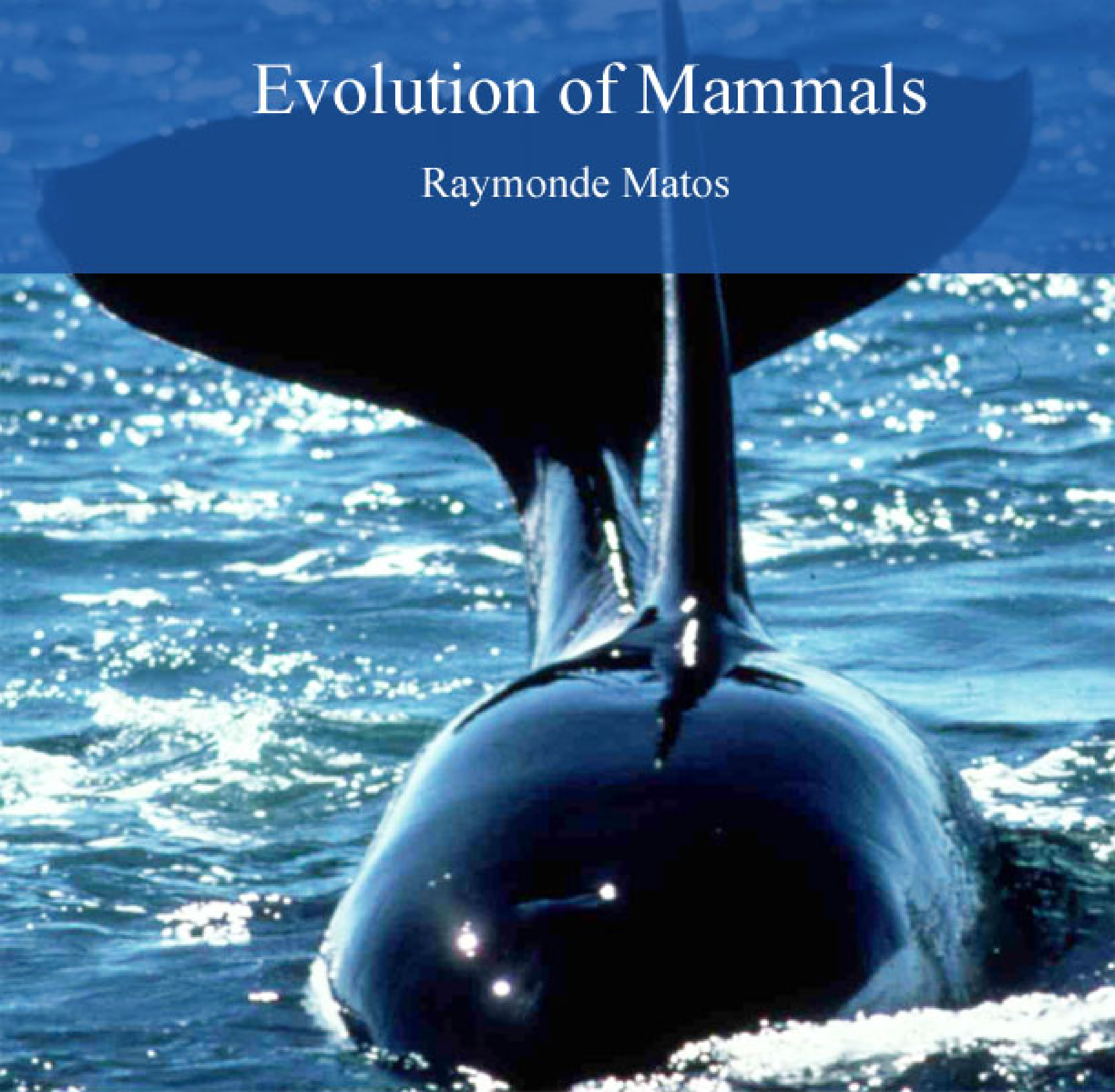
Evolution of Mammals

Raymonde Matos



First Edition, 2012

ISBN 978-81-323-3144-5

Published by:
Research World
4735/22 Prakashdeep Bldg,
Ansari Road, Darya Ganj,
Delhi - 110002
Email: info@wtbooks.com

Table of Contents

Chapter- 1

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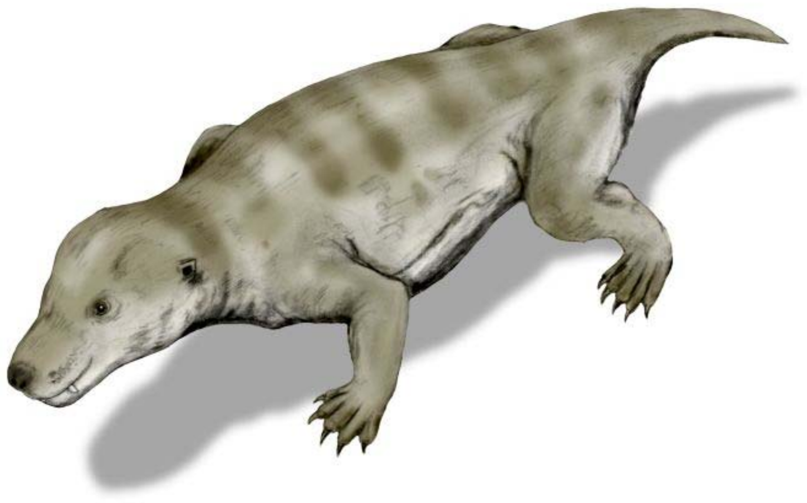


Restoration of *Thrinaxodon*, a member of the cynodont group, which includes the ancestors of mammals.

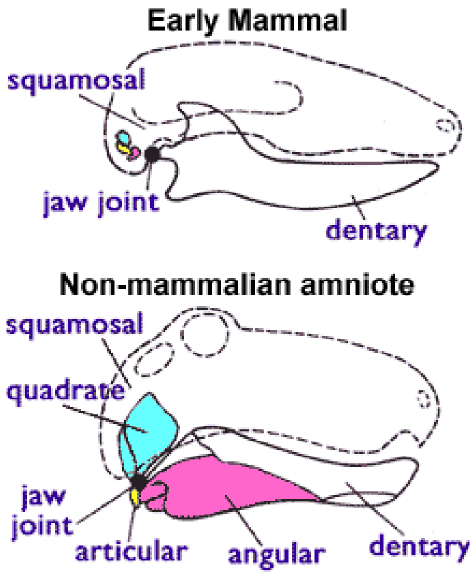
The **evolution of mammals** within the synapsid lineage (mammal-like-reptiles) was a gradual process that took approximately 70 million years, beginning in the mid-Permian. By the mid-Triassic, there were many species that looked like mammals, and the first true mammals appeared in the early Jurassic.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

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

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

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

Definition of "mammal"



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

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

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

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

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

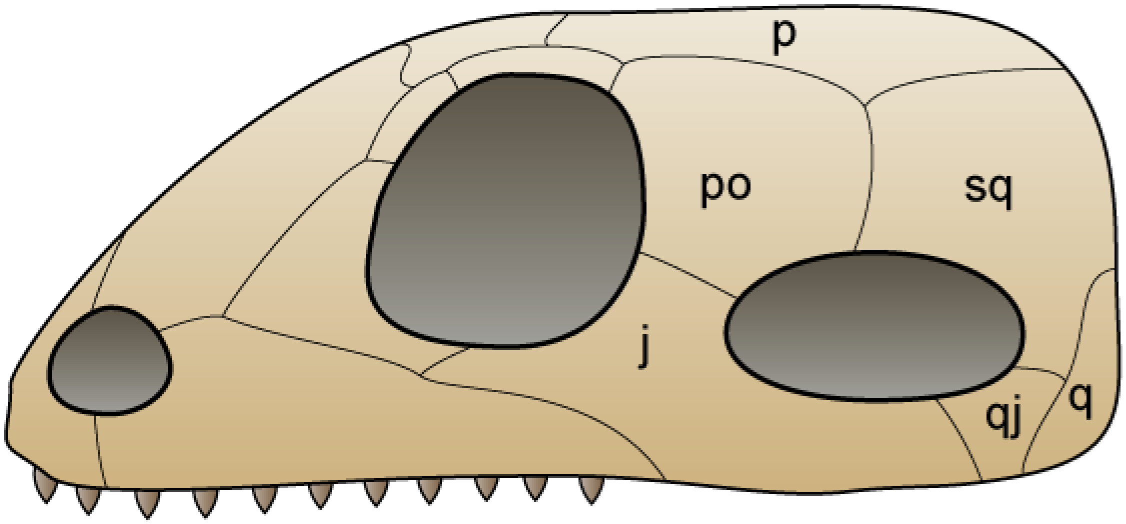
We may again ask the question, What is a mammal? Where we draw the line between reptile and mammal has no biological significance. It is purely a matter of convenience. There are two obvious choices, both immediately following a period of rapid evolution that make as definite a break as we can hope to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

Amniotes

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

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

Synapsids



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

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

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

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

Therapsids

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

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

- gradual development of a bony secondary palate. Most books and articles interpret this as a prequisite for the evolution of mammals' high metabolic rate, because it enabled these animals to eat and breathe at the same time. But some scientists point out that some modern ectotherms use a fleshy secondary palate to separate the mouth from the airway, and that a *bony* palate provides a surface on which the tongue can manipulate food, facilitating chewing rather than breathing. The interpretation of the bony secondary palate as an aid to chewing also suggests the development of a faster metabolism, since chewing makes it possible to digest food more quickly. In mammals the palate is formed by two specific bones, but various Permian therapsids had other combinations of bones in the right places to function as a palate.

- the dentary gradually becomes the main bone of the lower jaw.
- progress towards an erect limb posture, which would increase the animals' stamina by avoiding Carrier's constraint. But this process was erratic and very slow — for example: all herbivorous therapsids retained sprawling limbs (some late forms may have had semi-erect hind limbs); Permian carnivorous therapsids had sprawling forelimbs, and some late Permian ones also had semi-sprawling hindlimbs. In fact, modern monotremes still have semi-sprawling limbs.
- in the Triassic, progress towards the mammalian jaw and middle ear.
- there is plausible evidence of hair in Triassic therapsids, but none for Permian therapsids.
- some scientists have argued that some Triassic therapsids show signs of lactation.

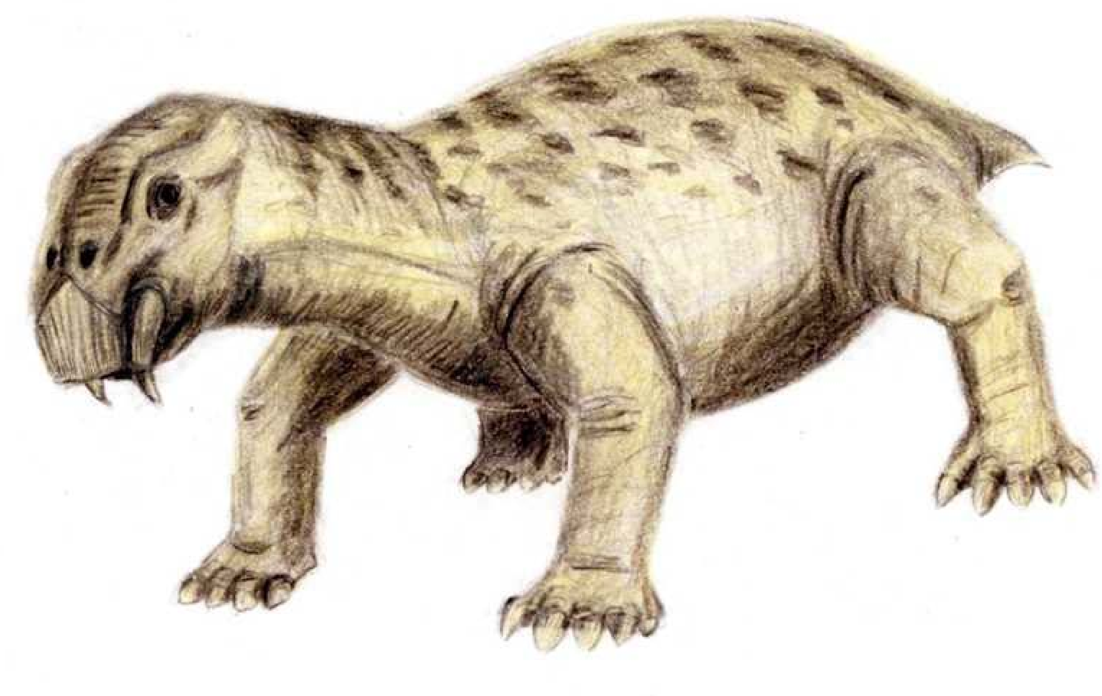
Biarmosuchia

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

Dinocephalians

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

Anomodonts



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

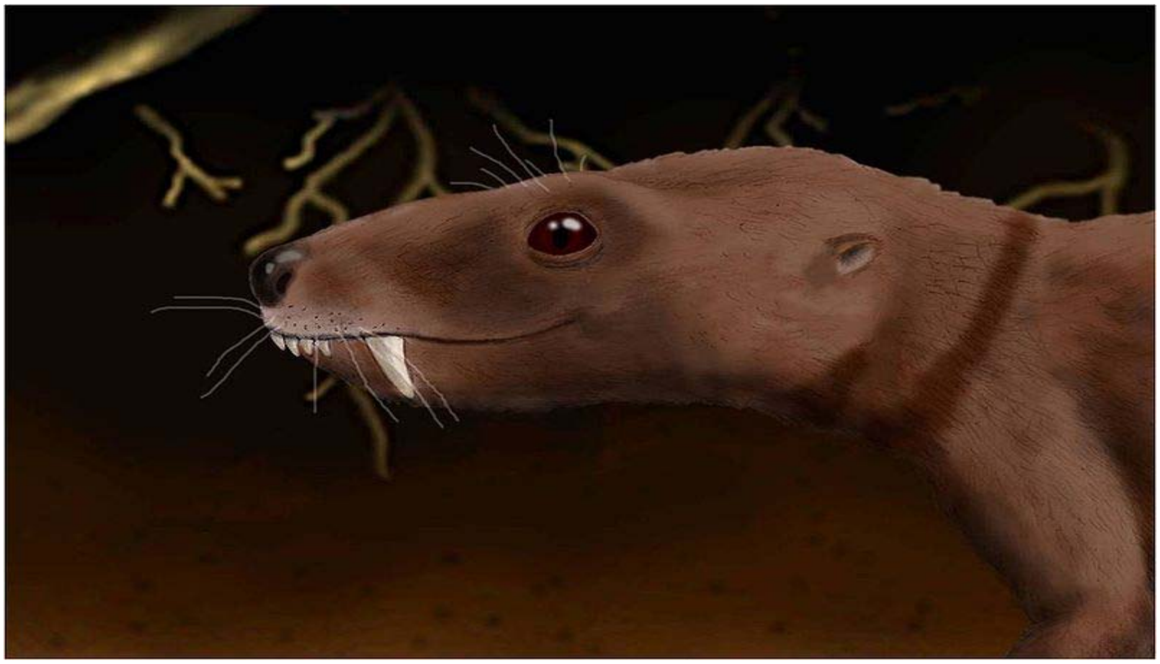
The anomodonts ("anomalous teeth") were the most successful of the herbivorous therapsids — one sub-group, the dicynodonts, survived almost to the end of the Triassic. But anomodonts were very different from modern herbivorous mammals, as their only teeth were a pair of fangs in the upper jaw and it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

Theriodonts

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

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

Cynodonts



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

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

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

Triassic takeover

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

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

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

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

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

From cynodonts to true mammals

Many uncertainties

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

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

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

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

As a result:

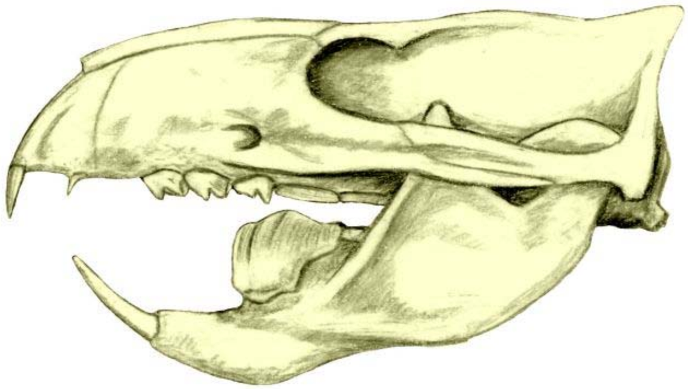
- In many cases it is difficult to assign a Mesozoic mammal or near-mammal fossil to a genus.
- All the available fossils of a genus seldom add up to a complete skeleton, and hence it is difficult to decide which genera are most like each other and therefore most likely to be closely-related. In other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

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

Mammals or mammaliformes?

