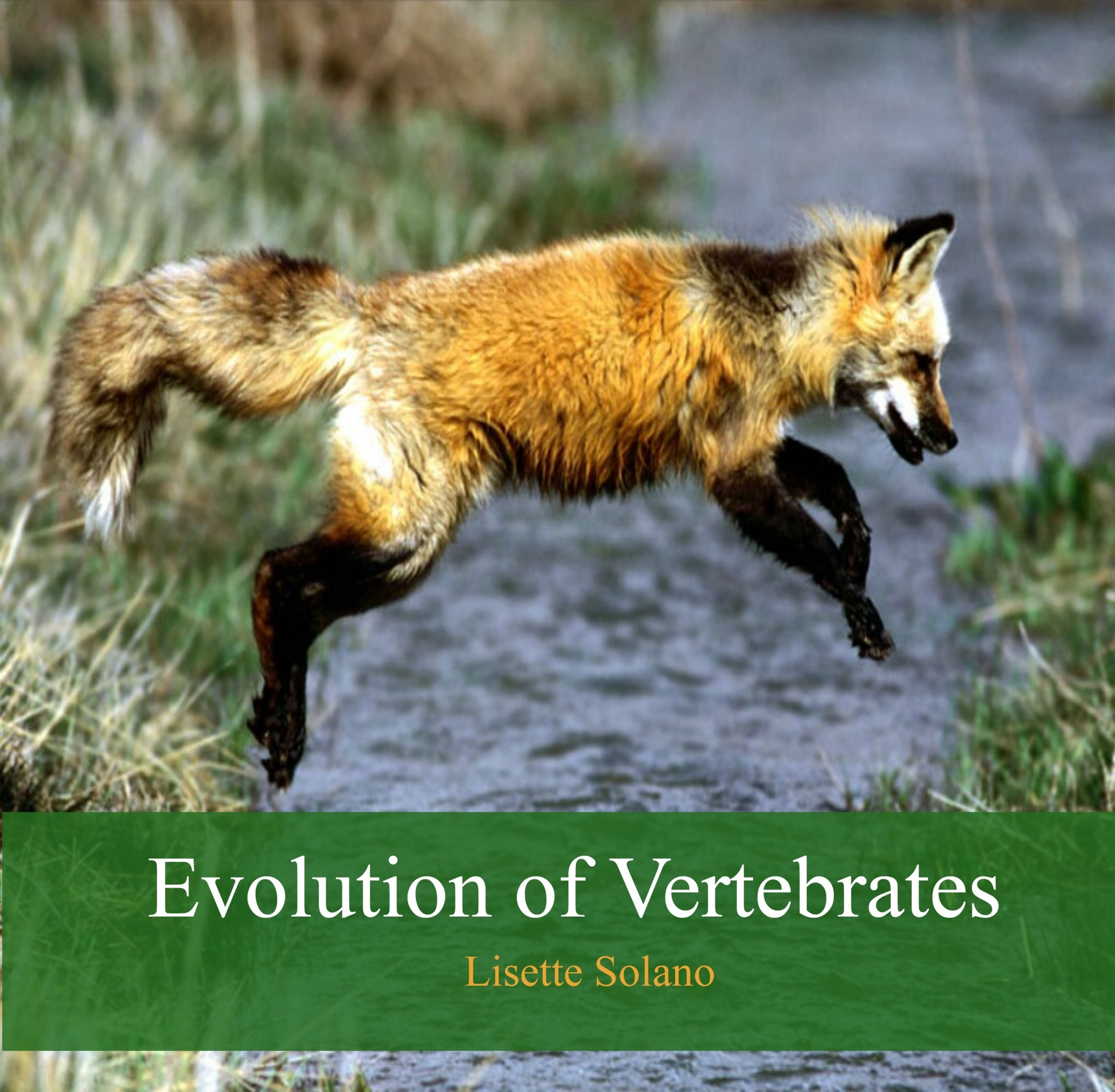

Evolution of Vertebrates

Lisette Solano

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Chapter- 1

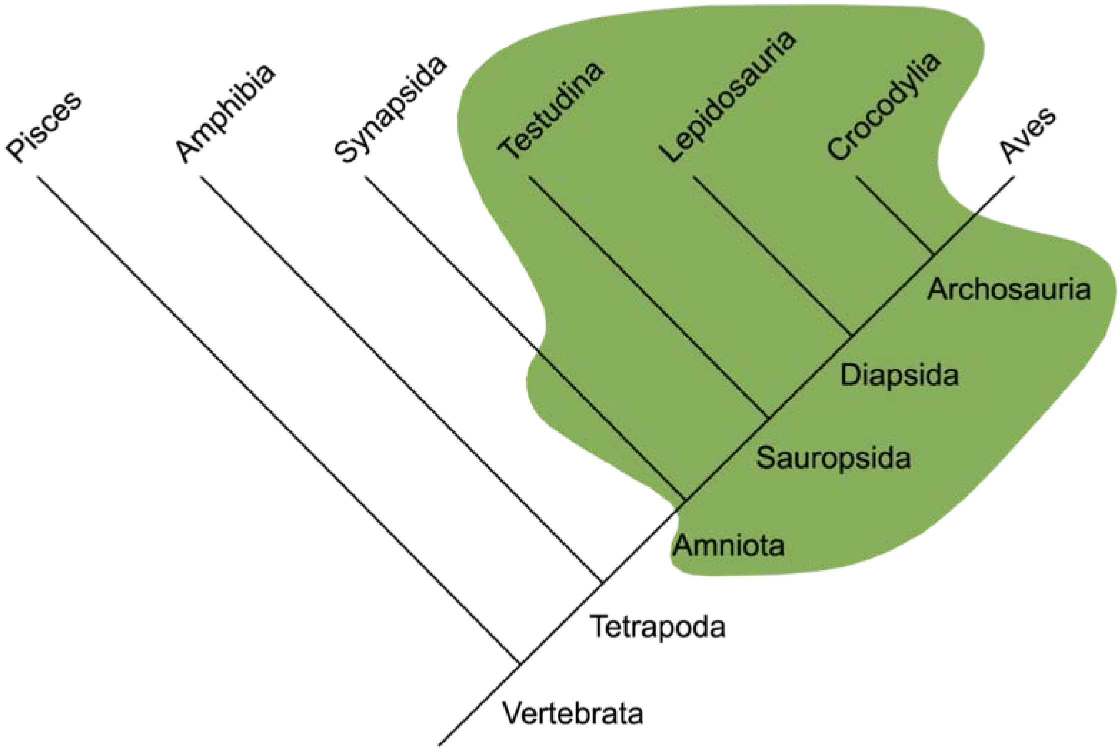
Evolution of Reptiles

A fossil of a Casineria. The earliest evidence of amniotes, although an amphibian, it laid eggs on land as reptiles do.

Reptiles arose about 310-320 million years ago during the Carboniferous period. Reptiles are defined as animals that have scales, lay land based hard shelled eggs, and possessing cold-blooded metabolisms. Today reptiles generally rank low in most ecological food chains, containing very few apex predators, but many examples of apex reptiles have existed in the past. Although reptiles have lower specie variation than in the past, they have an extremely diverse evolutionary history that has led to biological successes such as dinosaurs, mammals, and birds.

First reptiles

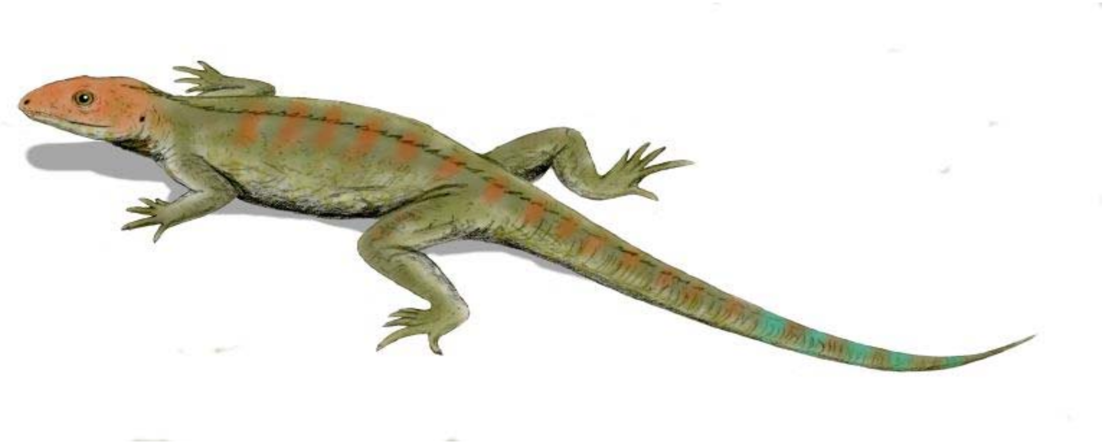
Rise from water



Reptiles (green field) are a paraphyletic group comprising all non-avian and non-mammalian amniotes.

Reptiles first arose from amphibians in the swamps of the late Carboniferous. Increasing evolutionary pressure and the vast untouched niches of the land powered the evolutionary changes in amphibians to gradually become more and more land based. Environmental selection propelled the development of certain traits, such as a stronger skeletal structure, muscles, and more protective coating (scales) became more favorable, the basic foundation of reptiles were founded. The evolution of lungs and legs are the main transitional steps towards reptiles, but the development of hard-shelled external eggs replacing the amphibious water bound eggs is the defining feature of the class reptilia (with the exception of certain squamates) and is what allowed amphibians to fully leave water. Another major difference from amphibians is the increased brain size, more specifically, the enlarged cerebrum and cerebellum. Although there brain size is small when compared to mammals and birds, these enhancements prove vital in hunting strategies of reptiles. The increased size of these two regions of the brain allowed for improved motor skills and an increase in sensory development.

Early reptiles

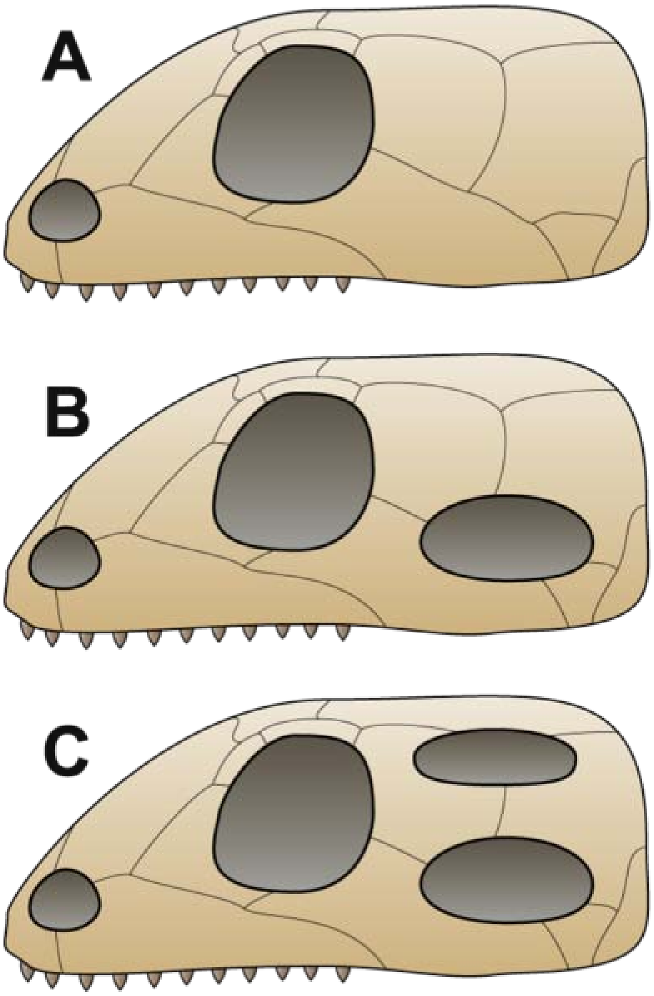


An early reptile *Hylonomus*

Mesozoic scene showing typical reptilian megafauna: the dinosaurs *Europasaurus holgeri* and *Iguanodon*, and the early bird *Archaeopteryx* perched on the foreground tree stump.

The origin of the reptiles lies about 320–310 million years ago, in the steaming swamps of the late Carboniferous period, when the first reptiles evolved from advanced reptiliomorph labyrinthodonts. The oldest known animal that may have been an amniote, i.e. a primitive reptile rather than an advanced amphibian is *Casineria*. A series of footprints from the fossil strata of Nova Scotia, dated to 315 million years show typical reptilian toes and imprints of scales. The tracks are attributed to *Hylonomus*, the oldest unquestionable reptile known. It was a small, lizard-like animal, about 20 to 30 cm (8–12 in) long, with numerous sharp teeth indicating an insectivorous diet. Other examples include *Westlothiana* (for the moment considered a reptiliomorph amphibian rather than a true amniote) and *Paleothyris*, both of similar build and presumably similar habit. One of the best known early reptiles is *Mesosaurus*, a genus from the early Permian that had returned to water, feeding on fish. The earliest reptiles were largely overshadowed by bigger labyrinthodont amphibians such as *Cochleosaurus*, and remained a small, inconspicuous part of the fauna until after the small ice age at the end of the Carboniferous.

Anapsids, synapsids, diapsids and sauropsids



A = Anapsid, B = Synapsid, C = Diapsid

The first reptiles were anapsids, having a solid skull with holes for only nose, eyes, spinal cord, etc. Very soon after the first reptiles appeared, they split into two branches. One branch, Synapsida (including both "mammal-like reptiles" and modern, extant mammals), had one opening in the skull roof behind each eye; the other branch, Diapsida, possessed a hole in their skulls behind each eye, along with a second hole located higher on the skull. The function of the holes in both groups was to lighten the skull and give room for the jaw muscles to move, allowing for a more powerful bite. Diapsids and later anapsids are classed as the "true reptiles", Sauropsida.

Turtles have been traditionally believed to be surviving anapsids, on the basis of their skull structure. The rationale for this classification was disputed, with some arguing that turtles are diapsids that reverted to this primitive state in order to improve their armor. Later morphological phylogenetic studies with this in mind placed turtles firmly within Diapsida. All molecular studies have strongly upheld the placement of turtles within diapsids, most commonly as a sister group to extant archosaurs.

Mammalian evolution

A basic cladogram of the origin of modern mammals from their closest reptilian relatives.

The main points to the transition from reptile to mammal was the evolution from scales to hair or fur, the evolution of warm-bloodedness, the loss of external eggs (except for in monotremes who have retained this trait), and the evolution mammary glands (the most defining trait in mammals that allow them to produce milk for offspring). The evolution of mammals was a gradual process that took approximately 70 million years, beginning in the mid-Permian. By the mid-Triassic, there were many species that looked like modern mammals, and the first true mammals appeared in the early Jurassic. The earliest known marsupial, *Sinodelphys*, appeared 125 million years ago in the early Cretaceous, around the same time as *Eomaia*, the first known eutherian (member of placentals' "parent" group); and the earliest known monotreme, *Teinolophos*, appeared two million years later.

Rise of dinosaurs

Permian reptiles

With the close of the Carboniferous, reptiles became the dominant tetrapod fauna. While the terrestrial reptiliomorph labyrinthodonts still existed, the synapsids evolved the first truly terrestrial megafauna (giant animals) in the form of pelycosaurs such as *Edaphosaurus* and the carnivorous *Dimetrodon*. In the mid-Permian period the climate turned dryer, resulting in a change of fauna: The primitive pelycosaurs were replaced by the more advanced therapsids.

The anapsid reptiles, whose massive skull roofs had no postorbital holes, continued and flourished throughout the Permian. The pareiasaurs reached giant proportions in the late

Permian, eventually disappearing at the close of the period (the turtles being possible survivors).

Early in the period, the diapsid reptiles split into two main lineages, the archosaurs (forefathers of crocodiles and dinosaurs) and the lepidosaurs (predecessors of modern snakes, lizards, and tuataras). Both groups remained lizard-like and relatively small and inconspicuous during the Permian.

The Mesozoic era, the "Age of Reptiles"

The close of the Permian saw the greatest mass extinction known. Most of the earlier anapsid/synapsid megafauna disappeared, being replaced by the archosauromorph diapsids. The archosaurs were characterized by elongated hind legs and an erect pose, the early forms looking somewhat like long-legged crocodiles. The archosaurs became the dominant group during the Triassic period, developing into the well-known dinosaurs and pterosaurs, as well as crocodiles and phytosaurs. Some of the dinosaurs developed into the largest land animals ever to have lived, making the Mesozoic era popularly known as the "Age of Reptiles". The dinosaurs also developed smaller forms, including the feather-bearing smaller theropods. In the mid-Jurassic period, these gave rise to the first birds.

The lepidosauromorph diapsids may have been ancestral to the sea reptiles. These reptiles developed into the sauropterygians in the early Triassic and the ichthyosaurs during the Middle Triassic. The mosasaurs also evolved in the Mesozoic era, emerging during the Cretaceous period.

The therapsids came under increasing pressure from the dinosaurs in the early Mesozoic and developed into increasingly smaller and more nocturnal forms, the first mammals being the only survivors of the line by the late Jurassic.

Bird evolution

An *Archaeopteryx* specimen in Berlin.

The main points to the transition from reptile to bird is the evolution from scales to feathers, the evolution of the beak (although independently evolved in other organisms), the hallofication of bones, development of flight, and warm-bloodedness.

The evolution of birds is thought to have begun in the Jurassic Period, with the earliest birds derived from theropod dinosaurs. Birds are categorized as a biological class, Aves. The earliest known species Aves is *Archaeopteryx lithographica*, from the Late Jurassic period, though 'Archaeopteryx is not commonly considered to have been a true bird, but a transitional species between Aves and Reptiles. Modern phylogenetics place birds in the dinosaur clade Theropoda. According to the current consensus, Aves and a sister group of the order Crocodilia, together are the sole living members of an unranked "reptile" clade, the Archosauria.

Demise of the dinosaurs

The close of the Cretaceous period saw the demise of the Mesozoic era reptilian megafauna. Along with massive amount of volcanic activity at the time, the meteor impact that created the K-T boundary is accepted as the main cause for this mass extinction event. Of the large marine reptiles, only sea turtles are left, and, of the dinosaurs, only the small feathered theropods survived in the form of birds. The end of the “Age of Reptiles” led into the “Age of Mammals”. Despite the change in phrasing, reptile diversification continued throughout the Cenozoic, with squamates undergoing a greater radiation than they did in the Mesozoic. Today squamates make up the majority of extant reptiles today (over 90%), filling many of the ecological niches left by the mammals who would take advantage of the niches left by the dinosaurs. There are approximately 8,700 extant species of reptiles, compared with 5,400 species of mammals.

Role reversal

After the Cretaceous-Tertiary extinction wiped out all of the non-avian dinosaurs (birds are generally regarded as the surviving dinosaurs) and several other mammalian groups, placental and marsupial mammals diversified into many new forms and ecological niches throughout the Tertiary era. Some reaching enormous sizes and almost as wide of a variation as the dinosaurs once did. Due to global climate changes such as a lowering in total oxygen levels and lower average temperatures, mammalian megafauna never quite reached the sky-scraper heights as did some sauropods. These evolutionary and climatic changes is what is responsible for all modern orders of mammals that are now on Earth, including humans.

The four orders of reptilia

Testudines

Testudines, or turtles, may have evolved from anaspids, but their exact origin is unknown and heavily debated. Fossils date back to around 220 million years ago and share remarkably similar characteristics. These first turtles retain the same body plan as do all modern testudines and are mostly herbivorous. With some feeding exclusively on small marine organisms. The trade-mark shell is believed to have evolved from extensions from there backbone and widened ribs which fused together. This is supported by the fossil of Odontochelys semitestacea, which has an incomplete shell originating from the ribs and back bone. This species also had teeth with its beak, giving more support to it being a transitional fossil, although this claim is still controversial. This shell evolved to protect itself from predators, but also slows down the land based species by a great amount. This has caused many species to go extinct in recent times. Because of alien species outcompeting the slow order for food and lack of ability to escape from humans, there are large amounts of endangered species in this order.

Sphenodontia

Sphenodontians arose in the mid Triassic and only consist of one genus tuatara, which only includes two endangered species on New Zealand and some other minor surrounding islands. Their evolutionary history is filled with many species. Recent paleogenetic discoveries show that tuataras are prone to quick speciation.

Squamata

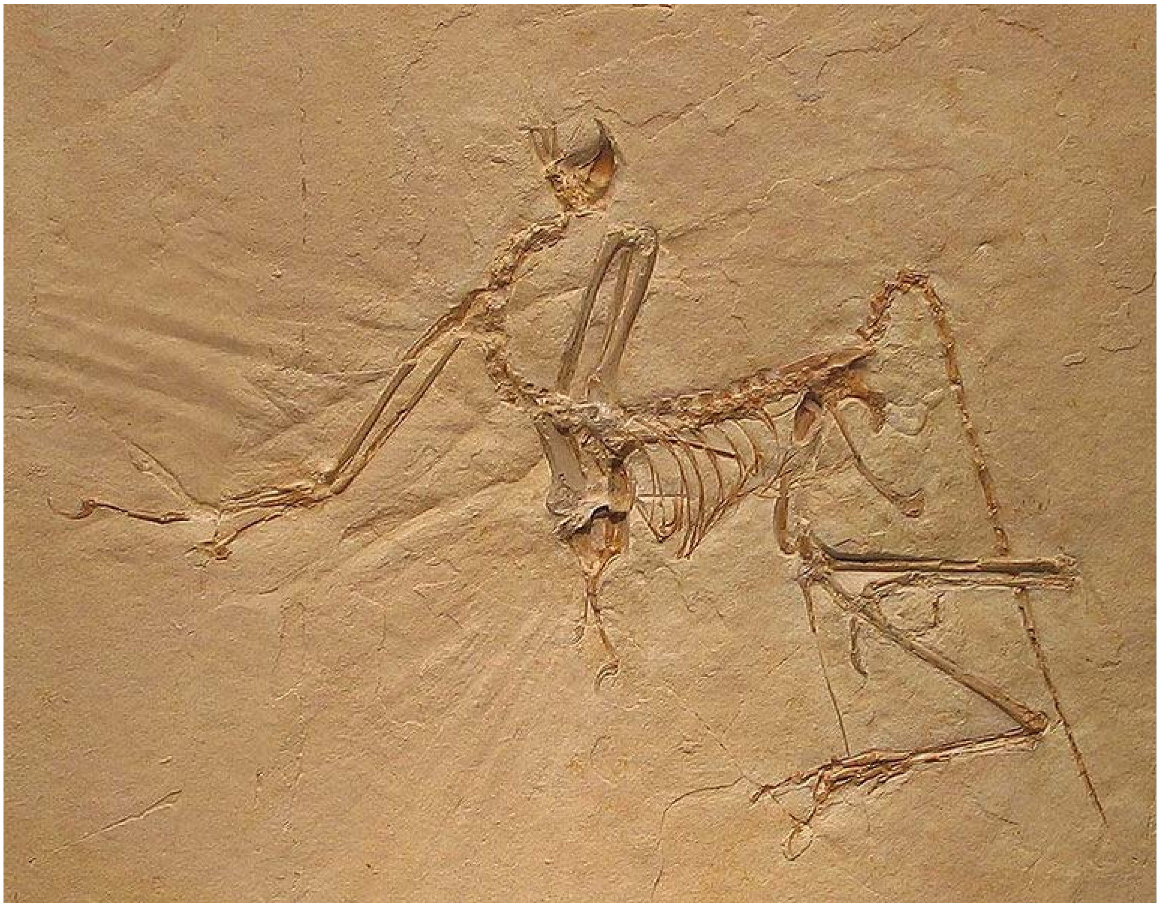
The most recent order of reptiles, squamates are recognized by having a movable quadrate bone (giving them upper-jaw movement) and possessing horny scales. They originate from the early Jurassic and are made up of the three suborders Lacertilia, Serpentes, and Amphisbaenia. Although they are the most recent order, squamates contain more species than any of the other reptilian orders. Squamates are a monophyletic group that is a sister group to the Sphenodontia or tuataras. The squamates and tuatara together are a sister group to crocodiles and birds, the extant archosaurs. Although squamate fossils first appear in the early Jurassic, mitochondrial phylogenetics suggests that they evolved in the late Permian. Most evolutionary relationships within the squamates are not yet completely worked out, with the relationship of snakes to other groups being most problematic. From morphological data, Iguanid lizards have been thought to have diverged from other squamates very early, but recent molecular phylogenies, both from mitochondrial and nuclear DNA, do not support this early divergence. Because snakes have a faster molecular clock than other squamates, and there are few early snake and snake ancestor fossils, it is difficult to resolve the relationship between snakes and other squamate groups.

Crocodilia

The first organisms that showed similar characteristics of Crocodilians would be the Crurotarsi who appeared during the early Triassic 250 million years ago. This quickly gave rise to the Eusuchia clade 220 million years ago which would eventually lead to the order of Crocodilians, first of which arose about 85 million years ago during the late cretaceous, originating from the Eusuchia clade. The earliest fossil evidence of eusuchians is of the species Isisfordia. Early species mainly feed on fish and vegetation. They were land-based, most having long legs (when compared to modern crocodiles) and many were bipeadal. As diversification increased, many apex predators arose, all of which is now extinct. Modern Crocodilia arose through specific evolutionary traits. The complete loss of bipedalism in trade for generally low quadrupedal stance for an easy and less noticeable entrance to bodies of water. The shape of the skull/jaw changed to allow further grasp along with up-ward pointing nostrils and eyes. Mimicry is evident, as the back of all crocodilia resemble some type floating log along with their general color scheme of brown and green to mimic moss or wood. There tail also took on a paddle shape to increase swimming speed. The only remaining groups to this order is the alligator, crocodile, caiman, and gharial.

Chapter- 2

Evolution of Birds



Archaeopteryx at Paläontologisches Museum München

The **evolution of birds** is thought to have begun in the Jurassic Period, with the earliest birds derived from theropod dinosaurs. Birds are categorized as a biological class, **Aves**. The earliest known species of class Aves is *Archaeopteryx lithographica*, from the Late Jurassic period, though *Archaeopteryx* is not commonly considered to have been a true bird. Modern phylogenies place birds in the dinosaur clade Theropoda. According to the current consensus, Aves and a sister group, the order Crocodilia, together are the sole living members of an unranked "reptile" clade, the Archosauria.

Phylogenetically, Aves is usually defined as all descendants of the most recent common ancestor of a specific modern bird species (such as the House Sparrow, *Passer domesticus*), and either *Archaeopteryx*, or some prehistoric species closer to Neornithes (to avoid the problems caused by the unclear relationships of *Archaeopteryx* to other theropods). If the latter classification is used then the larger group is termed Avialae. Currently, the relationship between dinosaurs, Archaeopteryx, and modern birds is still under debate.

Origins

There is significant evidence that birds evolved within theropod dinosaurs, specifically, that birds are members of Maniraptora, a group of theropods which includes dromaeosaurs and oviraptorids, among others. As more non-avian theropods that are closely related to birds are discovered, the formerly clear distinction between non-birds and birds becomes less so. Recent discoveries in northeast China (Liaoning Province), demonstrating that many small theropod dinosaurs had feathers, contribute to this ambiguity.

The basal bird *Archaeopteryx*, from the Jurassic, is well-known as one of the first "missing links" to be found in support of evolution in the late 19th century, though it is not considered a direct ancestor of modern birds. *Confuciusornis* is another early bird; it lived in the Early Cretaceous. Both may be predated by *Protoavis texensis*, though the fragmentary nature of this fossil leaves it open to considerable doubt whether this was a bird ancestor. Other Mesozoic birds include the *Confuciusornis*, the Enantiornithes, *Yanornis*, *Ichthyornis*, *Gansus*, and the Hesperornithiformes - a group of flightless divers resembling grebes and loons. The recently (2002) discovered dromaeosaur *Cryptovolans* (which may be a *Microraptor*) was capable of powered flight, possessed a sternal keel and had ribs with uncinate processes. In fact, *Cryptovolans* makes a better "bird" than *Archaeopteryx* which lacks some of these modern bird features. Because of this, some paleontologists have suggested that dromaeosaurs are actually basal birds whose larger members are secondarily flightless, i.e. that dromaeosaurs evolved within birds and not the other way around. Evidence for this theory is currently inconclusive, but digs continue to unearth fossils (especially in China) of the strange feathered dromaeosaurs. At any rate, it is fairly certain that flight utilizing feathered wings existed in the mid-Jurassic theropods and was "tried out" in several lineages and variants by the mid-Cretaceous, such as in *Confuciusornis*. This latter species had some peculiar features. For example, its vestigial tail was unfit for steering, and its wing shape seems rather specialized although the arm skeleton was still quite "dinosaurian").

Although ornithischian (bird-hipped) dinosaurs share the same hip structure as birds, birds actually originated from the saurischian (lizard-hipped) dinosaurs if the dinosaurian origin theory is correct. They thus arrived at their hip structure condition independently.

In fact, a bird-like hip structure also developed a third time among a peculiar group of theropods, the Therizinosauridae.

An alternate theory to the dinosaurian origin of birds, espoused by a few scientists, notably Larry Martin and Alan Feduccia, states that birds (including maniraptoran "dinosaurs") evolved from early archosaurs like *Longisquama*. This theory is contested by most other paleontologists and experts in feather development and evolution.

Adaptive radiation of birds

Modern birds are classified in Neornithes, which are now known to have evolved into some basic lineages by the end of the Cretaceous. The Neornithes are split into the paleognaths and neognaths.

Paleognathae

The paleognaths include the tinamous (found only in Central and South America) and the ratites which nowadays are found almost exclusively on the Southern Hemisphere. The ratites are large flightless birds, and include ostriches, rheas, cassowaries, kiwis and emus. A few scientists propose that the ratites represent an artificial grouping of birds which have independently lost the ability to fly in a number of unrelated lineages; in any case, the available data regarding their evolution is still very confusing.

Neognathae

The basal divergence from the remaining Neognathes was that of the Galloanserae, the superorder containing the Anseriformes (ducks, geese and swans), and the Galliformes (chickens, turkeys, pheasants, and their allies).

The dates for the splits are a matter of considerable debate amongst scientists. It is agreed that the Neornithes evolved in the Cretaceous and that the split between the Galloanserae and the other neognaths - the Neoaves - occurred before the K-T extinction event, but there are different opinions about whether the radiation of the remaining neognaths occurred before or after the extinction of the other dinosaurs. This disagreement is in part caused by a divergence in the evidence, with molecular dating suggesting a Cretaceous radiation, a small and equivocal neoavian fossil record from Cretaceous, and most living families turning up during the Paleogene. Attempts made to reconcile the molecular and fossil evidence have proved controversial.

On the other hand, two factors must be considered: First, molecular clocks cannot be considered reliable in the absence of robust fossil calibration, whereas the fossil record is naturally incomplete. Second, in reconstructed phylogenetic trees, the time and pattern of lineage separation corresponds to the evolution of the *characters* (such as DNA sequences, morphological traits etc.) studied, *not* to the actual evolutionary pattern of the lineages; these ideally should not differ by much, but may well do so in practice.

Considering this, it is easy to see that fossil data, compared to molecular data, tends to be more accurate in general, but also to underestimate divergence times: morphological traits, being the product of entire developmental genetics networks, usually only start to diverge some time *after* a lineage split would become apparent in DNA sequence comparison - especially if the sequences used contain many silent mutations.

