

The evolutionary history of the human foot

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Abstract

The human foot, with 26 skeletal elements and even more articulations, intrinsic and extrinsic muscles, is a highly complex structure. Functional analyses alone do not suffice to fully understand this complexity and therefore we set out to explore the evolutionary background of the human foot.

The first “foot” dates from the Late Devonian (approximately 400 million years ago), where the first tetrapods had developed a foot-like structure from an ancestral, multi-rayed fin, with (e.g. in *Ichtyostega*) at least five tarsal bones and seven toes with two to four phalanges. By the beginning of the Carboniferous, approx. 350 million years ago, tetrapods seem to have fixed on five toes. A next stage is seen in early amniotes (e.g. *Paleothyris*, 300 million years ago), in which the tarsal bones have fused to form the two tarsal bones astragalus and calcaneum (the later talus and calcaneus). A number of mid-tarsal bones were present as well. Only in the Eocene epoch (55-34 million years ago), primitive primates (e.g. adapids and omomyids) show a foot morphology that has shared derived features with extant primates. These primitive primates can be considered at the group that had the ancestral form of the modern primate foot.

Throughout evolution, primates have retained an arboreal lifestyle, and foot shape is characterised by a grasping (opposable) hallux and elongated distal segments. This pattern was still present in the common ancestor of humans and apes (e.g. represented by the primitive apes *Proconsul* or *Equatorius*), and is retained in all extant non-human primates.

For early hominins, postcranial remains are, unfortunately, scarce and the feet of *Australopithecus afarensis* and *A. africanus* (approx. 3.5 million years ago) are our best resource. Even though these species retained a number of primitive features in their feet (e.g. an opposable hallux or a flexible midfoot), they also show many derived

(human-like) features, (e.g. the ankle morphology, the ability to dorsiflex the toes), albeit in a different combination. Foot fossils from later hominins indicate further specialisations for bipedalism, such as an adducted and robust hallux, first seen in *Paranthropus robustus* and *Homo habilis* (both 1.8 Mya). Moreover, *H. habilis*, likely ancestral to modern humans, also shows a robust fifth metatarsal and a relative foot length similar to that of modern humans. Probably, they had no ape-like mid-tarsal break (flexible calcaneo-cuboid joint) any more. Near modern feet are first found in Neanderthals, whose feet likely differed from modern human feet in details.

An overview of the evolutionary history of the human foot may help understand why it has the highly complex structure we observe and why it functions (or sometimes malfunctions) the way it does.

Introduction

The human foot is a very complex structure, consisting of 26 bony elements (not counting the sesamoids), numerous ligaments, and intrinsic and extrinsic muscle/tendon complexes. Why is the foot this complex?

Functional studies have shown that the human foot combines multiple, potentially conflicting, functions during gait. For example, it is a flexible structure in the beginning of stance in order to dampen the impact and to adapt to the substrate. From midstance on, it becomes a rigid structure that helps in an efficient push-off. Combining these two functions in one anatomical structure requires some degree of complexity. There are more functions than this, e.g. keeping balance.

Nevertheless, even when functional aspects are taken into account, it remains difficult to understand why the foot is that complex - there still seems to be redundancy. Where does this come from?

We should bear in mind that the human foot is not designed by engineers “de novo”. It is the result of evolution by natural selection. Therefore, when trying to understand the modern human foot, we should consider both functional requirements of the foot and its evolutionary history.

The purpose of this paper is to present an overall outline of the evolutionary history of the foot. This is a very complex matter, and we can only present a brief introduction.

There is at least one work, the excellent book by Morton (1935), tackling the whole time span of the present paper. Even though this author’s insights were probably far ahead of his time, he was limited by the lack of fossils. He had no fossil foot specimens available, and the only old material known to him was *Australopithecus africanus* “Taung Child” (Dart, 1925). Other specimens were of more recent hominins: *Homo erectus* (then known as *Pithecanthropus erectus* “Java Man” Dubois,

1894 and *Sinanthropus pekinensis* “Peking Man”, Weidenreich, 1935) and the virtually modern Neanderthals. One of the older fossils known at that time, *Eoanthropus dawsoni* “Piltdown Man”, later turned out to be a hoax (Weiner, 1955).