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

Multituberculates

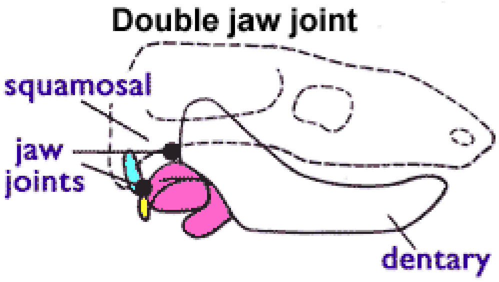


Skull of the multituberculate *Ptilodus*

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

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

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

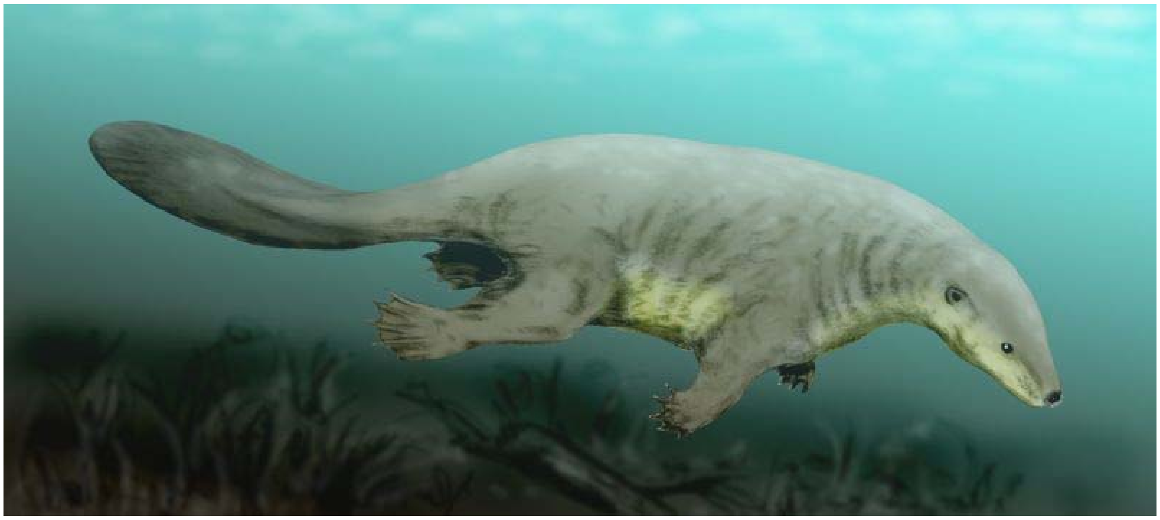


Morganucodontidae and other transitional forms had both types of jaw joint: dentary-squamosal (front) and articular-quadrate (rear).

Morganucodontidae

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

Docodonts

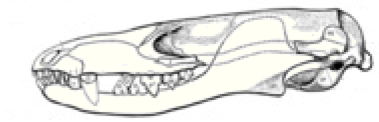


Reconstruction of *Castorocauda*. Note the fur and the adaptations for swimming (broad, flat tail; webbed feet) and for digging (robust limbs and claws).

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

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

Hadrocodium



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

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

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

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

The earliest true mammals

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

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

Australosphenida and Ausktribosphenidae

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

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

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

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

Monotremes

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

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

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

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

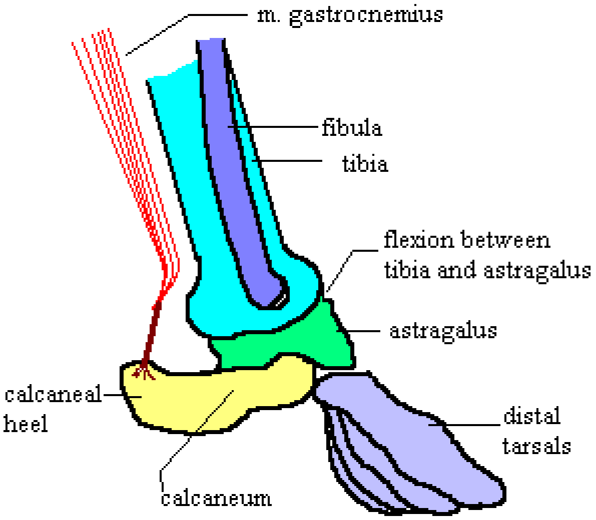
Unlike in other mammals, female monotremes do not have nipples and feed their young by "sweating" milk from patches on their bellies.

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

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

Theria

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



Therian form of crurotarsal ankle. Adapted with permission from Palaeos

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

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

Metatheria

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

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

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

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

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

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

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

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

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

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

Eutheria

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

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

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

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

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

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

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

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

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

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

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

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

Expansion of ecological niches in the Mesozoic

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

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

Repenomamus sometimes preyed on young dinosaurs

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

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

Evolution of major groups of living mammals

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

Fossil-based family tree of placental mammals

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

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

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

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

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

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

Family tree of placental mammals according to molecular phylogenetics

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

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

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

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

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

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

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

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

Timing of placental evolution

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

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

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

Evolution of mammalian features

Jaws and middle ears

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

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

Milk production (lactation)

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

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

Hair and fur

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

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

Erect limbs

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

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

Warm-bloodedness

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

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

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

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

Respiratory turbinates

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

Bony secondary palate

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

Diaphragm

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

Limb posture

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

Insulation (hair and fur)

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

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

Chapter- 2

Human Evolution

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

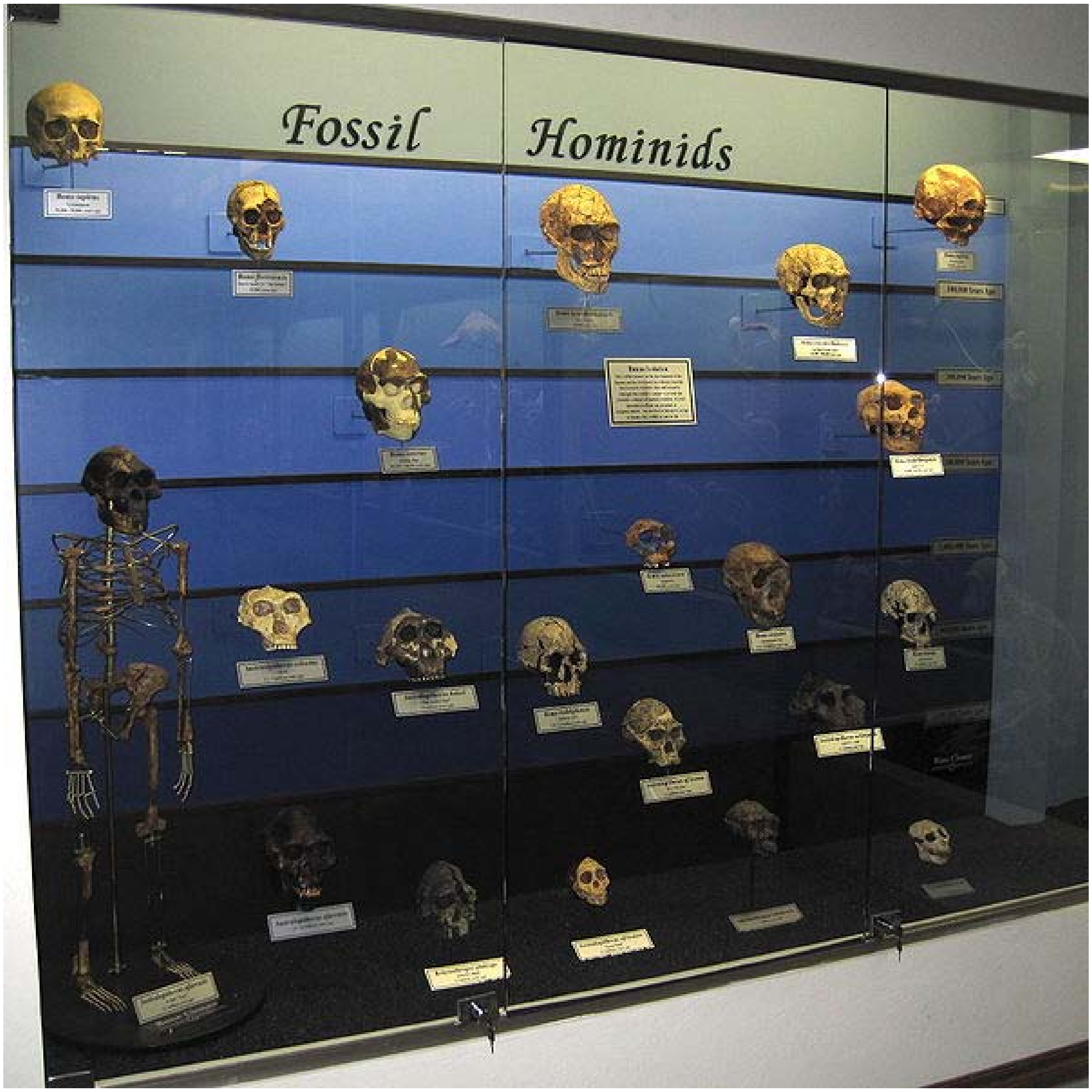
The term "human" in the context of human evolution refers to the genus *Homo*, but studies of human evolution usually include other hominids, such as the Australopithecines, from which the genus *Homo* had diverged by about 2.3 to 2.4 million years ago in Africa. Scientists have estimated that humans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

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

History of ideas

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

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



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

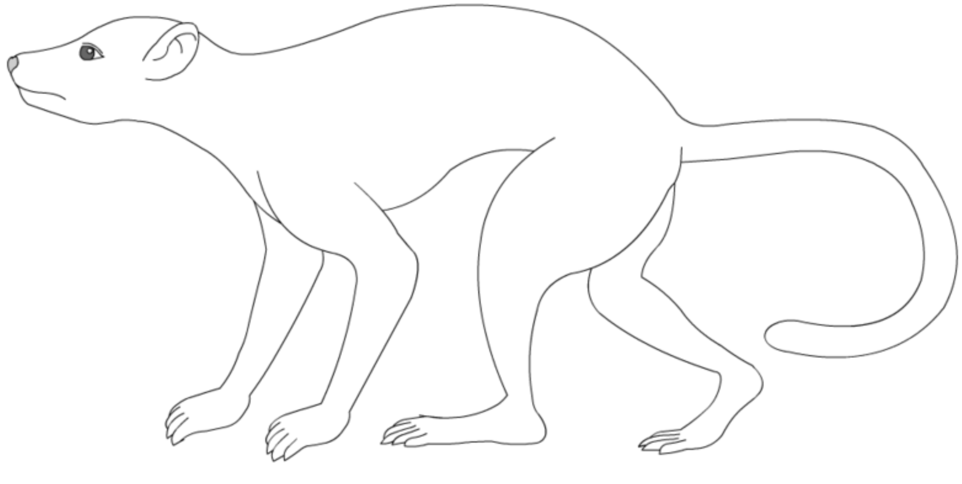
The first debates about the nature of human evolution arose between Thomas Huxley and Richard Owen. Huxley argued for human evolution from apes by illustrating many of the similarities and differences between humans and apes, and did so particularly in his 1863 book *Evidence as to Man's Place in Nature*.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

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

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

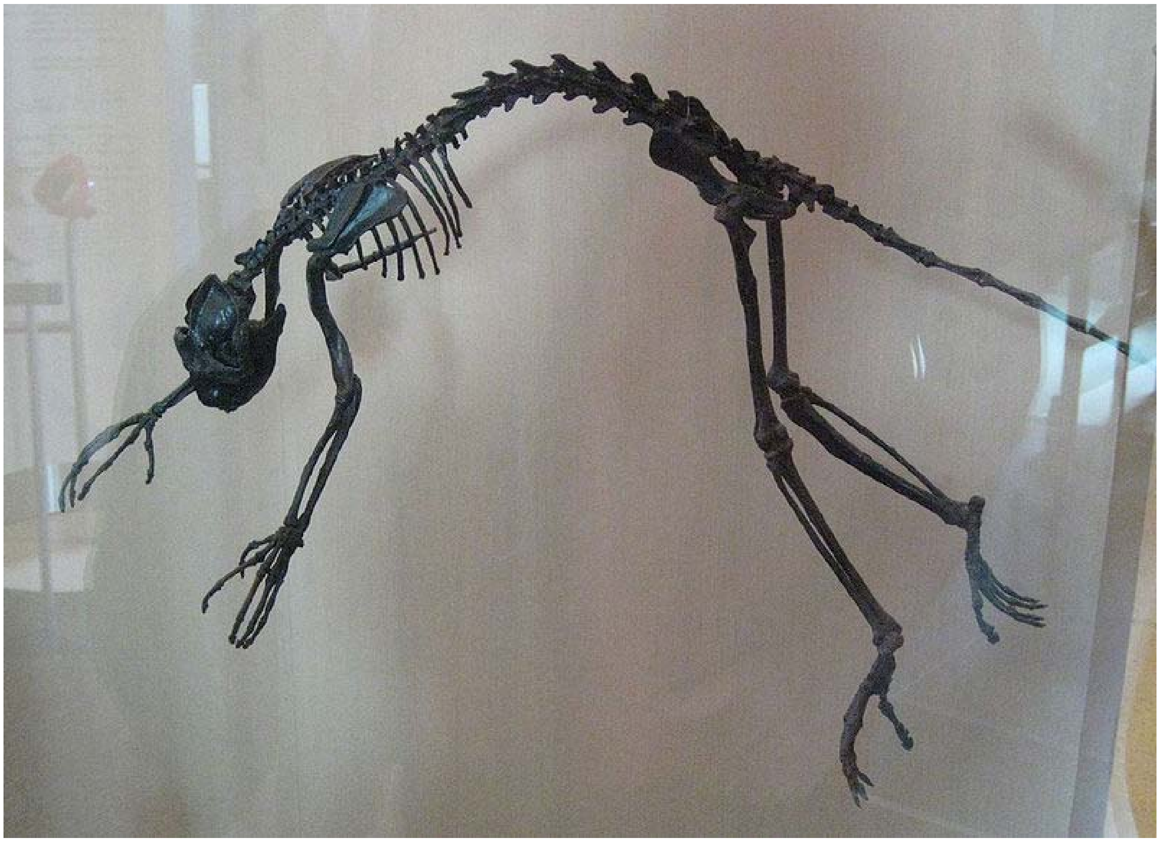
Before Homo

Evolution of the great apes



Plesiadapis

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



Notharctus

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

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

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

Reconstructed tailless *Proconsul* skeleton

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

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

Divergence of the human lineage from other Great Apes

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

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

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

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

Genus Homo

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

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

H. habilis and *H. gautengensis*

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

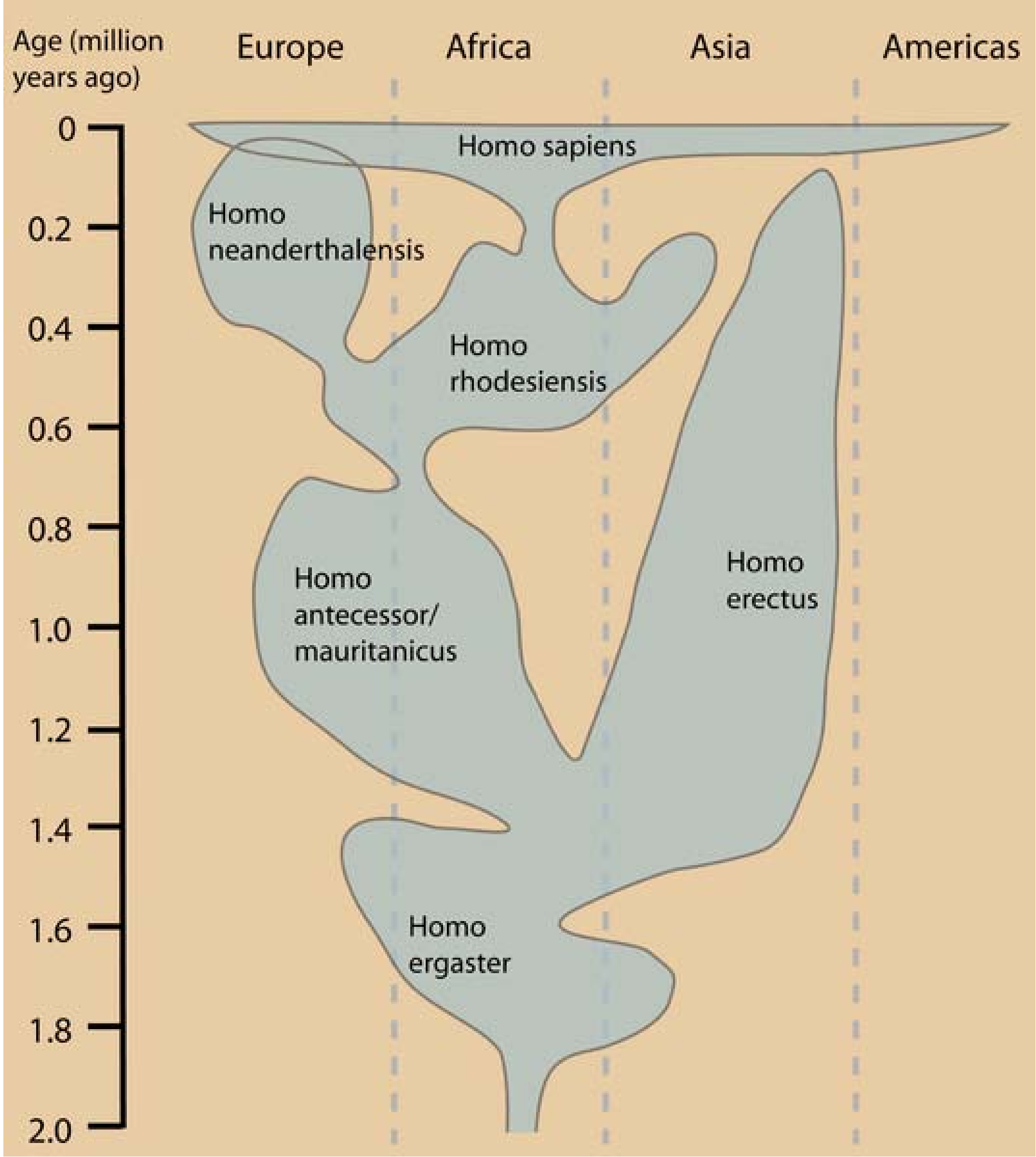
It was considered to be the first species of the genus *Homo* until May 2010, when a new species, *Homo gautengensis* was discovered in South Africa, that most likely arose earlier than *Homo habilis*.

