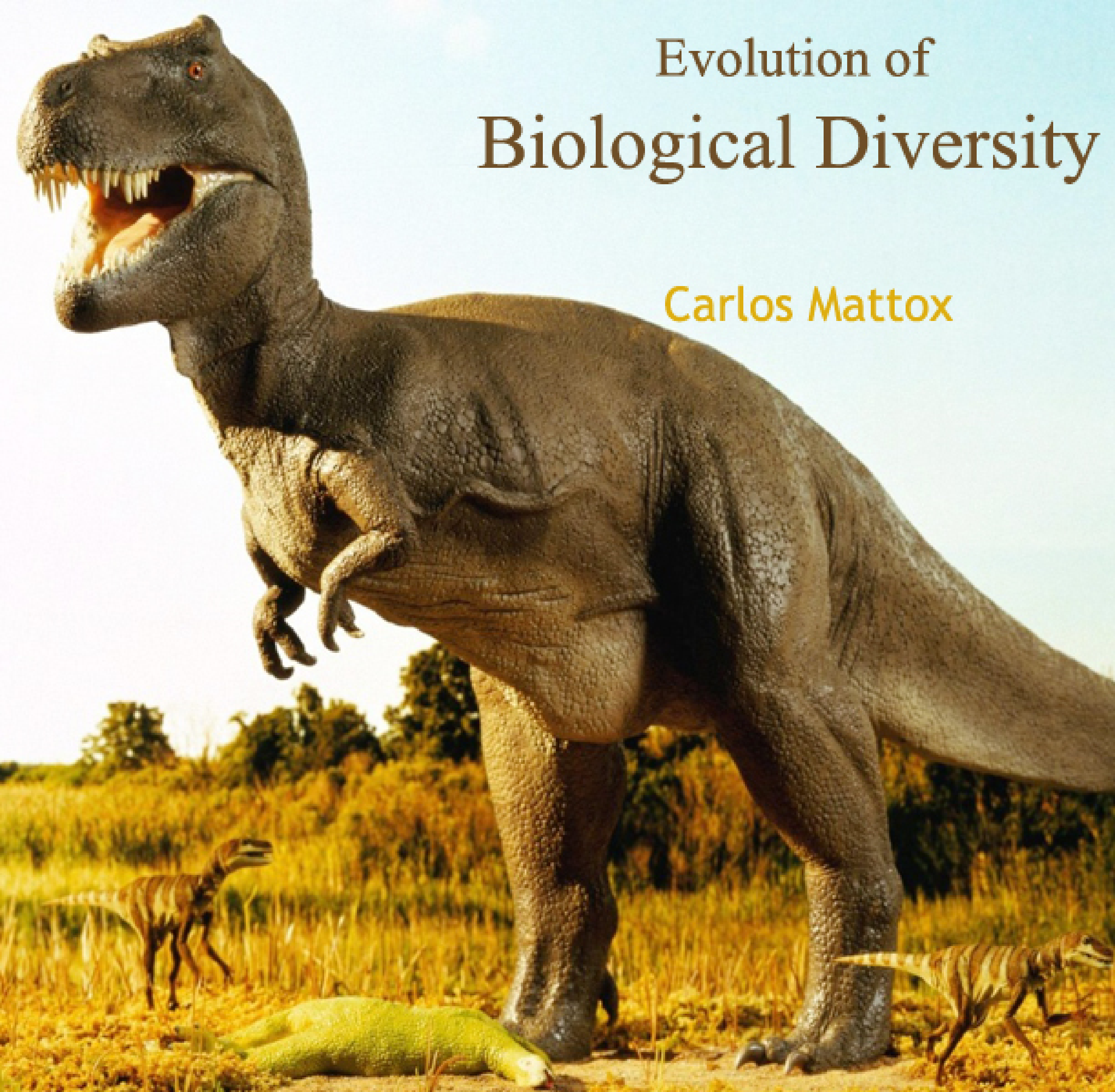
Evolution of Biological Diversity

Carlos Mattox



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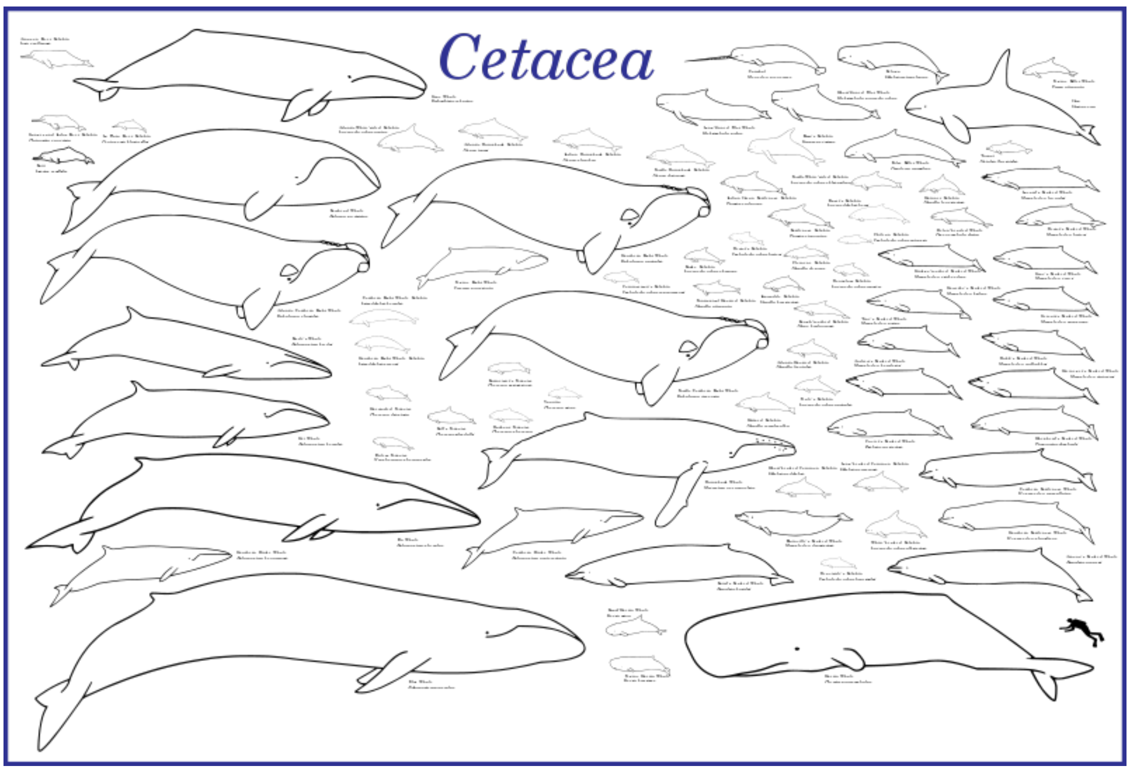
Evolution of Cetaceans



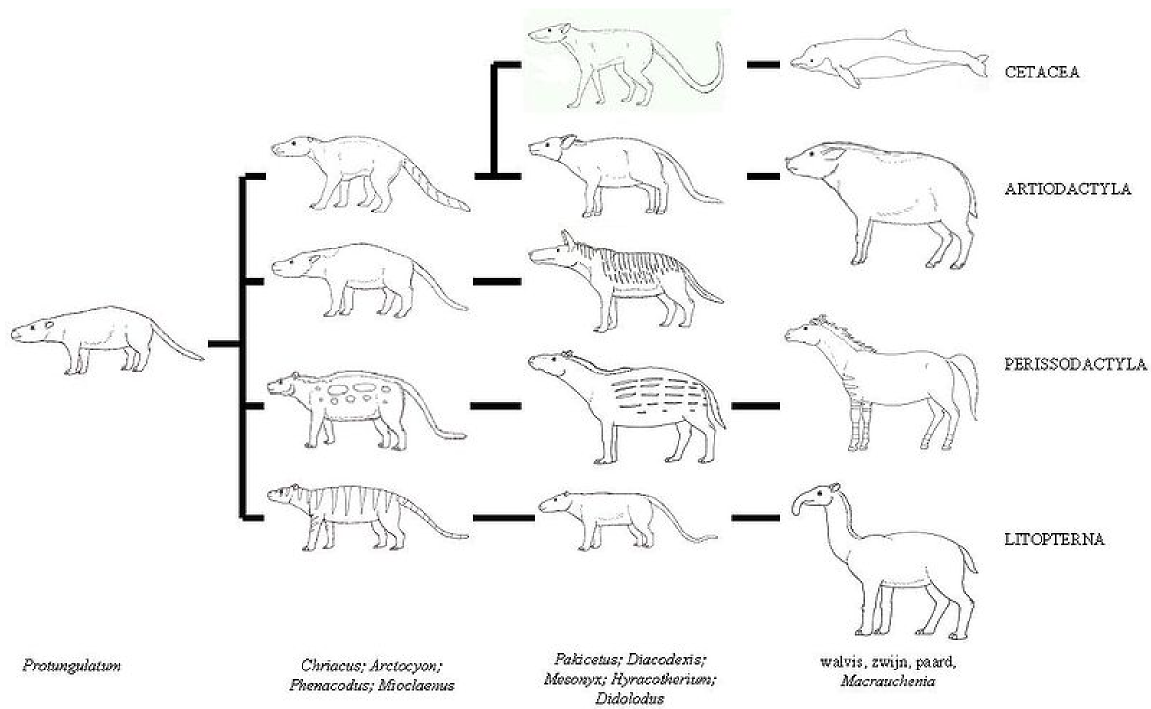
The approximately 80 modern species in the order Cetacea.

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

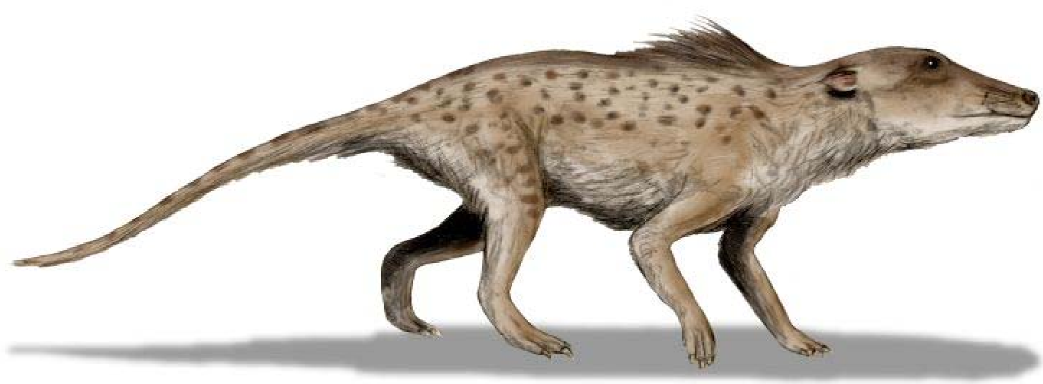


The family tree, including Ungulates.

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.

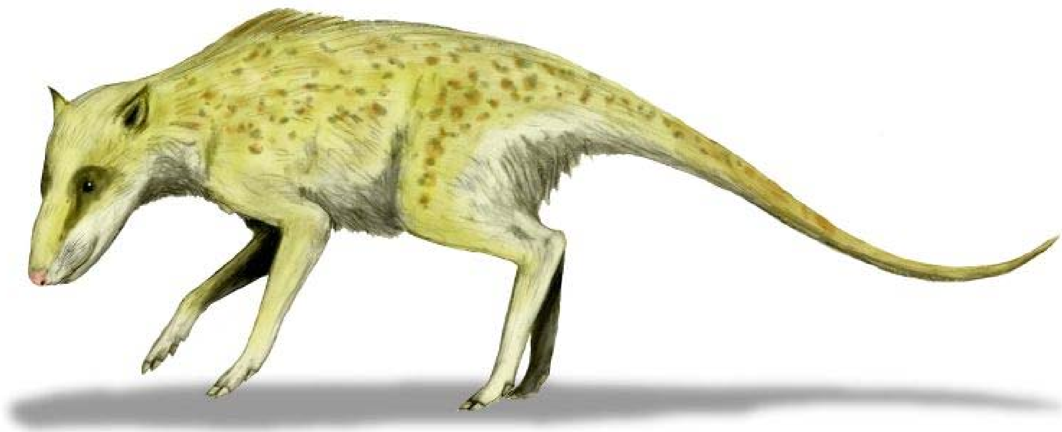
The recent discovery of *Pakicetus*, the earliest proto-whale (see below) supports the molecular data. The skeletons of *Pakicetus* demonstrate that whales did not derive directly from mesonychids. Instead, they are a form of artiodactyl (another type of ungulate) that began to take to the water after 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*

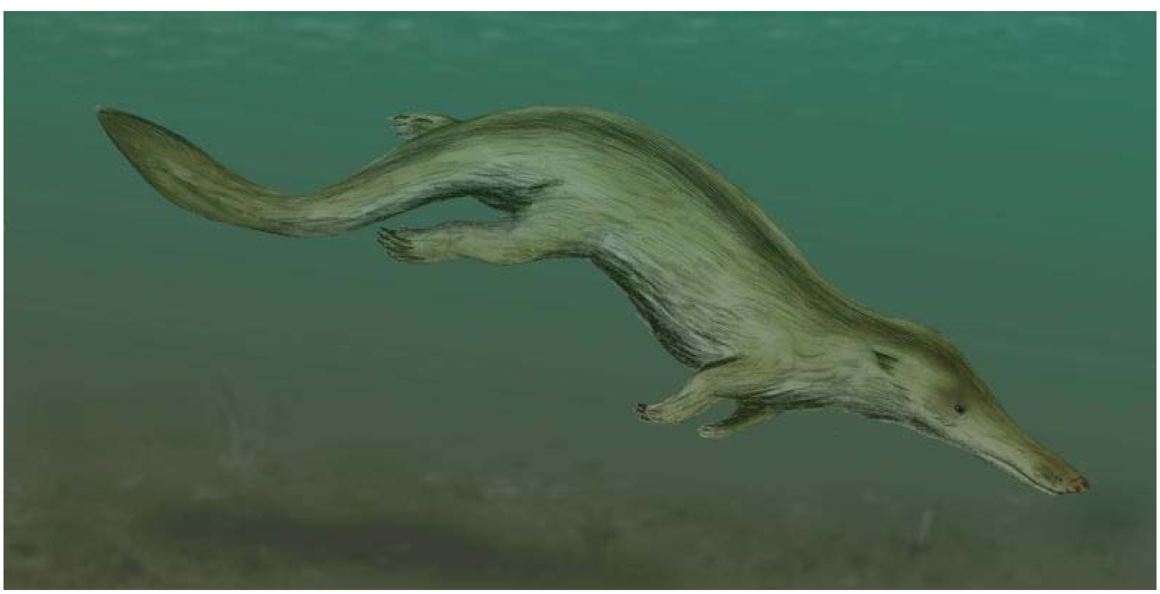
The pakicetids are hoofed-mammals that are sometimes classified as the earliest whales. They lived in the early Eocene, around 53 million years ago. They looked rather like dogs with hoofed feet and long, thick tails. They have been linked to whales by their ears: the structure of the auditory bulla 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

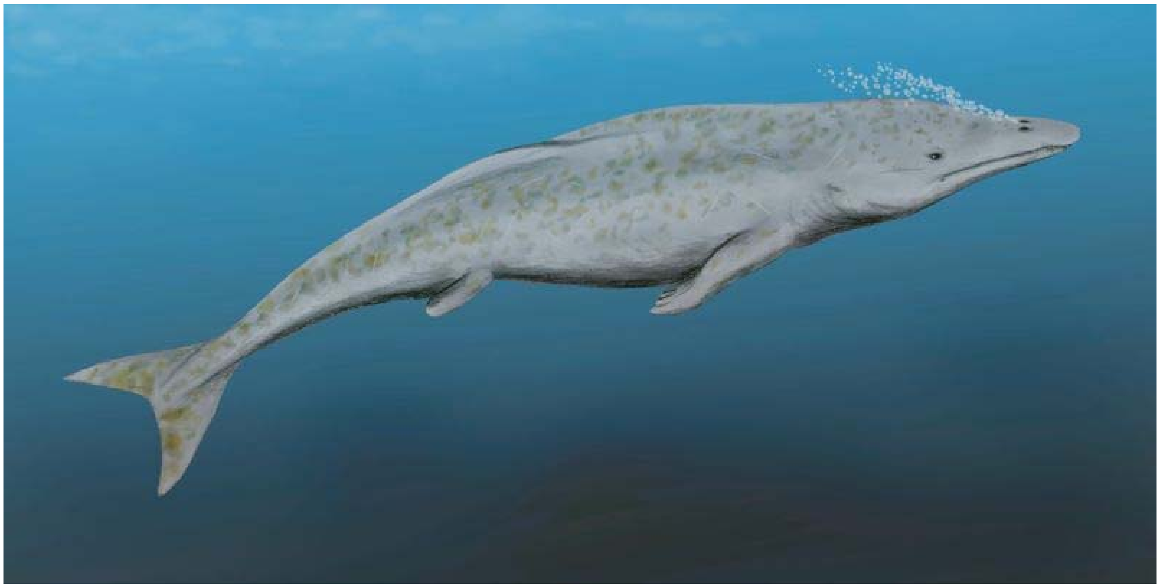
Reconstruction of *Ambulocetus natans*

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.

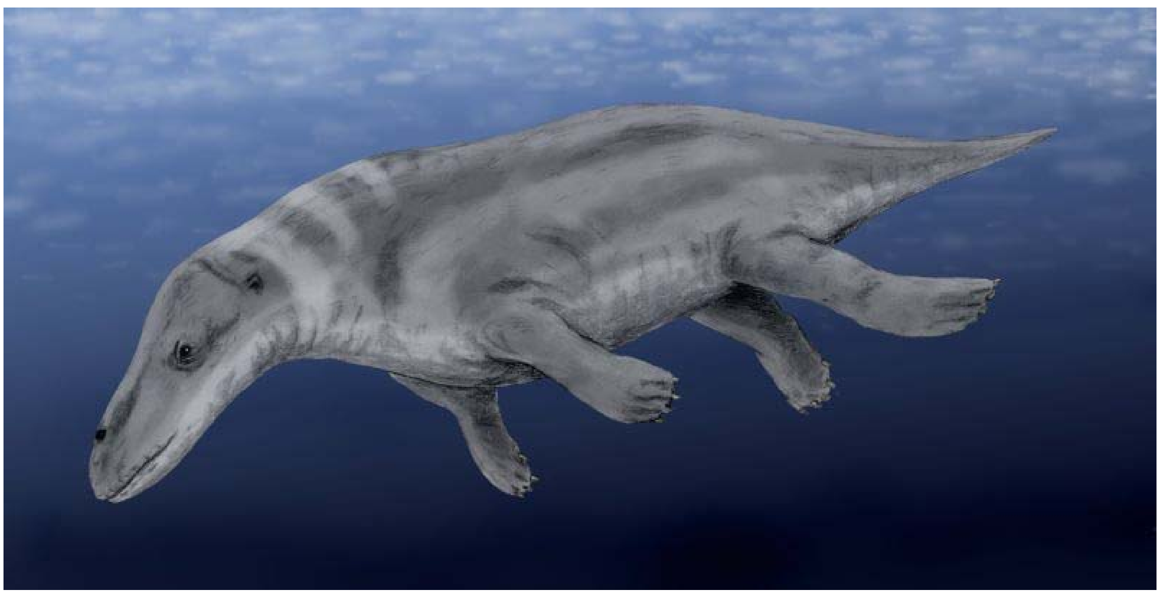
A smaller cousin of *Ambulocetus* was the remingtonocetidae family, which had longer snouts than *Ambulocetus*, and were slightly better adapted for underwater life. It has been speculated that they lived like modern sea otters, hunting for fish in the shallows.

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

Protocetids



Reconstruction of *Protocetus*

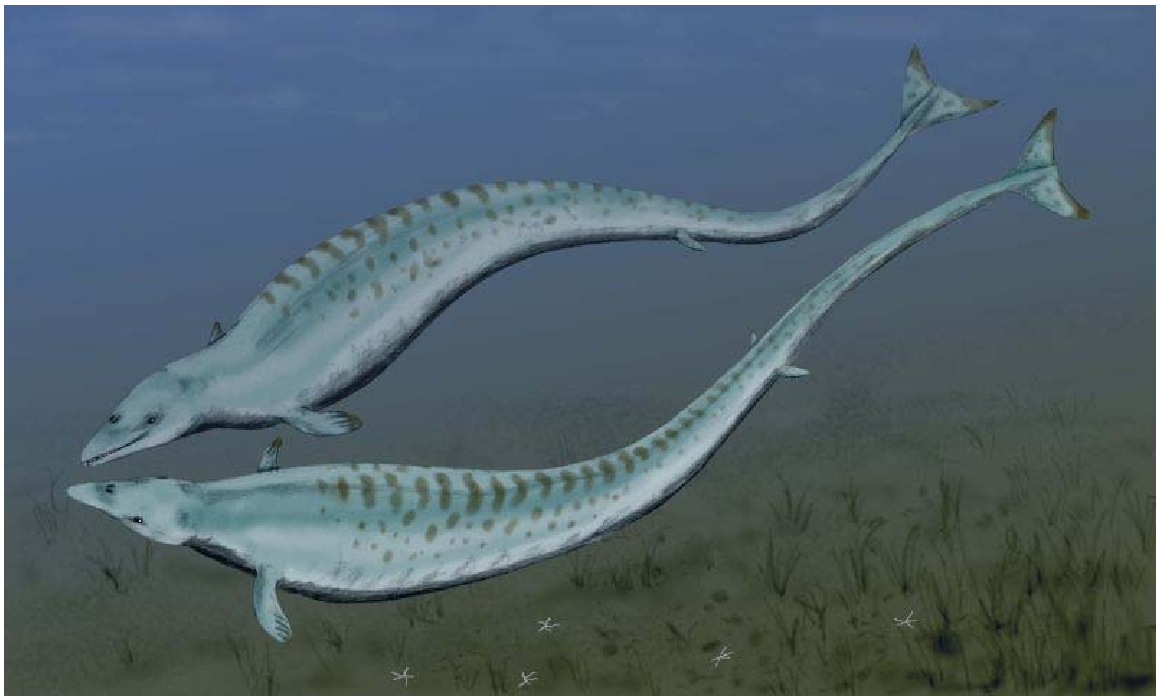


Reconstruction of *Rodhocetus*

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

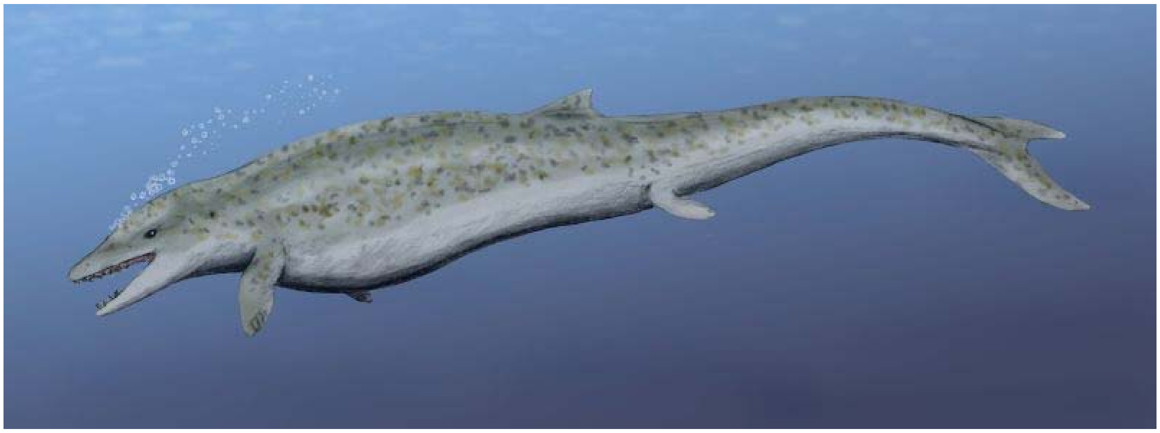
– was divided into loose vertebrae. However, the pelvis was still connected to one of the sacral vertebrae. Furthermore, the nasal openings are now halfway up the snout; a first step towards the telescoped condition in modern whales. Their supposed amphibious nature is supported by the discovery of a 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*