There are numerous recent papers tackling very specific topics in much more detail than we can do here. Without having the ambition of being complete, we will mention relevant studies where the interested reader can find up-to-date and detailed information.

In this paper we will (1) briefly address the process of evolution and then set out to explore (2) what a foot originated from (3) how this foot achieved the basic elements we find in humans (4) what the feet of known human-like ancestors looked like and (5) how the foot was “fine-tuned” to yield the modern human foot. Lastly, we will briefly discuss to what extent the feet seen in daily (clinical) practice reflect the “normal” human foot.

The process of evolution through natural selection

Organisms and their structures change over time. This process of evolution also applies to the foot. Most people are well aware of this - yet it may be useful to elaborate on the process of evolution as such, as it may help understand how a structure like the human foot has adapted to the function it performs, but not perfectly so.

Evolution is influenced both by processes driving change and by forces resisting it. In most cases (and in the case of hominin evolution), evolution proceeds mainly by natural selection: the most fit individuals (i.e. those having a selective advantage over others) will survive better and/or produce more offspring, thereby passing their genes on to following generations better than others. In this way, it can be understood e.g. why a well-developed longitudinal foot arch will evolve when endurance bipedal walking is important - this is a Darwinistic view that lets us understand why structures are so well adapted. But when looking more closely, we may in fact discover that structures rarely are “perfectly” adapted. The human foot may serve as an example of how a biological structure deviates from what a very good engineer would design. Why would this be the case?

One reason is that the process of evolution by natural selection involves several prerequisites (Arnold, 1983). As the first step, the feature and its variation within the population should be heritable and not just an expression of phenotypic plasticity. Second, this genetic variation should be reflected in a design variation. Design may be morphology but also e.g. physiology. Third, different designs should lead to differences in performance in a specific task (e.g. walking efficiency). Lastly, different performances should lead to different fitness. If one of these steps fails, evolution of the feature will not take place.

A second reason why structures may not evolve is that they may be constrained by pleiotropic effects: if a gene changes (e.g. one that regulates the number of toes), it may not only have the desired effect, but also a number of other, potentially un-

wanted, effects (Galis et al., 2001). Pleiotropy plays an important role in limb development.

A third reason is that evolution works generation by generation. In the case of hominins, characterised by very long generation times, this may slow down evolution. Moreover, hominin evolution has taken place over approximately 7 million years, which is a brief period in evolutionary terms. In contrast to this, the external factors driving evolution (i.e. changes in environment) can change very fast. This difference in speed may cause that the adapting structure is continuously lagging behind the conditions it is adapting to (cf. Red Queen Hypothesis, Van Valen, 1973). An analogue might be a heavy ship (“hominin”) trying to follow a speed boat (“environment”) that constantly changes direction: the ship may adjust its course to the speed boat, it may thoroughly follow the trail of the speed boat over the long term, but it may never catch up with it (“perfectly adapt”), unless the speed boat remains still (a stable external environment, approached e.g. by a tropical forest).

From fish fin to tetrapod foot

Up to the Devonian (416-360 million years ago, abbreviated “MYA” hereafter), vertebrate life was limited to aquatic habitats (hence the designation of this period as “The Age of Fishes”). One group of fish, then widespread, is particularly interesting in the present context: the Sarcopterygii or lobe-finned fishes. Lobe-finned fishes were aquatic, but likely lived near the bottom of dark and turbid water (Carroll, 1988) and might have crawled through vegetation, thereby imposing additional stress on the fins. Fossil representatives, of which *Eustenopteron* is best known (Fig. 1), had a well-developed and muscularised fin skeleton, unlike other groups whose fins consisted merely of soft fin rays. The proximal limb bones of the later tetrapods are already evident, although they retain the basic functions of fins (Carroll, 1988).

