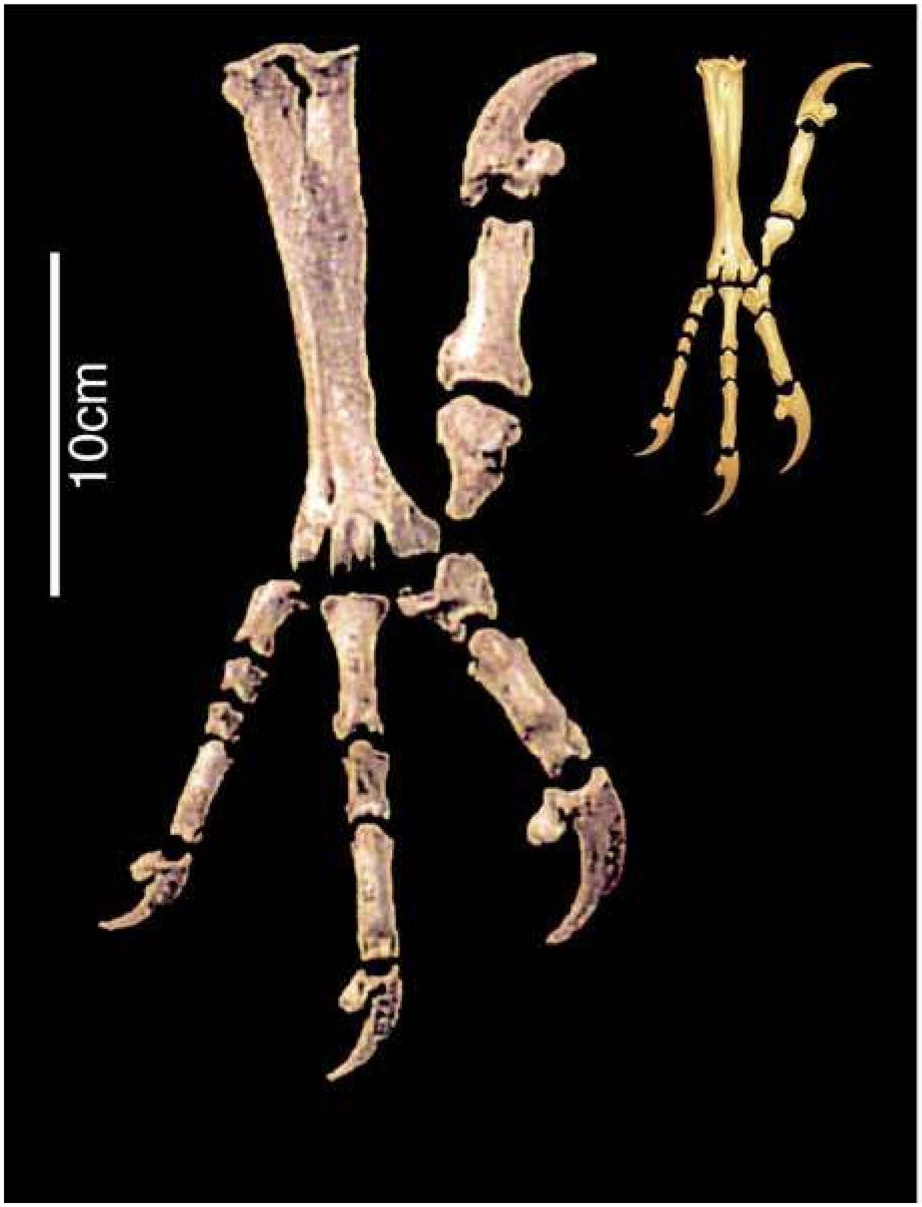
Skull

Early human settlers in New Zealand (the Māori arrived around 1280 CE) preyed heavily on large flightless birds, including all moa species, eventually hunting them to extinction. The loss of its natural prey caused the Haast's Eagle to become extinct as well around 1400 CE, when the last of its natural food sources were depleted.

A noted explorer, Charles Edward Douglas, claims in his journals that he had an encounter with two raptors of immense size in Landsborough River valley (probably during the 1870s), and that he shot and ate them. These birds might have been a last remnant of the species, but some might argue that there had not been suitable prey for a population of Haast's Eagle to maintain itself for about five hundred years before that date, and 19th century Māori lore was adamant that the *pouakai* was a bird not seen in living memory. Still, Douglas' observations on wildlife generally are trustworthy; a more probable explanation, given that the alleged three-metre wingspan described by Douglas is likely to have been a rough estimate, is that the birds were Eyles' Harriers. This was the largest known harrier (the size of a small eagle) — and a generalist predator — and although it is also assumed to have become extinct in prehistoric times, its dietary habits alone make it a more likely candidate for late survival.

Until recent human colonisation that introduced rodents and cats, the only mammals found on the islands of New Zealand were three species of bat, one of which recently has become extinct. Free from terrestrial mammalian competition and predatory threat, birds occupied or dominated all major niches in the New Zealand animal ecology because there were no threats to their eggs and chicks by small terrestrial animals. Moa were grazers, functionally similar to deer or cattle in other habitats, and Haast's Eagles were the hunters who filled the same niche as top-niche mammalian predators, such as tigers or lions.

Classification



Comparative morphology of Haast's Eagle with its closest living relative, the Little Eagle

DNA analysis has shown that this raptor is related most closely to the much smaller Little Eagle as well as the Booted Eagle (both of these two species were recently reclassified as belonging to the genus *Aquila*) and not, as previously thought, to the large Wedge-tailed Eagle. Thus, *Harpagornis moorei* may be reclassified as *Aquila moorei*, pending confirmation. *H. moorei* may have diverged from these smaller eagles as recently as 700,000 to 1.8 million years ago. Its increase in weight by ten to fifteen times over that period is the greatest and quickest evolutionary increase in weight of any known vertebrate. This was made possible in part by the presence of large prey and the absence of competition from other large predators.

Haast's Eagle was first classified by Julius von Haast in the 1870s, who named it *Harpagornis moorei* after George Henry Moore, the owner of the Glenmark Estate where bones of the bird had been found.

Chapter 9

Lion's Mane Jellyfish

Lion's mane jellyfish	
	
Conservation status	
Not evaluated (IUCN 3.1)	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Cnidaria
Subphylum:	Medusozoa
Class:	Scyphozoa
Order:	Semaeostomeae
Family:	Cyaneidae
Genus:	*Cyanea*
Species:	***C. capillata***
Binomial name	

Cyanea capillata
(Linnaeus, 1758)

The **lion's mane jellyfish** (***Cyanea capillata***) is the largest known species of jellyfish. Its range is confined to cold, boreal waters of the Arctic, northern Atlantic, and northern Pacific Oceans, seldom found farther south than 42°N latitude. Similar jellyfish, which may be the same species, are known to inhabit seas near Australia and New Zealand. The largest recorded specimen found, washed up on the shore of Massachusetts Bay in 1870, had a bell (body) with a diameter of 2.3 m (7 feet 6 inches) and tentacles 36.5 m (120 feet) long.

Taxonomy

Cyanea sp.

The taxonomy of *Cyanea* species is not fully agreed; some zoologists have suggested that all species within the genus should be treated as one. Two distinct taxa, however, occur together in at least the eastern North Atlantic, with the blue jellyfish (*Cyanea lamarckii* Péron & Lesueur, 1810) differing in blue (not red) color and smaller size (10–20 cm diameter, rarely 35 cm). Populations in the western Pacific around Japan are sometimes distinguished as *Cyanea nozakii* Kisinouye, 1891, or as a race, *Cyanea capillata nozakii*.

Sting

Most encounters cause temporary pain and localized redness. In normal circumstances, and in healthy individuals, their stings are not known to be fatal.

Description

Although capable of attaining a bell diameter of 2.5 m (8 feet), these jellyfish can greatly vary in size, those found in lower latitudes are much smaller than their far northern counterparts with bells about 50 cm (20 inches) in diameter. The tentacles of larger specimens may trail as long as 30 m (90 feet) or more. These extremely sticky tentacles are grouped into eight clusters, each cluster containing over 100 tentacles, arranged in a series of rows.

At 120 feet in length, the largest known specimen was longer than a Blue Whale and is generally considered the longest known animal in the world. However, in 1864, a Bootlace worm was found washed up on a Scottish shore that was 180 feet long. But because bootlace worms can easily stretch to several times their natural length, it is possible the worm did not actually grow to be that length.

The bell is divided into eight lobes, giving it the appearance of an eight-pointed star. An ostentatiously tangled arrangement of colorful arms emanates from the centre of the bell, much shorter than the silvery, thin tentacles which emanate from the bell's subumbrella.

Size also dictates coloration—larger specimens are a vivid crimson to dark purple while smaller specimens grade to a lighter orange or tan. These jellyfish are understandably named for their showy, trailing tentacles reminiscent of a lion's mane.

Ecology

A coldwater species, this jellyfish cannot cope with warmer waters. The jellyfish are pelagic for most of their lives but tend to settle in shallow, sheltered bays towards the end of their one-year lifespan. In the open ocean, lion's mane jellyfish act as floating oases for certain species, such as shrimp, medusafish, butterfish, harvestfish, and juvenile prowfish, providing both a reliable source of food and protection from predators.

Predators of the lion's mane jellyfish include seabirds, larger fish, other jellyfish species, and sea turtles. The jellyfish themselves feed mostly on zooplankton, small fish, ctenophores, and moon jellies.

Behavior and reproduction

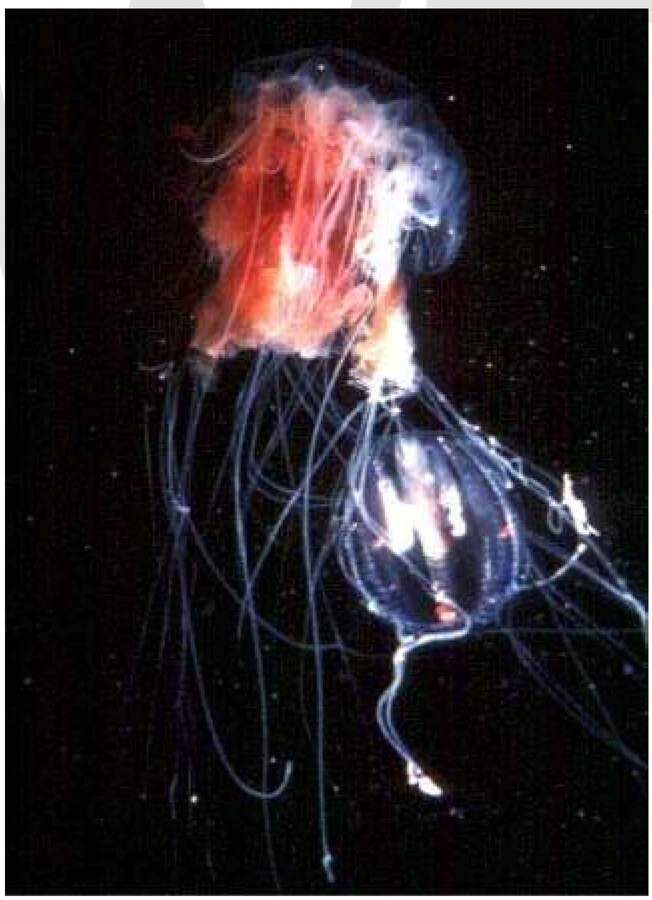
Small, dead Lion's Mane jelly washing up on the beach

Lion's mane jellyfish remain mostly very near the surface at no more than 20 m depth, their slow pulsations weakly driving them forwards; they depend on ocean currents whereby the jellies travel great distances. The jellyfish are most often spotted during the late summer and autumn, when they have grown to a large size and the currents begin to sweep them closer to shore.

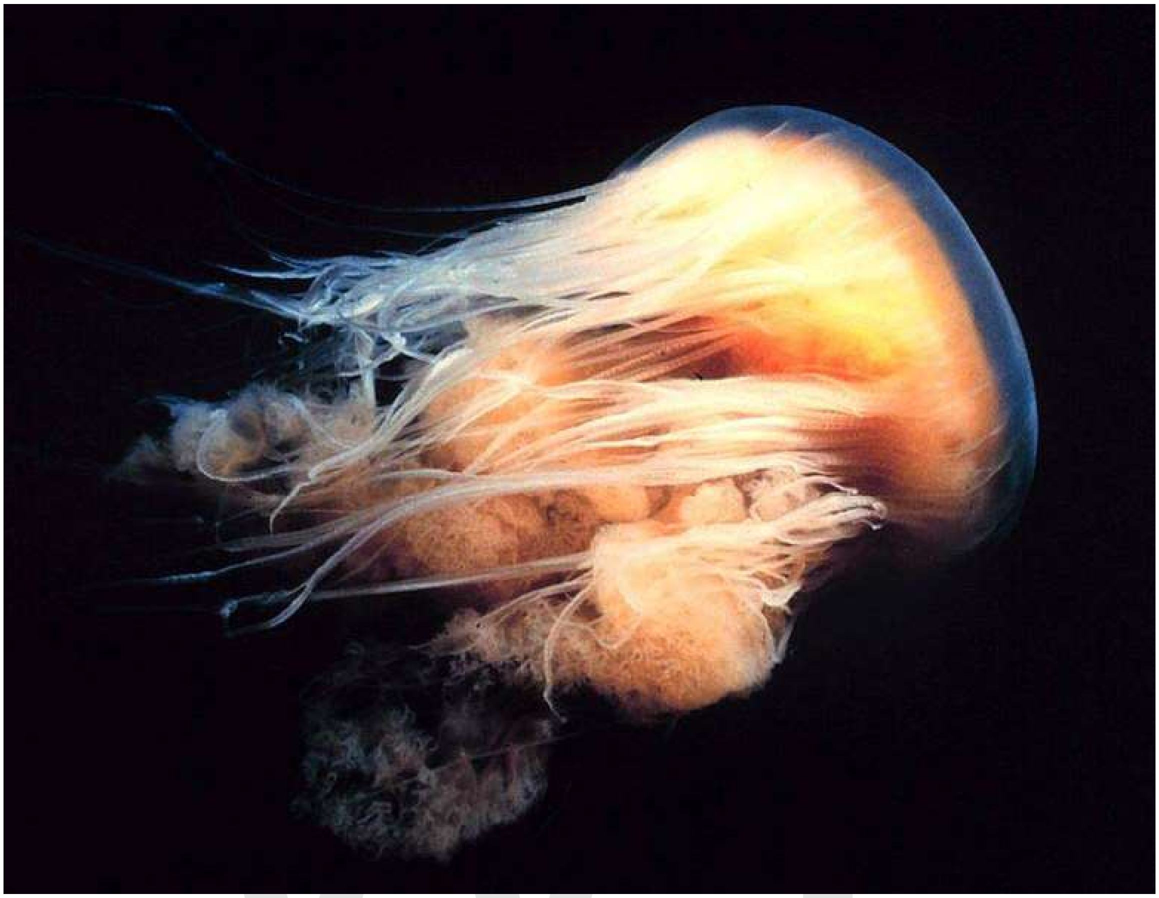
Like other jellyfish, Lions manes are capable of both sexual reproduction in the medusa stage and asexual reproduction in the polyp stage. Lion's mane jellyfish have four different stages in their year long life span, a larval stage, a polyp stage, an ephyrae stage and the medusa stage. The female jellyfish carries its fertilized eggs in its tentacle where the eggs grow into larva. When the larva are old enough, the female deposits them on a hard surface where the larva soon grow into polyps. The polyps begin to reproduce asexually, creating stacks of small creatures called ephyraes. The individual ephyraes break off the stacks, where they eventually grow into the medusa stage and become full grown jellyfish.

Human contact

On July 21, 2010, 50 to 100 people are thought to have been stung by the remains of a dead Lion's mane jellyfish that had broken up into countless pieces in Rye, New Hampshire in the United States. Considering the size of the species, it is possible but not likely that this mass incident was caused by a single specimen.



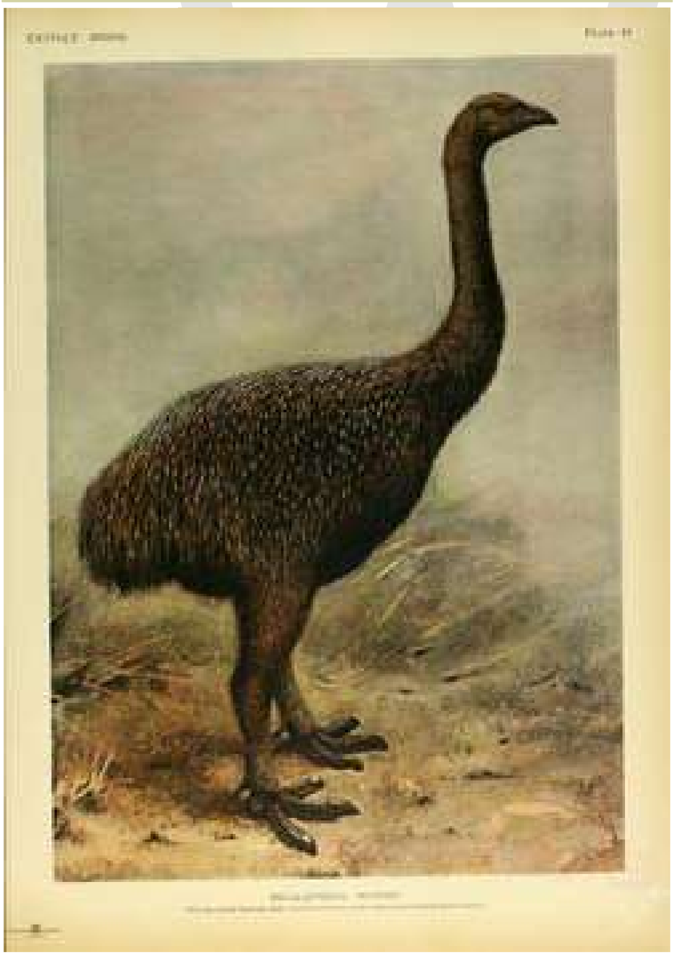
A lion's mane jelly capturing a sea gooseberry



Top view, Bonne Bay, NL, Canada

Chapter 10

Moa

Moa Temporal range: Miocene–Holocene Miocene - 1500 AD (Holocene)

Restoration of *Megalapteryx didinus*
Conservation status

Extinct (IUCN 3.1)

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Aves
Superorder:	Paleognathae
Order:	Struthioniformes
Family:	**†Dinornithidae** (Bonaparte, 1853)

Genera

†*Anomalopteryx* bush moa or lesser moa
†*Euryapteryx* stout-legged moa or coastal moa
†*Megalapteryx* upland moa
†*Dinornis* giant moa
†*Emeus* eastern moa
†*Pachyornis* Mappin's moa, heavy-footed moa, or crested moa

Diversity

6 genera, 11 species

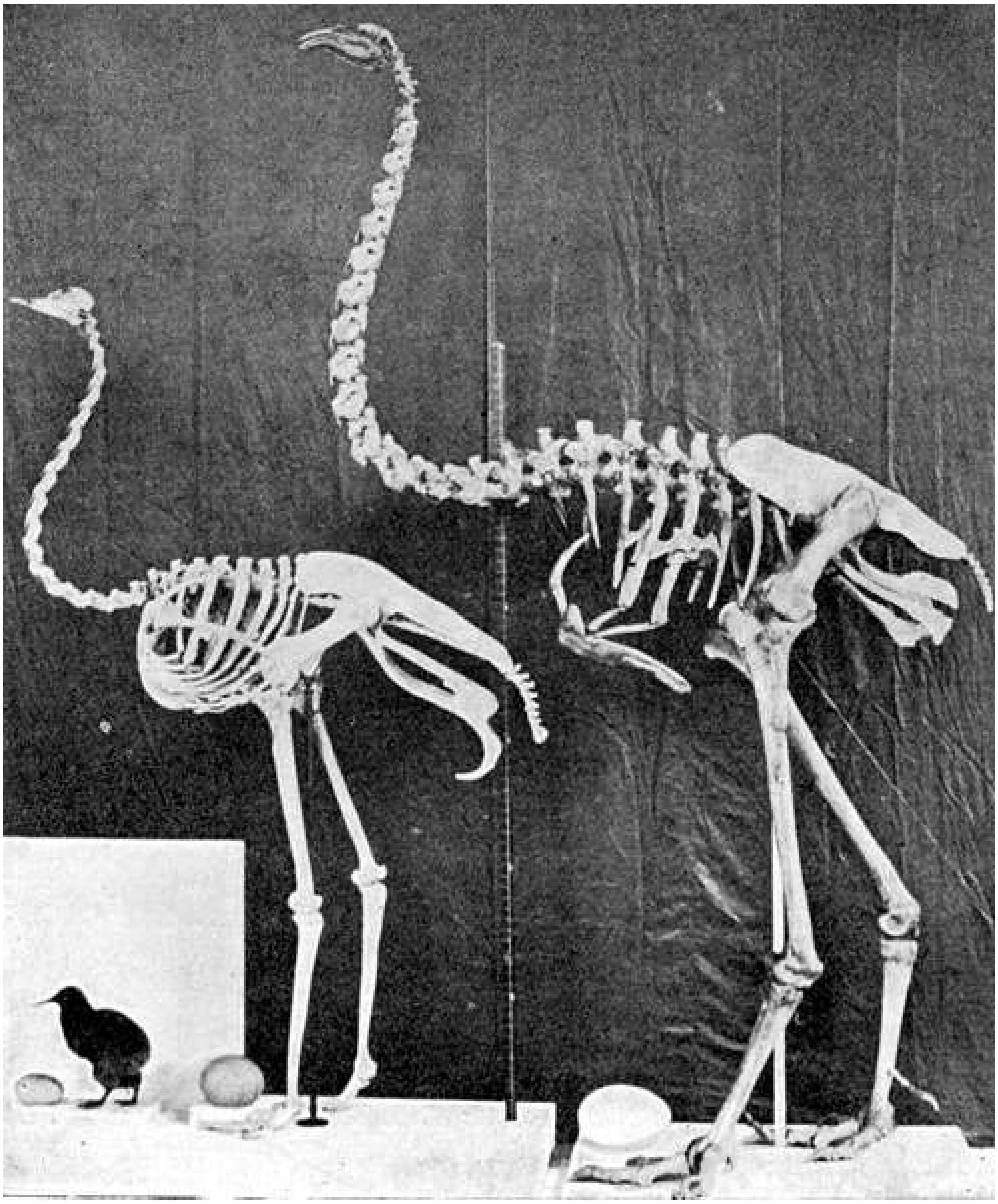
Synonyms

Dinornithes

The **moa** were eleven species (in six genera) of flightless birds endemic to New Zealand. The two largest species, *Dinornis robustus* and *Dinornis novaezelandiae*, reached about 3.7 m (12 ft) in height with neck outstretched, and weighed about 230 kg (510 lb).