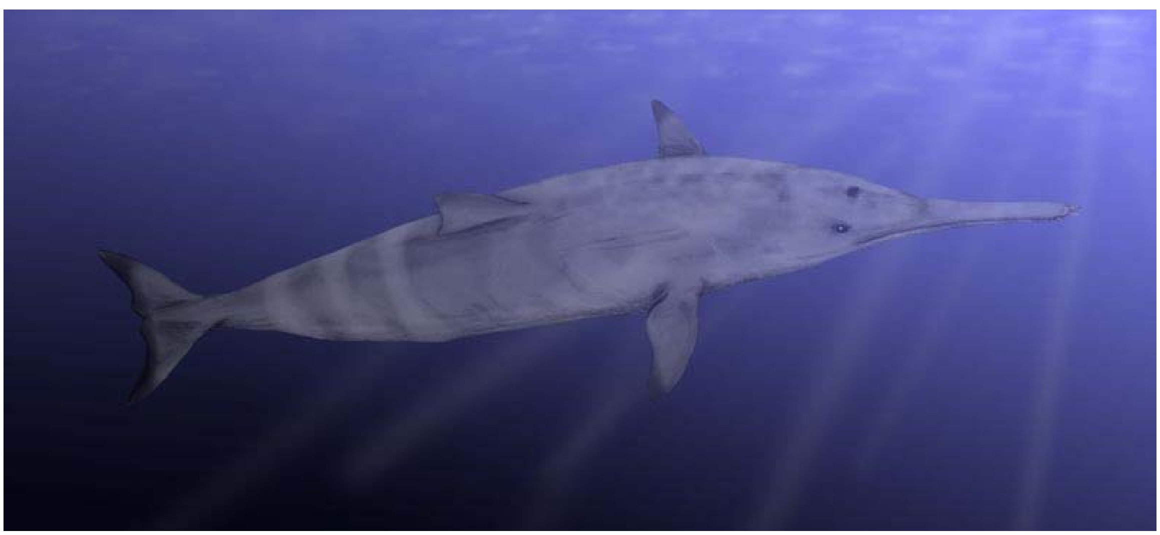
Basilosaurus (discovered in 1840 and initially mistaken for a reptile, hence its name) and *Dorudon* lived around 38 million years ago, and were fully recognizable whales which lived entirely in the ocean. *Basilosaurus* was as big as the larger modern whales, up to 18 m (60 ft) long; dorudontids were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

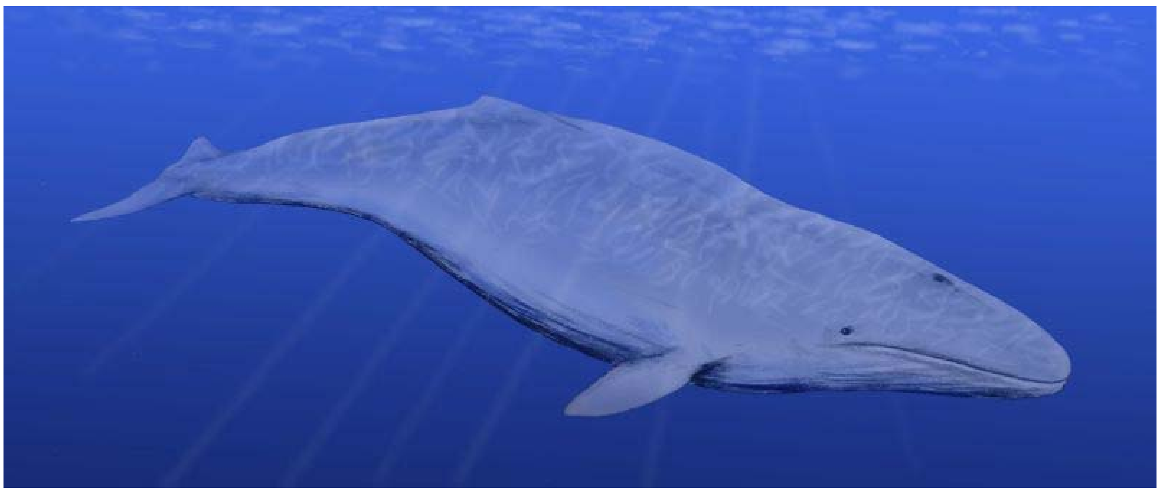
Early echolocation



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.

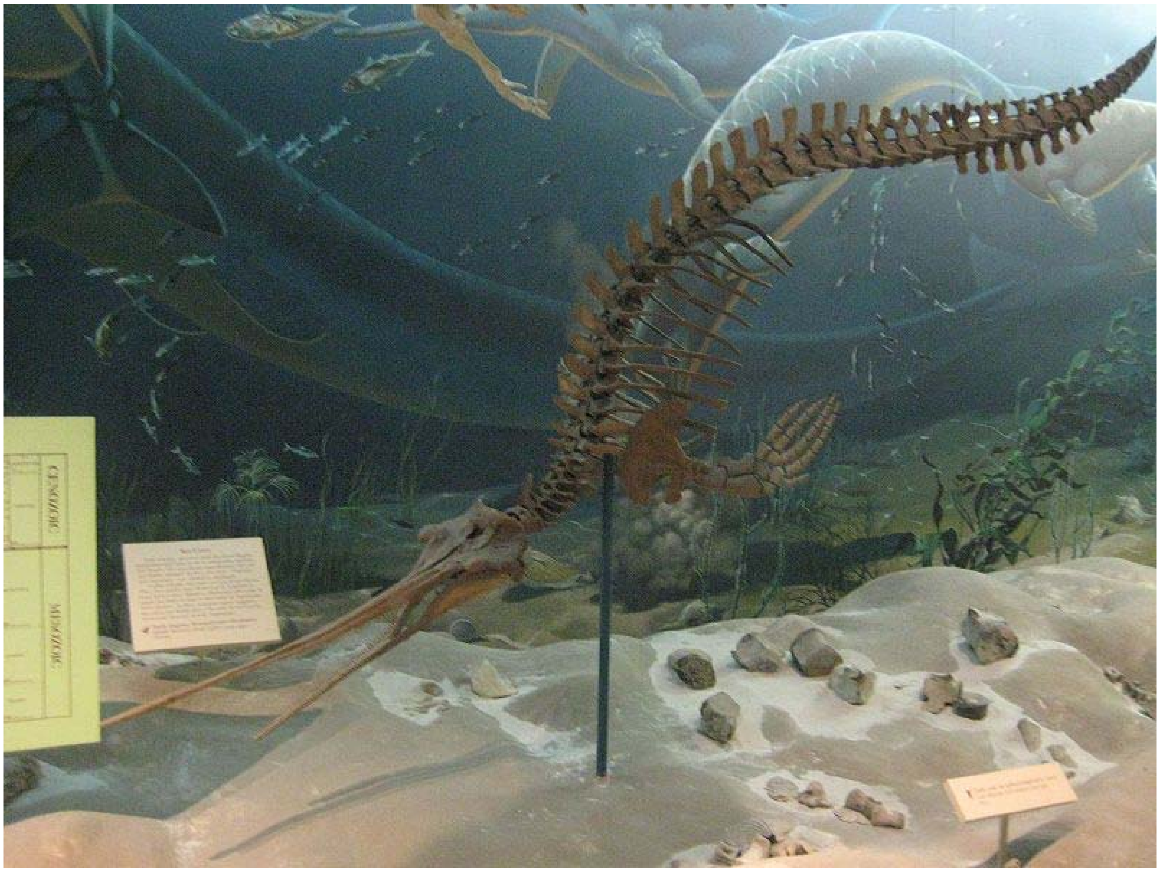
Early baleen whales



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

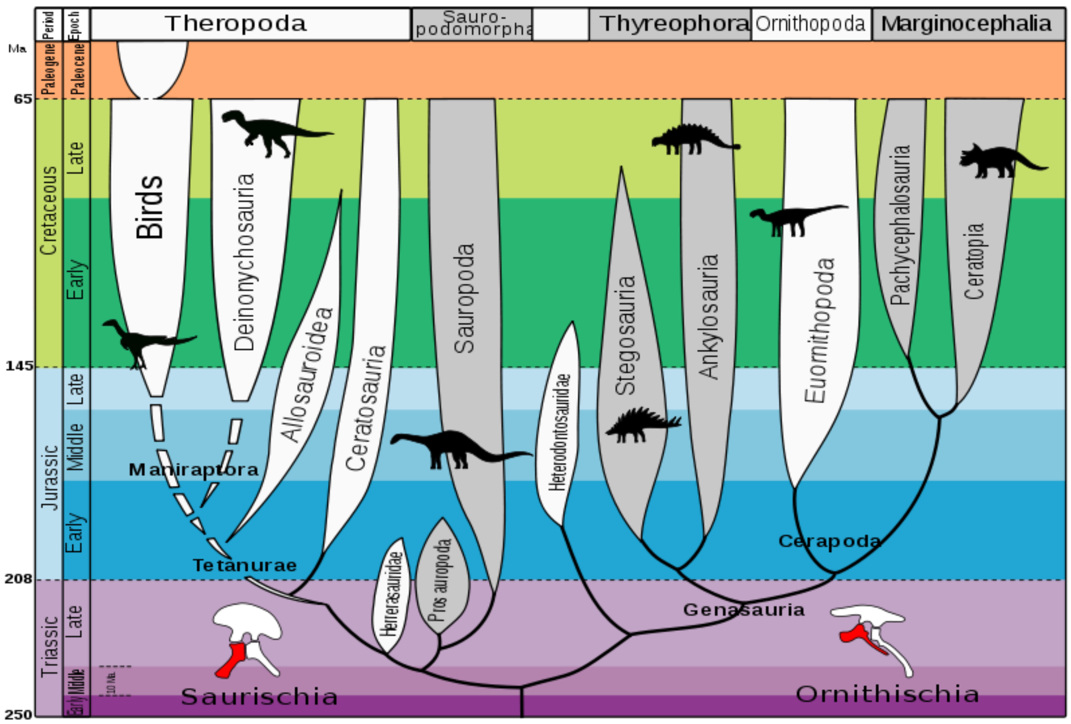
Today, the whale hind parts are internal and reduced. Occasionally, the genes that code for longer extremities cause a modern whale to develop miniature legs (known as atavism).

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.

Chapter- 2

Evolution of Dinosaurs



Evolution of dinosaurs

Dinosaurs evolved from the archosaurs 232-234 Ma (million years ago) in the Ladinian age, the latter part of the middle Triassic. Dinosauria is a well-supported clade, present in 98% of bootstraps. It is diagnosed by many features including loss of the postfrontal on the skull and an elongate deltopectoral crest on the humerus.

From archosaurs to dinosaurs

The process leading up the first dinosaurs can be followed through fossils of the early Archosaurs such as the Proterosuchidae, *Erythrosuchidae* and *Euparkeria* which have fossils dating back to 250 Ma, through mid-Triassic archosaurs such as *Ticinosuchus* 232-236 Ma. Crocodiles are also descendants of mid-Triassic archosaurs.

The dinosaurs can be defined as the last common ancestor of birds (Saurischia) and *Triceratops* (Ornithischia) and all the descendants of that ancestor. With that definition, the pterosaurs and several species of archosaurs narrowly miss out on being classed as dinosaurs. The pterosaurs are famous for flying through the Mesozoic skies on leathery wings. Archosaur genera that narrowly miss out on being classified as dinosaurs include *Schleromochlus* 220-225 Ma, *Lagerpeton* 230-232 Ma and *Marasuchus* 230-232 Ma.

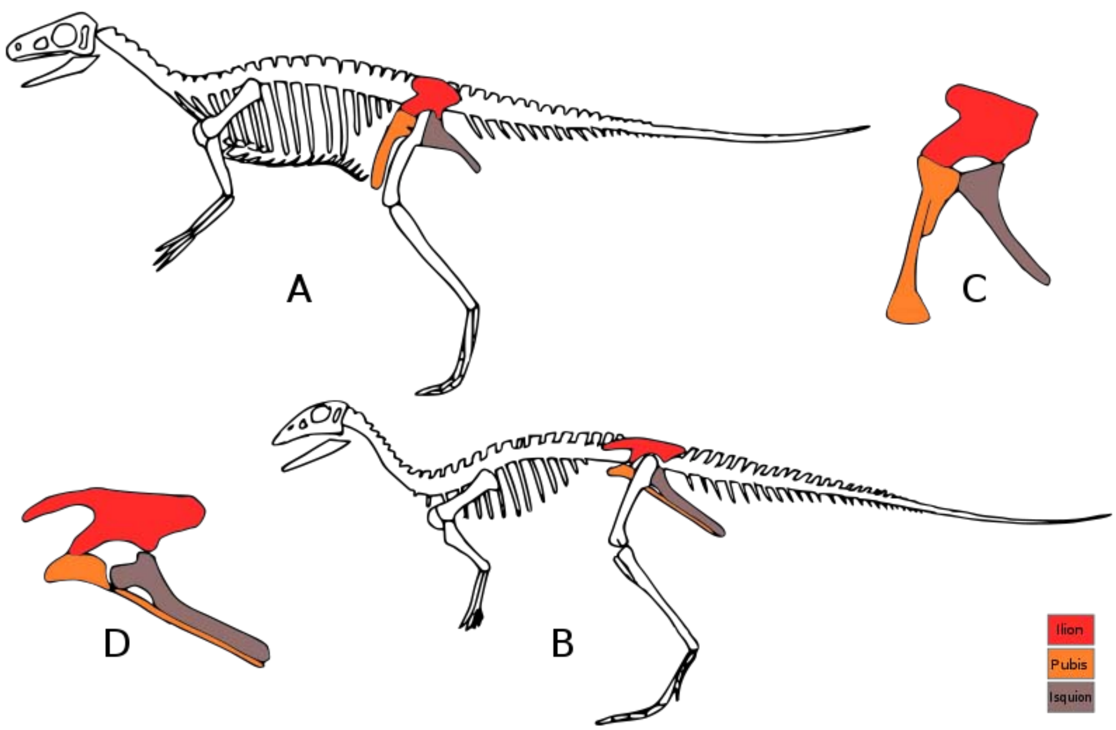
Earliest dinosaurs

The first known dinosaurs were bipedal predators that were one to two metres long.

Spondylosoma may or may not be a dinosaur; the fossils (all postcranial) are tentatively dated at 230-232 Ma.

The earliest confirmed dinosaur fossils include saurischian ('lizard-hipped') dinosaurs *Saturnalia* 225-232 Ma, *Herrerasaurus* 220-230 Ma, *Staurikosaurus* possibly 225-230 Ma, *Eoraptor* 220-230 Ma and *Alwalkeria* 220-230 Ma. *Saturnalia* may be a basal saurischian or a prosauropod. The others are basal saurischians.

Among the earliest ornithischian ('bird-hipped') dinosaurs is *Pisanosaurus* 220-230 Ma. Although *Lesothosaurus* comes from 195-206 Ma, skeletal features suggest that it branched from the main Ornithischia line at least as early as *Pisanosaurus*.



A. *Eoraptor*, an early saurischian, **B** *Lesothosaurus*, a primitive ornithischian, **C** *Staurikosaurus* (Saurischia) pelvis, **D** *Lesothosaurus* pelvis

It is clear from this figure that early saurischians resembled early ornithischians, but not modern crocodiles. Saurischians are distinguished from the ornithischians by retaining the ancestral configuration of bones in the pelvis. Another difference is in the skull, the upper skull of the Ornithischia is more solid and the joint connecting the lower jaw is more flexible; both are adaptations to herbivory and both can already be seen in *Lesothosaurus*.

Saurischia

Setting aside the basal Saurischia, the rest of the Saurischia are split into the Sauropodomorpha and Theropoda. The Sauropodomorpha is split into Prosauropoda and Sauropoda. The evolutionary paths taken by the Theropoda are very complicated. *The Dinosauria* (2004), a major reference work on dinosaurs, splits the Theropoda into groups Ceratosauria, Basal Tetanurae, Tyrannosauroidea, Ornithomimosauria, Therizinosauroidea, Oviraptorosauria, Troodontidae, Dromaeosauridae and Basal Avialae in turn. Each group branches off the main trunk at a later date.

Sauropodomorpha

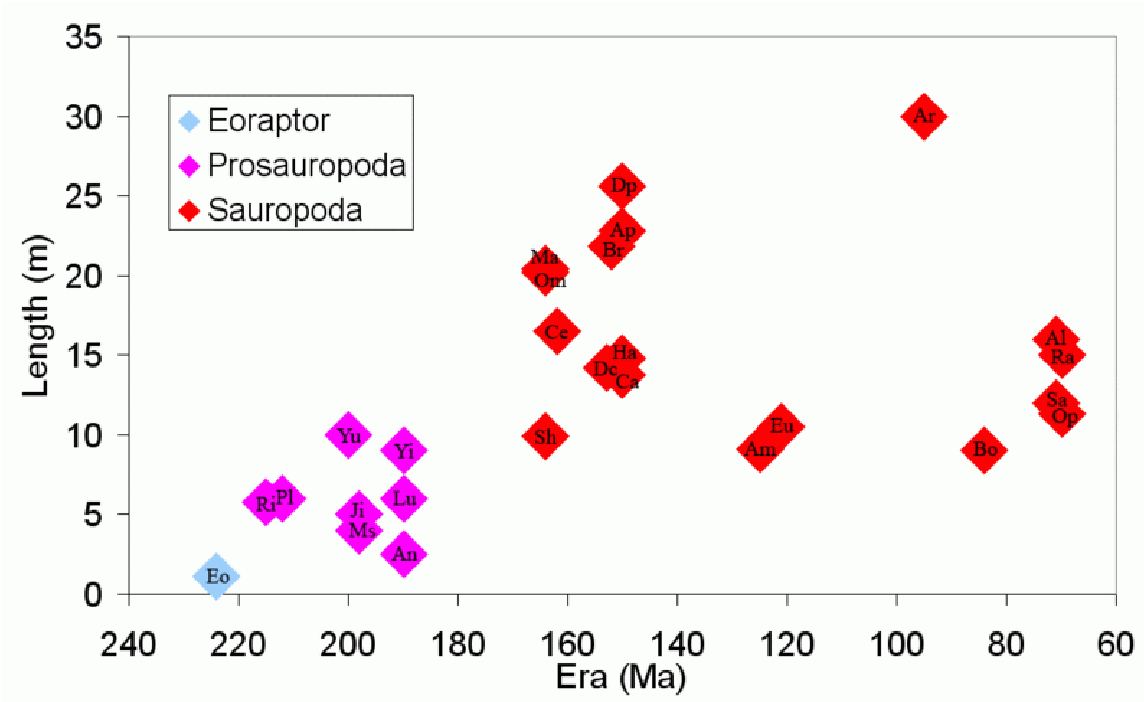
The first sauropodomorphs were prosauropods. Prosauropod fossils are known from the late Triassic to early Jurassic 227-180 Ma. They could be bipedal or quadrupedal and had developed long necks and tails and relatively small heads. They had lengths of 2.5 to 10 m and were primarily herbivorous. The earliest prosauropods, such as *Thecodontosaurus* from 205-220 Ma, still retained the ancestral bipedal stance and large head to body ratio.

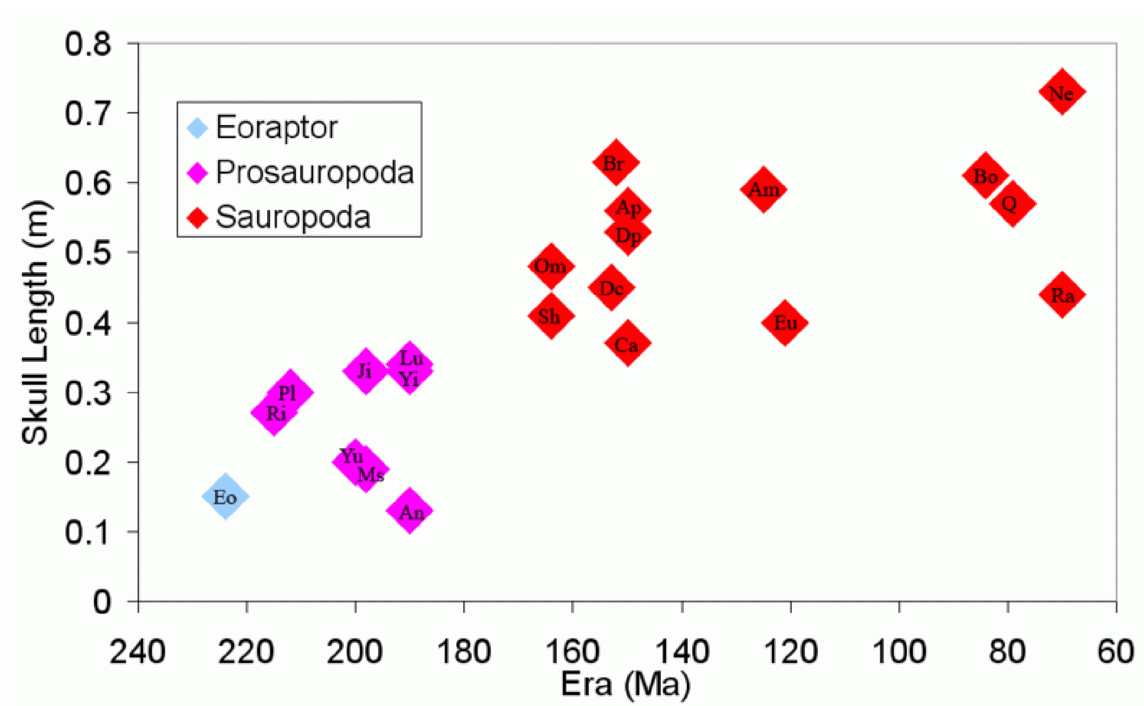
These evolved into the sauropods which became gigantic quadrupedal herbivores, some of which reached lengths of at least 26 m. Features defining this clade include a forelimb length to hindlimb length greater than 0.6. Most sauropods still had hindlimbs larger than forelimbs; one notable exception is *Brachiosaurus* whose long forelimbs suggest that it had evolved to feed from tall trees like a modern-day giraffe.

Sauropod fossils are found from the times of the earliest dinosaurs right up to the K-T extinction event, from 227 to 65 Ma. Most sauropods are known from the Jurassic, to be more precise between 227 and 121 Ma.

The Cretaceous sauropods form two groups. The Diplodocoidea lived from 121 to 65 Ma. The Titanosauriformes lived from 132 to 65 Ma. The latter clade consists of series of nested subgoups, the Titanosauria, the Titanosauridae and Saltasauridae. Both the Diplodocoidea and Titanosauriformes are descended from the Neosauropoda, the earliest of which lived in about 169 Ma.

The sauropods are famous for being the largest land animals that ever lived, and for having relatively small skulls. The enlargement of prosauropod and sauropod dinosaurs into these giants and the change in skull length is illustrated in the following charts.





Dinosaurs used in creating these charts are (in date order): Eo *Eoraptor*; Prosauropods Ri *Riojasaurus*, Pl *Plateosaurus*, Yu *Yunnanosaurus*, Ms *Massospondylus*, Ji *Jingshanosaurus*, An *Anchisaurus*, Lu *Lufengosaurus*, Yi *Yimenosaurus*, ; and Sauropods Sh *Shunosaurus*, Om *Omeisaurus*, Mm *Mamenchisaurus*, Ce *Cetiosaurus*, Dc

Dicraeosaurus, Br *Brachiosaurus*, Eu *Euhelopus*, Ap *Apatosaurus*, Ca *Camarasaurus*, Dp *Diplodocus*, Ha *Haplocanthosaurus*, Am *Amargasaurus*, Ar *Argentinosaurus (approx)*, Bo *Bonitasaura*, Q *Quaesitosaurus*, Al *Alamosaurus*, Sa *Saltasaurus*, Ra *Rapetosaurus*, Op *Opisthocoelicaudia*, Ne *Nemegtosaurus*.

With the exception of *Argentinosaurus* (included to fill a gap in time), these graphs show only the length of sauropods for whom near-complete fossil skeletons are known. It doesn't show other very large sauropods because these are only known from very incomplete skeletons. The ratio of skull length to body length is much higher in *Eoraptor* than in sauropods. The longest skull graphed is of *Nemegtosaurus*, which is not thought be a particularly large sauropod. The skull of *Nemegtosaurus* was found near the headless skeleton of 11 metre long *Opisthocoelicaudia*, and it has been suggested that they may be the same species, but see Nemegtosauridae.