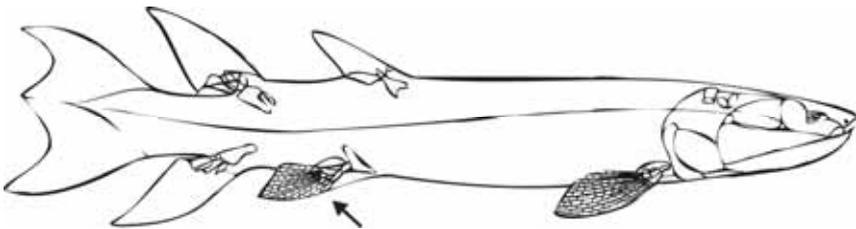


Figure 1: *Eustenopteron*, a lobe-finned fish. The arrow indicates the pelvic fin, which consists of multiple, stiff rays (after Andrews and Westall, 1970, in Carroll, 1988).

There are only a few Sarcopeterygian species living today, namely the lungfishes and the “living fossil” Coelacanth (*Latimeria*), which uses its paired fins in a manner much like that of the limbs in a trotting horse (Fricke et al., 1987). Even though it does not really “walk” under water in its natural environment, as previously thought, it is suggested that the trot-like “gait” of the paired fins might have facilitated the fish-tetrapod transition (Fricke & Hissmann, 1992), by being preadaptive.

Lobe-finned fishes were most likely the ancestors of tetrapods (Carroll, 1988), who first appeared as primitive amphibians. Interestingly, a transitional form (i.e. a tetrapod-like fish) was discovered recently: *Tiktaalik* (Daeschler et al., 2006). It had the overall body shape of a lobe-finned fish but with more arm-like front fins (hind fins have not been discovered yet).

Because amphibians do not fossilise well, there are not many species known. Foot bones were found for the most important species: *Ichtyostega* (Fig. 2a), *Acanthostega* and *Tulerpeton* (dated 363 MYA).

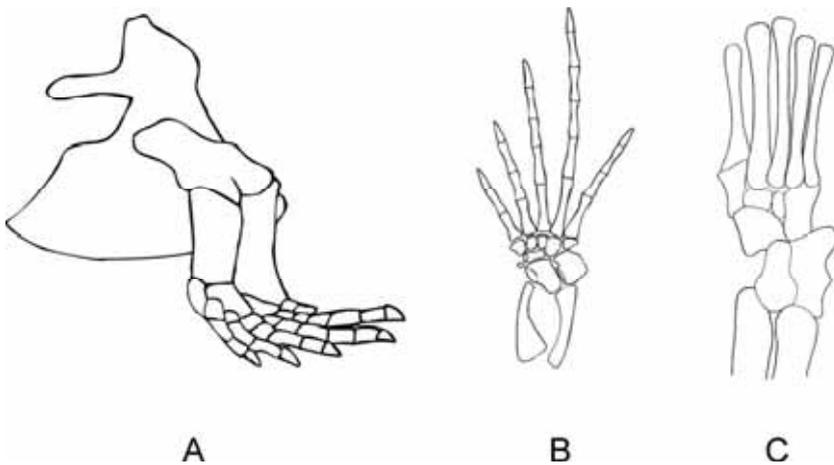


Figure 2: (a) Pelvic girdle and limb of *Ichtyostega*, a primitive amphibian (after Jarvik, 1955, in Carroll, 1988). (b) Lower leg and foot of *Paleothyris*, a primitive reptile (after Carroll, 1969, in Carroll, 1988). (c) Tarsus and metatarsus of *Asioryctes*, an early placental mammal that lived approximately 85 million years ago (Upper Cretaceous). Note that all foot bones, seen in modern humans, were present (after Kielan-Jaworowska, 1977, in Carroll, 1988).

These species had a clearly recognisable femur, tibia and fibula and their foot comprised of tarsal bones (e.g. tibiale, intermedium, fibulare, centrales), metatarsal segments and phalanges. The feet were unlike those of later tetrapods though, being typically polydactylous (6-8 digits were common in Devonian tetrapods), with more than three phalanges per toe. No full support of body weight by the feet was possible

in these species (but probably best in *Tulerpeton*). Even today, pentadactyly is not fixed in amphibians (e.g. four forelimb digits is typical here).