Classification of modern species

The phylogenetic classification of birds is a contentious issue. Sibley & Ahlquist's *Phylogeny and Classification of Birds* (1990) is a landmark work on the classification of birds (although frequently debated and constantly revised). A preponderance of evidence suggests that most modern bird orders constitute good clades. However, scientists are not in agreement as to the precise relationships between the orders; evidence from modern bird anatomy, fossils and DNA have all been brought to bear on the problem but no strong consensus has emerged. As of the mid-2000s, new fossil and molecular data provide an increasingly clear picture of the evolution of modern bird orders, and their relationships. For example, the Charadriiformes seem to consititute an ancient and distinct lineage, while the Mirandornithes and Cypselomorphae are supported by a wealth of anatomical and molecular evidence. Our understanding of the interrelationships of lower level taxa also continues to increase, particularly in the massively diverse perching bird order Passeriformes.

On June 27, 2008, the largest study of bird genetics was published. It overturns several hypothesized relationships, and will likely necessitate a wholesale restructuring of the avian phylogenetic tree.

Current evolutionary trends in birds

Evolution generally occurs at a scale far too slow to be witnessed by humans. However, bird species are currently going extinct at a far greater rate than any possible speciation or other generation of new species. The disappearance of a population, subspecies, or species represents the permanent loss of a range of genes.

Another concern with evolutionary implications is a suspected increase in hybridization. This may arise from human alteration of habitats enabling related allopatric species to overlap. Forest fragmentation can create extensive open areas, connecting previously isolated patches of open habitat. Populations that were isolated for sufficient time to diverge significantly, but not sufficient to be incapable of producing fertile offspring may now be interbreeding so broadly that the integrity of the original species may be compromised. For example, the many hybrid hummingbirds found in northwest South America may represent a threat to the conservation of the distinct species involved.

Several species of birds have been bred in captivity to create variations on wild species. In some birds this is limited to color variations, while others are bred for larger egg or meat production, for flightlessness or other characteristics.

Some species, like the rock pigeon or several species of crows have been successful living in man made environments. Because these new habitats are different from their far less numerous "natural" habitats these species are to a certain extent evolutionary adapting to living close to man. Such adaptions include color changes, increased memory, and enhanced intelligence. As seen in the New Caledonian Crow, which has been documented placing nuts infront of on-comming traffic as a means to open them and even waiting for the pedestrian light for the safe retrival of the crushed nut.

Chapter- 3

Origin of Birds

The famous Berlin specimen of *Archaeopteryx lithographica*

The **origin of birds** is a contentious and central topic within evolutionary biology. A close relationship between birds and dinosaurs was first proposed in the nineteenth century after the discovery of the primitive bird *Archaeopteryx* in Germany. To date, most researchers support the view that birds are a group of theropod dinosaurs that evolved during the Mesozoic Era.

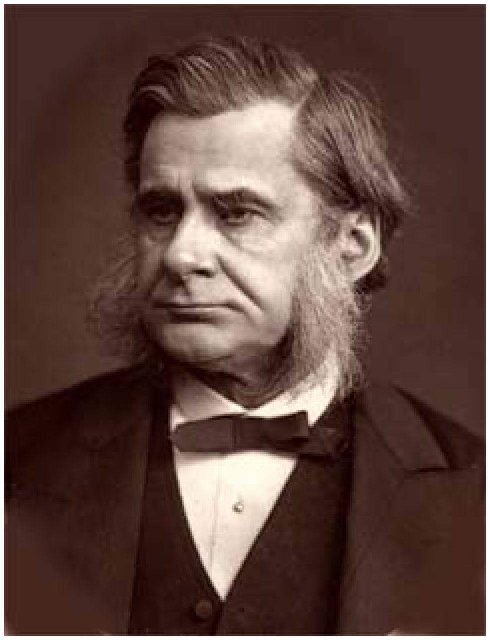
Birds share a myriad of unique skeletal features with dinosaurs. Moreover, fossils of more than twenty species of dinosaur have been collected which preserve feathers. There are even very small dinosaurs, such as *Microraptor* and *Anchiornis*, which have long, vaned, arm and leg feathers forming wings. The Jurassic basal avialan *Pedopenna* also shows these long foot feathers. Witmer (2009) has concluded that this evidence is sufficient to demonstrate that avian evolution went through a four-winged stage.

Fossil evidence also demonstrates that birds and dinosaurs shared features such as hollow, pneumatized bones, gastroliths in the digestive system, nest-building and brooding behaviors. The ground-breaking discovery of fossilized *Tyrannosaurus rex* soft tissue allowed a molecular comparison of cellular anatomy and protein sequencing of collagen tissue, both of which demonstrated that *T. rex* and birds are more closely related than either is to *Alligator*. A second molecular study robustly supported the relationship of birds to dinosaurs, though it did not place birds within Theropoda, as expected. This study utilized eight additional collagen sequences extracted from a femur of *Brachylophosaurus canadensis*, a hadrosaur.

Only a few scientists still debate the dinosaurian origin of birds, suggesting descent from other types of archosaurian reptiles. Among the consensus that supports dinosaurian ancestry, the exact sequence of evolutionary events that gave rise to the early birds within maniraptoran theropods is a hot topic. The origin of bird flight is a separate but related question for which there are also several proposed answers.

Research history

Huxley, *Archaeopteryx* and early research

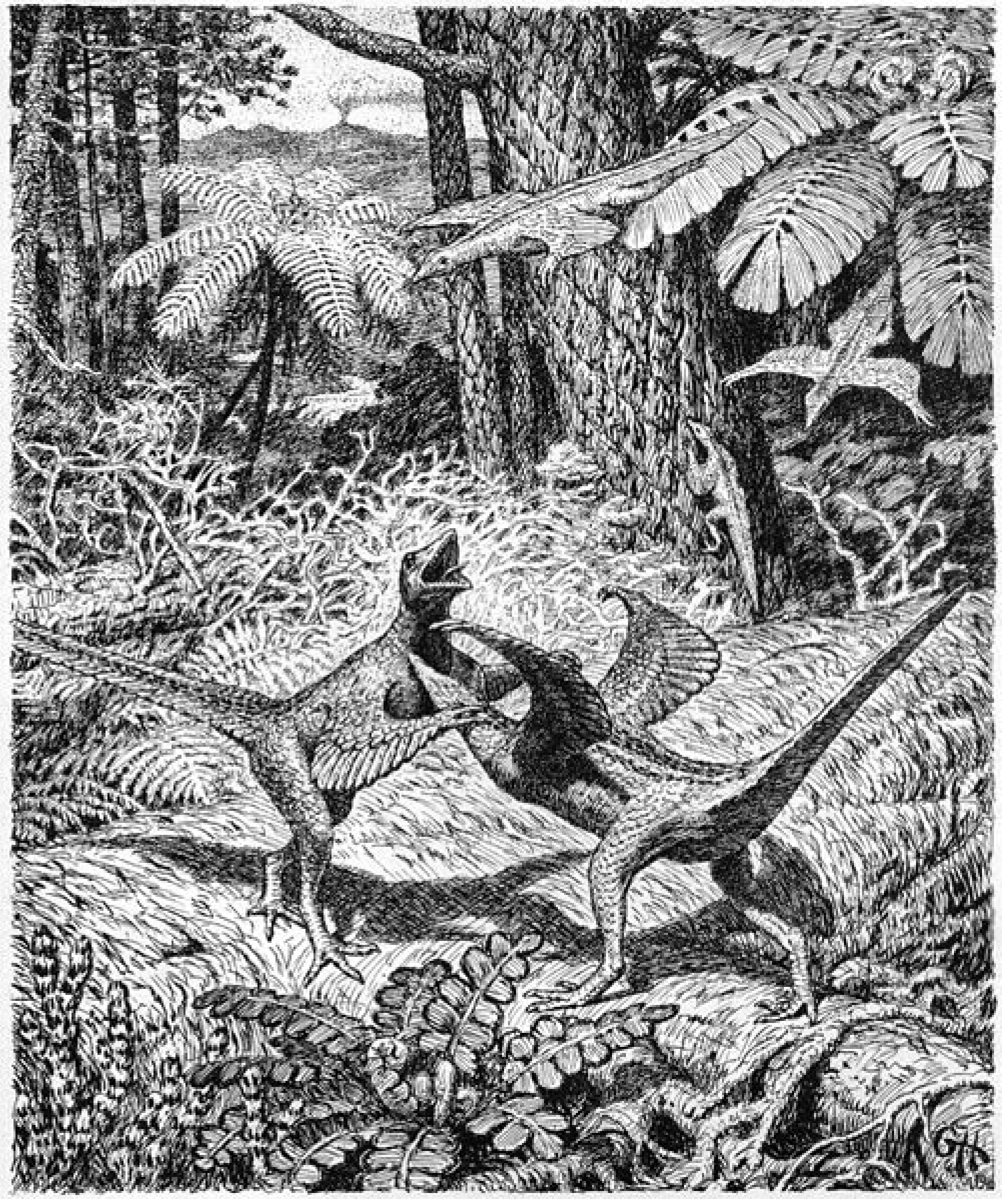


Thomas Henry Huxley (1825-1895)

Scientific investigation into the origin of birds began shortly after the 1859 publication of Charles Darwin's *On the Origin of Species*, the ground-breaking book which described his theory of evolution by natural selection. In 1860, a fossilized feather was discovered in Germany's Late Jurassic solnhofen limestone. Christian Erich Hermann von Meyer described this feather as *Archaeopteryx lithographica* the next year, and Richard Owen described a nearly complete skeleton in 1863, recognizing it as a bird despite many features reminiscent of reptiles, including clawed forelimbs and a long, bony tail.

Biologist Thomas Henry Huxley, known as "Darwin's Bulldog" for his ferocious support of the new theory of evolution, almost immediately seized upon *Archaeopteryx* as a transitional fossil between birds and reptiles. Starting in 1868, Huxley made detailed comparisons of *Archaeopteryx* with various prehistoric reptiles and found that it was most similar to dinosaurs like *Hypsilophodon* and *Compsognathus*. The discovery in the late 1870s of the iconic "Berlin specimen" of *Archaeopteryx*, complete with a set of reptilian teeth, provided further evidence. Huxley was the first to propose an evolutionary relationship between birds and dinosaurs, although he was opposed by the very influential Owen, who remained a staunch creationist. Huxley's conclusions were accepted by many biologists, including Baron Franz Nopcsa, while others, notably Harry Seeley, argued that the similarities were due to convergent evolution.

Heilmann and the thecodont hypothesis



Heilmann's hypothetical illustration of a pair of fighting 'Proaves' from 1916

A turning point came in the early twentieth century with the writings of Gerhard Heilmann of Denmark. An artist by trade, Heilmann had a scholarly interest in birds and from 1913 to 1916 published the results of his research in several parts, dealing with the anatomy, embryology, behavior, paleontology, and evolution of birds. His work, originally written in Danish as *Vor Nuvaerende Viden om Fuglenes Afstamning*, was compiled, translated into English, and published in 1926 as *The Origin of Birds*.

Like Huxley, Heilmann compared *Archaeopteryx* and other birds to an exhaustive list of prehistoric reptiles, and also came to the conclusion that theropod dinosaurs like *Compsognathus* were the most similar. However, Heilmann noted that birds possessed clavicles (collar bones) fused to form a bone called the furcula ("wishbone"), and while clavicles were known in more primitive reptiles, they had not yet been recognized in dinosaurs. Since he was a firm believer in Dollo's law, which states that evolution is not reversible, Heilmann could not accept that clavicles were lost in dinosaurs and re-evolved in birds. He was therefore forced to rule out dinosaurs as bird ancestors and ascribe all of their similarities to convergent evolution. Heilmann stated that bird ancestors would instead be found among the more primitive "thecodont" grade of reptiles. Heilmann's extremely thorough approach ensured that his book became a classic in the field, and its conclusions on bird origins, as with most other topics, were accepted by nearly all evolutionary biologists for the next four decades.

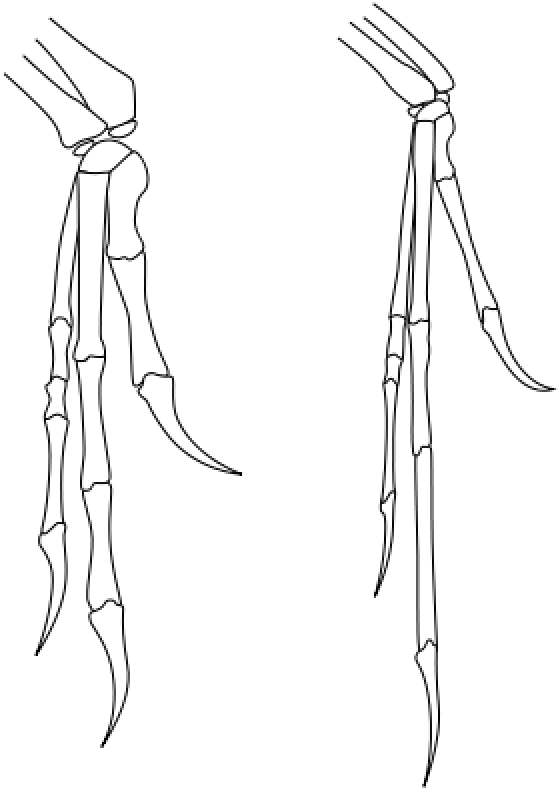
Bronze cast of the furcula of "Sue" the *Tyrannosaurus*, Field Museum

Clavicles are relatively delicate bones and therefore in danger of being destroyed or at least damaged beyond recognition. Nevertheless clavicles had been found in theropod dinosaurs before Heilman wrote his book, but had gone unrecognized. The absence of clavicles in dinosaurs became the orthodox view despite the discovery of clavicles in the primitive theropod *Segisaurus* in 1936. The next report of clavicles in a dinosaur was in 1983, and that was in a Russian article published before the end of the Cold War.

Contrary to what Heilman believed, paleontologists now accept that clavicles and in most cases furculae are a standard feature not just of theropods but of saurischian dinosaurs.

Up to late 2007 ossified furculae (i.e. made of bone rather than cartilage) have been found in nearly all types of theropods except the most basal ones, *Eoraptor* and *Herrerasaurus*. The original report of a furcula in the primitive theropod *Segisaurus* (1936) has been confirmed by a re-examination in 2005. Joined, furcula-like clavicles have also been found in *Massospondylus*, an Early Jurassic sauropodomorph.

Ostrom, *Deinonychus* and the Dinosaur Renaissance



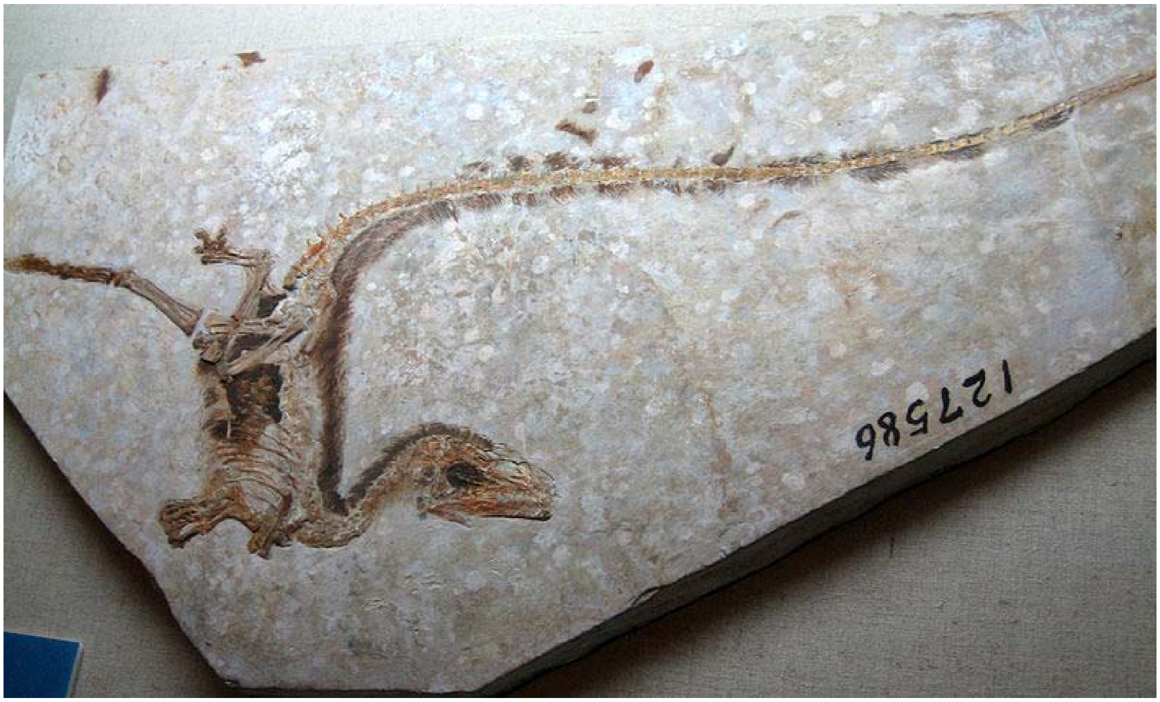
The similarity of the forelimbs of *Deinonychus* (left) and *Archaeopteryx* (right) led John Ostrom to revive the link between dinosaurs and birds.

The tide began to turn against the 'thecodont' hypothesis after the 1964 discovery of a new theropod dinosaur in Montana. In 1969, this dinosaur was described and named *Deinonychus* by John Ostrom of Yale University. The next year, Ostrom redescribed a specimen of *Pterodactylus* in the Dutch Teyler Museum as another skeleton of *Archaeopteryx*. The specimen consisted mainly of a single wing and its description made Ostrom aware of the similarities between the wrists of *Archaeopteryx* and *Deinonychus*.

In 1972, British paleontologist Alick Walker hypothesized that birds arose not from 'thecodonts' but from crocodile ancestors like *Sphenosuchus*. Ostrom's work with both theropods and early birds led him to respond with a series of publications in the mid-1970s in which he laid out the many similarities between birds and theropod dinosaurs, resurrecting the ideas first put forth by Huxley over a century before. Ostrom's recognition of the dinosaurian ancestry of birds, along with other new ideas about dinosaur metabolism, activity levels, and parental care, began what is known as the Dinosaur renaissance, which began in the 1970s and continues to this day.

Ostrom's revelations also coincided with the increasing adoption of phylogenetic systematics (cladistics), which began in the 1960s with the work of Willi Hennig. Cladistics is a method of arranging species based strictly on their evolutionary relationships, using a statistical analysis of their anatomical characteristics. In the 1980s, cladistic methodology was applied to dinosaur phylogeny for the first time by Jacques Gauthier and others, showing unequivocally that birds were a derived group of theropod dinosaurs. Early analyses suggested that dromaeosaurid theropods like *Deinonychus* were particularly closely related to birds, a result which has been corroborated many times since.

Modern research and feathered dinosaurs in China



Fossil of *Sinosauropteryx prima*.

The early 1990s saw the discovery of spectacularly preserved bird fossils in several Early Cretaceous geological formations in the northeastern Chinese province of Liaoning. In 1996, Chinese paleontologists described *Sinosauropteryx* as a new genus of bird from the Yixian Formation, but this animal was quickly recognized as a theropod dinosaur closely related to *Compsognathus*. Surprisingly, its body was covered by long filamentous structures. These were dubbed 'protofeathers' and considered to be homologous with the more advanced feathers of birds, although some scientists disagree with this assessment. Chinese and North American scientists described *Caudipteryx* and *Protarchaeopteryx* soon after. Based on skeletal features, these animals were non-avian dinosaurs, but their remains bore fully-formed feathers closely resembling those of birds. "Archaeoraptor," described without peer review in a 1999 issue of *National Geographic*, turned out to be a smuggled forgery, but legitimate remains continue to pour out of the Yixian, both legally and illegally. Feathers or "protofeathers" have been found on a wide variety of theropods in the Yixian, and the discoveries of extremely bird-like dinosaurs, as well as dinosaur-like primitive birds, have almost entirely closed the morphological gap between theropods and birds.

A small minority, including ornithologists Alan Feduccia and Larry Martin, continues to assert that birds are instead the descendants of earlier archosaurs, such as *Longisquama* or *Euparkeria*. Embryological studies of bird developmental biology have raised questions about digit homology in bird and dinosaur forelimbs. However, due to the cogent evidence provided by comparative anatomy and phylogenetics, as well as the dramatic feathered dinosaur fossils from China, the idea that birds are derived dinosaurs, first championed by Huxley and later by Nopcsa and Ostrom, enjoys near-unanimous support among today's paleontologists.

Phylogeny

Archaeopteryx has historically been considered the first bird, or *Urvogel*. Although newer fossil discoveries eliminated the gap between theropods and *Archaeopteryx*, as well as the gap between *Archaeopteryx* and modern birds, phylogenetic taxonomists, in keeping with tradition, almost always use *Archaeopteryx* as a specifier to help define Aves. Aves has more rarely been defined as a crown group consisting only of modern birds. Nearly all palaeontologists regard birds as coelurosaurian theropod dinosaurs. Within Coelurosauria, multiple cladistic analyses have found support for a clade named Maniraptora, consisting of therizinosauroids, oviraptorosaurs, troodontids, dromaeosaurids, and birds. Of these, dromaeosaurids and troodontids are usually united in the clade Deinonychosauria, which is a sister group to birds (together forming the node-clade Eumaniraptora) within the stem-clade Paraves.

Other studies have proposed alternative phylogenies in which certain groups of dinosaurs that are usually considered non-avian are suggested to have evolved from avian ancestors. For example, a 2002 analysis found oviraptorosaurs to be basal avians. Alvarezsaurids, known from Asia and the Americas, have been variously classified as basal maniraptorans, paravians, the sister taxon of ornithomimosaurs, as well as specialized early birds. The genus *Rahonavis*, originally described as an early bird, has been identified as a non-avian dromaeosaurid in several studies. Dromaeosaurids and troodontids themselves have also been suggested to lie within Aves rather than just outside it.

Features linking birds and dinosaurs

Many distinct anatomical features are shared by birds and theropod dinosaurs. Some of the more interesting similarities are discussed here:

Feathers

Parts of a feather

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. Discovered just two years after Darwin's seminal *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 Liaoning province, northeastern China, which was part of an island continent during the Cretaceous period. Though feathers have been found only in the lagerstätte of the Yixian Formation and a few other places, 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.

A recent development in the debate centers around the discovery of impressions of "protofeathers" surrounding many dinosaur fossils. These protofeathers suggest that the tyrannosauroids may have been feathered. However, others claim that these protofeathers are simply the result of the decomposition of collagenous fiber that underlaid the dinosaurs' integument.

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

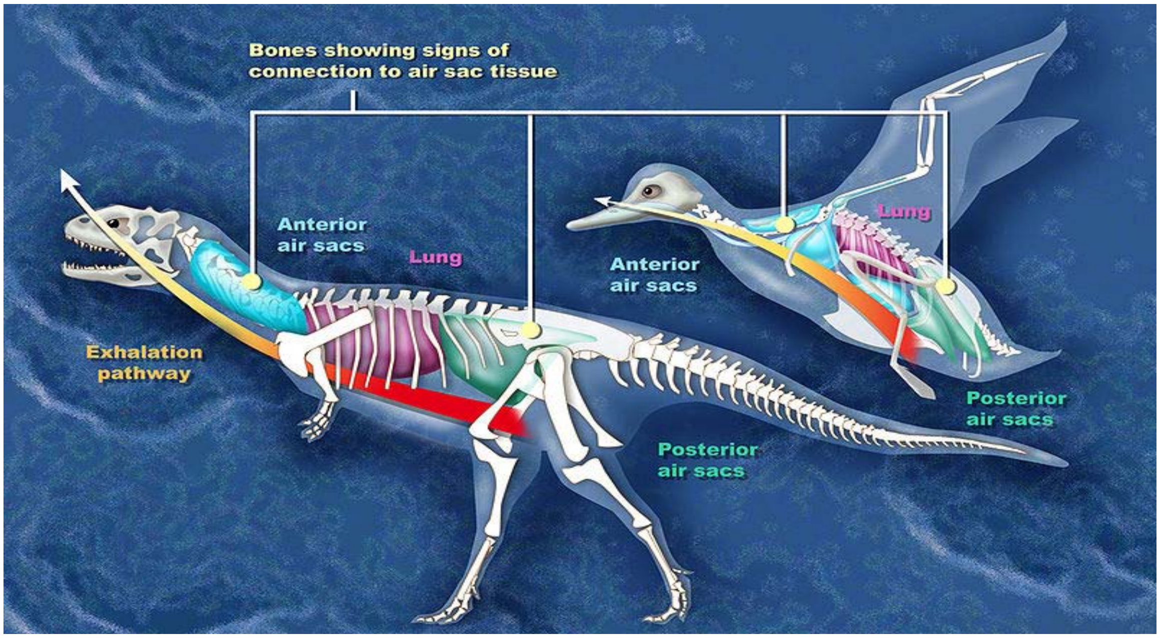
The feathered dinosaurs discovered so far include *Beipiaosaurus*, *Caudipteryx*, *Dilong*, *Microraptor*, *Protarchaeopteryx*, *Shuvuuia*, *Sinornithosaurus*, *Sinosauropteryx*, and *Jinfengopteryx*, along with dinosaur-like birds, such as *Confuciusornis*, which are anatomically closer to modern avians. All of them have been found in the same area and formation, in northern China. The Dromaeosauridae family, in particular, seems to have been heavily feathered and at least one dromaeosaurid, *Cryptovolans*, may have been capable of flight.

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 the more important link for paleontologists. Furthermore, it is increasingly clear that the relationship between birds and dinosaurs, and the evolution of flight, are more complex topics than previously realized. For example, while it was once believed that birds evolved within dinosaurs in one linear progression, some scientists, most notably Gregory S. Paul, conclude that dinosaurs such as the dromaeosaurs may have evolved within birds, losing the power of flight while keeping their feathers in a manner similar to the modern ostrich and other ratites.

Comparisons of bird and dinosaur skeletons, as well as cladistic analysis, strengthens the case for the link, particularly for a branch of theropods called maniraptors. Skeletal similarities include the neck, pubis, wrist (semi-lunate carpal), arm and pectoral girdle, shoulder blade, clavicle, and breast bone.

Lungs



Comparison between the air sacs of *Majungasaurus* and a bird

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 M. O'Connor of Ohio University. The lungs of theropod dinosaurs (carnivores that walked on two legs and had birdlike 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. The study was funded in part by the National Science Foundation.

Heart and sleeping posture

Modern computed tomography (CT) scans of a dinosaur chest cavity (conducted in 2000) found the apparent remnants of complex four-chambered hearts, 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. A recently discovered troodont fossil demonstrates that the dinosaurs slept like certain modern birds, with their heads tucked under their arms. This behavior, which may have helped to keep the head warm, is also characteristic of modern birds.

Reproductive biology

When laying eggs, female birds grow a special type of bone in their limbs. This medullary bone, which is rich in calcium, forms a layer inside the hard outer bone that is used to make eggshells. The presence of endosteally-derived bone tissues lining the interior marrow cavities of portions of a *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 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.

Brooding and care of young

A nesting *Citipati osmolskae* specimen, at the American Museum of Natural History in New York.

Several *Citipati* specimens have been found resting over the eggs in its nest in a position most reminiscent of brooding.

Numerous dinosaur species, for example *Maiasaura*, have been found in herds mixing both very young and adult individuals, suggesting rich interactions between them.

A dinosaur embryo was found without teeth, which suggests some parental care was required to feed the young dinosaur, possibly the adult dinosaur regurgitated food into the young dinosaur's mouth. This behaviour is seen in numerous bird species; parent birds regurgitate food into the hatchling's mouth.

Gizzard stones

Both birds and dinosaurs use gizzard stones. These stones are swallowed by animals to aid digestion and break down food and hard fibres once they enter the stomach. When found in association with fossils, gizzard stones are called gastroliths. Gizzard stones are also found in some fish (mullets, mud shad, and the gilaroo, a type of trout) and in crocodiles.

Molecular evidence and soft tissue

Fossil of a juvenile individual of Scipionyx samniticus. The fossil preserves clear traces of soft tissues.

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*, Dr. 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. The seven collagen types obtained from the bone fragments, compared to collagen data from living birds (specifically, a chicken), suggest that older theropods and birds are closely related.

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 Dr. Schweitzer's discovery, are not yet clear; study and interpretation of the specimens is ongoing.

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 have putatively been detected in dinosaur fossils, including hemoglobin.

Debates

Origin of bird flight

Debates about the origin of bird flight are almost as old as the idea that birds evolved within dinosaurs, which arose soon after the discovery of *Archaeopteryx* in 1862. Two theories have dominated most of the discussion since then: the cursorial ("from the ground up") theory proposes that birds evolved from small, fast predators that ran on the ground; the arboreal ("from the trees down") theory proposes that powered flight evolved from unpowered gliding by arboreal (tree-climbing) animals. A more recent theory, "wing-assisted incline running" (WAIR), is a variant of the cursorial theory and proposes that wings developed their aerodynamic functions as a result of the need to run quickly up very steep slopes, for example to escape from predators.

Cursorial ("from the ground up") theory

Reconstruction of *Rahonavis*, a ground-dwelling feathered dinosaur that some researchers think was well-equipped for flight.

The cursorial theory of the origin of flight was first proposed by Samuel Wendell Williston, and elaborated upon by Baron Nopcsa. This hypothesis proposes that some fast-running animals with long tails used their arms to keep their balance while running. Modern versions of this theory differ in many details from the Williston-Nopcsa version, mainly as a result of discoveries since Nopcsa's time.

Nopcsa theorized that increasing the surface area of the outstretched arms could have helped small cursorial predators to keep their balance, and that the scales of the forearms became elongated, evolving into feathers. The feathers could also have been used as a trap to catch insects or other prey. Progressively, the animals would have leapt for longer distances, helped by their evolving wings. Nopcsa also proposed that there were three main stages in the evolution of flight. First, passive flight was realized, in which the developed wing structures served as a sort of parachute. Second, active flight was possible, in which the animal achieved flight by flapping its wings. He used *Archaeopteryx* as an example of this second stage. Finally, birds gained the ability to soar.

It is now thought that feathers did not evolve from scales, as feathers are made of different proteins. More seriously, Nopcsa's theory assumes that feathers evolved as part of the evolution of flight, and recent discoveries prove that assumption is false.

Feathers are very common in coelurosaurian dinosaurs (including the early tyrannosauroid *Dilong*). Modern birds are classified as coelurosaurs by nearly all palaeontologists, though not by a few ornithologists. The modern version of the "from the ground up" hypothesis argues that birds' ancestors were small, *feathered*, ground-running predatory dinosaurs (rather like roadrunners in their hunting style) that used their forelimbs for balance while pursuing prey, and that the forelimbs and feathers later evolved in ways that provided gliding and then powered flight. The most widely-suggested original functions of feathers include thermal insulation and competitive displays, as in modern birds.

All of the *Archaeopteryx* fossils come from marine sediments and it has been suggested that wings may have helped the birds run over water in the manner of the *Jesus Christ Lizard* (Common basilisk).

Most recent refutations of the "from the ground up" hypothesis attempt to refute the modern version's assumption that birds are modified coelurosaurian dinosaurs. The strongest attacks are based on embryological analyses which conclude that birds' wings are formed from digits 2, 3, and 4 (corresponding to the index, middle, and ring fingers in humans; the first of a bird's three digits forms the alula, which they use to avoid stalling in low-speed flight, for example when landing); but the hands of coelurosaurs are formed by digits 1, 2, and 3 (thumb and first two fingers in humans). However these embryological analyses were immediately challenged on the embryological grounds that the "hand" often develops differently in clades that have lost some digits in the course of their evolution, and that birds' "hands" do develop from digits 1, 2, and 3.