The relationship between the evolution of large herbivores and large plants remains uncertain. About 50% of the plants over the time of the dinosaurs were conifers, they increased in number in the Triassic until stabilising in about 190 Ma. Cycads formed the second largest group until about 120 Ma. Ferns were present in roughly constant numbers the whole time. Flowering plants began about 120 Ma and by the end of the period had taken over from the cycads. All dinosaur herbivores appear to have been adversely affected by the extinction event at the end of the Jurassic.

Theropoda

By far the earliest fossils of Theropoda (not counting the basal saurischians) are of the Coelophysoidea, including *Coelophysis* and others, from late Triassic and early Jurassic 227-180 Ma. Cladistic analysis sometimes connects these to the group called Ceratosauria. Principal features of both include changes in the pelvic girdle and hind limb that differ between the sexes. Other ceratosauria first appear in the late Jurassic of western North America.

These are followed by the basal Tetanurae, of whom fossils have been found from the mid Jurassic to past the end of the early Cretaceous 180 Ma to 94 Ma. They have a relatively short maxillary tooth row. They did not all branch off the evolutionary line leading to coelurosaurs at the same time. Basal tetanurans include Megalosauridae, spinosaurids, a diverse clade of allosaurs, and several genera of less certain affinities, including *Compsognathus*. With the exception of *Compsognathus* they are large-bodied. Allosaurs form a distinct long-lived clade that share some cranial characters. They include the well known *Allosaurus* and *Sinraptor* among others.

The great radiation of Theropoda into many different clades of Coelurosauria must have happened in the mid to late Jurassic, because *Archaeopteryx* was around in about 152-154 Ma, and cladistic analysis has shown that many other groups of Coelurosauria branched off before that. Fossil evidence from China suggests that the earliest feathers were found on the primitive Coelurosauria. The most primitive of these, e.g. on the tyrannosauroid *Dilong*, were simply hollow-cored fibres that would have been useful for insulation but useless for flying.

Occasional bones and cladistic analyses point to the Tyrannosauroidea branching off from the other Theropoda early, in the middle Jurassic, although nearly complete skeletons haven't yet appeared before *Eotyrannus* from 121-127 Ma, and the many close relatives of *Tyrannosaurus* itself don't appear before 84 Ma, near the end of the late Cretaceous.

Ornithomimosauria fossils are known from 127 to 65 Ma. The earliest branch from the main line of Ornithomimosauria is believed to be *Harpymimus*.

The Therizinosauroidea are unusual theropods in being almost all vegetarian. Fossil Therizinosauroidea are known from 127 to 65 Ma.

Maniraptorans include Oviraptorosauria, Deinonychosaurs and birds. They are characterized by an ulna with a curved shaft.

Oviraptorosaurian fossils are known from 127 to 65 Ma. They have a toothless skull that is extremely modified. The skeleton has an unusually short tail.

Deinonychosaurs, named after the enlarged sickle-shaped second digit of the hand, are closely related to birds. They have two distinct families, Troodontidae and Dromaeosauridae. Troodontid fossils are known from 127 to 65 Ma. They have the more slender build, and longer limbs. The earliest named troodontid fossil known is *Sinornithoides*. Dromaeosaurid fossils are known from about 127 to 65 Ma with the exception of *Utahraptor*. The skeletal remains of *Utahraptor* are about 127-144 Ma. This is interesting because according to a recent cladistic analysis, *Utahraptor* is about as far from the ancestral Theropoda as it is possible to get, further than *Archaeopteryx*. Dromaeosaurids have a larger second digit; this family includes the well known dinosaurs *Dromaeosaurus*, *Deinonychus* and *Velociraptor*.

Ancient birds (Avialae) include both the Aves, which are defined as descendants of the common ancestor of modern birds and *Archaeopteryx*, and the more primitive *Epidendrosaurus*. Fossil birds stretch down from 154 Ma through the K-T extinction event at 65 Ma to the present day. Scores of complete skeletons have now been found of the more recent *Confuciusornis*, which is an early representative of the Ornithurae. Ornithurans all have a bony pygostyle, to which tail feathers are anchored.

Ornithischia

Ornithischia, as the name indicates, was coined for the birdlike pelvic girdle, although they are not the ancestors of birds.

The ornithischian skull and dentition was modified very early by a herbivorous diet. *Lesothosaurus* separated early, but the skull of *Lesothosaurus* already shows such adaptations, with broad proportions, a less flexible upper jaw, and a more mobile connection for the lower jaw.

The major clades were already established by the early Jurassic. The ornithischians divided into armoured thyreophorans and unarmoured ornithopods and marginocephalians.

Thyreophorans

Surface body armour (scutes) is the most striking feature of the thyreophorans. *Scutellosaurus* has these but otherwise differs little from *Lesothosaurus*. It has a long tail and combined bipedal-quadrupedal posture that separates it from all later thyreophorans including Stegosauria and Ankylosauria. These two clades, although quite different in overall appearance, share many unusual features in the skull and skeleton.

Stegosaurs are easily recognised by the prominent row of plates above the spine and ling spines on the tail. Most stegosaurs, but not *Stegosaurus*, also have a spine over each shoulder. These spines and plates have evolved from the earlier surface scutes. *Huayangosaurus* is the oldest and most primitive known stegosaur.

Ankylosaurs are easily recognised by their extensive body armour. The skull is heavily ossified. Early in their evolution, ankylosaurs split into the Nodosauridae and Ankylosauridae, distinguished by features of the skull.

Ornithopoda

Ornithopods fall into one of three distinct clades - Heterodontosauridae, Hypsilophodontidae, and Iguanodontia.

Heterodontosaurids are very small (body length < 1 m) and lived in the early to late Jurassic. Apart from *Abrictosaurus* all have a short upper canine and longer lower canine. The forelimbs in known fossils are unusually long.

Hypsilophodontids more closely resemble their ancestors than the heterodontosaurids do. The most distinctive features are short scapula and rod-shaped pre-pubic process. The earliest is *Agilisaurus* from the middle Jurassic of China.

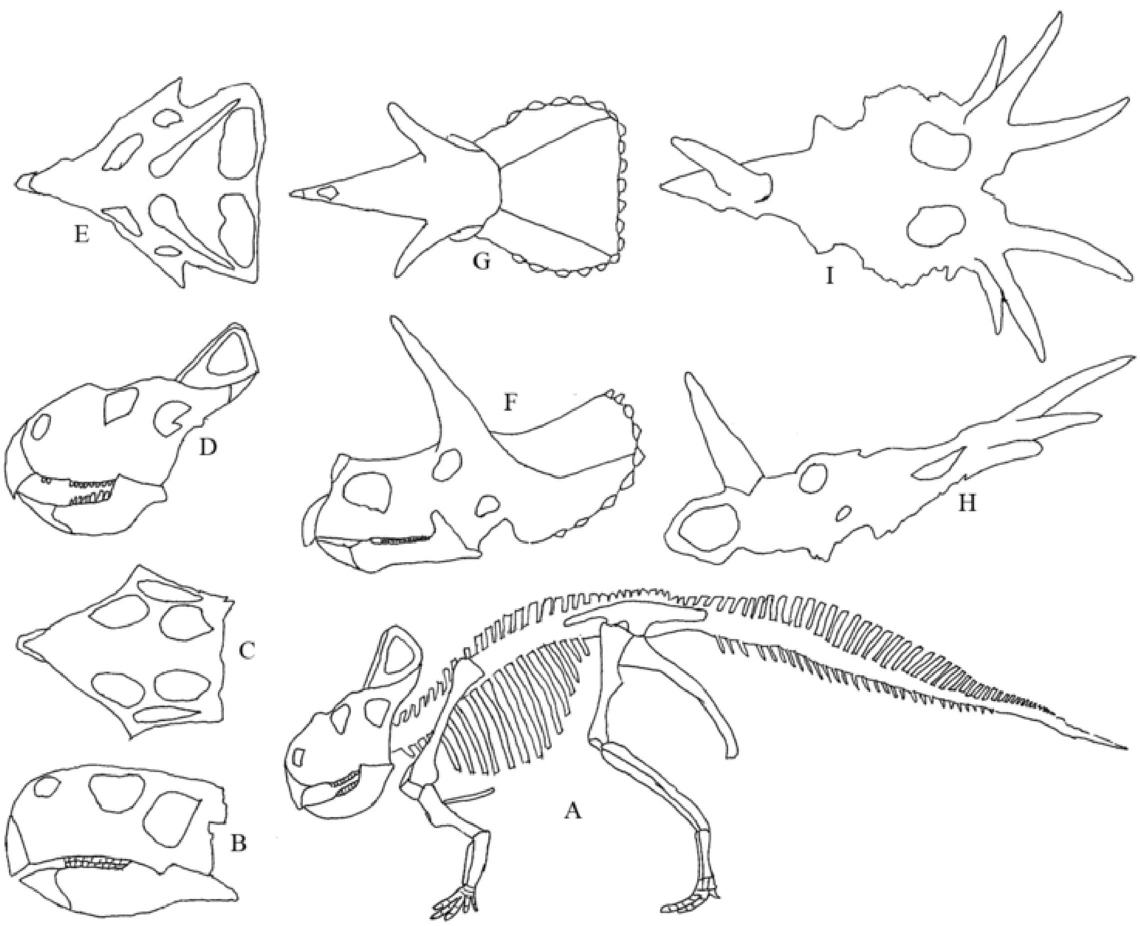
Iguanodontians are a diverse but morphologically tight knit array of genera known from fossils of the late Cretaceous. Significant modifications include the evolution of tooth batteries, a ligament-bound metacarpus and a digitigrade hand posture. *Tenontosaurus* is the most basal iguanodontian. Others include *Iguanodon*, *Camptosaurus* and *Muttaburrasaurus*.

Marginocephalia

Marginocephalia are named for a shelf that projects over the back of the skull. They include the pachycephalosaurians and ceratopsians.

Pachycephalosaurs are best known for their thick upper fronts to their skull. The oldest known is *Stenopelix*, from the early Cretaceous of Europe.

Ceratopsians, famous for *Protoceratops*, *Triceratops* and *Styracosaurus* illustrate the evolution of frilled and horned skulls. The frills evolved from the shelf common to all Marginocephalia. Ceratopsians are separated into basal ceratopsians, including the parrot-beaked *Psittacosaurus*, and neoceratopsians.



Diversity of ceratopsian skulls. A) Skeleton of *Protoceratops*. B) to I) Skulls. B) & C) *Psittacosaurus* side & top. D) & E) *Protoceratops* side & top. F) & G) *Triceratops* side & top. H) & I) *Styracosaurus* side (without lower jaw) & top.

The sequence of ceratopsian evolution in the Cretaceous is roughly from *Psittacosaurus* (121 -99 Ma) to *Protoceratops* (83 Ma) to (*Triceratops* 67 Ma and *Styracosaurus*

72 Ma). In side view the skull of *Psittacosaurus* bears very little resemblance to that of *Styracosaurus* but in top view a similar pentagonal arrangement can be seen.

Fossil record

The first few lines of primitive dinosaurs diversified rapidly through the Triassic period; dinosaur species quickly evolved the specialised features and range of sizes needed to exploit nearly every terrestrial ecological niche. During the period of dinosaur predominance, which encompassed the ensuing Jurassic and Cretaceous periods, nearly every known land animal larger than 1 meter in length was a dinosaur.

One measure of the quality of the fossil record is obtained by comparing the date of first appearance with the order of branching of a cladogram based on the shape of fossil elements. Close correspondence exists for ornithiscians, saurischians and subgroups. The cladogram link between coelophysids and ceratosaurs is an exception, it would place the origin of coelophysids much too late. The simplest explanation is convergent evolution - ceratosaur bones evolved independently into a shape that resembles that of the earlier coelophysids. The other possibility is that ceratosaurs evolved much earlier than the fossil record suggests.

Most dinosaur fossils have been found in the Norian-Sinemurian, Kimmeridgian-Tithonian, and Campanian-Maastrichtian periods. Continuity of lineages across the intervening gaps shows that those gaps are artifacts of preservation rather than any reduction in diversity or abundance.

In many instances, cladistic analysis shows that ancestral lineages of varying durations fall in those gaps. The length of missing ancestral lineages in 1997 range from 25 Ma (*Lesothosaurus*, Genasauria, Hadrosauroidea, Sauropoda, Neoceratopsia, Coelurosauria) to 85 Ma (Carcharodontosauridae). Because the dinosaurian radiation began at small body size, the unrecorded early history may be due to less reliable fossilization of smaller species. However, some missing lineages, notably of Carcharodontosauridae and Abelisauridae, require alternative explanations because the missing range extends across stages rich in fossil material.

Evolutionary trends

Body size

Body size is important because of its correlation with metabolism, diet, life history, geographic range and extinction rate. The modal body mass of dinosaurs lies between 1 and 10 tons throughout the Mesozoic and across all major continental regions. That said, there was a trend towards increasing body size within many dinosaur clades, including the Thyreophora, Ornithopoda, Pachycephalosauria, Ceratopsia, Sauropomorpha, and basal Theropoda. Marked decreases in body size have also occurred in some lineages, but are more sporadic. The best known example is the decrease in body size leading up to the first birds; *Archaeopteryx* was below 10 kg in weight, and later aves *Confuciusornis* and *Sinornis* are starling- to pigeon-sized.

Mobility

The ancestral dinosaur was a biped. The evolution of a quadrupedal posture occurred four times, among the ancestors of Euornithopoda, Thyreophora, Ceratopsia and Sauropodomorpha. In all four cases this was associated with an increase in body size, and in all four cases the trend is unidirectional without reversal.

Dinosaurs exhibit a pattern of the reduction and loss of fingers on the lateral side of the hand (digits III, IV and V). The primitive function of the dinosaur hand is grasping with a partially opposable thumb, rather than weight-bearing.

Effect of food sources

The ancestral dinosaur was a carnivore. Herbivory among dinosaurs arose three times, at the origin of the ornithischian, sauropodomorph, and therizinosaurid clades. Individual therizinosaurids are herbivorous or omnivorous. Herbivory among the ornithischians and sauropodomorphs was never reversed.

The potential co-evolution of plants and herbivorous dinosaurs has been subject to extensive speculation. The appearance of prosauropods in the late Triassic has been tentatively linked either to the demise or diversification of types of flora at that time. The rise of ceratopsids and iguanodont and hadrosaurid ornithopods in the Cretaceous has been tentatively linked to the angiosperm radiation. Unfortunately, there are still no hard data on dietary preferences of herbivorous dinosaurs, apart from data on chewing technique and gastroliths.

Biogeography

Dinosaurian faunas, which were relatively uniform in character when Pangaea began to break up, became markedly differentiated by the close of the Cretaceous. Biogeography is based on the splitting of an ancestral species by the emplacement of a geographic barrier. Interpretation is limited by a lack of fossil evidence for eastern North America, Madagascar, India, Antarctica and Australia. No unequivocal proof of the biogeographical action on Dinosaur species has been obtained, but some authors have outlined centres of origin for many dinosaur groups, multiple dispersal routes, and intervals of geographic isolation.

Dinosaurs that have been given as evidence of biogeography include abelisaurid theropods from South America and possibly else where on Gondwana.

Relationships between dinosaurs show abundant evidence of dispersal from one region of the globe to another. Tetanuran theropods travelled widely through western North America, Asia, South America, Africa and Antarctica. Pachycephalosaurs and ceratopsians show clear evidence of multiple bidirectional dispersion events across Beringa.

Extinction

The Cretaceous–Tertiary extinction event, which occurred 65.5 million years ago at the end of the Cretaceous period, caused the extinction of all dinosaurs except for the line that had already given rise to the first birds.

Chapter- 3

Evolutionary History of Cephalopods

The cephalopods have a long geological history, with the first nautiloids found in late Cambrian strata, and purported stem-group representatives present in the earliest Cambrian lagerstätten.

The class developed during the middle Cambrian, and underwent pulses of diversification during the Ordovician period to become diverse and dominant in the Paleozoic and Mesozoic seas. Small shelly fossils such as *Tommotia* were once interpreted as early cephalopods, but today these tiny fossils are recognized as sclerites of larger animals, and the earliest accepted cephalopods date to the Middle Cambrian Period. During the Cambrian, cephalopods are most common in shallow near-shore environments, but they have been found in deeper waters too. Cephalopods were thought to have "undoubtedly" arisen from within the tryblidiid monoplacophoran clade. However genetic studies suggest that they are more basal, forming a sister group to the scaphopoda but otherwise basal to all other major mollusc classes.

Traditional view of origins

The cephalopods were once thought to have evolved from a monoplacophoran-like ancestor with a curved, tapering shell, and to be closely related to the gastropods (snails). The similarity of the early shelled cephalopod *Plectronoceras* to some gastropods was used in support of this view. The development of a siphuncle would have allowed the shells of these early forms to become gas-filled (thus buoyant) in order to support them and keep the shells upright while the animal crawled along the floor, and separated the true cephalopods from putative ancestors such as *Knightoconus*, which lacked a siphuncle. Negative buoyancy (i.e. the ability to float) would have come later, followed by swimming in the Plectronocerida and eventually jet propulsion in more derived cephalopods. However, because chambered shells are found in a range of molluscs – monoplacophora and gastropods as well as cephalopods – a siphuncle is essential to ally a fossil shell conclusively to the cephalopoda. Chambered gastropods can be distinguished from cephalopod shells by the absence of a siphuncle, the irregular spacing of septa, the layering of the shell and (in younger or unmetamorphosed rocks) its microstructure, and the relatively thick width of the shell. The earliest such shells do not have the muscle scars which would be expected if they truly had a monoplacophoran affinity. Additionally, the discovery that *Nectocaris pteryx*, which did not have a shell and appeared to possess jet propulsion in the manner of "derived" cephalopods, complicated the question of the order in which cephalopod features developed.

Early shelly record

Fossil orthoconic nautiloid from the Ordovician of Kentucky; an internal mold showing siphuncle and half-filled camerae, both encrusted.

Understanding of early cephalopod origins is by necessity biased by the available fossil material, which on the whole consists of shelly fossils. Critical fossils are detailed below; since their stratigraphic age has guided the interpretation of the fossils, they are listed in descending order of age.

Cambrian cephalopods

With the exception of the shelly genera *Ectenolites* and *Eoclarkoceras*, none of the 30+ Cambrian cephalopod genera are known to have survived into the Ordovician. Cambrian cephalopods differ from their descendants by account of their small size (a few centimetres in length); long, tapering shells; smooth shell surfaces; closely-spaced septa; and lack of deposits in their body chamber; several more specific features are also only seen in certain groups of Cambrian cephalopod.

Knightoconus

Knightoconus is a Cambrian monoplacophoran thought to represent an ancestor to the cephalopods. It had a chambered, conical shell, but lacked a siphuncle. Although earlier molluscan fossils are also septate, *Knightoconus* is the latest septate mollusc before the first sipunculate cephalopods – a point that has been taken to prove its relevance to the cephalopoda. The absence of this siphuncle has been taken as evidence against cephalopod ancestry – how, it is argued, could a siphuncle evolve to penetrate existing septa? The prevailing argument suggests that a strand of tissue remained attached to the previous septum as the mollusc moved forwards and deposited its next septum, producing an obstacle to the complete closure of the septum and becoming mineralised itself. 10 or more septa are found in mature individuals, occupying around a third of the shell – septa form very early and have been found in specimens as small as 2 mm in length. Septa are uniformly spaced, which is inconsistent with a gastropod affinity. Unlike monoplacophoran fossils, there is no evidence of muscle scarring in *Knightoconus* fossils.

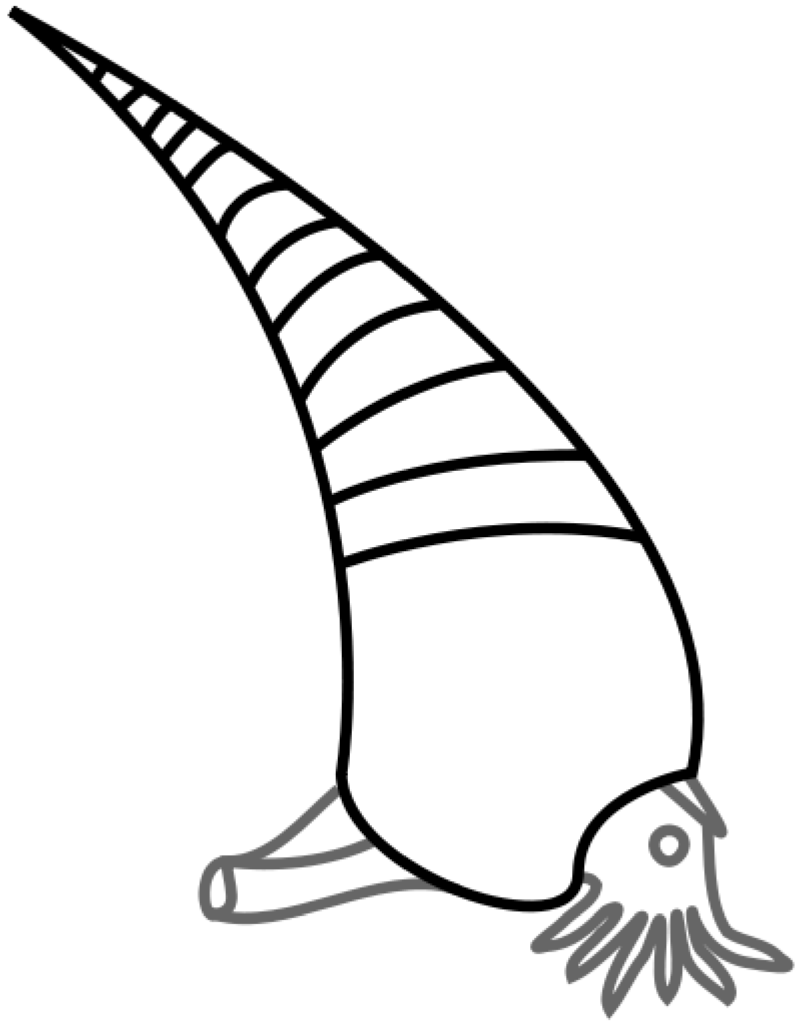
Plectronoceras

Plectronoceras is arguably the earliest known crown-group cephalopod, dating to the Upper Cambrian. Its 14 known specimens hail from the basal Fengshan Formation (north-east China) of the earliest Fengshanian stage. None of the fossils are complete, and none show the tip or opening of the shell. Approximately half of its shell was filled with septa; 7 were recorded in a 2 cm shell. Its shell contains transverse septa separated by about half a millimetre, with a siphuncle on its concave side. Its morphology matches closely to that hypothesised for the last common ancestor of all cephalopods, and the Plectronocerida have been said to be the ancestors of the Ellesmerocerids, the first "true cephalopods".

Yochelcionellids

The Yochelcionellids have given rise to the "snorkel hypothesis". These fossils are aseptate helcionellids with a snorkel-like tube on one surface. The snorkel has been seized upon as characteristic of a cephalopod-like water circulatory system, or perhaps as a precursor to the siphuncle. However, neither of these theories have been borne out.

Ellesmerocerida



Sketch of the soft-part anatomy of early ellesmeroceridans

The earliest true cephalopod order to emerge was the Ellesmerocerida, which were quite small organisms; their shells were slightly curved, and the internal chambers were closely spaced. The siphuncle penetrated the septa with meniscus-like holes. This marks an important difference from the earlier cephalopods, whose siphuncle was positioned at the edge of the septum and against the shell wall. On the basis of muscle scars preserved in such genera as *Paradakeoceras* and *Levisoceras*, these animals are reconstructed with a straight body and dorsal shell, with the head at the anterior, concave surface of the shell, and the funnel – consisting of a pair of folds in the foot – at the rear — not juxtaposed with the head as in later, oncocerid-like forms.

Early Ordovician diversity

The Ellesmerocerids were the only shelled cephalopods that survived the end-Cambrian extinction, and all subsequent cephalopods, which diversified throughout the Ordovician period, are thus thought to be derived from these forms.