H. rudolfensis and *H. georgicus*

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

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

H. ergaster and *H. erectus*



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

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

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

H. cepranensis and *H. antecessor*

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

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

H. heidelbergensis

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

H. rhodesiensis, and the Gawis cranium

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

H. neanderthalensis

Le Ferrassie Neanderthal skull (cast)

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

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

H. sapiens

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

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

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

H. floresiensis

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

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

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

Denisova hominin

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

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

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

Comparative table of *Homo* species

Comparative table of *Homo* species

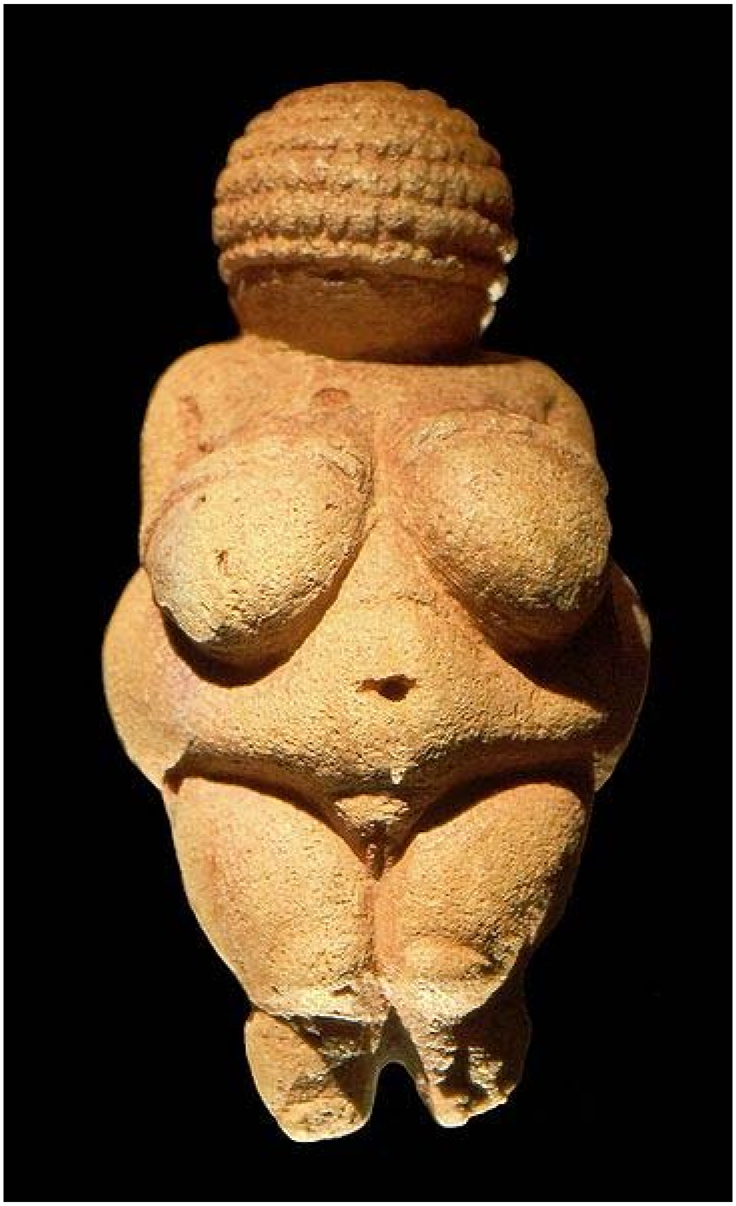
Species	Lived when (Ma)	Lived where	Adult height	Adult mass	Cranial capacity (cm³)	Fossil record	Discovery / publication of name
H. antecessor	1.2 – 0.8	Spain	1.75 m (5.7 ft)	90 kg (200 lb)	1,000	2 sites	1997
H. cepranensis	0.9 – 0.8?	Italy			1,000	1 skull cap	1994/2003
H. erectus	1.5 – 0.2	Africa, Eurasia (Java, China, India, Caucasus)	1.8 m (5.9 ft)	60 kg (130 lb)	850 (early) – 1,100 (late)	Many	1891/1892
H. ergaster	1.9 – 1.4	Eastern and Southern Africa	1.9 m (6.2 ft)		700–850	Many	1975
H. floresiensis	0.10? – 0.012	Indonesia	1.0 m (3.3 ft)	25 kg (55 lb)	400	7 individuals	2003/2004
H. gautengensis	>2 – 0.6	South Africa	1.0 m (3.3 ft)			1 individual	2010/2010
H. georgicus	1.8	Georgia			600	4 individuals	1999/2002
H. habilis	2.3 – 1.4	Africa	1.0–1.5 m (3.3–4.9 ft)	33–55 kg (73–120 lb)	510–660	Many	1960/1964
H. heidelbergensis	0.6 – 0.35	Europe, Africa, China	1.8 m (5.9 ft)	60 kg (130 lb)	1,100–1,400	Many	1908
H. neanderthalensis	0.35 – 0.03	Europe, Western Asia	1.6 m (5.2 ft)	55–70 kg (120–150 lb) (heavily built)	1,200–1,900	Many	(1829)/1864
H. rhodesiensis	0.3 – 0.12	Zambia			1,300	Very few	1921
H. rudolfensis	1.9	Kenya				1 skull	1972/1986
H. sapiens idaltu	0.16 – 0.15	Ethiopia			1,450	3 craniums	1997/2003
H. sapiens sapiens (modern humans)	0.2 – present	Worldwide	1.4–1.9 m (4.6–6.2 ft)	50–100 kg (110–220 lb)	1,000–1,850	Still living	—/1758

Use of tools

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

Fire, one of the greatest human discoveries

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



Venus of Willendorf, an example of Paleolithic art

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

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

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

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

Stone tools

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

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

Modern humans and the "Great Leap Forward" debate

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

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

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

Models of human evolution

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

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

Multiregional model

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

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

Out of Africa

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

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

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

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

Recent and current human evolution

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

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

Genetics

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

Notable human evolution researchers

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

- Mary Leakey, a British archaeologist and anthropologist whose discoveries in

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

Chapter- 3

Evolution of Mammalian Auditory Ossicles

The **evolution of mammalian auditory ossicles** is one of the most well-documented and important evolutionary events, demonstrating both numerous transitional forms as well as an excellent example of exaptation, the re-purposing of existing structures during evolution.

In reptiles, the eardrum is connected to the inner ear via a single bone, the stapes or stirrup, while the upper and lower jaws contain several bones not found in mammals. Over the course of the evolution of mammals, one lower and one upper jaw bone (the articular and quadrate) lost their purpose in the jaw joint and were put to new use in the middle ear, connecting to the stapes and forming a chain of three bones (collectively called the ossicles) which amplify sounds and allow more acute hearing. In mammals, these three bones are known as the malleus, incus, and stapes (hammer, anvil, and stirrup respectively).

The evidence that the malleus and incus are homologous to the reptilian articular and quadrate was originally embryological, and since this discovery an abundance of transitional fossils has both supported the conclusion and given a detailed history of the transition. The evolution of the stapes was an earlier and distinct event.

Reichert–Gaupp theory

The relationship between the reptilian jaw bones and mammalian middle-ear bones was first established on the basis of embryology and comparative anatomy by Reichert (in 1837, before the publication of On the Origin of Species in 1859) and advanced by Gaupp, and this is known as the *Reichert–Gaupp Theory*.

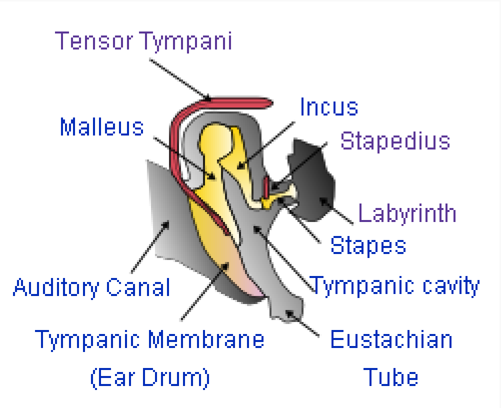
In the course of the development of the embryo, the incus and malleus arise from the same First Pharyngeal arch as the Mandible and Maxilla, and are served by mandibular and maxillary division of the Trigeminal Cranial nerve.

...the discovery that the mammalian malleus and incus were actually homologues of visceral elements of the "reptilian" jaw articulation ... ranks as one of the milestones in the history of comparative biology.

... it is one of the triumphs of the long series of researches on the extinct Theromorph reptiles, begun by Owen (1845), and continued by Seeley, Broom, and Watson, to have revealed the intermediate steps by which the change may have occurred from an inner quadrate to an outer squamosal articulation ...

There are also more recent studies in the genetic basis for the development of the ossicles from the embryonic arch. and relating this to evolutionary history.

"*Bapx1*, also known as *Nkx3.2*, is the vertebrate homologue of the *Drosophila* gene *Bagpipe*. A member of the NK2 class of homeobox genes ..." and this gene is implicated in the change from the jaw bones of non-mammals to the ossicles of mammals. Yet the transition between the "reptilian" jaw and the "mammalian" inner ear was not bridged in the fossil record until the 1950s with the elaboration of such fossils as the now-famous *Morganucodon*.



A typical mammalian middle ear: sound makes the tympanum (ear-drum) vibrate; 3 small bones, the malleus, incus and stapes, transmit the vibrations to the Labyrinth (inner ear), which transforms the vibrations into nerve signals.

Definitive mammalian middle ear

The mammalian middle ear contains three tiny bones known as the ossicles: malleus, incus, and stapes. The ossicles are a complex system of levers whose functions include: reducing the amplitude of the vibrations; increasing the amount of energy transmitted. The details of these effects vary noticeably between different mammal species, even when the species are as closely related as humans and chimpanzees.

Evolutionary history

Definition of "mammal"

Living mammal species can be identified by the presence in females of mammary glands which produce milk. Other features are required when classifying fossils, since mammary glands and other soft-tissue features are not visible in fossils. Paleontologists therefore use a distinguishing feature that is shared by all living mammals (including monotremes), but is not present in any of the early Triassic therapsids ("mammal-like reptiles"): mammals use two bones for hearing that all other amniotes use for eating. The earliest amniotes had a jaw joint composed of the articular (a small bone at the back of the lower jaw) and the quadrate (a small bone at the back of the upper jaw). All non-mammalian amniotes use this system including lizards, crocodilians, dinosaurs (and their descendants the birds) and therapsids; so the only ossicle in their middle ears is the stapes. But mammals have a different jaw joint, composed only of the dentary (the lower jaw bone which carries the teeth) and the squamosal (another small skull bone). And in mammals the quadrate and articular bones have become the incus and malleus bones in the middle ear.

Summary of the fossil evidence

Here is a very simplified "family tree" of the various lineages involved:

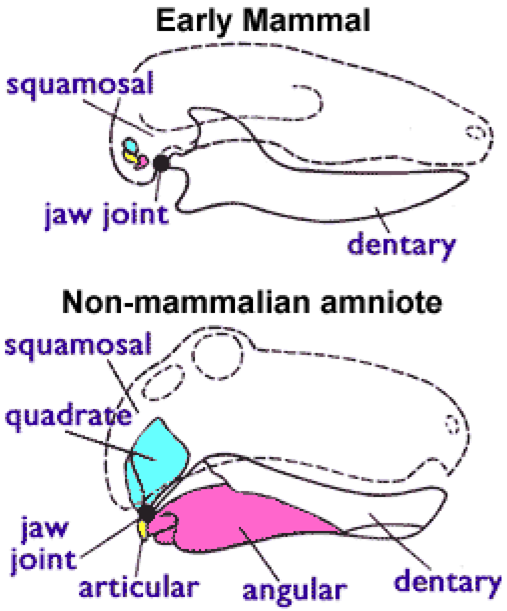
```
--Tetrapods------
    |       ("4 legged"; the earliest breathed via gills)
    |
    +-- Amphibians ----------------------------------------------
    |
    `--------Reptiliomorphs-----
               |         ("reptile-like" amphibians)
               |
               `--Amniotes------
                    |
                    +--Sauropsids ("lizard faces")---------------
                         |     (lizards, crocodilians, dinosaurs, birds
                         |      Testudines; and some extinct groups)
                         |
                         `--Synapsids------
                              |
                              `--Pelycosaurs----
                                   |
                                   `--Therapsids-----
                                        |
                                        `--Mammals---------------
```

The first fully terrestrial vertebrates were amniotes - their eggs had internal membranes which allowed the developing embryo to breathe but kept water in. This allowed amniotes to lay eggs on dry land, while amphibians generally need to lay their eggs in water. The first amniotes apparently arose in the late Carboniferous from the ancestral reptiliomorphs (a group of amphibians whose only living descendants are amniotes).

Within a few million years two important amniote lineages became distinct: mammals' synapsid ancestors and the sauropsids, from which lizards, snakes, crocodilians, dinosaurs and birds are descended.

The earliest known fossils of all these groups date from about 320 to 315M years ago. Unfortunately it is difficult to be sure about when each of them evolved, since vertebrate fossils from the late Carboniferous are very rare, and therefore the actual first occurrences of each of these types of animal might have been considerably earlier.

The pattern in most of the following sections is that each successive more "advanced" group started with the more "primitive" jaws and ears of its predecessors, then developed more mammal-like jaws and ears, and so on. The evolution of mammalian jaw joints and ears did not proceed neatly in step with the evolution of other mammalian features; or, to put it another way, all but the last of the various stages into which paleontologists divide the evolution towards the mammalian condition are not defined by their jaw joints and ears.



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

Early tetrapod and amniote ears

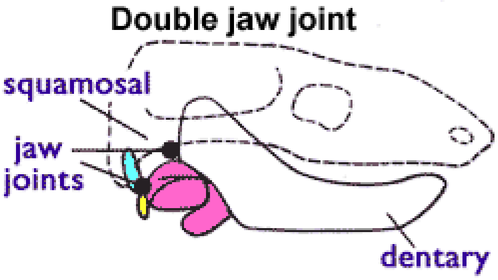
In modern amniotes (including mammals), the middle ear collects airborne sounds through an ear drum and transmits the vibrations to the inner ear via thin cartilaginous and ossified structures, which usually include the stapes (a stirrup-shaped auditory ossicle). But the earliest tetrapods, amphibians and amniotes probably did not have ear drums. In fact ear drums apparently evolved independently three to six times, in:

stegocephalians (very primitive amphibians); in anurans (the amphibian group that includes frogs and toads); in synapsids (mammals and their extinct relatives), in diapsids (the most important sauropsid group, including lizards, crocodiles, dinosaurs and birds); perhaps separately in anapsids (turtles and their extinct relatives), if turtles are not modified diapsids; probably in seymouriamorphs (a group of reptiliomorphs); and possibly in some temnospondyls (primitive amphibians). In all basal members of the 3 major clades of amniotes (synapsids, eureptiles, and parareptiles) the stapes bones are relatively massive props that support the braincase, and this function prevents them from being used as part of the hearing system. But there is increasing evidence that synapsids, eureptiles and parareptiles developed eardrums connected to the inner ear by stapes during the Permian.

Early therapsid jaws and ears

The jaws of early synapsids, including the ancestors of mammals, were similar to those of other tetrapods of the time, with a lower jaw consisting of a tooth-bearing dentary bone and several smaller posterior bones. The jaw joint consisted of the articular bone in the lower jaw and the quadrate in the upper jaw. The early pelycosaurs (late Carboniferous and early Permian) most probably did not have tympanic membranes (external eardrums), and their massive stapes bones supported the braincase, with the lower ends resting on the quadrates. But their descendants the therapsids (including mammals' ancestors) probably did have tympanic membranes and these probably were in contact with the quadrate bones; and the stapes bones were still in contact with the quadrates but functioned as auditory ossicles rather than braincase supports; so the therapsids' quadrates had a dual function, as part of the jaw joint and as parts of the hearing system.

Twin-jointed jaws



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

During the Permian and early Triassic the dentary of therapsids, including the ancestors of mammals, continually enlarged while other jaw bones were reduced. Eventually, the dentary was able to make contact with the squamosal, a bone in the upper jaw located anterior to the quadrate, allowing two simultaneous jaw joints - an anterior "mammalian" joint between the dentary and squamosal and a posterior "reptilian" joint between the quadrate and articular. This "twin-jointed jaw" can be seen in late cynodonts and early mammaliforms. *Morganucodon* is one of the first discovered and most thoroughly studied of the mammaliforms, since an unusually large number of morganucodont fossils have been found, and

Morganucodon is an almost perfect intermediate in this respect (the "twin-jointed jaw") between the higher mammal-like reptiles on the one hand and the typical mammals on the other.

(note: "mammal-like reptiles" is an obsolete term for the therapsids)

Mammal-like jaws and ears

As the dentary continued to enlarge during the Triassic, the older quadrate-articular joint fell out of use. Some of the bones were lost, but the quadrate (which is directly connected to the stapes), the articular (connected to the quadrate) and the angular (connected to the articular) became free-floating and associated with the stapes. This occurred at least twice in the mammaliformes ("almost-mammals"). The Multituberculates, which lived from about 160M years ago (mid-Jurassic) to about 35M years ago (early Oligocene) had jaw joints that consisted of only the dentary and squamosal bones, and the quadrate and articular bones were part of the middle ear; but other features of their teeth, jaws and skulls are significantly different from those of mammals.