Moa are members of the order Struthioniformes (or ratites) although some sources also recognise these as the separate order Dinornithiformes. The eleven species of moa are the only wingless birds, lacking even the vestigial wings which all other ratites have. They were the dominant herbivores in New Zealand forest, shrubland and subalpine ecosystems for thousands of years, and until the arrival of the Māori were hunted only by the Haast's Eagle. It is generally considered that most, if not all, species of Moa died out by Maori hunting and habitat decline before European discovery and settlement.

Taxonomy



Comparison of a kiwi, ostrich, and *Dinornis*, each with its egg

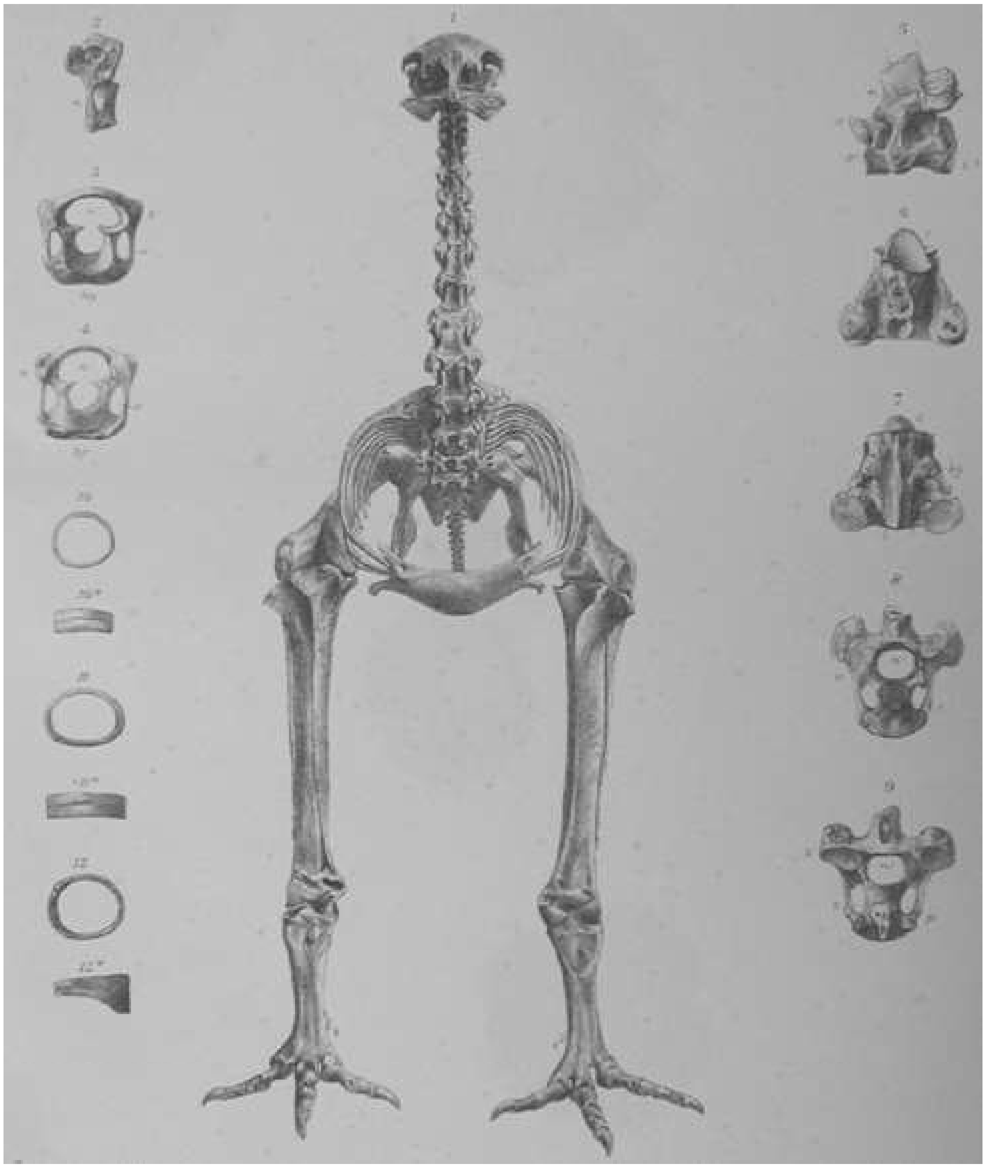
The kiwi were formerly regarded as the closest relatives of the moa, but comparisons of their DNA in a paper published in 2005 suggested moa were more closely related to the Australian emu and cassowary. However research published in 2010 found that the moa's closest cousins were not the emu and cassowary but smaller terrestrial South American birds called the tinamous which are able to fly.

Although dozens of species were described in the late 19th century and early 20th century, many were based on partial skeletons and turned out to be synonyms. Currently, eleven species are formally recognised, although recent studies using ancient DNA recovered from bones in museum collections suggest that distinct lineages exist within some of these. One factor that has caused much confusion in moa taxonomy is the intraspecific variation of bone sizes, between glacial and inter-glacial periods as well as sexual dimorphism being evident in several species. *Dinornis* seems to have had the most pronounced sexual dimorphism, with females being up to 150% as tall and 280% as heavy as males—so much bigger that they were formerly classified as separate species until 2003.

Although moa were traditionally reconstructed in an upright position to create impressive height, analysis of their vertebral articulation indicates that they probably carried their heads forward, in the manner of a kiwi. This would have allowed them to graze on low-level vegetation, while being able to lift their heads and browse trees when necessary.

Ancient DNA analyses have determined that there were a number of cryptic evolutionary lineages in several moa genera. These may eventually be classified as species or subspecies; *Megalapteryx benhami* (Archey) which is synonymised with *M. didinus* (Owen) because the bones of both share all essential characters. Size differences can be explained by a north-south cline combined with temporal variation such that specimens were larger during the Otiran glacial period (the last ice age in New Zealand). Similar temporal size variation is known for the North Island *Pachyornis mappini*. Some of the other 'Large' ranges in variation for moa species can probably be explained by similar geographic and temporal factors.

Sometimes, the Dinornithidae are considered to be a full order (Dinornithiformes), in which case the subfamilies listed below would be advanced to full family status (replacing "-inae" with "-idae").



Anomalopteryx didiformus skeleton

Emeus crassus fossil, Zoologisk Museum, Copenhagen

Thus, the currently recognised genera and species are:

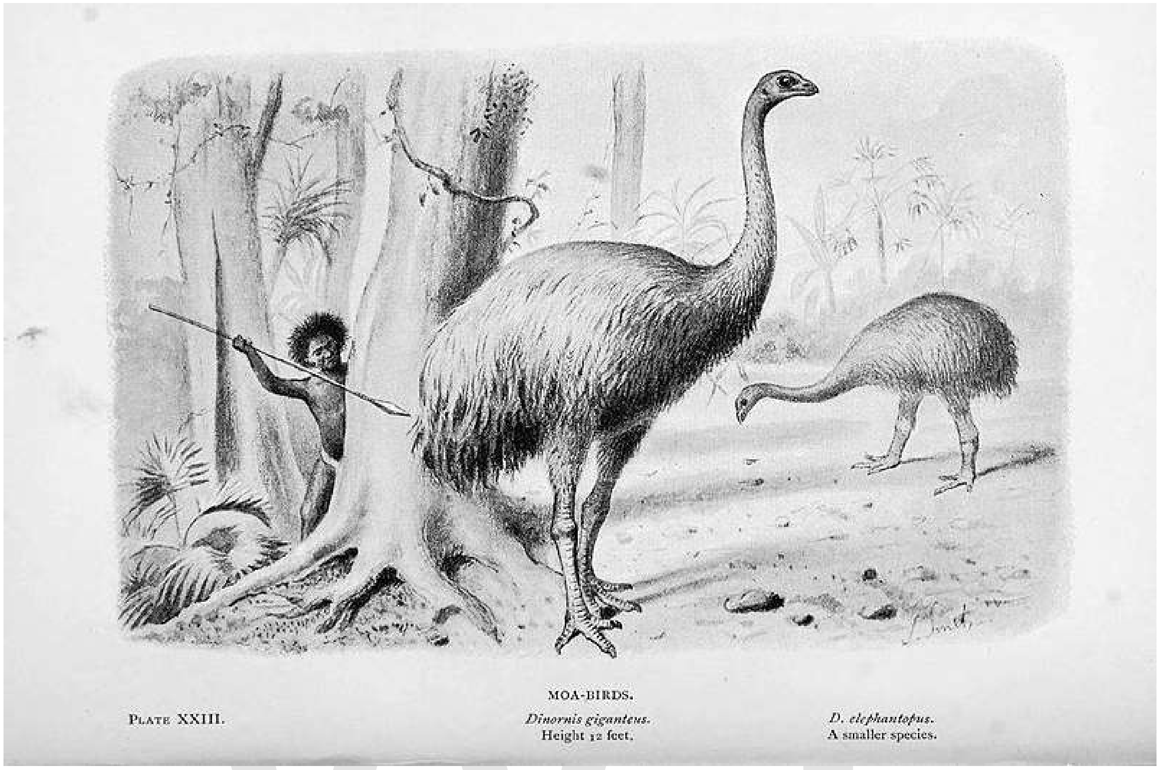
- Family †**Dinornithidae** - Moa
    - Subfamily **Megalapteryginae** - Megalapteryx Moa
        - Genus ***Megalapteryx***
            - Upland Moa, *Megalapteryx didinus (South Island, New Zealand)*
    - Subfamily **Anomalopteryginae** - Lesser Moa
        - Genus ***Anomalopteryx***
            - Bush Moa, *Anomalopteryx didiformis* (South Island, New Zealand)

    - Genus ***Euryapteryx***
        - North Island Broad-billed Moa, *Euryapteryx curtus* (North Island, New Zealand)
        - Stout-legged Moa, *Euryapteryx geranoides* (South Island, New Zealand)
    - Genus ***Emeus***
        - Eastern Moa, *Emeus crassus* (South Island, New Zealand)
    - Genus ***Pachyornis***
        - Heavy-footed Moa, *Pachyornis elephantopus* (South Island, New Zealand)
        - Mappin's Moa, *Pachyornis mappini* (North Island, New Zealand)
        - Crested Moa, *Pachyornis australis* (South Island, New Zealand)
        - *Pachyornis* new lineage A (North Island, New Zealand)
        - *Pachyornis* new lineage B (South Island, New Zealand)
- Subfamily **Dinornithinae** - Giant Moa
    - Genus ***Dinornis***
        - *Dinornis struthoides* (South Island, New Zealand)
        - North Island Giant Moa, *Dinornis novaezealandiae* (North Island, New Zealand)
        - South Island Giant Moa, *Dinornis giganteus* (South Island, New Zealand)
        - *Dinornis* new lineage A (South Island, New Zealand)
        - *Dinornis* new lineage B (South Island, New Zealand)

Regional faunas

Analyses of fossil moa bone assemblages have provided detailed data on the habitat preferences of individual moa species, and revealed distinctive regional moa faunas:

South Island



Restoration of *Dinornis giganteus* and *Pachyornis elephantopus*, both from the South Island

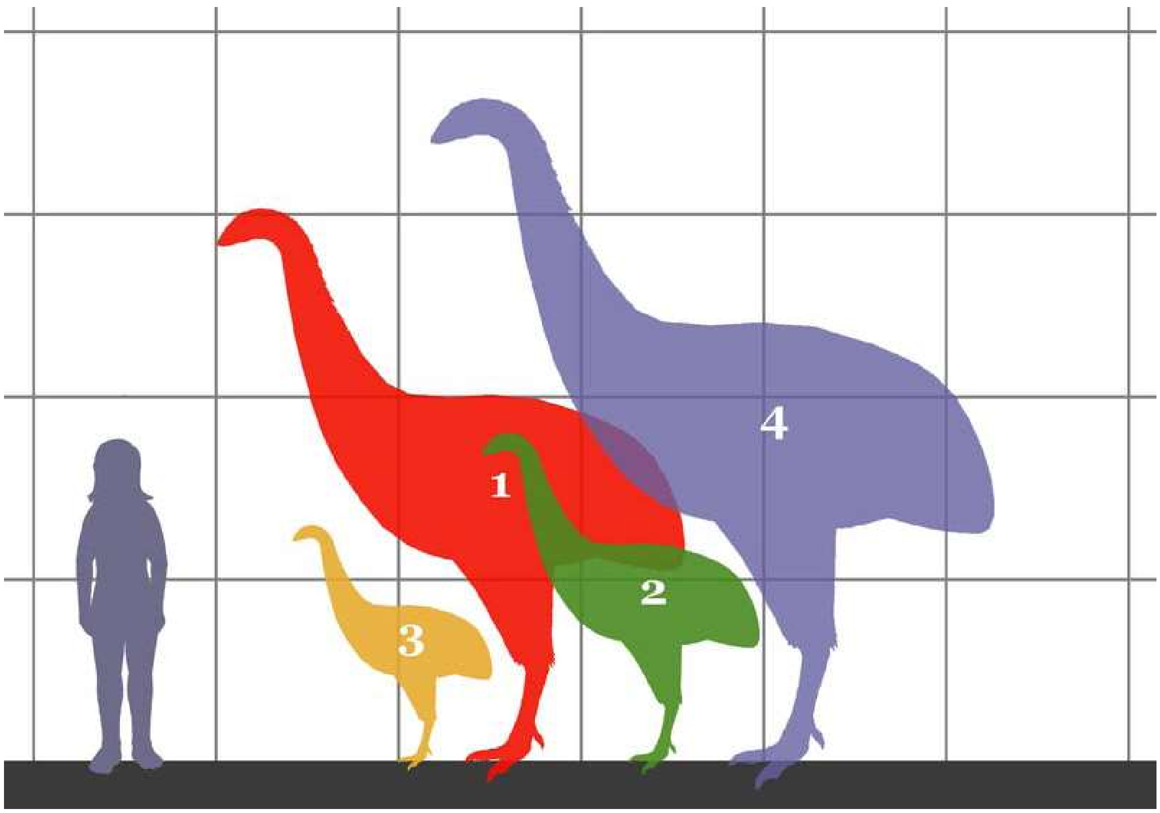
The two main faunas identified in the South Island include: 1. The fauna of the high rainfall west coast beech (*Nothofagus*) forests that included *Anomalopteryx didiformis* and *Dinornis giganteus*; and 2. The fauna of the dry rainshadow forest and shrublands east of the Southern Alps that included *Pachyornis elephantopus*, *Euryapteryx gravis*, *Emeus crassus* and *Dinornis robustus*. The two other moa species that existed in the South Island; *Pachyornis australis* and *Megalapteryx didinus* might be included in a 'subalpine fauna', along with the widespread *Dinornis robustus*. *P. australis* is the rarest of the moa species, and the only one yet to have been found in Maori middens. Its bones have been found in caves in the northwest Nelson and Karamea districts (such as Honeycomb Hill Cave), and some sites around the Wanaka district. *M. didinus* is more widespread. Its name 'upland moa' reflects the fact its bones are commonly found in the subalpine zone. However, it also occurred down to sea level where there was suitable steep and rocky terrain (such as Punakaiki on the west coast and Central Otago).

North Island

Significantly less is known about North Island paleofaunas, due to a paucity of fossil sites compared to the South Island; however, the basic pattern of moa-habitat relationships were the same. Although the South Island and the North Island shared some moa species

(*Euryapteryx gravis*, *Anomalopteryx didiformis*), most were exclusive to one island, reflecting divergence over several thousand years since lower sea level had resulted in a land bridge across Cook Strait. In the North Island, *Dinornis novaezealandiae* and *Anomalopteryx didiformis* dominated in high rainfall forest habitat; a similar pattern to the South Island. The other moa species present in the North Island (*Euryapteryx gravis*, *E. curtus*, and *Pachyornis geranoides*) tended to inhabit drier forest and shrubland habitats. *P. geranoides* occurred throughout the North Island, while the distributions of *E. gravis* and *E. curtus* were almost mutually exclusive, the former having only been found in coastal sites around the southern half of the North Island.

Biology



Size comparison between 4 moa species and a human. **1.** *D. giganteus*. **2.** *E.crassus*. **3.** *A. didiformis* **4.** *D. novaezelandiae*

Evolution

Because moa are a group of flightless birds with no vestiges of wing bones, questions have been raised about how they arrived in New Zealand, and from where. It is suggested that ancestral moa were already in New Zealand as it broke away from Antarctica 70 million years ago. Cretaceous Antarctica, as evidenced by plant fossils, was subtropical, and supported an environment lush with vegetation. Richard Dawkins suggests that Antarctica, "provided a clement and ratite-friendly land bridge linking Africa and South America on one side of the world to Australia and New Zealand on the other...".

Sexual Dimorphism

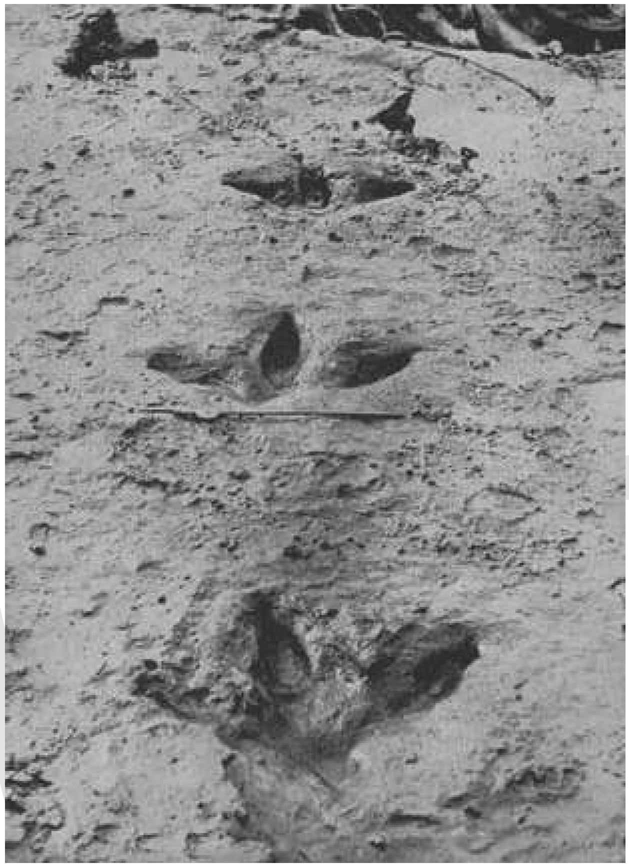
It has been long suspected that the pairs of species of moa described as *Euryapteryx curtus*/*E. exilis*, *Emeus huttonii*/*E. crassus*, and *Pachyornis septentrionalis*/*P. mappini* constituted males and females, respectively. This has been confirmed by analysis for sex-specific genetic markers of DNA extracted from bone material. For example, prior to 2003 there were three species of *Dinornis* recognised: South Island giant moa (*D. giganteus*), North Island giant moa (*D. novaezealandiae*) and slender moa (*D. struthioides*). However, DNA showed that all *D. struthioides* were in fact males, and all *D. giganteus* were females. Therefore the three species of *Dinornis* were reclassified as two species, one each formerly occurring on New Zealand's North Island (*D. novaezealandiae*) and South Island (*D. robustus*); *robustus* however, comprises three distinct genetic lineages and may eventually be classified as many species as discussed above.