Early cephalopods had fine shells that could not cope with the pressures of deep water. In the mid Tremadoc, these were supplemented by larger shells around 20 cm in length; these larger forms included straight and coiled shells, and fall into the orders Endocerida (with wide siphuncles) and Tarphycerida (with narrow siphuncles).

By the mid Ordovician these orders are joined by the Orthocerids, whose first chambers are small and spherical, and Lituitids, whose siphuncles are thin. The Oncocerids also appear during this time; they are restricted to shallow water and have short exogastric conchs. The mid Ordovician saw the first cephalopods with septa strong enough to cope with the pressures associated with deeper water, and could inhabit depths greater than 100–200 m. The wide-siphuncled Actinocerida and the Discocerida both emerged during the Darriwilian. The direction of coiling would prove to be crucial to the future success of the lineages; endogastric coiling would only permit large size to be attained with a straight shell, whereas exogastric coiling – initially rather rare – permitted the spirals familiar from the fossil record to develop, with their corresponding large size and diversity. (Endogastric mean the shell is curved so as the ventral or lower side is longitudinally concave (belly in); exogastric means the shell is curved so as the ventral side is longitudinally convex (belly out) allowing the funnel to be pointed backwards beneath the shell.)

Curved shells brought a number of benefits. Firstly, minerals are not required in as large quantities, as each successive whorl builds on the one before. Also, the organism is more stable (its centre of mass coincides with its centre of buoyancy) and more manoeuvrable.

Early cephalopods were likely predators near the top of the food chain. In the Early Palaeozoic, their range was far more restricted than today; they were mainly constrained to sub-littoral regions of shallow shelves of the low latitudes, and usually occur in association with thrombolites. A more pelagic habit was gradually adopted as the Ordovician progressed. Deep-water cephalopods, whilst rare, have been found in the Lower Ordovician – but only in high-latitude waters.

Fossils mistaken for cephalopods

A number of fossils have historically been considered to represent components of the cephalopods' history, but been reinterpreted on the basis of additional material.

Volborthella

When it was discovered in 1888, it was thought that the early Cambrian *Volborthella* was a cephalopod. However discoveries of more detailed fossils showed that *Volborthella*'s small, conical shell was not secreted but built from grains of the mineral silicon dioxide (silica); neither was it septate. This illusion was a result of the laminated texture of the organisms' tests. Therefore, *Volborthella*'s classification is now uncertain.

Shelbyoceras

Because the characters differentiating monoplacophora from cephalopods are few, several monoplacophora have been mistaken for cephalopod ancestors. One such genus is *Shelbyoceras*, which was reclassified based on a depressed groove that forms a band around the shell, which is similar to a feature seen in *Hypseloconus*. The septa in this genus are either closely or irregularly spaced.

Kirengellids

The Kirengellids are a group of shells that, whilst originally aligned to the monoplacophoran ancestry of the cephalopods, have been reinterpreted as brachiopods.

Coleoidea

An ammonitic ammonoid with the body chamber missing, showing the septal surface (especially at right) with its undulating lobes and saddles.

The ancestors of coleoids (including most modern cephalopods) and the ancestors of the modern nautilus, had diverged by the Floian Age of the Early Ordovician Period, over 470 million years ago. We know this because the orthocerids were the first known representatives of the neocephalopoda, were ultimately the ancestors of ammonoids and coleoids, and had appeared by the Floian. It is widely held that the Bactritida, an Silurian–Triassic group of orthocones, are paraphyletic to the coleoids and ammonoids – that is, the latter groups arose from within the Bactritida. An increase in the diversity of the coleoids and ammonoids is observed around the start of the Devonian period, and corresponds with a profound increase in fish diversity. This could represent the origin of the two derived groups.

Unlike most modern cephalopods, most ancient varieties had protective shells. These shells at first were conical but later developed into curved nautiloid shapes seen in modern nautilus species. It is thought that competitive pressure from fish forced the shelled forms into deeper water, which provided an evolutionary pressure towards shell loss and gave rise to the modern coleoids, a change which led to greater metabolic costs associated with the loss of buoyancy, but which allowed them to recolonise shallow waters. However, some of the straight-shelled nautiloids evolved into belemnites, out of which some evolved into squid and cuttlefish. The loss of the shell may also have resulted from evolutionary pressure to increase manoeuvrability, resulting in a more fish-like habit. This pressure may have increased as a result of the increased complexity of fish in the late Palaeozoic, increasing the competitive pressure. Internal shells still exist in many non-shelled living cephalopod groups but most truly shelled cephalopods, such as the ammonites, became extinct at the end of the Cretaceous.

Organ origins

The tentacles of the ancestral cephalopod developed from the mollusc's foot; the ancestral state is thought to have had five pairs of tentacles which surround the mouth. Smell-detecting organs evolved very early in the cephalopod lineage.

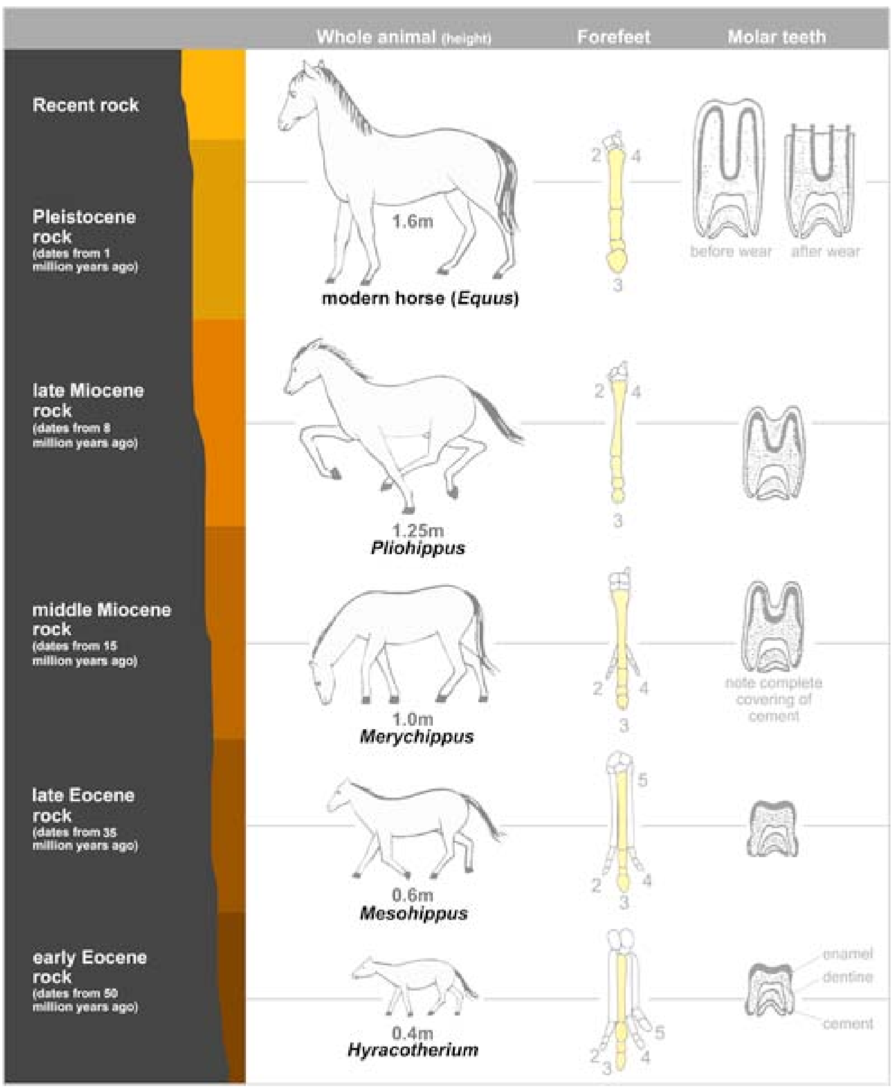
The earliest cephalopods, like *Nautilus* and some coeloids, appeared to be able to propel themselves forwards by directing their jet backwards. Because they had an external shell, they would not have been able to generate their jets by contracting their mantle, so must have used alternate methods: such as by contracting their funnels or moving the head in and out of the chamber.

Exceptional preservation

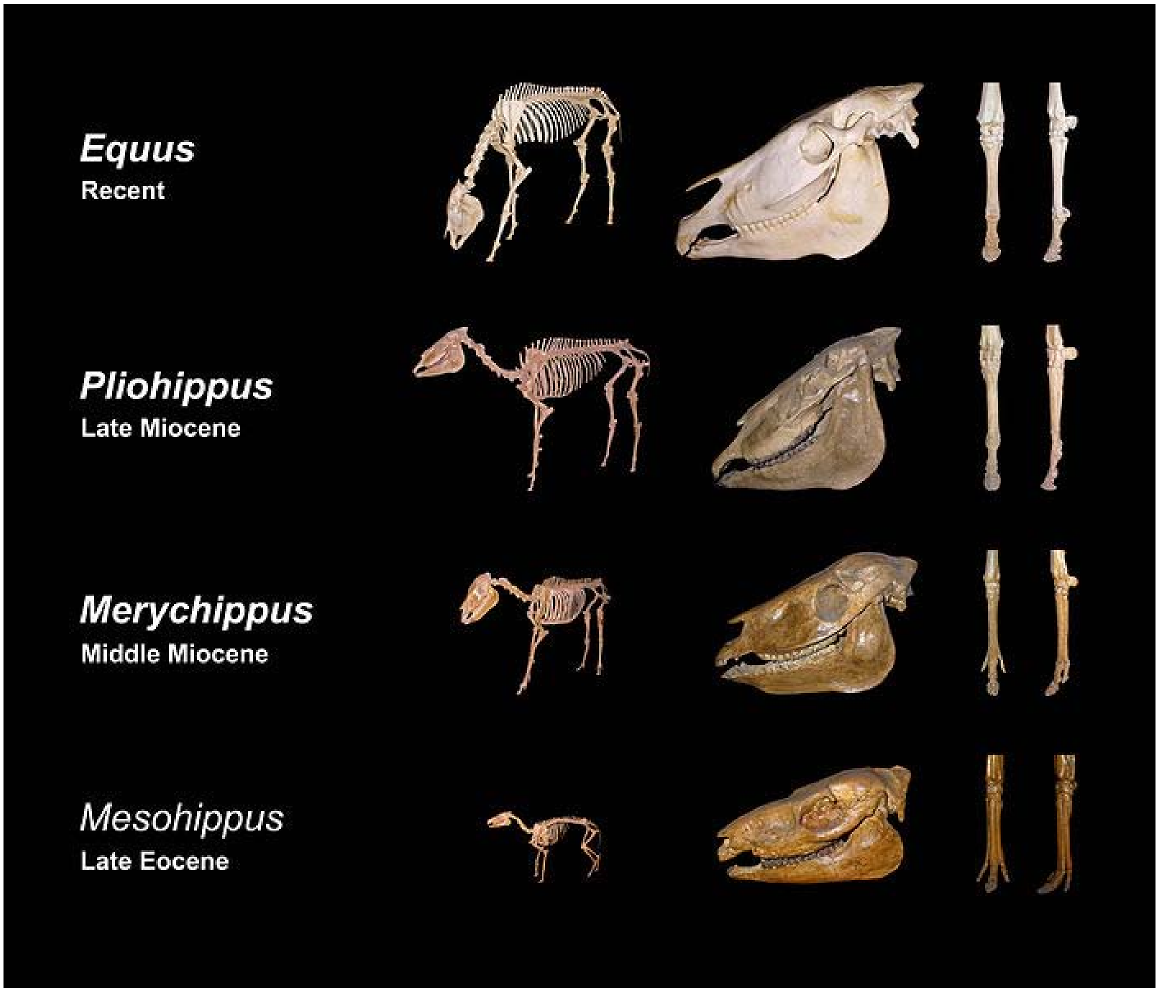
The preservation of cephalopod soft parts is not entirely unusual; soft-bodied fossils, especially of coeloids (squid), are relatively widespread in the Jurassic, but phosphatized remains are unknown before this period. On the other hand, soft parts – including a possible ink sac — are known from the Paleozoic Hunsrück Slate and Francis Creek shale.

Chapter- 4

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



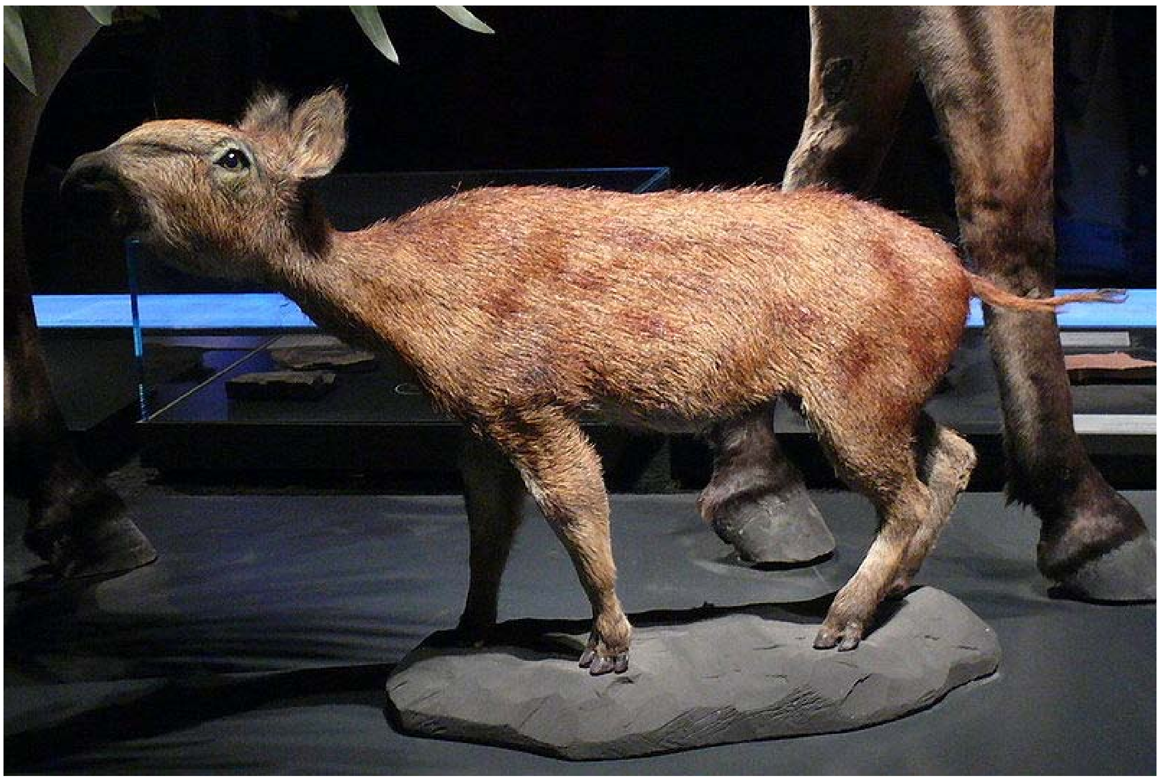
Skeletal evolution

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.

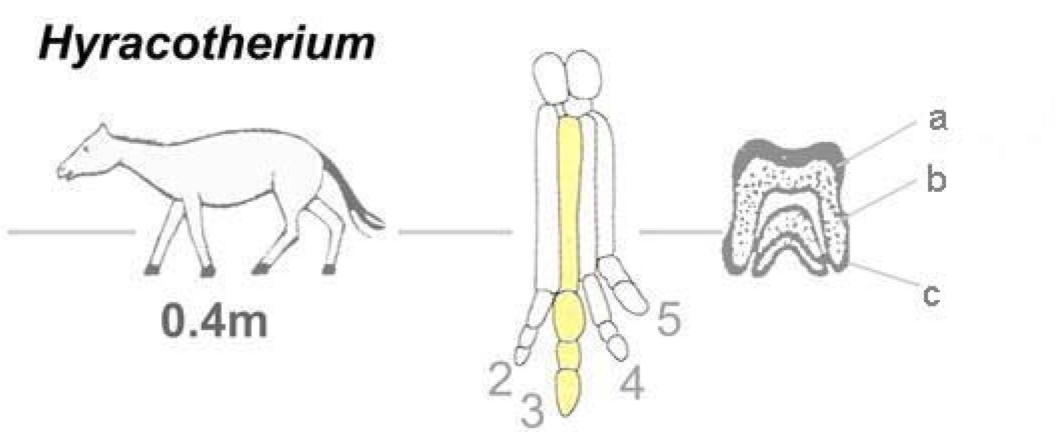
Detailed fossil information on the rate and distribution of new equid species has also revealed the progression between species was not as smooth and consistent as was once believed. Although some transitions, such as that of *Dinohippus* to *Equus*, were indeed gradual progressions, a number of others, 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

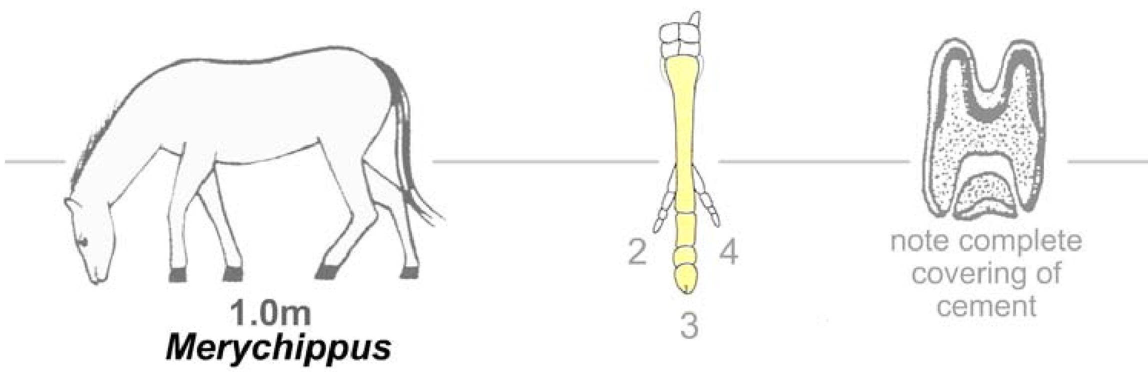
Fossil *Megahippus mckennai*

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 Ma ago.

Modern horses

Equus

Skull of a giant extinct horse of the *Equus* genus, *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- 5

Peppered Moth Evolution

Biston betularia f. typica, the white-bodied peppered moth.


Biston betularia f. carbonaria, the black-bodied peppered moth.

The **evolution of the peppered moth** over the last two hundred years has been studied in detail. Originally, the vast majority of peppered moths had light colouration, which effectively camouflaged them against the light-coloured trees and lichens which they rested upon. However, because of widespread pollution during the Industrial Revolution in England, many of the lichens died out, and the trees that peppered moths rested on became blackened by soot, causing most of the light-coloured moths, or ***typica***, to die off from predation. At the same time, the dark-coloured, or *melanic*, moths, ***carbonaria***, flourished because of their ability to hide on the darkened trees.

Since then, with improved environmental standards, light-coloured peppered moths have again become common, but the dramatic change in the peppered moth's population has remained a subject of much interest and study, and has led to the coining of the term ***industrial melanism*** to refer to the genetic darkening of species in response to pollutants. As a result of this relatively simple and easy-to-understand circumstances of the adaptation, the peppered moth has become a common example used in explaining or demonstrating natural selection.

Genetics

Evolution is defined as "a change in the frequency of an allele within a gene pool", an occurrence that causes a population's genetically inherited traits to change over successive generations. Evolution in the wild is chiefly caused by two mechanisms: natural selection, the process by which individual organisms with beneficial traits are more likely to survive and reproduce, and genetic drift, the statistical drift over time of allele frequencies in a population from random sampling effects in the formation of successive generations.

J.W. Tutt first proposed the "differential bird predation hypothesis" in 1896, as a mechanism of natural selection. The melanic morphs were better camouflaged against the bark of trees without foliose lichen, whereas the *typica* morphs were better camouflaged against trees with lichens. As a result, birds would find and eat those morphs that were not camouflaged with increased frequency.

In 1924, J.B.S. Haldane calculated, using a simple general selection model, the selective advantage necessary for the recorded evolution of peppered moths, based on the assumption that in 1848 the frequency of dark-coloured moths was 2%, and by 1895 it was 95%. The dark-coloured, or melanic, form would have had to be one and a half times as fit as the typical, light-coloured form. Even taking into consideration the errors in the model, this reasonably excluded the stochastic process of genetic drift, because the changes were too fast.

In peppered moths, the allele for dark-bodied moths is dominant, while the allele for light-bodied moths is recessive, meaning that the *typica* moths have a phenotype (visible or detectable characteristic) that is only seen in a homozygous genotype (an organism that has two copies of the same allele), and never in a heterozygous one. This helps explain how dramatically quickly the population changed when being selected for dark colouration.

The peppered moth *Biston betularia* is also a model of parallel evolution in the incidence of melanism in the British form (f. carbonaria) and the American form (f. swettaria) as they are indistinguishable in appearance. Genetic analysis indicates that both phenotypes are inherited as autosomal dominants. Cross hybridizations indicate the phenotypes are produced by isoalleles at a single locus.

Environmental changes

Typica and *carbonaria* morphs resting on the same tree. The light-colored *typica* (below the bark's scar) is nearly invisible on this pollution-free tree, camouflaging it from predators.

Before the Industrial Revolution, the peppered moth was mostly found in a light grey form with little black speckled spots. The light-bodied moths were able to blend in with the light-coloured lichens and tree bark, and the less common black moth was more likely to be eaten by birds. As a result of the common light-coloured lichens and English trees, therefore, the light-coloured moths were much more effective at hiding from predators, and the frequency of the dark allele was about 0.01%.

During the early decades of the Industrial Revolution in England, the countryside between London and Manchester was blanketed with soot from the new coal-burning factories. Many of the light-bodied lichens died from sulphur dioxide emissions, and the trees became covered with soot. This led to an increase in bird predation for light-coloured moths, as they no longer blended in as well in their polluted ecosystem: indeed, their bodies now dramatically contrasted with the colour of the bark. Dark-coloured moths, on the other hand, were camouflaged very well by the blackened trees.

Although a majority of light-coloured moths initially continued to be produced, most of them didn't survive, while the dark-coloured moths flourished. As a result, over the course of many generations of moths, the allele frequency gradually shifted towards the dominant allele, as more and more dark-bodied moths survived to reproduce. By the mid-19th century, the number of dark-coloured moths had risen noticeably, and by 1895, the percentage of dark-coloured moths in the Manchester peppered moth population was reported at 98%, a dramatic change (by almost 1000%) from the original frequency. This evolved darkening in colour as a result of industrialization has come to be known as *industrial melanism* as a result.

While evidence of increasing frequency of melanic forms in the Lepidoptera was available during Darwin's lifetime — the first observations were made in 1848 — current understanding is that it was not until 1896, 14 years after Darwin's death, that Tutt explicitly linked melanism with natural selection. However, a recent article reports that melanism in the Lepidoptera had been linked to natural selection prior to Tutt. Albert Brydges Farn (1841–1921), a British entomologist, wrote to Darwin on the 18th November 1878 to discuss his observation of colour variations in the Annulet moth (then *Gnophos obscurata*, now *Charissa obscurata*). In his letter, Farn mentions the existence of different colour morphs, describing how each is matched to the habitats in which they are found (dark morphs on peat, white morphs on chalk cliffs) and refers explicitly to this variability as pointing to 'survival of the fittest'.

In modern times, because of cleaner air standards in Europe and North America, the dark-bodied moth is becoming less frequent, again demonstrating the adaptive shifts in the peppered moth population.

Rise and fall of phenotype frequency

Melanism has appeared in the European and North American peppered moth populations. Information about the rise in frequency is scarce. Much more is known about the subsequent fall in phenotype frequency, as it has been measured by lepidopterists using moth traps.

Though a black peppered moth was found in 1811, this can be seen as an aberrant morph caused by a recurrent mutation that was probably selected out of the population. The first *carbonaria* to be found was caught in Manchester, England in 1848, but was only reported 16 years later in 1864 by Edleston. Edleston notes that by 1864 it was the more common morph in his garden in Manchester. Steward compiled data for the first recordings of the peppered moth by locality, and deduced that the carbonaria morph was the result of a single mutation that subsequently spread. By 1895, it had reached a reported frequency of 98% in Manchester.