In the lineage most closely related to mammals, the jaws of *Hadrocodium* (about 195M years ago in the very early Jurassic) suggest that it or a very close ancestor may have been the first to have a nearly fully mammalian middle ear: it lacks the trough at the rear of the lower jaw, over which the eardrum stretched in therapsids and earlier mammaliformes, and the absence of this trough which suggests that *Hadrocodium*'s ear was part of the cranium, as it is in mammals, and hence that the former articular and quadrate had migrated to the middle ear and become the malleus and incus; but *Hadrocodium*'s dentary has a "bay" at the rear which mammals lack, a hint that that its dentary bone retained the same shape that it would have had if the articular and quadrate had remained part of the jaw joint. It has been suggested that a relatively large trough in the jaw bone of the early Cretaceous monotreme *Teinolophos* provides evidence of a pre-mammalian jaw joint, because therapsids and many mammaliforms had such troughs, in which the articular and angular bones "docked", and therefore that *Teinolophos* had a pre-mammalian middle ear; and therefore that the mammalian middle ear ossicles evolved indepedendently in monotremes and in other mammals. But a more recent analysis of *Teinolophos* concluded that the animal was a full-fledged platypus and the trough was a channel for the large number of nerves that collect signals from the electrical and vibration sensors in the bill (this is a signature feature of the platypi within monotremes), and therefore that the trough is not evidence that *Teinolophos* had a pre-mammalian jaw joint and a pre-mammalian middle ear. Ironically Rich and Vickers-Rich were among the authors of the 2005 paper on which they later cast doubt.

A recently discovered intermediate form is the primitive mammal Yanoconodon, from 125 million years ago in the Mesozoic, in which the ossicles have separated from the jaw and serve the hearing function in the middle ear, yet maintain a slender connection to the jaw via the ossified Meckel's cartilage, which in more advanced mammals dissolves during development.

How these changes affected hearing

The frequency range and sensitivity of the ear is dependent upon the shape and arrangement of the middle-ear bones. In early synapsids such as the pelycosaurs, the quadrate and articular had to function as the jaw joint, and this severely limited how far these bones could be modified to alter the frequency range of the ear. But once these bones were no longer involved in the jaw joint, variations which affected hearing would not also affect jaw joint function, and this allowed unconstrained evolution of the mammalian hearing apparatus. By the Jurassic, the typical mammalian ear had evolved, in which the angular had become the tympanic annula (a bony support for the tympanic membrane), while the articular and quadrate had become the malleus and incus, respectively, connected in series with the stapes. This series of three bones acts as an amplification system to allow enhanced hearing.

The transition between these two states is one of the most well-documented and supported in all of evolution, and newly discovered fossils from this transitional period have recently improved our understanding of this transition. But they also suggest that it was not a simple linear process from the early therapsid jaw (quadrate-articular joint) and middle ear (with stapes as the only ossicles) to the modern mammalian condition.

Natural selection

It has been suggested that natural selection could be a factor in the preservation of the structure of the middle ear in mammals. Many of the earliest mammals were quite small, and the dentition indicates that they were insectivorous. If they were "warm-blooded" (homeothermous), like modern mammals, then they could have been nocturnal. This fits with the popular image of small, nocturnal insectivorous mammals surviving in niches not accessible to the large, dominant contemporary dinosaurs. The enhanced hearing, particularly in the higher frequencies, would be helpful for nocturnal animals, in particular for detecting insects. This scenario is consistent with selective advantage being a contributory factor to the transition.

Summary

While the stapes is present in many types of tetrapods, the addition of the incus and malleus (also known as quadrate and articular) in the middle ear is a signature feature of mammals, distinguishing them from reptiles and all other vertebrates. They therefore have the appearance of representing a discontinuity in the tree of life. But in the early 19th century, it was hypothesized that these bones are not a total novelty, but are the equivalents of two bones which non-mammals have in their jaws. This hypothesis made sense, not only of the existence of these middle-ear bones, but also of certain other features of the anatomy, such as the paths taken by nerves in the head.

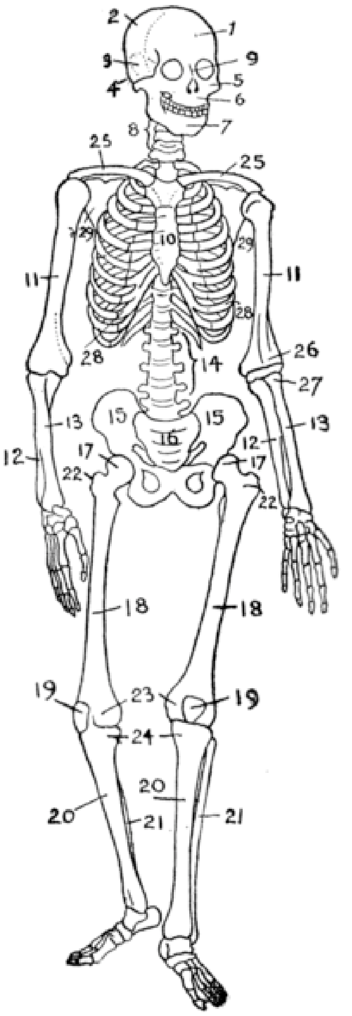
As evolutionary biology began to be expanded upon, this relationship became treated as one of common descent. For the evolutionary explanation to make sense, it seemed to demand that there would be a transition in function between being part of the feeding mechanism in the joint of the jaw and serving only in hearing; and this would mean that somehow there had to be an intermediate connecting these two quite different functions. With the discovery of *Morganucodon* and other fossils, there were concrete examples of this. There was a double jaw joint: the "older reptilian", as well as the "newer mammalian", in the same animal. This meant a confirmation of the pattern of inference from comparative anatomy to evolutionary biology.

The earliest mammals were generally small animals, probably nocturnal insectivores. This suggests a plausible evolutionary mechanism driving the change, for with these small bones in the middle ear, a mammal has extended its range of hearing for higher-pitched sounds which would improve the detection of insects in the dark. Natural selection would account for the success of this feature. And still one more connection with another part of biology: genetics suggested a mechanism for this transition, the kind of major change of function seen elsewhere in the world of life being studied by Evodevo.

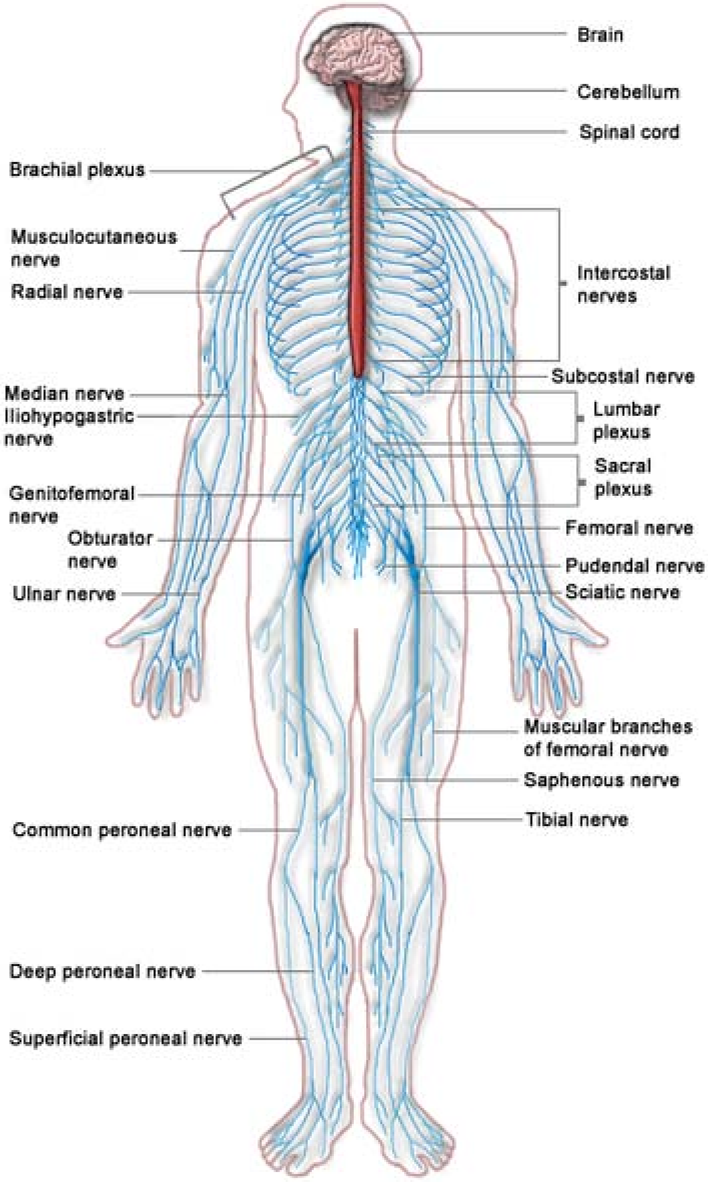
Chapter- 4

Mammal Anatomy

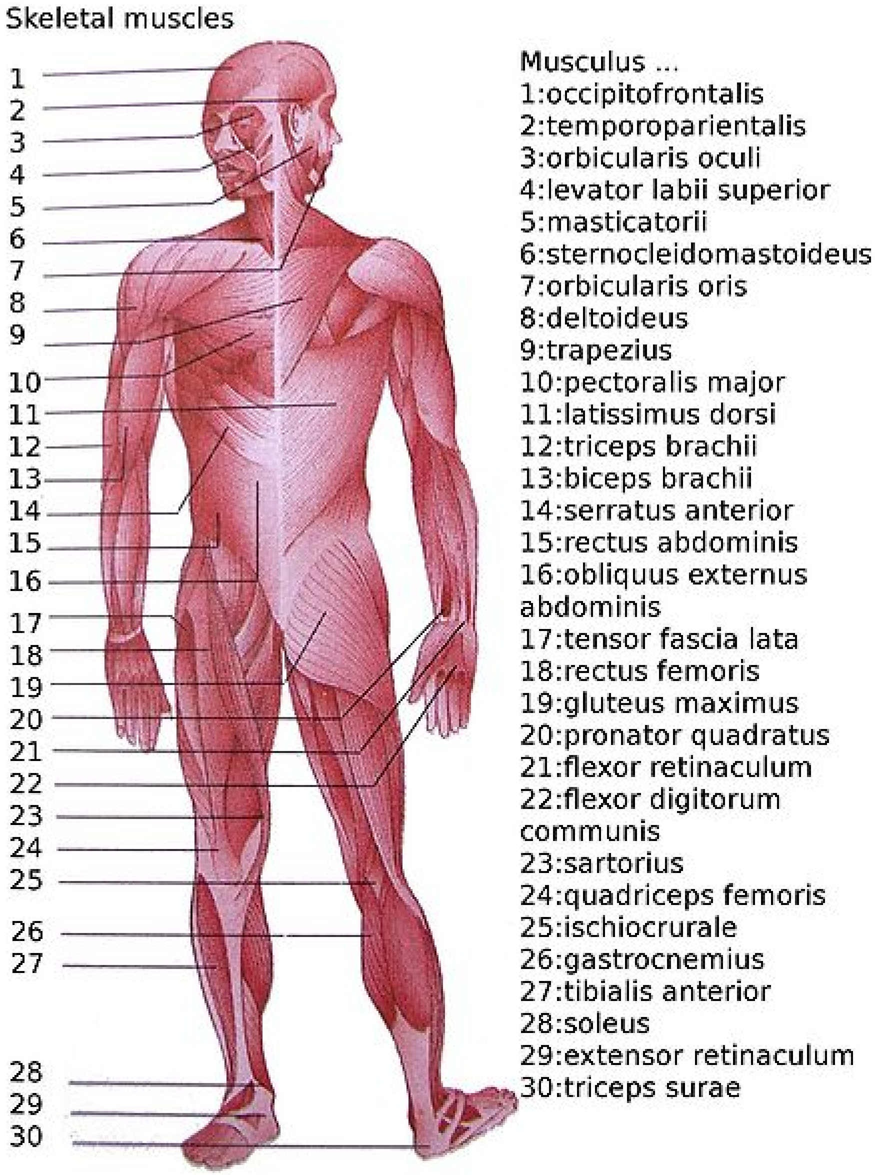
Human anatomy



The skeleton



The nervous system


Skeletal muscles
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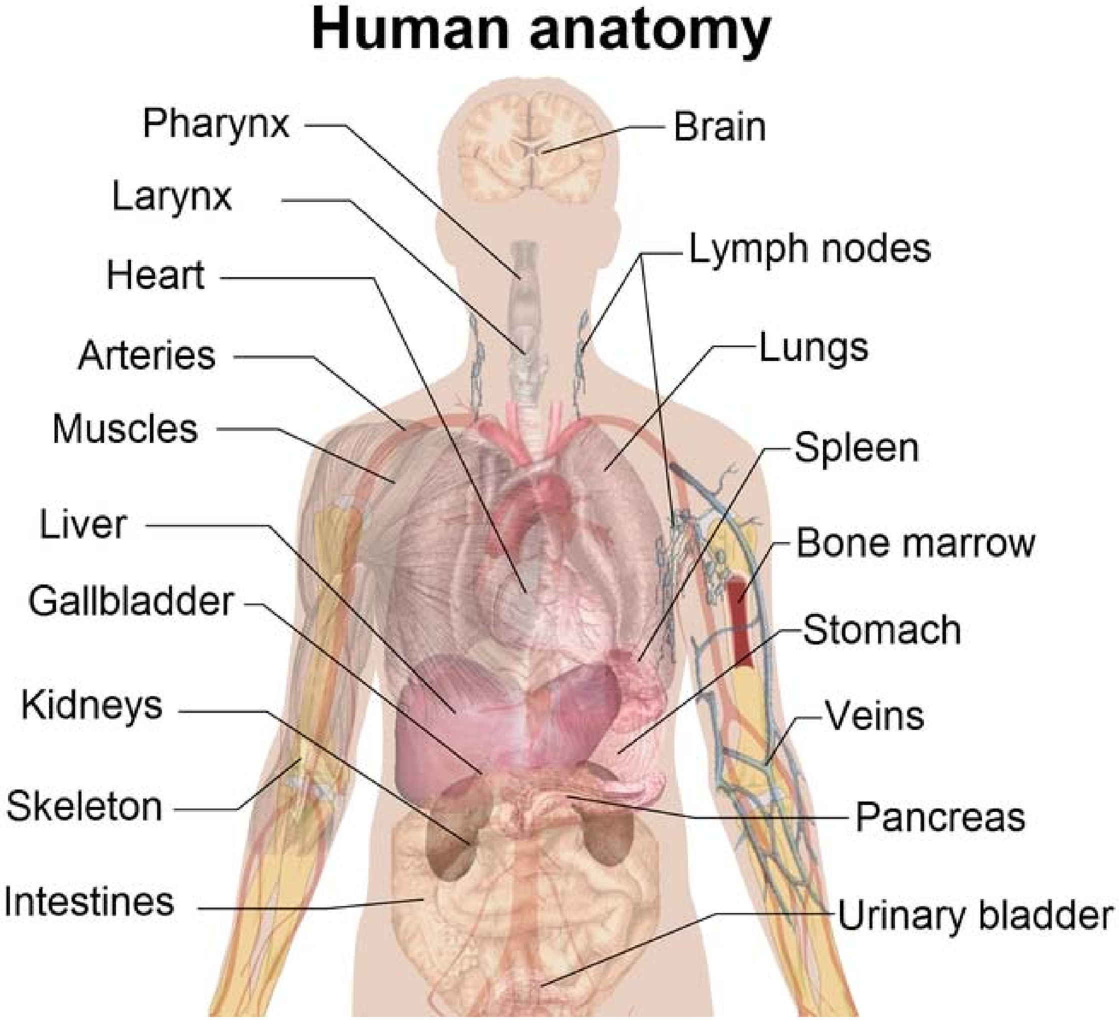
Musculus ...
1:occipitofrontalis
2:temporoparientalis
3:orbicularis oculi
4:levator labii superior
5:masticatorii
6:sternocleidomastoideus
7:orbicularis oris
8:deltoideus
9:trapezius
10:pectoralis major
11:latissimus dorsi
12:triceps brachii
13:biceps brachii
14:serratus anterior
15:rectus abdominis
16:obliquus externus abdominis
17:tensor fascia lata
18:rectus femoris
19:gluteus maximus
20:pronator quadratus
21:flexor retinaculum
22:flexor digitorum communis
23:sartorius
24:quadriceps femoris
25:ischiocrurale
26:gastrocnemius
27:tibialis anterior
28:soleus
29:extensor retinaculum
30:triceps surae

The muscles



The internal organs and their contents

Human anatomy (gr. ἀνατομία, "dissection", from ἀνά, "up", and τέμνειν, "cut"), which, with human physiology and biochemistry, is a complementary basic medical science, is primarily the scientific study of the morphology of the human body. Anatomy is subdivided into gross anatomy and microscopic anatomy. Gross anatomy (also called topographical anatomy, regional anatomy, or anthropotomy) is the study of anatomical structures that can be seen by unaided vision. Microscopic anatomy is the study of minute anatomical structures assisted with microscopes, which includes histology (the study of the organization of tissues), and cytology (the study of cells). Anatomy, physiology (the study of function) and biochemistry (the study of the chemistry of living structures) are complementary basic medical sciences when applied to the human body. As such, these subjects are usually taught together (or in tandem) to students in the medical sciences.

In some of its facets human anatomy is closely related to embryology, comparative anatomy and comparative embryology, through common roots in evolution; for example, much of the human body maintains the ancient segmental pattern that is present in all vertebrates with basic units being repeated, which is particularly obvious in the vertebral column and in the ribcage, and can be traced from very early embryos.

The human body consists of biological systems, that consist of organs, that consist of tissues, that consist of cells and connective tissue.

The history of anatomy has been characterized, over a long period of time, by a continually developing understanding of the functions of organs and structures in the body. Methods have also advanced dramatically, advancing from examination of animals through dissection of preserved cadavers (dead human bodies) to technologically complex techniques developed in the 20th century.