Diet

Dinornis giganteus skull at the Museum für Naturkunde, Berlin

Although feeding moa were never observed by scientists their diet has been deduced from fossilised contents of their gizzards, coprolites, as well as indirectly through morphological analysis of skull and beak, and stable isotope analysis of their bones. Moa fed on a range of plant species and plant parts, including fibrous twigs and leaves taken from low trees and shrubs. The beak of *Pachyornis elephantopus* was analogous to a pair of secateurs, and was able to clip the fibrous leaves of New Zealand flax (*Phormium tenax*) and twigs up to at least 8mm in diameter. Like many other birds, moa swallowed *gizzard stones* (gastroliths), which were retained in their muscular gizzards, providing a grinding action that allowed them to eat coarse plant material. These stones were commonly smooth, rounded quartz pebbles, but stones over 110 millimetres (4 in) in length have been found amongst preserved moa gizzard contents. *Dinornis* gizzards could often contain several kilograms of stones.

Locomotion



Preserved footprints of a large moa found in 1911

Approximately eight moa trackways, with fossilised moa footprint impressions in fluvial silts have been found throughout the North Island, including Waikanae Creek (1872), Napier (1887), Manawatu River (1895), Marton (1896), Palmerston North (1911), Ragitikei River (1939), and underwater in Lake Taupo (1973). Analysis of the spacing of these tracks indicate walking speeds of between 3 and 5 km/h (1.75–3 mph).

Breeding

Examination of growth rings present in moa cortical bone has revealed that these birds were K-strategists, as are many other large endemic New Zealand birds. They are characterised by having low fecundity and a long maturation period, taking approximately ten years to reach adult size. The large *Dinornis* species took the same length of time to reach adult size as small moa species, and as a result had accelerated rate of skeletal growth during their juvenile years.

Eggs

Fragments of moa eggshell are often encountered in archaeological sites and sand dunes around the New Zealand coast. Thirty six whole moa eggs exist in museum collections and vary greatly in size (from 120–240 millimetres (4.7–9.4 in) in length and 91–178 millimetres (3.6–7.0 in) wide). The outer surface of moa eggshell is characterised by small slit-shaped pores. The eggs of most moa species were white, although those of the upland moa (*Megalapteryx didinus*) were blue-green. A 2010 study by Huynen et al. has found that the eggs of certain species were fragile, only around a millimeter in thickness: "Unexpectedly, several thin-shelled eggs were also shown to belong to the heaviest moa of the genera *Dinornis*, *Euryapteryx* and *Emeus*, making these, to our knowledge, the most fragile of all avian eggs measured to date. Moreover, sex-specific DNA recovered from the outer surfaces of eggshells belonging to species of *Dinornis* and *Euryapteryx* suggest that these very thin eggs were likely to have been incubated by the lighter males. The thin nature of the eggshells of these larger species of moa, even if incubated by the male, suggests that egg breakage in these species would have been common if the typical contact method of avian egg incubation was used." Despite the bird's extinction, the high yield of DNA available from recovered fossilized eggs has allowed the moa to have its genome sequenced.

Nests

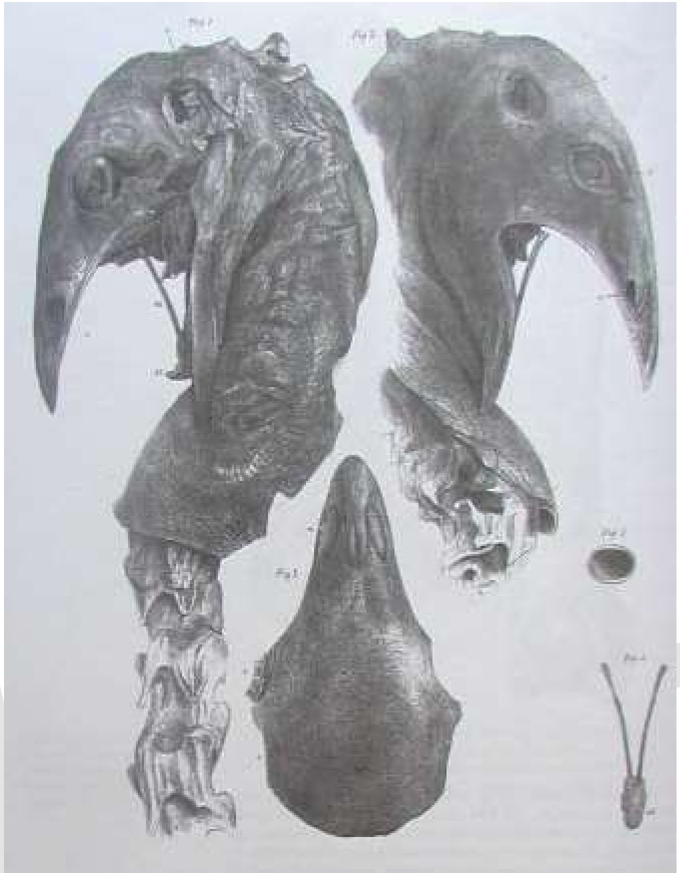
There is no evidence to suggest that moa were colonial nesters. While evidence of moa nesting is often inferred from accumulations of eggshell fragments found in caves and rock shelters, little evidence exists of the nests themselves. Excavations of rock shelters in the eastern North Island during the 1940s uncovered moa nests, which were described as "*small depressions obviously scratched out in the soft dry pumice*". Moa nesting material has also been recovered from rock shelters in the Central Otago region of the South Island, where the dry climate has resulted in the preservation of plant material used to construct the nesting platform (including twigs that have been clipped by moa bills). Seeds and pollen within moa coprolites found amongst the nesting material provide evidence that the nesting season was late spring to summer.

Vocalisation

Although there is no surviving record of what sounds moa made, some idea of their calls can be gained from fossil evidence. The trachea of moa were supported by many small rings of bone known as tracheal rings. Excavation of these rings from articulated skeletons has shown that at least two moa genera (*Euryapteryx* and *Emeus*) exhibited tracheal elongation, that is, their trachea were up to 1 metre (3 ft) long and formed a large loop within the body cavity. These are the only ratites known to exhibit this feature, which is also present in several other bird groups including swans, cranes and guinea fowl. The feature is associated with deep, resonant vocalisations that can travel long distances.

Feathers and soft tissues

Preserved *Megalapteryx* foot, Natural History Museum



Megalapteryx didinus head

Several remarkable examples of moa remains have been found that exhibit soft tissues (muscle, skin, feathers), preserved through desiccation when the bird died in a naturally dry site (for example, a cave with a constant dry breeze blowing through it). Most of these specimens have been found in the semi-arid Central Otago region, the driest part of New Zealand. These include:

- Dried muscle on bones of a female *Dinornis robustus* found at Tiger Hill in the Manuherikia River Valley by gold miners in 1864 (currently held by Yorkshire Museum)
- Several bones of *Emeus crassus* with muscle attached, and a row of neck vertebrae with muscle, skin and feathers collected from Earnscleugh Cave near the town of Alexandra in 1870 (currently held by Otago Museum)
- An articulated foot of a male *Dinornis robustus* with skin and foot pads preserved found in a crevice on the Knobby Range in 1874 (currently held by Otago Museum)
- The type specimen of *Megalapteryx didinus* found near Queenstown in 1878
- The lower leg of *Pachyornis elephantopus* with skin and muscle from the Hector Range in 1884; (currently held by the Zoology Department, Cambridge University)

- The complete feathered leg of a *Megalapteryx didinus* from Old Man Range in 1894 (currently held by Otago Museum)
- The head of a *Megalapteryx didinus* found near Cromwell sometime prior to 1949 (currently held by the Museum of New Zealand).

Two specimens are known from outside the Central Otago region:

- A complete foot of *Megalapteryx didinus* found in a cave on Mount Owen near Nelson in 1980s (currently held by the Museum of New Zealand)
- A skeleton of *Anomalopteryx didiformis* with muscle, skin and feather bases collected from a cave near Te Anau in 1980.

In addition to these specimens, loose moa feathers have been collected from caves and rockshelters in the southern South Island, and so some idea of the moa plumage can be gained. The preserved leg of *Megalapteryx didinus* from the Old Man Range reveals that this species was feathered right down to the foot. This is likely to have been an adaptation to living in high altitude snowy environments, and is also seen in the Darwin's Rhea which lives in a similar seasonally snowy habitat. Moa feathers are up to 23 centimetres (9 in) long and a range of colours have been reported, including reddish brown, white, yellowish and purplish. Dark feathers with white or creamy tips have also been found, and indicate that some moa species may have had plumage with a speckled appearance.

Extinction

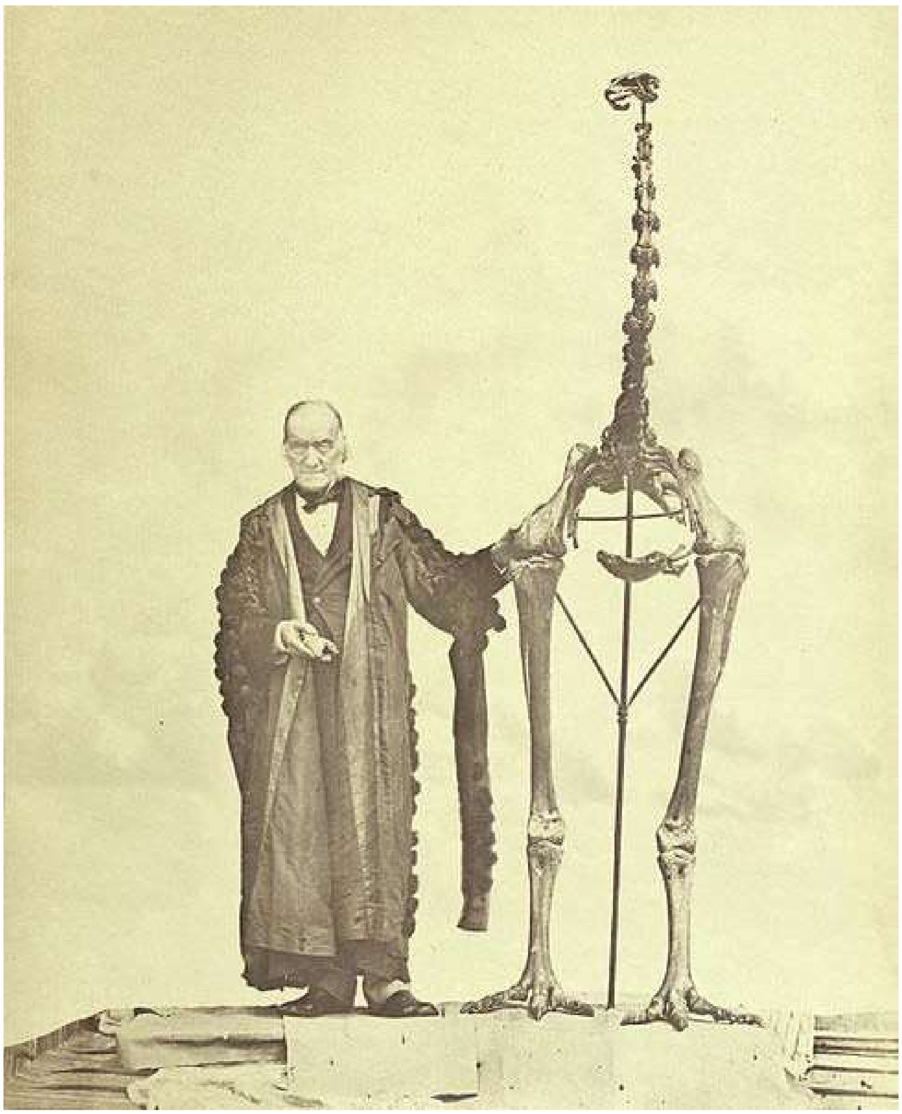
Early 20th century reconstruction of a moa hunt

The moa's only predator was the massive Haast's Eagle—until the arrival of human settlers.

The Māori arrived sometime before A.D. 1300, and all moa genera were soon driven to extinction by hunting and, to a lesser extent, forest clearance. By about A.D. 1400 almost all moa are generally thought to have become extinct, along with the Haast's Eagle which had relied on them for food. Recent research using carbon-14 dating of middens strongly suggests that this took less than a hundred years, rather than the period of exploitation lasting several hundred years which had been earlier believed.

Some authors have speculated that a few *Megalapteryx didinus* may have persisted in remote corners of New Zealand until the 18th and even 19th centuries, but the view is not widely accepted. Some Māori hunters claimed to be in pursuit of the moa as late as the 1770s. Whalers and sealers recalled seeing monstrous birds along the coast of the South Island, and in the 1820s a man named George Pauley made an unverified claim of seeing a moa in the Otago Region of New Zealand. An expedition in the 1850s under Lieutenant A. Impey reported two Emu-like birds on a hillside, on the South Island, and an 1861 story from the Nelson Examiner told of three-toed footprints measuring 36 centimetres (14 in) between Takaka and Riwaka, found by a surveying party, and finally in 1878 the Otago Witness published an account from a farmer and his shepherd.

Discovery by science



Sir Richard Owen with *Dinornis robustus* skeleton

Joel Polack, a trader who lived on the East Coast of the North Island from 1834 to 1837, records in 1838 that he had been shown 'several large fossil ossifications' found near Mt Hikurangi. He was certain that these were the bones of a species of emu or ostrich, noting that 'the Natives add that in times long past they received the traditions that very large birds had existed, but the scarcity of animal food, as well as the easy method of entrapping them, has caused their extermination'. Polack further noted that he had received reports from Māori that a 'species of Struthio' still existed in remote parts of the South Island. Dieffenbach also refers to a fossil from the area near Mt Hikurangi, and surmises that it belongs to 'a bird, now extinct, called Moa (or Movie) by the natives'. In 1839, John W. Harris, a Poverty Bay flax trader who was a natural history enthusiast, was given a piece of unusual bone by a Māori who had found it in a river bank. He showed the 15 centimetres (6 in) fragment of bone to his uncle, John Rule, a Sydney surgeon, who sent it to Richard Owen who at that time was working at the Hunterian Museum at the Royal College of Surgeons in London. Owen became a noted biologist, anatomist and paleontologist at the British Museum.

Owen puzzled over the fragment for almost four years. He established it was part of the femur of a big animal, but it was uncharacteristically light and honeycombed. Owen announced to a skeptical scientific community and the world that it was from a giant extinct bird like an ostrich, and named it *Dinornis*. His deduction was ridiculed in some quarters but was proved correct with the subsequent discoveries of considerable quantities of moa bones throughout the country, sufficient to reconstruct skeletons of the birds.

In July 2004, the Natural History Museum in London placed on display the moa bone fragment Owen had first examined, to celebrate 200 years since his birth, and in memory of Owen as founder of the museum.

Moa bone deposits

Since the discovery of the first moa bones in the late 1830s, thousands more have been found. They occur in a range of late Quaternary and Holocene sedimentary deposits, but are most common in three main types of site:

Caves

Moa bones scattered across the floor of 'Moa Cave', Honeycomb Hill Cave System. This cave is a closed scientific reserve.

Bones are commonly found in Caves or ‘tomo’ (Maori word for doline or sinkhole; often used to refer to pitfalls or vertical cave shafts). The two main ways that the moa bones were deposited in such sites were: 1. Birds that entered the cave to nest or escape bad weather, and subsequently died in the cave; and 2. Birds that fell into a vertical shaft and were unable to escape. Moa bones (and the bones of other extinct birds) have been found in caves throughout New Zealand, especially in the limestone/marble areas of northwest Nelson, Karamea, Waitomo and Te Anau.

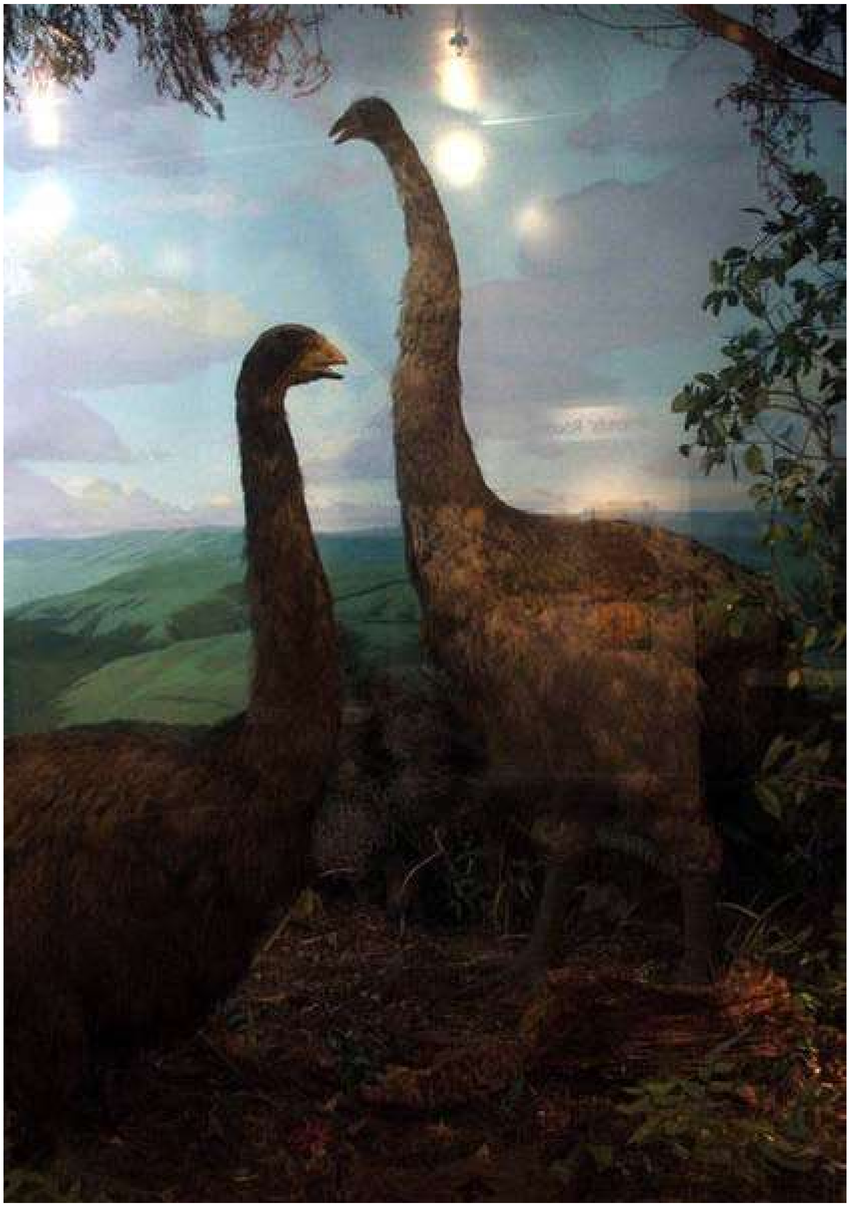
Dunes

Moa bones and eggshell fragments sometimes occur in active coastal sand dunes, where they may erode from paleosols and concentrate in ‘blowouts’ between dune ridges. Many such moa bones predate human settlement, although some can originate from Maori midden sites which frequently occur in dunes near harbours and river mouths (for example the large moa hunter sites at Shag River, Otago and Wairau Bar, Marlborough).