From around 1962 to the present, the phenotype frequency of *carbonaria* has steadily fallen. Its decline has been measured more accurately than its rise, because of more rigorous scientific studies being conducted. Notably, Bernard Kettlewell conducted a national survey in 1956, Bruce Grant conducted a similar one in early 1996. , and L.M. Cook in 2003.

Similar results were found in America. Melanic forms have not been found in Japan. It is believed that this is because peppered moths in Japan do not inhabit industrialised regions.

Predation experiments

The Great Tit, an insectivorous bird.

In 1896 J. W. Tutt hypothesised that the increased proportion of *carbonaria* resulted from differential bird predation giving an advantage to the melanistic phenotype in polluted regions, but not in unpolluted regions where the light coloured *typica* moths had the advantage. Various experiments have been performed on predation of the peppered moth and each has supported this hypothesis.

The most famous experiments on the peppered moth were carried out by Bernard Kettlewell under the supervision of E. B. Ford, who helped him gain a grant from the Nuffield Foundation to perform the experiments. In one of Kettlewell's experiments, moths were released into a large (18 m by 6 m) aviary, where they were fed on by Great Tits (*Parus major*). In 1953, Kettlewell experimented at Cadbury Nature Reserve in Birmingham, England, marking, releasing and recapturing marked moths. He found that in this polluted woodland *typica* morphs were preferentially preyed. He thus showed that the melanistic phenotype was important to the survival of peppered moths in such a habitat. Kettlewell repeated the experiment in 1955 at unpolluted woodland in Dorset and again in the polluted woods in Birmingham. He was accompanied by Nico Tinbergen, and they made a film together. Further studies by others found similar results, culminating in 1996 when reporting work on both sides of the Atlantic found a correlation between changes in melanic frequencies and pollution levels.

An experiment in field biology will always suffer from some level of artificiality, but that has to be balanced against practicality, costs and in this case the history of field biology; the most important aspect is that an experiment generates useful statistics. The only previous experiments of this type were R.A. Fisher and E.B. Ford's (1947) with the scarlet tiger moth.

Michael Majerus in his 1998 book *Melanism: Evolution in Action* discussed criticisms concerning Kettlewell's experimental methods. Criticism and controversy arose when the book was misrepresented in reviews, and the story was picked up by creationist campaigners. The journalist Judith Hooper suggested in her book *Of Moths and Men* (2002) that Kettlewell committed scientific fraud. Careful studies of Kettlewell's surviving papers by Rudge (2005) and Young (2004) have revealed that Hooper's allegation of fraud is unjustified, and "that Hooper does not provide one shred of evidence to support this serious allegation".

In 2000 Majerus developed plans for experiments to establish where peppered moths rest through the day, and to examine if the various valid criticisms of Kettlewell's experimental protocols could have altered the qualitative validity of his conclusions. In the following year he piloted a new field predation experiment designed to overcome criticisms that Kettlewell had used too few release sites, resulting in the density of moths being too high; moths had been released onto tree trunks rather than branches; moths released during the day might not have found the best places to hide; mixtures of wild-caught and lab-bred moths might have behaved differently; and the behaviour of translocated moths might have changed because of local adaptation. During the main experiment in Cambridge over the seven years 2001-2007 Majerus noted the natural resting positions of the moths, and of the 135 moths examined over half were on tree branches, mostly on the lower half of the branch, 37% were on tree trunks, mostly on the north side, and only 12.6% were resting on or under twigs. Following correspondence with Hooper he added an experiment to find if bat predation might have skewed the results – this found that bats preyed equally on both forms of the moth. He observed a number of species of bird preying on the moths, and the overall data led him to conclude that differential bird predation was a major factor responsible for the decline in *carbonaria* frequency compared to *typica* in Cambridge during the study period. He described his results as a complete vindication of the peppered moth story, and said "If the rise and fall of the peppered moth is one of the most visually impacting and easily understood examples of Darwinian evolution in action, it should be taught. It provides after all the proof of evolution."

Alternative hypotheses

Several alternative hypotheses to explain industrial melanism, particularly noted in the peppered moth, were proposed during the 1920s and 1930s. Some dissenters within the scientific community have criticized the peppered moth story, notably Sargent *et al.* (1998), but peppered moth researchers remain unconvinced.

Several alternative selection mechanisms have been proposed. Note that a change in allele frequency, be it caused by natural selection, mutation, migration or genetic drift by definition, is differential. However, the magnitude of the changes observed can only be accounted for by natural selection. It can be seen from population genetics that a non-differential change will not cause evolution. If the allele frequencies are denoted by the algebraic terms p and q, and (say) $p = 0.6$ and $q = 0.4$, then a non-differential reduction in population size from say 2000 to 100 individuals, will still produce the same values of (approximately) $p = 0.6$ and $q = 0.4$.

Phenotypic induction

John William Heslop-Harrison (1920) rejected Tutt's differential bird predation hypothesis, on the basis that he did not believe that birds ate moths. Instead he advocated the idea that pollutants could cause changes to the soma and germ plasm of the organism. The origin of this hypothesis probably has its roots in the 1890s, when it was proposed as a form of Lamarckism. It is important to note its historical context.

Hasebroek (1925) was the first who tried to prove this hypothesis, he contended that air pollution altered lepidopteran physiology, thus producing an excess of black pigment. He exposed pupae of Lepidoptera to various doses of pollutant gases, namely hydrogen sulfide (H_2S), ammonia (NH_3) and "pyredin" (presumably his spelling of pyridine). He used eight species in his studies, four of which were species of butterfly that did not exhibit melanism. Ford (1964) contends that Hasebroek's illustrations showed that the abnormal forms that appeared were not melanics, and Hasebroek failed to study their genetics.

Heslop Harrison (Harrison and Garrett 1926; Harrison 1928) suggested that the increase of melanic moths in industrialised regions was due to "mutation pressure", not to selection by predators which he regarded as negligible. Salts of lead and manganese were present in the airborne pollutant particles, and he suggested that these caused the mutation of genes for melanin production but of no others. He used *Selenia bilunaria* and *Tephrosia bistortata* as material. The larvae were fed with leaves that had incorporated these salts and melanics subsequently appeared.

Similar experiments by Hughes McKenney (1932) and Thomasen and Lemche (1933) failed to replicate these results. However, the statistician and geneticist Ronald Fisher, showed that Heslop Harrison's controls were inadequate. This hypothesis, however, appeared to be falsified by breeding experiments. Further evidence, if it were needed, is likely to come from research into the biochemistry of melanism.

Criticism and controversy

Creationists have disputed the occurrence or significance of the melanic *carbonaria* morph increasing in frequency.

In recent years, the use of the peppered moth as an example of evolution has come under attack by advocates of intelligent design and other creationists, who allege that it is not reliable as evidence of evolution.

Creationists have argued that the "peppered moth story" showed only microevolution, rather than speciation or other changes at the larger macroevolutionary scale. Biologists agree that this example shows natural selection causing evolution within a species, demonstrating rapid and obvious adaptiveness with such change, and accept that it is not proof of the theory of evolution as a whole. However, though creationists accept "microevolution" of varieties within a "kind", they claim that "macroevolution" does not happen. To biologists there is no dividing line between the two, and in the modern evolutionary synthesis the same mechanisms are seen operating at various scales to cause both evolution within species and speciation at a macroevolution level or wider changes, the only difference being of time and scale.

Another common, but unfounded, criticism involves well-known pictures of moths resting on trunks, used in many textbooks. These photos were prepared (dead moths pinned to branches), which has been conflated into the idea that all the studies were staged, ignoring the point that professional photography to illustrate textbooks uses dead insects because of the considerable difficulty in getting good images of small, relatively fast moving, animals, and that the studies actually consisted of observational data rather than using such photographs. The photographs in Michael Majerus's 1998 book

Melanism: Evolution in Action are unstaged pictures of live moths in the wild, and the photographs of moths on tree-trunks, apart from some slight blurring, look no different than the "staged" photographs.

Furthermore, while an experiment did involve the gluing of dead moths to trees, this practice was just one of many different ways used to study different individual elements of the overall hypothesis. This particular experiment was not meant to exactly reproduce natural conditions, but instead was used to assess how the numbers of moths available (their density) affected the foraging practices of birds.

The methodology of Bernard Kettlewell's classic study was questioned in a review by the biologist Jerry Coyne in *Nature* of Michael Majerus's 1998 book *Melanism: Evolution in Action* which includes a critique of Kettlewell's experiment, matching a similar 1998 analysis by Sargent *et al.* Coyne stated that the most serious problem found by Majerus was that only two peppered moths had been found on tree trunks. He also noted that the white moths had increased in numbers before the lichen had returned, and that Kettlewell's findings of moths choosing matching backgrounds had not been replicated in later experiments. Coyne compared his reaction to "the dismay attending my discovery, at the age of 6, that it was my father and not Santa who brought the presents on Christmas Eve". He concluded that "for the time being we must discard *Biston* as a well-understood example of natural selection in action, although it is clearly a case of evolution. There are many studies more appropriate for use in the classroom", and that further studies of the animal's habits were needed. At the beginning of his second paragraph on the peppered moths, Majerus emphasises that the wealth of additional data obtained since Kettlewell's initial predation papers does not undermine the basic qualitative deductions from that work, and that differential bird predation of the dark and light moths in habitats affected by industrial pollution to different degrees (directional selection) "is the primary influence of the evolution of melanism in the peppered moth". Coyne had erred in his statement that only two peppered moths had been found on tree trunks, as the book gives the resting positions of 47 peppered moths Majerus had found in the wild between 1964 and 1996; twelve were on tree trunks (six exposed, six unexposed), twenty were at the trunk/branch joint, and fifteen resting on branches. Majerus found that the review did not reflect the factual content of the book or his own views, and cites an assessment by the entomologist Donald Frack that there was essentially no resemblance between the book and Coyne's review, which appeared to be a summary of the Sargent et al. paper rather than Majerus's book.

The review was subsequently picked up by journalist Robert Matthews, who wrote an article for *The Sunday Telegraph*, March 14, 1999, claiming that "Evolution experts are quietly admitting that one of their most cherished examples of Darwin's theory, the rise and fall of the peppered moth, is based on a series of scientific blunders. Experiments using the moth in the Fifties and long believed to prove the truth of natural selection are now thought to be worthless, having been designed to come up with the 'right' answer". Majerus regarded this view as surprising, and not one that would be shared by those involved in the field. He noted numerous scientific inaccuracies, misquotations and misrepresentations here, but thought this was common in press reports. He stated that he had spoken to Matthews for over half an hour and had to explain many details as Matthews hadn't read the book, but "Even then, he got nearly everything wrong."

The story was taken up by creationists, and at a seminar presenting his wedge strategy on March 13, 1999, the leading intelligent design proponent Phillip E. Johnson asserted that the moths "do not sit on tree trunks", "moths had to be glued to the trunks" for pictures and that the experiments were "fraudulent" and a "scam." This led Frack to exchanges with intelligent design proponent Jonathan Wells, who conceded that Majerus listed six moths on exposed tree trunks (out of 47), but argued that this was "an insignificant proportion". Wells wrote an essay on the subject, a shortened version of which appeared in *The Scientist* of May 24, 1999, claiming that "In 25 years of fieldwork, C.A. Clarke and his colleagues found only one peppered moth on a tree trunk", and concluding that "The fact that peppered moths do not normally rest on tree trunks invalidates Kettlewell's experiments". In 2000 he wrote *Icons of Evolution: Why much of what we Teach About Evolution is Wrong*, which claims "What the textbooks don't explain, however, is that biologists have known since the 1980s that the classical story has some serious flaws. The most serious is that peppered moths in the wild don't even rest on tree trunks. The textbook photographs, it turns out, have been staged." The arguments put by Wells have been dismissed by Majerus, Cook and peppered moth researcher Bruce Grant who describes Wells as distorting the picture by selectively omitting or scrambling references in a way that is basically dishonest.

On November 27, 2000, the school board of Pratt County, Kansas continued efforts to favor intelligent design teaching by requiring the use of specific resources. These included here by Jerry Coyne, who wrote to object strongly to this creationist misrepresentation of his critical re-evaluation, emphasising that the moth story is a sound example of evolution produced by natural selection and stating that his call for additional research was only to resolve uncertainty regarding bird predation as the cause of the natural selection and evolutionary change. Bruce Grant also wrote to challenge allegations of fraud in the moth experiments based on misrepresentations by Wells.

In 2002, Judith Hooper's *Of Moths and Men* added to the chorus of accusations of scientific fraud. She accused Kettlewell of manipulating his data to prove his hypothesis. The book received strong criticism from the scientific press (e.g., Coyne, B.C. Clarke, Grant). Majerus described it as "littered with errors, misrepresentations, misinterpretations and falsehoods".

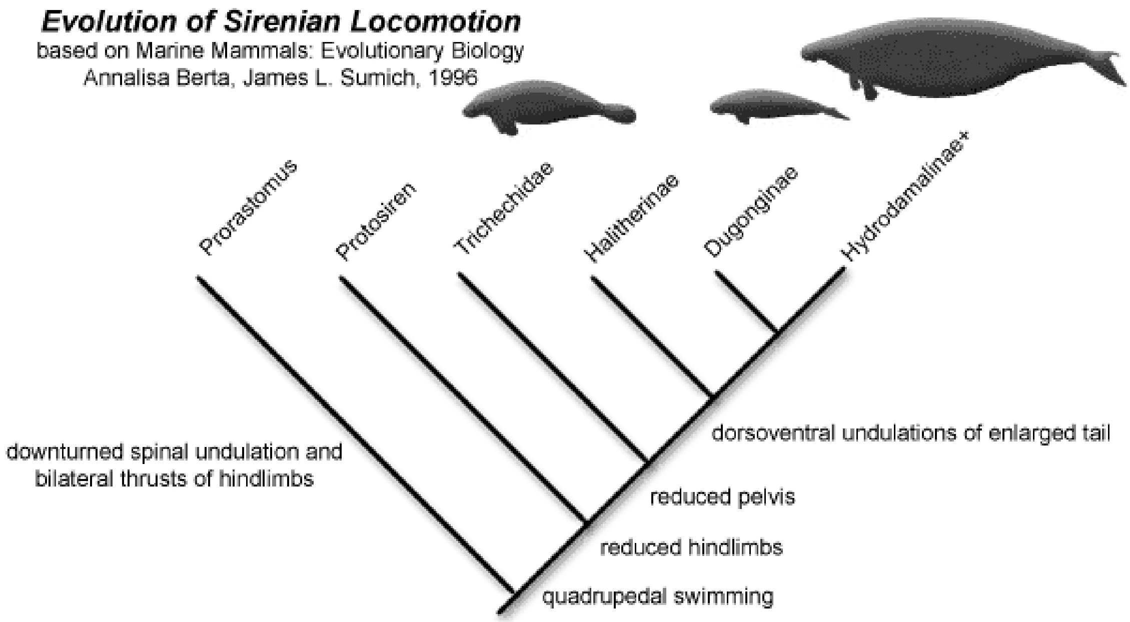
Chapter- 6

Evolution of Sirenians

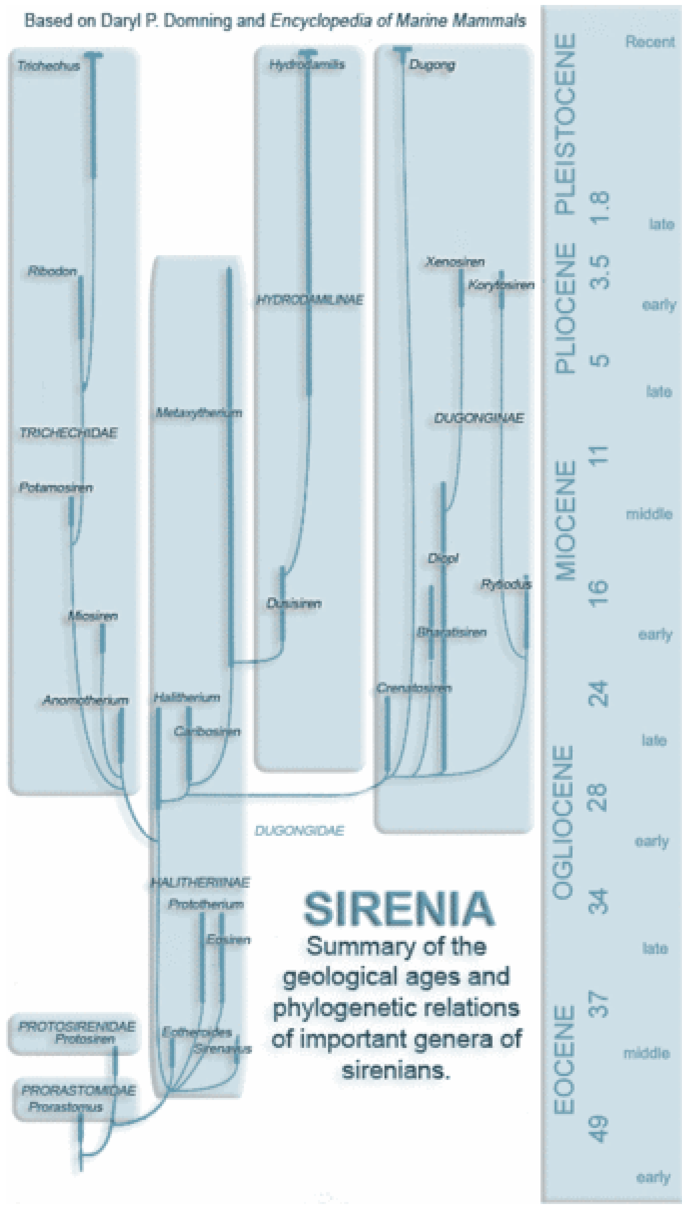
A manatee's toenails. Manatee share common ancestry with Elephants.

Sirenia is the order of placental mammals which comprise modern "sea cows" (manatees and the Dugong) and their extinct relatives. They are the only extant herbivorous marine mammals and the only group of herbivorous mammals to have become completely aquatic. Sirenians are thought to have a 50-million-year-old fossil record (early Eocene-recent). They attained modest diversity during the Oligocene and Miocene, but have since declined as a result of climatic cooling, oceanographic changes, and human interference. Two genera and four species are extant: *Trichechus* which includes the three species of manatee that live along the Atlantic coasts and in rivers and coastlines of the Americas and western Africa, and *Dugong* which is found in the Indian and Pacific oceans.

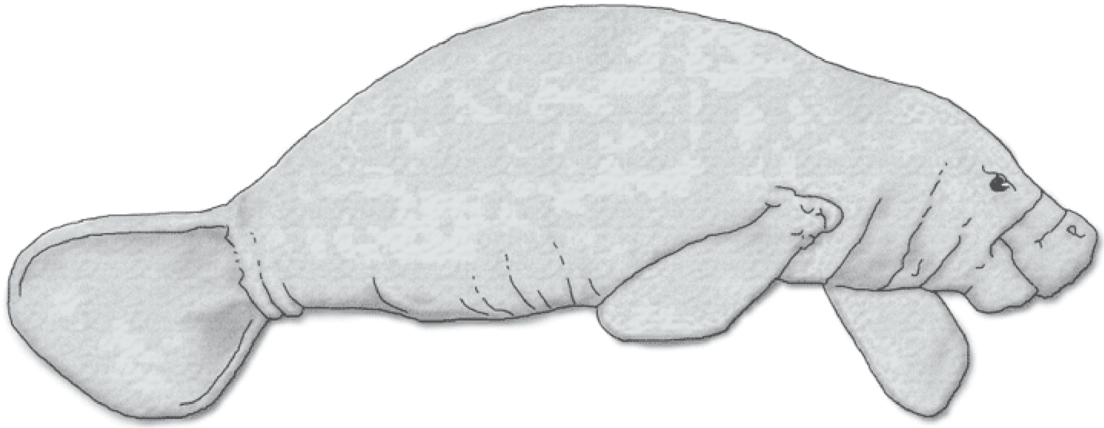
Origins



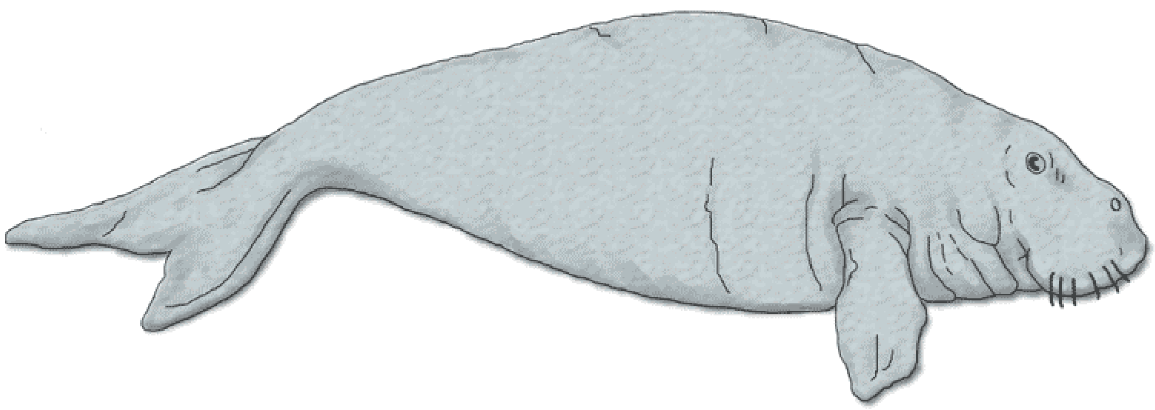
Evolution of Sirenian Locomotion, based on Berta and Sumich, 1999.



Evolution of Sirenia, based on Daryl P. Domning and *Encyclopedia of Marine Mammals*.

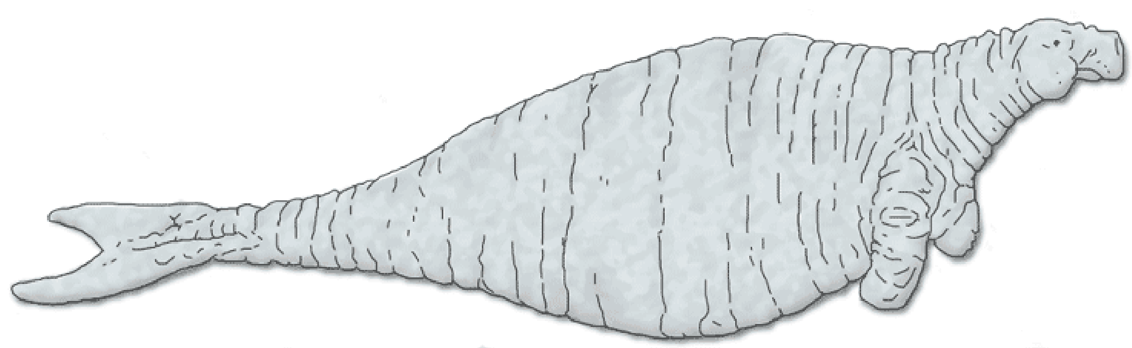


Amazonian Manatee.



Dugong.

West Indian Manatee.



Steller's Sea Cow (extinct).

Sirenians, along with Proboscidea (elephants), group together with the extinct Desmostylia and likely the extinct Embrithopoda to form the Tethytheria. Tethytheria is thought to have evolved from primitive hoofed mammals ("condylarths") along the shores of the ancient Tethys Ocean.

Tethytheria, combined with Hyracoidea (hyraxes) forms a clade called Paenungulata. Paenungulata and Tethytheria (especially the latter) are among the least controversial mammalian clades, with strong support from morphological and molecular interpretations. The ancestry of Sirenia is remote from that of Cetacea and Pinnipedia, although they are thought to have evolved an aquatic lifestyle around the same time.

Fossil history

Prorastomus, an early sirenian from the Eocene

The first appearance of sirenians in the fossil record was during the early Eocene, and by the late Eocene, sirenians had significantly diversified. Inhabitants of rivers, estuaries, and nearshore marine waters, they were able to spread rapidly. The most primitive sirenian known to date, *Prorastomus*, was found in Jamaica, not the Old World.