Wing-assisted incline running

The WAIR hypothesis was prompted by observation of young chukar chicks, and proposes that wings developed their aerodynamic functions as a result of the need to run quickly up very steep slopes such as tree trunks, for example to escape from predators. This makes it a specialized type of cursorial ("from the ground up") theory. Note that in this scenario birds need *downforce* to give their feet increased grip. But early birds, including *Archaeopteryx*, lacked the shoulder mechanism by which modern birds' wings produce swift, powerful upstrokes; since the downforce on which WAIR depends is generated by upstrokes, it seems that early birds were incapable of WAIR.

Arboreal ("from the trees down") theory

The remarkable four-winged *Microraptor*, a "cousin" of the birds.

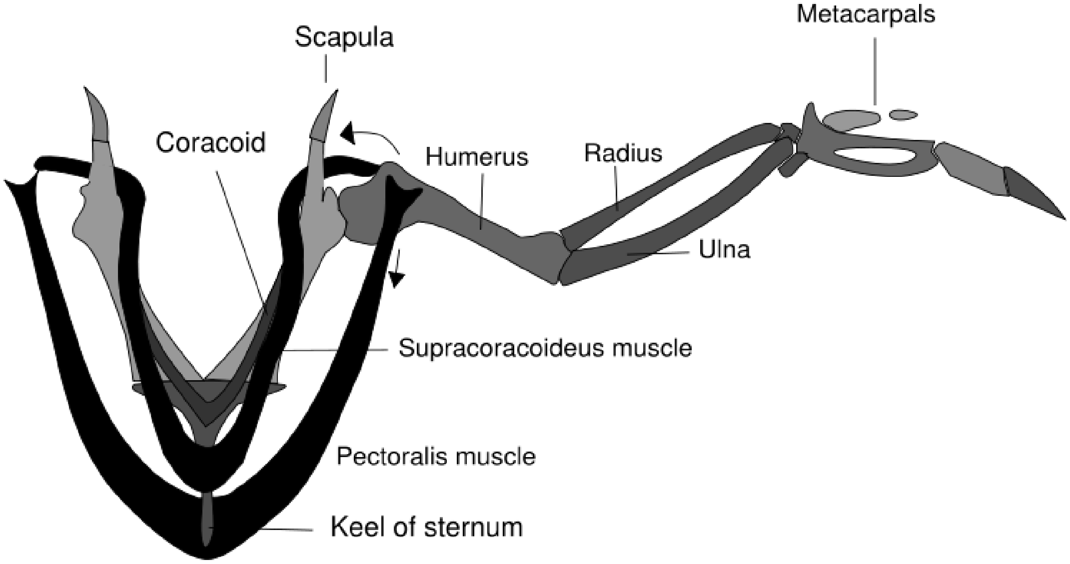
Most versions of the arboreal hypothesis state that the ancestors of birds were very small dinosaurs that lived in trees, springing from branch to branch. This small dinosaur already had feathers, which were co-opted by evolution to produce longer, stiffer forms that were useful in aerodynamics, eventually producing wings. Wings would have then evolved and become increasingly refined as devices to give the leaper more control, to parachute, to glide, and to fly in stepwise fashion. The arboreal hypothesis also notes that, for arboreal animals, aerodynamics are far more energy efficient, since such animals simply fall in order to achieve minimum gliding speeds.

Several small dinosaurs from the Jurassic or Early Cretaceous, all with feathers, have been interpreted as possibly having arboreal and/or aerodynamic adaptations. These include *Epidendrosaurus*, *Epidexipteryx*, *Microraptor*, *Pedopenna*, and *Anchiornis*. *Anchiornis* is particularly important to this subject, as it is the smallest known non - avian dinosaur, and it lived at the beginning of the Late Jurassic, long before *Archaeopteryx*.

Analysis of the proportions of the toe bones of the most primitive birds *Archaeopteryx* and *Confuciusornis*, compared to those of living species, suggest that the early species may have lived both on the ground and in trees.

One study suggested that the earliest birds and their immediate ancestors did not climb trees. This study determined that the amount of toe claw curvature of early birds was more like that seen in modern ground-foraging birds than in perching birds.

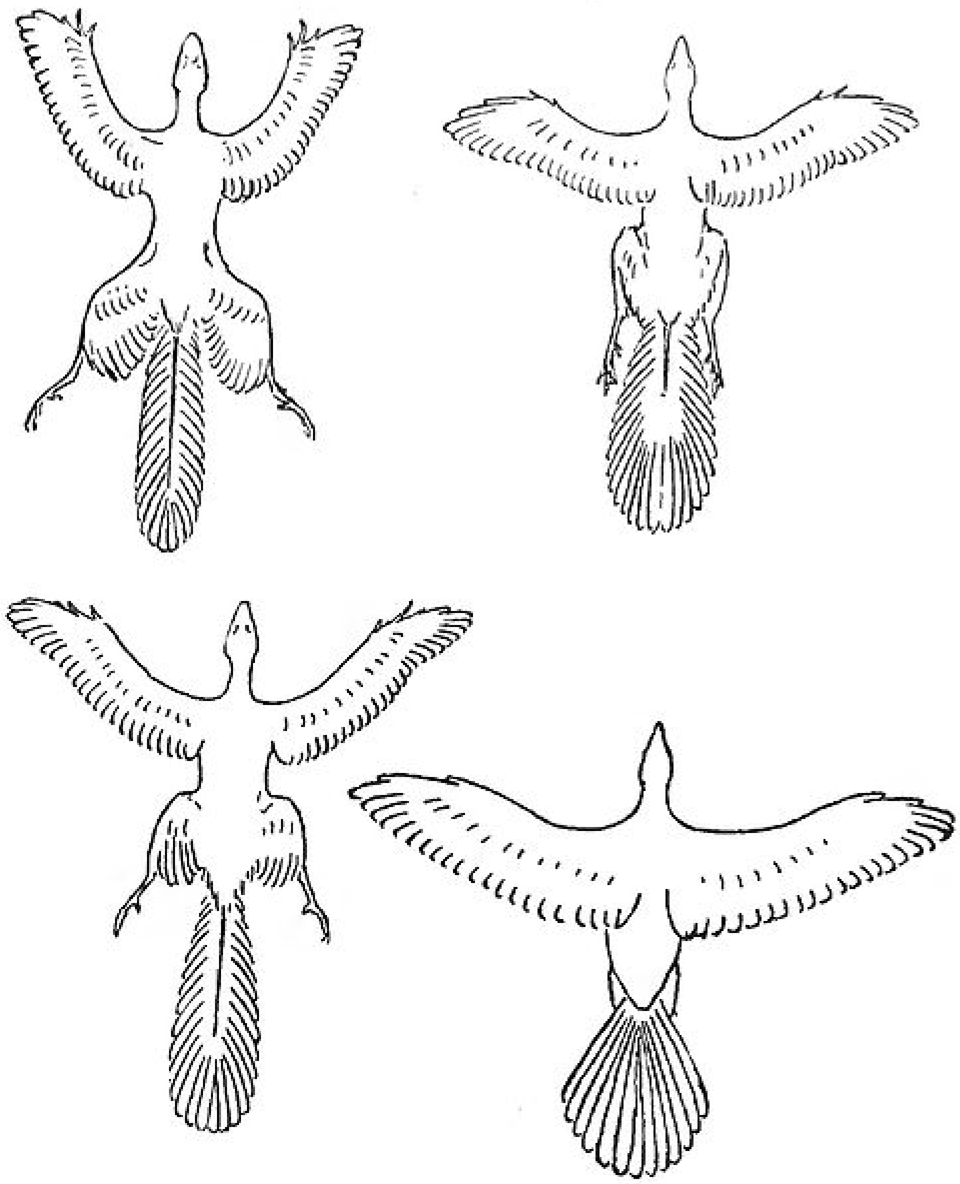
Diminished significance of *Archaeopteryx*



The supracoracoideus works using a pulley-like system to lift the wing while the pectorals provide the powerful downstroke

Archaeopteryx was the first and for a long time the only known feathered Mesozoic animal (or dinosaur, if one accepts the majority view that birds are modified dinosaurs). As a result, discussion of the evolution of birds and of bird flight centered on *Archaeopteryx* at least until the mid-1990s.

There has been debate about whether *Archaeopteryx* could really fly. It appears that *Archaeopteryx* had the brain structures and inner-ear balance sensors that birds use to control their flight. *Archaeopteryx* also had a wing feather arrangement like that of modern birds and similarly asymmetrical flight feathers on its wings and tail. But *Archaeopteryx* lacked the shoulder mechanism by which modern birds' wings produce swift, powerful upstrokes; this may mean that it and other early birds were incapable of flapping flight and could only glide.



Proposed development of flight in a book from 1922: Tetrapteryx, *Archaeopteryx*, Hypothetical Stage, Modern Bird

But the discovery since the early 1990s of many feathered dinosaurs means that *Archaeopteryx* is no longer the key figure in the evolution of bird flight. Other small, feathered coelurosaurs from the Cretaceous and Late Jurassic show features that may be precursors of avian flight, for example: *Rahonavis*, a ground-runner which had a *Velociraptor*-like raised sickle claw on the second toe and which some paleontologists think was better adapted for flight than *Archaeopteryx*; *Epidendrosaurus*, an arboreal dinosaur that may provide some support for the "from the trees down" theory; *Microraptor*, an arboreal dinosaur that may have been capable of powered flight but, if so, more like a biplane, as it had well-developed feathers on its legs. As early as 1915, some scientists had argued that the evolution of bird flight may have gone through a four-winged (or *tetrapteryx*) stage.

Secondary flightlessness in dinosaurs

hypothesis, credited to Gregory Paul and propounded in his books *Predatory Dinosaurs of the World* (1988) and *Dinosaurs of the Air* (2002), suggests that some groups of non-flying carnivorous dinosaurs, especially deinonychosaurs but perhaps others such as oviraptorosaurs, therizinosaurs, alvarezsaurids and ornithomimosaurs, are actually descended from birds. Paul also proposed that the bird ancestor of these groups was more advanced in its flight adaptations than *Archaeopteryx*. This would mean that *Archaeopteryx* is thus less closely related to extant birds than these dinosaurs are.

Paul's hypothesis received additional support when Mayr *et al.* (2005) analyzed a new, tenth specimen of *Archaeopteryx*, and concluded that *Archaeopteryx* was the sister clade to the Deinonychosauria, but that the more advanced bird *Confuciusornis* was within the Dromaeosauridae. This result supports Paul's hypothesis, suggesting that the Deinonychosauria and the Troodontidae are part of Aves, the bird lineage proper, and secondarily flightless. This paper, however, excluded all other birds and thus did not sample their character distributions. The paper was criticized by Corfe and Butler (2006) who found the authors could not support their conclusions statistically. Mayr *et al.* agreed that the statistical support was weak, but added that it is also weak for the alternative scenarios.

Paul's hypothesis about the position of *Archaeopteryx* is not supported by current cladistic analyses which generally find that *Archaeopteryx* is closer to birds, within the clade *Avialae*, than it is to deinonychosaurs or oviraptorosaurs. However, the version of this theory stating that some non-flying carnivorous dinosaurs may have had flying ancestors is supported by some fossils. Especially, *Microraptor*, *Pedopenna*, and *Anchiornis* all have winged feet, share many features, and lie close to the base of the clade Paraves. This suggests that the ancestral paravian was a four-winged glider, and that larger Deinonychosaurs secondarily lost the ability to glide, while the bird lineage increased in aerodynamic ability as it progressed.

Digit homology

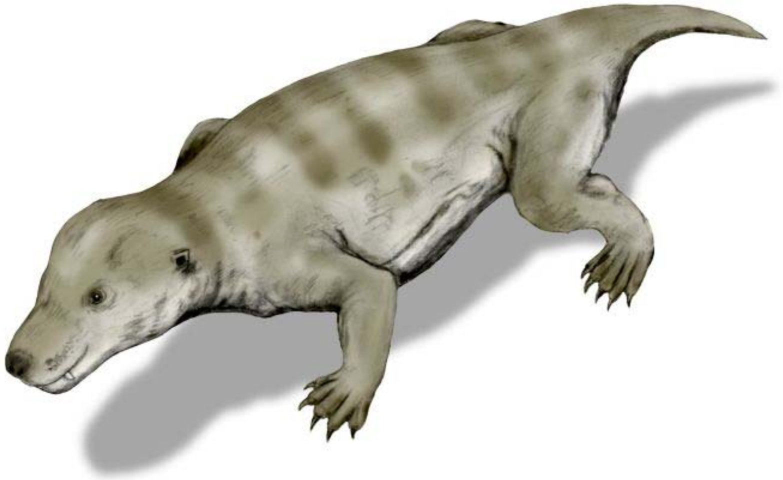
There is a debate between embryologists and paleontologists whether the hands of theropod dinosaurs and birds are essentially different, based on phalangeal counts, a count of the number of phalanges (fingers) in the hand. This is an important and fiercely debated area of research because its results may challenge the consensus that birds are descendants of dinosaurs.

Embryologists and some paleontologists who oppose the bird-dinosaur link, have long numbered the digits of birds II-III-IV on the basis of multiple studies of the development in the egg. This is based on the fact that in most amniotes, the first digit to form in a 5-fingered hand is digit IV, which develops a primary axis. Therefore, embryologists have identified the primary axis in birds as digit IV, and the surviving digits as II-III-IV. The fossils of advanced theropod (Tetanurae) hands appear to have the digits I-II-III (some genera within Avetheropoda also have a reduced digit IV). If this is true, then the II-III-IV development of digits in birds is an indication against theropod (dinosaur) ancestry. However, with no ontogenical (developmental) basis to definitively state which digits are which on a theropod hand (because no non-avian theropods can be observed growing and developing today), the labelling of the theropod hand is not absolutely conclusive.

Paleontologists have traditionally identified avian digits as I-II-III. They argue that the digits of birds number I-II-III, just as those of theropod dinosaurs do, by the conserved phalangeal formula. The phalangeal count for archosaurs is 2-3-4-5-3; many archosaur lineages have a reduced number of digits, but have the same phalangeal formula in the digits that remain. In other words, paleontologists assert that archosaurs of different lineages tend to lose the same digits when digit loss occurs, from the outside to the inside. The three digits of dromaeosaurs, and *Archaeopteryx* have the same phalangeal formula of I-II-III as digits I-II-III of basal archosaurs. Therefore, the lost digits would be V and IV. If this is true, then modern birds would also possess digits I-II-III. Also, one research team has proposed a frame-shift in the digits of the theropod line leading to birds (thus making digit I into digit II, II to III, and so forth). However, such frame shifts are rare in amniotes and would have had to occur solely in the forelimbs and not the hindlimbs (a condition presently unknown in any animal) in the bird-theropod lineage in order to be consistent with the theropod origin of birds. This is called *Lateral Digit Reduction* (LDR) versus *Bilateral Digit Reduction* (BDR)

Chapter- 4

Evolution of Mammals



Restoration of *Thrinaxodon*, a member of the cynodont group, which includes the ancestors of mammals.

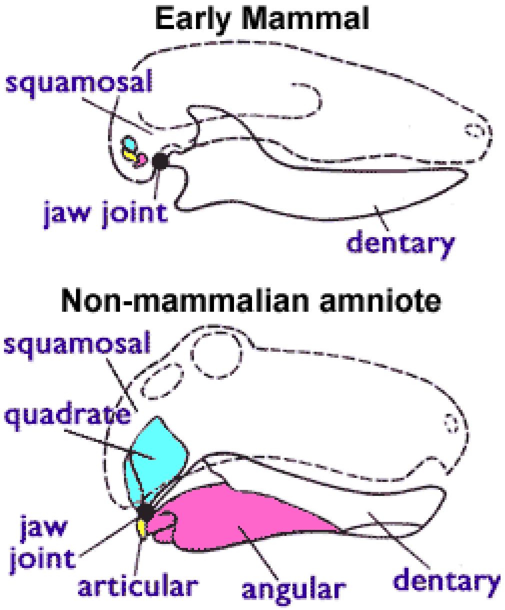
The **evolution of mammals** within the synapsid lineage (mammal-like-reptiles) was a gradual process that took approximately 70 million years, beginning in the mid-Permian. By the mid-Triassic, there were many species that looked like mammals, and the first true mammals appeared in the early Jurassic. The earliest known marsupial, *Sinodelphys*, appeared 125 million years ago in the early Cretaceous, around the same time as *Eomaia*, the first known eutherian (member of placentals' "parent" group); and the earliest known monotreme, *Teinolophos*, appeared two million years later. After the Cretaceous-Tertiary extinction wiped out the non-avian dinosaurs (birds are generally regarded as the surviving dinosaurs) and several other mammalian groups, placental and marsupial mammals diversified into many new forms and ecological niches throughout the Tertiary, by the end of which all modern orders had appeared.

From the point of view of phylogenetic nomenclature, mammals are the only surviving synapsids. The synapsid lineage became distinct from the sauropsid ("reptile") lineage in the late Carboniferous period, between 320 and 315 million years ago, and were the most common and largest land vertebrates of the Permian period. But in the Triassic period a previously obscure group of sauropsids, the archosaurs, became the dominant vertebrates and one archosaur group, the dinosaurs, dominated the rest of the Mesozoic era. These changes forced the Mesozoic mammaliforms ("nearly mammals") into nocturnal niches, and may have contributed greatly to the development of mammalian traits such as endothermy, hair and a large brain. Later in the Mesozoic mammals spread into other ecological niches, for example aquatic, gliding and even preying on dinosaurs.

Most of the evidence consists of fossils. For many years fossils of Mesozoic mammals and their immediate ancestors were very rare and fragmentary, but since the mid 1990s there have been many important new finds, especially in China. The relatively new techniques of molecular phylogenetics have also shed light on some aspects of mammalian evolution by estimating the timing of important divergence points for modern species. When used carefully, these techniques often, but not always, agree with the fossil record.

Although mammary glands are a signature feature of modern mammals, little is known about the evolution of lactation, and virtually nothing is known about the evolution of another distinctive feature, the neocortex region of the brain. This is because these soft tissues are not often preserved in the fossil record. Hence, most study of the evolution of mammals centers around the development of the middle ear bones from components of the ancestral amniote jaw joint. Other much-studied aspects include the evolution of erect limb posture, a bony secondary palate, fur and hair, and warm-bloodedness.

Definition of "mammal"



Mammalian and non-mammalian jaws. In the mammal configuration, the quadrate and articular bones are much smaller and form part of the middle ear. Note that in mammals the lower jaw consists of only the dentary bone.

Living mammal species can be identified by the presence of milk-producing mammary glands in females. Other features are required when classifying fossils, since mammary glands and other soft-tissue features are not visible in fossils.

Paleontologists therefore use a distinguishing feature that is shared by all living mammals (including monotremes) but is not present in any of the early Triassic therapsids: Mammals use two bones for hearing that all other amniotes use for eating. The earliest amniotes had a jaw joint composed of the articular (a small bone at the back of the lower jaw) and the quadrate (a small bone at the back of the upper jaw). All non-mammalian amniotes use this system including lizards, crocodilians, dinosaurs (and their descendants the birds), and therapsids. But mammals have a different jaw joint, composed only of the dentary (the lower jaw bone, which carries the teeth) and the squamosal (another small skull bone). In mammals, the quadrate and articular bones have become the incus and malleus bones in the middle ear.

Mammals also have a double occipital condyle; they have two knobs at the base of the skull that fit into the topmost neck vertebra, and other vertebrates have a single occipital condyle. But paleontologists use only the jaw joint and middle ear as criteria for identifying fossil mammals, as it would be confusing if they found a fossil that had one feature but not the other (e.g. a mammalian jaw and ear but a non-mammalian single occipital condyle).

Due to the incremental changes in transitional fossils, it has been said

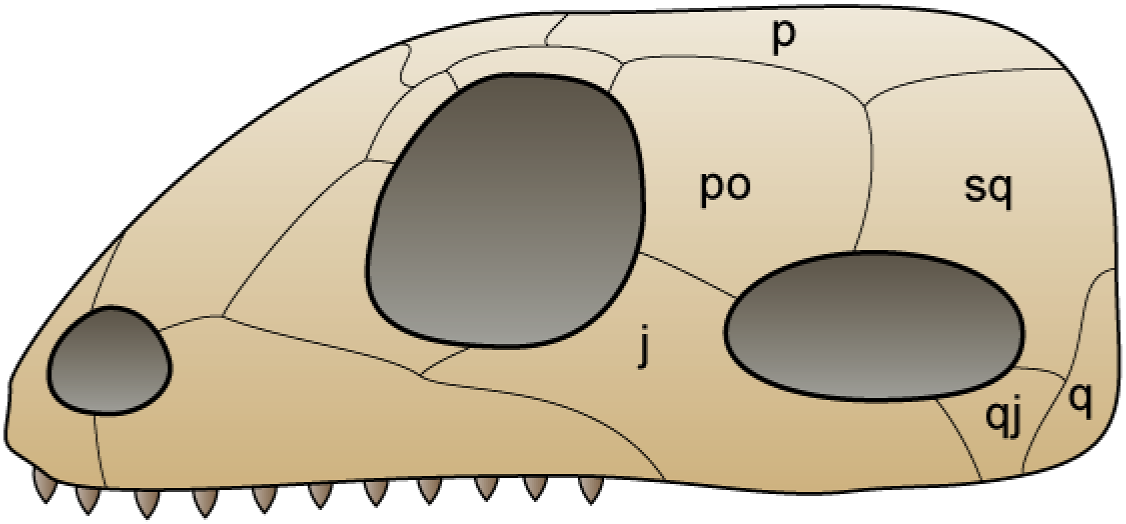
We may again ask the question, What is a mammal? Where we draw the line between reptile and mammal has no biological significance. It is purely a matter of convenience. There are two obvious choices, both immediately following a period of rapid evolution that make as definite a break as we can hope to find.

Amniotes

The first fully terrestrial vertebrates were amniotes — their eggs had internal membranes that allowed the developing embryo to breathe but kept water in. This allowed amniotes to lay eggs on dry land, while amphibians generally need to lay their eggs in water (a few amphibians, such as the Surinam toad, have evolved other ways of getting round this limitation). The first amniotes apparently arose in the late Carboniferous from the ancestral reptiliomorphs.

Within a few million years two important amniote lineages became distinct: mammals' synapsid ancestors and the sauropsids, from which lizards, snakes, crocodilians, dinosaurs and birds are descended. The earliest known fossils of synapsids and sauropsids (such as Archaeothyris and Hylonomus resp.) date from about 320 to 315 million years ago. Unfortunately it is difficult to be sure about when each of them evolved, since vertebrate fossils from the late Carboniferous are very rare, and therefore the actual first occurrences of each of these types of animal might have been considerably earlier.

Synapsids



The original synapsid skull structure has one hole behind each eye, in a fairly low position on the skull (lower right in this image).

Synapsid skulls are identified by the distinctive pattern of the holes behind each eye, which served the following purposes:

- made the skull lighter without sacrificing strength.
- saved energy by using less bone.
- probably provided attachment points for jaw muscles. Having attachment points further away from the jaw made it possible for the muscles to be longer and therefore to exert a strong pull over a wide range of jaw movement without being stretched or contracted beyond their optimum range.

Early Permian terrestrial fossils indicate that one synapsid group, the pelycosaurs, were the most common land vertebrates of their time and included the largest land animals of the time.

Therapsids

Therapsids descended from pelycosaurs in the middle Permian and took over their position as the dominant land vertebrates. They differ from pelycosaurs in several features of the skull and jaws, including larger temporal fenestrae and incisors that are equal in size.

The therapsids went through a series of stages, beginning with animals that were very like their pelycosaur ancestors and ending with some that could easily be mistaken for mammals:

- gradual development of a bony secondary palate. Most books and articles interpret this as a prequisite for the evolution of mammals' high metabolic rate, because it enabled these animals to eat and breathe at the same time. But some scientists point out that some modern ectotherms use a fleshy secondary palate to separate the mouth from the airway, and that a *bony* palate provides a surface on which the tongue can manipulate food, facilitating chewing rather than breathing. The interpretation of the bony secondary palate as an aid to chewing also suggests the development of a faster metabolism, since chewing makes it possible to digest food more quickly. In mammals the palate is formed by two specific bones, but various Permian therapsids had other combinations of bones in the right places to function as a palate.
- the dentary gradually becomes the main bone of the lower jaw.
- progress towards an erect limb posture, which would increase the animals' stamina by avoiding Carrier's constraint. But this process was erratic and very slow — for example: all herbivorous therapsids retained sprawling limbs (some late forms may have had semi-erect hind limbs); Permian carnivorous therapsids had sprawling forelimbs, and some late Permian ones also had semi-sprawling hindlimbs. In fact, modern monotremes still have semi-sprawling limbs.
- in the Triassic, progress towards the mammalian jaw and middle ear.
- there is plausible evidence of hair in Triassic therapsids, but none for Permian therapsids.
- some scientists have argued that some Triassic therapsids show signs of lactation.

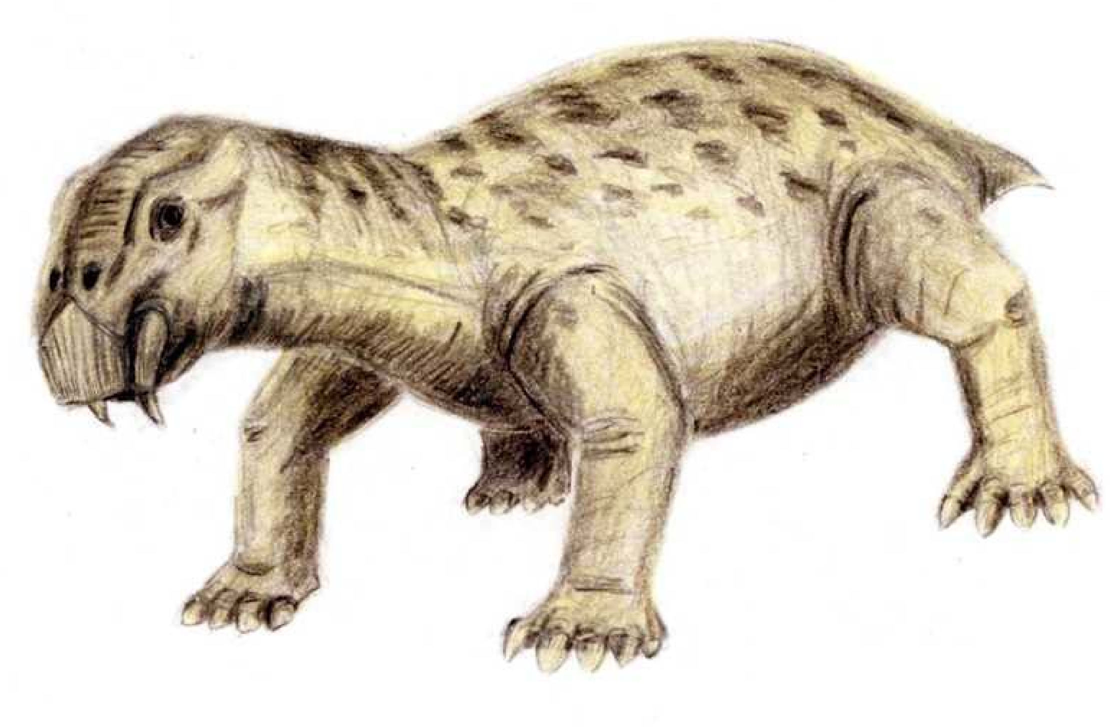
Biarmosuchia

The Biarmosuchia were the most primitive and pelycosaur-like of the therapsids.

Dinocephalians

Dinocephalians ("terrible heads") were large, some as large as a rhinoceros, and included both carnivores and herbivores. Some of the carnivores had semi-erect hindlimbs, but all dinocephalians had sprawling forelimbs. In many ways they were very primitive therapsids, for example they had no secondary palate and their jaws were rather "reptilian".

Anomodonts



Lystrosaurus, one of the few species of dicynodonts that survived the Permian-Triassic extinction event

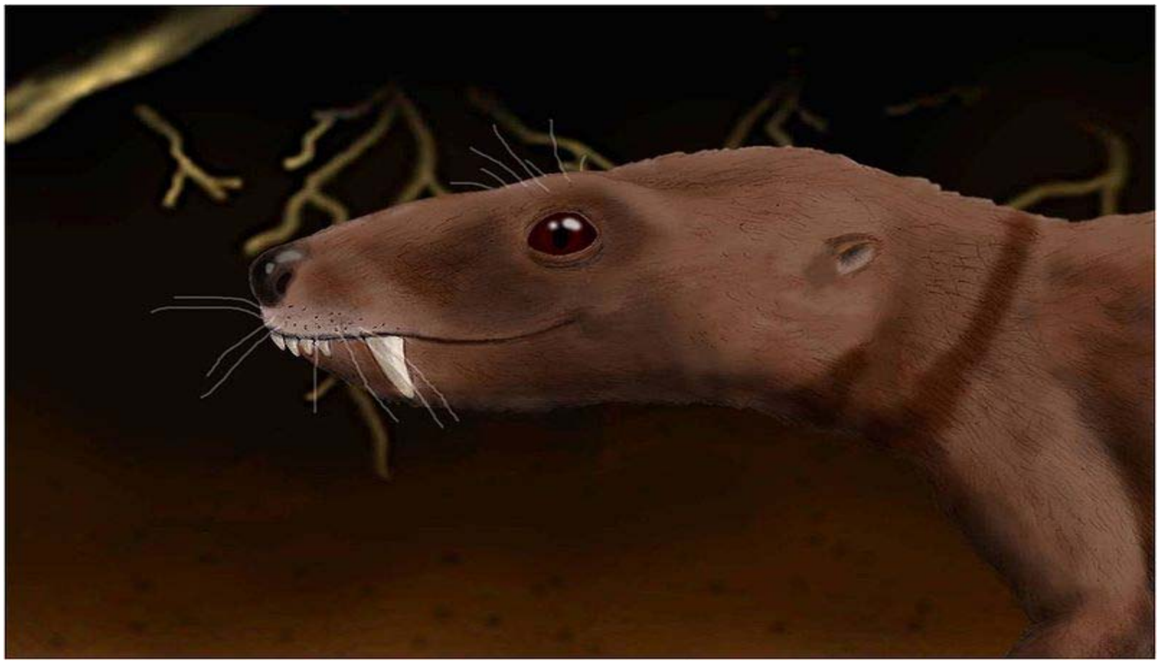
The anomodonts ("anomalous teeth") were the most successful of the herbivorous therapsids — one sub-group, the dicynodonts, survived almost to the end of the Triassic. But anomodonts were very different from modern herbivorous mammals, as their only teeth were a pair of fangs in the upper jaw and it is generally agreed that they had beaks like those of birds or ceratopsians.

Theriodonts

The theriodonts ("beast teeth") and their descendants had jaw joints in which the lower jaw's articular bone tightly gripped the skull's very small quadrate bone. This allowed a much wider gape, and one group, the carnivorous gorgonopsians ("gorgon faces"), took advantage of this to develop "sabre teeth". But the theriodont's jaw hinge had a longer term significance — the much reduced size of the quadrate bone was an important step in the development of the mammalian jaw joint and middle ear.