Swamps/mirings

Densely intermingled moa bones have been encountered in swamps throughout New Zealand. The most well-known example is at Pyramid Valley in north Canterbury, where bones from at least 183 individual moa have been excavated. Many explanations were proposed to account for how these deposits had formed, ranging from poisonous spring waters to floods and wildfires. However the currently accepted explanation is that the bones accumulated at a slow rate over thousands of years, from birds that had entered the swamps to feed and became trapped in the soft sediment.

Claims of moa survival



Reconstruction of two moa species, Otago Museum, Dunedin. Otago Museum holds the world's largest collection of moa remains.

The moa is thought to be extinct, but there has been occasional speculation—since at least the late 19th century, and as recently as 1993 and 2008—that some moa may still exist, particularly in the rugged wilderness of South Westland and Fiordland. Cryptozoologists and others reputedly continue to search for them, but their claims and supporting evidence (such as of purported footprints or blurry photos) have earned little attention from mainstream experts, and are widely considered pseudoscientific.

The rediscovery of the takahē in 1948 after none had been seen since 1898 showed that rare birds may exist undiscovered for a long time. However, the takahē is a much smaller bird than the moa, and was rediscovered after its tracks were identified—yet no reliable evidence of moa tracks has ever been found, and experts still contend that moa survival is extremely unlikely, since this would involve the ground-dwelling birds living unnoticed in a region visited often by hunters and hikers.

Chapter 11

Dinosaur

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

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

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

- **†Ornithischia**
    - †Cerapoda
    - †Thyreophora
- **Saurischia**
    - †Sauropodomorpha
    - Theropoda

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

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

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

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

Etymology

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

Modern definition

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

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

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

From the point of view of cladistics, birds are dinosaurs, but in ordinary speech the word "dinosaur" does not include birds. Additionally, referring to dinosaurs that are not birds as "non-avian dinosaurs" is cumbersome.

General description

Stegosaurus skeleton, Field Museum, Chicago

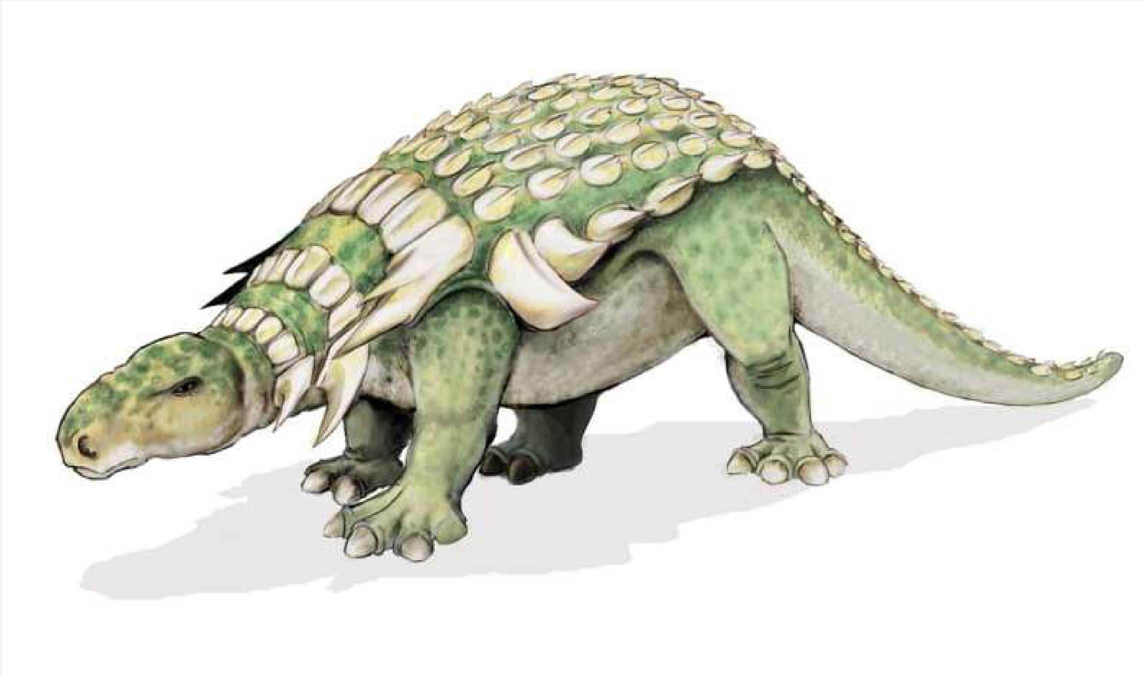
Using one of the above definitions, dinosaurs (aside from birds) can be generally described as terrestrial archosaurian reptiles with limbs held erect beneath the body, that existed from the Late Triassic (first appearing in the Carnian faunal stage) to the Late Cretaceous (going extinct at the end of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

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

Distinguishing anatomical features

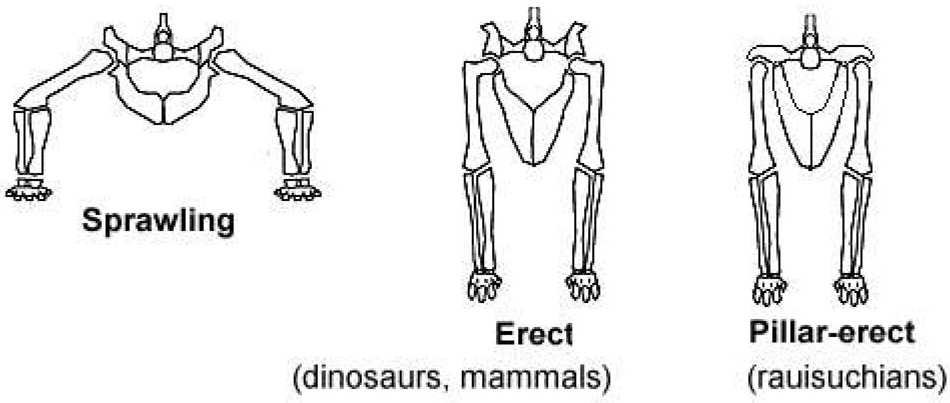
While recent discoveries have made it more difficult to present a universally agreed-upon list of dinosaurs' distinguishing features, nearly all dinosaurs discovered so far share certain modifications to the ancestral archosaurian skeleton. Although some later groups of dinosaurs featured further modified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

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



Edmontonia was an armored dinosaur of the group Ankylosauria

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



Hip joints and hindlimb postures

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

Natural history

Origins and early evolution

Marasuchus, a dinosaur-like ornithodiran

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

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

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

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

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

Low diversification in the Cretaceous

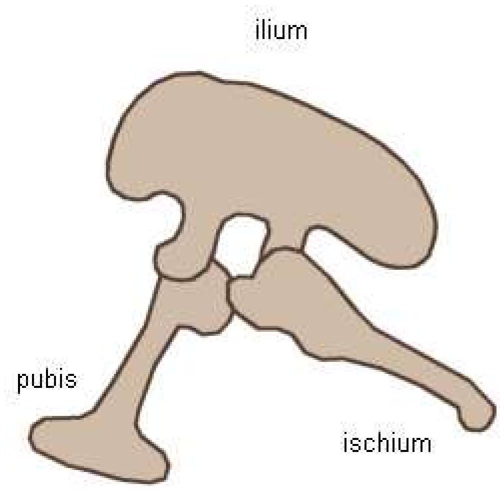
Statistical analyses based on raw data suggest that dinosaurs diversified, i.e. the number of species increased, in the Late Cretaceous. However in July 2008 Graeme T. Lloyd *et al.* argued that this apparent diversification was an illusion caused by sampling bias, because Late Cretaceous rocks have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

Classification

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

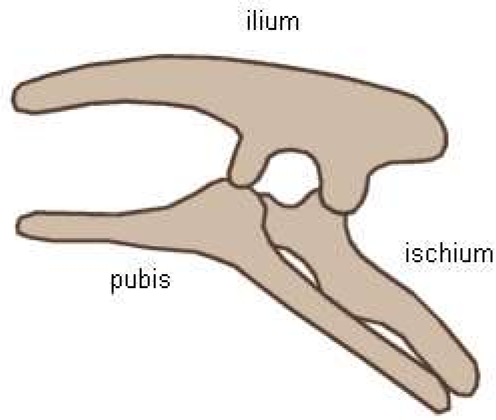
Collectively, dinosaurs are usually regarded as a superorder or an unranked clade. They are divided into two orders, Saurischia and Ornithischia, depending upon pelvic structure. Saurischia includes those taxa sharing a more recent common ancestor with birds than with Ornithischia, while Ornithischia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

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



Saurischian pelvis structure (left side)

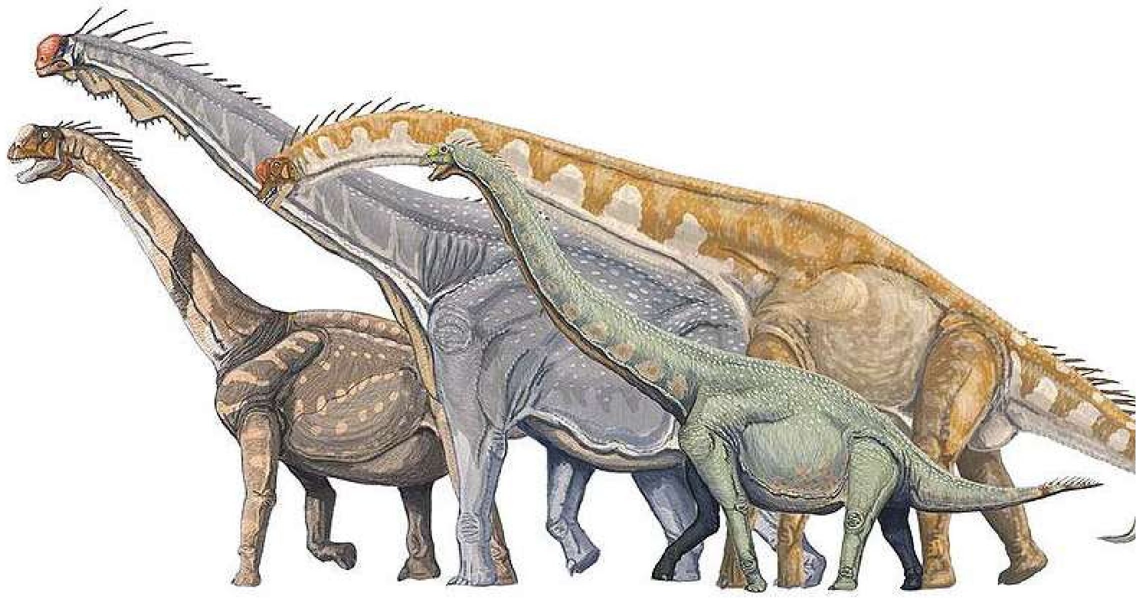
Tyrannosaurus pelvis (showing saurischian structure – left side)



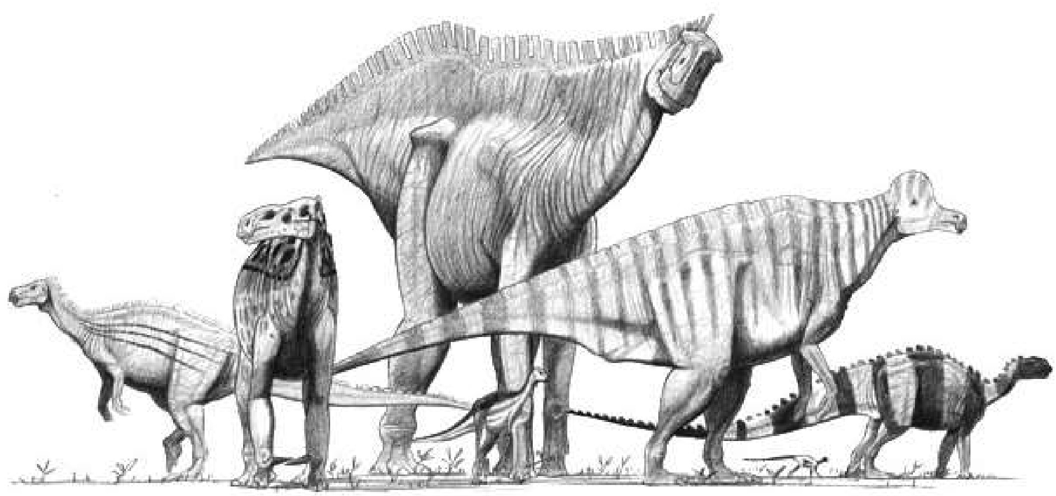
Ornithischian pelvis structure (left side)

Edmontosaurus pelvis (showing ornithischian structure – left side)

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



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



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

- Dinosauria
    - Saurischia (theropods and sauropods)

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

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

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

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

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

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

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

- †Ornithischians (diverse bipedal and quadrupedal herbivores)

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

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

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

Evolution and paleobiogeography

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

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

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

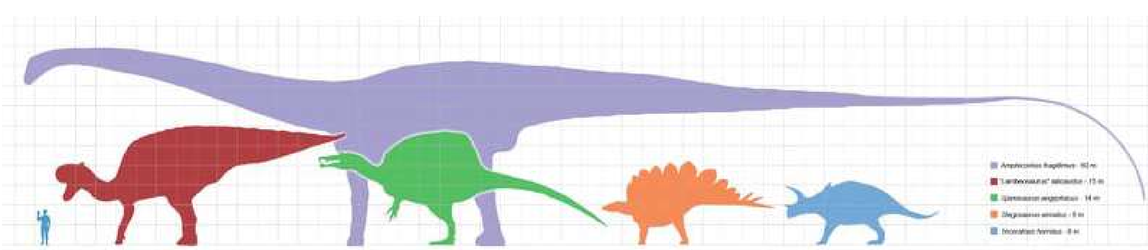
There were three general dinosaur faunas in the Late Cretaceous. In the northern continents of North America and Asia, the major theropods were tyrannosaurids and various types of smaller maniraptoran theropods, with a predominantly ornithischian herbivore assemblage of hadrosaurids, ceratopsians, ankylosaurids,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

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

Paleobiology

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

Size



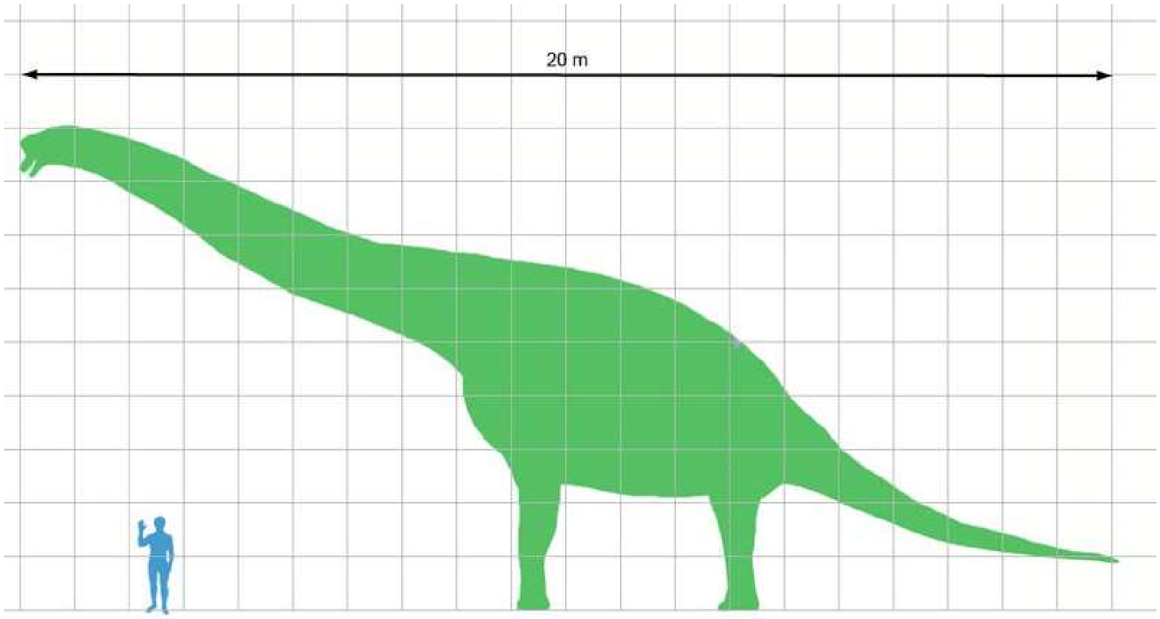
Scale diagram comparing the largest known dinosaurs in five major clades and a human

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

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

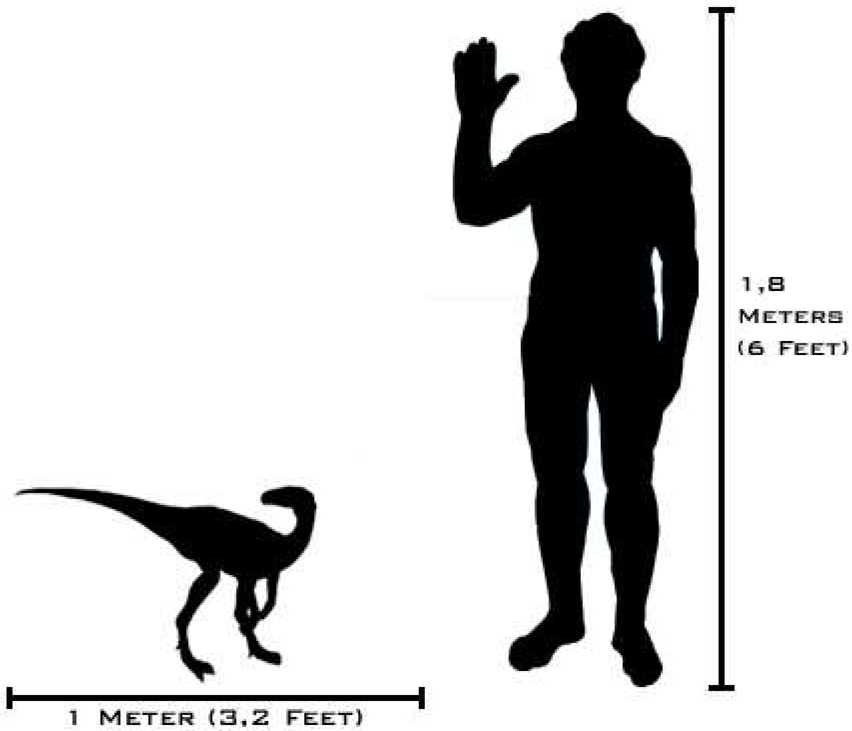
Largest and smallest

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



Comparative size of *Giraffatitan*

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



Comparative size of *Eoraptor*

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

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

Behavior

A nesting ground of *Maiasaura* was discovered in 1978

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

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

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

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

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

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

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

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

Communication and vocalization

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

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

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

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

Physiology

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

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

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

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

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

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

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

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

Soft tissue and DNA

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

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

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

Newer research, published in PloS One (30 July 2008), has challenged the claims that the material found is the soft tissue of *Tyrannosaurus*. Thomas Kaye of the University of Washington and his co-authors contend that what was really inside the tyrannosaur bone was slimy biofilm created by bacteria that coated the voids once occupied by blood vessels and cells. The researchers found that what previously had been identified as remnants of blood cells, because of the presence of iron, were actually framboids, microscopic mineral spheres bearing iron. They found similar spheres in a variety of other fossils from various periods, including an ammonite. In the ammonite they found the spheres in a place where the iron they contain could not have had any relationship to the presence of blood.