The earliest known sea cows, of the families Prorastomidae and Protosirenidae, are both confined to the Eocene, and were about the size of a pig, four legged amphibious creatures. By the time the Eocene drew to a close, came the appearance of the Dugongidae; sirenians had acquired their familiar fully-aquatic streamlined body with flipper-like front legs with no hind limbs, powerful tail with horizontal caudal fin, with up and down movements which move them through the water, like cetaceans.

The last of the sirenian families who made their appearance, Trichechidae, apparently arose from early dugongids in the late Eocene or early Oligocene. The current fossil record documents all major stages in hindlimb and pelvic reduction to the extreme reduction in the modern manatee pelvis, providing an example of dramatic morphological change among fossil vertebrates.

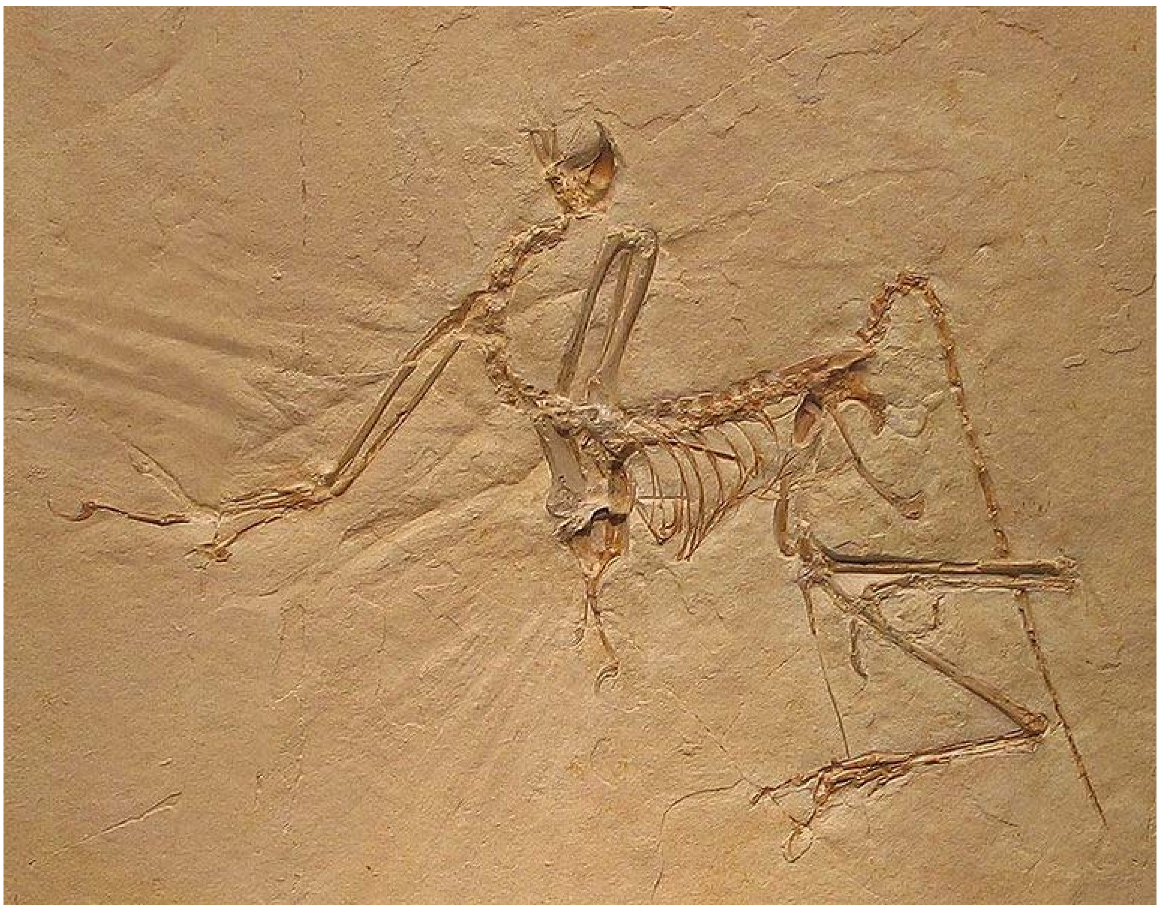
Since sirenians first evolved, they have been herbivores, likely depending on seagrasses and aquatic angiosperms (flowering plants) for food. To the present, almost all have remained tropical, marine and angiosperm consumers. Sea cows are shallow divers with large lungs. They have heavy skeletons to help them stay submerged; the bones are pachyostotic (swollen) and osteosclerotic (dense), especially the ribs which are often found as fossils.

Eocene sirenians, like Mesozoic mammals but in contrast to other Cenozoic ones, have five instead of four premolars, giving them a 3.1.5.3 dental formula. Whether this condition is truly a primitive retention in sirenians is still under debate.

Although cheek teeth are relied on for identifying species in other mammals, they do not vary to a significant degree among sirenians in their morphology, but are almost always low-crowned (brachyodont) with two rows of large, rounded cusps (bunobilophodont). The most easily identifiable parts of sirenian skeletons are the skull and mandible, especially the frontal and other skull bones. With the exception of a pair of tusk-like first upper incisors present in most species, front teeth (incisors and canines) are lacking in all, except the earliest sirenians.

Chapter- 7

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 from 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 from 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.

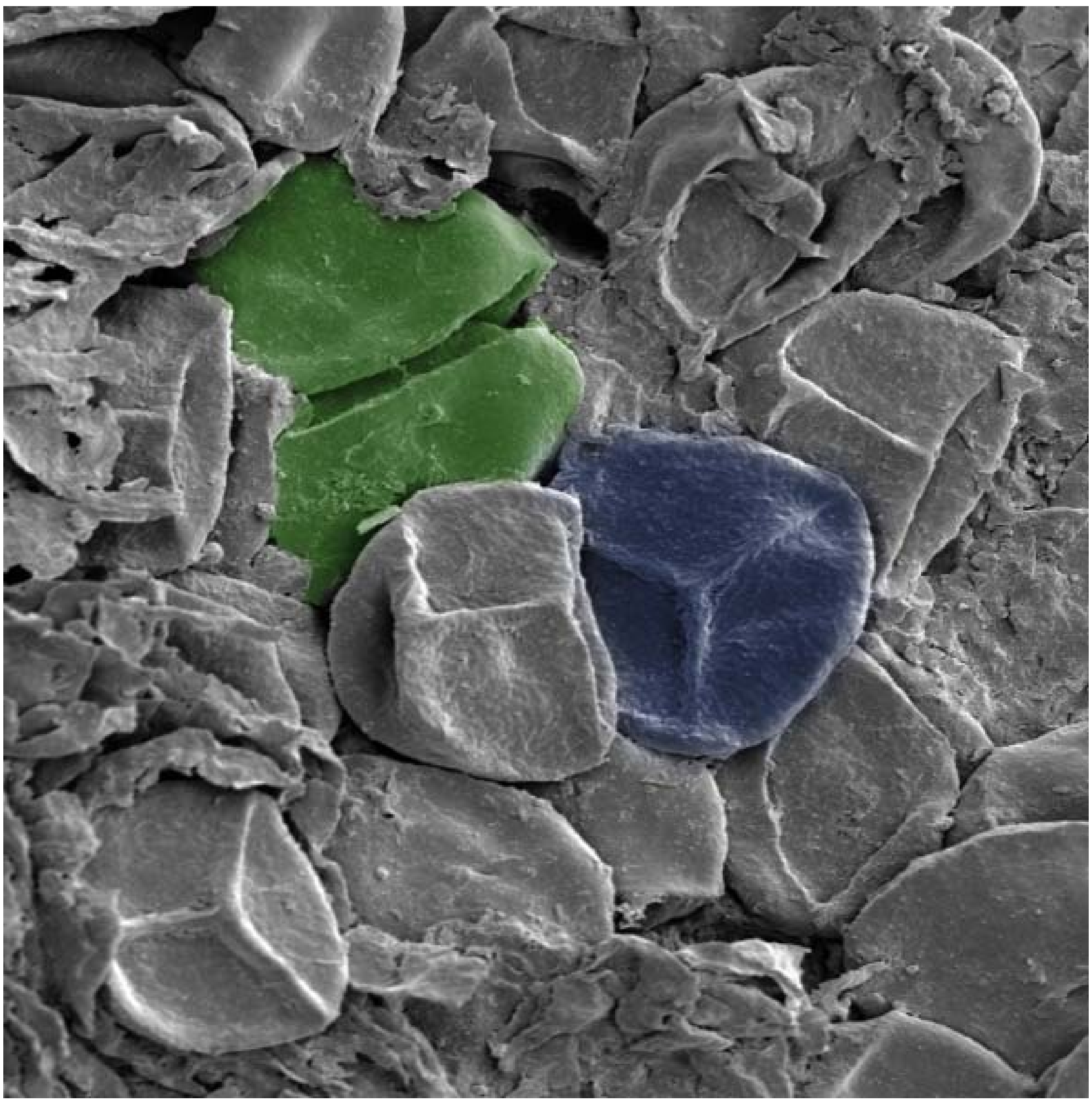
Another concern with evolutionary implications is a suspected increase in hybridization. This may arise from human alteration of habitats enabling related allopatric species to overlap. Forest fragmentation can create extensive open areas, connecting previously isolated patches of open habitat. Populations 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.

Chapter- 8

Evolutionary History of Plants



A late Silurian sporangium. **Green**: A spore tetrad. **Blue**: A spore bearing a trilete mark – the *Y*-shaped scar. The spores are about 30-35 μm across

The **evolution of plants** has resulted in increasing levels of complexity, from the earliest algal mats, through bryophytes, lycopods, ferns to the complex gymnosperms and angiosperms of today. While the groups which appeared earlier continue to thrive, especially in the environments in which they evolved, each new grade of organisation has eventually become more "successful" than its predecessors by most measures.

Evidence suggests that an algal scum formed on the land 1,200 million years ago, but it was not until the Ordovician Period, around 450 million years ago, that land plants appeared. These began to diversify in the late Silurian Period, around 420 million years ago, and the fruits of their diversification are displayed in remarkable detail in an early Devonian fossil assemblage from the Rhynie chert. This chert preserved early plants in cellular detail, petrified in volcanic springs. By the middle of the Devonian Period most of the features recognised in plants today are present, including roots, leaves and secondary wood, and by late Devonian times seeds had evolved. Late Devonian plants had thereby reached a degree of sophistication that allowed them to form forests of tall trees. Evolutionary innovation continued after the Devonian period. Most plant groups were relatively unscathed by the Permo-Triassic extinction event, although the structures of communities changed. This may have set the scene for the evolution of flowering plants in the Triassic (~200 million years ago), which exploded in the Cretaceous and Tertiary. The latest major group of plants to evolve were the grasses, which became important in the mid Tertiary, from around 40 million years ago. The grasses, as well as many other groups, evolved new mechanisms of metabolism to survive the low CO_2 and warm, dry conditions of the tropics over the last 10 million years.

Colonisation of land

The Devonian period marks the beginning of extensive land colonization by plants, which through their effects on erosion and sedimentation brought about significant climatic change.

Land plants evolved from chlorophyte algae, perhaps as early as 510 million years ago; their closest living relatives are the charophytes, specifically Charales. Assuming that the Charales' habit has changed little since the divergence of lineages, this means that the land plants evolved from a branched, filamentous, haplontic alga, dwelling in shallow fresh water, perhaps at the edge of seasonally desiccating pools. Co-operative interactions with fungi may have helped early plants adapt to the stresses of the terrestrial realm.

Plants were not the first photosynthesisers on land, though: consideration of weathering rates suggests that organisms were already living on the land 1,200 million years ago, and microbial fossils have been found in freshwater lake deposits from 1,000 million years ago, but the carbon isotope record suggests that they were too scarce to impact the atmospheric composition until around 850 million years ago. These organisms were probably small and simple, forming little more than an "algal scum".

The first evidence of plants on land comes from spores of Mid-Ordovician age (early Llanvirn, ~470 million years ago). These spores, known as cryptospores, were produced either singly (monads), in pairs (diade) or groups of four (tetrads), and their microstructure resembles that of modern liverwort spores, suggesting they share an equivalent grade of organisation. It could be that atmospheric 'poisoning' prevented eukaryotes from colonising the land prior to this, or it could simply have taken a great time for the necessary complexity to evolve.

Trilete spores similar to those of vascular plants appear soon afterwards, in Upper Ordovician rocks. Depending exactly when the tetrad splits, each of the four spores may bear a "trilete mark", a *Y*-shape, reflecting the points at which each cell was squashed up against its neighbours. However, in order for this to happen, the spore walls must be sturdy and resistant at an early stage. This resistance is closely associated with having a desiccation-resistant outer wall – a trait only of use when spores have to survive out of water. Indeed, even those embryophytes that have returned to the water lack a resistant wall, thus don't bear trilete marks. A close examination of algal spores shows that none have trilete spores, either because their walls are not resistant enough, or in those rare cases where it is, the spores disperse before they are squashed enough to develop the mark, or don't fit into a tetrahedral tetrad.

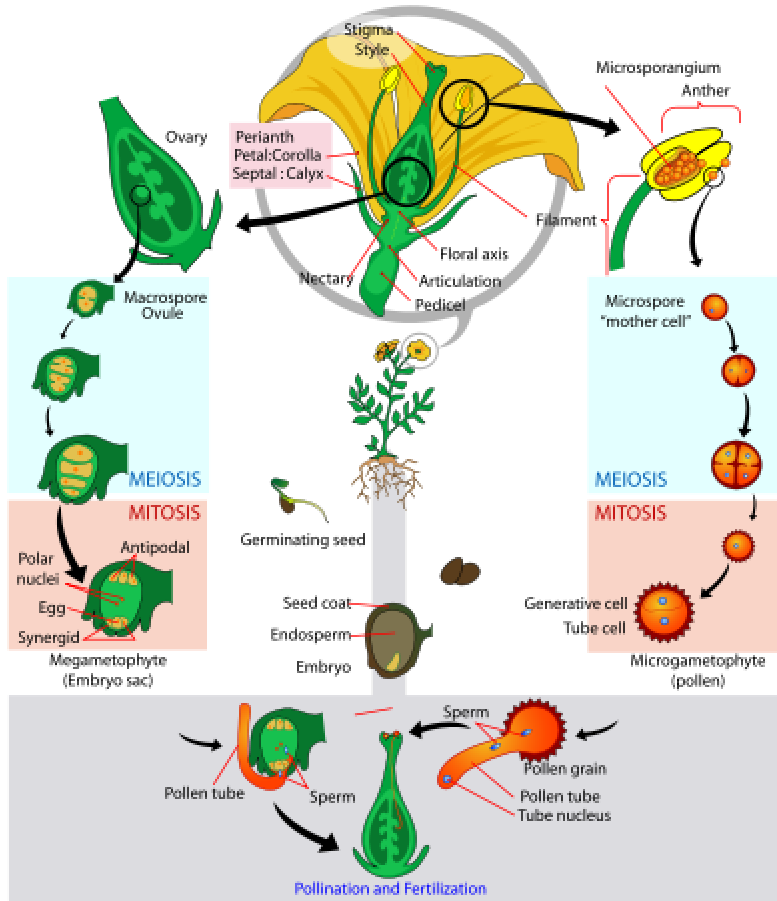
The earliest megafossils of land plants were thalloid organisms, which dwelt in fluvial wetlands and are found to have covered most of an early Silurian flood plain. They could only survive when the land was waterlogged.

Once plants had reached the land, there were two approaches to dealing with desiccation. The bryophytes avoid it or give in to it, restricting their ranges to moist settings, or drying out and putting their metabolism "on hold" until more water arrives. Tracheophytes resist desiccation. They all bear a waterproof outer cuticle layer wherever they are exposed to air (as do some bryophytes), to reduce water loss – but since a total covering would cut them off from CO_2 in the atmosphere, they rapidly evolved stomata – small openings to allow gas exchange. Tracheophytes also developed vascular tissue to aid in the movement of water within the organisms (see below), and moved away from a gametophyte dominated life cycle (see below). Vascular tissue also facilitated upright growth without the support of water and paved the way for the evolution of larger plants on land.

The establishment of a land-based flora permitted the accumulation of oxygen in the atmosphere as never before, as the new hordes of land plants pumped it out as a waste product. When this concentration rose above 13%, it permitted the possibility of wildfire. This is first recorded in the early Silurian fossil record by charcoalified plant fossils. Apart from a controversial gap in the Late Devonian, charcoal is present ever since.

Charcoalification is an important taphonomic mode. Wildfire drives off the volatile compounds, leaving only a shell of pure carbon. This is not a viable food source for herbivores or detritovores, so is prone to preservation; it is also robust, so can withstand pressure and display exquisite, sometimes sub-cellular, detail.

Changing life cycles



Angiosperm life cycle

All multicellular plants have a life cycle comprising two generations or phases. One is termed the **gametophyte**, has a single set of chromosomes (denoted **1N**), and produces gametes (sperm and eggs). The other is termed the **sporophyte**, has paired chromosomes (denoted **2N**), and produces spores. The gametophyte and sporophyte may appear identical – homomorphy – or may be very different – heteromorphy.

The pattern in plant evolution has been a shift from homomorphy to heteromorphy. The algal ancestors to land plants were almost certainly haplobiontic, being haploid for all their life cycles, with a unicellular zygote providing the 2N stage. All land plants (i.e. embryophytes) are diplobiontic – that is, both the haploid and diploid stages are multicellular. Two trends are apparent: bryophytes (liverworts, mosses and hornworts) have developed the gametophyte, with the sporophyte becoming almost entirely dependent on it; vascular plants have developed the sporophyte, with the gametophyte being particularly reduced in the seed plants.

There are two competing theories to explain the appearance of a diplobiontic lifecycle.

The **interpolation theory** (also known as the antithetic or intercalary theory) holds that the sporophyte phase was a fundamentally new invention, caused by the mitotic division of a freshly germinated zygote, continuing until meiosis produces spores. This theory implies that the first sporophytes would bear a very different morphology to the gametophyte, on which they would have been dependent. This seems to fit well with what we know of the bryophytes, in which a vegetative thalloid gametophyte is parasitised by simple sporophytes, which often comprise no more than a sporangium on a stalk. Increasing complexity of the ancestrally simple sporophyte, including the eventual acquisition of photosynthetic cells, would free it from its dependence on a gametophyte, as we see in some hornworts (*Anthoceros*), and eventually result in the sporophyte developing organs and vascular tissue, and becoming the dominant phase, as in the tracheophytes (vascular plants). This theory may be supported by observations that smaller *Cooksonia* individuals must have been supported by a gametophyte generation. The observed appearance of larger axial sizes, with room for photosynthetic tissue and thus self-sustainability, provides a possible route for the development of a self-sufficient sporophyte phase.

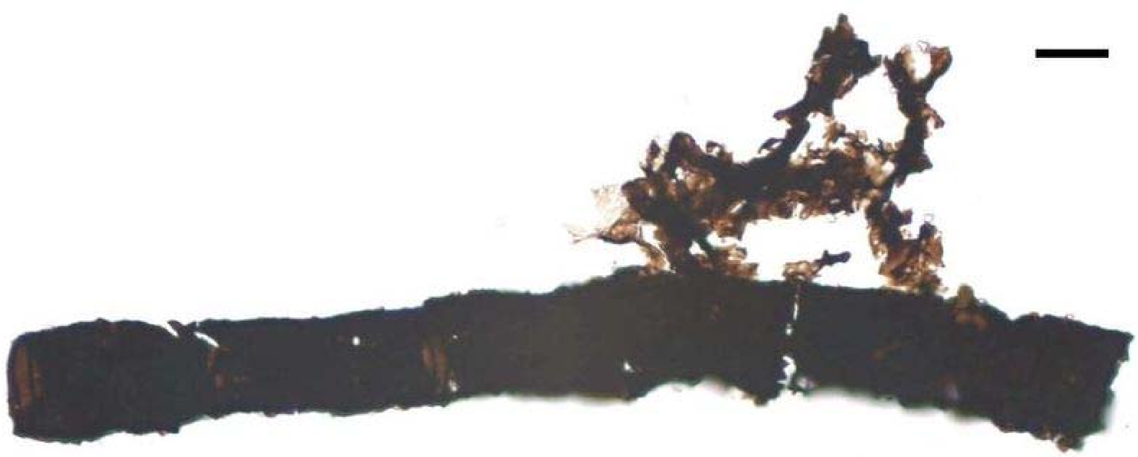
The alternative hypothesis is termed the **transformation theory** (or homologous theory). This posits that the sporophyte appeared suddenly by a delay in the occurrence of meiosis after the zygote germinated. Since the same genetic material would be employed, the haploid and diploid phases would look the same. This explains the behaviour of some algae, which produce alternating phases of identical sporophytes and gametophytes. Subsequent adaption to the desiccating land environment, which makes sexual reproduction difficult, would result in the simplification of the sexually active gametophyte, and elaboration of the sporophyte phase to better disperse the waterproof spores. The tissue of sporophytes and gametophytes preserved in the Rhynie chert is of similar complexity, which is taken to support this hypothesis.

Water transport

In order to photosynthesise, plants must uptake CO_2 from the atmosphere. However, this comes at a price: while stomata are open to allow CO_2 to enter, water can evaporate. Water is lost much faster than CO_2 is absorbed, so plants need to replace it, and have developed systems to transport water from the moist soil to the site of photosynthesis. Early plants sucked water between the walls of their cells, then evolved the ability to control water loss (and CO_2 acquisition) through the use of stomata. Specialised water transport tissues soon evolved in the form of hydroids, tracheids, then secondary xylem, followed by an endodermis and ultimately vessels.

The high CO_2 levels of Silurian-Devonian times, when plants were first colonising land, meant that the need for water was relatively low . As CO_2 was withdrawn from the atmosphere by plants, more water was lost in its capture, and more elegant transport mechanisms evolved. As water transport mechanisms, and waterproof cuticles, evolved, plants could survive without being continually covered by a film of water. This transition from poikilohydry to homoiohydry opened up new potential for colonisation. Plants were then faced with a balance, between transporting water as efficiently as possible and preventing transporting vessels to implode and cavitate.

During the Silurian, CO_2 was readily available, so little water needed expending to acquire it. By the end of the Carboniferous, when CO_2 levels had lowered to something approaching today's, around 17 times more water was lost per unit of CO_2 uptake. However, even in these "easy" early days, water was at a premium, and had to be transported to parts of the plant from the wet soil to avoid desiccation. This early water transport took advantage of the **cohesion-tension** mechanism inherent in water. Water has a tendency to diffuse to areas that are drier, and this process is accelerated when water can be wicked along a fabric with small spaces. In small passages, such as that between the plant cell walls (or in tracheids), a column of water behaves like rubber – when molecules evaporate from one end, they literally pull the molecules behind them along the channels. Therefore transpiration alone provided the driving force for water transport in early plants. However, without dedicated transport vessels, the cohesion-tension mechanism cannot transport water more than about 2 cm, severely limiting the size of the earliest plants. This process demands a steady supply of water from one end, to maintain the chains; to avoid exhausing it, plants developed a waterproof cuticle. Early cuticle may not have had pores but did not cover the entire plant surface, so that gas exchange could continue. However, dehydration at times was inevitable; early plants cope with this by having a lot of water stored between their cell walls, and when it comes to it sticking out the tough times by putting life "on hold" until more water is supplied.



A banded tube from the late Silurian/early Devonian. The bands are difficult to see on this specimen, as an opaque carbonaceous coating conceals much of the tube. Bands are just visible in places on the left half of the image. Scale bar: 20 µm

In order to be free from the constraints of small size and constant moisture that the parenchymatic transport system inflicted, plants needed a more efficient water transport system. During the early Silurian, they developed specialized cells, which were lignified (or bore similar chemical compounds) to avoid implosion; this process coincided with cell death, allowing their innards to be emptied and water to be passed through them. These wider, dead, empty cells were a million times more conductive than the inter-cell method, giving the potential for transport over longer distances, and higher CO_2 diffusion rates.

The first macrofossils to bear water-transport tubes *in situ* are the early Devonian pretracheophytes *Aglaophyton* and *Horneophyton*, which have structures very similar to the **hydroids** of modern mosses. Plants continued to innovate new ways of reducing the resistance to flow within their cells, thereby increasing the efficiency of their water transport. Bands on the walls of tubes, in fact apparent from the early Silurian onwards, are an early improvisation to aid the easy flow of water. Banded tubes, as well as tubes with pitted ornamentation on their walls, were lignified and, when they form single celled conduits, are considered to be **tracheids**. These, the "next generation" of transport cell design, have a more rigid structure than hydroids, allowing them to cope with higher levels of water pressure. Tracheids may have a single evolutionary origin, possibly within the hornworts, uniting all tracheophytes (but they may have evolved more than once).