Study

Generally, physicians, dentists, physiotherapists, nurses, paramedics, radiographers, and students of certain biological sciences, learn gross anatomy and microscopic anatomy from anatomical models, skeletons, textbooks, diagrams, photographs, lectures, and tutorials. The study of microscopic anatomy (or histology) can be aided by practical experience examining histological preparations (or slides) under a microscope; and in addition, medical and dental students generally also learn anatomy with practical experience of dissection and inspection of cadavers (dead human bodies). A thorough working knowledge of anatomy is required for all medical doctors, especially surgeons, and doctors working in some diagnostic specialities, such as histopathology and radiology.

Human anatomy, physiology, and biochemistry are basic medical sciences, which are generally taught to medical students in their first year at medical school. Human anatomy can be taught regionally or systemically; that is, respectively, studying anatomy by bodily regions such as the head and chest, or studying by specific systems, such as the nervous or respiratory systems. The major anatomy textbook, Gray's Anatomy, has recently been reorganized from a systems format to a regional format, in line with modern teaching.

Anatomy in arts

Gross anatomy has become a key part of visual arts. Basic concepts of how muscles and bones function and deform with movement is key to drawing, painting or animating a human figure. Many books such as "Human Anatomy for Artists: The Elements of Form", are written as a guide to drawing the human body anatomically correct. Leonardo da Vinci sought to improve his art through a better understanding of human anatomy. In the process he advanced both human anatomy and its representation in art.

Approaches

Regional groups

- Head and neck – includes everything above the thoracic inlet.
- Upper limb – includes the hand, wrist, forearm, elbow, arm, and shoulder.
- Thorax – the region of the chest from the thoracic inlet to the thoracic diaphragm.
- Human abdomen to the pelvic brim or to the pelvic inlet.
- The back – the spine and its components, the vertebrae, sacrum, coccyx, and intervertebral disks.
- Pelvis and Perineum – the pelvis consists of everything from the pelvic inlet to the pelvic diaphragm. The perineum is the region between the sex organs and the anus.
- Lower limb – everything below the inguinal ligament, including the hip, the thigh, the knee, the leg, the ankle, and the foot.

Internal organs (by region)

Head and neck

- Brain
    - Amygdala
    - Basal ganglia
    - Brain stem
        - medulla
        - midbrain
        - pons
    - Cerebellum
    - Cerebral cortex
    - Hypothalamus
    - Limbic system

- Eye
- Pituitary
- Thyroid and Parathyroids

Thorax

- Heart
- Lung
- Esophagus
- Thymus
- Pleura

Abdomen and pelvis (both sexes)

- Adrenals
- Appendix
- Bladder
- Gallbladder
- Large intestine
- Small intestine
- Kidney
- Liver
- Pancreas
- Spleen
- Stomach

Male pelvis

- Prostate
- Testes

Female pelvis

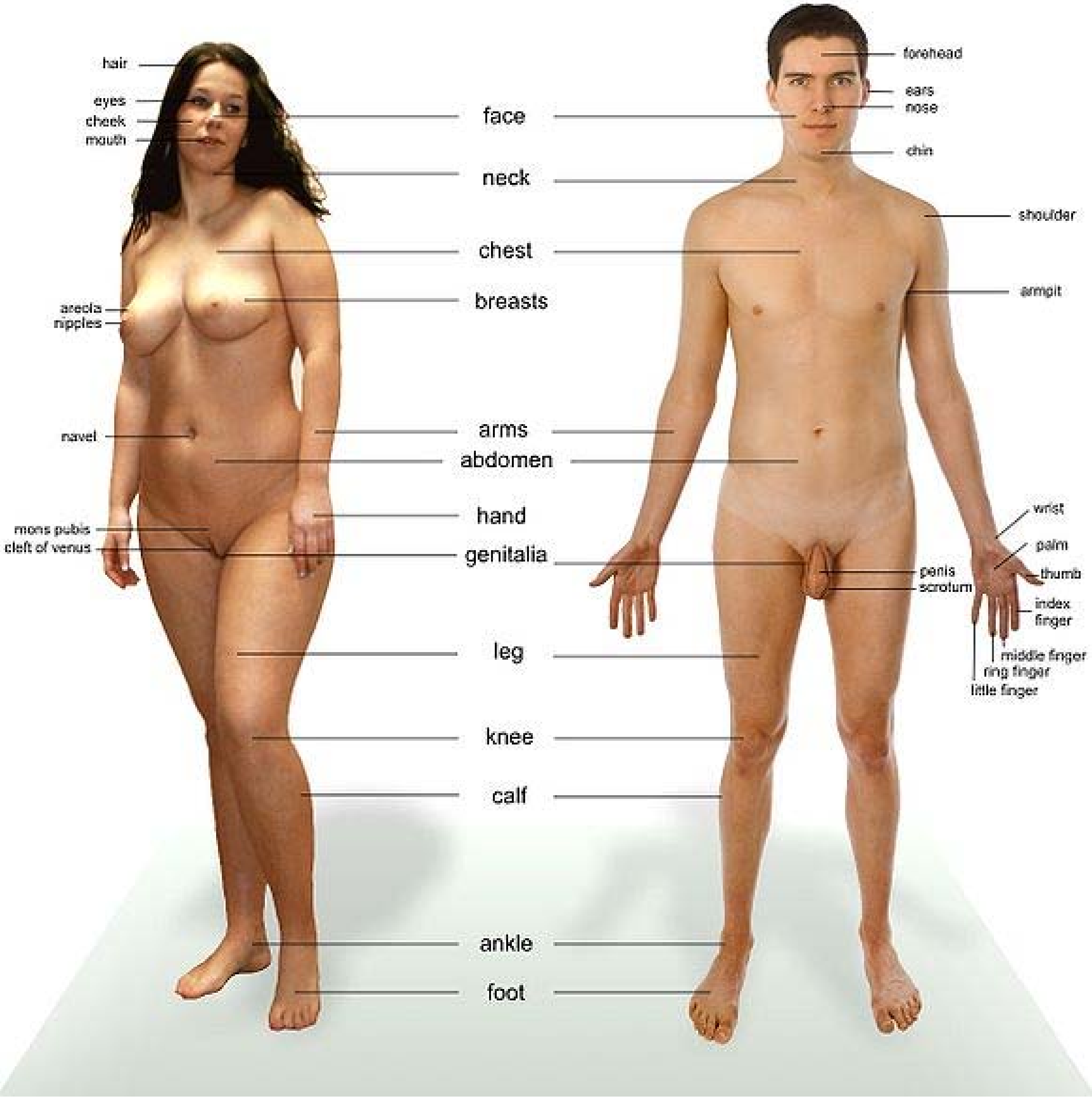
- Ovaries
- Uterus

Major organ systems

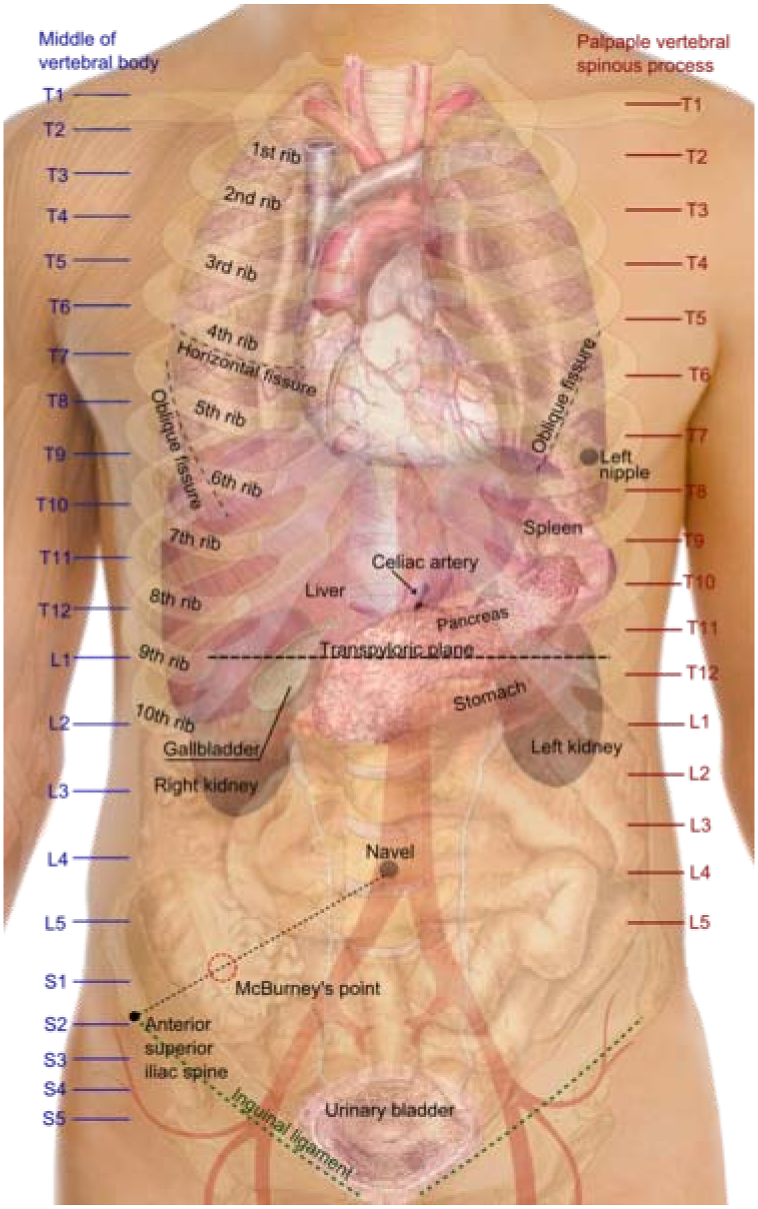
- Circulatory system: pumping and channeling blood to and from the body and lungs with heart, blood, and blood vessels.
- Digestive System: digestion and processing food with salivary glands, esophagus, stomach, liver, gallbladder, pancreas, intestines, rectum, and anus.
- Endocannabinoid system: neuromodulatory lipids and receptors involved in a variety of physiological processes including appetite, pain-sensation, mood, motor learning, synaptic plasticity, and memory.
- Endocrine system: communication within the body using hormones made by endocrine glands such as the hypothalamus, pituitary or pituitary gland, pineal body or pineal gland, thyroid, parathyroids, and adrenals or adrenal glands
- Integumentary system: skin, hair and nails
- Immune system: the system that fights off disease; composed of leukocytes, tonsils, adenoids, thymus, and spleen.
- Lymphatic system: structures involved in the transfer of lymph between tissues and the blood stream, the lymph and the nodes and vessels that transport it.
- Musculoskeletal system: muscles provide movement and a skeleton provides structural support and protection with bones, cartilage, ligaments, and tendons.
- Nervous system: collecting, transferring and processing information with brain, spinal cord, peripheral nerves, and nerves

- Reproductive system: the sex organs; in the female; ovaries, fallopian tubes, uterus, vagina, mammary glands, and in the male; testes, vas deferens, seminal vesicles, prostate, and penis.
- Respiratory system: the organs used for breathing, the pharynx, larynx, trachea, bronchi, lungs, and diaphragm.
- Urinary system: kidneys, ureters, bladder and urethra involved in fluid balance, electrolyte balance and excretion of urine.
- Vestibular system: contributes to our balance and our sense of spatial orientation.

Superficial anatomy



Superficial anatomy of female and male human body



Surface projections of the major organs of the trunk, using the vertebral column and rib cage as main reference points of superficial anatomy

Superficial anatomy or surface anatomy is important in human anatomy being the study of anatomical landmarks that can be readily identified from the contours or other reference points on the surface of the body. With knowledge of superficial anatomy, physicians gauge the position and anatomy of the associated deeper structures.

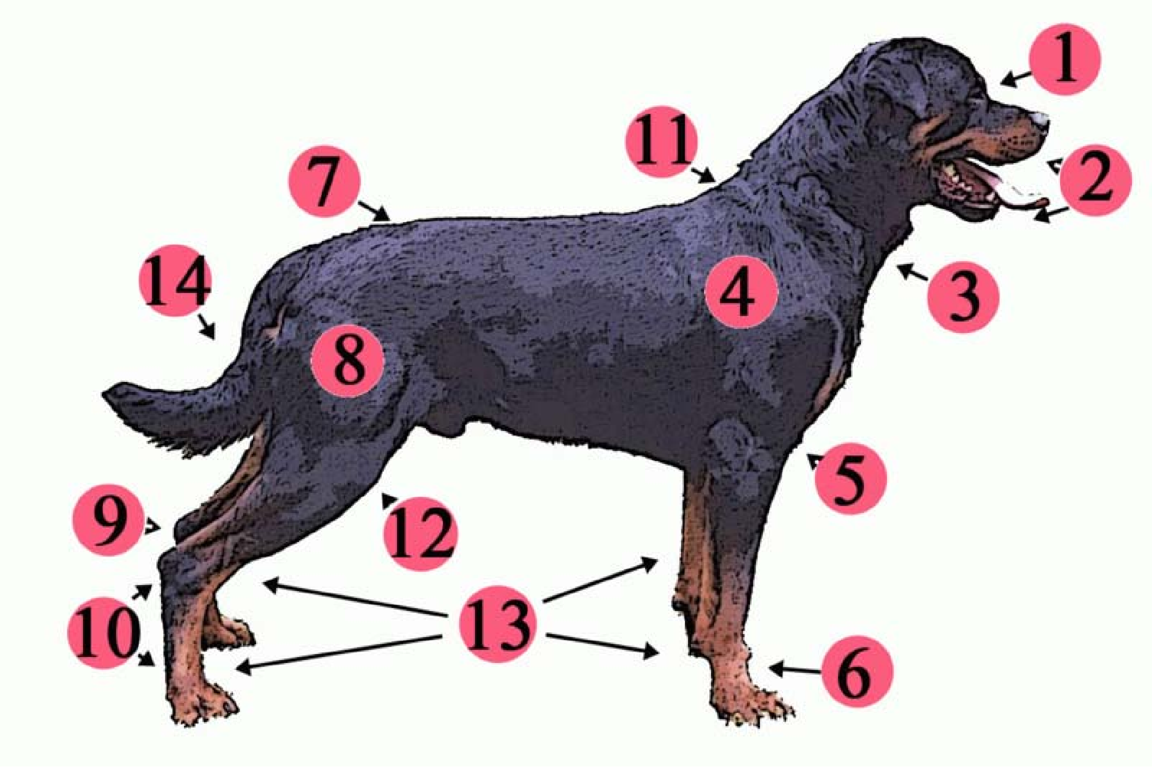
Common names of well known parts of the human body, from top to bottom:

- Head – Forehead – Jaw – Cheek – Chin
- Neck – Shoulder
- Arm – Elbow – Wrist – Hand – Finger – Thumb

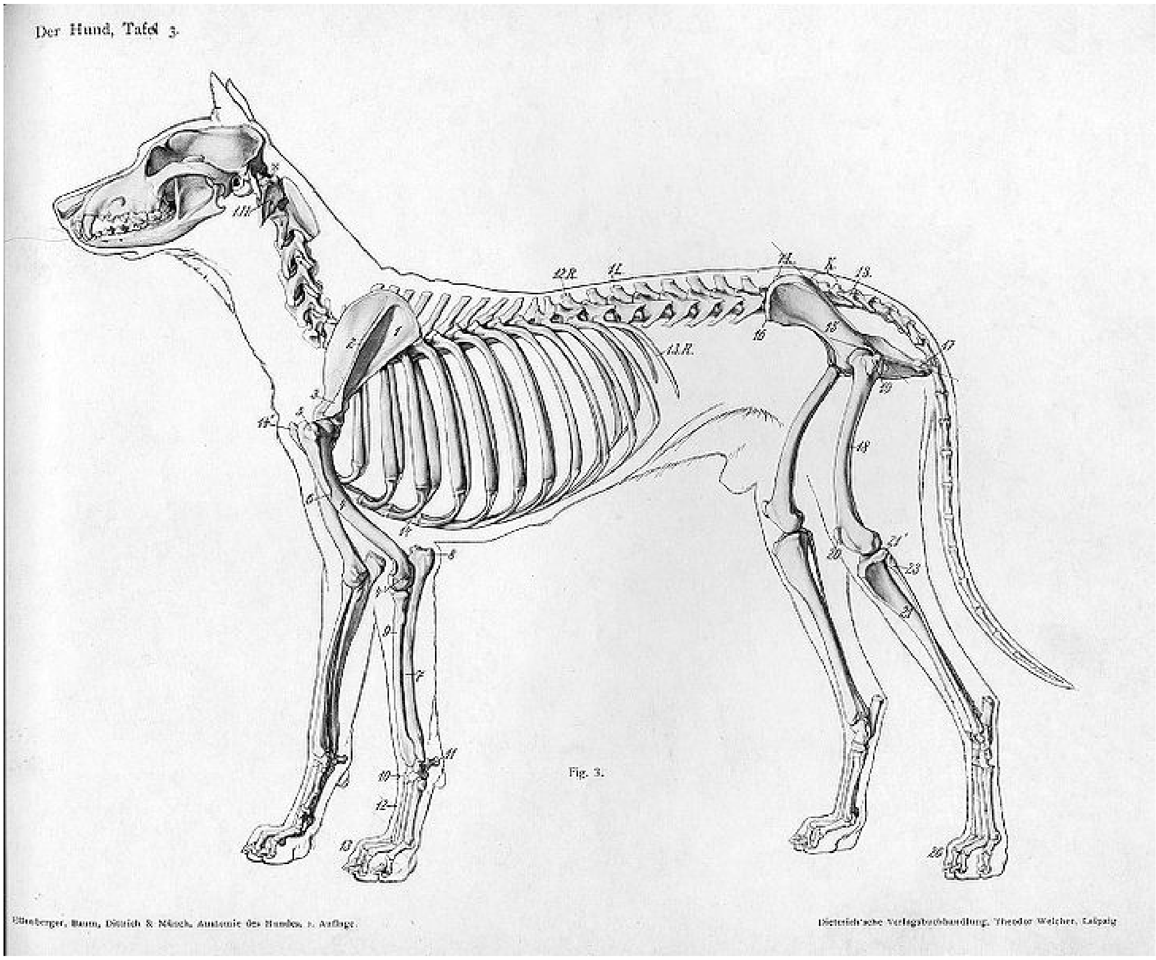
- Spine – Chest – Thorax
- Abdomen – Groin
- Hip – Buttocks – Leg – Thigh – Knee – Calf – Heel – Ankle – Foot – Toe
- Eye, ear, nose, mouth, teeth, tongue, throat, adam's apple, breast, penis, scrotum, clitoris, vulva, navel are also superficial structures.