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

Feathers and the origin of birds

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

Feathers

The famous Berlin Specimen of *Archaeopteryx lithographica*

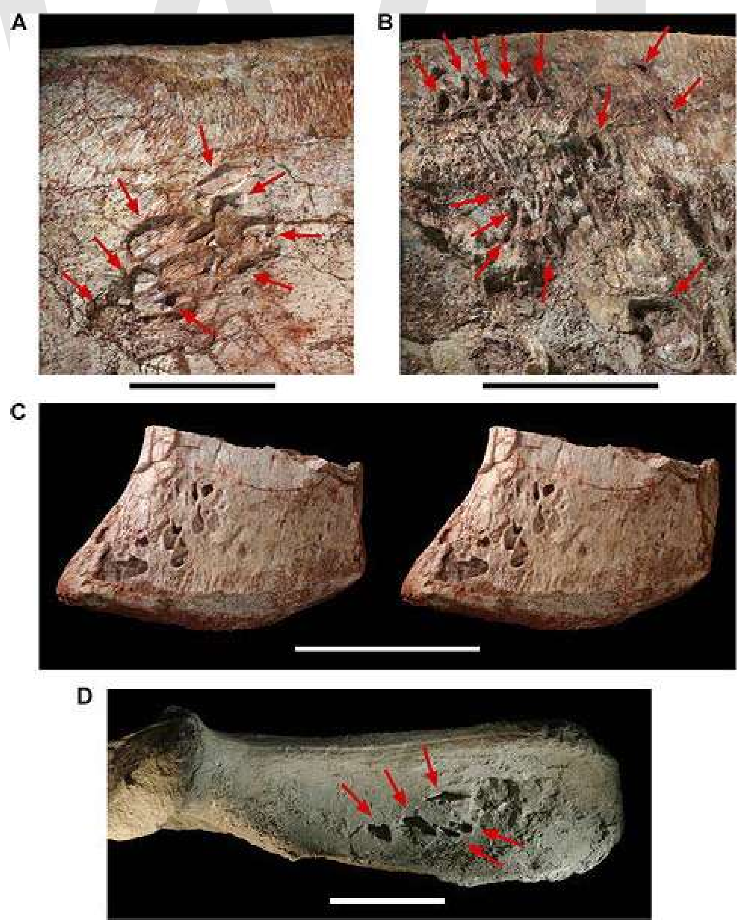
Archaeopteryx, the first good example of a "feathered dinosaur", was discovered in 1861. The initial specimen was found in the Solnhofen limestone in southern Germany, which is a *lagerstätte*, a rare and remarkable geological formation known for its superbly detailed fossils. *Archaeopteryx* is a transitional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

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

Skeleton

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

Soft anatomy



Pneumatopores on the left ilium of *Aerosteon riocoloradensis*

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

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

Reproductive biology

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

Behavioral evidence

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

Extinction

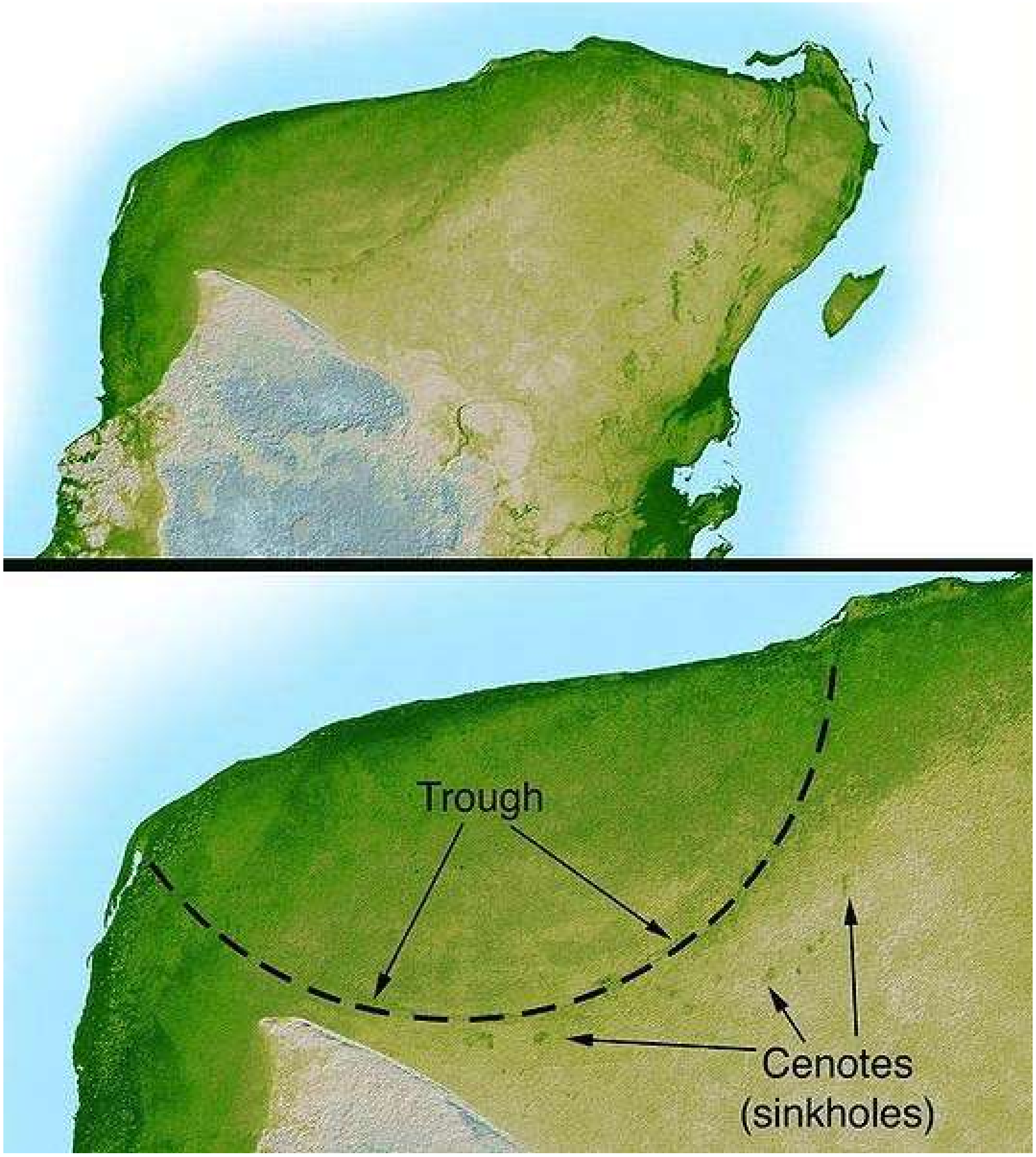
Non-avian dinosaurs suddenly became extinct approximately 65 million years ago. Many other groups of animals also became extinct at this time, including ammonites (nautilus-like mollusks), mosasaurs, plesiosaurs, pterosaurs, most birds, and many groups of mammals. This mass extinction is known as the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

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

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

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

Impact event



The Chicxulub Crater at the tip of the Yucatán Peninsula; the impactor that formed this crater may have caused the dinosaur extinction.

The asteroid collision theory, which was brought to wide attention in 1980 by Walter Alvarez and colleagues, links the extinction event at the end of the Cretaceous period to a bolide impact approximately 65.5 million years ago. Alvarez *et al.* proposed that a sudden increase in iridium levels, recorded around the world in the period's rock stratum, was direct evidence of the impact. The bulk of the evidence now suggests that a bolide 5 to 15 kilometers (3 to 9 mi) wide hit in the vicinity of the Yucatán Peninsula, creating the approximately 180 km (110 mi) Chicxulub Crater and triggering the mass extinction.

Scientists are not certain whether dinosaurs were thriving or declining before the impact event. Some scientists propose that the meteorite caused a long and unnatural drop in Earth's atmospheric temperature, while others claim that it would have instead created an unusual heat wave.

Although the speed of extinction cannot be deduced from the fossil record alone, various models suggest that the extinction was extremely rapid. The consensus among scientists who support this theory is that the impact caused extinctions both directly (by heat from the meteorite impact) and also indirectly (via a worldwide cooling brought about when matter ejected from the impact crater reflected thermal radiation from the sun).

In September 2007, U.S. researchers led by William Bottke of the Southwest Research Institute in Boulder, Colorado, and Czech scientists used computer simulations to identify the probable source of the Chicxulub impact. They calculated a 90% probability that a giant asteroid named Baptistina, approximately 160 km (100 mi) in diameter, orbiting in the asteroid belt which lies between Mars and Jupiter, was struck by a smaller unnamed asteroid about 55 km (35 mi) in diameter about 160 million years ago. The impact shattered Baptistina, creating a cluster which still exists today as the Baptistina family. Calculations indicate that some of the fragments were sent hurtling into earth-crossing orbits, one of which was the 10 km (6 mi) wide meteorite which struck Mexico's Yucatan peninsula 65 million years ago, creating the Chicxulub crater.

A similar but more controversial explanation proposes that "passages of the [hypothetical] solar companion star Nemesis through the Oort comet cloud would trigger comet showers." One or more of these comets then collided with the Earth at approximately the same time, causing the worldwide extinction. As with the impact of a single asteroid, the end result of this comet bombardment would have been a sudden drop in global temperatures, followed by a protracted cool period.

Deccan Traps

Before 2000, arguments that the Deccan Traps flood basalts caused the extinction were usually linked to the view that the extinction was gradual, as the flood basalt events were thought to have started around 68 million years ago and lasted for over 2 million years. However, there is evidence that two-thirds of the Deccan Traps were created in only 1 million years about 65.5 million years ago, and so these eruptions would have caused a fairly rapid extinction, possibly over a period of thousands of years, but still longer than would be expected from a single impact event.

The Deccan Traps could have caused extinction through several mechanisms, including the release into the air of dust and sulphuric aerosols, which might have blocked sunlight and thereby reduced photosynthesis in plants. In addition, Deccan Trap volcanism might have resulted in carbon dioxide emissions, which would have increased the greenhouse effect when the dust and aerosols cleared from the atmosphere. Before the mass extinction of the dinosaurs, the release of volcanic gases during the formation of the Deccan Traps "contributed to an apparently massive global warming. Some data point to an average rise in temperature of 8 °C (14 °F) in the last half million years before the impact [at Chicxulub]."

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

Failure to adapt to changing conditions

Lloyd *et al.* (2008) noted that, in the Mid Cretaceous, the flowering, angiosperm plants became a major part of terrestrial ecosystems, which had previously been dominated by gymnosperms such as conifers. Dinosaur coprolite–fossilized dung–indicate that, while some ate angiosperms, most herbivorous dinosaurs ate mainly gymnosperms. Statistical analysis by Lloyd *et al.* concluded that, contrary to earlier studies, dinosaurs did not diversify very much in the Late Cretaceous. Lloyd *et al.* suggested that dinosaurs' failure to diversify as ecosystems were changing doomed them to extinction.

Possible Paleocene survivors

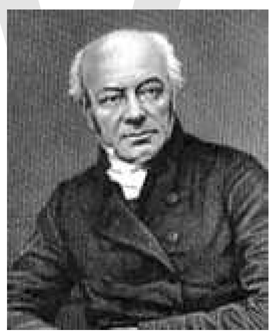
Non-avian dinosaur remains are occasionally found above the K–T boundary. In 2001, paleontologists Zielinski and Budahn reported the discovery of a single hadrosaur leg-bone fossil in the San Juan Basin, New Mexico, and described it as evidence of Paleocene dinosaurs. The formation in which the bone was discovered has been dated to the early Paleocene epoch, approximately 64.5 million years ago. If the bone was not re-deposited into that stratum by weathering action, it would provide evidence that some dinosaur populations may have survived at least a half million years into the Cenozoic Era. Other evidence includes the finding of dinosaur remains in the Hell Creek Formation up to 1.3 meters (51 in) above (40000 years later than) the K–T boundary. Similar reports have come from other parts of the world, including China. Many scientists, however, dismissed the supposed Paleocene dinosaurs as re-worked, i.e. washed out of their original locations and then re-buried in much later sediments. However, direct dating of the bones themselves has supported the later date, with U-Pb dating methods resulting in a precise age of 64.8 ± 0.9 million years ago. If correct, the presence of a handful of dinosaurs in the early Paleocene would not change the underlying facts of the extinction.

History of discovery

Dinosaur fossils have been known for millennia, although their true nature was not recognized. The Chinese, whose modern word for dinosaur is *konglong* (恐龍, or "terrible dragon"), considered them to be dragon bones and documented them as such.

For example, *Hua Yang Guo Zhi*, a book written by Zhang Qu during the Western Jin Dynasty, reported the discovery of dragon bones at Wucheng in Sichuan Province. Villagers in central China have long unearthed fossilized "dragon bones" for use in traditional medicines, a practice that continues today. In Europe, dinosaur fossils were generally believed to be the remains of giants and other creatures killed by the Great Flood.

Scholarly descriptions of what would now be recognized as dinosaur bones first appeared in the late 17th century in England. Part of a bone, now known to have been the femur of a *Megalosaurus*, was recovered from a limestone quarry at Cornwell near Chipping Norton, Oxfordshire, England, in 1676. The fragment was sent to Robert Plot, Professor of Chemistry at the University of Oxford and first curator of the Ashmolean Museum, who published a description in his *Natural History of Oxfordshire* in 1677. He correctly identified the bone as the lower extremity of the femur of a large animal, and recognized that it was too large to belong to any known species. He therefore concluded it to be the thigh bone of a giant human similar to those mentioned in the Bible. In 1699, Edward Lhuyd, a friend of Sir Isaac Newton, was responsible for the first published scientific treatment of what would now be recognized as a dinosaur when he described and named a sauropod tooth, "Rutellum implicatum", that had been found in Caswell, near Witney, Oxfordshire.



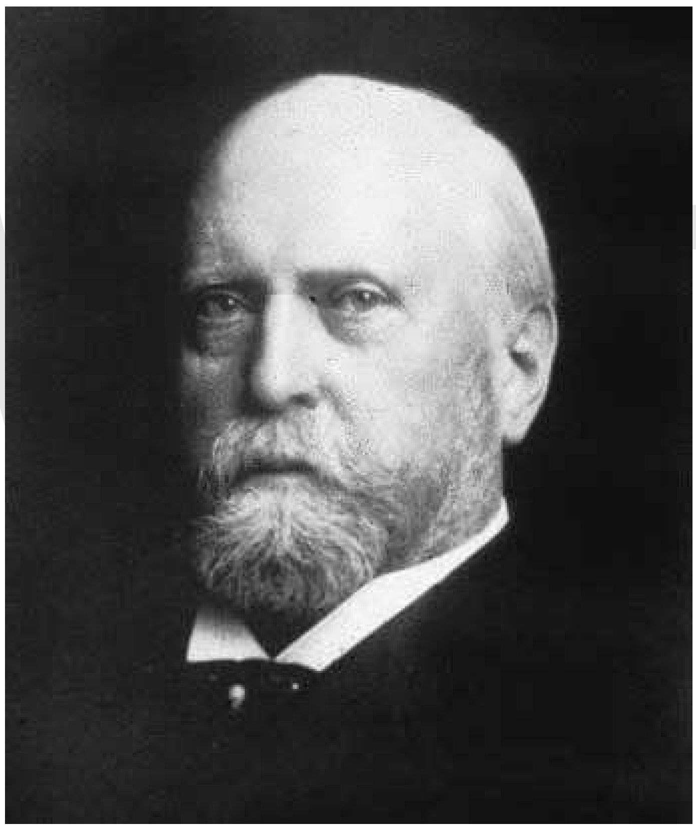
William Buckland

Between 1815 and 1824, the Rev William Buckland, a professor of geology at Oxford University, collected more fossilized bones of *Megalosaurus* and became the first person to describe a dinosaur in a scientific journal. The second dinosaur genus to be identified, *Iguanodon*, was discovered in 1822 by Mary Ann Mantell – the wife of English geologist Gideon Mantell. Gideon Mantell recognized similarities between his fossils and the bones of modern iguanas. He published his findings in 1825.

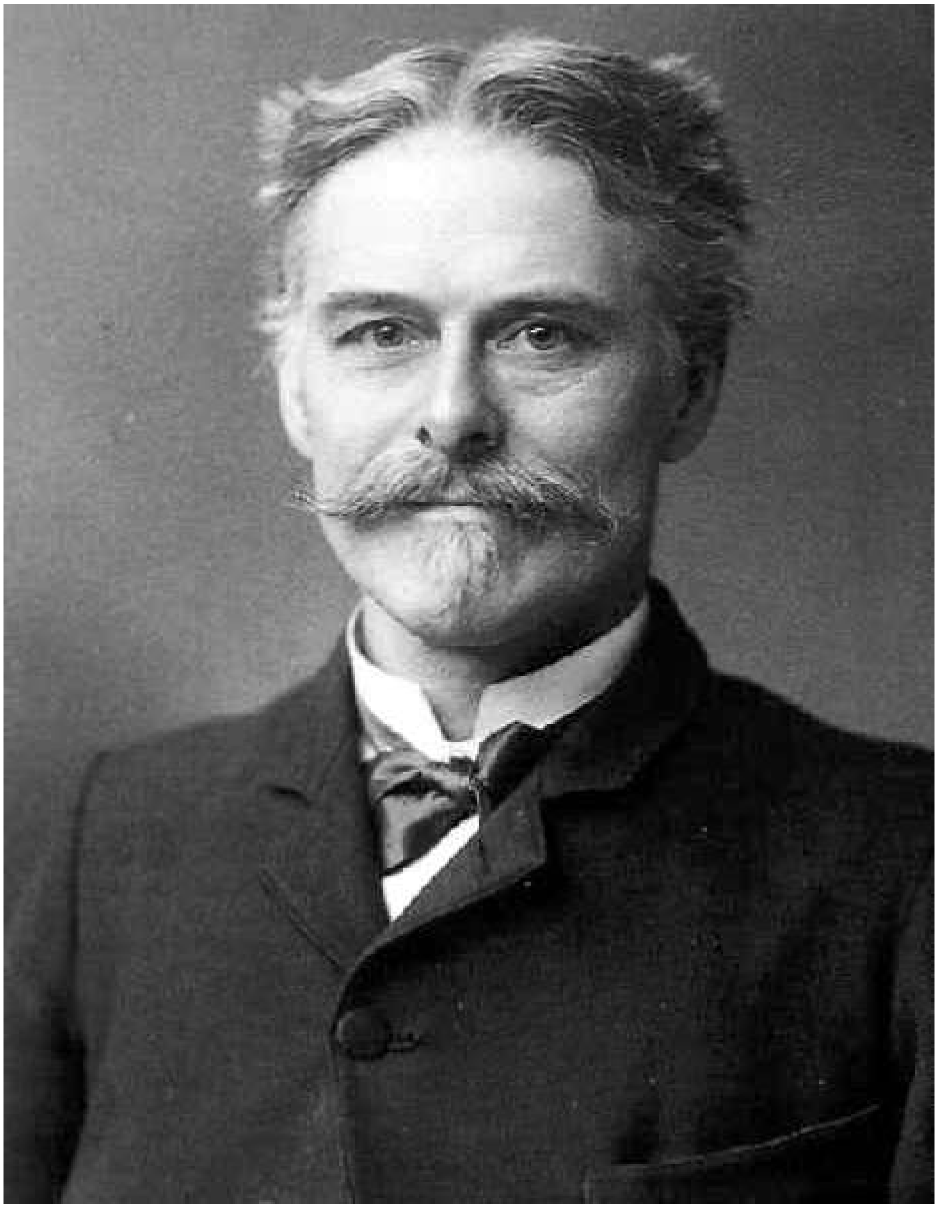
The study of these "great fossil lizards" soon became of great interest to European and American scientists, and in 1842 the English paleontologist Richard Owen coined the term "dinosaur". He recognized that the remains that had been found so far, *Iguanodon*, *Megalosaurus* and *Hylaeosaurus*, shared a number of distinctive features, and so decided to present them as a distinct taxonomic group. With the backing of Prince Albert of Saxe-Coburg-Gotha, the husband of Queen Victoria, Owen established the Natural History

Museum in South Kensington, London, to display the national collection of dinosaur fossils and other biological and geological exhibits.

In 1858, the first known American dinosaur was discovered, in marl pits in the small town of Haddonfield, New Jersey (although fossils had been found before, their nature had not been correctly discerned). The creature was named *Hadrosaurus foulkii*. It was an extremely important find: *Hadrosaurus* was one of the first nearly complete dinosaur skeletons found (the first was in 1834, in Maidstone, Kent, England), and it was clearly a bipedal creature. This was a revolutionary discovery as, until that point, most scientists had believed dinosaurs walked on four feet, like other lizards. Foulke's discoveries sparked a wave of dinosaur mania in the United States.



Othniel Charles Marsh, 19th century photograph



Edward Drinker Cope, 19th century photograph

Dinosaur mania was exemplified by the fierce rivalry between Edward Drinker Cope and Othniel Charles Marsh, both of whom raced to be the first to find new dinosaurs in what came to be known as the Bone Wars. The feud probably originated when Marsh publicly pointed out that Cope's reconstruction of an *Elasmosaurus* skeleton was flawed: Cope had inadvertently placed the plesiosaur's head at what should have been the animal's tail end. The fight between the two scientists lasted for over 30 years, ending in 1897 when Cope died after spending his entire fortune on the dinosaur hunt. Marsh 'won' the contest primarily because he was better funded through a relationship with the US Geological Survey. Unfortunately, many valuable dinosaur specimens were damaged or destroyed due to the pair's rough methods: for example, their diggers often used dynamite to unearth bones (a method modern paleontologists would find appalling). Despite their unrefined methods, the contributions of Cope and Marsh to paleontology were vast: Marsh unearthed 86 new species of dinosaur and Cope discovered 56, a total of 142 new species. Cope's collection is now at the American Museum of Natural History in New York, while Marsh's is on display at the Peabody Museum of Natural History at Yale University.