The gorgonopsians still had some primitive features: no bony secondary palate (but other bones in the right places to perform the same functions); sprawling forelimbs; hindlimbs that could operate in both sprawling and erect postures. But the therocephalians ("beast heads"), which appear to have arisen at about the same time as the gorgonopsians, had additional mammal-like features, e.g. their finger and toe bones had the same number of phalanges (segments) as in early mammals (and the same number that primates have, including humans).

Cynodonts



Artist's conception of the cynodont *Trirachodon* within a burrow

The cynodonts, a theriodont group that also arose in the late Permian, include the ancestors of all mammals — one sub-group, the trithelodonts, is widely regarded as the most likely to contain mammals' ancestor. Cynodonts' mammal-like features include further reduction in the number of bones in the lower jaw; a secondary bony palate; cheek teeth with a complex pattern in the crowns; the brain filled the endocranial cavity.

Multi-chambered burrows have been found, containing as many as 20 skeletons of the Early Triassic cynodont *Trirachodon*; the animals are thought to have been drowned by a flash flood. The extensive shared burrows indicate that these animals were capable of complex social behaviors.

Triassic takeover

The catastrophic Permian-Triassic mass extinction killed off about 70 percent of terrestrial vertebrate species, and the majority of land plants. As a result

- Ecosystems and food chains collapsed, and the recovery took about 6 million years.
- The survivors had to re-start the struggle for dominance of their former ecological niches — even the cynodonts, which had seemed on the way to dominance at the end of the Permian.

But the cynodonts lost out to a previously obscure group of sauropsids, the archosaurs (which include the ancestors of crocodilians, dinosaurs and birds). This reversal of fortunes is often called the "Triassic takeover". Several explanations have been offered for it, but the most likely is that the early Triassic was predominantly arid and therefore archosaurs' superior water conservation gave them a decisive advantage (all known sauropsids have glandless skins and excrete uric acid, which requires less water to keep it sufficiently liquid than urea, which marsupial and placental mammals excrete and presumably therapsids excreted). The Triassic takeover was gradual — in the earliest part of the Triassic cynodonts were the main predators and lystrosaurs were the main herbivores, but by the mid-Triassic archosaurs dominated all the large carnivore and herbivore niches.

But the Triassic takeover may have been a vital factor in the evolution of cynodonts into mammals. The cynodonts' descendants were only able to survive as small, mainly nocturnal insectivores. As a result:

- The therapsid trend towards differentiated teeth with precise occlusion accelerated, because of the need to hold captured arthropods and crush their exoskeletons.
- Nocturnal life required advances in thermal insulation and temperature regulation to enable the ancestors of mammals to be active in the cool of the night.
- Acute senses of hearing and smell became vital.
    - This accelerated the development of the mammalian middle ear, and therefore of the mammalian jaw since bones that had been part of the jaw joint became part of the middle ear.
    - The increase in the size of the olfactory and auditory lobes of the brain increased brain weight as a total percentage of body weight. Brain tissue requires a disproportionate amount of energy. The need for more food to support the enlarged brains increased the pressures for improvements in insulation, temperature regulation and feeding.
- As a side-effect of the nocturnal life, discerning colors became less important (they lost two out of four opsins), and this is reflected in the fact that most mammals have poor color vision, including the "lower primates" such as lemurs.

From cynodonts to true mammals

Many uncertainties

While the Triassic takeover probably accelerated the evolution of mammals, it made life more difficult for paleontologists because good fossils of the nearly-mammals are extremely rare, mainly because they were mostly smaller than rats:

- They were largely restricted to environments that are less likely to provide good fossils. The best terrestrial environments for fossilization are floodplains, where seasonal floods quickly cover dead animals in a protective layer of silt that is later compressed into sedimentary rock. But floodplains are dominated by medium to

large animals, and the Triassic therapsids and near-mammals could not compete with archosaurs in the medium to large size range.
- Their delicate bones were vulnerable to being destroyed before they could be fossilized — by scavengers (including fungi and bacteria) and by being trodden on.
- Small fossils are harder to spot and more vulnerable to being destroyed by weathering and other natural stresses before they are discovered.

In fact it was said as recently as the 1980s that all the Mesozoic fossils of mammals and near-mammals could be contained in a few shoeboxes — and they were mostly teeth, which are the most durable of all tissues. Since then, the number of Mesozoic fossil mammals has increased, from 116 genera known in 1979 to about 310 in 2007, with an increase in quality such that "at least 18 Mesozoic mammals are represented by nearly complete skeletons".

As a result:

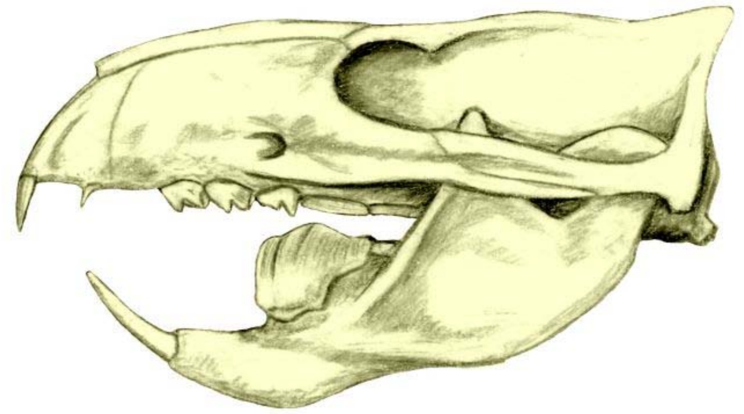
- In many cases it is difficult to assign a Mesozoic mammal or near-mammal fossil to a genus.
- All the available fossils of a genus seldom add up to a complete skeleton, and hence it is difficult to decide which genera are most like each other and therefore most likely to be closely-related. In other words, it becomes very difficult to classify them by means of cladistics, which is the most reliable and least subjective method currently available.

So the evolution of mammals in the Mesozoic is full of uncertainties, although there is no room for doubt that true mammals did first appear in the Mesozoic.

Mammals or mammaliformes?

One result of these uncertainties has been a change in the paleontologists' definition of "mammal". For a long time a fossil was considered a mammal if it met the jaw-ear criterion (the jaw joint consists only of the squamosal and dentary; and the articular and the quadrate bones have become the middle ear's malleus and incus). But more recently some paleontologists have usually defined "mammal" as the crown group mammals, i.e. the last common ancestor of monotremes, marsupials and placentals and all of its descendants. The need to address the animals that are more mammal-like than cynodonts, but less closely related to monotremes, marsupials and placentals, lead to erecting the group mammaliformes to accommodate these primitive forms. Mammaliformes is a paraphyletic taxon, representing the early radiation of mammals after the jaw-ear criterion. Although this now appears to be the majority approach, some paleontologists have resisted it because it simply moves most of the problems into the new taxon (a paraphyletic one at that) without solving the original problem; the Mammaliformes includes some animals with "mammalian" jaw joints and some with "reptilian" (articular-to-quadrate) jaw joints; and the newer definition of "mammal" and "mammaliformes" depend on last common ancestors of both groups, which have not yet been found.

Multituberculates

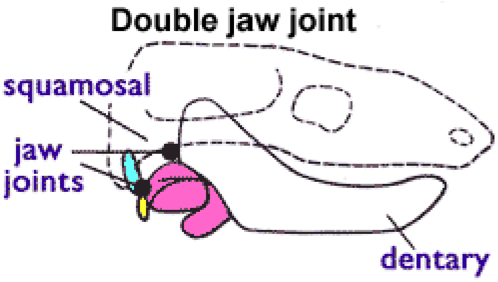


Skull of the multituberculate *Ptilodus*

Multituberculates (named for the multiple tubercles on their "molars") are often called the "rodents of the Mesozoic" but this is an example of convergent evolution rather than meaning that they are closely related to the Rodentia. At first sight they look like mammals: their jaw joints consists of only the dentary and squamosal bones, and the quadrate and articular bones are part of the middle ear; their teeth are differentiated, occlude and have mammal-like cusps; they have a zygomatic arch; the structure of the pelvis suggests that they gave birth to tiny helpless young, like modern marsupials. And they lived for over 120 million years (from mid Jurassic, about 160M years ago, to early Oligocene, about 35M years ago), which in terms of clade longevity would make them the most successful mammaliformes ever. But a closer look shows that they are very different from modern mammals:

- Their "molars" have two parallel rows of tubercles, unlike the tribosphenic (three-peaked) molars of early mammals.
- The chewing action is completely different. Mammals chew with a side-to-side grinding action, which means that usually the molars occlude on only one side at a time. Multituberculates' jaws were incapable of side-to-side movement and chewed by dragging the lower teeth backwards against the upper ones as the jaw closed.
- The anterior (forward) part of the zygomatic arch mostly consists of the maxilla (upper jawbone) rather than the jugal, and the jugal is a small bone in a little slot in the maxillary process (extension).
- The squamosal does not form part of the braincase.
- The rostrum (snout) is unlike that of mammals, in fact it looks more like that of a pelycosaur such as *Dimetrodon*. The multituberculate rostrum is box-like, with

the large flat maxillae forming the sides, the nasal the top, and the tall premaxilla at the front.

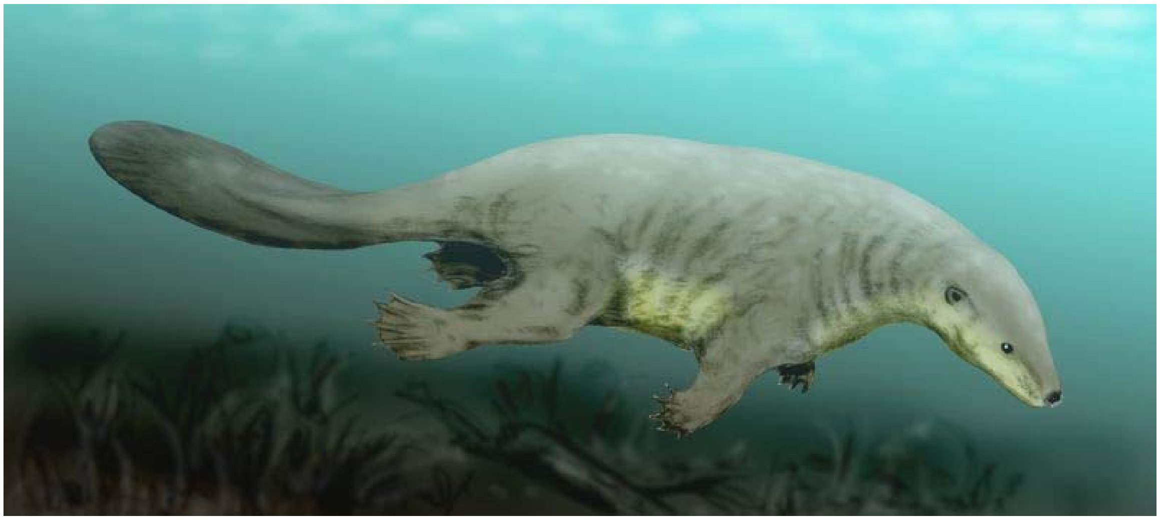


Morganucodontidae and other transitional forms had both types of jaw joint: dentary-squamosal (front) and articular-quadrate (rear).

Morganucodontidae

The Morganucodontidae first appeared in the late Triassic, about 205M years ago. They are an excellent example of transitional fossils, since they have both the dentary-squamosal and articular-quadrate jaw joints. They were also one of the first discovered and most thoroughly studied of the mammaliformes, since an unusually large number of morganucodont fossils have been found.

Docodonts

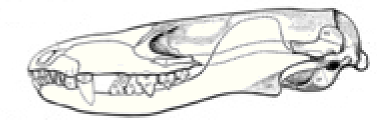


Reconstruction of *Castorocauda*. Note the fur and the adaptations for swimming (broad, flat tail; webbed feet) and for digging (robust limbs and claws).

The most notable member of the docodonts is *Castorocauda* ("beaver tail"), which lived in the mid Jurassic about 164M years ago and was first discovered in 2004 and described in 2006. *Castorocauda* was not a typical docodont (most were omnivores) and not a true mammal, but it is extremely important in the study of the evolution of mammals because the first find was an almost complete skeleton (a real luxury in paleontology) and it breaks the "small nocturnal insectivore" stereotype:

- It was noticeably larger than most Mesozoic mammal-like fossils — about 17 in (43 cm) from its nose to the tip of its 5-inch (130 mm) tail, and may have weighed 500–800 g (18–28 oz).
- It provides the earliest absolutely certain evidence of hair and fur. Previously the earliest was *Eomaia*, a true mammal from about 125M years ago.
- It had aquatic adaptations including flattened tail bones and remnants of soft tissue between the toes of the back feet, suggesting that they were webbed. Previously the earliest known semi-aquatic mammal-like animals were from the Eocene, about 110M years later.
- *Castorocauda's* powerful forelimbs look adapted for digging. This feature and the spurs on its ankles make it resemble the platypus, which also swims and digs.
- Its teeth look adapted for eating fish: the first two molars had cusps in a straight row, which made them more suitable for gripping and slicing than for grinding; and these molars are curved backwards, to help in grasping slippery prey.

Hadrocodium



Hadrocodium skull. The jaw joint is fully mammalian (squamosal-dentary only) and farther forward than in earlier transitional forms.

The consensus family tree above shows *Hadrocodium* as an "aunt" of true mammals, while symmetrodonts and kuehneotheriids are more closely related to true mammals. But fossils of symmetrodonts and kuehneotheriids are so few and fragmentary that they are poorly understood and may be paraphyletic. On the other hand there are good fossils of *Hadrocodium* (about 195M years ago in the very early Jurassic) and they have some important features:

- The jaw joint consists only of the squamosal and dentary bones, and the jaw contains no smaller bones to the rear of the dentary, unlike the therapsid design.
- In therapsids and most mammaliformes the eardrum stretched over a trough at the rear of the lower jaw. But *Hadrocodium* had no such trough, which suggests its ear was part of the cranium, as it is in mammals — and hence that the former articular and quadrate had migrated to the middle ear and become the malleus and incus. On the other hand the dentary has a "bay" at the rear that mammals lack. This suggests that *Hadrocodium's* dentary bone retained the same shape that it would have had if the articular and quadrate had remained part of the jaw joint, and therefore that *Hadroconium* or a very close ancestor may have been the first to have a fully mammalian middle ear.
- Therapsids and earlier mammaliforms had their jaw joints very far back in the skull, partly because the ear was at the rear end of the jaw but also had to be close

to the brain. This arrangement limited the size of the braincase, because it forced the jaw muscles to run round and over it. *Hadrocodium's* braincase and jaws were no longer bound to each other by the need to support the ear, and its jaw joint was further forward. In its descendants or those of animals with a similar arrangement, the brain case was free to expand without being constrained by the jaw and the jaw was free to change without being constrained by the need to keep the ear near the brain — in other words it now became possible for mammal-like animals both to develop large brains and to adapt their jaws and teeth in ways that were purely specialized for eating.

The earliest true mammals

This part of the story introduces new complications, since true mammals are the only group that still has living members:

- One has to distinguish between extinct groups and those that have living representatives.
- One often feels compelled to try to explain the evolution of features that do not appear in fossils. This endeavor often involves Molecular phylogenetics, a technique that has become popular since the mid-1980s but is still often controversial because of its assumptions, especially about the reliability of the molecular clock.

Australosphenida and Ausktribosphenidae

Ausktribosphenidae is a group name that has been given to some rather puzzling finds that:

- appear to have tribosphenic molars, a type of tooth that is otherwise known only in placentals and marsupials.
- come from mid Cretaceous deposits in Australia — but Australia was connected only to Antarctica, and placentals originated in the northern hemisphere and were confined to it until continental drift formed land connections from North America to South America, from Asia to Africa and from Asia to India (the late Cretaceous map at shows how the southern continents are separated).
- are represented only by skull and jaw fragments, which is not very helpful.

Australosphenida is a group that has been defined in order to include the Ausktribosphenidae and monotremes. *Asfaltomylos* (mid- to late Jurassic, from Patagonia) has been interpreted as a basal australosphenid (animal that has features shared with both Ausktribosphenidae and monotremes; lacks features that are peculiar to Ausktribosphenidae or monotremes; also lacks features that are absent in Ausktribosphenidae and monotremes) and as showing that australosphenids were widespread throughout Gondwanaland (the old Southern hemisphere super-continent).

But recent analysis of *Teinolophos* suggests *Teinolophos* (about 115M years ago) was a "crown group" (advanced and relatively specialised) monotreme, so the basal (most primitive) monotremes must have appeared considerably earlier; that some alleged Australosphenids were also "crown group" monotremes (e.g. *Steropodon*); and that other alleged Australosphenids (e.g. *Ausktribosphenos*, *Bishops*, *Ambondro*, *Asfaltomylos*) are therefore more closely related to and possibly members of the Therian mammals.

Monotremes

The earliest known monotreme is *Teinolophos*, which lived about 123M years ago in Australia. Recent (2007, published 2008) analysis suggest that it was not a basal (primitive, ancestral) monotreme but a full-fledged platypus, and therefore that the platypus and echidna lineages diverged considerably earlier and that basal monotremes were even earlier.

A more recent study (2009), however, has suggested that while Teinolophis was a type of platypus, it also was a basal monotreme and predated the radiation of modern monotremes. The semi-aquatic lifestyle of platypuses prevented them from being outcompeted by the marsupials that migrated to Australia millions of years ago, since joeys need to keep attached to their mothers and would drown if their mothers ventured into water. Genetic evidence has determined that echidnas diverged from the platypus lineage as recently as 19-48M when they made their transition from semi-aquatic to terrestrial lifestyle.

Monotremes have some features that may be inherited from the original amniotes:

- they use the same orifice to urinate, defecate and reproduce ("monotreme" means "one hole") — as lizards and birds also do.
- they lay eggs that are leathery and uncalcified, like those of lizards, turtles and crocodilians.

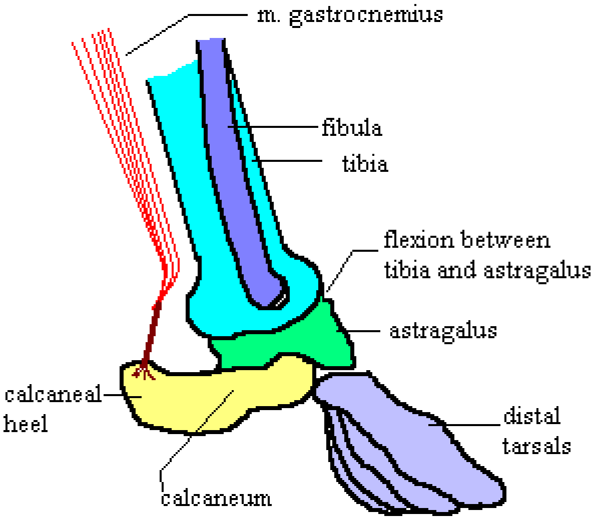
Unlike in other mammals, female monotremes do not have nipples and feed their young by "sweating" milk from patches on their bellies.

Of course these features are not visible in fossils, and the main characteristics from paleontologists' point of view are:

- a slender dentary bone in which the coronoid process is small or non-existent.
- the external opening of the ear lies at the posterior base of the jaw.
- the jugal bone is small or non-existent.
- a primitive pectoral girdle with strong ventral elements: coracoids, clavicles and interclavicle. Note: therian mammals have no interclavicle.
- sprawling or semi-sprawling forelimbs.

Theria

Theria ("beasts") is a name applied to the hypothetical group from which both metatheria (which include marsupials) and eutheria (which include placentals) descended. Although no convincing fossils of basal therians have been found (just a few teeth and jaw fragments), metatheria and eutheria share some features that one would expect to have been inherited from a common ancestral group:



Therian form of crurotarsal ankle. Adapted with permission from Palaeos

- no interclavicle.
- coracoid bones non-existent or fused with the shoulder blades to form coracoid processes.
- a type of crurotarsal ankle joint in which: the main joint is between the tibia and astragalus; the calcaneum has no contact with the tibia but forms a heel to which muscles can attach. (The other well-known type of crurotarsal ankle is seen in crocodilians and works differently — most of the bending at the ankle is between the calcaneum and astragalus).
- tribosphenic molars.

Tribosphenic molars have been found in fossils from Madagascar, which indicates that therian mammals are at least 167 million years old.

Metatheria

The living Metatheria are all marsupials ("animals with pouches"). A few fossil genera such as the Mongolian late Cretaceous *Asiatherium* may be marsupials or members of some other metatherian group(s).

The oldest known marsupial is *Sinodelphys*, found in 125M-year old early Cretaceous shale in China's northeastern Liaoning Province. The fossil is nearly complete and includes tufts of fur and imprints of soft tissues.

Didelphimorphia (common opossums of the Western Hemisphere) first appeared in the late Cretaceous and still have living representatives, probably because they are mostly semi-arboreal unspecialized omnivores.

The best-known feature of marsupials is their method of reproduction:

- The mother develops a kind of yolk sack in her womb that delivers nutrients to the embryo. Embryos of bandicoots, koalas and wombats additionally form placenta-like organs that connect them to the uterine wall, although the placenta-like organs are smaller than in placental mammals and it is not certain that they transfer nutrients from the mother to the embryo.
- Pregnancy is very short, typically 4 to 5 weeks. The embryo is born at a very young age of development, and is usually less than 2 in (5.1 cm) long at birth. It has been suggested that the short pregnancy is necessary to reduce the risk that the mother's immune system will attack the embryo.
- The newborn marsupial uses its forelimbs (with relatively strong hands) to climb to a nipple, which is usually in a pouch on the mother's belly. The mother feeds the baby by contracting muscles over her mammary glands, as the baby is too weak to suck. The newborn marsupial's need to use its forelimbs in climbing to the nipple has prevented the forelimbs from evolving into paddles or wings and has therefore prevented the appearance of aquatic or truly flying marsupials (although there are several marsupial gliders).

Palate of thylacine, showing one of the paired palatal fenestrae (top left), which are a signature feature of marsupials.

Although some marsupials look very like some placentals (the thylacine or "marsupial wolf" is a good example), marsupial skeletons have some features that distinguish them from placentals:

- Some, including the thylacine, have 4 molars. No placentals have more than 3.

- All have a pair of palatal fenestrae, window-like openings on the bottom of the skull (in addition to the smaller nostril openings).

Marsupials also have a pair of marsupial bones (sometimes called "epipubic bones"), which support the pouch in females. But these are not unique to marsupials, since they have been found in fossils of multituberculates, monotremes, and even eutherians — so they are probably a common ancestral feature that disappeared at some point after the ancestry of living placental mammals diverged from that of marsupials. Some researchers think the epipubic bones' original function was to assist locomotion by supporting some of the muscles that pull the thigh forwards.

Eutheria

The living Eutheria ("true beasts") are all placentals. But the earliest known eutherian, *Eomaia*, found in China and dated to 125M years ago, has some features that are more like those of marsupials (the surviving metatherians):

Fossil of *Eomaia* in the Hong Kong Science Museum.

- Epipubic bones extending forwards from the pelvis, which are not found in any modern placental, but are found in all other mammals — non-placental

eutherians, marsupials, monotremes and mammaliformes — and even in the cynodont therapsids that are closest to mammals. Their function is to stiffen the body during locomotion. This stiffening would be harmful in pregnant placentals, whose abdomens need to expand.
- A narrow pelvic outlet, which indicates that the young were very small at birth and therefore pregnancy was short, as in modern marsupials. This suggests that the placenta was a later development.
- 5 incisors in each side of the upper jaw. This number is typical of metatherians, and the maximum number in modern placentals is 3, except for homodonts such as the armadillo. But *Eomaia's* molar to premolar ratio (it has more pre-molars than molars) is typical of eutherians, including placentals, and not normal in marsupials.

Eomaia also has a Meckelian groove, a primitive feature of the lower jaw that is not found in modern placental mammals.

These intermediate features are consistent with molecular phylogenetics estimates that the placentals diversified about 110M years ago, 15M years after the date of the *Eomaia* fossil.

Eomaia also has many features that strongly suggest it was a climber, including several features of the feet and toes; well-developed attachment points for muscles that are used a lot in climbing; and a tail that is twice as long as the rest of the spine.

Placentals' best-known feature is their method of reproduction:

- The embryo attaches itself to the uterus via a large placenta via which the mother supplies food and oxygen and removes waste products.
- Pregnancy is relatively long and the young are fairly well-developed at birth. In some species (especially herbivores living on plains) the young can walk and even run within an hour of birth.

It has been suggested that the evolution of placental reproduction was made possible by retroviruses that:

- make the interface between the placenta and uterus into a syncytium, i.e. a thin layer of cells with a shared external membrane. This allows the passage of oxygen, nutrients and waste products but prevents the passage of blood and other cells, which would cause the mother's immune system to attack the fetus.
- reduce the aggressiveness of the mother's immune system (which is good for the foetus but makes the mother more vulnerable to infections).

From a paleontologist's point of view, eutherians are mainly distinguished by various features of their teeth, ankles and feet.

Expansion of ecological niches in the Mesozoic

There is still some truth in the "small, nocturnal insectivores" stereotype but recent finds, mainly in China, show that some mammaliforms and true mammals were larger and had a variety of lifestyles. For example:

- *Castorocauda*, a member of Docodonta which lived in the middle Jurassic about 164 million years, was about 42.5 cm (16.7 in) long, weighed 500–800 g (18–28 oz), had limbs that were adapted for swimming and digging and teeth adapted for eating fish.
- *Multituberculates*, are allotherians that survived for over 125 million years (from mid Jurassic, about 160M years ago, to early Oligocene, about 35M years ago) are often called the "rodents of the Mesozoic", because they had continuously-growing incisors like those of modern rodents.

Repenomamus sometimes preyed on young dinosaurs

- *Fruitafossor*, from the late Jurassic period about 150 million years ago, was about the size of a chipmunk and its teeth, forelimbs and back suggest that it broke open the nest of social insects to prey on them (probably termites, as ants had not yet appeared).
- *Volaticotherium*, allotherians from the boundary the early Cretaceous about 125M years ago, is the earliest-known gliding mammal and had a gliding membrane that

stretched out between its limbs, rather like that of a modern flying squirrel. This also suggests it was active mainly during the day.
- *Repenomamus*, tricodonts from the early Cretaceous 130 million years ago, was a stocky, badger-like predator that sometimes preyed on young dinosaurs. Two species have been recognized, one more than 1 m (39 in) long and weighing about 12–14 kg (26–31 lb), the other less than 0.5 m (20 in) long and weighing 4–6 kg (8.8–13 lb).

Evolution of major groups of living mammals

There are currently vigorous debates between traditional paleontologists ("fossil-hunters") and molecular phylogeneticists about how and when the true mammals diversified, especially the placentals. Generally the traditional paelontologists date the appearance of a particular group by the earliest known fossil whose features make it likely to be a member of that group, while the molecular phylogeneticists suggest that each lineage diverged earlier (usually in the Cretaceous) and that the earliest members of each group were anatomically very similar to early members of other groups and differed only in their genes. These debates extend to the definition of and relationships between the major groups of placentals — the controversy about Afrotheria is a good example.

Fossil-based family tree of placental mammals

Here is a very simplified version of a typical family tree based on fossils, based on Cladogram of Mammalia - Palaeos. It tries to show the nearest thing there is at present to a consensus view, but some paleontologists have very different views, for example:

- The most common view is that placentals originated in the southern hemisphere, but some paleontologists argue that they first appeared in Laurasia (old supercontinent containing modern Asia, N. America and Europe).
- Paleontologists differ about when the first placentals appeared, with estimates ranging from 20M years before the end of the Cretaceous to just after the end of the Cretaceous. And molecular biologists argue for a much earlier origin.
- Most paleontologists suggest that placentals should be divided into Xenarthra and the rest, but a few think these animals diverged later.

For the sake of brevity and simplicity the diagram omits some extinct groups in order to focus on the ancestry of well-known modern groups of placentals — **X** marks extinct groups. The diagram also shows the following:

- the age of the oldest known fossils in many groups, since one of the major debates between traditional paleontologists and molecular phylogeneticists is about when various groups first became distinct.
- well-known modern members of most groups.

This family tree contains some surprises and puzzles. For example:

- The closest living relatives of cetaceans (whales, dolphins, porpoises) are artiodactyls, hoofed animals, which are almost all pure vegetarians.
- Bats are fairly close relatives of primates.
- The closest living relatives of elephants are the aquatic sirenians, while their next relatives are hyraxes, which look more like well-fed guinea pigs.
- There is little correspondence between the structure of the family (what was descended from what) and the dates of the earliest fossils of each group. For example the earliest fossils of perissodactyls (the living members of which are horses, rhinos and tapirs) date from the late Paleocene but the earliest fossils of their "sister group" the Tubulidentata date from the early Miocene, nearly 50M years later. Paleontologists are fairly confident about the family relationships, which are based on cladistic analyses, and believe that fossils of the ancestors of modern aardvarks have simply not been found yet.

Family tree of placental mammals according to molecular phylogenetics

Molecular phylogenetics uses features of organisms' genes to work out family trees in much the same way as paleontologists do with features of fossils — if two organisms' genes are more similar to each other than to those of a third organism, the two organisms are more closely related to each other than to the third.

Molecular phylogeneticists have proposed a family tree that is very different from the one with which paleontologists are familiar. Like paleontologists, molecular phylogeneticists have different ideas about various details, but here is a typical family tree according to molecular phylogenetics: Note that the diagram shown here omits extinct groups, as one cannot extract DNA from fossils.

Here are the most significant of the many differences between this family tree and the one familiar to paleontologists:

- The top-level division is between Atlantogenata and Boreoeutheria, instead of between Xenarthra and the rest. But some molecular phylogeneticists have proposed a 3-way top-level split between Xenarthra, Afrotheria and Boreoeutheria.
- Afrotheria contains several groups that are only distantly related according to the paleontologists' version: Afroinsectiphilia ("African insectivores"), Tubulidentata (aardvarks, which paleontologists regard as much closer to odd-toed ungulates than to other members of Afrotheria), Macroscelidea (elephant shrews, usually regarded as close to rabbits and rodents). The only members of Afrotheria that paleontologists would regard as closely related are Hyracoidea (hyraxes), Proboscidea (elephants) and Sirenia (manatees, dugongs).
- Insectivores are split into 3 groups: one is part of Afrotheria and the other two are distinct sub-groups within Boreoeutheria.
- Bats are closer to Carnivora and odd-toed ungulates than to primates and Dermoptera (colugos).

- Perissodactyla (odd-toed ungulates) are closer to Carnivora and bats than to Artiodactyla (even-toed ungulates).

The grouping together of the Afrotheria has some geological justification. All surviving members of the Afrotheria originate from South American or (mainly) African lineages — even the Indian elephant, which diverged from an African lineage about 7.6 million years ago. As Pangaea broke up Africa and South America separated from the other continents less than 150M years ago, and from each other between 100M and 80M years ago. The earliest known eutherian mammal is *Eomaia*, from about 125M years ago. So it would not be surprising if the earliest eutherian immigrants into Africa and South America were isolated there and radiated into all the available ecological niches.

Nevertheless these proposals have been controversial. Paleontologists naturally insist that fossil evidence must take priority over deductions from samples of the DNA of modern animals. More surprisingly, these new family trees have been criticised by other molecular phylogeneticists, sometimes quite harshly:

- Mitochondrial DNA's mutation rate in mammals varies from region to region — some parts hardly ever change and some change extremely quickly and even show large variations between individuals within the same species.
- Mammalian mitochondrial DNA mutates so fast that it causes a problem called "saturation", where random noise drowns out any information that may be present. If a particular piece of mitochondrial DNA mutates randomly every few million years, it will have changed several times in the 60 to 75M years since the major groups of placental mammals diverged.