Dog anatomy

Dog anatomy includes the same internal structures that are in humans. Details of structures vary tremendously from breed to breed, more than in any other animal species, wild or domesticated, as dogs vary from the tiny Chihuahua to the giant Irish Wolfhound.



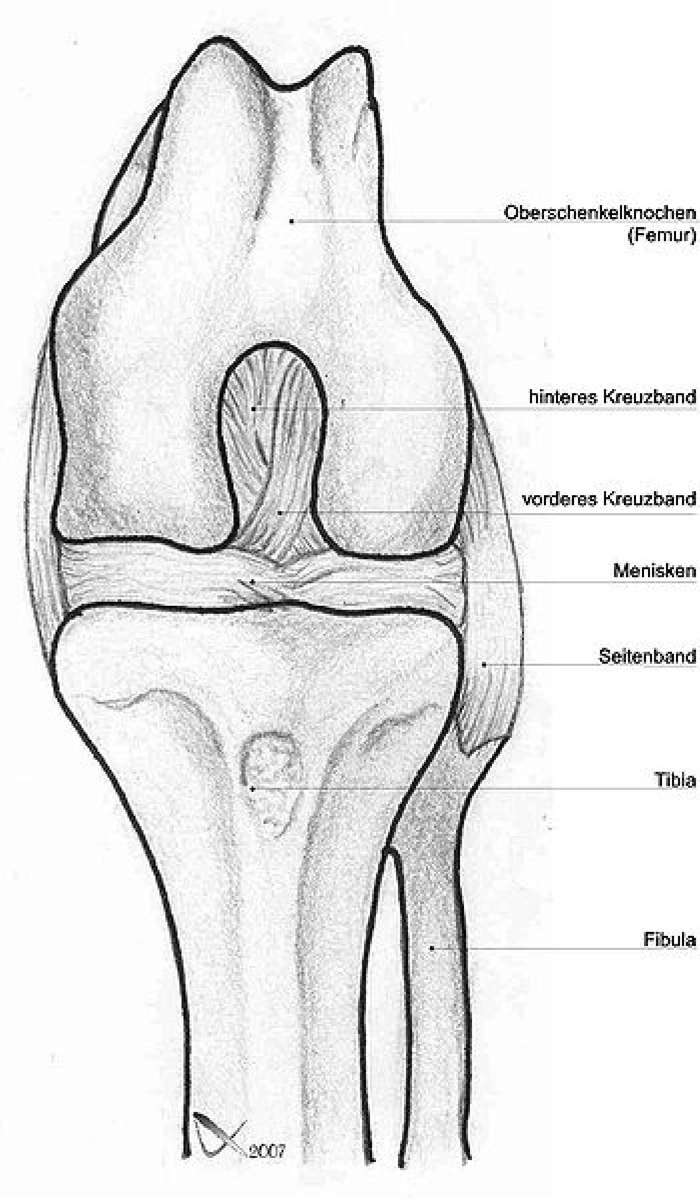
Croup 8.Leg (thigh and hip) 9.Hock 10.Hind feet 11.Withers 12.Stifle 13.Paws 14.Tail



Skeleton of a domestic dog

Skull of a dog

Physical characteristics



Dog knee

Like most predatory mammals, the dog has powerful muscles, a cardiovascular system that supports both sprinting and endurance, and teeth for catching, holding, and tearing.

The dog's ancestral skeleton provided the ability to run and leap. Their legs are designed to propel them forward rapidly, leaping as necessary, to chase and overcome prey. Consequently, they have small, tight feet, walking on their toes; their rear legs are fairly rigid and sturdy; the front legs are loose and flexible, with only muscle attaching them to the torso.

Although selective breeding has changed the appearance of many breeds, all dogs retain the basic ingredients from their distant ancestors. Dogs have disconnected shoulder bones (lacking the collar bone of the human skeleton) that allow a greater stride length for running and leaping. They walk on four toes, front and back, and have vestigial dewclaws (dog thumbs) on their front legs and sometimes on their rear legs.When a dog has extra dewclaws in addition to the usual one on each front leg, the dog is said to be "double dewclawed".

There is some debate about whether a dewclaw helps dogs to gain traction when they run because, in some dogs, the dewclaw makes contact when they are running and the nail on the dewclaw often wears down in the same way that the nails on their other toes do, from contact with the ground. However, in many dogs the dewclaws never make contact with the ground; in this case, the dewclaw's nail never wears away, and it is then often trimmed to keep it to a safe length.

The dewclaws are not dead appendages. They can be used to lightly grip bones and other items that dogs hold with the paws. However, in some dogs these claws may not appear to be connected to the leg at all except by a flap of skin; in such dogs the claws do not have a use for gripping as the claw can easily fold or turn.

There is also some debate as to whether dewclaws should be surgically removed. The argument for removal states that dewclaws are a weak digit, barely attached to the leg, so that they can rip partway off or easily catch on something and break, which can be extremely painful and prone to infection. Others say the pain of removing a dewclaw is far greater than any other risk. For this reason, removal of dewclaws is illegal in many countries. There is, perhaps, an exception for hunting dogs, who can sometimes tear the dewclaw while running in overgrown vegetation. If a dewclaw is to be removed, this should be done when the dog is a puppy, sometimes as young as 3 days old, though it can also be performed on older dogs if necessary (though the surgery may be more difficult then). The surgery is fairly straight-forward and may even be done with only local anesthetics if the digit is not well connected to the leg. Unfortunately many dogs can't resist licking at their sore paws following the surgery, so owners need to remain vigilant.

In addition, for those dogs whose dewclaws make contact with the ground when they run, it is possible that removing them could be a disadvantage for a dog's speed in running and changing of direction, particularly in performance dog sports such as dog agility.

The dog's ancestor was about the size of a Dingo, and its skeleton took about 10 months to mature. Today's toy breeds have skeletons that mature in only a few months, while giant breeds such as the Mastiffs take 16 to 18 months for the skeleton to mature. Dwarfism has affected the proportions of some breeds' skeletons, as in the Basset Hound.

Knowledge of basic anatomy also helps when competing in dog shows or contests.

Size

Researchers have identified a particular piece of genetic material that is common to every small-dog breed and, in turn, is probably responsible for making them tiny. The study, published in 2007, found a regulatory sequence (not a gene) next to the gene IGF1; together the gene and regulatory sequence together are known as a haplotype that "is a major contributor to body size in all small dogs." Medium and large size dogs do not usually have the regulatory sequence, although the small-size sequence was found in the Rottweiler breed. The study included 3,241 dogs from 143 breeds. The researchers concluded the genetic instructions to make dogs small must be at least 12,000 years old, and it is not found in wolves. Another study has shown that lap dogs (small dogs) are among the oldest dog types.

Modern dog breeds show more variation in size, appearance, and behavior than any other domestic animal. Within the range of extremes, dogs generally share attributes with their wild ancestors, the wolves. Dogs are predators and scavengers, possessing sharp teeth and strong jaws for attacking, holding, and tearing their food. Although selective breeding has changed the appearance of many breeds, all dogs retain basic traits from their distant ancestors. Like many other predatory mammals, the dog has powerful muscles, fused wristbones, a cardiovascular system that supports both sprinting and endurance, and teeth for catching and tearing.

Sight

A Greyhound, one of many breeds of sighthound

Like most mammals, dogs are dichromats and have color vision equivalent to red-green color blindness in humans. Different breeds of dogs have different eye shapes and dimensions, and they also have different retina configurations. Dogs with long noses have a "*visual streak*" which runs across the width of the retina and gives them a very wide field of excellent vision, while those with short noses have an "*area centralis*" — a central patch with up to three times the density of nerve endings as the *visual streak* — giving them detailed sight much more like a human's.

Some breeds, particularly the sighthounds, have a field of vision up to 270° (compared to 180° for humans), although broad-headed breeds with short noses have a much narrower field of vision, as low as 180°.

Hearing

According to hypertextbook.com, the frequency range of dog hearing is approximately 40 Hz to 60,000 Hz. Dogs detect sounds as low as the 16 to 20 Hz frequency range (compared to 20 to 70 Hz for humans) and above 45 kHz (compared to 13 to 20 kHz for humans), and in addition have a degree of ear mobility that helps them to rapidly pinpoint the exact location of a sound. Eighteen or more muscles can tilt, rotate and raise or lower a dog's ear. Additionally, a dog can identify a sound's location much faster than a human can, as well as hear sounds up to four times the distance that humans are able to. Those with more natural ear shapes, like those of wild canids like the fox, generally hear better than those with the floppier ears of many domesticated species.

Smell

Scent hounds, especially the Bloodhound, are bred for their keen sense of smell.

Dogs have nearly 220 million smell-sensitive cells over an area about the size of a pocket handkerchief (compared to 5 million over an area the size of a postage stamp for humans). According to nhm.org, dogs can sense odours at concentrations nearly 100 million times lower than humans can. According to Dummies.com, the percentage of the dog's brain that is devoted to analyzing smells is actually 40 times larger than that of a human. Some dog breeds have been selectively bred for excellence in detecting scents, even compared to their canine brethren.

The highly sensitive nose of a dog.

Coat

Domestic dogs often display the remnants of counter-shading, a common natural camouflage pattern. The general theory of countershading is that an animal that is lit from above will appear lighter on its upper half and darker on its lower half where it will usually be in its own shade. This is a pattern that predators can learn to watch for. A countershaded animal will have dark coloring on its upper surfaces and light coloring below. This reduces the general visibility of the animal. One reminder of this pattern is that many breeds will have the occasional "blaze", stripe, or "star" of white fur on their chest or undersides.

Dogs diverged from a now-extinct Asian wolf between 12,000 and 15,000 years ago, according to recent DNA studies. In that time, the long nose and heavy grey-colored double coat of the wolf has changed into the wide variety of dog shapes and coats and colors seen today. The change was due at first to genetic changes that occurred as the original dogs learned to tolerate the presence of humans, as shown in the research on foxes by Dmitri Belyaev in his Farm-Fox Experiment. The research found that a genetic change to tameness brought along other unexpected changes as well; one notable change was in the coats, changed from a typical fox coat to a spotted coat resembling a dog's coat. As ancient dogs learned to live near humans and became less like wolves, their appearance changed as well, long before any selective breeding was done by people.

A Stanford University School of Medicine study published in Science in October, 2007 found the genetics that explain coat colors in other mammals such as in horse coats and in cat coats, did not apply to dogs. The project took samples from 38 different breeds to find the gene (a beta defensin gene) responsible for dog coat color. One version produces yellow dogs, and a mutation produces black. All dog coat colors are modifications of black or yellow. For example, the white in white miniature schnauzers is a cream color, not albinism (a genotype of e/e at MC1R.)

Modern dog breeds exhibit a diverse array of fur coats, including dogs without fur, such as the Mexican Hairless Dog. Dog coats vary in texture, color, and markings, and a specialized vocabulary has evolved to describe each characteristic.

Tail

There are many different shapes for dog tails: straight, straight up, sickle, curled, cork-screw. In some breeds, the tail is traditionally docked to avoid injuries (especially for hunting dogs). It can happen that some puppies are born with a short tail or no tail in some breeds.

Puppy characteristics

This probably 15 weeks old German shepherd mongrel already shows an upward erection trend of the ears, with varying grades of erection during the day

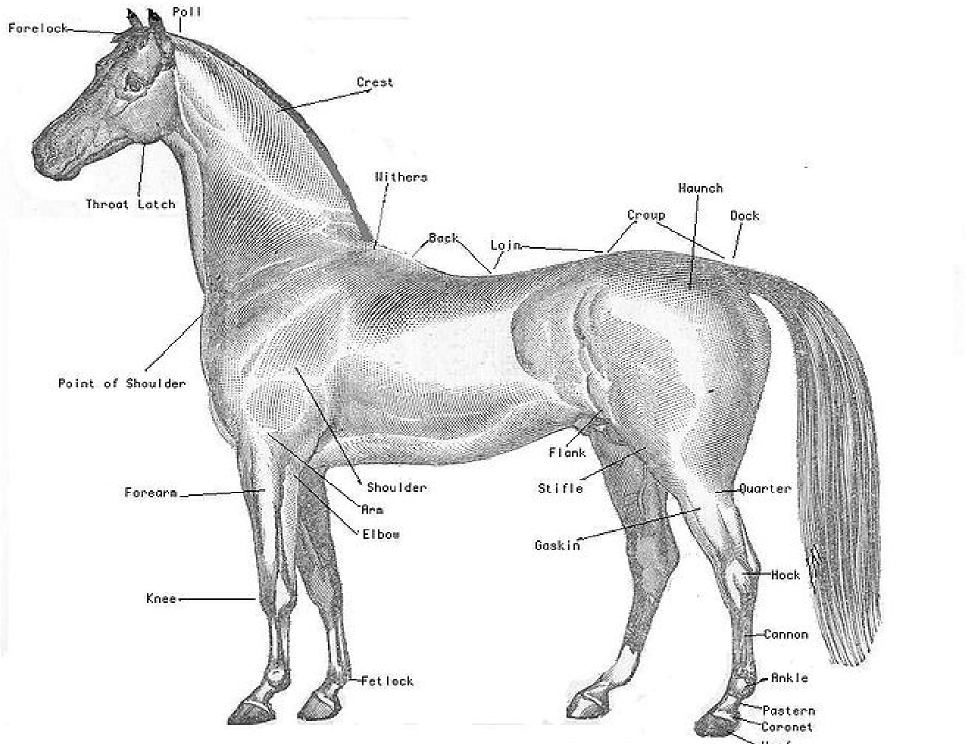
Puppies often have characteristics that do not last beyond early puppyhood. Eye color often changes from blue to its adult color as the puppy matures. The coat color may change: Kerry Blue Terrier puppies have black coats at birth and change to blue with maturity, and Dalmatians are white and gain their spots with age. The ear shape will also often change, especially with erect-eared breeds such as the German Shepherd Dog which have soft ears at birth, but the cartilage strengthens with age. Labrador Retrievers and other swimming dogs, start of with a very fluffy puppy coat, and over time the water proof layer grows. Puppies that are going to grow into larger dogs, often will have over sized paws to begin with, and then the rest of them grow to fit.

Temperature regulation

It is a common misconception that dogs do not sweat. They do sweat, mainly through the footpads, but only a small fraction of a dog's excess heat is lost this way. Primarily, dogs regulate their body temperature through panting. Panting moves cooling air over the moist surfaces of the tongue and lungs, rejecting heat to the atmosphere.

Dogs possess a rete mirabile, a complex of intermingled small arteries and veins, in the carotid sinus at the base of their neck. This acts to thermally isolate the head, containing the brain, the most temperature-sensitive organ, from the body, containing the muscles, where most of the heat is generated. The result is that dogs can sustain intense physical exertion over a prolonged time in a hot environment, compared to animals which lack this apparatus; thus, a dog chasing a jackrabbit through the desert may not be able to outrun the rabbit, but it can continue the chase until the rabbit slows due to overheating.

Equine anatomy



Based on an engraving of "Gold Dust" from *Manning's Illustrated Horse Book*
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Parts of a Horse

Equine anatomy refers to the gross and microscopic anatomy of horses and other equids, including donkeys, and zebras. While all anatomical features of equids are described in the same terms as for other animals by the International Committee on Veterinary Gross Anatomical Nomenclature in the book Nomina Anatomica Veterinaria, there are many horse-specific colloquial terms used by equestrians.

External anatomy

- **back**: the area where the saddle goes, begins at the end of the withers, extends to the last thoracic vertebrae. (Colloquially includes the loin or "coupling," though technically incorrect usage)
- **barrel**: the main body area of the horse, enclosing the rib cage and the major internal organs.
- **cannon** or **cannon bone**: The area between the knee or hock and the fetlock joint, sometimes called the "shin" of the horse, though technically it is the metacarpal III.
- **chestnut**: a callosity on the inside of each leg
- **chin groove**: the part of the horse's head behind the lower lip and chin. (the area that dips down slightly on the lower jaw). Area where the curb chain of certain bits is fastened.
- **coronet** or **coronary band**: The ring of soft tissue just above the horny hoof that blends into the skin of the leg.
- **crest**: the upper portion of the neck where the mane grows.
- **croup**: the topline of the horse's hindquarters, beginning at the hip, extending proximate to the sacral vertebrae and stopping at the dock of the tail (where the coccygeal vertebrae begin). Sometimes called "rump."
- **dock**: the point where the tail connects to the croup of the horse.
- **elbow**: The joint of the front leg at the point where the belly of the horse meets the leg. Homologous to the elbow in humans.
- **ergot**: a callosity on the back of the fetlock
- **fetlock**: Sometimes called the "ankle" of the horse, though it is not the same skeletal structure as an ankle in humans. Known to anatomists as the metacarpophalangeal (front) or metatarsophalangeal (hind) joint; homologous to the "ball" of the foot or the metacarpophalangeal joints of the fingers in humans.
- **flank**: Where the hind legs and the barrel of the horse meet, specifically the area right behind the rib cage and in front of the stifle joint.
- **forearm**: the area of the front leg between the knee and elbow. Consists of the fused radius and ulna, and all the tissue around these bones. Anatomically the antebrachium.
- **forelock**: the continuation of the mane, which hangs from between the ears down onto the forehead of the horse.
- **frog**: the highly elastic wedge-shaped mass on the underside of the hoof, which normally makes contact with the ground every stride, supports both the locomotion and circulation of the horse.
- **gaskin**: the large muscle on the hind leg, just above the hock, below the stifle. Homologous to the calf of a human.