After 1897, the search for dinosaur fossils extended to every continent, including Antarctica. The first Antarctic dinosaur to be discovered, the ankylosaurid *Antarctopelta oliveroi*, was found on Ross Island in 1986, although it was 1994 before an Antarctic species, the theropod *Cryolophosaurus ellioti*, was formally named and described in a scientific journal.

Current dinosaur "hot spots" include southern South America (especially Argentina) and China. China in particular has produced many exceptional feathered dinosaur specimens due to the unique geology of its dinosaur beds, as well as an ancient arid climate particularly conducive to fossilization.

The "dinosaur renaissance"

The field of dinosaur research has enjoyed a surge in activity that began in the 1970s and is ongoing. This was triggered, in part, by John Ostrom's discovery of *Deinonychus*, an active predator that may have been warm-blooded, in marked contrast to the then-prevailing image of dinosaurs as sluggish and cold-blooded. Vertebrate paleontology has become a global science. Major new dinosaur discoveries have been made by paleontologists working in previously unexploited regions, including India, South America, Madagascar, Antarctica, and most significantly China (the amazingly well-preserved feathered dinosaurs in China have further consolidated the link between dinosaurs and their conjectured living descendants, modern birds). The widespread application of cladistics, which rigorously analyzes the relationships between biological organisms, has also proved tremendously useful in classifying dinosaurs. Cladistic analysis, among other modern techniques, helps to compensate for an often incomplete and fragmentary fossil record.

Cultural depictions

By human standards, dinosaurs were creatures of fantastic appearance and often enormous size. As such, they have captured the popular imagination and become an enduring part of human culture. Entry of the word "dinosaur" into the common vernacular reflects the animals' cultural importance: in English, "dinosaur" is commonly used to describe anything that is impractically large, slow-moving, obsolete, or bound for extinction.

Public enthusiasm for dinosaurs first developed in Victorian England, where in 1854, three decades after the first scientific descriptions of dinosaur remains, the famous dinosaur sculptures were unveiled in London's Crystal Palace Park. The Crystal Palace dinosaurs proved so popular that a strong market in smaller replicas soon developed. In subsequent decades, dinosaur exhibits opened at parks and museums around the world, ensuring that successive generations would be introduced to the animals in an immersive and exciting way. Dinosaurs' enduring popularity, in its turn, has resulted in significant public funding for dinosaur science, and has frequently spurred new discoveries. In the United States, for example, the competition between museums for public attention led directly to the Bone Wars of the 1880s and 1890s, during which a pair of feuding paleontologists made enormous scientific contributions.

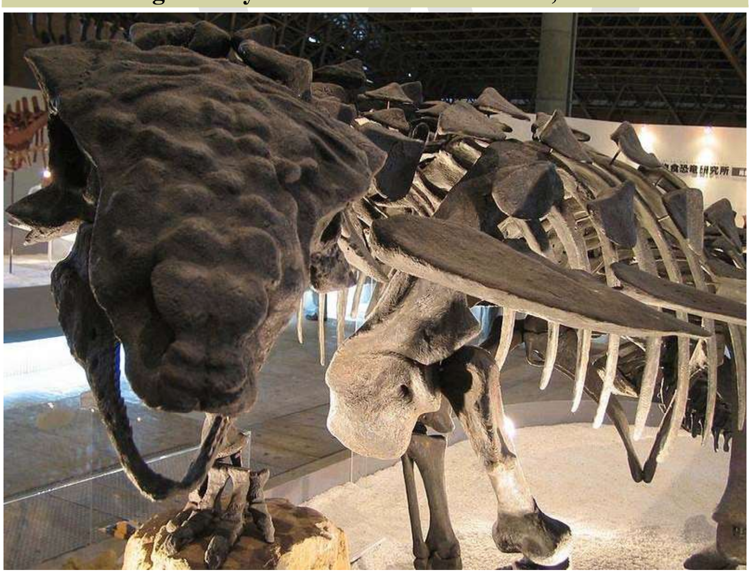
The popular preoccupation with dinosaurs has ensured their appearance in literature, film and other media. Beginning in 1852 with a passing mention in Charles Dickens' *Bleak House*, dinosaurs have been featured in large numbers of fictional works. Sir Arthur Conan Doyle's 1912 book *The Lost World*, the iconic 1933 film *King Kong*, 1954's *Godzilla* and its many sequels, the best-selling 1990 novel *Jurassic Park* by Michael Crichton and its 1993 film adaptation are just a few notable examples of dinosaur appearances in fiction. Authors of general-interest non-fictional works about dinosaurs, including some prominent paleontologists, have often sought to use the animals as a way to educate readers about science in general. Dinosaurs are ubiquitous in advertising; numerous companies have referenced dinosaurs in printed or televised advertisements, either in order to sell their own products or in order to characterize their rivals as slow-moving, dim-witted or obsolete.

Chapter 12

Thyreophora and Ornithischia

Thyreophora

Thyreophorans Fossil range: Early Jurassic-Late Cretaceous, 190–65.5 Ma	



Mymoorapelta.

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Superorder:	Dinosauria
Order:	†Ornithischia
Suborder:	**†Thyreophora** Nopcsa, 1915
Infraorders	

- †Ankylosauria
- †Stegosauria

The **Thyreophora** ("shield bearers", often known simply as "armored dinosaurs" - Greek: *θυρεος*, a large oblong shield, like a door and *φορεω*, I carry) were a subgroup of the ornithischian dinosaurs. They were armored herbivorous dinosaurs, living from the early Jurassic until the end of the Cretaceous.

Thyreophorans are characterized by the presence of body armor lined up in longitudinal rows along the body. Primitive forms had simple, low, keeled scutes or osteoderms whereas more derived forms developed more elaborate structures including spikes and plates. Most thyreophorans had relatively small brains for their body size.

Thyreophorans include well-known suborders such as the **Ankylosauria** and **Stegosauria** as well as lesser-known groups. Among the Ankylosauria, the two main groups are the Ankylosaurids and Nodosaurids. In both groups, the forelimbs were much shorter than the hindlimbs, and this was particularly exaggerated in stegosaurs. The clade has been defined as the group consisting of all species more closely related to *Ankylosaurus* than to *Triceratops*. Thyreophora is the sister group of the Cerapoda within the Genasauria.

Ankylosaurids are noted by the presence of a large tail club composed of distended vertebrae that have fused into a single mass. They were heavy-set and heavily armored from head to tail in bony armor, even down to minor features such as the eyelids. Spikes and nodules, often of horn, were set into the armor. The head was flat, stocky, with little or no "neck", roughly shovel-shaped and characterized by two spikes on either side of the head approximately where the ears and cheeks were. *Euoplocephalus tutus* is perhaps the best-known ankylosaurid.

Nodosaurids, the other family in the Ankylosauria, may actually include the ancestors of the ankylosaurids. They lived during the middle Jurassic (approx 170 mya) on up through the late Cretaceous (65 mya) and, while armored as the ankylosaurids, did not have a tail club. Instead, the bony bumps and spikes that covered the rest of their body continued out to the tail and/or were augmented with sharp spines. Two examples of nodosaurs are *Sauropelta* and *Edmontonia*, the latter most notable for its formidable forward-pointing shoulder spikes.

The **Stegosauria** suborder comprises the **Stegosauridae** and **Huayangosauridae**. These dinosaurs lived mostly from the Middle to Late Jurassic, although some fossils have been found in the Early Cretaceous. Stegosaurs had very small heads with simple, leaf-like teeth. Stegosaurs possessed rows of plates and/or spikes running down the dorsal midline and elongated dorsal vertebra. It has been suggested that stegosaur plates functioned in control of body temperature (thermoregulation) and/or were used as a display to identify members of a species, as well as to attract mates and intimidate rivals. Well known stegosaurs are *Stegosaurus* and *Kentrosaurus*.

Taxonomy

- **SUBORDER THYREOPHORA**
  - *Emausaurus*
  - *Scutellosaurus*
  - ?*Tatisaurus*
    - **Eurypoda**
      - **Infraorder Ankylosauria**
        - ?Family Scelidosauridae (may be basal group)
          - *Bienosaurus*
          - *Lusitanosaurus*
          - *Scelidosaurus*
        - *Antarctopelta*
        - *Minmi*
        - Family Ankylosauridae
        - Family Nodosauridae
      - **Infraorder Stegosauria**
        - Family Huayangosauridae
        - Family Stegosauridae

"Tyreophorus"

"Tyreophorus" is an informal generic name, attributed to Friedrich von Huene, 1929, that is sometimes seen in lists of dinosaurs. It is probably a typographical error; von Huene intended to assign indeterminate remains to Thyreophora *incertae sedis*, but at some point in the process of publication, the text was revised to make it appear that he was creating a new generic name "Tyreophorus" (as described by George Olshevsky in a 1999 post to the Dinosaur Mailing List). The name is undescribed and has not been used seriously.

Ornithischia

Ornithischians Fossil range: Late Triassic–Late Cretaceous, 228–65 Ma	

Edmontosaurus pelvis (showing ornithischian structure – left side) Oxford University Museum of Natural History

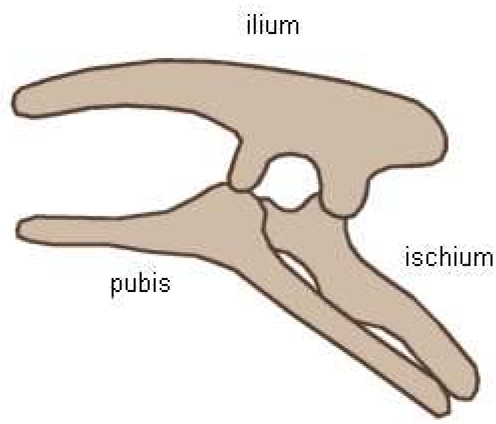
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Superorder:	Dinosauria
Order:	†**Ornithischia** Seeley, 1888

Subgroups

- †Fabrosauridae
- †Heterodontosauridae
- †Lesothosauridae
- †Pisanosauridae
- †Genasauria
    - †Cerapoda
    - †Thyreophora

Ornithischia or **Predentata** is an extinct order of beaked, herbivorous dinosaurs. The name *ornithischia* is derived from the Greek *ornitheos* (*ορνιθειος*) meaning 'of a bird' and *ischion* (*ισχιον*) meaning 'hip joint'. They are known as the 'bird-hipped' dinosaurs because of their bird-like hip structure, even though birds actually descended from the 'lizard-hipped' dinosaurs (the saurischians). Being herbivores that sometimes lived in herds, they were more numerous than the saurischians. They were prey animals for the theropods and were smaller than the sauropods.

Characteristics



Ornithischian pelvic structure (left side)

The Dinosauria superorder was divided into the two orders Ornithischia and Saurischia by Harry Seeley in 1887. This division, which has generally been accepted, is based on the evolution of the pelvis into a more bird-like structure (although birds did not descend from these dinosaurs), details in the vertebrae and armor and the possession of a 'predentary' bone. The predentary is an extra bone in the front of the lower jaw, which extends the dentary (the main lower jaw bone). The predentary coincides with the premaxilla in the upper jaw. Together they form a beak-like apparatus used to clip off plant material.

The ornithischian pubis bone points downward and toward the tail (backwards), parallel with the ischium, with a forward-pointing process to support the abdomen. This makes a four-pronged pelvic structure. In contrast to this, the saurischian pubis points downward and toward the head (forwards), as in ancestral lizard types. Ornithischians also had smaller antorbital fenestrae (holes in front of their eye sockets) than did saurischians, and a wider, more stable pelvis. A bird-like pubis arrangement, parallel to the vertebral column, evolved independently three times in dinosaur evolution, namely in the ornithischians, in the therizinosauroids and in bird-like dromaeosaurids.

Ornithischians shifted from bipedal to quadrupedal posture at least three times in their evolutionary history and have been shown to have been capable of adopting both postures early in their evolutionary history.

Classification

Taxonomy

Linnaean ranks after Benton (2004):

- **Order Ornithischia**
    - Genus *Eocursor*
    - Genus *Pisanosaurus*
    - Family Fabrosauridae
    - Family Heterodontosauridae
    - Family Lesothosauridae
    - **Suborder Thyreophora** – (armored dinosaurs)
        - Family Scelidosauridae
        - **Infraorder Stegosauria**
        - **Infraorder Ankylosauria**
    - **Suborder Cerapoda**
        - **Infraorder Ornithopoda**
            - Family Hypsilophodontidae*
            - Family Hadrosauridae – (duck-billed dinosaurs)
        - **Infraorder Pachycephalosauria**
        - **Infraorder Ceratopsia** – (horned dinosaurs)

Phylogeny

Genasaurian ornithischians are divided into two clades: the Thyreophora and the Cerapoda. The Thyreophora include the Stegosauria (like the armored *Stegosaurus*) and the Ankylosauria (like *Ankylosaurus*). The Cerapoda include the Marginocephalia (Ceratopsia like the frilled ceratopsidae and Pachycephalosauria) and the Ornithopoda (including duck-bills (hadrosaurs) such as *Edmontosaurus)*. The Cerapoda are a relatively recent concept (Sereno, 1986).

Chapter 13

Saurischia (Type of Dinosaur)

Saurischians **Fossil range: Late Triassic-Recent 231.4–0 Ma**	
	
Tyrannosaurus rex saurischian pelvis and hind limbs (left side).	
Scientific classification	
Kingdom:	Animalia

Phylum:	Chordata
Class:	Reptilia
Superorder:	Dinosauria
Order:	**Saurischia** Seeley, 1888

Subgroups

- †Herrerasauridae?
- **Eusaurischia**
    - †Sauropodomorpha
    - Theropoda

Saurischia from the Greek *sauros* (*σαυρος*) meaning 'lizard' and *ischion* (*ισχιον*) meaning 'hip joint') is one of the two orders, or basic divisions, of dinosaurs. In 1888, Harry Seeley classified dinosaurs into two orders, based on their hip structure. Saurischians ('lizard-hipped') are distinguished from the ornithischians ('bird-hipped') by retaining the ancestral configuration of bones in the hip.

All carnivorous dinosaurs (the theropods) are saurischians, as are one of the two primary lineages of herbivorous dinosaurs, the sauropodomorphs. At the end of the Cretaceous Period, all non-avian saurischians became extinct. This is referred to as the Cretaceous-Tertiary extinction event. Avians (modern birds), as direct descendants of one group of theropod dinosaurs, are considered to be a sub-clade of saurischian dinosaurs in phylogenetic classification.

Description

Saurischians are distinguished from ornithischians by their three-pronged pelvic structure, with the pubis pointed forward. The ornithischians' pelvis is arranged with the pubis rotated backward, parallel with the ischium, often also with a forward-pointing process, giving a four-pronged structure.

The ornithischian hip structure is superficially similar to that of birds, which led Seeley to name them "**bird-hipped dinosaurs**," though he did not propose any specific relationship with birds. He termed saurischians "lizard-hipped" dinosaurs because they retained the ancestral hip anatomy also found in modern lizards.

However, as later study revealed, the hip structure possessed by modern birds actually evolved independently from the "lizard-hipped" saurischians (specifically, a sub-group of saurischians called the Maniraptora) in the Jurassic Period. In this example of convergent evolution, birds developed hips oriented similar to the earlier ornithischian hip anatomy, in both cases possibly as an adaptation to a herbivorous or omnivorous diet.

Classification

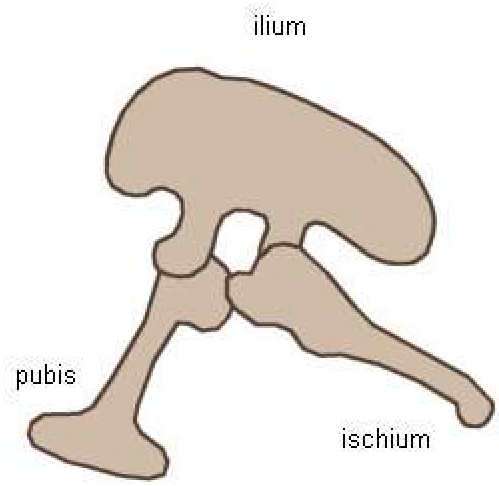


Diagram of saurischian pelvic structure (left side).

In his paper naming the two groups, Seeley reviewed previous classification schemes put forth by other paleontologists to divide up the traditional Order Dinosauria. He preferred one that had been put forward by Othniel Charles Marsh in 1878, which divided dinosaurs into four Orders: Sauropoda, Theropoda, Ornithopoda, and Stegosauria (these names are still used today in much the same way to refer to suborders or clades within Saurischia and Ornithischia).

Seeley, however, wanted to formulate a classification that would take into account a single primary difference between major dinosaurian groups based on a characteristic that also differentiated them from other reptiles. He found this in the configuration of the hip bones, and found that all four of Marsh's orders could be divided neatly into two major groups based on this feature. He placed the Stegosauria and Ornithopoda in the Ornithischia, and the Theropoda and Sauropoda in the Saurischia. Furthermore, Seeley used this major difference in the hip bones, along with many other noted differences between the two groups, to argue that "dinosaurs" were not a natural grouping at all, but rather two distinct orders that had arisen independently from more primitive archosaurs. This concept that "dinosaur" was an outdated term for two distinct orders lasted many decades in the scientific and popular literature, and it was not until the 1960s that scientists began to again consider the possibility that saurischians and ornithischians were more closely related to each other than they were to other archosaurs.

Although his concept of a paraphyletic Dinosauria is no longer accepted by most paleontologists, Seeley's basic division of the two dinosaurian groups has stood the test of time, and has been supported by modern cladistic analysis of relationships among dinosaurs. One alternate hypothesis challenging Seeley's classification was proposed by Robert T. Bakker in his 1986 book *The Dinosaur Heresies*. Bakker's classification separated the theropods into their own group and placed the two groups of herbivorous dinosaurs (the sauropodomorphs and ornithischians) together in a separate group he named the Phytodinosauria ('plant dinosaurs'). The Phytodinosauria hypothesis was based partly on the supposed link between ornithischians and prosauropods, and the idea that the former had evolved directly from the later, possibly by way of an enigmatic family that seemed to possess characters of both groups, the segnosaurs. However, it was later found that segnosaurs were actually an unusual type of herbivorous theropod saurischians closely related to birds, and the Phytodinosauria hypothesis fell out of favor.

Taxonomy

Mounted skeletons of *Tyrannosaurus* (left) and *Apatosaurus* (right) in the hall of saurischian dinosaurs at the American Museum of Natural History.

- **Order Saurischia**
    - Infraorder †Herrerasauria
        - **Suborder †Sauropodomorpha**
            - †Guaibasauridae
            - Infraorder †Prosauropoda
            - Infraorder †Sauropoda
        - **Suborder Theropoda**
            - *†Eoraptor*
            - *†Tawa*
            - Infraorder †Carnosauria
            - Infraorder †Ceratosauria
            - Infraorder †Deinonychosauria
            - Infraorder †Ornithomimosauria
            - Infraorder †Oviraptorosauria

Additionally, the genera *Teyuwasu* and *Agnosphitys* may represent early saurischians, or more primitive non-dinosaurs.

Chapter 14

Theropoda (Type of Dinosaur)

Theropods
Fossil range:
Late Triassic–Late Cretaceous, 228–65 Ma
Descendant taxon Aves survives to present

Mounted replica of a *Tyrannosaurus rex* skeleton

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Superorder:	Dinosauria
Order:	Saurischia
(unranked):	Eusaurischia
Suborder:	**Theropoda** Marsh, 1881

Subgroups

- †*Eodromaeus*
- †*Eoraptor*?
- †Herrerasauridae?
- †*Tawa*
- **Avepoda**
  - †Coelophysoidea
  - **Neotheropoda**
    - †Ceratosauria
    - †Dilophosauridae
    - Tetanurae

Theropods suborder name *theropoda* meaning "beast feet") is both a suborder of bipedal saurischian dinosaurs, and a clade consisting of that suborder and its descendants (including modern birds). Dinosaurs belonging to the suborder *theropoda* were primarily carnivorous, although a number of theropod groups evolved herbivory, omnivory, and insectivory. Theropods first appeared during the Carnian age of the late Triassic period about 230 million years ago (Ma) and included the sole large terrestrial carnivores from the Early Jurassic until at least the close of the Cretaceous, about 65 Ma. In the Jurassic, birds evolved from small specialized coelurosaurian theropods, and are today represented by 9,900 living species.