Timing of placental evolution

Recent molecular phylogenetic studies suggest that most placental orders diverged about 100M to 85M years ago, but that modern families first appeared in the late Eocene and early Miocene.

Some paleontologists object that no placental fossils have been found from before the end of the Cretaceous — for example *Maelestes gobiensis*, from about 75M years ago, is a eutherian but not a true placental. Many Cretaceous fossil sites contain well-preserved lizards, salamanders, birds, and mammals, but not the modern forms of mammals. It is likely that they simply did not exist, and that the molecular clock runs fast during major evolutionary radiations. On the other hand there is fossil evidence from 85 million years ago of hoofed animals that may be ancestors of modern ungulates.

Fossils of the earliest members of most modern groups date from the Paleocene, a few date from later and very few from the Cretaceous, before the extinction of the dinosaurs. But some paleontologists, influenced by molecular phylogenetic studies, have used statistical methods to extrapolate *backwards* from fossils of members of modern groups and concluded that primates arose in the late Cretaceous. However statistical studies of the fossil record confirm that mammals were restricted in size and diversity right to the end of the Cretaceous, and rapidly grew in size and diversity during the Early Paleocene.

Evolution of mammalian features

Jaws and middle ears

Hadrocodium, whose fossils date from the early Jurassic, provides the first clear evidence of fully mammalian jaw joints and middle ears, in which the jaw joint is formed by the dentary and squamosal bones while the articular and quadrate move to the middle ear, where they are known as the incus and malleus. Curiously it is usually classified as a member of the mammaliformes rather than a as a true mammal.

One analysis of the monotreme *Teinolophos* suggested that this animal had a pre-mammalian jaw joint formed by the angular and quadrate bones and that the typical mammalian middle ear evolved twice independently, in monotremes and in therian mammals, but this idea has been disputed. In fact 2 of the suggestion's authors co-authored a later paper that reinterpreted the same features as evidence that *Teinolophos* was a full-fledged platypus, which means it would have had a mammalian jaw joint and middle ear.

Milk production (lactation)

It has been suggested that lactation's original function was to keep eggs moist. Much of the argument is based on monotremes (egg-laying mammals):

- Monotremes do not have nipples but secrete milk from a hairy patch on their bellies.
- During incubation, monotremes' eggs are covered in a sticky substance whose origin is not known. Before the eggs are laid, their shells have only three layers. Afterwards a fourth layer appears, and its composition is different from that of the original three. The sticky substance and the fourth layer may be produced by the mammary glands.
- If so, that may explain why the patches from which monotremes secrete milk are hairy — it is easier to spread moisture and other substances over the egg from a broad, hairy area than from a small, bare nipple.

Hair and fur

The first clear evidence of hair or fur is in fossils of *Castorocauda*, from 164M years ago in the mid Jurassic.

From 1955 onwards some scientists have interpreted the foramina (passages) in the maxillae (upper jaws) and premaxillae (small bones in front of the maxillae) of cynodonts as channels that supplied blood vessels and nerves to vibrissae (whiskers), and suggested that this was evidence of hair or fur. But foramina do not necessarily show that an animal had vibrissae — for example the modern lizard *Tupinambis* has foramina that are almost identical to those found in the non-mammalian cynodont Thrinaxodon.

Erect limbs

The evolution of erect limbs in mammals is incomplete — living and fossil monotremes have sprawling limbs. In fact some scientists think that the parasagittal (non-sprawling) limb posture is a synapomorphy (distinguishing characteristic) of the Boreosphenida, a group that contains the Theria and therefore includes the last common ancestor of modern marsupials and placentals — and therefore that all earlier mammals had sprawling limbs.

Sinodelphys (the earliest known marsupial) and *Eomaia* (the earliest known eutherian) lived about 125M years ago, so erect limbs must have evolved before then.

Warm-bloodedness

"Warm-bloodedness" is a complex and rather ambiguous term, because it includes some or all of the following:

- **Endothermy**, i.e. the ability to generate heat internally rather than via behaviors such as basking or muscular activity.
- **Homeothermy**, i.e. maintaining a fairly constant body temperature.
- **Tachymetabolism**, i.e. maintaining a high metabolic rate, particularly when at rest. This requires a fairly high and stable body temperature, since biochemical processes run about half as fast if an animal's temperature drops by 10°C; most enzymes have an optimum operating temperature and their efficiency drops rapidly outside the preferred range.

Since scientists cannot know much about the internal mechanisms of extinct creatures, most discussion focuses on homeothermy and tachymetabolism.

Modern monotremes have a lower body temperature and more variable metabolic rate than marsupials and placentals. So the main question is when a monotreme-like metabolism evolved in mammals. The evidence found so far suggests Triassic cynodonts may have had fairly high metabolic rates, but is not conclusive.

Respiratory turbinates

Modern mammals have respiratory turbinates, convoluted structures of thin bone in the nasal cavity. These are lined with mucous membranes that warm and moisten inhaled air and extract heat and moisture from exhaled air. An animal with respiratory turbinates can maintain a high rate of breathing without the danger of drying its lungs out, and therefore may have a fast metabolism. Unfortunately these bones are very delicate and therefore have not yet been found in fossils. But rudimentary ridges like those that support respiratory turbinates have been found in Triassic therapsids such as *Thrinaxodon* and *Diademodon*, which suggests that they may have had fairly high metabolic rates.

Bony secondary palate

Mammals have a secondary bony palate, which separates the respiratory passage from the mouth, allowing them to eat and breathe at the same time. Secondary bony palates have been found in the more advanced cynodonts and have been used as evidence of high metabolic rates. But some cold-blooded vertebrates have secondary bony palates (crocodilians and some lizards), while birds, which are warm-blooded, do not have them.

Diaphragm

A muscular diaphragm helps mammals to breathe, especially during strenuous activity. For a diaphragm to work, the ribs must not restrict the abdomen, so that expansion of the chest can be compensated for by reduction in the volume of the abdomen and *vice versa*. The advanced cynodonts have very mammal-like rib cages, with greatly reduced lumbar ribs. This suggests that these animals had diaphragms, were capable of strenuous activity for fairly long periods and therefore had high metabolic rates. On the other hand these mammal-like rib cages may have evolved to increase agility. But the movement of even advanced therapsids was "like a wheelbarrow", with the hindlimbs providing all the thrust while the forelimbs only steered the animal, in other words advanced therapsids were not as agile as either modern mammals or the early dinosaurs. So the idea that the main function of these mammal-like rib cages was to increase agility is doubtful.

Limb posture

The therapsids had sprawling forelimbs and semi-erect hindlimbs. This suggests that Carrier's constraint would have made it rather difficult for them to move and breathe at the same time, but not as difficult as it is for animals such as lizards, which have completely sprawling limbs. But cynodonts (advanced therapsids) had costal plates that stiffened the rib cage and therefore may have reduced sideways flexing of the trunk while moving, which would have made it a little easier for them to breathe while moving . These facts suggest that advanced therapsids were significantly less active than modern mammals of similar size and therefore may have had slower metabolisms.

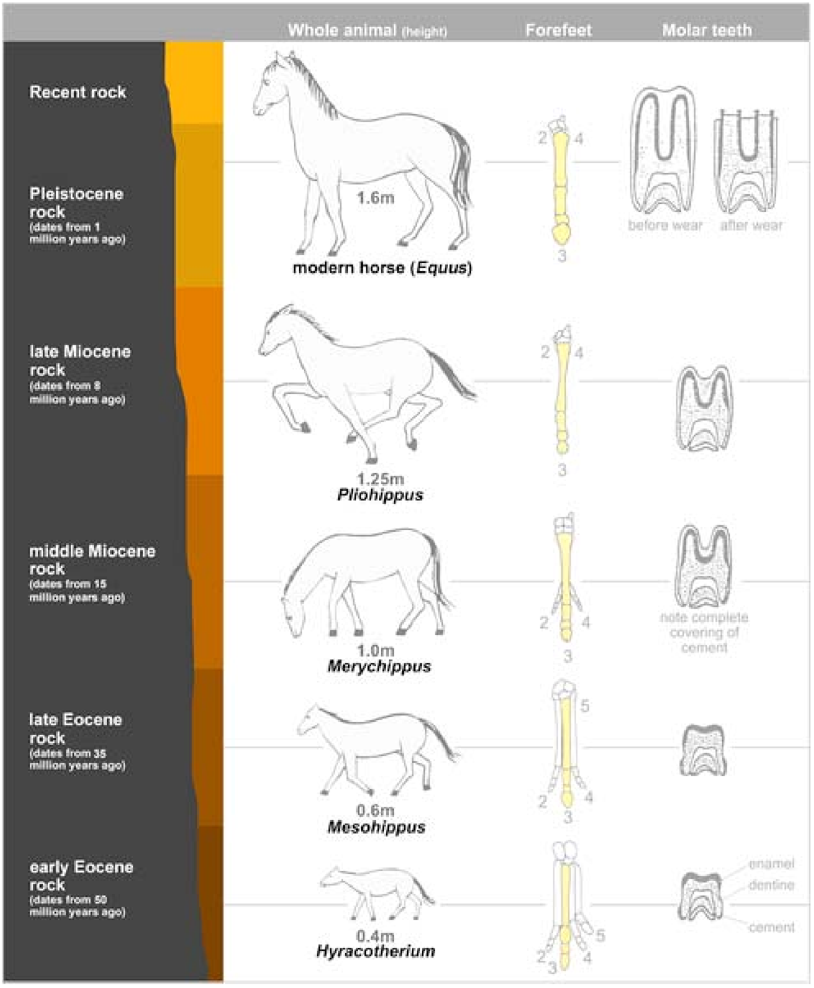
Insulation (hair and fur)

Insulation is the "cheapest" way to maintain a fairly constant body temperature, without consuming energy to produce more body heat. Therefore, possession of hair or fur would be good evidence of homeothermy but would not be such strong evidence of a high metabolic rate.

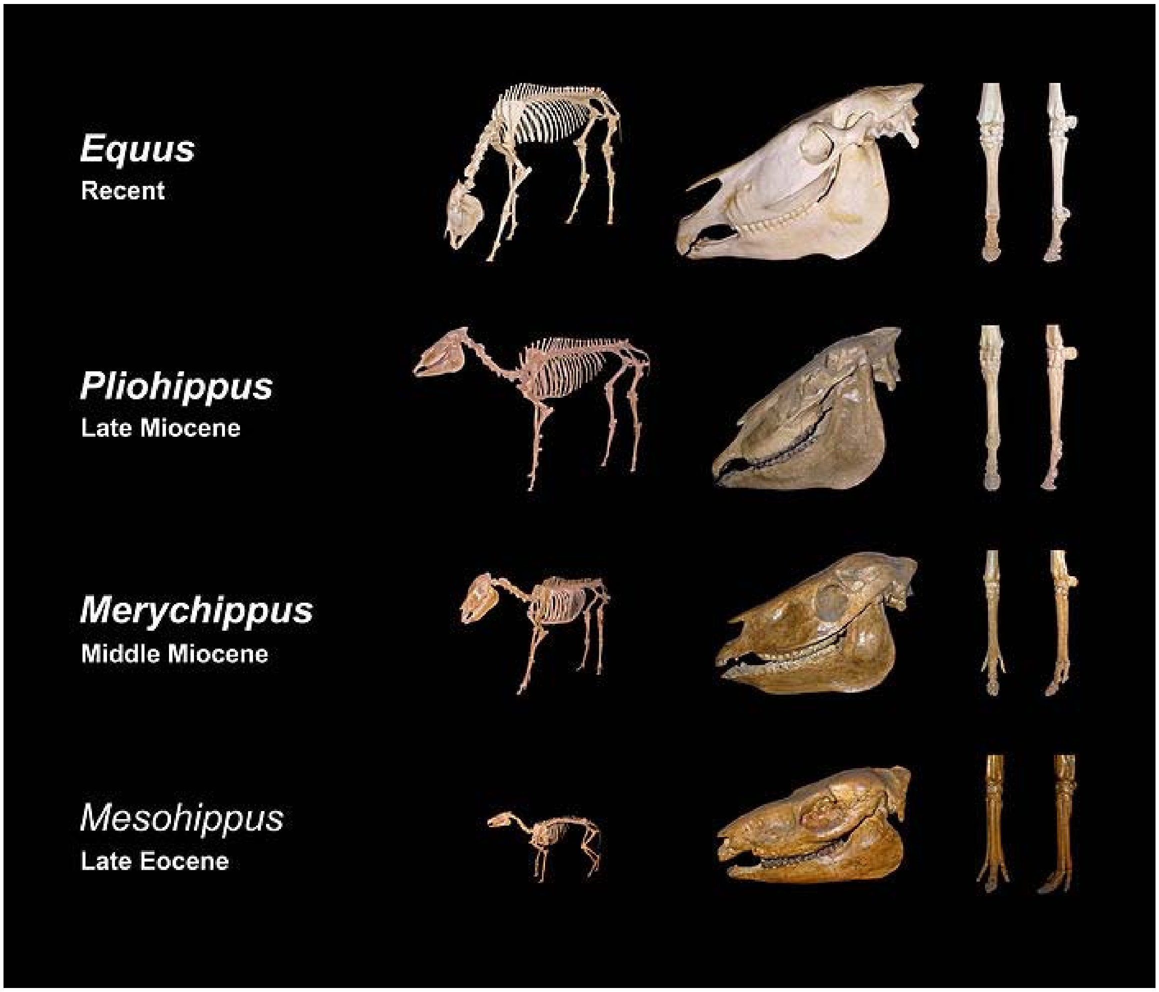
The first clear evidence of hair or fur is in fossils of *Castorocauda*, from 164M years ago in the mid Jurassic; arguments that advanced therapsids had hair are unconvincing.

Chapter- 5

Evolution of the Horse



This image shows a representative sequence but should not be construed to represent a "straight-line" evolution of the horse. Reconstruction, left forefoot skeleton (third digit emphasized yellow) and longitudinal section of molars of selected prehistoric horses



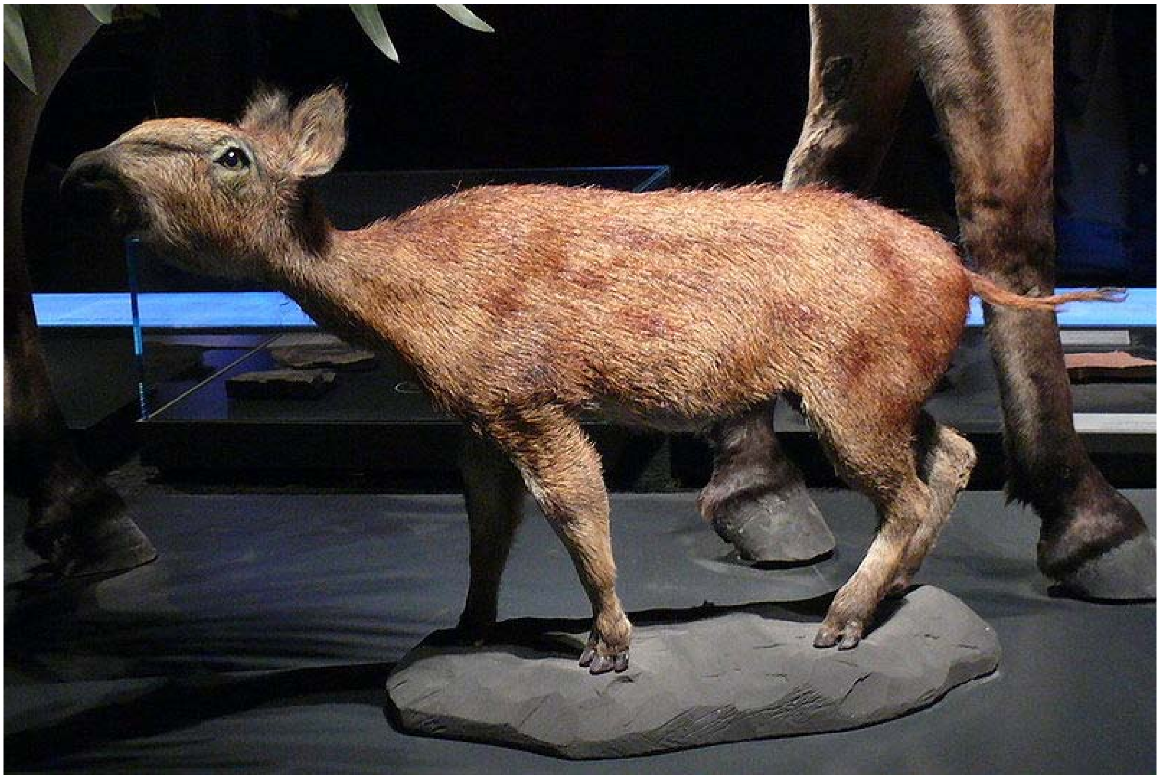
Skeletal evolution

The **evolution of the horse** pertains to the phylogenetic ancestry of the modern horse from the fox-sized, forest-dwelling *Hyracotherium* over geologic time scales. Paleozoologists have been able to piece together a more complete picture of the modern horse's evolutionary lineage than that of any other animal.

The horse belongs to an order known as Perissodactyla, or "odd-toed ungulates", which all share hoofed feet and an odd number of toes on each foot, as well as mobile upper lips and a similar tooth structure. This means that horses share a common ancestry with tapirs and rhinoceroses. The perissodactyls originally arose in the late Paleocene, less than 10 million years after the Cretaceous-Tertiary extinction event. This group of animals appears to have been originally specialized for life in tropical forests, but whereas tapirs and, to some extent, rhinoceroses, retained their jungle specializations, modern horses are adapted to life on drier land in the much-harsher climatic conditions of the steppes. Other species of *Equus* are adapted to a variety of intermediate conditions.

The early ancestors of the modern horse walked on several spread-out toes, an accommodation to life spent walking on the soft, moist grounds of primeval forests. As grass species began to appear and flourish, the equids' diets shifted from foliage to grasses, leading to larger and more durable teeth. At the same time, as the steppes began to appear, the horse's predecessors needed to be capable of greater speeds to outrun predators. This was attained through the lengthening of limbs and the lifting of some toes from the ground in such a way that the weight of the body was gradually placed on one of the longest toes, the third.

History of research



Restoration of *Eurohippus parvulus*, Museum für Naturkunde, Berlin

Horses were absent from the Americas until the Spanish brought domestic horses from Europe, beginning in 1493, and escaped horses quickly established large wild herds. The early naturalist Buffon suggested in the 1760s that this was an indication of inferiority of fauna in the New World, then later reconsidered this idea. William Clark's 1807 expedition to Big Bone Lick found "leg and foot bones of the Horses" which were included with other fossils sent to Thomas Jefferson and evaluated by the anatomist Caspar Wistar, but neither commented on the significance of this find.

The first equid fossil was found in the gypsum quarries in Montmartre, Paris in the 1820s. The tooth was sent to the Paris Conservatory, where it was identified by Georges Cuvier who identified it as a browsing equine related to the tapir. His sketch of the entire animal matched later skeletons found at the site.

During the *Beagle* survey expedition the young naturalist Charles Darwin had remarkable success with fossil hunting in Patagonia. On 10 October 1833 at Santa Fe, Argentina, he was "filled with astonishment" when he found a horse's tooth in the same stratum as fossil giant armadillos, and wondered if it might have been washed down from a later layer, but concluded that this was "not very probable". After the expedition returned in 1836, the anatomist Richard Owen confirmed the tooth was from an extinct species which he subsequently named *Equus curvidens*, and remarked that "This evidence of the former existence of a genus, which, as regards South America, had become extinct, and has a second time been introduced into that Continent, is not one of the least interesting fruits of Mr. Darwin's palæontological discoveries."

In 1848 a study *On the fossil horses of America* by Joseph Leidy systematically examined Pleistocene horse fossils from various collections, including that of the Academy of Natural Sciences and concluded at least two ancient horse species had existed in North America: *Equus curvidens* and another which he named *Equus americanus*. A decade later, however, he found the latter name had already been taken and renamed it *Equus complicatus*. In the same year, he visited Europe and was introduced by Owen to Darwin.

The original sequence of species believed to have evolved into the horse was based on fossils discovered in North America in the 1870s by paleontologist Othniel Charles Marsh. The sequence, from *Hyracotherium* (popularly called ***Eohippus***) to the modern horse (*Equus*), was popularized by Thomas Huxley and became one of the most widely-known examples of a clear evolutionary progression. The horse's evolutionary lineage became a common feature of biology textbooks, and the sequence of transitional fossils was assembled by the American Museum of Natural History into an exhibit which emphasized the gradual, "straight-line" evolution of the horse.

Since then, as the number of equid fossils has increased, the actual evolutionary progression from *Hyracotherium* to *Equus* has been discovered to be much more complex and multi-branched than was initially supposed. The straight, direct progression from the former to the latter has been replaced by a more elaborate model with numerous branches in different directions, of which the modern horse is only one of many. It was first recognized by George Gaylord Simpson in 1951 that the modern horse was not the "goal" of the entire lineage of equids, it is simply the only genus of the many horse lineages that has survived.

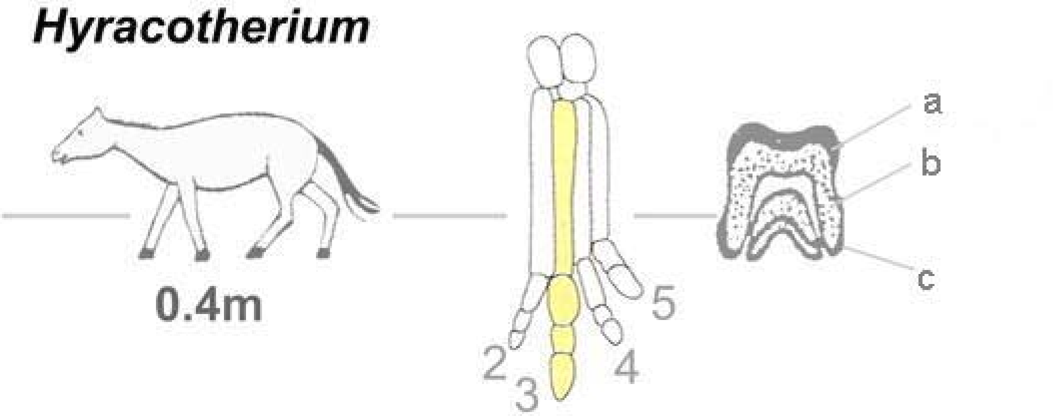
Detailed fossil information on the rate and distribution of new equid species has also revealed the progression between species was not as smooth and consistent as was once believed. Although some transitions, such as that of *Dinohippus* to *Equus*, were indeed gradual progressions, a number of others, such as that of *Epihippus* to *Mesohippus*, were relatively abrupt and sudden in geologic time, taking place over only a few million years. Both anagenesis (gradual change in an entire population's gene frequency) and cladogenesis (a population "splitting" into two distinct evolutionary branches) occurred, and many species coexisted with "ancestor" species at various times. The change in equids' traits was also not always a "straight line" from *Hyracotherium* to *Equus*: some traits reversed themselves at various points in the evolution of new equid species, such as size and the presence of facial *fossae*, and it is only in retrospect that certain evolutionary trends can be recognized.

Eocene and Oligocene: early equids

Hyracotherium

The earliest animal to bear recognizably horse-like anatomy was the *Hyracotherium* ("hyrax-like beast"). Its scientific name is derived from initial confusion over early partial fossils' relationship with living species: Richard Owen likened early *Hyracotherium* fossils "to a hare in one passage and to something between a hog and a hyrax in another". A later name for the *Hyracotherium*, "eohippus" ("dawn horse"), is also popular, though the earlier name takes precedence due to scientific naming conventions.

Hyracotherium lived in the Ypresian (early Eocene), about 52 mya (million years ago). It was an animal approximately the size of a fox (250–450 mm in height), with a relatively short head and neck and a springy, arched back. It had 44 low-crowned teeth, in the typical arrangement of an omnivorous, browsing mammal: 3 incisors, 1 canine, 4 premolars, and 3 molars on each side of the jaw. Its molars were uneven, dull, and bumpy, and used primarily for grinding foliage. The cusps of the molars were slightly connected in low crests. The *Hyracotherium* browsed on soft foliage and fruit, probably scampering between thickets in the mode of a modern muntjac; the *Hyracotherium* had a small brain, and possessed especially small frontal lobes.



Hyracotherium, with left forefoot (third metacarpal colored) and tooth (a enamel; b dentin; c cement) detailed.

Its limbs were decently long relative to its body, already showing the beginnings of adaptations for running. However, all of the major leg bones were unfused, leaving the legs flexible and rotatable. Its wrist and hock joints were low to the ground. The forelimbs had developed five toes, out of which only four were equipped with a small proto-hoof; the large fifth "toe-thumb" was off the ground. The hind limbs had three out of the five toes equipped with small hooves, while the vestigial first and fifth toes did not touch the ground. Its feet were padded, much like a dog's, but with the small hooves on each toe in place of claws.

For a span of about 20 million years, the *Hyracotherium* thrived with few significant evolutionary changes. The most significant change was in the teeth, which began to adapt to the changing diet of *Hyracotheria*, as these early Equidae shifted from a mixed diet of fruits and foliage to one focused increasingly on browsing foods. During the Eocene, a *Hyracotherium* species (most likely *Hyracotherium vassacciense*) branched out into various new types of Equidae. Thousands of complete, fossilized skeletons of these animals have been found in the Eocene layers of North American strata, mainly in the Wind River basin in Wyoming. Similar fossils have also been discovered in Europe, such as *Propalaeotherium* (which is not considered ancestral to the modern horse).

Orohippus

Approximately 50 million years ago, in the early-to-middle Eocene, *Hyracotherium* smoothly transitioned into *Orohippus* over a gradual series of changes. Although its name means "mountain horse", *Orohippus* was not a true horse and did not live in the mountains. It resembled *Hyracotherium* in size, but had a slimmer body, an elongated head, slimmer forelimbs, and longer hind legs, all of which are characteristics of a good jumper. Although *Orohippus* was still pad-footed, the vestigial outer toes of *Hyracotherium* were not present in the *Orohippus*; there were four toes on each forelimb, and three on each hind leg.

The most dramatic change between *Hyracotherium* and *Orohippus* was in the teeth: the first of the premolar teeth were dwarfed, the last premolar shifted in shape and function into a molar, and the crests on the teeth became more pronounced. Both of these factors gave the teeth of *Orohippus* greater grinding ability, suggesting that *Orohippus* ate tougher plant material.

Epihippus

In the mid-Eocene, about 47 million years ago, *Epihippus*, a genus which continued the evolutionary trend of increasingly efficient grinding teeth, evolved from *Orohippus*. *Epihippus* had five grinding, low-crowned cheek teeth with well-formed crests. A late species of *Epihippus*, sometimes referred to as *Duchesnehippus intermedius*, had teeth similar to Oligocene equids, although slightly less developed. Whether *Duchesnehippus* was a subgenus of *Epihippus* or a distinct genus is disputed.

Mesohippus

In the late Eocene and the early stages of the Oligocene epoch (32–24 mya), the climate of North America became drier, and the earliest grasses began to evolve. The forests were yielding to flatlands, home to grasses and various kinds of brush. In a few areas these plains were covered in sand, creating the type of environment resembling the present-day prairies.

In response to the changing environment, the then-living species of Equidae also began to change. In the late Eocene, they began developing tougher teeth and becoming slightly larger and leggier, allowing for faster running speeds in open areas, and thus for evading predators in non-wooded areas. About 40 mya, *Mesohippus* ("middle horse") suddenly developed in response to strong new selective pressures to adapt, beginning with the species *Mesohippus celer* and soon followed by *Mesohippus westoni*.

In the early Oligocene, *Mesohippus* was one of the more widespread mammals in North America. It walked on three toes on each of its front and hind feet (the first and fifth toes remained, but were small and not used in walking). The third toe was stronger than the outer ones, and thus more weighted; the fourth front toe was diminished to a vestigial nub. Judging by its longer and slimmer limbs, *Mesohippus* was an agile animal.

Mesohippus was slightly larger than *Epihippus*, about 610 mm (24") at the shoulder. Its back was less arched, and its face, snout, and neck were somewhat longer. It had significantly larger cerebral hemispheres, and had a small, shallow depression on its skull called a *fossa*, which in modern horses is quite detailed. The fossa serves as a useful marker for identifying an equine fossil's species. *Mesohippus* had six grinding "cheek teeth", with a single premolar in front—a trait all descendant Equidae would retain. *Mesohippus* also had the sharp tooth crests of *Epihippus*, improving its ability to grind down tough vegetation.

Miohippus

Around 36 million years ago, soon after the development of *Mesohippus*, *Miohippus* ("lesser horse") emerged, the earliest species being *Miohippus assiniboiensis*. Like *Mesohippus*, *Miohippus*'s evolution was relatively abrupt, though a few transitional fossils linking the two genera have been found. It was once believed that *Mesohippus* had anagenetically evolved into *Miohippus* by a gradual series of progressions, but new evidence has shown that *Miohippus*'s evolution was cladogenetic: a *Miohippus* population split off from the main *Mesohippus* genus, coexisted with *Mesohippus* for around 4 million years, and then over time came to replace *Mesohippus*.

Miohippus was significantly larger than its predecessors, and its ankle joints had subtly changed. Its facial fossa was larger and deeper, and it also began to show a variable extra crest in its upper cheek teeth, a trait that became a characteristic feature of equine teeth.

Miohippus ushered in a major new period of diversification in Equidae. While *Mesohippus* died out in the mid-Oligocene, *Miohippus* continued to thrive, and in the early Miocene (24–5.3 mya), it began to rapidly diversify and speciate. It branched out into two major groups, one of which adjusted to the life in forests once again, while the other remained suited to life on the prairies.

Miocene and Pliocene: true equines

Kalobatippus

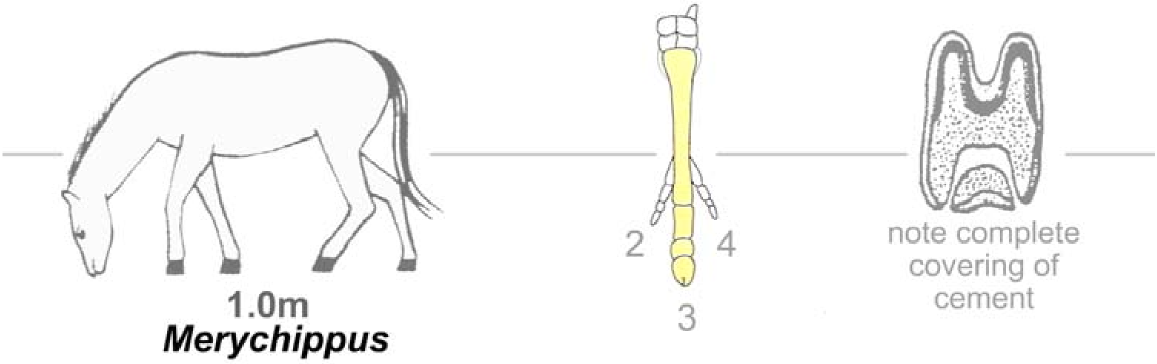
Fossil *Megahippus mckennai*

The forest-suited form was *Kalobatippus* (or *Miohippus intermedius*, depending on whether it was a new genus or species), whose second and fourth front toes were long, well-suited travel on the soft forest floors. *Kalobatippus* probably gave rise to *Anchitherium*, which travelled to Asia via the Bering Strait land bridge, and from there to Europe. In both North America and Eurasia, larger-bodied genera evolved from *Anchitherium*; *Sinohippus* in Eurasia and *Hypohippus* and *Megahippus* in North America. *Hypohippus* became extinct by the late Miocene.