- **girth'** ***or*** *heartgirth*: the area right behind the elbow of the horse, where the girth of the saddle would go, this area should be where the barrel is at its greatest diameter in a properly-conditioned horse that is not pregnant or obese.
- **hindquarters**: the large, muscular area of the hind legs, above the stifle and behind the barrel of the horse.
- **hock**: The tarsus of the horse (hindlimb equivalent to the human ankle and heel), the large joint on the hind leg.
- **hoof**: The foot of the horse. The hoof wall is the tough outside covering of the hoof that comes into contact with the ground. The hoof wall is, in many respects, a much larger and stronger version of the human fingernail.
- **jugular groove**: the line of indentation on the lower portion of the neck, can be seen from either side, just above the windpipe. Beneath this area run the jugular vein, the carotid artery and part of the sympathetic trunk.
- **knee**: the carpus of the horse (equivalent to the human wrist), the large joint in the front legs, above the cannon bone
- **loin**: the area right behind the saddle, going from the last rib of the horse to the croup. Anatomically approximate to the lumbar spine.
- **mane**: long and relatively coarse hair growing from the dorsal ridge of the neck, lying on either the left or right side of the neck).
- **muzzle**: the chin, mouth, and nostrils of the horse's face.
- **pastern**: The connection between the coronet and the fetlock. Made up of the middle and proximal phalanx.
- **poll**: commonly refers to the poll joint at the beginning of the horse's neck, immediately behind the ears, a slight depression at the joint where the atlas (C1) meets the occipital crest. Anatomically, the occipital crest itself is the "poll."
- **splints**: bones found on each of the legs, on either side of the cannon bone (8 total). Partially vestigial, these bones support the corresponding carpal bones in the forelimb, and the corresponding tarsal bones in the hindlimb. Anatomically referred to as Metacarpal/Metatarsal II (on the medial aspect (inside)) and IV (on the lateral aspect (outside)).
- **shoulder**: made up of the scapula and associated muscles. Runs from the withers to the point of shoulder (the joint at the front of the chest, i.e. the glenoid). The angle of the shoulder has a great effect on the horse's movement and jumping ability, and is an important aspect of equine conformation.
- **stifle**: Corresponds to the knee of a human, consists of the articulation between femur and tibia, as well as the articulation between patella and femur.
- **tail**: consists of both the living part of the tail (which consists of the coccygeal vertebrae, muscules, and ligaments), as well as the long hairs which grow from the living part
- **throatlatch**: The point at which the windpipe meets the head at the underside of the jaw.
- **withers**: the highest point of the thoracic vertebrae, the point just above the tops of the shoulder blades. Seen best with horse standing square and head slightly lowered. The height of the horse is measured at the withers in "hands."

Digestive system

Horses and other Equids evolved as grazing animals, adapted to eating small amounts of the same kind of food all day long. In the wild, the horse adapted to eating prairie grasses in semi-arid regions and traveling significant distances each day in order to obtain adequate nutrition. Therefore, the digestive system of a horse is about 100 feet (30 m) long, and most of this is intestines.

The mouth

Digestion begins in the mouth, which is also called the "oral cavity." It is made up of the teeth, the hard palate, the soft palate, the tongue and related muscles, the cheeks and the lips. Horses also have three pairs of salivary glands, the parotid (largest salivary gland and located near the poll), submaxillary (located in the jaw), and sublingual (located under the tongue). Horses select pieces of forage and pick up finer foods, such as grain, with their sensitive, prehensile lips. The front teeth of the horse, called incisors, clip forage, and food is then pushed back in the mouth by the tongue, and ground up for swallowing by the premolars and molars.

The esophagus

The esophagus is about 4–5 feet in length, and carries food to the stomach. A muscular ring, called the cardiac sphincter, connects the stomach to the esophagus. This sphincter is very well developed in horses. This and the oblique angle at which the esophagus connects to the stomach explains why horses cannot vomit. The esophagus is also the area of the digestive tract where horses may suffer from choke.

The stomach

Horses have a relatively small stomach for their size, and this limits the amount of feed a horse can take in at one time. The average sized horse (800 to 1200 lb) has a stomach with a capacity of only four gallons, and works best when it contains about two gallons. Because the stomach empties when 2/3 full, whether stomach enzymes have completed their processing of the food or not, and doing so prevents full digestion and proper utilization of feed, continuous foraging or several small feedings per day are preferable to one or two large ones. The horse stomach consists of a non-glandular proximal region (saccus cecus), divided by a distinct border, the margo plicata, from the glandular distal stomach.

In the stomach, assorted acids and the enzyme pepsin break down food. Pepsin allows for the further breakdown of proteins into amino acid chains. Other enzymes include resin and lipase. Additionally, the stomach absorbs some water, as well as ions and lipid soluble compounds. The end product is food broken down into chyme. It then leaves the stomach through the pyloric valve, which controls the flow of food out of stomach.

The small intestine

The horse’s small intestine is 50 to 70 feet (21 m) long and holds 10 to 12 gallons. This is the major digestive organ, and where most nutrients are absorbed. It has three parts, the duodenum, jejunum and ileum. The majority of digestion occurs in the duodenum while the majority of absorption occurs in the jejunum. Bile from the liver aids in digesting fats in the duodenum combined with enzymes from the pancreas and small intestine . Horses do not have a gall bladder, so bile flows constantly. Most food is digested and absorbed into the bloodstream from the small intestine, including proteins, simple carbohydrate, fats, and vitamines A, D, and E. Any remaining liquids and roughage move into the large intestine.

The large intestine

Cecum

The cecum is the first section of the large intestine. It is also known as the "water gut" or "hind gut." It is a cul-de-sac pouch, about 4 feet (1.2 m) long that holds 7 to 8 gallons. It contains bacteria that digest cellulose plant fiber through fermentation. These bacteria feed upon digestive chyme, and also produce certain fat-soluble vitamins which are absorbed by the horse. The reason horses must have their diets changed slowly is so the bacteria in the cecum are able to modify and adapt to the different chemical structure of new feedstuffs. Too abrupt a change in diet can cause colic, as the new food is not properly digested.

Colon

The large colon, small colon, and rectum make up the remainder of the large intestine. The large colon is 10–12 feet long and holds up to 20 gallons of semi-liquid matter. It is made up of the right lower (ventral) colon, the left lower (ventral) colon, the left upper (dorsal) colon, the right upper (dorsal) colon, and the transverse colon, in that order. Three flexures are also named; the sternal flexure, between right and left ventral colon; the pelvic flexure, between left dorsal and left ventral colon; the diaphragmatic flexure, between left dorsal and right dorsal colon. The main purpose of the large colon is to absorb carbohydrates, which were broken down from cellulose in the cecum. Due to its many twists and turns, it is a common place for a type of horse colic called an impaction.

The small colon is 10–12 feet in length and holds only 5 gallons of material. It is the area where the majority of water in the horse's diet is absorbed, and is the place where fecal balls are formed. The rectum is about one foot long, and acts as a holding chamber for waste matter, which is then expelled from the body via the anus.

Reproductive system

Mare

The reproductive system of the mare is responsible for controlling gestation, birth, lactation, as well as the estrous cycle and mating behavior of the mare. It lies ventral to the 4th or 5th lumbar vertebrae, although its position within the mare can vary depending on the movement of the intestines and distention of the bladder.

The mare has two ovaries, usually 7–8 cm in length and 3–4 cm thick, that generally tend to decrease in size as the mare ages. The ovaries connect to the fallopian tubes (oviducts), which serve to move the ovum from the ovary to the uterus. To do so, the oviducts are lined with a layer of cilia, which produce a current that flows toward the uterus. Each oviduct attaches to one of the two horns of the uterus, which are approximately 20–25 cm in length. These horns attach to the body of the uterus (18–20 cm long). Caudal to the uterus is the cervix, about 5–7 cm long, which enters the vagina. Usually 3.5–4 cm in diameter, it can expand to allow the passage of the foal. The vagina of the mare is 15–20 cm long, and is quite elastic, allowing it to expand. The vulva is the external opening of the vagina, and consists of the clitoris and two labia. It lies ventral to the rectum. The mare has two mammary glands, which are smaller in virgin mares. They have two ducts each, which open externally.

Stallion

The reproductive system of the stallion is responsible for the sexual behavior and secondary sex characteristics (such as a large crest) of the stallion. The external genitalia comprise:

- the testes, which are suspended horizontally within the scrotum. The testes of an average stallion are ovoids 8 to 12 cm long;
- the penis, within the prepuce, also known as the "sheath." When not erect, the penis is housed within the prepuce, 50 cm long and 2.5 to 6 cm in diameter with the distal end 15 to 20 cm. When erect, the penis doubles in length and thickness and the glans increases by 3 to 4 times. The urethra opens within the **urethral fossa**, a small pouch at the distal end of the glans.

The internal genitalia comprise the accessory sex glands:

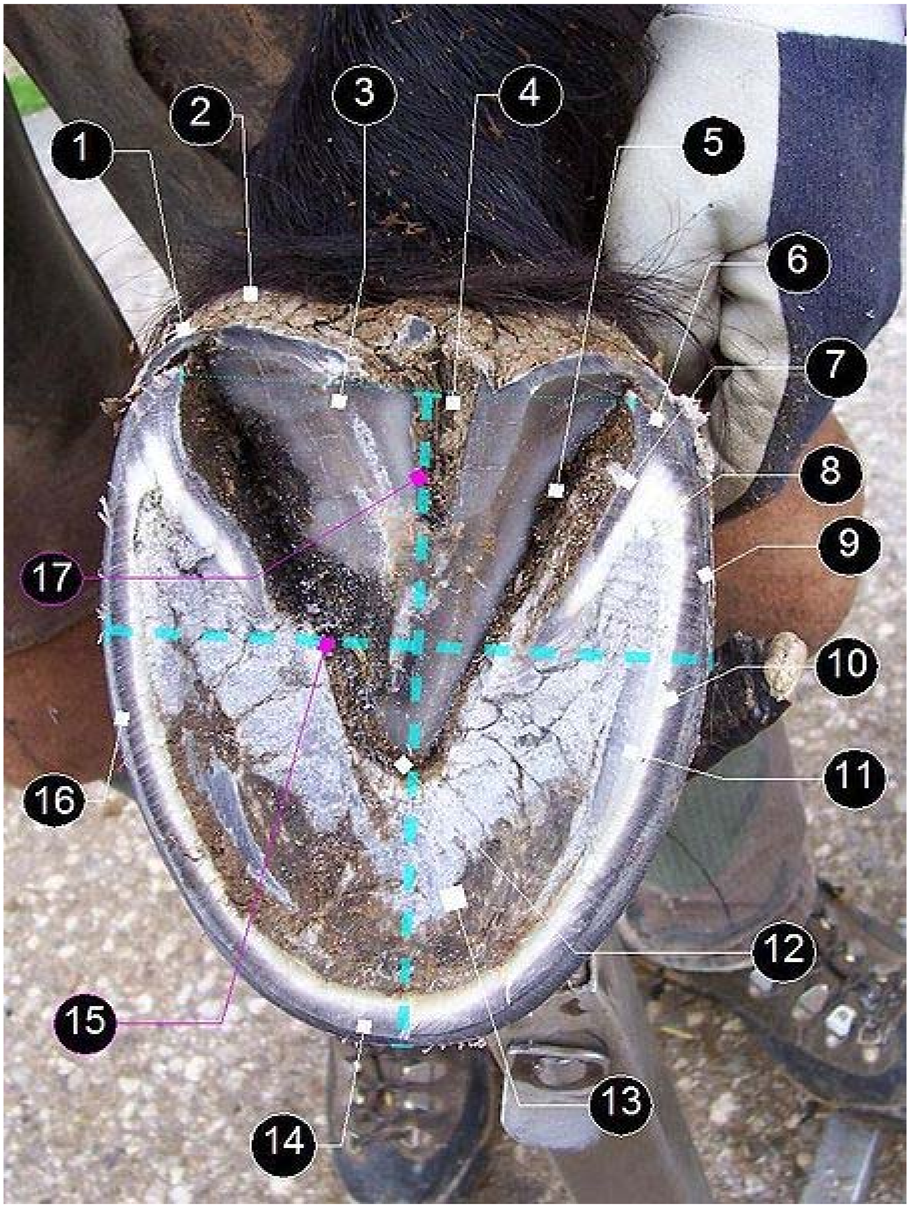
- vesicular glands;
- prostate gland; and
- bulbourethral glands.

These contribute fluid to the semen at ejaculation, but are not strictly necessary for fertility

Teeth

A horse's teeth include incisors, premolars, molars, and sometimes canine teeth. A horse's incisors, premolars, and molars, once fully developed, continue to erupt throughout its lifetime as the grinding surface is worn down through chewing. Because of this pattern of wear, a rough estimate of a horse's age can be made from an examination of the teeth.

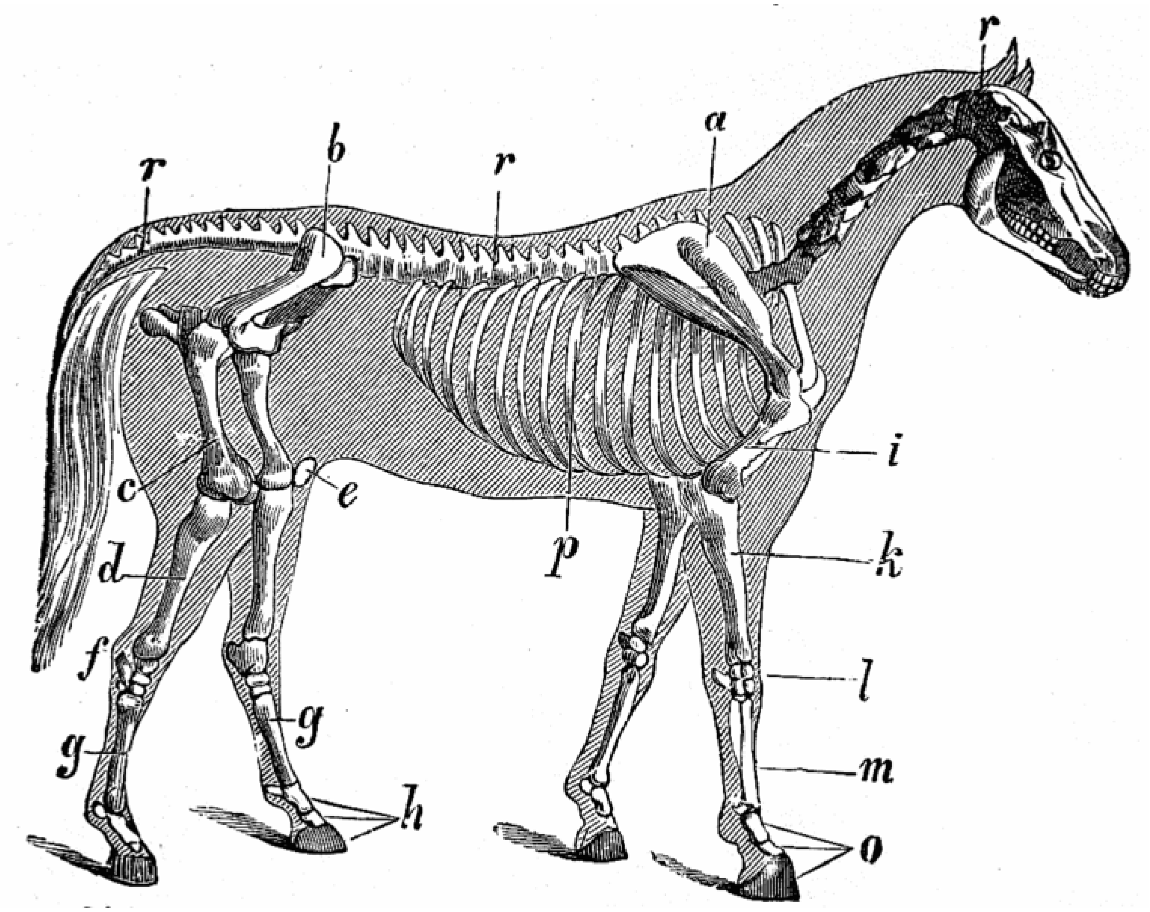
Feet/Hooves



1- Heel perioplium, 2-Bulb, 3-Frog, 4-Frog cleft, 5-Lateral groove, 6-Heel, 7-Bar, 8-Seat-of-corn, 9-Pigmented walls 10-Water line, 11-White line, 12-Apex of the frog, 13-Sole, 14-Toe, 15-How to measure hoof width (blue dotted line), 16-Quarter, 17-How to measure length (blue dotted line)

The hoof of the horse encases the second and third phalanx of the lower limbs, analogous to the fingertip or toe tip of a human. In essence, a horse travels on its "tiptoes." The hoof wall is a much larger, thicker and stronger version of the human fingernail or toenail, made up of similar materials, primarily keratin, a very strong protein molecule. The horse's hoof contains a high proportion of sulfur-containing amino acids which contribute to its resilience and toughness.