Among the features linking theropod dinosaurs to birds are the three-toed foot, a furcula (wishbone), air-filled bones and (in some cases) feathers and brooding of the eggs.

Paleobiology

Diet

Specimen of the troodontid *Jinfengopteryx elegans*, with seeds preserved in the stomach region

While historically generalized as exclusively carnivorous dinosaurs, theropods in fact displayed a wide range of diets. All early finds of theropod fossils showed them to be primarily carnivorous. Theropod specimens known to scientists in the 19th and early 20th centuries all showed sharp teeth with serrated edges for cutting flesh, and some specimens even showed direct evidence of predatory behavior. For example, a *Compsognathus* fossil was found with a lizard in its stomach, and a *Velociraptor* specimen was found locked in combat with a *Protoceratops* (a type of ornithischian dinosaur).

The first confirmed non-carnivorous theropods found were the therizinosaurs, originally known as segnosaurs. First thought to be prosauropods, these enigmatic dinosaurs were later proven to be highly specialized, herbivorous theropods. Therizinosaurs possessed large abdomens for processing plant food, and small heads with beaks and leaf-shaped teeth. Further study of maniraptoran theropods and their relationships showed that therizinosaurs were not the only member of this group to abandon carnivory. Several other lineages of maniraptors show adaptations for an omnivorous diet, including seed-eating (some troodontids) and insect-eating (many avialans and alvarezsaurs). Oviraptorosaurs, ornithomimosaurs and advanced troodontids were likely omnivorous as well, and some theropods (such as *Masiakasaurus* and the spinosaurids) appear to have specialized in catching fish.

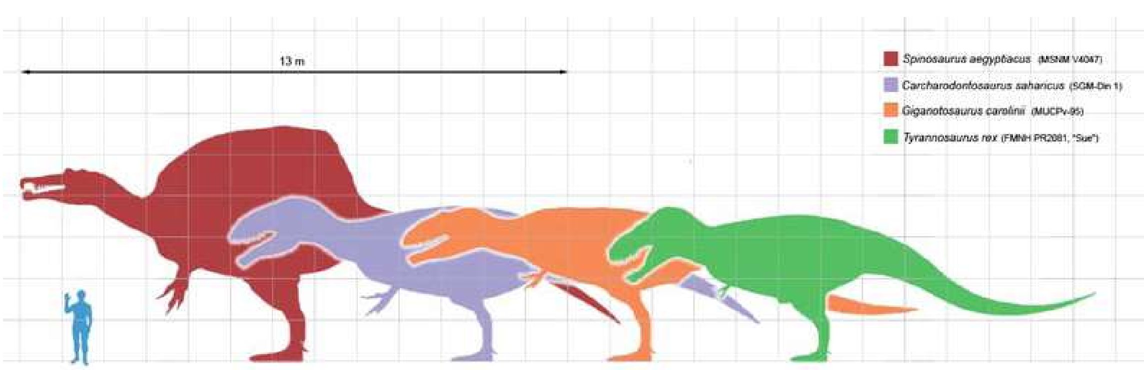
Skin, scales and feathers

Mesozoic theropods were also very diverse in terms of skin texture and covering. Though feather-like structures are known in the related ornithischian dinosaurs, evidence of feathers or feather-like structures has not been reported for any theropods less advanced than the coelurosaurs. More primitive theropods show evidence that their skin was covered in small, bumpy scales. In some species, these were interspersed with larger scales with bony cores, or osteoderms. This type of skin is best known in the ceratosaur *Carnotaurus*, which has been preserved with extensive skin impressions.

The most primitive known protofeathered theropods are the compsognathids and early tyrannosauroids, both coelurosaurs. These early forms had feathers which were relatively short and composed of simple, possibly branching filaments. Simple filaments are also seen in therizinosaurs, which also possessed large, stiffened "quill"-like feathers.

Most feathered theropods, including modern birds, usually retain scales only on the feet. Some forms seem to have mixed feathers elsewhere on the body as well. *Scansoriopteryx* preserved scales on the underside of the tail, and *Juravenator* may have been predominantly scaly with some simple filaments interspersed. On the other hand, some theropods were completely covered with feathers, such as the troodontid *Anchiornis*, which even had feathers on the feet and toes.

Size



Size comparison of selected giant theropod dinosaurs.

Tyrannosaurus was the largest and most popular theropod known to the general public for many decades. Since its discovery, however, a number of other giant carnivorous dinosaurs have been described, including *Spinosaurus*, *Carcharodontosaurus*, and *Giganotosaurus*. The original *Spinosaurus* specimens (as well as newer fossils described in 2006) support the idea that *Spinosaurus* is larger than *Tyrannosaurus*, showing that *Spinosaurus* was possibly 6 meters longer and at least 1 metric ton heavier than *Tyrannosaurus*. There is still no clear explanation for exactly why these animals grew so much larger than the predators that came before and after them.

The smallest non-avialan theropod known from adult specimens is the troodontid *Anchiornis huxleyi*, at 110 grams in weight and 34 centimeters (1 ft) in length. When modern birds are included, the Bee Hummingbird *Mellisuga helenae* is smallest at 1.9 g and 5.5 cm (2.2 in) long.

Nervous system and senses

Although rare, complete casts of theropod endocrania are known from fossils. Theropod endocrania can also be reconstructed from preserved brain cases without damaging valuable specimens by using a computed tomography scan and 3D reconstruction software. These finds are of evolutionary significance because they help document the emergence of the neurology of modern birds from that of earlier reptiles. An increase in the proportion of the brain occupied by the cerebrum seems to have occurred with the advent of the Coelurosauria and "continued throughout the evolution of maniraptorans and early birds."

Forelimb morphology

The clawed left hand of an *Allosaurus*.

Shortened forelimbs in relation to hind legs was a common trait among theropods, most notably in the abelisaurids (such as *Carnotaurus*) and the tyrannosaurids (such as *Tyrannosaurus*). This trait was, however, not universal: spinosaurids had well developed forelimbs, so also did many coelurosaurs. One genus, *Xuanhanosaurus*, has also been claimed to have been quadrupedal because of its comparatively robust forelimbs, but this is no longer thought to be likely.

The hands are also very different among the different groups. the most common is an appendage consisting of 3 fingers, the digits I, II and III (or possibly II, III and IV) with sharp claws. Some basal theropods (*Herrerasaurus*, *Eoraptor*) had 4 digits, and also a reduced metacarpal V. Ceratosaurians usually had 4 digits, while most tetanurans had 3.

The forelimbs' scope of use is also believed to have also been different among different families. The spinosaurids could have used their powerful forelimbs to hold fishes. Some small coelurosaurus (dromaeosaurids, scansoriopterygids) are believed to have used their forelimbs to climb in trees, and birds, which are believed to be descendants of theropods, use them for flight.

Forelimb movement

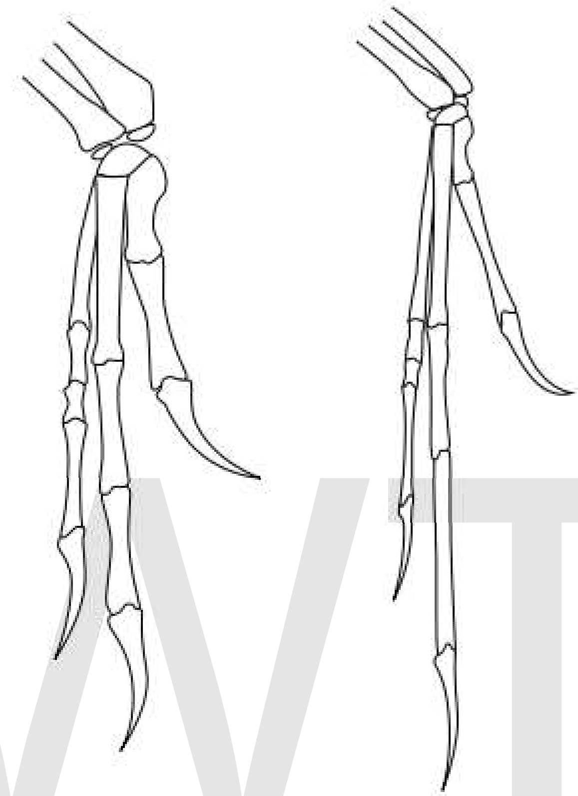
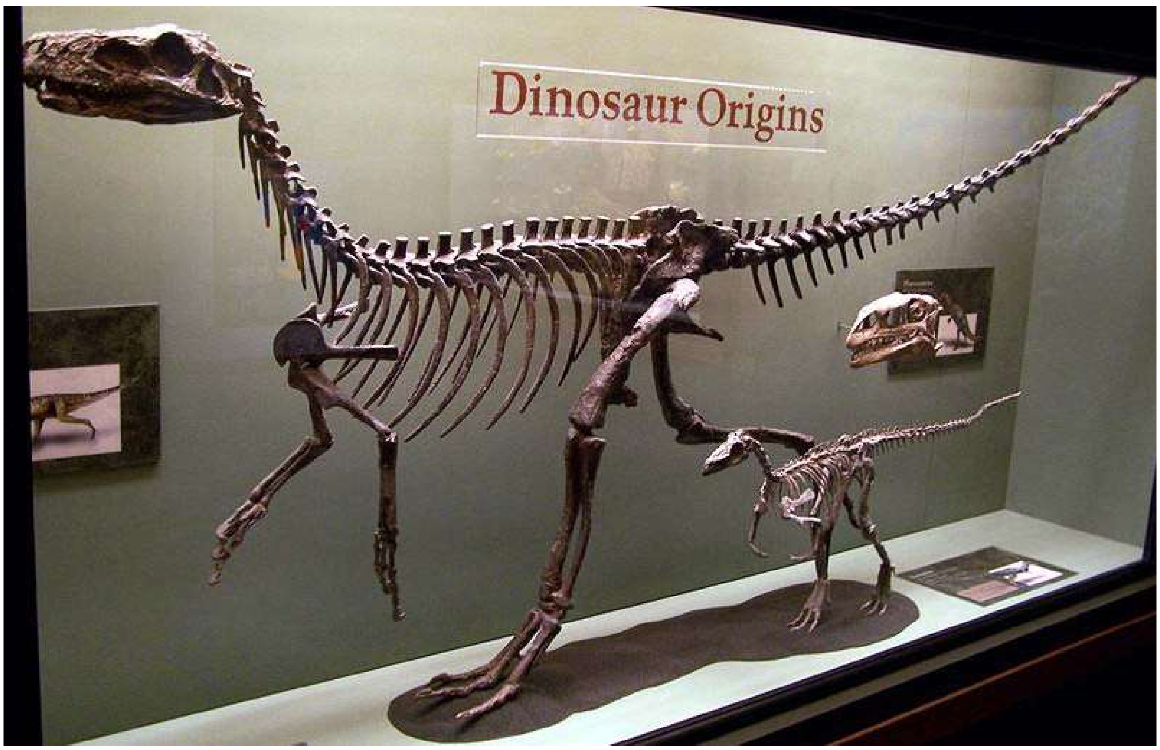


Diagram of *Deinonychus* (left) and *Archaeopteryx* (right) forelimbs illustrating wing-like posture

Contrary to the way theropods have often been reconstructed in art and the popular media, the range of motion of theropod forelimbs was severely limited, especially compared with the forelimb dexterity of humans and other primates. Most notably, theropods and other bipedal saurischian dinosaurs (including the bipedal prosauropods) could not pronate their hands—that is, they could not rotate the forearm so that the palms faced the ground or backwards towards the legs. In humans, pronation is achieved by motion of the radius relative to the ulna (the two bones of the forearm). In saurischian dinosaurs, however, the end of the radius near the elbow was actually locked into a groove of the ulna, preventing any movement. Movement at the wrist was also limited in many species, forcing the entire forearm and hand to move as a single unit with little flexibility. In theropods and prosauropods, the only way for the palm to face the ground would have been by lateral splaying of the entire forelimb, as in a bird raising its wing.

In carnosaurs like *Acrocanthosaurus*, the hand itself retained a relatively high degree of flexibility, with mobile fingers. This was also true of more basal theropods such as herrerasaurs and dilophosaurs. Coelurosaurs showed a shift in the use of the forearm, with greater flexibility at the shoulder allowing the arm to be raised towards the horizontal plane, and to even greater degrees in flying birds. However, in coelurosaurs such as ornithomimosaurs and especially dromaeosaurs, the hand itself had lost most flexibility, with highly inflexible fingers. Dromaeosaurs and other maniraptorans also showed increased mobility at the wrist not seen in other theropods, thanks to the presence of a specialized half-moon shaped wrist bone (the semi-lunate carpal) that allowed the whole hand to fold backward towards the forearm in the manner of modern birds.

Evolutionary history



The possible early forms *Herrerasaurus* (large) and *Eoraptor* (small)

During the late Triassic, a number of primitive proto-theropod and theropod dinosaurs existed and evolved alongside each other.

The earliest and most primitive of the theropod dinosaurs were the carnivorous *Eodromaeus* and the herrerasaurids of Argentina (as well as, possibly, the omnivorous *Eoraptor*). The herrerasaurs existed during the early late Triassic (Late Carnian to Early Norian). They were found in North America and South America and possibly also India and Southern Africa. The herrerasaurs were characterised by a mosaic of primitive and advanced features. Some paleontologists have in the past considered the herrerasaurians to be members of Theropoda, while other theorized the group to be basal saurischians, and may even have evolved prior to the saurischian-ornithischian split. Cladistic analysis following the discovery of *Tawa*, another Triassic dinosaur, suggests the herrerasaurs likely were early theropods.

The earliest and most primitive unambiguous theropods (or alternatively, "Eutheropoda" - 'True Theropods') are the Coelophysoidea. The Coelophysoidea were a group of widely distributed, lightly built and potentially gregarious animals. They included small hunters like *Coelophysis* and (possibly) larger predators like *Dilophosaurus*. These successful animals continued from the Late Carnian (early Late Triassic) through to the Toarcian (late Early Jurassic). Although in the early cladistic classifications they were included under the Ceratosauria and considered a side-branch of more advanced theropods, they may have been ancestral to all other theropods (which would make them a paraphyletic group).

The somewhat more advanced ceratosaurs (including *Ceratosaurus* and *Carnotaurus*) appeared during the Early Jurassic and continued through to the Late Jurassic in Laurasia. They competed alongside their more anatomically advanced tetanuran relatives and—in the form of the abelisaur lineage—lasted to the end of the Cretaceous in Gondwana.

The Tetanurae are more specialised again than the ceratosaurs. They are subdivided into the basal Megalosauroidea (alternately Spinosauroidea) and the more derived Avetheropoda. Megalosauridae were primarily Middle Jurassic to Early Cretaceous predators, and their spinosaurid relatives' remains are mostly from Early and Middle Cretaceous rocks. Avetheropoda, as their name indicates, were more closely related to birds and are again divided into the Allosauroidea (the diverse carcharodontosaurs) and the Coelurosauria (a very large and diverse dinosaur group including the birds).

Thus, during the late Jurassic, there were no fewer than four distinct lineages of theropods—ceratosaurs, megalosaurs, allosaurs, and coelurosaurs—preying on the abundance of small and large herbivorous dinosaurs. All four groups survived into the Cretaceous, and three of those—the ceratosaurs, coelurosaurs, and allosaurs—survived to end of the period, where they were geographically separate, the ceratosaurs and allosaurs in Gondwana, and the coelurosaurs in Laurasia.

Of all the theropod groups, the coelurosaurs were by far the most diverse. Some coelurosaur groups that flourished during the Cretaceous were the tyrannosaurids (including *Tyrannosaurus*) the dromaeosaurids (including *Velociraptor* and *Deinonychus*, which are remarkably similar in form to the oldest known bird, *Archaeopteryx*), the bird-like troodontids and oviraptorosaurs, the ornithomimosaurs (or "ostrich dinosaurs"), the strange giant-clawed herbivorous therizinosaurs, and the avialans, which include modern birds and is the only dinosaur lineage to survive the Cretaceous-Paleogene extinction event. While the roots of these various groups are found in the Middle Jurassic, they only became abundant during the Early Cretaceous. A few paleontologists, such as Gregory S. Paul, have suggested that some or all of these advanced theropods were actually descended from flying dinosaurs or proto-birds like *Archaeopteryx* that lost the ability to fly and returned to a terrestrial habitat.

Classification

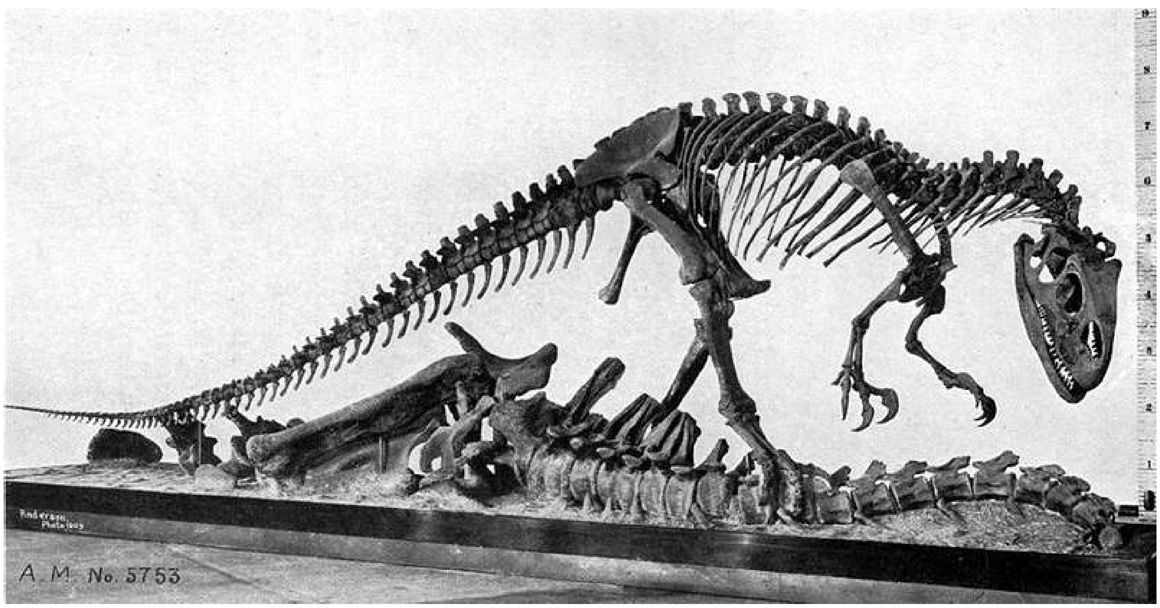
History of classification

Othniel Charles Marsh, who coined the name Theropoda. Photo c. 1870.

The name Theropoda (meaning "beast feet") was first coined by O.C. Marsh in 1881. Marsh initially named Theropoda as a suborder to include the family Allosauridae, but later expanded its scope, re-ranking it as an order to include a wide array of "carnivorous" dinosaur families, including Megalosauridae, Compsognathidae, Ornithomimidae, Plateosauridae and Anchisauridae (now known to be herbivorous prosauropods) and Hallopodidae (now known to be relatives of crocodilians). Due to the scope of Marsh's

Order Theropoda, it came to replace a previous taxonomic group that Marsh's rival E.D. Cope had created in 1866 for the carnivorous dinosaurs, **Goniopoda** ("angled feet").

By the early 20th century, some paleontologists, such as Friedrich von Huene, no longer considered carnivorous dinosaurs to have formed a natural group. Huene abandoned the name Theropoda, instead using Harry Seeley's Order Saurischia, which Huene divided into the suborders Coelurosauria and Pachypodosauria. Huene placed most of the small theropod groups into Coelurosauria, and the large theropods and prosauropods into Pachypodosauria, which he considered ancestral to the Sauropoda (prosauropods were still thought of as carnivorous at this time, owing to the incorrect association of rauisuchian skulls and teeth with prosauropod bodies, in animals such as *Teratosaurus*). In W.D. Matthew and Barnum Brown's 1922 description of the first known dromaeosaurid (*Dromaeosaurus albertensis*), they became the first paleontologists to exclude prosauropods from the carnivorous dinosaurs, and attempted to revive the name Goniopoda for that group, though neither of these suggestions were accepted by other scientists.