Parahippus

The *Miohippus* population that remained on the steppes is believed to be ancestral to *Parahippus*, a North American animal about the size of a small pony, with a prolonged skull and a facial structure resembling the horses of today. Its third toe was stronger and larger, and carried the main weight of the body. Its four premolars resembled the molar teeth and the first were small and almost nonexistent. The incisive teeth of *Parahippus*, like those of its predecessors, had a crown as humans do; however, the top incisors had a trace of a shallow crease marking the beginning of the core/cup.

Merychippus



Merychippus, an effective grazer and runner.

In the middle of the Miocene epoch, the grazer *Merychippus* flourished. *Merychippus* had wider molars than its predecessors, which are believed to have been used for crunching the hard grasses of the steppes. The hind legs, which were relatively short, had side toes equipped with small hooves, but they probably only touched the ground when running. *Merychippus* radiated into at least 19 additional grassland species.

Hipparion

Protohippus simus

Three lineages within Equidae are believed to be descended from the numerous varieties of *Merychippus*: *Hipparion*, *Protohippus* and *Pliohippus*. The most different from *Merychippus* was *Hipparion*. The main difference was in the structure of tooth enamel: in comparison with other Equidae, the inside, or tongue side, had a completely isolated parapet. A complete and well-preserved skeleton of the North American *Hipparion* shows an animal the size of a small pony. They were very slim, rather like antelopes, and were adapted to life on dry prairies. On its slim legs, *Hipparion* had three toes equipped with small hooves, but the side toes did not touch the ground.

In North America, *Hipparion* and its relatives (*Cormohipparion*, *Nannippus*, *Neohipparion*, and *Pseudhipparion*), proliferated into many kinds of equids, at least one of which managed to migrate to Asia and Europe during the Miocene epoch. (European *Hipparion* differs from American *Hipparion* in its smaller body size – the best-known discovery of these fossils was near Athens.)

Pliohippus

Pliohippus pernix

Pliohippus arose from *Callippus* in the middle Miocene, around 12 mya. It was very similar in appearance to *Equus*, though it had two long extra toes on both sides of the hoof, externally barely visible as callused stubs. The long and slim limbs of *Pliohippus* reveal a quick-footed steppe animal.

Until recently, *Pliohippus* was believed to be the ancestor of present-day horses because of its many anatomical similarities. However, though *Pliohippus* was clearly a close relative of *Equus*, its skull had deep facial *fossae*, whereas *Equus* had no *fossae* at all. Additionally, its teeth were strongly curved, unlike the very straight teeth of modern horses. Consequently, it is unlikely to be the ancestor of the modern horse; instead, it is a likely candidate for the ancestor of *Astrohippus*.

Dinohippus

Dinohippus was the most common species of Equidae in North America during the late Pliocene. It was originally thought that *Dinohippus* was monodactyl, but a 1981 fossil find in Nebraska shows that some were tridactyl.

Plesippus

Mounted skeleton of Hagerman Horse (Equus simplicidens)

Plesippus is often considered an intermediate stage between *Dinohippus* and the extant genus, *Equus*.

The famous fossils found near Hagerman, Idaho were originally thought to be a part of the genus *Plesippus*. Hagerman Fossil Beds (Idaho) is a Pliocene site, dating to about 3.5 mya. The fossilized remains were originally called *Plesippus shoshonensis*, but further study by paleontologists determined that fossils represented the oldest remains of the genus *Equus*. Their estimated average weight was 425 kg, roughly the size of an Arabian horse.

At the end of the Pliocene, the climate in North America began to cool significantly and most of the animals were forced to move south. One population of *Plesippus* moved across the Bering land bridge into Eurasia around 2.5 Mya.

Modern horses

Equus

Skull of a giant extinct horse of the genus Equus, E. eisenmannae

The genus *Equus*, which includes all extant equines, is believed to have evolved from *Dinohippus*, via the intermediate form *Plesippus*. One of the oldest species is *Equus simplicidens*, described as zebra-like with a donkey-shaped head. The oldest material to date is ~3.5 million years old from Idaho, USA. The genus appears to have spread quickly into the Old World, with the similarly aged *Equus livenzovensis* documented from western Europe and Russia.

Molecular phylogenies indicate that the most recent common ancestor of all modern equids (members of the genus *Equus*) lived ~5.6 (3.9-7.8) mya. The oldest divergencies are the Asian hemiones (subgenus *E. (Asinus))*, including the Kulan, Onager, and Kiang), followed by the African zebras (subgenera *E. (Dolichohippus)*, and *E. (Hippotigris)*). All other modern forms including the domesticated horse (and many fossil Pliocene and Pleistocene forms) belong to the subgenus *E. (Equus)* which diverged ~4.8 (3.2-6.5) million years ago.

Pleistocene horse fossils have been assigned to a multitude of species, with over 50 species of equines described from the Pleistocene of North America alone, although the taxonomic validity of most of these has been called into question. Recent genetic work on fossils has found evidence for only three genetically divergent equid lineages in Pleistocene North and South America. These results suggest that all North American fossils of caballine-type horses (which also include the domesticated horse and Przewalski's Horse of Europe and Asia), as well as South American fossils traditionally placed in the subgenus *E. (Amerhippus)* belong to the same species: *E. ferus*. Remains attributed to a variety of species and lumped as New World stilt-legged horses (including *E. francisci*, *E. tau*, *E. quinni* and potentially N. American Pleistocene fossils previously attributed to *E. cf. hemiones*, and *E. (Asinus) cf. kiang*) likely all belong to a second species endemic to N. America, which despite a superficial resemblance to species in the subgenus *E. (Asinus)* (and hence occasionally referred to as North American Ass) is closely related to *E. ferus*. Surprisingly, the third species, endemic to S. America, and traditionally referred to as *Hippidion*, originally believed to be descended from Pliohippus, was shown to be a third species in the genus *Equus*, closely related to the New World stilt-legged horse. The temporal and regional variation in body size and morphological features within each lineage indicates extraordinary intraspecific plasticity. Such environment-driven adaptative changes would explain why the taxonomic diversity of Pleistocene equids has been overestimated on morphoanatomical grounds.

According to these results, it appears that the genus *Equus* evolved from a *Dinohippus*-like ancestor ~4-7 mya. It rapidly spread into the Old World and there diversified into the various species of asses and zebras. A North American lineage of the subgenus *E. (Equus)* evolved into the New World stilt-legged horse (**NWSLH**). Subsequently, populations of this species entered South America as part of the Great American Interchange shortly after the formation of the Isthmus of Panama and evolved into the form currently referred to as "*Hippidion*" ~2.5 million years ago. "*Hippidion*" is thus unrelated to the morphologically similar *Pliohippus*, which presumably went extinct during the Miocene. Both the NWSLH and "*Hippidium*" show adaptations to dry, barren ground, whereas the shortened legs of "*Hippidion*" may have been a response to sloped terrain. In contrast, the geographic origin of the closely related modern *E. ferus* is not resolved. However, genetic results on extant and fossil material of Pleistocene age indicate two clades, potentially subspecies, one of which had a holarctic distribution spanning from Europe through Asia and across North America and would become the founding stock of the modern domesticated horse. The other population appears to have been restricted to N. America. One or more N. American populations of *E. ferus* entered S. America ~1.0-1.5 million years ago, leading to the forms currently known as "*E. (Amerhippus)*", which represent an extinct geographic variant or race of *E. ferus*, however.

Pleistocene extinctions

Digs in western Canada have unearthed clear evidence that horses existed in North America until about 12,000 years ago. However, all Equidae in North America ultimately became extinct. The causes of this extinction (simultaneous with the extinctions of a variety of other American megafauna) have been a matter of debate. Given the suddenness of the event and the fact that these mammals had been flourishing for millions of years previously, something quite unusual must have happened. There are two main hypotheses. The first attributes extinction to climate change. For example, in Alaska, beginning approximately 12,500 years ago, the grasses characteristic of a steppe ecosystem gave way to shrub tundra, which was covered with unpalatable plants. Another hypothesis suggests extinction was linked to overexploitation of naive prey by newly arrived humans. Extinctions were roughly simultaneous with the end of the most recent glacial advance and the appearance of the big-game-hunting Clovis culture. Several studies have indicated that humans probably arrived in Alaska at the same time or shortly before the local extinction of horses. Additionally, it has been proposed that the steppe-tundra vegetation transition in Beringia may have been a consequence, rather than a cause, of the extinction of megafaunal grazers.

In Eurasia, horse fossils began occurring frequently again in archaeological sites in Kazakhstan and the southern Ukraine about 6,000 years ago. From then on, it is probable that domesticated horses as well as the knowledge of capturing, taming, and rearing horses spread relatively quickly, with wild mares from several wild populations being incorporated en route.

Return to the Americas

Horses only returned to the Americas with Christopher Columbus in 1493. These were Iberian horses first brought to Hispaniola and later to Panama, Mexico, Brazil, Peru, Argentina, and, in 1538, Florida. The first horses to return to the main continent were 16 specifically identified horses brought by Hernan Cortes. Subsequent explorers, such as Coronado and De Soto brought ever-larger numbers, some from Spain and other from breeding establishments set up by the Spanish in the Caribbean. Later, as Spanish missions were founded on the mainland, horses would eventually be lost or stolen, and proliferated into large herds of feral horses that became known as mustangs.

The indigenous peoples of the Americas did not have a specific word for horses, and came to refer to them in various languages as a type of dog or deer (in one case, "elk-dog").

Details

Toes

The ancestors of the horse came to walk only on the end of the third toe and both side toes. Skeletal remnants show obvious wear on the back of both sides of metacarpal and metatarsal bones, commonly called the “splint bones”. They are the remnants of the second and the fourth toe. Modern horses retain the splint bones; it is often believed that they are a useless attachment, but they in fact play an important role in supporting the carpal joints (front knee) and even the tarsal joints (hock).

Teeth

Throughout the phylogenetic development, the teeth of the horse underwent significant changes. The type of the original omnivorous teeth with short, "bumpy" molars, with which the prime members of the evolutionary line distinguished themselves, gradually changed into the teeth common to herbivorous mammals. They became long (as much as 100 mm), roughly cubical molars equipped with a flat grinding surface. In conjunction with the teeth, during the horse’s evolution the elongation of the facial part of the skull is apparent, and can also be observed in the backward set eyeholes. In addition, the relatively short neck of the equine ancestors became longer with equal elongation of the legs. Finally, the size of the body grew as well.

Chapter- 6

Human Evolution

Human evolution, or *anthropogeny*, is the origin and evolution of *Homo sapiens* as a distinct species from other hominids, great apes and placental mammals. The study of human evolution uses many scientific disciplines, including physical anthropology, primatology, archaeology, linguistics and genetics.

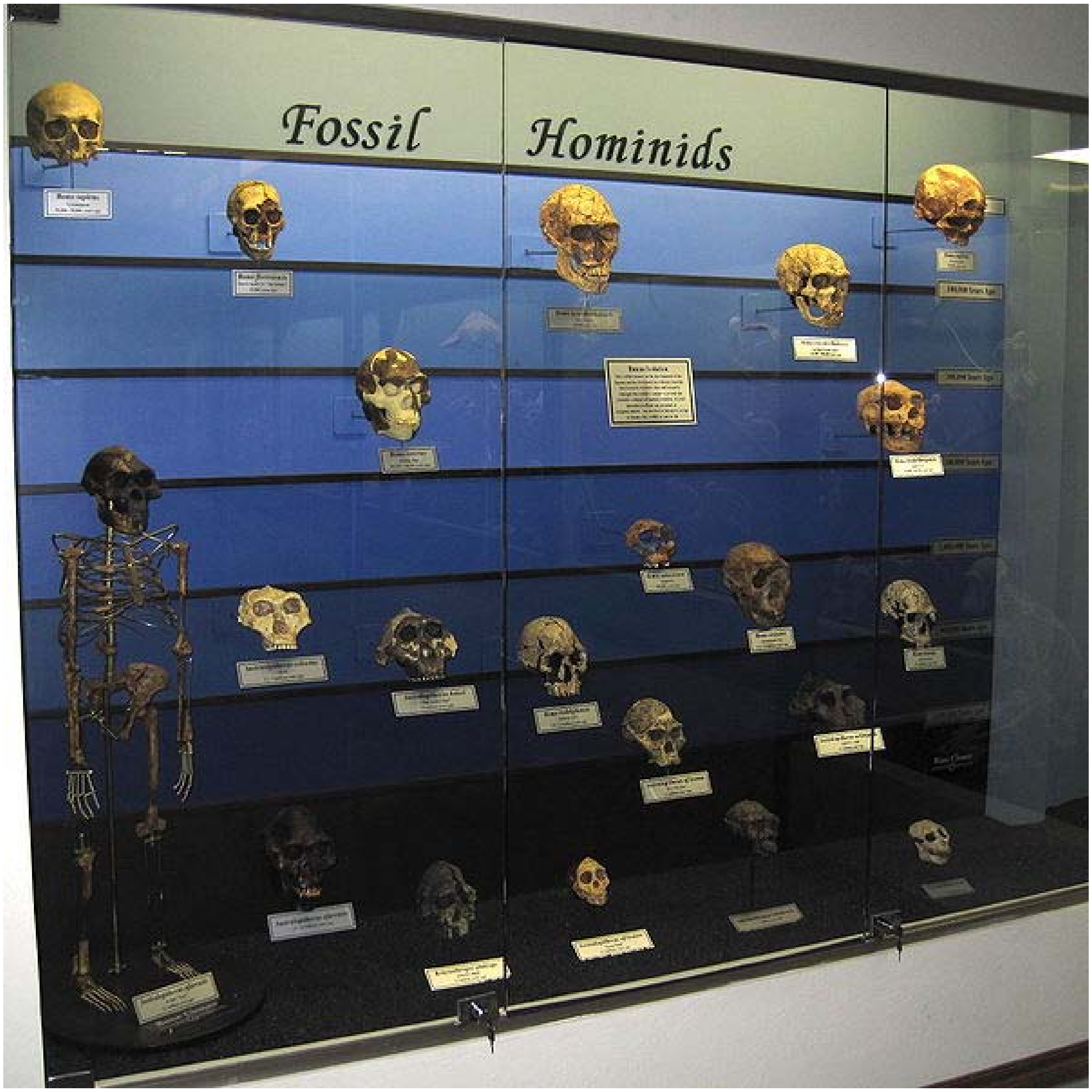
The term "human" in the context of human evolution refers to the genus *Homo*, but studies of human evolution usually include other hominids, such as the Australopithecines, from which the genus *Homo* had diverged by about 2.3 to 2.4 million years ago in Africa. Scientists have estimated that humans branched off from their common ancestor with chimpanzees about 5–7 million years ago. Several species and subspecies of *Homo* evolved and are now extinct. These include *Homo erectus*, which inhabited Asia, and *Homo sapiens neanderthalensis*, which inhabited Europe. Archaic *Homo sapiens* evolved between 400,000 and 250,000 years ago.

The dominant view among scientists concerning the origin of anatomically modern humans is the "Out of Africa" or recent African origin hypothesis, which argues that *Homo sapiens* arose in Africa and migrated out of the continent around 50,000 to 100,000 years ago, replacing populations of *Homo erectus* in Asia and *Homo neanderthalensis* in Europe. Scientists supporting the alternative multiregional hypothesis argue that *Homo sapiens* evolved as geographically separate but interbreeding populations stemming from a worldwide migration of *Homo erectus* out of Africa nearly 2.5 million years ago. This theory has been contradicted by recent evidence, although it has been suggested that non Homo sapiens Neanderthal genomes may have contributed about 4% of non-African heredity, and the recently discovered *Denisova* hominin may have contributed 6% of the genome of Melanesians.

History of ideas

The word *homo*, the name of the biological genus to which humans belong, is Latin for "human". It was chosen originally by Carolus Linnaeus in his classification system. The word "human" is from the Latin *humanus*, the adjectival form of *homo*. The Latin "homo" derives from the Indo-European root, *dhghem*, or "earth".

Carolus Linnaeus and other scientists of his time also considered the great apes to be the closest relatives of humans due to morphological and anatomical similarities. The possibility of linking humans with earlier apes by descent only became clear after 1859 with the publication of Charles Darwin's *On the Origin of Species*. This argued for the idea of the evolution of new species from earlier ones. Darwin's book did not address the question of human evolution, saying only that "Light will be thrown on the origin of man and his history".



Fossil Hominid Evolution Display at The Museum of Osteology, Oklahoma City, USA

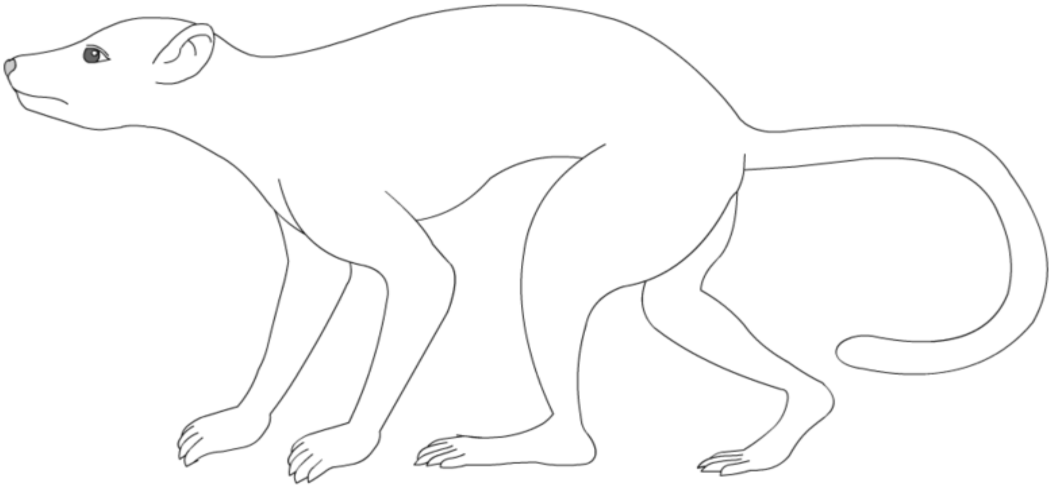
The first debates about the nature of human evolution arose between Thomas Huxley and Richard Owen. Huxley argued for human evolution from apes by illustrating many of the similarities and differences between humans and apes, and did so particularly in his 1863 book *Evidence as to Man's Place in Nature*. However, many of Darwin's early supporters (such as Alfred Russel Wallace and Charles Lyell) did not agree that the origin of the mental capacities and the moral sensibilities of humans could be explained by natural selection. Darwin applied the theory of evolution and sexual selection to humans when he published *The Descent of Man* in 1871.

A major problem was the lack of fossil intermediaries. It was only in the 1920s that such fossils were discovered in Africa. In 1925, Raymond Dart described *Australopithecus africanus*. The type specimen was the Taung Child, an Australopithecine infant discovered in a cave. The child's remains were a remarkably well-preserved tiny skull and an endocranial cast of the individual's brain. Although the brain was small (410 cm^3), its shape was rounded, unlike that of chimpanzees and gorillas, and more like a modern human brain. Also, the specimen showed short canine teeth, and the position of the foramen magnum was evidence of bipedal locomotion. All of these traits convinced Dart that the Taung baby was a bipedal human ancestor, a transitional form between apes and humans.

The classification of humans and their relatives has changed considerably over time. The gracile Australopithecines are now thought to be ancestors of the genus *Homo*, the group to which modern humans belong. Both Australopithecines and *Homo sapiens* are part of the tribe Hominini. Recent data suggests Australopithecines were a diverse group and that *A. africanus* may not be a direct ancestor of modern humans. Reclassification of Australopithecines that originally were split into either gracile or robust varieties has put the latter into a family of its own, *Paranthropus*. Taxonomists place humans, Australopithecines and related species in the same family as other great apes, in the Hominidae.

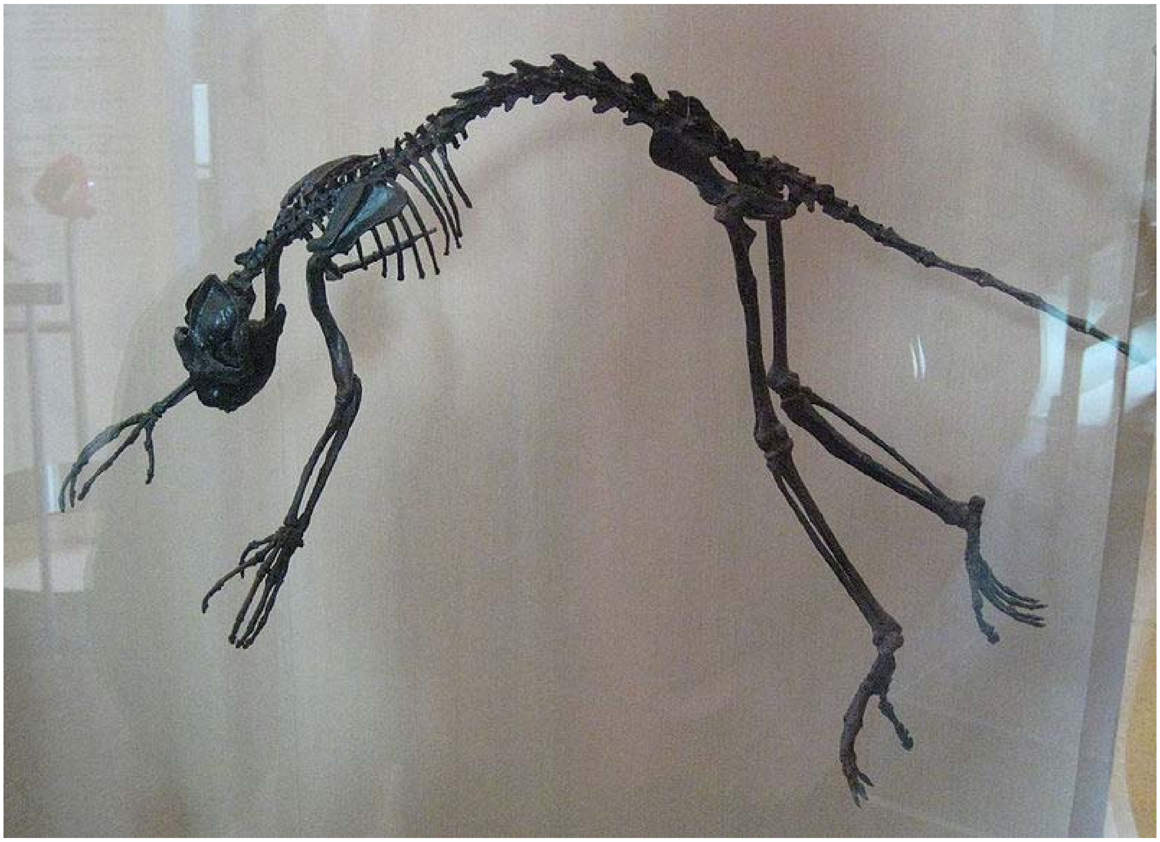
Before Homo

Evolution of the great apes



Plesiadapis

The evolutionary history of the primates can be traced back 65 million years, as one of the oldest of all surviving placental mammal groups. The oldest known primate-like mammal species, the Plesiadapis, come from North America, but they were widespread in Eurasia and Africa during the tropical conditions of the Paleocene and Eocene.



Notharctus

The beginning of modern climates was marked by the formation of the first Antarctic ice in the early Oligocene around 30 million years ago. A primate from this time was *Notharctus*. Fossil evidence found in Germany in the 1980s was determined to be about 16.5 million years old, some 1.5 million years older than similar species from East Africa and challenging the original theory regarding human ancestry originating on the African continent.

David Begun says that these primates flourished in Eurasia and that the lineage leading to the African apes and humans— including Dryopithecus—migrated south from Europe or Western Asia into Africa. The surviving tropical population, which is seen most completely in the upper Eocene and lowermost Oligocene fossil beds of the Fayum depression southwest of Cairo, gave rise to all living primates—lemurs of Madagascar, lorises of Southeast Asia, galagos or "bush babies" of Africa, and the anthropoids; platyrrhines or New World monkeys, and catarrhines or Old World monkeys and the great apes and humans.

The earliest known catarrhine is *Kamoyapithecus* from uppermost Oligocene at Eragaleit in the northern Kenya Rift Valley, dated to 24 million years ago. Its ancestry is generally thought to be species related to *Aegyptopithecus*, *Propliopithecus*, and *Parapithecus* from the Fayum, at around 35 million years ago. In 2010, *Saadanius* was described as a close relative of the last common ancestor of the crown catarrhines, and tentatively dated to 29–28 million years ago, helping to fill an 11-million-year gap in the fossil record.

Reconstructed tailless *Proconsul* skeleton

In the early Miocene, about 22 million years ago, the many kinds of arboreally adapted primitive catarrhines from East Africa suggest a long history of prior diversification. Fossils at 20 million years ago include fragments attributed to *Victoriapithecus*, the earliest Old World Monkey. Among the genera thought to be in the ape lineage leading up to 13 million years ago are *Proconsul*, *Rangwapithecus*, *Dendropithecus*, *Limnopithecus*, *Nacholapithecus*, *Equatorius*, *Nyanzapithecus*, *Afropithecus*, *Heliopithecus*, and *Kenyapithecus*, all from East Africa. The presence of other generalized non-cercopithecids of middle Miocene age from sites far distant—*Otavipithecus* from cave deposits in Namibia, and *Pierolapithecus* and *Dryopithecus* from France, Spain and Austria—is evidence of a wide diversity of forms across Africa and the Mediterranean basin during the relatively warm and equable climatic regimes of the early and middle Miocene. The youngest of the Miocene hominoids, *Oreopithecus*, is from 9 million year old coal beds in Italy.

Molecular evidence indicates that the lineage of gibbons (family Hylobatidae) became distinct from Great Apes between 18 and 12 million years ago, and that of orangutans (subfamily Ponginae) became distinct from the other Great Apes at about 12 million years; there are no fossils that clearly document the ancestry of gibbons, which may have originated in a so-far-unknown South East Asian hominoid population, but fossil proto-orangutans may be represented by *Ramapithecus* from India and *Griphopithecus* from Turkey, dated to around 10 million years ago.

Divergence of the human lineage from other Great Apes

Species close to the last common ancestor of gorillas, chimpanzees and humans may be represented by *Nakalipithecus* fossils found in Kenya and *Ouranopithecus* found in Greece. Molecular evidence suggests that between 8 and 4 million years ago, first the gorillas, and then the chimpanzees (genus *Pan*) split off from the line leading to the humans; human DNA is approximately 98.4% identical to that of chimpanzees when comparing single nucleotide polymorphisms. The fossil record of gorillas and chimpanzees is quite limited. Both poor preservation (rain forest soils tend to be acidic and dissolve bone) and sampling bias probably contribute to this problem.

Other hominines likely adapted to the drier environments outside the equatorial belt, along with antelopes, hyenas, dogs, pigs, elephants, and horses. The equatorial belt contracted after about 8 million years ago. Fossils of these hominans - the species in the human lineage following divergence from the chimpanzees - are relatively well known.

The earliest are *Sahelanthropus tchadensis* (7 Ma) and *Orrorin tugenensis* (6 Ma), followed by:

- *Ardipithecus* (5.5–4.4 Ma), with species *Ar. kadabba* and *Ar. ramidus*;
- *Australopithecus* (4–1.8 Ma), with species *Au. anamensis*, *Au. afarensis*, *Au. africanus*, *Au. bahrelghazali*, *Au. garhi*, and *Au. sediba*;
- *Kenyanthropus* (3–2.7 Ma), with species *Kenyanthropus platyops*;
- *Paranthropus* (3–1.2 Ma), with species *P. aethiopicus*, *P. boisei*, and *P. robustus*;
- *Homo* (2 Ma–present), with species *Homo habilis*, *Homo rudolfensis*, *Homo ergaster*, *Homo georgicus*, *Homo antecessor*, *Homo cepranensis*, *Homo erectus*, *Homo heidelbergensis*, *Homo rhodesiensis*, *Homo neanderthalensis*, *Homo sapiens idaltu*, *Archaic Homo sapiens*, *Homo floresiensis*.

Genus Homo

Homo sapiens is the only extant species of its genus, *Homo*. While some other, extinct, *Homo* species might have been ancestors of *Homo sapiens*, many were likely our "cousins", having speciated away from our ancestral line. There is not yet a consensus as to which of these groups should count as separate species and which as subspecies. In some cases this is due to the dearth of fossils, in other cases it is due to the slight differences used to classify species in the *Homo* genus. The Sahara pump theory (describing an occasionally passable "wet" Sahara Desert) provides an explanation of the early variation in the genus *Homo*.

Based on archaeological and paleontological evidence, it has been possible to infer, to some extent, the ancient dietary practices of various *Homo* species and to study the role of diet in physical and behavioral evolution within *Homo*.

H. habilis and H. gautengensis

Homo habilis lived from about 2.4 to 1.4 Ma. *Homo habilis* evolved in South and East Africa in the late Pliocene or early Pleistocene, 2.5–2 Ma, when it diverged from the Australopithecines. *Homo habilis* had smaller molars and larger brains than the Australopithecines, and made tools from stone and perhaps animal bones. One of the first known hominids, it was nicknamed 'handy man' by its discoverer, Louis Leakey due to its association with stone tools. Some scientists have proposed moving this species out of *Homo* and into *Australopithecus* due to the morphology of its skeleton being more adapted to living on trees rather than to moving on two legs like *Homo sapiens*.