Skeletal system



A horse's skeleton

The skeleton of the horse has three major functions in the body. It protects vital organs, provides framework, and supports soft parts of the body. Horses have 205 bones, which are divided into the appendicular skeleton (the legs) and the axial skeleton (the skull, vertebral column, sternum, and ribs). Both pelvic and thoracic limbs contain the same number of bones, 20 bones per limb. Bones are connected to muscles via tendons and other bones via ligaments. Bones are also used to store minerals, and are the site of red blood cell formation.

Ligaments and tendons

Ligaments

Ligaments attach bone to bone or bone to tendon, and are vital in stabilizing joints as well as supporting structures. They are made up of fibrous material that is generally quite strong. Due to their relatively poor blood supply, ligament injuries generally take a long time to heal.

Tendons

Tendons are cords of connective tissue attaching muscle to bone, cartilage or other tendons. They are a major contributor to shock absorption, are necessary for support of the horse's body, and translate the force generated by muscles into movement. Tendons are classified as flexors (flex a joint) or extensors (extend a joint). However, some tendons will flex multiple joints while extending another (the flexor tendons of the hind limb, for example, will flex the fetlock, pastern, and coffin joint, but extend the hock joint). In this case, the tendons (and associated muscles) are named for their most distal action (digital flexion).

Tendons form in the embryo from fibroblasts which become more tightly packed as the tendon grows. As tendons develop they lay down collagen, which is the main structural protein of connective tissue. As tendons pass near bony prominences, they are protected by a fluid filled synovial structure, either a tendon sheath or a sac called a bursa.

Tendons are easily damaged if placed under too much strain, which can result in a painful, and possibly career-ending, injury. Tendinitis is most commonly seen in high performance horses that gallop or jump. When a tendon is damaged the healing process is slow because tendons have a poor blood supply, reducing the availability of nutrients and oxygen to the tendon. Once a tendon is damaged the tendon will always be weaker, because the collagen fibres tend to line up in random arrangements instead of the stronger linear pattern. Scar tissue within the tendon decreases the overall elasticity in the damaged section of the tendon as well, causing an increase in strain on adjacent uninjured tissue.

Muscular system

When a muscle contracts, it pulls a tendon, which acts on the horse's bones to move them. Muscles are commonly arranged in pairs so that they oppose each other (they are "antagonists"), with one flexing the joint (a flexor muscle) and the other extending it (extensor muscle). Therefore, one muscle of the pair must be relaxed in order for the other muscle in the pair to contract and bend the joint properly. A muscle is made up of several muscle bundles, which in turn are made up of muscle fibers. Muscle fibers have myofibrils, which are able to contract due to actin and myosin. A muscle together with its tendon and bony attachments form an extensor or flexor unit.

Respiratory system and smell

The horse's respiratory system consists of the nostrils, pharynx, larynx, trachea, diaphragm, and lungs. Additionally, the nasolacrimal duct and sinuses are connected to the nasal passage. The horse's respiratory system not only allows the animal to breathe, but also is important in the horse's sense of smell (olfactory ability) as well as in communicating.

Circulatory system

The horse's circulatory system includes the four-chambered heart, averaging 8.5 lb (3.9 kg) in weight, as well as the blood and blood vessels. Its main purpose is to circulate blood throughout the body to deliver oxygen and nutrients to tissues, and to remove waste from these tissues. The frog (the V shaped part on the bottom of the horses hoof)is a very important part of the circulatory system. The frog consists of blood vessel filled tissue. When the horse steps, the ground pushes upward compressing the frog and causing the digital cushion to sqeeze the blood upward and back up the leg towards the heart. Helping the heart work against gravity.

The eye

A horse's eye

The horse has the largest eye of all land mammals, and is designed to help the horse as a prey animal. It provides the horse with a wide field of monocular vision, as well as good visual acuity and some ability to see color. Because the horse's vision is closely tied to his behavior, the horse's visual abilities are often taken into account when handling and training the animal.

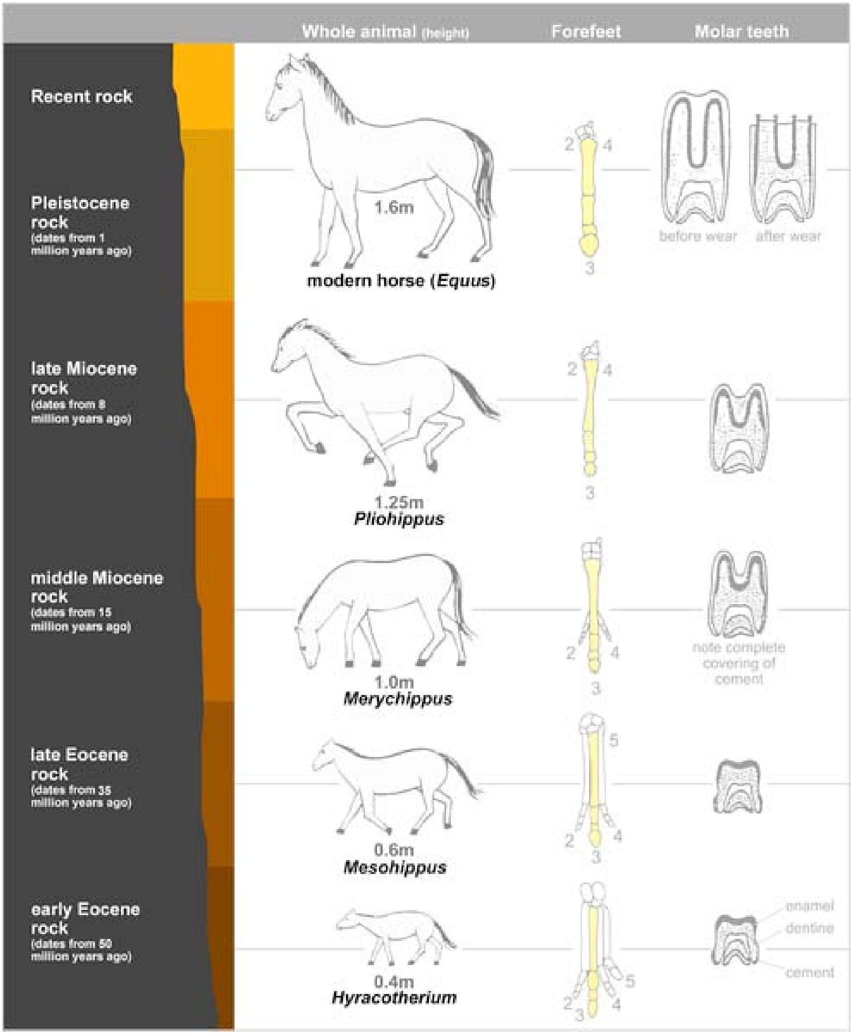
Hearing

The pinna of a horse's ears can rotate in any direction to pick up sounds

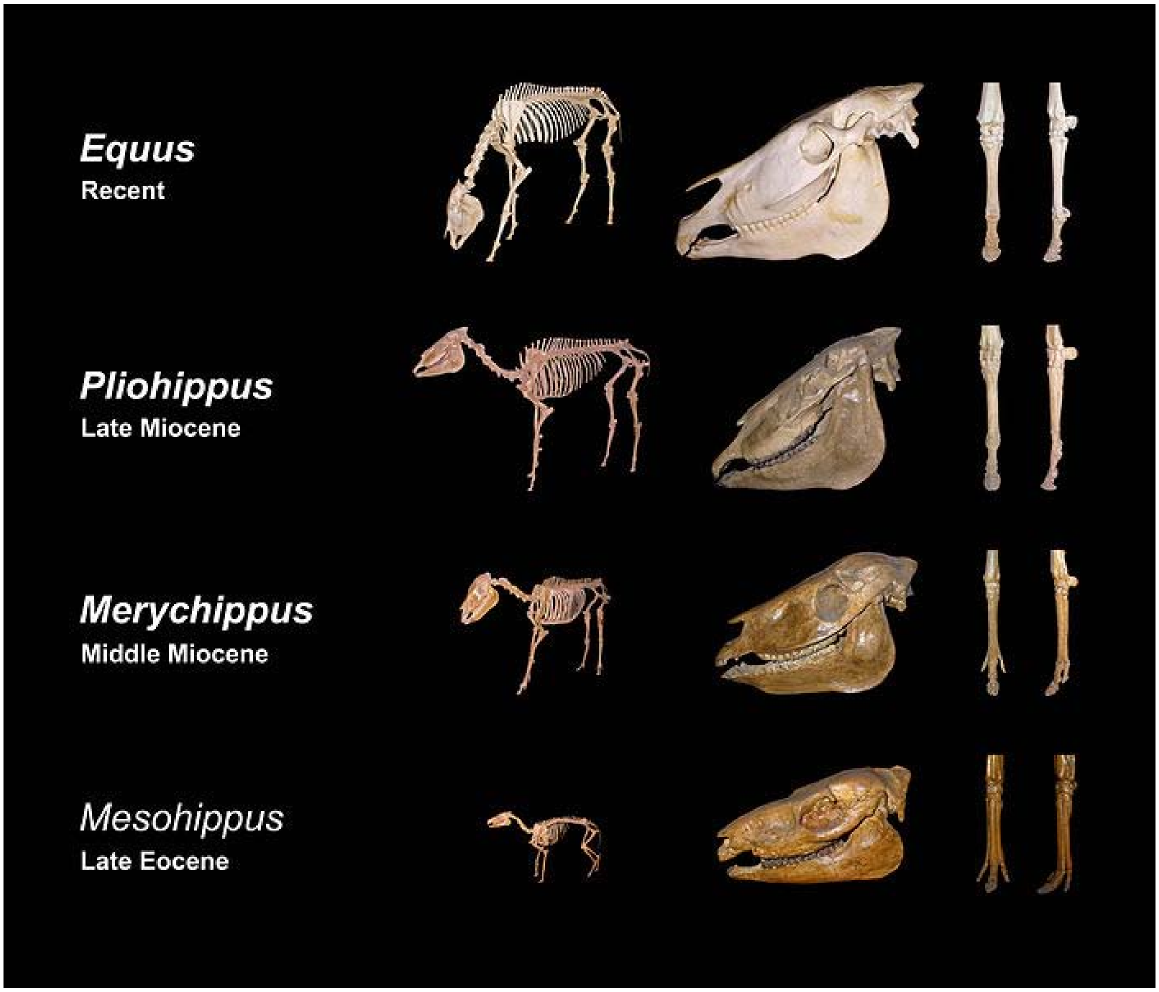
The hearing of horses is good, superior to that of humans, and the pinna of each ear can rotate up to 180°, giving the potential for 360° hearing without having to move the head. Often, the eye of the horse is looking in the same direction as the ear is directed

Chapter- 5

Evolution of the Horse



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



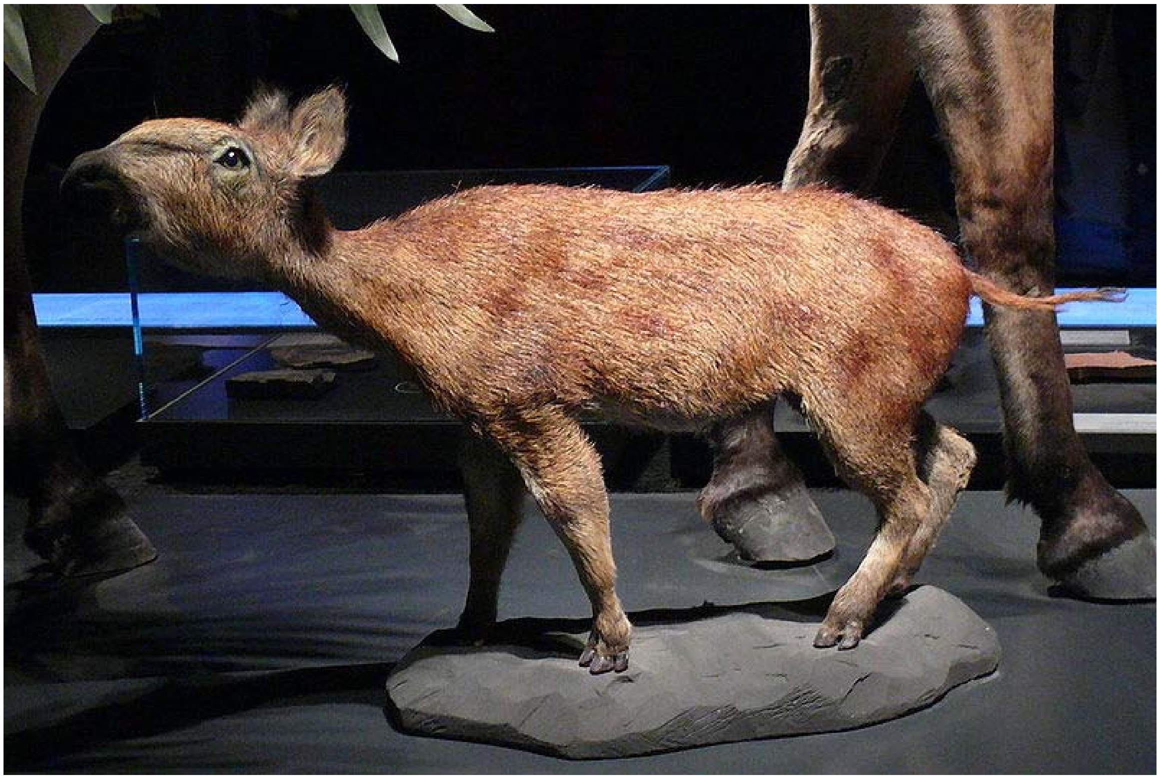
Skeletal evolution

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

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

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

History of research



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

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

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

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

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

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

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

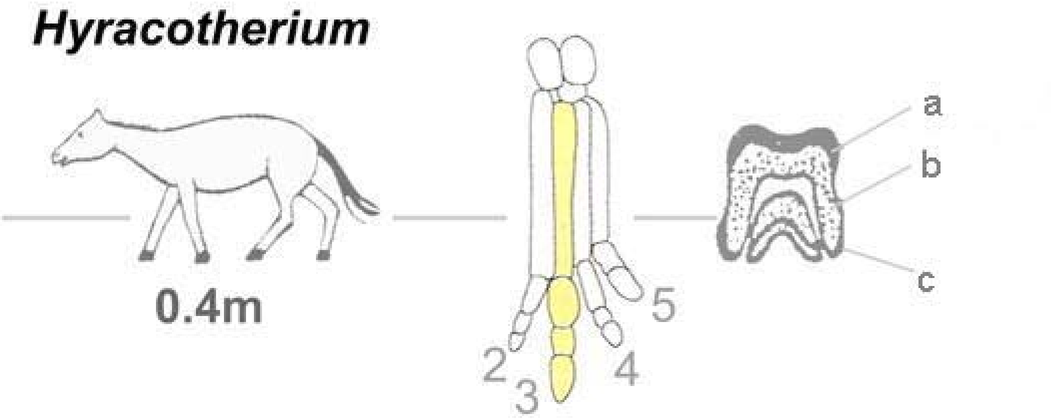
Detailed fossil information on the rate and distribution of new equid species has also revealed the progression between species was not as smooth and consistent as was once believed. Although some transitions, such as that of *Dinohippus* to *Equus*, were indeed gradual progressions, a number of others,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

Eocene and Oligocene: early equids

Hyracotherium

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

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



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

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

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

Orohippus

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

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

Epihippus

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

Mesohippus

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

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

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

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

Miohippus

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

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

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

Miocene and Pliocene: true equines

Kalobatippus

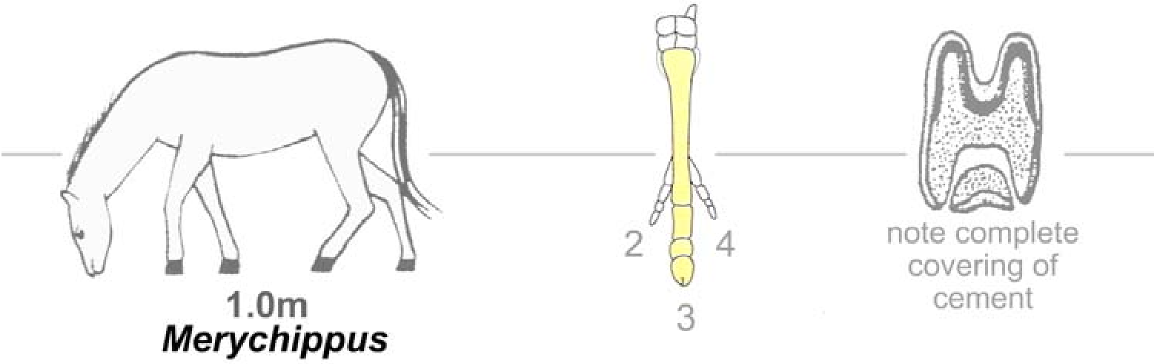
Fossil *Megahippus mckennai*

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

Parahippus

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

Merychippus



Merychippus, an effective grazer and runner.

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

Hipparion

Protohippus simus

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

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

Pliohippus

Pliohippus pernix

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

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

Dinohippus

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

Plesippus

Mounted skeleton of Hagerman Horse (*Equus simplicidens*)

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

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

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

Modern horses

Equus

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

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

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

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

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

Pleistocene extinctions

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

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

Return to the Americas

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

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

Details

Toes

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

Teeth

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