Water transport requires regulation, and dynamic control is provided by stomata. By adjusting the amount of gas exchange, they can restrict the amount of water lost through transpiration. This is an important role where water supply is not constant, and indeed stomata appear to have evolved before tracheids, being present in the non-vascular hornworts.

An endodermis probably evolved during the Silu-Devonian, but the first fossil evidence for such a structure is Carboniferous. This structure in the roots covers the water transport tissue and regulates ion exchange (and prevents unwanted pathogens etc. from entering the water transport system). The endodermis can also provide an upwards pressure, forcing water out of the roots when transpiration is not enough of a driver.

Once plants had evolved this level of controlled water transport, they were truly homoiohydric, able to extract water from their environment through root-like organs rather than relying on a film of surface moisture, enabling them to grow to much greater size. As a result of their independence from their surroundings, they lost their ability to survive desiccation – a costly trait to retain.

During the Devonian, maximum xylem diameter increased with time, with the minimum diameter remaining pretty constant. By the middle Devonian, the tracheid diameter of some plant lineages had plateaued. Wider tracheids allow water to be transported faster, but the overall transport rate depends also on the overall cross-sectional area of the xylem bundle itself. The increase in vascular bundle thickness further seems to correlate with the width of plant axes, and plant height; it is also closely related to the appearance of leaves and increased stomatal density, both of which would increase the demand for water.

While wider tracheids with robust walls make it possible to achieve higher water transport pressures, this increases the problem of cavitation. Cavitation occurs when a bubble of air forms within a vessel, breaking the bonds between chains of water molecules and preventing them from pulling more water up with their cohesive tension. A tracheid, once cavitated, cannot have its embolism removed and return to service (except in a few advanced angiosperms which have developed a mechanism of doing so). Therefore it is well worth plants' while to avoid cavitation occurring. For this reason, pits in tracheid walls have very small diameters, to prevent air entering and allowing bubbles to nucleate. Freeze-thaw cycles are a major cause of cavitation. Damage to a tracheid's wall almost inevitably leads to air leaking in and cavitation, hence the importance of many tracheids working in parallel.

Cavitation is hard to avoid, but once it has occurred plants have a range of mechanisms to contain the damage. Small pits link adjacent conduits to allow fluid to flow between them, but not air – although ironically these pits, which prevent the spread of embolisms, are also a major cause of them. These pitted surfaces further reduce the flow of water through the xylem by as much as 30%. Conifers, by the Jurassic, developed an ingenious improvement, using valve-like structures to isolate cavitated elements. These torus-margo structures have a blob floating in the middle of a donut; when one side depressurises the blob is sucked into the torus and blocks further flow. Other plants simply accept cavitation; for instance, oaks grow a ring of wide vessels at the start of each spring, none of which survive the winter frosts. Maples use root pressure each spring to force sap upwards from the roots, squeezing out any air bubbles.

Growing to height also employed another trait of tracheids – the support offered by their lignified walls. Defunct tracheids were retained to form a strong, woody stem, produced in most instances by a secondary xylem. However, in early plants, tracheids were too mechanically vulnerable, and retained a central position, with a layer of tough sclerenchyma on the outer rim of the stems. Even when tracheids do take a structural role, they are supported by sclerenchymatic tissue.

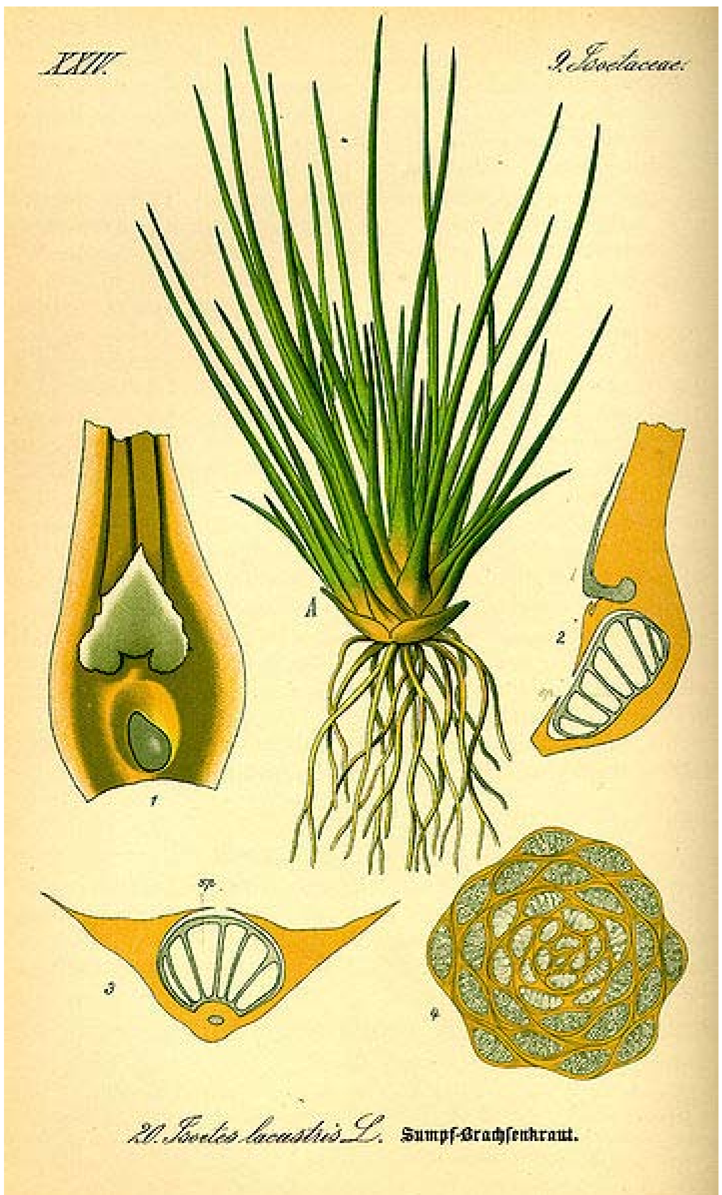
Tracheids end with walls, which impose a great deal of resistance on flow; vessel members have perforated end walls, and are arranged in series to operate as if they were one continuous vessel. The function of end walls, which were the default state in the Devonian, was probably to avoid embolisms. An embolism is where an air bubble is created in a tracheid. This may happen as a result of freezing, or by gases dissolving out of solution. Once an embolism is formed, it usually cannot be removed; the affected cell cannot pull water up, and is rendered useless.

End walls excluded, the tracheids of prevascular plants were able to operate under the same hydraulic conductivity as those of the first vascular plant, *Cooksonia*.

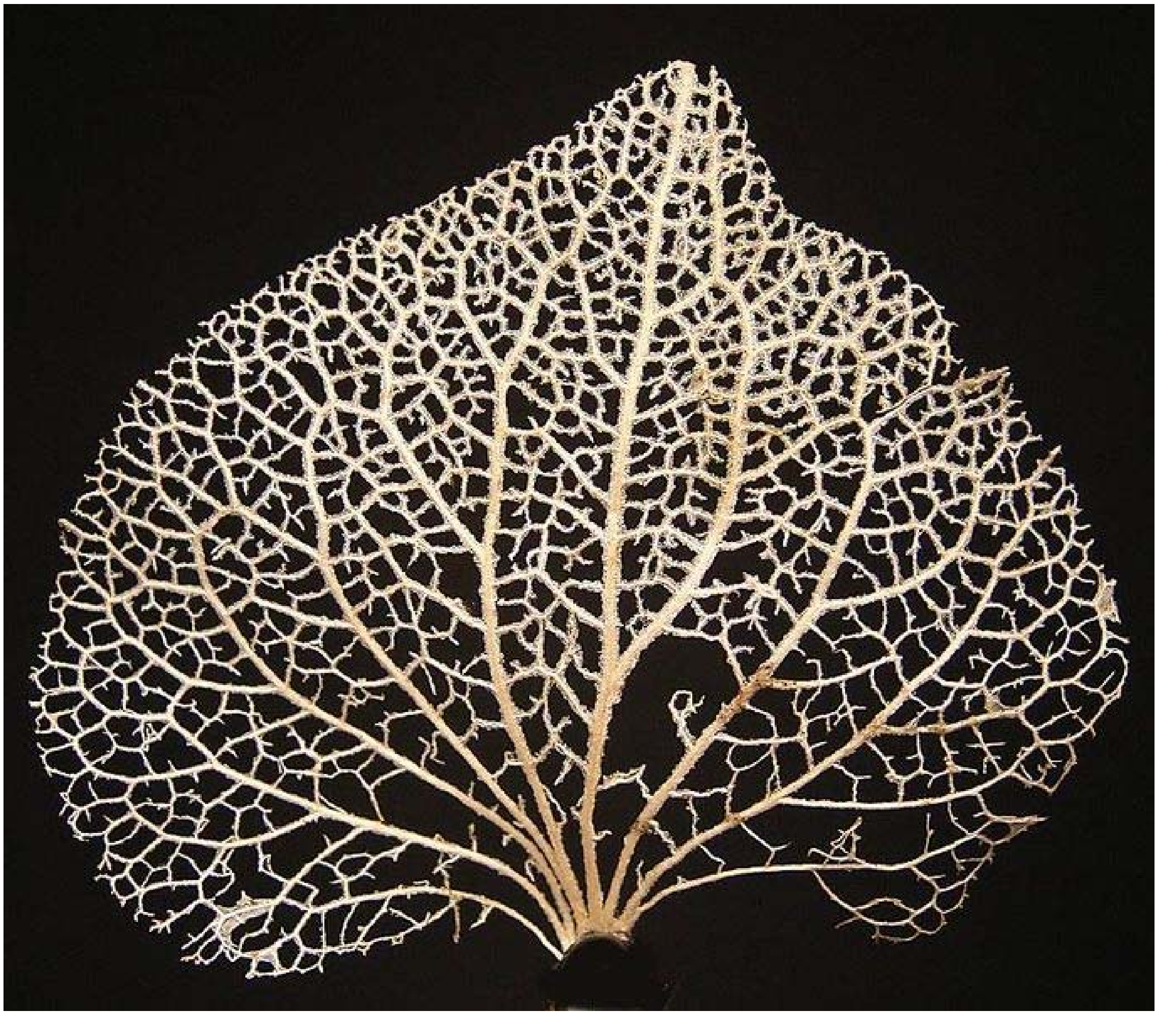
The size of tracheids is limited as they comprise a single cell; this limits their length, which in turn limits their maximum useful diameter to 80 μm. Conductivity grows with the fourth power of diameter, so increased diameter has huge rewards; **vessel elements**, consisting of a number of cells, joined at their ends, overcame this limit and allowed larger tubes to form, reaching diameters of up to 500 μm, and lengths of up to 10 m.

Vessels first evolved during the dry, low CO_2 periods of the late Permian, in the horsetails, ferns and Selaginellales independently, and later appeared in the mid Cretaceous in angiosperms and gnetophytes. Vessels allow the same cross-sectional area of wood to transport around a hundred times more water than tracheids! This allowed plants to fill more of their stems with structural fibres, and also opened a new niche to vines, which could transport water without being as thick as the tree they grew on. Despite these advantages, tracheid-based wood is a lot lighter, thus cheaper to make, as vessels need to be much more reinforced to avoid cavitation.

Evolution of leaves



The lycopod *Isoetes* bears microphylls with a single vascular trace.



The branching pattern of megaphyll veins may belie their origin as webbed, dichotomising branches.

Leaves today are, in almost all instances, an adaptation to increase the amount of sunlight that can be captured for photosynthesis. Leaves certainly evolved more than once, and probably originated as spiny outgrowths to protect early plants from herbivory.

The rhyniophytes of the Rhynie chert comprised nothing more than slender, unornamented axes. The early to middle Devonian trimerophytes, therefore, are the first evidence we have of anything that could be considered leafy. This group of vascular plants are recognisable by their masses of terminal sporangia, which adorn the ends of axes which may bifurcate or trifurcate. Some organisms, such as *Psilophyton*, bore enations. These are small, spiny outgrowths of the stem, lacking their own vascular supply.

Around the same time, the zosterophyllophytes were becoming important. This group is recognisable by their kidney-shaped sporangia, which grew on short lateral branches close to the main axes. They sometimes branched in a distinctive H-shape. The majority of this group bore pronounced spines on their axes. However, none of these had a vascular trace, and the first evidence of vascularised enations occurs in the Rhynie genus *Asteroxylon*. The spines of *Asteroxylon* had a primitive vasuclar supply – at the very least, leaf traces could be seen departing from the central protostele towards each individual "leaf". A fossil known as *Baragwanathia* appears in the fossil record slightly earlier, in the late Silurian. In this organism, these leaf traces continue into the leaf to form their mid-vein. One theory, the "enation theory", holds that the leaves developed by outgrowths of the protostele connecting with existing enations, but it is also possible that microphylls evolved by a branching axis forming "webbing".

Asteroxylon and *Baragwanathia* are widely regarded as primitive lycopods. The lycopods are still extant today, familiar as the quillwort *Isoetes* and the club mosses. Lycopods bear distinctive microphylls – leaves with a single vascular trace. Microphylls could grow to some size – the Lepidodendrales boasted microphylls over a meter in length – but almost all just bear the one vascular bundle. (An exception is the branching *Selaginella*).

The more familiar leaves, megaphylls, are thought to have separate origins – indeed, they appeared four times independently, in the ferns, horsetails, progymnosperms, and seed plants. They appear to have originated from dichotomising branches, which first overlapped (or "overtopped") one another, and eventually developed "webbing" and evolved into gradually more leaf-like structures. So megaphylls, by this "teleome theory", are composed of a group of webbed branches – hence the "leaf gap" left where the leaf's vascular bundle leaves that of the main branch resembles two axes splitting. In each of the four groups to evolve megaphylls, their leaves first evolved during the late Devonian to early Carboniferous, diversifying rapidly until the designs settled down in the mid Carboniferous.

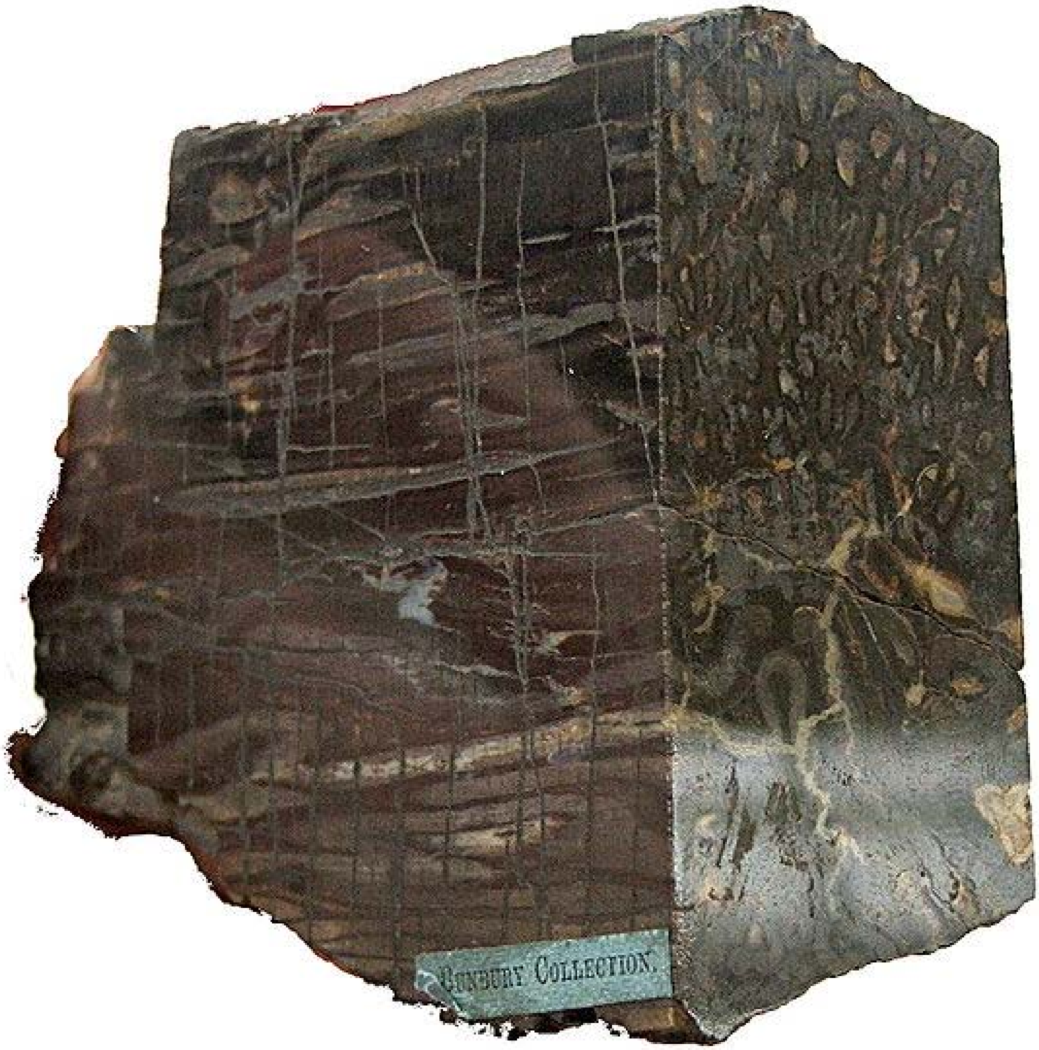
The cessation of further diversification can be attributed to developmental constraints, but why did it take so long for leaves to evolve in the first place? Plants had been on the land for at least 50 million years before megaphylls became significant. However, small, rare mesophylls are known from the early Devonian genus *Eophyllophyton* – so development could not have been a barrier to their appearance. The best explanation so far incorporates observations that atmospheric CO_2 was declining rapidly during this time – falling by around 90% during the Devonian. This corresponded with an increase in stomatal density by 100 times. Stomata allow water to evaporate from leaves, which causes them to curve. It appears that the low stomatal density in the early Devonian meant that evaporation was limited, and leaves would overheat if they grew to any size. The stomatal density could not increase, as the primitive steles and limited root systems would not be able to supply water quickly enough to match the rate of transpiration.

Clearly, leaves are not always beneficial, as illustrated by the frequent occurrence of secondary loss of leaves, famously exemplified by cacti and the "whisk fern" *Psilotum*.

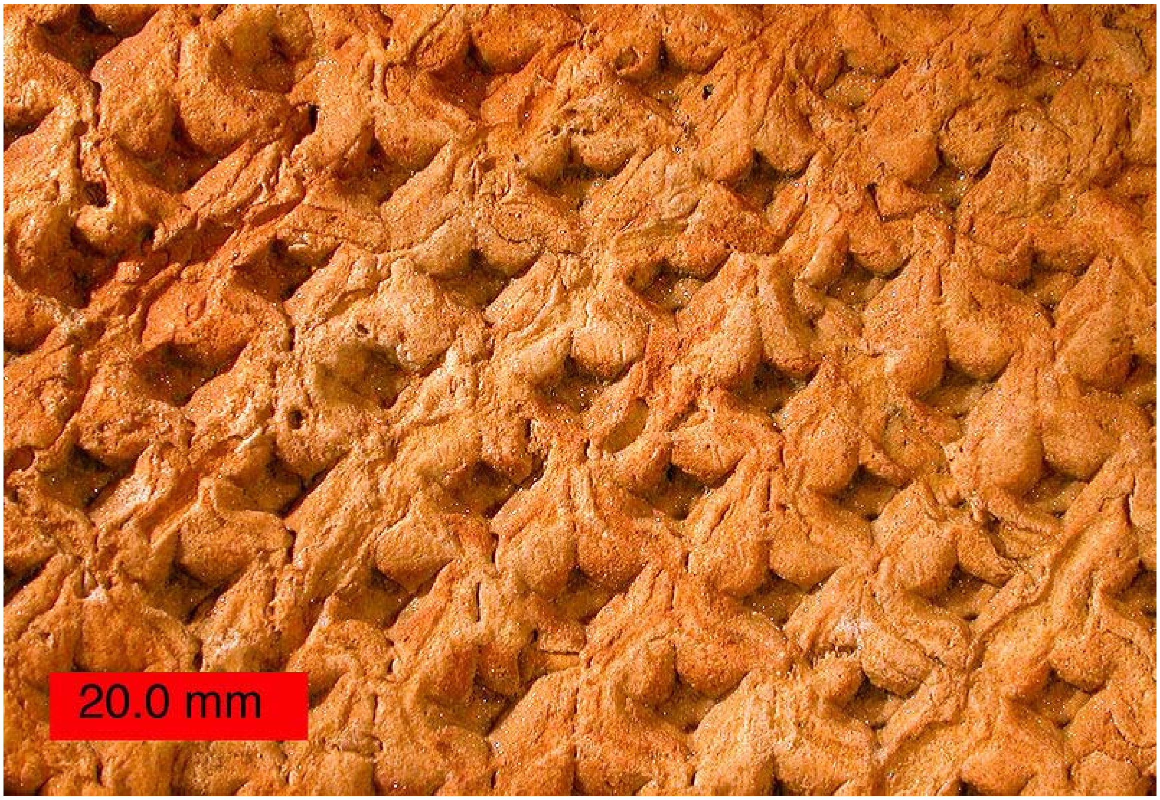
Secondary evolution can also disguise the true evolutionary origin of some leaves. Some genera of ferns display complex leaves which are attached to the pseudostele by an outgrowth of the vascular bundle, leaving no leaf gap. Further, horsetail (*Equisetum*) leaves bear only a single vein, and appear for all the world to be microphyllous; however, in the light of the fossil record and molecular evidence, we conclude that their forbears bore leaves with complex venation, and the current state is a result of secondary simplification.

Deciduous trees deal with another disadvantage to having leaves. The popular belief that plants shed their leaves when the days get too short is misguided; evergreens prospered in the Arctic circle during the most recent greenhouse earth. The generally accepted reason for shedding leaves during winter is to cope with the weather – the force of wind and weight of snow are much more comfortably weathered without leaves to increase surface area. Seasonal leaf loss has evolved independently several times and is exhibited in the ginkgoales, pinophyta and angiosperms. Leaf loss may also have arisen as a response to pressure from insects; it may have been less costly to lose leaves entirely during the winter or dry season than to continue investing resources in their repair.

Evolution of trees



The trunk of early tree fern *Psaronius*, showing internal structure. The top of the plant would have been to the left of the image



External mold of *Lepidodendron* trunk showing leaf scars from the Upper Carboniferous of Ohio

The early Devonian landscape was devoid of vegetation taller than waist height. Without the evolution of a robust vascular system, taller heights could not be attained. There was, however, a constant evolutionary pressure to attain greater height. The most obvious advantage is the harvesting of more sunlight for photosynthesis – by overshadowing competitors – but a further advantage is present in spore distribution, as spores (and, later, seeds) can be blown greater distances if they start higher. This may be demonstrated by *Prototaxites*, thought to be a late Silurian fungus reaching eight metres in height.

In order to attain arborescence, early plants needed to develop woody tissue that would act as both support and water transport. To understand wood, we must know a little of vascular behaviour. The stele of plants undergoing "secondary growth" is surrounded by the vascular cambium, a ring of cells which produces more xylem (on the inside) and phloem (on the outside). Since xylem cells comprise dead, lignified tissue, subsequent rings of xylem are added to those already present, forming wood.

The first plants to develop this secondary growth, and a woody habit, were apparently the ferns, and as early as the middle Devonian one species, *Wattieza*, had already reached heights of 8 m and a tree-like habit.

Other clades did not take long to develop a tree-like stature; the late Devonian *Archaeopteris*, a precursor to gymnosperms which evolved from the trimerophytes, reached 30 m in height. These progymnosperms were the first plants to develop true wood, grown from a bifacial cambium, of which the first appearance is in the mid Devonian *Rellimia*. True wood is only thought to have evolved once, giving rise to the concept of a "lignophyte" clade.