Only in amniote vertebrates (reptiles, birds and mammals) is pentadactyly the normal condition. Most amniotes have five toes or digits, even though secondary reductions are well documented (e.g. in hoofed animals). Where does this five-rayed bauplan come from, and why is it so stable? This question is not completely understood, and indeed neither is the whole fin-foot transition, but the following insights may be useful.

Fin rays are suitable for swimming, but not for the high loads associated with crawling and terrestrial locomotion. Probably in order to withstand these loads, stiffer bones, phalanges, appeared (for overviews of this stage, see Herkner, 1999, Coates et al., 2002, and Clack, 2004). The number of digits, five, may have been a good compromise between strength and the ability to swim, as early tetrapods were still aquatic. We know that, during embryogenesis, the rays of the hands and feet (the autopodium) result from apoptosis: in fact, separate toes do not originate from tissue growth, but by programmed cell death of tissue between the future toes. From this point of view, more rays would lead to decreased strength.

Pentadactyly is very stable, being determined by highly conservative genes (i.e. Hox genes, Hinchliffe, 2002). Moreover, pleiotropic effects (see above) are involved. Indeed, in clinical practice, polydactylous feet (i.e. feet with six or more toes) are associated with other abnormalities (Watanabe et al., 1992). The reason why these pleiotropic effects may be so important in limb formation, is that the latter is a very early process in embryonic development, at the crucial stage of organogenesis (Galis et al., 2001; for overview, see also Shubin et al., 1997, and Shubin, 2002).

In the middle Carboniferous (362-290 MYA) we find the first amniotes. These were primitive "reptiles" which looked quite similar to today's insect-eating lizards. A fossil representative is *Paleothyris* (300 MYA, Fig. 2b) (Benton, 1997). It had an astragalus (later to become the talus of primates), which is formed from the previous tibiale, intermedium and a centrale. The fibulare had enlarged and became the calcaneum (the later calcaneus). The foot was five-rayed but the toes had 2-5 phalanges (Benton, 1997).

Among the later reptiles, the therapsids (250 MYA) are most interesting in the present context. *Thrinaxodon*, a representative closely related to early mammals, had made the shift from a sprawling posture to a more erect posture, i.e. the hindlimbs were held closer under the body, instead of being held sideways, at right angles to it. This was a major change, enabling longer strides, and is associated with major changes in the anatomy of the hind limb and foot, e.g. the calcaneum projected posteriorly, like the calcaneus in mammals and humans.

Placental mammals, such as *Asioryctes* (164-45 MYA; Cretaceous, Fig. 2c) show an anatomy that was likely ancestral to all later placental mammals (Carroll, 1988). The foot consisted of an astragalus ("talus") which was positioned fully dorsal to the calcaneum, a cuboid, naviculare, three cuneiforms, five metatarsals and phalanges. So

the basic structure of the human foot was present, although the shape and proportions of the bones differed strongly. Early placental mammals had claws, not nails, a feature that was preserved until the plesiadapids, a group strongly related to the first primates (Boyd & Silk, 2000).

The primate foot

Early primates flourished during the Early Eocene, about 55 MYA (Rose, 1995). The most abundant then, were the adapids. These arboreal primates had grasping feet with nails (thus, no claws any more) and probably resembled today's lemurs (Boyd & Silk, 2000).