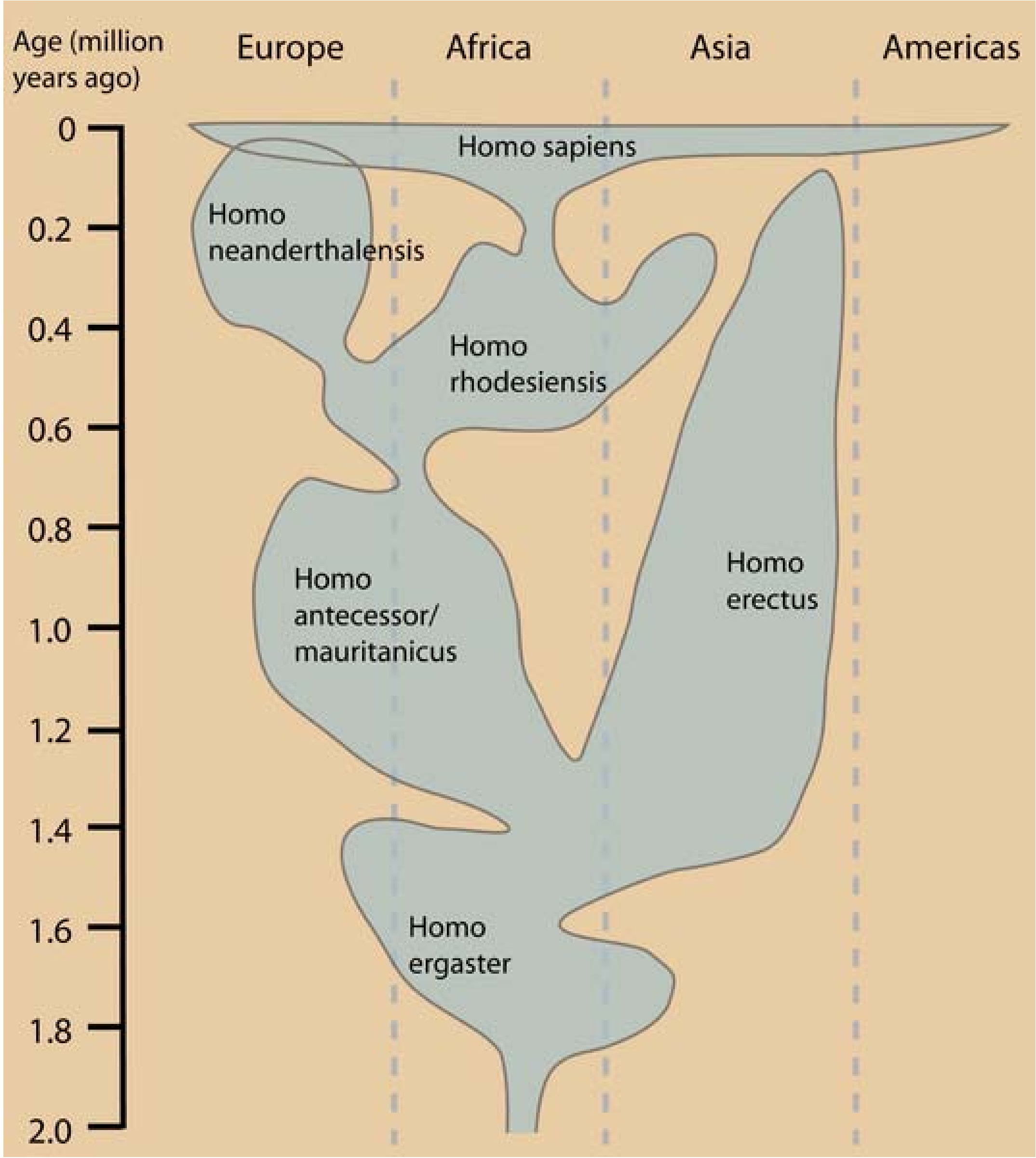
It was considered to be the first species of the genus *Homo* until May 2010, when a new species, *Homo gautengensis* was discovered in South Africa, that most likely arose earlier than *Homo habilis*.

H. rudolfensis and H. georgicus

These are proposed species names for fossils from about 1.9–1.6 Ma, the relation of which with *Homo habilis* is not yet clear.

- *Homo rudolfensis* refers to a single, incomplete skull from Kenya. Scientists have suggested that this was another *Homo habilis*, but this has not been confirmed.
- *Homo georgicus*, from Georgia, may be an intermediate form between *Homo habilis* and *Homo erectus*, or a sub-species of *Homo erectus*.

H. ergaster and H. erectus



One current view of the temporal and geographical distribution of hominid populations. Other interpretations differ mainly in the taxonomy and geographical distribution of hominid species.

The first fossils of *Homo erectus* were discovered by Dutch physician Eugene Dubois in 1891 on the Indonesian island of Java. He originally gave the material the name *Pithecanthropus erectus* based on its morphology that he considered to be intermediate between that of humans and apes. *Homo erectus* (H erectus) lived from about 1.8 Ma to about 70,000 years ago (which would indicate that they were probably wiped out by the Toba catastrophe; however, *Homo erectus soloensis* and *Homo floresiensis* survived it). Often the early phase, from 1.8 to 1.25 Ma, is considered to be a separate species, *Homo ergaster*, or it is seen as a subspecies of *Homo erectus*, *Homo erectus ergaster*. In the early Pleistocene, 1.5–1 Ma, in Africa, Asia, and Europe, some populations of *Homo habilis* are thought to have evolved larger brains and made more elaborate stone tools; these differences and others are sufficient for anthropologists to classify them as a new species, *Homo erectus*. In addition *Homo erectus* was the first human ancestor to walk truly upright. This was made possible by the evolution of locking knees and a different location of the foramen magnum (the hole in the skull where the spine enters). They may have used fire to cook their meat.

A famous example of *Homo erectus* is Peking Man; others were found in Asia (notably in Indonesia), Africa, and Europe. Many paleoanthropologists now use the term *Homo ergaster* for the non-Asian forms of this group, and reserve *Homo erectus* only for those fossils that are found in Asia and meet certain skeletal and dental requirements which differ slightly from *H. ergaster*.

H. cepranensis and H. antecessor

These are proposed as species that may be intermediate between *H. erectus* and *H. heidelbergensis*.

- *H. antecessor* is known from fossils from Spain and England that are dated 1.2 Ma–500 ka.
- *H. cepranensis* refers to a single skull cap from Italy, estimated to be about 800,000 years old.

H. heidelbergensis

H. heidelbergensis (Heidelberg Man) lived from about 800,000 to about 300,000 years ago. Also proposed as *Homo sapiens heidelbergensis* or *Homo sapiens paleohungaricus*.

H. rhodesiensis, and the Gawis cranium

- *H. rhodesiensis*, estimated to be 300,000–125,000 years old. Most current experts believe Rhodesian Man to be within the group of *Homo heidelbergensis*, though other designations such as Archaic Homo sapiens and Homo sapiens rhodesiensis have also been proposed.
- In February 2006 a fossil, the Gawis cranium, was found which might possibly be a species intermediate between *H. erectus* and *H. sapiens* or one of many evolutionary dead ends. The skull from Gawis, Ethiopia, is believed to be 500,000–250,000 years old. Only summary details are known, and no peer reviewed studies have been released by the finding team. Gawis man's facial features suggest its being either an intermediate species or an example of a "Bodo man" female.

H. neanderthalensis

Le Ferrassie Neanderthal skull (cast)

H. neanderthalensis lived from 400,000 to about 30,000 years ago. Also proposed as *Homo sapiens neanderthalensis*. Evidence from sequencing mitochondrial DNA indicated that no significant gene flow occurred between *H. neanderthalensis* and *H. sapiens*, and, therefore, the two were separate species that shared a common ancestor about 660,000 years ago. In 1997, Mark Stoneking stated: "These results [based on mitochondrial DNA extracted from Neanderthal bone] indicate that Neanderthals did not contribute mitochondrial DNA to modern humans… Neanderthals are not our ancestors". Subsequent investigation of a second source of Neanderthal DNA supported these findings.

However, the 2010 sequencing of the Neanderthal genome indicated that Neanderthals did indeed interbreed with *H. sapiens circa* 75,000 BC (after *H. sapiens* moved out from Africa, but before they separated into Europe, the Middle East, and Asia). Nearly all modern humans have 1% to 4% of their DNA derived from Neanderthal DNA. This 1–4% bit of DNA is only present in non-African humans. However, supporters of the multiregional hypothesis point to recent studies indicating non-African nuclear DNA heritage dating to one Ma, although the reliability of these studies has been questioned. Competition from *Homo sapiens* probably contributed to Neanderthal extinction. They could have coexisted in Europe for as long as 10,000 years.

H. sapiens

H. sapiens (the adjective *sapiens* is Latin for "wise" or "intelligent") have lived from about 250,000 years ago to the present. Between 400,000 years ago and the second interglacial period in the Middle Pleistocene, around 250,000 years ago, the trend in skull expansion and the elaboration of stone tool technologies developed, providing evidence for a transition from *H. erectus* to *H. sapiens*. The direct evidence suggests there was a migration of *H. erectus* out of Africa, then a further speciation of *H. sapiens* from *H. erectus* in Africa. A subsequent migration within and out of Africa eventually replaced the earlier dispersed *H. erectus*. This migration and origin theory is usually referred to as the *recent single origin* or Out of Africa theory. Current evidence does not preclude some multiregional evolution or some admixture of the migrant *H. sapiens* with existing *Homo* populations. This is a hotly debated area of paleoanthropology.

Current research has established that humans are genetically highly homogenous; that is, the DNA of individuals is more alike than usual for most species, which may have resulted from their relatively recent evolution or the possibility of a population bottleneck resulting from cataclysmic natural events such as the Toba catastrophe. Distinctive genetic characteristics have arisen, however, primarily as the result of small groups of people moving into new environmental circumstances. These adapted traits are a very small component of the *Homo sapiens* genome, but include various characteristics such as skin color and nose form, in addition to internal characteristics such as the ability to breathe more efficiently at high altitudes.

H. sapiens idaltu, from Ethiopia, is an extinct sub-species who lived about 160,000 years ago.

H. floresiensis

H. floresiensis, which lived from approximately 100,000 to 12,000 before present, has been nicknamed *hobbit* for its small size, possibly a result of insular dwarfism. *H. floresiensis* is intriguing both for its size and its age, being a concrete example of a recent species of the genus *Homo* that exhibits derived traits not shared with modern humans. In other words, *H. floresiensis* share a common ancestor with modern humans, but split from the modern human lineage and followed a distinct evolutionary path. The main find was a skeleton believed to be a woman of about 30 years of age. Found in 2003 it has been dated to approximately 18,000 years old. The living woman was estimated to be one meter in height, with a brain volume of just 380 cm^3 (considered small for a chimpanzee and less than a third of the *H. sapiens* average of 1400 cm^3).

However, there is an ongoing debate over whether *H. floresiensis* is indeed a separate species. Some scientists presently believe that *H. floresiensis* was a modern *H. sapiens* suffering from pathological dwarfism. This hypothesis is supported in part, because some modern humans who live on Flores, the island where the skeleton was found, are pygmies. This coupled with pathological dwarfism, it is argued, could indeed create a hobbit-like human. The other major attack on *H. floresiensis* is that it was found with tools only associated with *H. sapiens*.

The hypothesis of pathological dwarfism, however, fails to explain additional anatomical features that are unlike those of modern humans (diseased or not) but much like those of ancient members of our genus. Aside from cranial features, these features include the form of bones in the wrist, forearm, shoulder, knees, and feet.

Denisova hominin

In 2008, archaeologists working at the site of Denisova Cave in the Altai Mountains of Siberia uncovered a small bone fragment from the fifth finger of a juvenile hominin, dubbed the "X-woman" (referring to the maternal descent of mitochondrial DNA), or the Denisova hominin. Artifacts, including a bracelet, excavated in the cave at the same level were carbon dated to around 40,000 BP. As DNA had survived in the fossil fragment due to the cool climate of the Denisova Cave, a team of scientists from the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany sequenced mtDNA extracted from the fragment.

The analysis indicated that modern humans, Neanderthals, and the Denisova hominin last shared a common ancestor around 1 million years ago. Modern humans are known to have overlapped with Neanderthals in Europe for more than 10,000 years, and the discovery raises the possibility that Neanderthals, modern humans and the Denisovan hominin may have co-existed together.

The DNA analysis further indicated that this new hominin species was the result of an early migration out of Africa, distinct from the later out-of-Africa migrations associated with Neanderthals and modern humans, but also distinct from the earlier African exodus of *Homo erectus*. Professor Chris Stringer, human origins researcher at London's Natural History Museum and one of the leading proponents of the recent single-origin hypothesis, remarked: "This new DNA work provides an entirely new way of looking at the still poorly understood evolution of humans in central and eastern Asia." Pääbo noted that the existence of this distant branch creates a much more complex picture of humankind during the Late Pleistocene.

Comparative table of *Homo* species

Comparative table of *Homo* species

Species	Lived when (Ma)	Lived where	Adult height	Adult mass	Cranial capacity (cm³)	Fossil record	Discovery / publication of name
H. antecessor	1.2 – 0.8	Spain	1.75 m (5.7 ft)	90 kg (200 lb)	1,000	2 sites	1997
H. cepranensis	0.9 – 0.8?	Italy			1,000	1 skull cap	1994/2003
H. erectus	1.5 – 0.2	Africa, Eurasia (Java, China, India, Caucasus)	1.8 m (5.9 ft)	60 kg (130 lb)	850 (early) – 1,100 (late)	Many	1891/1892
H. ergaster	1.9 – 1.4	Eastern and Southern Africa	1.9 m (6.2 ft)		700–850	Many	1975
H. floresiensis	0.10? – 0.012	Indonesia	1.0 m (3.3 ft)	25 kg (55 lb)	400	7 individuals	2003/2004
H. gautengensis	>2 – 0.6	South Africa	1.0 m (3.3 ft)			1 individual	2010/2010
H. georgicus	1.8	Georgia			600	4 individuals	1999/2002
H. habilis	2.3 – 1.4	Africa	1.0–1.5 m (3.3–4.9 ft)	33–55 kg (73–120 lb)	510–660	Many	1960/1964
H. heidelbergensis	0.6 – 0.35	Europe, Africa, China	1.8 m (5.9 ft)	60 kg (130 lb)	1,100–1,400	Many	1908
H. neanderthalensis	0.35 – 0.03	Europe, Western Asia	1.6 m (5.2 ft)	55–70 kg (120–150 lb) (heavily built)	1,200–1,900	Many	(1829)/1864
H. rhodesiensis	0.3 – 0.12	Zambia			1,300	Very few	1921
H. rudolfensis	1.9	Kenya				1 skull	1972/1986
H. sapiens idaltu	0.16 – 0.15	Ethiopia			1,450	3 craniums	1997/2003

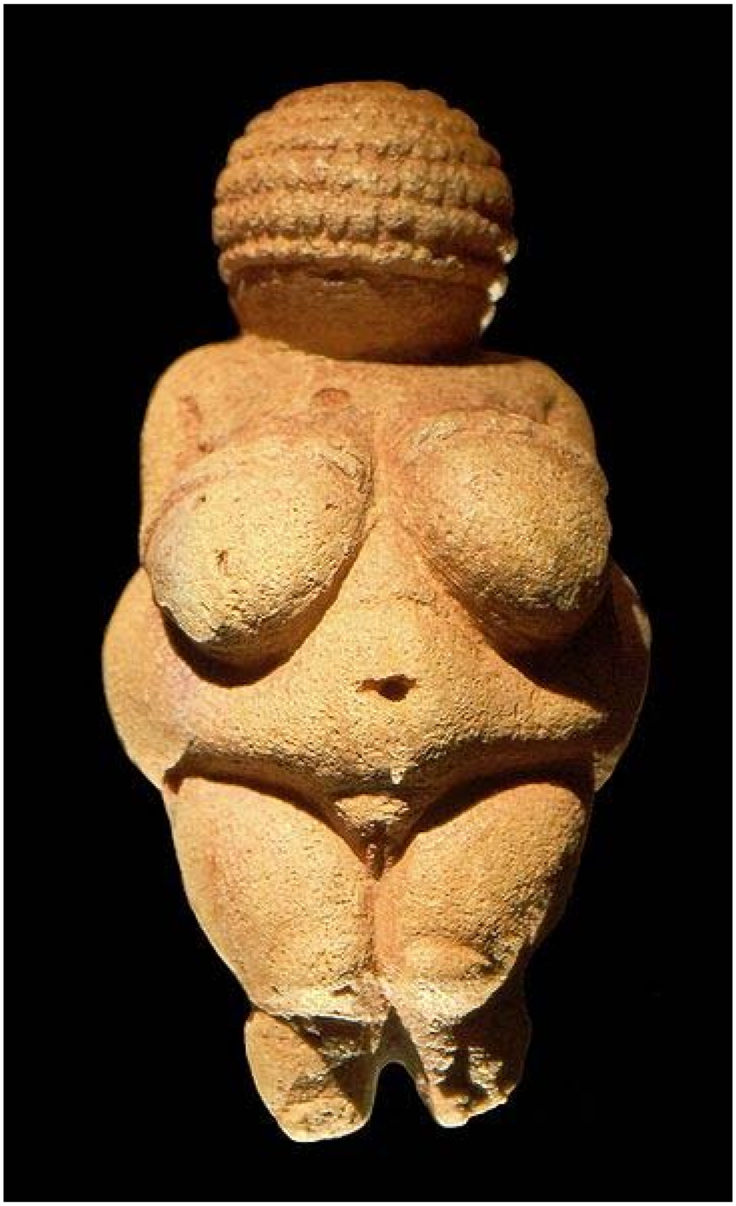
H. sapiens sapiens (modern humans)	0.2 – present	Worldwide	1.4–1.9 m (4.6–6.2 ft)	50–100 kg (110–220 lb)	1,000–1,850	Still living	—/1758

Use of tools

"A sharp rock", an Oldowan pebble tool, the most basic of human stone tools

Fire, one of the greatest human discoveries

An Acheulean hand axe, the pinnacle of *Homo erectus* stone working



Venus of Willendorf, an example of Paleolithic art

Using tools has been interpreted as a sign of intelligence, and it has been theorized that tool use may have stimulated certain aspects of human evolution—most notably the continued expansion of the human brain. Paleontology has yet to explain the expansion of this organ over millions of years despite being extremely demanding in terms of energy consumption. The brain of a modern human consumes about 20 watts (400 kilocalories per day), which is one fifth of the energy consumption of a human body. Increased tool use would allow hunting for energy-rich meat products, and would enable processing more energy-rich plant products. Researchers have suggested that early hominids were thus under evolutionary pressure to increase their capacity to create and use tools.

Precisely when early humans started to use tools is difficult to determine, because the more primitive these tools are (for example, sharp-edged stones) the more difficult it is to decide whether they are natural objects or human artifacts. There is some evidence that the australopithecines (4 Ma) may have used broken bones as tools, but this is debated.

It should be noted that many species make and use tools, but it is the human species that dominates the areas of making and using more complex tools. The oldest known tools are the "Oldowan stone tools" from Ethiopia. It was discovered that these tools are from 2.5 to 2.6 million years old, which predates the earliest known "Homo" species. There is no known evidence that any "Homo" specimens appeared by 2.5 Ma. A Homo fossil was found near some Oldowan tools, and its age was noted at 2.3 million years old, suggesting that maybe the Homo species did indeed create and use these tools. It is surely possible, but not solid evidence. Bernard Wood noted that "Paranthropus" coexisted with the early Homo species in the area of the "Oldowan Industrial Complex" over roughly the same span of time. Although there is no direct evidence that points to Paranthropus as the tool makers, their anatomy lends to indirect evidence of their capabilities in this area. Most paleoanthropologists agree that the early "Homo" species were indeed responsible for most of the Oldowan tools found. They argue that when most of the Oldowan tools were found in association with human fossils, Homo was always present, but Paranthropus was not.

In 1994, Randall Susman used the anatomy of opposable thumbs as the basis for his argument that both the Homo and Paranthropus species were toolmakers. He compared bones and muscles of human and chimpanzee thumbs, finding that humans have 3 muscles that chimps lack. Humans also have thicker metacarpals with broader heads, making the human hand more successful at precision grasping than the chimpanzee hand. Susman defended that modern anatomy of the human thumb is an evolutionary response to the requirements associated with making and handling tools and that both species were indeed toolmakers.

Stone tools

Stone tools are first attested around 2.6 Ma, when *H. habilis* in Eastern Africa used so-called pebble tools, choppers made out of round pebbles that had been split by simple strikes. This marks the beginning of the Paleolithic, or Old Stone Age; its end is taken to be the end of the last Ice Age, around 10,000 years ago. The Paleolithic is subdivided into the Lower Paleolithic (Early Stone Age, ending around 350,000–300,000 years ago), the Middle Paleolithic (Middle Stone Age, until 50,000–30,000 years ago), and the Upper Paleolithic.

The period from 700,000–300,000 years ago is also known as the Acheulean, when *H. ergaster* (or *erectus*) made large stone hand-axes out of flint and quartzite, at first quite rough (Early Acheulian), later "retouched" by additional, more subtle strikes at the sides of the flakes. After 350,000 BP (Before Present) the more refined so-called Levallois technique was developed. It consisted of a series of consecutive strikes, by which scrapers, slicers ("racloirs"), needles, and flattened needles were made. Finally, after about 50,000 BP, ever more refined and specialized flint tools were made by the Neanderthals and the immigrant Cro-Magnons (knives, blades, skimmers). In this period they also started to make tools out of bone.

Modern humans and the "Great Leap Forward" debate

Until about 50,000–40,000 years ago the use of stone tools seems to have progressed stepwise. Each phase (*H. habilis*, *H. ergaster*, *H. neanderthalensis*) started at a higher level than the previous one, but once that phase started further development was slow. These *Homo* species were culturally conservative, but after 50,000 BC modern human culture started to change at a much greater speed. Jared Diamond, author of *The Third Chimpanzee*, and some anthropologists characterize this as a "Great Leap Forward".

Modern humans started burying their dead, making clothing out of hides, developing sophisticated hunting techniques (such as using trapping pits or driving animals off cliffs), and engaging in cave painting. As human culture advanced, different populations of humans introduced novelty to existing technologies: artifacts such as fish hooks, buttons and bone needles show signs of variation among different populations of humans, something that had not been seen in human cultures prior to 50,000 BP. Typically, *H. neanderthalensis* populations do not vary in their technologies.

Among concrete examples of Modern human behavior, anthropologists include specialization of tools, use of jewellery and images (such as cave drawings), organization of living space, rituals (for example, burials with grave gifts), specialized hunting techniques, exploration of less hospitable geographical areas, and barter trade networks. Debate continues as to whether a "revolution" led to modern humans ("the big bang of human consciousness"), or whether the evolution was more gradual.

Models of human evolution

Today, all humans belong to one population of *Homo sapiens sapiens,* undivided by species barrier. However, according to the "Out of Africa" model this is not the first species of hominids: the first species of genus *Homo*, *Homo habilis*, evolved in East Africa at least 2 Ma, and members of this species populated different parts of Africa in a relatively short time. *Homo erectus* evolved more than 1.8 Ma, and by 1.5 Ma had spread throughout the Old World.

Anthropologists have been divided as to whether current human population evolved as one interconnected population (as postulated by the Multiregional Evolution hypothesis), or evolved only in East Africa, speciated, then migrated out of Africa and replaced human populations in Eurasia (called the "Out of Africa" Model or the "Complete Replacement" Model).

Multiregional model

Multiregional evolution, a *model to account for the pattern of human evolution*, was proposed by Milford H. Wolpoff in 1988. Multiregional evolution holds that human evolution from the beginning of the Pleistocene 2.5 million years BP to the present day has been within a single, continuous human species, evolving worldwide to modern *Homo sapiens*.

According to the multiregional hypothesis, fossil and genomic data are evidence for worldwide human evolution and contradict the recent speciation postulated by the Recent African origin hypothesis. The fossil evidence was insufficient for Richard Leakey to resolve this debate. Studies of haplogroups in Y-chromosomal DNA and mitochondrial DNA have largely supported a recent African origin. Evidence from autosomal DNA also supports the Recent African origin. However the presence of archaic admixture in modern humans remains a possibility and has been suggested by some studies.

Out of Africa

According to the Out of Africa model, developed by Chris Stringer and Peter Andrews, modern *H. sapiens* evolved in Africa 200,000 years ago. *Homo sapiens* began migrating from Africa between 70,000 – 50,000 years ago and eventually replaced existing hominid species in Europe and Asia. Out of Africa has gained support from research using mitochondrial DNA (mtDNA). After analysing genealogy trees constructed using 133 types of mtDNA, researchers concluded that all were descended from a woman from Africa, dubbed Mitochondrial Eve. Out of Africa is also supported by the fact that mitochondrial genetic diversity is highest among African populations.

There are differing theories on whether there was a single exodus or several. A multiple dispersal model involves the Southern Dispersal theory, which has gained support in recent years from genetic, linguistic and archaeological evidence. In this theory, there was a coastal dispersal of modern humans from the Horn of Africa around 70,000 years ago. This group helped to populate Southeast Asia and Oceania, explaining the discovery of early human sites in these areas much earlier than those in the Levant. A second wave of humans dispersed across the Sinai peninsula into Asia, resulting in the bulk of human population for Eurasia. This second group possessed a more sophisticated tool technology and was less dependent on coastal food sources than the original group. Much of the evidence for the first group's expansion would have been destroyed by the rising sea levels at the end of the Holocene era. The multiple dispersal model is contradicted by studies indicating that the populations of Eurasia and the populations of Southeast Asia and Oceania are all descended from the same mitochondrial DNA lineages, which support a single migration out of Africa that gave rise to all non-African populations.

The broad study of African genetic diversity headed by Dr. Sarah Tishkoff found the San people to express the greatest genetic diversity among the 113 distinct populations sampled, making them one of 14 "ancestral population clusters". The research also located the origin of modern human migration in south-western Africa, near the coastal border of Namibia and Angola.

According to the Toba catastrophe theory to which some anthropologists and archeologists subscribe, the supereruption of Lake Toba on Sumatra island in Indonesia roughly 70,000 years ago had global consequences, killing most humans then alive and creating a population bottleneck that affected the genetic inheritance of all humans today.

Recent and current human evolution

Natural selection is being observed in contemporary human populations, with recent findings demonstrating the population which is at risk of the severe debilitating disease kuru has significant over-representation of an immune variant of the prion protein gene G127V versus non-immune alleles. Scientists postulate one of the reasons for the rapid selection of this genetic variant is the lethality of the disease in non-immune persons. Other reported evolutionary trends in other populations include a lengthening of the reproductive period, reduction in cholesterol levels, blood glucose and blood pressure.

In their 2009 book *The 10,000 Year Explosion*, Gregory Cochran and Henry Harpending argue that human evolution has accelerated since and as a result of the development of agriculture and civilisation since some 50,000 years ago, and that there are consequently substantial genetic differences between different current human populations.

Genetics

Human evolutionary genetics studies how one human genome differs from the other, the evolutionary past that gave rise to it, and its current effects. Differences between genomes have anthropological, medical and forensic implications and applications. Genetic data can provide important insight into human evolution.

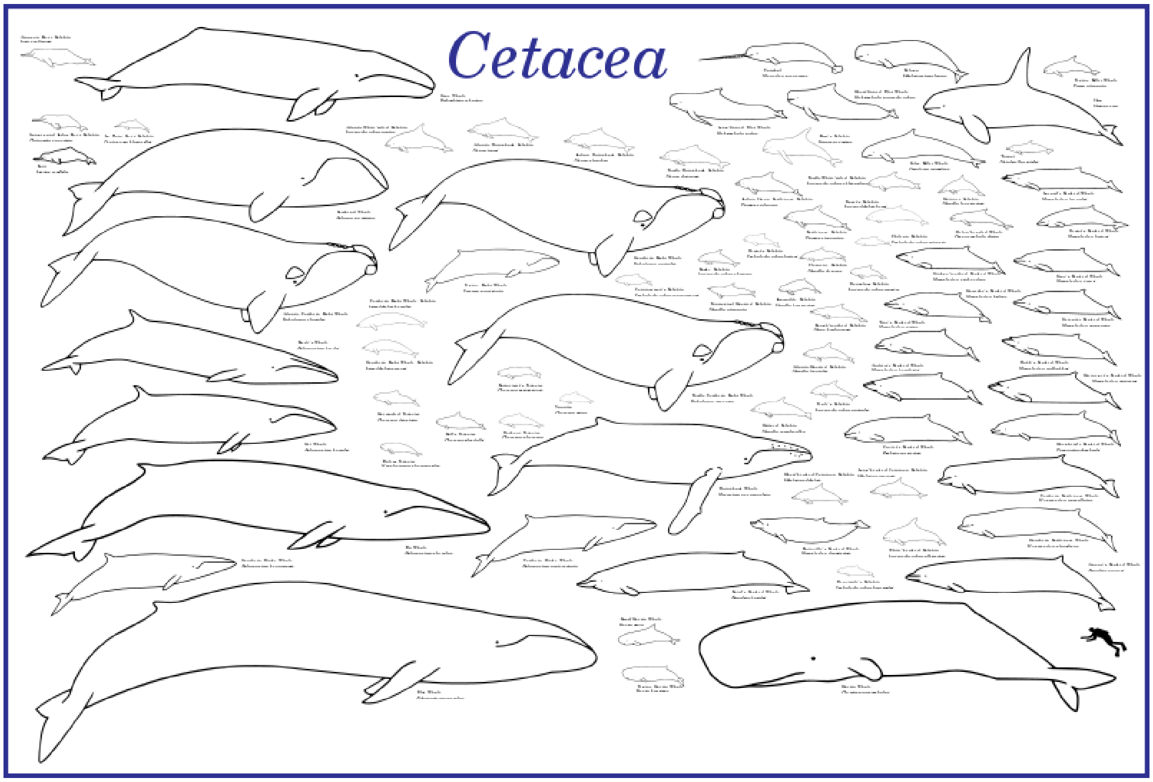
Notable human evolution researchers

- Robert Broom, a Scottish physician and palaeontologist whose work on South Africa led to the discovery and description of the Paranthropus genus of hominins, and of "Mrs. Ples"
- Raymond Dart, an Australian anatomist and palaeoanthropologist, whose work at Taung, in South Africa, led to the discovery of *Australopithecus africanus*
- Charles Darwin, a British naturalist who documented considerable evidence that species originate through evolutionary change
- Henry McHenry, an American anthropologist who specializes in studies of human evolution, the origins of bipedality, and paleoanthropology
- Donald Johanson, credited with the discovery of *Australopithecus afarensis*
- Jeffrey Laitman, an American anatomist and physical anthropologist whose work has explored the evolution of the vocal tract and speech
- Louis Leakey, an African archaeologist and naturalist whose work was important in establishing human evolutionary development in Africa

- Mary Leakey, a British archaeologist and anthropologist whose discoveries in Africa include the Laetoli footprints
- Richard Leakey, an African paleontologist and archaeologist, son of Louis and Mary Leakey
- Svante Pääbo, a Swedish biologist specializing in evolutionary genetics
- David Pilbeam, a paleoanthropologist, researcher and writer on a range of topics involving human and primate evolution.
- Jeffrey H. Schwartz, an American physical anthropologist and professor of biological anthropology
- Chris Stringer, anthropologist, leading proponent of the recent single origin hypothesis
- Alan Templeton, geneticist and statistician, proponent of the multiregional hypothesis
- Philip V. Tobias, a South African palaeoanthropologist is one of the world's leading authorities on the evolution of humankind
- Erik Trinkaus, a prominent American paleoanthropologist and expert on Neanderthal biology and human evolution
- Milford H. Wolpoff, an American paleoanthropologist who is the leading proponent of the multiregional evolution hypothesis.