These *Archaeopteris* forests were soon supplemented by lycopods, in the form of lepidodendrales, which topped 50m in height and 2m across at the base. These lycopods rose to dominate late Devonian and Carboniferous coal deposits. Lepidodendrales differ from modern trees in exhibiting determinate growth: after building up a reserve of nutrients at a low height, the plants would "bolt" to a genetically determined height, branch at that level, spread their spores and die. They consisted of "cheap" wood to allow their rapid growth, with at least half of their stems comprising a pith-filled cavity. Their wood was also generated by a unifacial vascular cambium – it did not produce new phloem, meaning that the trunks could not grow wider over time.

The horsetail *Calamites* was next on the scene, appearing in the Carboniferous. Unlike the modern horsetail *Equisetum*, *Calamites* had a unifacial vascular cambium, allowing them to develop wood and grow to heights in excess of 10 m. They also branched multiple times.

While the form of early trees was similar to that of today's, the groups containing all modern trees had yet to evolve.

The dominant groups today are the gymnosperms, which include the coniferous trees, and the angiosperms, which contain all fruiting and flowering trees. It was long thought that the angiosperms arose from within the gymnosperms, but recent molecular evidence suggests that their living representatives form two distinct groups. It must be noted that the molecular data has yet to be fully reconciled with morphological data, but it is becoming accepted that the morphological support for paraphyly is not especially strong. This would lead to the conclusion that both groups arose from within the pteridosperms, probably as early as the Permian.

The angiosperms and their ancestors played a very small role until they diversified during the Cretaceous. They started out as small, damp-loving organisms in the understory, and have been diversifying ever since the mid -Cretaceous, to become the dominant member of non-boreal forests today.

Evolution of roots

The roots (bottom image) of lepidodendrales are thought to be functionally equivalent to the stems (top), as the similar appearance of "leaf scars" and "root scars" on these specimens from different species demonstrates.

Roots are important to plants for two main reasons: Firstly, they provide anchorage to the substrate; more importantly, they provide a source of water and nutrients from the soil. Roots allowed plants to grow taller and faster.

The onset of roots also had effects on a global scale. By disturbing the soil, and promoting its acidification (by taking up nutrients such as nitrate and phosphate), they enabled it to weather more deeply, promoting the draw-down of CO_2 with huge implications for climate. These effects may have been so profound they led to a mass extinction.

But how and when did roots evolve in the first place? While there are traces of root-like impressions in fossil soils in the late Silurian, body fossils show the earliest plants to be devoid of roots. Many had tendrils which sprawled along or beneath the ground, with upright axes or thalli dotted here and there, and some even had non-photosynthetic subterranean branches which lacked stomata. The distinction between root and specialised branch is developmental; true roots follow a different developmental trajectory to stems. Further, roots differ in their branching pattern, and in possession of a root cap. So while Silu-Devonian plants such as *Rhynia* and *Horneophyton* possessed the physiological equivalent of roots, roots – defined as organs differentiated from stems – did not arrive until later. Unfortunately, roots are rarely preserved in the fossil record, and our understanding of their evolutionary origin is sparse.

Rhizoids – small structures performing the same role as roots, usually a cell in diameter – probably evolved very early, perhaps even before plants colonised the land; they are recognised in the Characeae, an algal sister group to land plants. That said, rhizoids probably evolved more than once; the rhizines of lichens, for example, perform a similar role. Even some animals (*Lamellibrachia*) have root-like structures!

More advanced structures are common in the Rhynie chert, and many other fossils of comparable early Devonian age bear structures that look like, and acted like, roots. The rhyniophytes bore fine rhizoids, and the trimerophytes and herbaceous lycopods of the chert bore root-like structure penetrating a few centimetres into the soil. However, none of these fossils display all the features borne by modern roots. Roots and root-like structures became increasingly more common and deeper penetrating during the Devonian period, with lycopod trees forming roots around 20 cm long during the Eifelian and Givetian. These were joined by progymnosperms, which rooted up to about a metre deep, during the ensuing Frasnian stage. True gymnosperms and zygopterid ferns also formed shallow rooting systems during the Famennian period.

The rhizomorphs of the lycopods provide a slightly approach to rooting. They were equivalent to stems, with organs equivalent to leaves performing the role of rootlets. A similar construction is observed in the extant lycopod *Isoetes*, and this appears to be evidence that roots evolved independently at least twice, in the lycophytes and other plants.

A vascular system is indispensable to a rooted plants, as non-photosynthesising roots need a supply of sugars, and a vascular system is required to transport water and nutrients from the roots to the rest of the plant. These plants are little more advanced than their Silurian forbears, without a dedicated root system; however, the flat-lying axes can be clearly seen to have growths similar to the rhizoids of bryophytes today.

By the mid-to-late Devonian, most groups of plants had independently developed a rooting system of some nature. As roots became larger, they could support larger trees, and the soil was weathered to a greater depth. This deeper weathering had effects not only on the aforementioned drawdown of CO_2, but also opened up new habitats for colonisation by fungi and animals.

Roots today have developed to the physical limits. They penetrate many metres of soil to tap the water table. The narrowest roots are a mere 40 µm in diameter, and could not physically transport water if they were any narrower. The earliest fossil roots recovered, by contrast, narrowed from 3 mm to under 700 µm in diameter; of course, taphonomy is the ultimate control of what thickness we can see.

Arbuscular mycorrhizae

The efficiency of many plants' roots is increased via a symbiotic relationship with a fungal partner. The most common are arbuscular mycorrhizae (AM), literally "tree-like fungal roots". These comprise fungi which invade some root cells, filling the cell membrane with their hyphae. They feed on the plant's sugars, but return nutrients generated or extracted from the soil (especially phosphate), which the plant would otherwise have no access to.

This symbiosis appears to have evolved early in plant history. AM are found in all plant groups, and 80% of extant vascular plants, suggesting an early ancestry; a "plant"-fungus symbiosis may even have been the step that enabled them to colonise the land, and indeed AM are abundant in the Rhynie chert; the association occurred even before there were true roots to colonise, and is has even been suggested that roots evolved in order to provide a more comfortable habitat for mycorrhizal fungi.

Evolution of seeds

The fossil seed *Trigonocarpus*

Early land plants reproduced in the fashion of ferns: spores germinated into small gametophytes, which produced sperm. These would swim across moist soils to find the female organs (archegonia) on the same or another gametophyte, where they would fuse with an ovule to produce an embryo, which would germinate into a sporophyte.

This mode of reproduction restricted early plants to damp environments, moist enough that the sperm could swim to their destination. Therefore, early land plants were constrained to the lowlands, near shores and streams. The development of heterospory freed them from this constraint.

Heterosporic organisms, as their name suggests, bear spores of two sizes – microspores and megaspores. These would germinate to form microgametophytes and megagametophytes, respectively. This system paved the way for seeds: taken to the extreme, the megasporangia could bear only a single megaspore tetrad, and to complete the transition to true seeds, three of the megaspores in the original tetrad could be aborted, leaving one megaspore per megasporangium.

The transition to seeds continued with this megaspore being "boxed in" to its sporangium while it germinates. Then, the megagametophyte is contained within a waterproof integument, which forms the bulk of the seed. The microgametophyte – a pollen grain which has germinated from a microspore – is employed for dispersal, only releasing its desiccation-prone sperm when it reaches a receptive megagametophyte.

Lycopods go a fair way down the path to seeds without ever crossing the threshold. Fossil lycopod megaspores reaching 1 cm in diameter, and surrounded by vegetative tissue, are known – these even germinate into a megagametophyte *in situ*. However, they fall short of being seeds, since the nucellus, an inner spore-covering layer, does not completely enclose the spore. A very small slit remains, meaning that the seed is still exposed to the atmosphere. This has two consequences – firstly, it means it is not fully resistant to desiccation, and secondly, sperm do not have to "burrow" to access the archegonia of the megaspore.

The first "spermatophytes" (literally:seed plants) – that is, the first plants to bear true seeds – are called **pteridosperms**: literally, "seed ferns", so called because their foliage consisted of fern-like fronds, although they were not closely related to ferns. The oldest fossil evidence of seed plants is of Late Devonian age and they appear to have evolved out of an earlier group known as the progymnosperms. These early seed plants ranged from trees to small, rambling shrubs; like most early progymnosperms, they were woody plants with fern-like foliage. They all bore ovules, but no cones, fruit or similar. While it is difficult to track the early evolution of seeds, we can trace the lineage of the seed ferns from the simple trimerophytes through homosporous Aneurophytes.

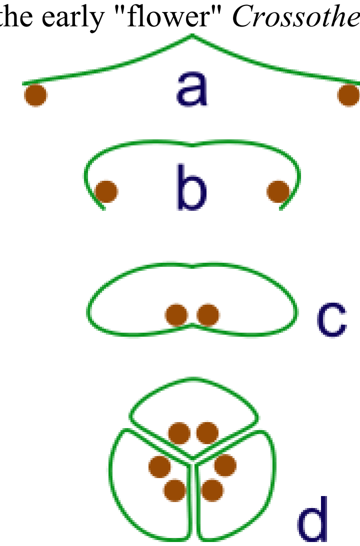
This seed model is shared by basically all gymnosperms (literally: "naked seeds"), most of which encase their seeds in a woody or fleshy (the yew, for example) cone, but none of which fully enclose their seeds. The angiosperms ("vessel seeds") are the only group to fully enclose the seed, in a carpel.

Fully enclosed seeds opened up a new pathway for plants to follow: that of seed dormancy. The embryo, completely isolated from the external atmosphere and hence protected from desiccation, could survive some years of drought before germinating. Gymnosperm seeds from the late Carboniferous have been found to contain embryos, suggesting a lengthy gap between fertilisation and germination. This period is associated with the entry into a greenhouse earth period, with an associated increase in aridity. This suggests that dormancy arose as a response to drier climatic conditions, where it became advantageous to wait for a moist period before germinating. This evolutionary breakthrough appears to have opened a floodgate: previously inhospitable areas, such as dry mountain slopes, could now be tolerated, as were soon covered by trees.

Seeds offered further advantages to their bearers: they increased the success rate of fertilised gametophytes, and because a nutrient store could be "packaged" in with the embryo, the seeds could germinate rapidly in inhospitable environments, reaching a size where it could fend for itself more quickly. For example, without an endosperm, seedlings growing in arid environments would not have the reserves to grow roots deep enough to reach the water table before they expired. Likewise, seeds germinating in a gloomy understory require an additional reserve of energy to quickly grow high enough to capture sufficient light for self-sustenance. A combination of these advantages gave seed plants the ecological edge over the previously dominant genus *Archaeopteris*, this increasing the biodiversity of early forests.

Evolution of flowers

The pollen bearing organs of the early "flower" *Crossotheca*



The evolution of syncarps.
a: sporangia borne at tips of leaf
b: Leaf curls up to protect sporangia

c: leaf curls to form enclosed roll
d: grouping of three rolls into a syncarp

Flowers are modified leaves possessed only by the group known as the angiosperms, which are relatively late to appear in the fossil record. Colourful and/or pungent structures surround the cones of plants such as cycads and gnetales, making a strict definition of the term "flower" elusive.

The flowering plants have long been assumed to have evolved from within the *gymnosperms*; according to the traditional morphological view, they are closely allied to the gnetales. However, as noted above, recent molecular evidence is at odds to this hypothesis, and further suggests that gnetales are more closely related to some gymnosperm groups than angiosperms, and that extant gymnosperms form a distinct clade to the angiosperms, the two clades diverging some 300 million years ago.

The relationship of stem groups to the angiosperms is of utmost importance in determining the evolution of flowers; stem groups provide an insight into the state of earlier "forks" on the path to the current state. If we identify an unrelated group as a stem group, then we will gain an incorrect image of the lineages' history. The traditional view that flowers arose by modification of a structure similar to that of the gnetales, for example, no longer bears weight in the light of the molecular data.

Convergence increases our chances of misidentifying stem groups. Since the protection of the megagametophyte is evolutionarily desirable, it would be unsurprising if many separate groups stumbled upon protective encasements independently. Distinguishing ancestry in such a situation, especially where we usually only have fossils to go on, is tricky – to say the least.

In flowers, this protection is offered by the carpel, an organ believed to represent an adapted leaf, recruited into a protective role, shielding the ovules. These ovules are further protected by a double-walled integument.

Penetration of these protective layers needs something more that a free-floating microgametophyte. Angiosperms have pollen grains comprising just three cells. One cell is responsible for drilling down through the integuments, and creating a conduit for the two sperm cells to flow down. The megagametophyte has just seven cells; of these, one fuses with a sperm cell, forming the nucleus of the egg itself, and another other joins with the other sperm, and dedicates itself to forming a nutrient-rich endosperm. The other cells take auxiliary roles. This process of "double fertilisation" is unique and common to all angiosperms.

The inflorescences of the Bennettitales are strikingly similar to flowers

In the fossil record, there are three intriguing groups which bore flower-like structures. The first is the Permian pteridosperm *Glossopteris*, which already bore recurved leaves resembling carpels. The Triassic *Caytonia* is more flower-like still, with enclosed ovules – but only a single integument. Further, details of their pollen and stamens set them apart from true flowering plants.

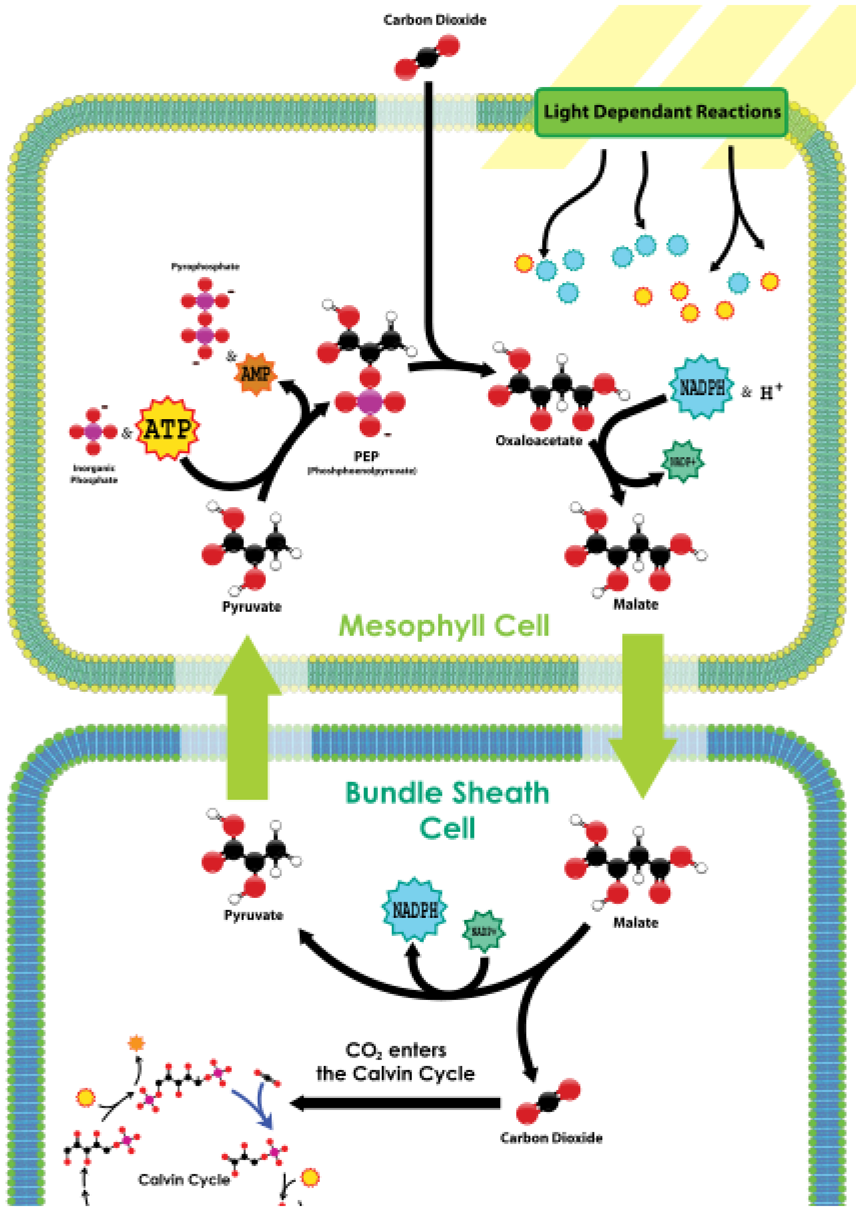
The Bennettitales bore remarkably flower-like organs, protected by whorls of bracts which may have played a similar role to the petals and sepals of true flowers; however, these flower-like structures evolved independently, as the Bennettitales are more closely related to cycads and ginkgos than to the angiosperms.

However, no true flowers are found in any groups save those extant today. Most morphological and molecular analyses place *Amborella*, the nymphaeales and

Austrobaileyaceae in a basal clade dubbed "ANA". This clade appear to have diverged in the early Cretaceous, around 130 million years ago – around the same time as the earliest fossil angiosperm, and just after the first angiosperm-like pollen, 136 million years ago. The magnoliids diverged soon after, and a rapid radiation had produced eudicots and monocots by 125 million years ago. By the end of the Cretaceous 65.5 million years ago, over 50% of today's angiosperm orders had evolved, and the clade accounted for 70% of global species. It was around this time that flowering trees became dominant over conifers

The features of the basal "ANA" groups suggest that angiosperms originated in dark, damp, frequently disturbed areas. It appears that the angiosperms remained constrained to such habitats throughout the Cretaceous – occupying the niche of small herbs early in the successional series. This may have restricted their initial significance, but given them the flexibility that accounted for the rapidity of their later diversifications in other habitats.

Advances in metabolism



The C_4 carbon concentrating mechanism

The most recent major innovation by the plants is the development of the C_4 metabolic pathway.

Photosynthesis is not quite as simple as adding water to CO_2 to produce sugars and oxygen. A complex chemical pathway is involved, facilitated along the way by a range of enzymes and co-enzymes. The enzyme RuBisCO is responsible for "fixing" CO_2 – that is, it attaches it to a carbon-based molecule to form a sugar, which can be used by the plant, releasing an oxygen molecule along the way. However, the enzyme is notoriously inefficient, and just as effectively will also fix oxygen instead of CO_2 in a process called photorespiration. This is energetically costly as the plant has to use energy to turn the products of photorepsiration back into a form that can react with CO_2.

Concentrating carbon

To work around this inefficiency, C_4 plants evolved carbon concentrating mechanisms. These work by increasing the concentration of CO_2 around RuBisCO, thereby increasing the amount of photosynthesis and decreasing photorespiration. The process of concentrating CO_2 around RuBisCO requires more energy than allowing gases to diffuse, but under certain conditions – i.e. warm temperatures (>25°C), low CO_2 concentrations, or high oxygen concentrations – pays off in terms of the decreased loss of sugars through photorespiration.

One, C_4 metabolism, employs a so-called Kranz anatomy. This transports CO_2 through an outer mesophyll layer, via a range of organic molecules, to the central bundle sheath cells, where the CO_2 is released. In this way, CO_2 is concentrated near the site of RuBisCO operation. Because RuBisCO is operating in an environment with much more CO_2 than it otherwise would be, it performs more efficiently.

A second method, CAM photosynthesis, temporally separates photosynthesis from the action of RuBisCO. RuBisCO only operates during the day, when stomata are sealed and CO_2 is provided by the breakdown of the chemical malate. More CO_2 is then harvested from the atmosphere when stomata open, during the cool, moist nights, reducing water loss.

Evolutionary record

These two pathways, with the same effect on RuBisCO, evolved a number of times independently – indeed, C_4 alone arose in 18 different plant families. The C_4 construction is most famously used by a subset of grasses, while CAM is employed by many succulents and cacti. The trait appears to have emerged during the Oligocene, around 25 to 32 million years ago; however, they did not become ecologically significant until the Miocene, -1 million years ago. Remarkably, some charcoalified fossils preserve tissue organised into the Kranz anatomy, with intact bundle sheath cells, allowing the presence C_4 metabolism to be identified without doubt at this time. In deducing their distribution and significance, we resort to the use of isotopic markers. C_3 plants preferentially use the lighter of two isotopes of carbon in the atmosphere, ^{12}C, which is more readily involved in the chemical pathways involved in its fixation. Because C_4 metabolism involves a further chemical step, this effect is accentuated. Plant material can be analysed to deduce the ratio of the heavier ^{13}C to ^{12}C. This ratio is denoted $\delta^{13}C$. C_3 plants are on average around 14‰ (parts per thousand) lighter than the atmospheric ratio, while C_4 plants are about 28‰ lighter. The $\delta^{13}C$ of CAM plants depends on the percentage of carbon fixed at night relative to what is fixed in the day, being closer to C_3 plants if they fix most carbon in the day and closer to C_4 plants if they fix all their carbon at night.

It's troublesome procuring original fossil material in sufficient quantity to analyse the grass itself, but fortunately we have a good proxy: horses. Horses were globally widespread in the period of interest, and browsed almost exclusively on grasses. There's an old phrase in isotope palæontology, "you are what you eat (plus a little bit)" – this refers to the fact that organisms reflect the isotopic composition of whatever they eat, plus a small adjustment factor. There is a good record of horse teeth throughout the globe, and their $\delta^{13}C$ has been measured. The record shows a sharp negative inflection around -1 million years ago, during the Messinian, and this is interpreted as the rise of C_4 plants on a global scale.

When is C_4 an advantage?

While C_4 enhances the efficiency of RuBisCO, the concentration of carbon is highly energy intensive. This means that C_4 plants only have an advantage over C_3 organisms in certain conditions: namely, high temperatures and low rainfall. C_4 plants also need high levels of sunlight in order to thrive. Models suggest that without wildfires removing shade-casting trees and shrubs, there would be no space for C_4 plants. But wildfires have occurred for 400 million years – why did C_4 take so long to arise, and then appear independently so many times? The Carboniferous period (~300 million years ago) had notoriously high oxygen levels – almost enough to allow spontaneous combustion – and very low CO_2, but there is no C_4 isotopic signature to be found. And there doesn't seem to be a sudden trigger for the Miocene rise.

During the Micoene, the atmosphere and climate was relatively stable. If anything, CO_2 increased gradually from 14 to 9 million years ago before settling down to concentrations similar to the Holocene. This suggests that it did not have a key role in invoking C_4 evolution. Grasses themselves (the group which would give rise to the most occurrences of C_4) had probably been around for 60 million years or more, so had had plenty of time to evolve C_4, which in any case is present in a diverse range of groups and thus evolved independently. There is a strong signal of climate change in South Asia; increasing aridity – hence increasing fire frequency and intensity – may have led to an increase in the importance of grasslands. However, this is difficult to reconcile with the North American record. It is possible that the signal is entirely biological, forced by the fire- (and elephant?)- driven acceleration of grass evolution – which, both by increasing weathering and incorporating more carbon into sediments, reduced atmospheric CO_2 levels. Finally, there is evidence that the onset of C_4 from 9 to 7 million years ago is a biased signal, which only holds true for North America, from where most samples originate; emerging evidence suggests that grasslands evolved to a dominant state at least 15Ma earlier in South America.

Evolutionary trends

The process of evolution works slightly differently in plants than animals. Differences in plant physiology and reproduction mean that while the same evolutionary principles of natural selection apply, the finer nuances of their effect are radically different.

One major difference is the ability of plants to reproduce clonally, and the totipotent nature of their cells, allowing them to reproduce asexually much more easily than most animals. They are also capable of polyploidy – where more than two chromosome sets are inherited from parents. This allows relatively fast bursts of evolution to occur. The long periods of dormancy that seed plants can employ also makes them less vulnerable to extinction, as they can "sit out" the tough periods and wait until more clement times to leap back to life.

The effect of these differences is most profoundly seen during extinction events. These events, which wiped out between 6 and 62% of terrestrial animal families, had "negligible" effect on plant families. However, the ecosystem structure is significantly rearranged, with the abundances and distributions of different groups of plants changing profoundly. These effects are perhaps due to the higher diversity within families, as extinction – which *was* common at the species level – was very selective. For example, wind-pollinated species survived better than insect-pollinated taxa, and specialised species generally lost out. In general, the surviving taxa were rare before the extinction, suggesting that they were generalists who were poor competitors when times were easy, but prospered when specialised groups went extinct and left ecological niches vacant.