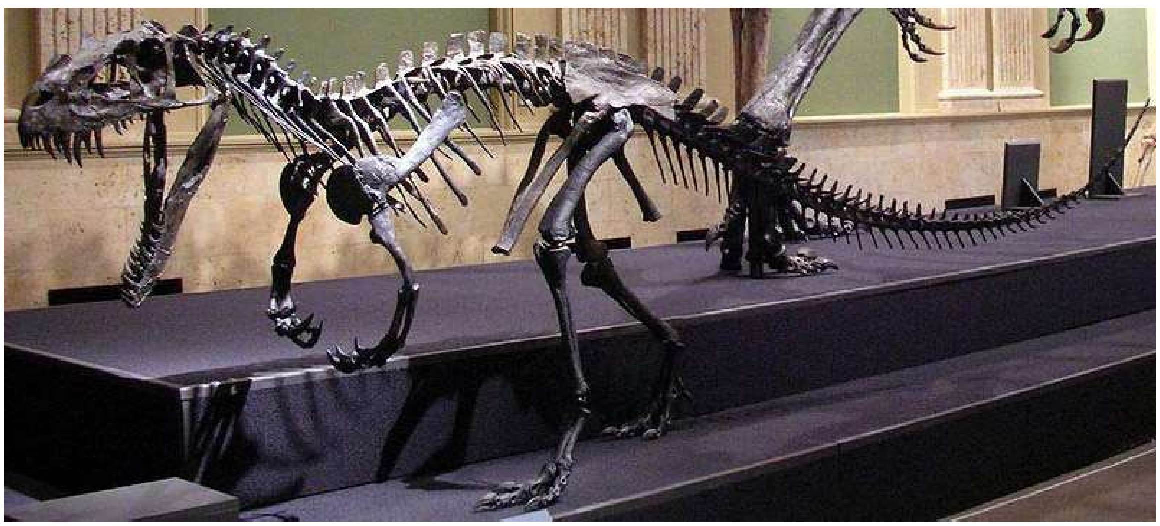


Allosaurus was one of the first dinosaurs classified as a theropod

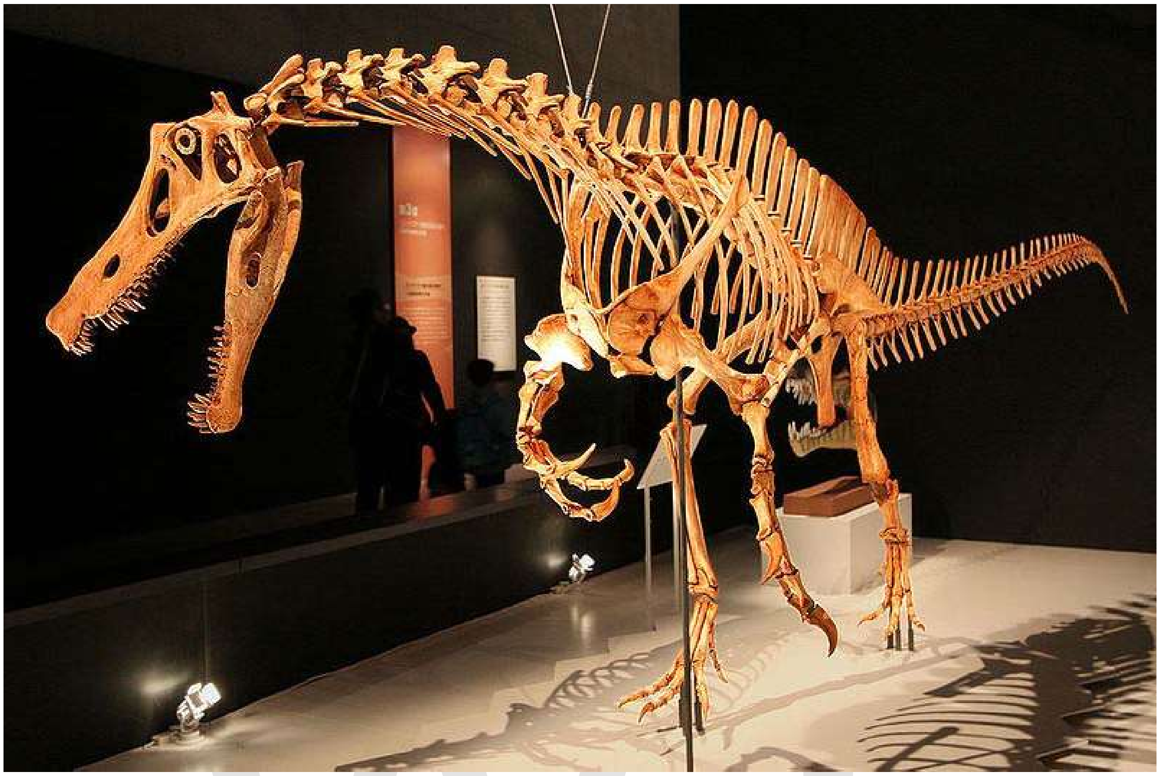
It was not until 1956 that Theropoda came back into use as a taxon containing the carnivorous dinosaurs and their descendants, when Alfred Romer re-classified the Order Saurischia into two suborders, Theropoda and Sauropoda. This basic division has survived into modern paleontology, with the exception of, again, the Prosauropoda, which Romer included as an infraorder of theropods. Romer also maintained a division between Coelurosauria and Carnosauria (which he also ranked as infraorders). This dichotomy was upset by the discovery of *Deinonychus* and *Deinocheirus* in 1969, neither of which could be classified easily as "carnosaurs" or "coelurosaurs." In light of these and other discoveries, by the late 1970s Rinchen Barsbold created a new series of theropod infraorders: Coelurosauria, Deinonychosauria, Oviraptorosauria, Carnosauria, Ornithomimosauria, and Deinocheirosauria.

With the advent of cladistics and phylogenetic nomenclature in the 1980s, and their development in the 1990s and 2000s, a clearer picture of theropod relationships began to emerge. Several major theropod groups were named by Jacques Gauthier in 1986, including the clade Tetanurae for one branch of a basic theropod split with another group, the Ceratosauria. As more information about the link between dinosaurs and birds came to light, the more bird-like theropods were grouped in the clade Maniraptora (also named by Gauthier in 1986). These new developments also came with a recognition among most scientists that birds arose directly from maniraptoran theropods and, with the abandonment of ranks in cladistic classification, the re-evaluation of birds as a subset of theropod dinosaurs that happened to have survived the Mesozoic extinctions into the present.

Major groups



Ceratosaurus, a ceratosaur



Irritator, a spinosaur

Microraptor, a deinonychosaur

Theropods are a highly diverse group, and many major Mesozoic lineages have been identified:

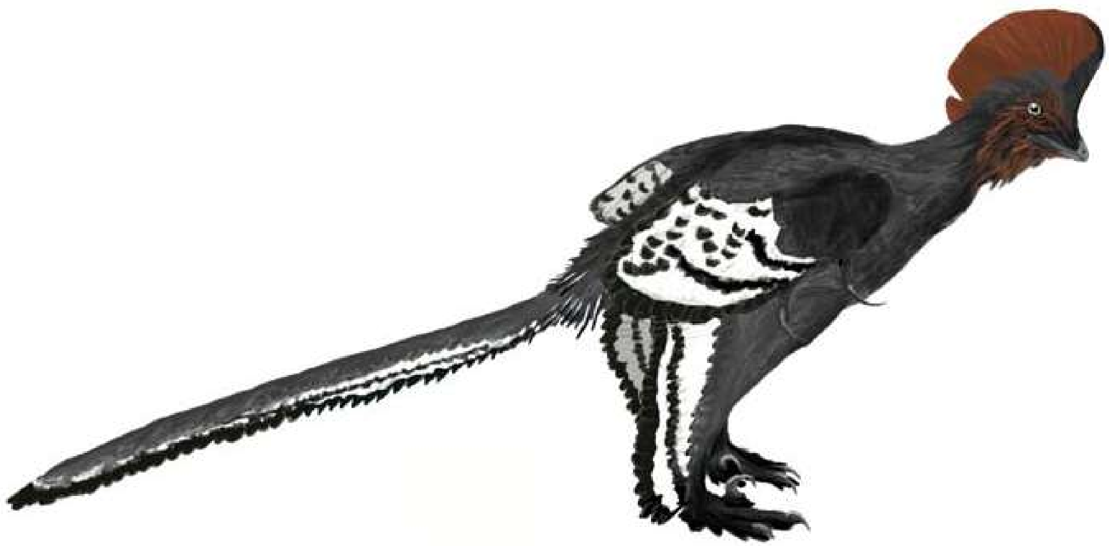
- †Herrerasaurids, probably early theropods, though they may be more primitive saurischians or even non-dinosaurs
- †Coelophysoids, primitive theropods including *Coelophysis*
- †Ceratosaurians, including *Ceratosaurus* and abelisaurids. The latter were important Late Cretaceous predators in southern continents
- †Dilophosaurids, crested theropods sometimes allied with the coelophysoids
- Tetanurans, a major grouping of more advanced theropods
    - †Megalosauroids, including the crocodile-skulled spinosaurids
    - Avetheropods, more advanced and bird-like theropods
        - †Allosauroids, including *Allosaurus* and close relatives like the carcharodontosaurids
        - Coelurosaurians, a diverse lineage with a wide range of body sizes, diets and niches
            - †Tyrannosauroids, small to gigantic carnivores, often with reduced forelimbs
            - †Ornithomimosaurians, "ostrich-mimics", mostly toothless and probably omnivorous
            - Maniraptorans, birds and their closest relatives, all possessed feathers, many omnivorous or herbivorous
                - †Therizinosaurs, bipedal herbivores with large hand claws and small heads
                - †Alvarezsaurs, small bird-like insectivores with extremely short forelimbs
                - †Oviraptorosaurians, mostly toothless; their diet and lifestyle are uncertain
                - †Deinonychosaurs, popularly known as "raptors", extremely bird-like omnivores with some pure carnivores
                - Avialans, the group including modern birds (the only living dinosaurs) and other winged theropods
                    - †Scansoriopterygids, small insectivorous theropods that may have lived in trees
                    - Avians, traditional birds

Relationships

The following cladogram is adapted from Weishampel *et al.*, 2004. It retains Coelophysoidea as possible ceratosaurs, as opposed to many recent studies placing them outside ceratosaurs and ancestral to both ceratosaurs and tetanurae.

Chapter 15

Feathered Dinosaur (Type of Dinosaur)



Artist's impression of *Anchiornis*, illustrating feather arrangement and colors

The realization that dinosaurs are closely related to birds raised the obvious possibility of **feathered dinosaurs**. Fossils of *Archaeopteryx* include well-preserved feathers, but it was not until the early 1990s that clearly non-avian dinosaur fossils were discovered with preserved feathers. Today more than twenty genera of dinosaurs, mostly theropods, are known to have been feathered. Most fossils are from the Yixian formation in China. The fossil feathers of one specimen, *Shuvuuia deserti*, have tested positive for beta-keratin, the main protein in bird feathers, in immunological tests.

Early hypotheses

The Berlin *Archaeopteryx*

Shortly after the 1859 publication of Charles Darwin's *On the Origin of Species*, British biologist and evolution-defender Thomas Henry Huxley proposed that birds were descendants of dinosaurs. He compared the skeletal structure of *Compsognathus*, a small theropod dinosaur, and the 'first bird' *Archaeopteryx lithographica* (both of which were found in the Upper Jurassic Bavarian limestone of Solnhofen). He showed that, apart from its hands and feathers, *Archaeopteryx* was quite similar to *Compsognathus*. In 1868 he published *On the Animals which are most nearly intermediate between Birds and Reptiles*, making the case. The leading dinosaur expert of the time, Richard Owen, disagreed, claiming *Archaeopteryx* as the first bird outside dinosaur lineage. For the next century, claims that birds were dinosaur descendants faded, with more popular birdancestry hypotheses including 'crocodylomorph' and 'thecodont' ancestors, rather than dinosaurs or other archosaurs.

In 1964, John Ostrom described *Deinonychus antirrhopus*, a theropod whose skeletal resemblance to birds seemed unmistakable. Ostrom became a leading proponent of the theory that birds are direct descendants of dinosaurs. Further comparisons of bird and dinosaur skeletons, as well as cladistic analysis strengthened the case for the link, particularly for a branch of theropods called maniraptors. Skeletal similarities include the neck, the pubis, the wrists (semi-lunate carpal), the 'arms' and pectoral girdle, the shoulder blade, the clavicle and the breast bone. In all, over a hundred distinct anatomical features are shared by birds and theropod dinosaurs.

Other researchers drew on these shared features and other aspects of dinosaur biology and began to suggest that at least some theropod dinosaurs were feathered. The first restoration of a feathered dinosaur was Sarah Landry's depiction of a feathered "Syntarsus" (now renamed *Megapnosaurus* or considered a synonym of *Coelophysis*), in Robert T. Bakker's 1975 publication *Dinosaur Renaissance*. Gregory S. Paul was probably the first paleoartist to depict maniraptoran dinosaurs with feathers and protofeathers, starting in the late 1970s.

By the 1990s, most paleontologists considered birds to be surviving dinosaurs and referred to 'non-avian dinosaurs' (all extinct), to distinguish them from birds (aves). Before the discovery of feathered dinosaurs, the evidence was limited to Huxley and Ostrom's comparative anatomy. Some mainstream ornithologists, including Smithsonian Institution curator Storrs L. Olson, disputed the links, specifically citing the lack of fossil evidence for feathered dinosaurs.

Fossil evidence

Sinosauropteryx fossil, first fossil of a non-avian dinosaur with feathers

After a century of hypotheses without conclusive evidence, well-preserved fossils of feathered dinosaurs were discovered during the 1990s, and more continue to be found. The fossils were preserved in a Lagerstätte — a sedimentary deposit exhibiting remarkable richness and completeness in its fossils — in Liaoning, China. The area had repeatedly been smothered in volcanic ash produced by eruptions in Inner Mongolia 124 million years ago, during the Early Cretaceous Period. The fine-grained ash preserved the living organisms that it buried in fine detail. The area was teeming with life, with millions of leaves, angiosperms (the oldest known), insects, fish, frogs, salamanders, mammals, turtles, lizards and crocodilians discovered to date.

The most important discoveries at Liaoning have been a host of feathered dinosaur fossils, with a steady stream of new finds filling in the picture of the dinosaur-bird connection and adding more to theories of the evolutionary development of feathers and flight. Norell et al. (2007) reported quill knobs from an ulna of *Velociraptor mongoliensis*, and these are strongly correlated with large and well-developed secondary feathers.

A nesting *Citipati osmolskae* specimen, at the AMNH.

Behavioural evidence, in the form of an oviraptorosaur on its nest, showed another link with birds. Its forearms were folded, like those of a bird. Although no feathers were preserved, it is likely that these would have been present to insulate eggs and juveniles.

Genuine feathers?

There have been claims that the supposed feathers of the Chinese fossils were a preservation artifact. Despite doubts, the fossil feathers have roughly the same appearance as those of birds fossilized in the same locality, so there is no serious reason to think they are of different nature; moreover, no non-theropod fossil from the same site shows such an artifact, but sometimes show unambiguous hair (some mammals) or scales (some reptiles).

The "Archaeoraptor" fake

In 1999, a supposed 'missing link' fossil of an apparently feathered dinosaur named "Archaeoraptor liaoningensis", found in Liaoning Province, northeastern China, turned out to be a forgery. Comparing the photograph of the specimen with another find, Chinese paleontologist Xu Xing came to the conclusion that it was composed of two portions of different fossil animals. His claim made *National Geographic* review their research and they too came to the same conclusion. The bottom portion of the "Archaeoraptor" composite came from a legitimate feathered dromaeosaurid now known as *Microraptor*, and the upper portion from a previously-known primitive bird called *Yanornis*.

Current knowledge

List of dinosaur genera preserved with evidence of feathers

Fossil of *Sinornithosaurus millenii*, the first evidence of feathers in dromaeosaurids.

Fossil cast of NGMC 91, a probable specimen of *Sinornithosaurus*.

Jinfengopteryx elegans fossil

A number of non-avian dinosaurs are now known to have been feathered. Direct evidence of feathers exists for the following genera, listed in the order currently accepted evidence was first published. In all examples, the evidence described consists of feather impressions, except those marked with an asterisk (*), which denotes genera known to have had feathers based on skeletal or chemical evidence, such as the presence of quill knobs.

1. *Avimimus** (1987)
2. *Sinosauropteryx* (1996)
3. *Protarchaeopteryx* (1997)
4. *Caudipteryx* (1998)
5. *Rahonavis** (1998)
6. *Shuvuuia* (1999)
7. *Sinornithosaurus* (1999)
8. *Beipiaosaurus* (1999)
9. *Microraptor* (2000)
10. *Nomingia** (2000)

11. *Cryptovolans* (2002)
12. *Scansoriopteryx* (2002)
13. *Psittacosaurus*? (2002)
14. *Yixianosaurus* (2003)
15. *Dilong* (2004)
16. *Pedopenna* (2005)
17. *Jinfengopteryx* (2005)
18. *Juravenator* (2006)
19. *Sinocalliopteryx* (2007)
20. *Velociraptor** (2007)
21. *Similicaudipteryx* (2008)
22. *Epidexipteryx* (2008)
23. *Anchiornis* (2009)
24. *Tianyulong*? (2009)
25. *Concavenator**? (2010)

- The ornithmomimosaur *Pelecanimimus* was initially reported to preserve filamentous feathers. However, subsequent detailed study of the structure showed them to be muscle fibers.

- Note, filamentous structures in some ornithischian dinosaurs (*Psittacosaurus*, *Tianyulong*) and pterosaurs may or may not be homologous with the feathers and protofeathers of theropods.

Primitive feather types

The evolution of feather structures is thought to have proceeded from simple hollow filaments through several stages of increasing complexity, ending with the large, deeply rooted, feathers with strong pens (rachis), barbs and barbules that birds display today.

Some evidence suggests that the original function of simple feathers was insulation. In particular, preserved patches of skin in large, derived, tyrannosauroids show scutes, while those in smaller, more primitive, forms show feathers. This may indicate that the larger forms had complex skins, with both scutes and filaments, or that tyrannosauroids may be like rhinos and elephants, having filaments at birth and then losing them as they developed to maturity. An adult *Tyrannosaurus rex* weighed about as much as an African Elephant. If large tyrannosauroids were endothermic, they would have needed to radiate heat efficiently, and feathers would have interfered with this.

It is not known with certainty at what point in archosaur phylogeny the earliest simple “protofeathers” arose, or if they arose once or, independently, multiple times. Filamentous structures are clearly present in pterosaurs, and long, hollow quills have been reported in specimens of the ornithischian dinosaurs *Psittacosaurus* and *Tianyulong*. In 2009 Xu et al. noted that the hollow, unbranched, stiff integumentary structures found on a specimen of *Beipiaosaurus* were strikingly similar to the integumentary structures of *psittacosaurus* and pterosaurs. They suggested that all of these structures may have been inherited from a common ancestor much earlier in the evolution of archosaurs, possibly in an ornithodire from the Middle Triassic or earlier.

Display feathers are also known from dinosaurs that are very primitive members of the bird lineage, or Avialae. The most primitive example is *Epidexipteryx*, which had a short tail with extremely long, ribbon - like, feathers. Oddly enough, the fossil does not preserve wing feathers, suggesting that *Epidexipteryx* was either secondarily flightless, or that display feathers evolved before flight feathers in the bird lineage.

Phylogeny and the inference of feathers in other dinosaurs

Fossil feather impressions are extremely rare and they require exceptional preservation conditions to form. Therefore only a few feathered dinosaur genera have been identified so far. However, through a process called phylogenetic bracketing, scientists can infer the presence of feathers on poorly-preserved specimens. All fossil feather specimens have been found to show certain similarities. Due to these similarities and through developmental research almost all scientists agree that feathers could only have evolved once in dinosaurs. Feathers would then have been passed down to all later, more derived species (although it is possible that some lineages lost feathers secondarily). If a dinosaur falls at a point on an evolutionary tree within the known feather-bearing lineages, scientists assume it too had feathers, unless conflicting evidence is found. This technique can also be used to infer the type of feathers a species may have had, since the developmental history of feathers is now reasonably well-known.

The scientists who described the (apparently unfeathered) *Juravenator* performed a genealogical study of coelurosaurs, including distribution of various feather types. Based on the placement of feathered species in relation to those that have not been found with any type of skin impressions, they were able to infer the presence of feathers in certain dinosaur groups. The following simplified cladogram follows these results, and shows the likely distribution of plumaceous (downy) and pennaceous (vaned) feathers among theropods. Note that the authors inferred pennaceous feathers for *Velociraptor* based on phylogenetic bracketing, a prediction later confirmed by fossil evidence.