Chapter- 7

Evolution of Cetaceans



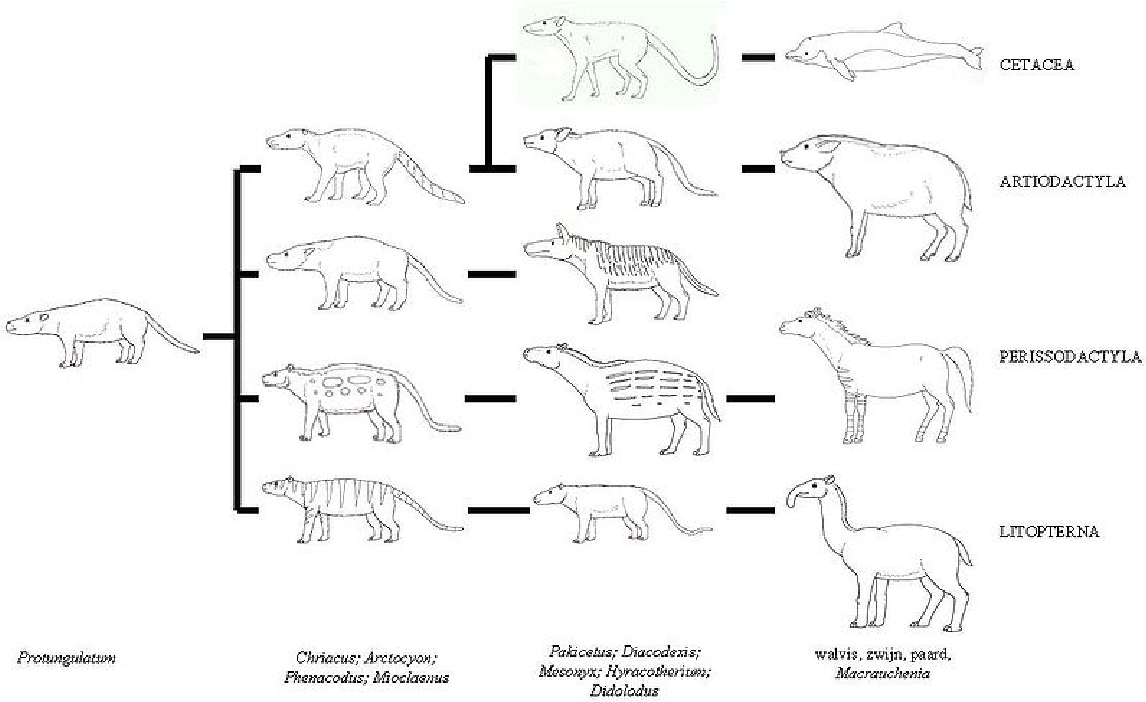
The approximately 80 modern species in the order Cetacea.

The cetaceans (whales, dolphins and porpoises) are marine mammal descendants of land mammals. Their terrestrial origins are indicated by:

- Their need to breathe air from the surface;
- The bones of their fins, which resemble the limbs of land mammals
- The vertical movement of their spines, characteristic more of a running mammal than of the horizontal movement of fish.

The question of how land animals evolved into ocean-going leviathans was a mystery until recent discoveries in Pakistan revealed several stages in the transition of cetaceans from land to sea.

Earliest ancestors

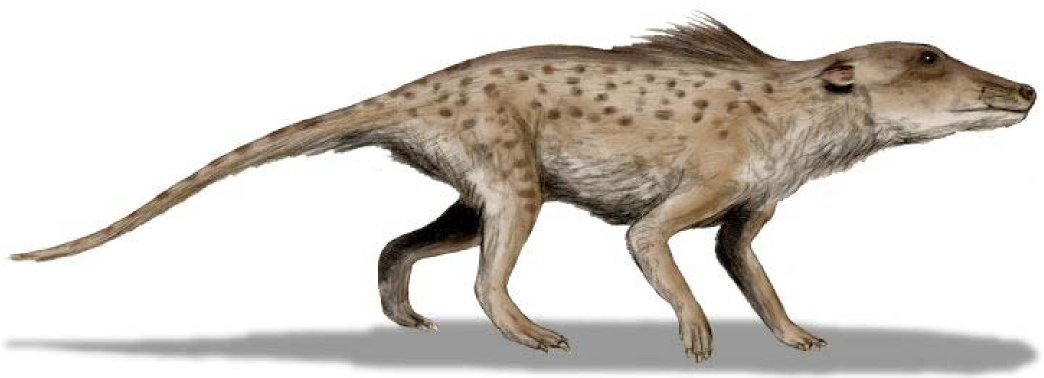


The family tree, including Ungulates.

The traditional theory of cetacean evolution was that whales were related to the mesonychids, an extinct order of carnivorous ungulates (hoofed animals), which looked rather like wolves with hooves and were a sister group of artiodactyls. These animals possessed unusual triangular teeth that are similar to those of whales. For this reason, scientists had long believed that whales evolved from a form of mesonychid; however, more recent molecular phylogeny data suggest that whales are more closely related to the artiodactyls, specifically the hippopotamus. The strong evidence for a clade combining cetaceans and artiodactyls is further discussed under the entry Cetartiodactyla. However, hippos' anthracothere ancestors do not appear in the fossil record until millions of years after Pakicetus, the first known whale ancestor.

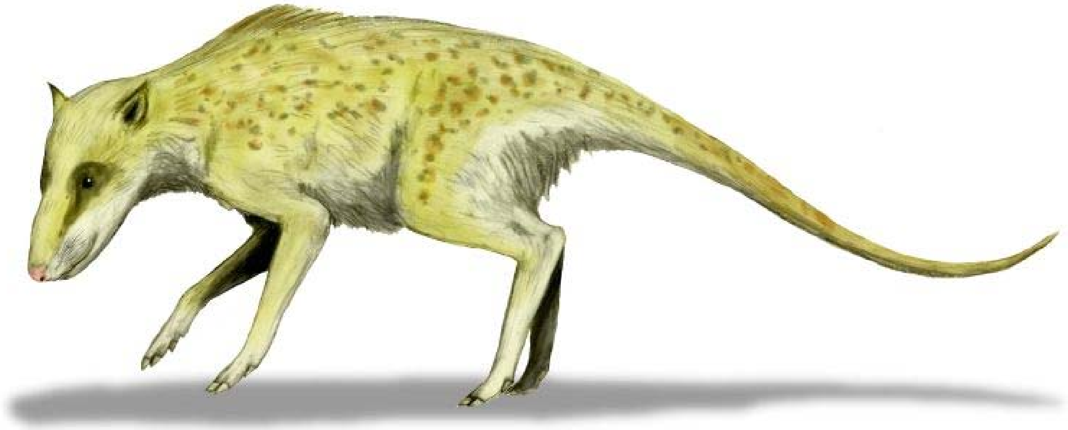
The recent discovery of *Pakicetus*, the earliest proto-whale supports the molecular data. The skeletons of *Pakicetus* demonstrate that whales did not derive directly from mesonychids. Instead, they are a form of artiodactyl (another type of ungulate) that began to take to the water after the artiodactyl family split from the mesonychids. In other words, the proto-whales were early artiodactyls that retained aspects of their mesonychid ancestry (such as the triangular teeth) which modern artiodactyls have since lost. An interesting implication is that the earliest ancestors of all hoofed mammals were probably at least partly carnivorous or scavengers, today's artiodactyls and perissodactyls having switched to a plant diet later in their evolution. Whales, due to the readier availability of animal prey and their need for higher caloric content, in order to live as marine endotherms, naturally retained their carnivorous diet, as did mesonychids, who were however out-competed by better-adapted animals like the Carnivora later on (mesonychids became specialized carnivores when the overall availability of large animal prey was still low; thus their adaptation was likely at a disadvantage when new forms had filled the gaps left by the dinosaurs).

The earliest cetaceans: Pakicetids or Indohyus?



Reconstruction of *Pakicetus*

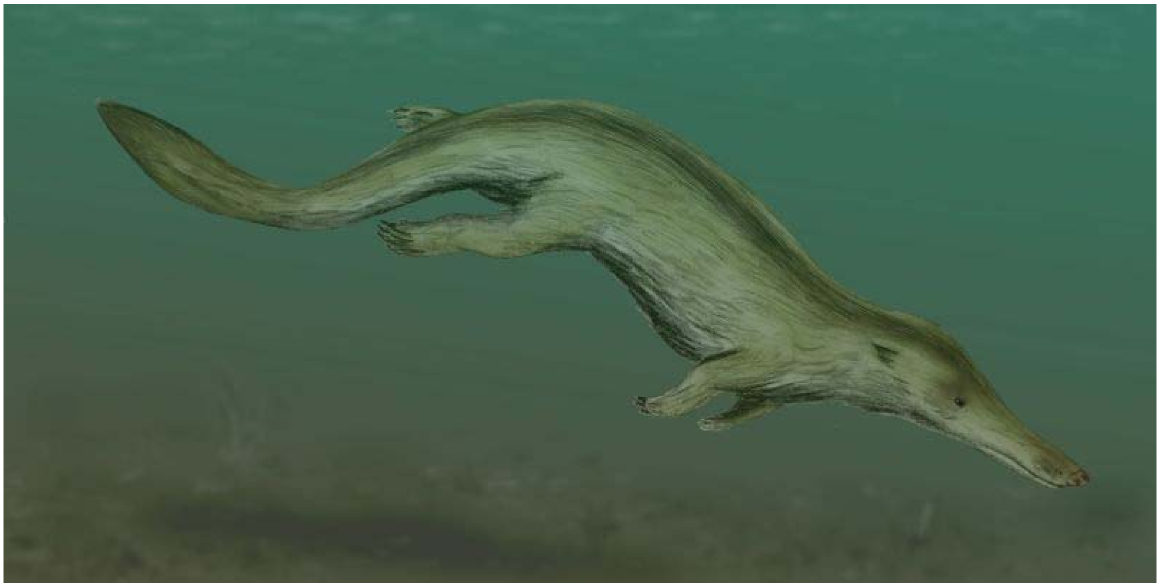
The pakicetids are hoofed-mammals that are sometimes classified as the earliest whales. They lived in the early Eocene, around 53 million years ago. They looked rather like dogs with hoofed feet and long, thick tails. They have been linked to whales by their ears: the structure of the auditory bulla is formed from the ectotympanic bone only. The shape of the ear region in *Pakicetus* is highly unusual and only resembles the skulls of whales. The feature is diagnostic for cetaceans and is found in no other species. It was initially thought that the ears of *Pakicetus* were adapted for underwater hearing, but, as would be expected from the anatomy of the rest of this creature, the ears of *Pakicetus* are specialized for hearing on land, and if *Pakicetus* is related to the ancestors of whales, underwater hearing must have been a later adaptation. According to Thewissen, the teeth of *Pakicetus* also resemble the teeth of fossil whales, being less like a dog's incisors, with a serrated triangular shape, similar to a shark's tooth, which is another link to more modern whales.



Reconstruction of *Indohyus*.

Thewissen has since found the same ear structure in fossils of a small deer-like creature, *Indohyus*, which lived about 48 million years ago in Kashmir. About the size of a raccoon or domestic cat, this herbivorous creature shared some of the traits of whales, and showed signs of adaptations to aquatic life, including a thick and heavy outer coating to bones which is similar to the bones of modern creatures such as the hippopotamus, and reduces buoyancy so that they can stay underwater. This suggests a similar survival strategy to the African mousedeer or water chevrotain which, when threatened by a bird of prey, dives into water and hides beneath the surface for up to four minutes.

Ambulocetids and remingtonocetids



Reconstruction of *Kutchicetus*, a remingtonocetid

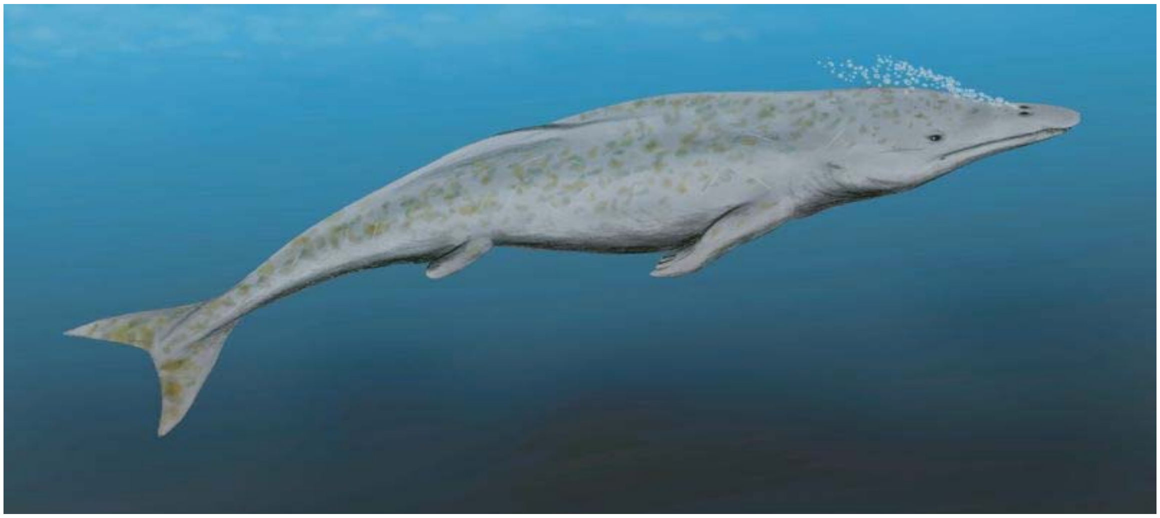
Reconstruction of *Ambulocetus natans*

The most remarkable of the recent discoveries in Pakistan has been *Ambulocetus*, which looked like a three-metre long mammalian crocodile. *Ambulocetus* was clearly amphibious, as its back legs are better adapted for swimming than for walking on land, and it probably swam by undulating its back vertically, as otters, seals and whales do. It has been speculated that Ambulocetids hunted like crocodiles, lurking in the shallows to snatch unsuspecting riparian prey and fish.

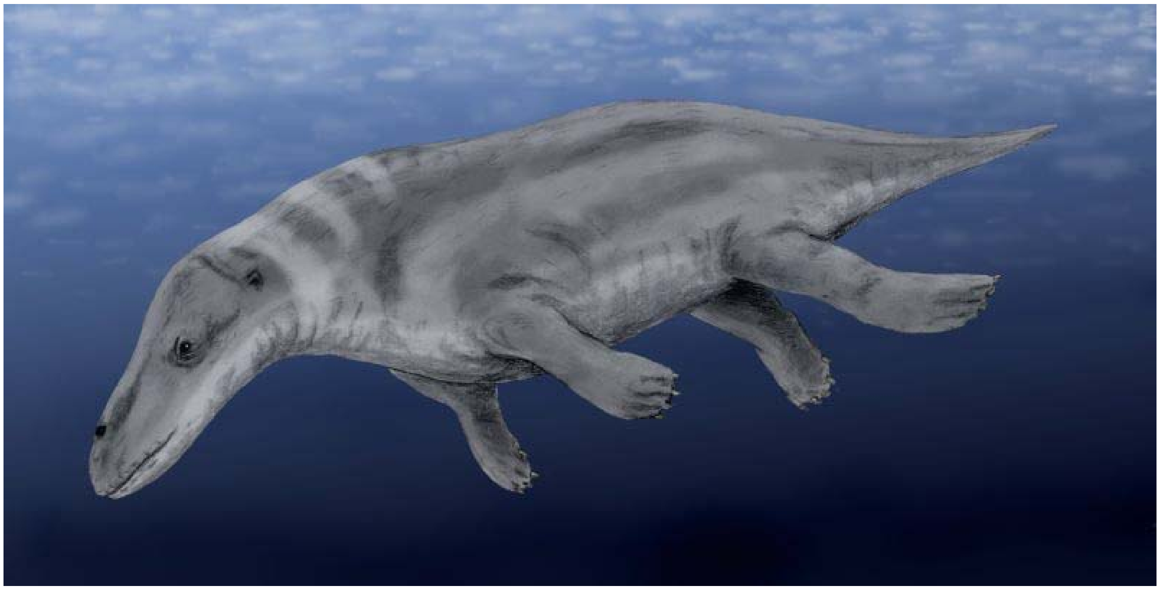
A smaller cousin of *Ambulocetus* was the remingtonocetidae family, which had longer snouts than *Ambulocetus*, and were slightly better adapted for underwater life. It has been speculated that they lived like modern sea otters, hunting for fish in the shallows.

In both groups, the nasal openings were at the tip of the snout, like in land-mammals.

Protocetids



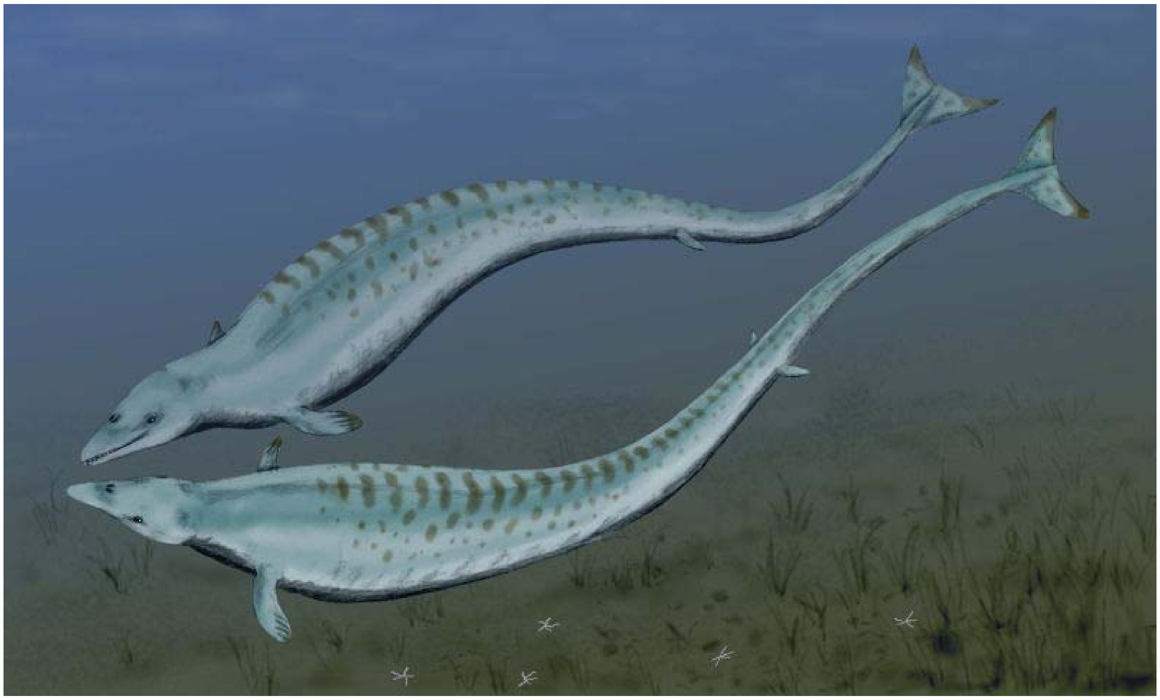
Reconstruction of *Protocetus*



Reconstruction of *Rodhocetus*

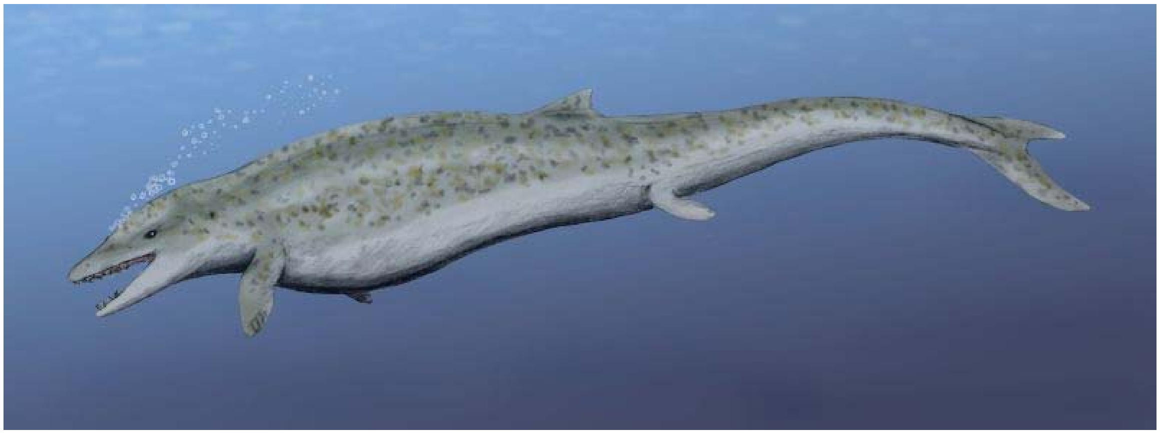
The protocetids form a diverse and heterogeneous group known from Asia, Europe, Africa, and North America. There were many genera, and some of these are very well known (e.g., *Rodhocetus*). Known protocetids had large fore- and hindlimbs that could support the body on land, and it is likely that they lived amphibiously: in the sea and on land. It is unclear at present whether protocetids had flukes (the horizontal tail fin of modern cetaceans). However, what is clear is that they are adapted even further to an aquatic life-style. In *Rodhocetus*, for example, the sacrum – a bone that in land-mammals is a fusion of five vertebrae that connects the pelvis with the rest of the vertebral column – was divided into loose vertebrae. However, the pelvis was still connected to one of the sacral vertebrae. Furthermore, the nasal openings are now halfway up the snout; a first step towards the telescoped condition in modern whales. Their supposed amphibious nature is supported by the discovery of a pregnant *Maiacetus*, in which the fossilised fetus was positioned for a head-first delivery, suggesting that *Maiacetus* gave birth on land. The ungulate ancestry of these early whales is still underlined by characteristics like the presence of hoofs at the ends of toes in *Rodhocetus*.

Basilosaurids and dorudontids: fully marine cetaceans



Reconstruction of *Basilosaurus*

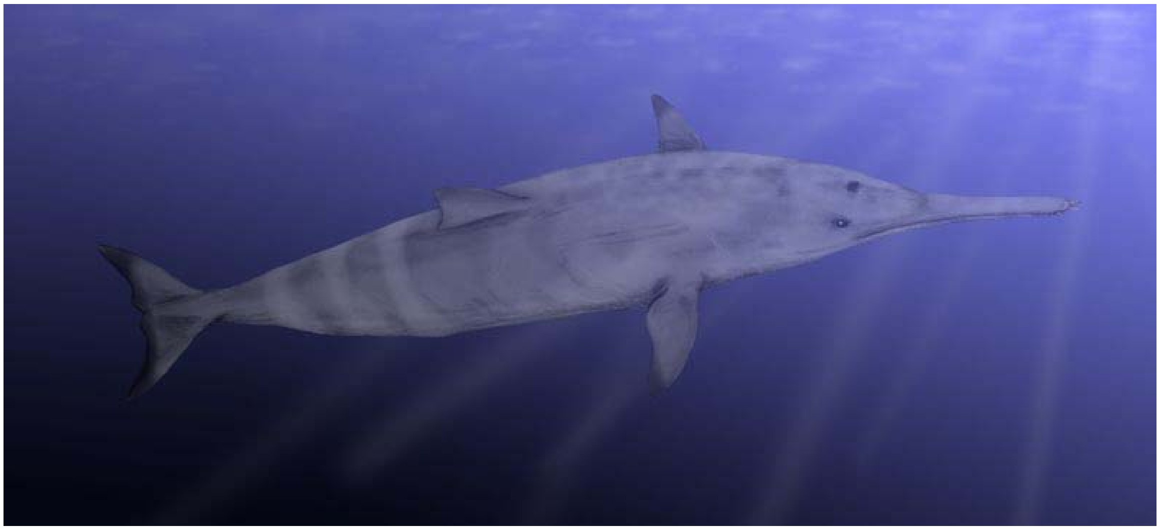
Basilosaurus (discovered in 1840 and initially mistaken for a reptile, hence its name) and *Dorudon* lived around 38 million years ago, and were fully recognizable whales which lived entirely in the ocean. *Basilosaurus* was as big as the larger modern whales, up to 18 m (60 ft) long; dorudontids were smaller, about 5 m (16 ft) long.



Reconstruction of *Dorudon*

Although they look very much like modern whales, basilosaurids and dorudontids lacked the 'melon organ' that allows their descendants to use echolocation as effectively as modern whales. They had small brains; this suggests they were solitary and did not have the complex social structure of some modern cetaceans. *Basilosaurus* had two tiny but well-formed hind legs which were probably used as claspers when mating; they are a small reminder of the lives of their ancestors. Interestingly, the pelvic bones associated with these hind limbs was now no longer connected to the vertebral column as it was in protocetids. Essentially, any sacral vertebrae can no longer be clearly distinguished from the other vertebrae.

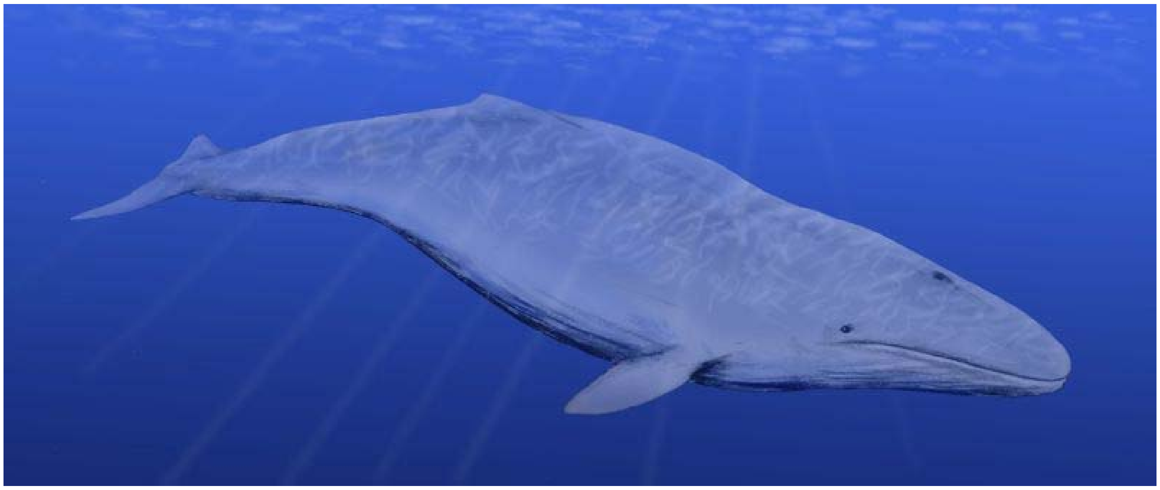
Early echolocation



Reconstruction of *Squalodon*

Toothed whales (Odontocetes) echolocate by creating a series of clicks emitted at various frequencies. Sound pulses are emitted through their melon-shaped foreheads, reflected off objects, and retrieved through the lower jaw. Skulls of *Squalodon* show evidence for the first hypothesized appearance of echolocation. *Squalodon* lived from the early to middle Oligocene to the middle Miocene, around 33-14 million years ago. *Squalodon* featured several commonalities with modern Odontocetes. The cranium was well compressed, the rostrum telescoped outward (a characteristic of the modern suborder Odontoceti), giving *Squalodon* an appearance similar to that of modern toothed whales. However, it is thought unlikely that squalodontids are direct ancestors of living dolphins.

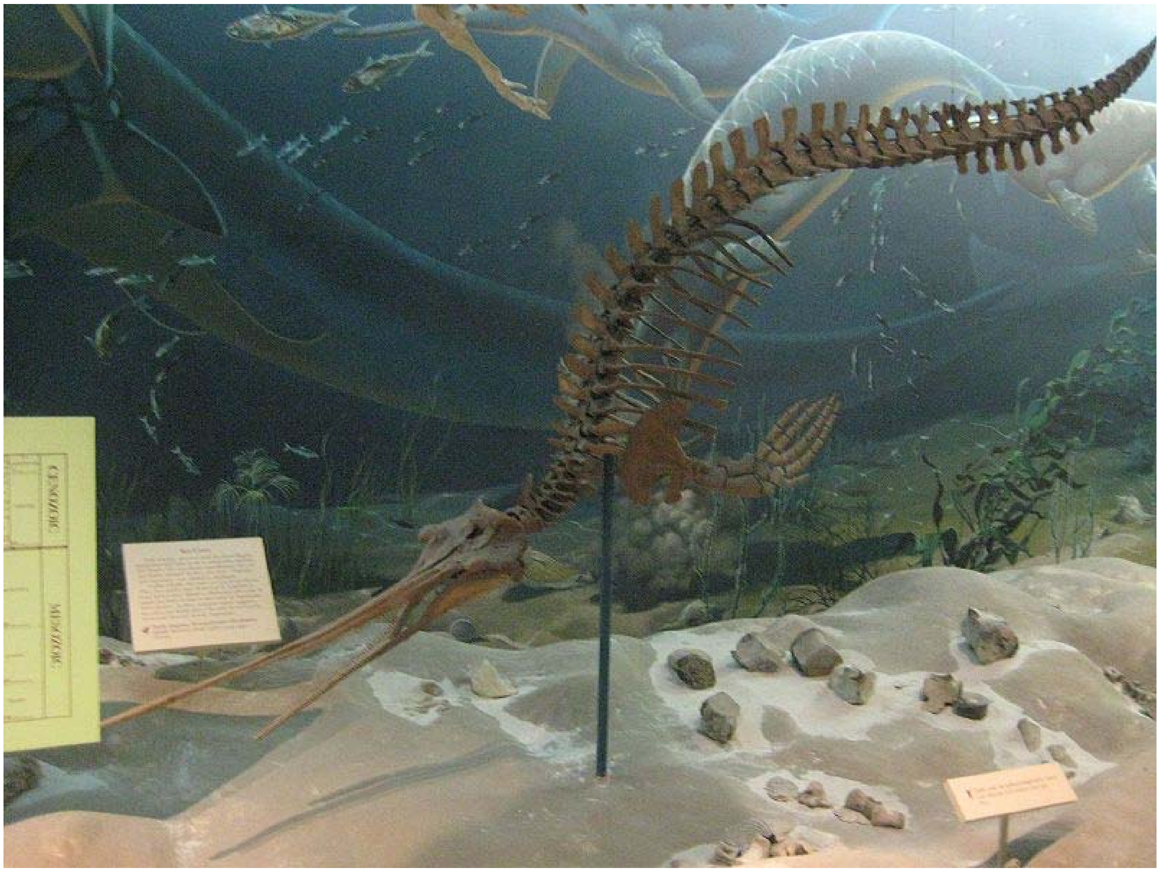
Early baleen whales



Reconstruction of *Cetotherium*

All modern mysticetes are large filter-feeding or baleen whales, though the exact means by which baleen is used differs among species (gulp-feeding with balaenopterids, skim-feeding with balaenids, and bottom ploughing with eschrichtiids). The first members of some modern groups appeared during the middle Miocene. These changes may have been a result of worldwide environmental change and physical changes in the oceans. A large scale change in ocean current and temperature could have initiated the radiation of modern mysticetes, leading to the demise of the archaic forms. Generally it is speculated the four modern mysticete families have separate origins among the cetotheres. Modern baleen whales, Balaenopteridae (rorquals and humpback whale, *Megaptera novaengliae*), Balaenidae (right whales), Eschrichtiidae (gray whale, *Eschrictius robustus*), and Neobalaenidae (pygmy right whale, *Caperea marginata*) all have derived characteristics presently unknown in any cetothere.

Early dolphins



Skeleton of *Xiphiacetus sp.*

During the early Miocene (about 20 Ma), echolocation developed in its modern form. Various extinct dolphin-like families flourished. Early dolphins include *Kentriodon* and *Hadrodelphis*. These belong to Kentriodontidae, which were small to medium-sized toothed cetaceans with largely symmetrical skulls, and thought likely to include ancestors of some modern species. Kentriodontids date to the late Oligocene to late Miocene. Kentriodontines ate small fish and other nectonic organisms; they are thought to have been active echolocators, and might have formed schools. Diversity, morphology and distribution of fossils appear parallel to some modern species.

Skeletal evolution

Today, the whale hind parts are internal and reduced. Occasionally, the genes that code for longer extremities cause a modern whale to develop miniature legs (known as atavism).

Whereas early cetaceans such as the *Pakicetus* had the nasal openings at the end of the snout, in later species such as the *Rodhocetus*, the openings had begun to drift toward the top of the skull. This is known as nasal drift.

The nostrils of modern whales have become modified into blowholes that allow them to break to the surface, inhale, and submerge with convenience. The ears began to move inward as well, and, in the case of *Basilosaurus*, the middle ears began to receive vibrations from the lower jaw. Today's modern toothed whales use the 'melon organ', a pad of fat, for echolocation.