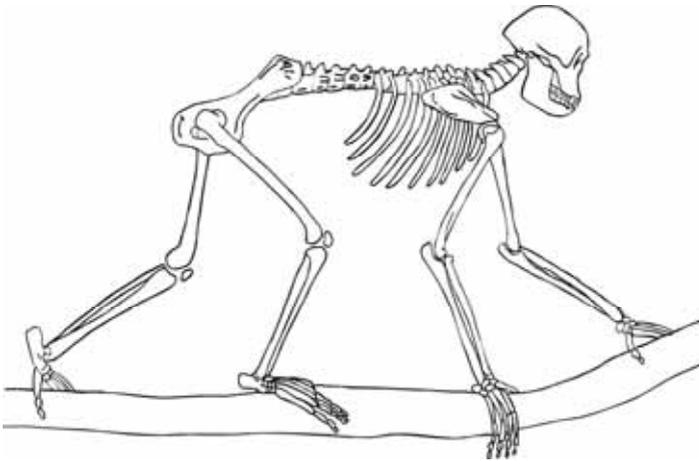


Figure 3: *Proconsul*, and early ape (see text for details) (after Boyd & Silk, 2000).

Later, during the Late Oligocene, the earliest hominoids (apes and humans) lived, *Proconsul* (20-17 MYA, Fig. 3) being the best known representative. It still was a generalized arboreal quadruped (see Berillon, 2000, for an analysis of its grasping feet), which may have engaged to some degree in suspension. The most recent of fossil hominoids are dated 16-13 MYA. *Nacholapithecus* (Nakatsukasa et al., 1998; Ishida et al., 1999) is a recently discovered representative which is highly interesting because it was tail-less and likely engaged habitually in orthograde postures (vertical climbing, hoisting, bridging), with associated morphological adaptations (see Nakatsukasa, 2004). After these findings there is a gap in the fossil record (excluding one species only known from a maxilla) until the first specimens considered hominin (see below).

Based on the fossil findings, Nakatsukasa (2004) proposed a scenario for the transition of early hominoid, to hominin locomotion. Generalised arboreal quadrupedalism would have led to an increased importance of forelimb suspension and orthograde behaviours, which would later lead to upright bipedalism. Such a scenario is consistent with Crompton et al. (2003), but more classical hypotheses propose a terrestrial/quadrupedal stage (Gebo, 1992) or vertical climbing stage (Fleagle et al., 1981).

For a description of extant primate feet, we refer to the paper by Vereecke & Van Sint Jan (2008; this volume).

Hominins

Modern humans and the two ape species in genus *Pan* (i.e. the chimpanzee and the bonobo) share a common ancestor (see e.g. Goodman, 1999) possibly 7 MYA (as suggested by fossil findings), although molecular data suggest the split to be slightly more recent (Chen & Li, 2001; Salem et al., 2003), maybe around 5 to 6 MYA. The latter dates are quite recent in evolutionary terms, and extant humans and the *Pan* apes only differ by 1.24% in their genetic material, which is a smaller difference than that between *Pan* species and the gorilla (Chen & Li, 2001).

The species that lived after the split with the *Pan* genus, in the clade that led to modern humans (and its side branches) is referred to as hominids or hominins. The term hominid (from the family Hominidae) is very frequently used in the literature, even though, strictly speaking, this family includes the extant great apes. Therefore, we have adapted the term hominin (from the tribe Hominini) for the purpose of the present paper; it is more correct from a phylogenetic point of view (see Aiello & Dean, 1990). Habitual bipedalism is generally regarded the benchmark for hominin status, and since this feature can not always be deduced unequivocally from early fossils, their position as hominin is often debated (see below).

Some of the hominins known to date most likely are our ancestors, while other species were sister groups that became extinct. There is considerable debate as to the reconstruction of the human family line (see e.g. Lieberman, 2001 for an overview of possible hominin relationships and Cela-Conde & Ayala, 2003 for an overview of hominin genera). Several species of hominins have coexisted at several times and places, perhaps as recently as a few thousand years ago (*Homo sapiens* and *H. floresiensis*, see below).

Hominin evolution took place over the geological epochs of, probably, the Miocene (23-5.3 MYA) and definitely the Pliocene (5.3-1.8 MYA) and the Pleistocene (1.8 MYA - 115 000 years ago).

Known hominins, their locomotion and their feet

Compared to apes, the hominin fossil record is quite rich (in fact only very recently a first fossil representative of the ape genus *Pan* was discovered, McBrearty & Jablon-ski, 2005). Still, important new findings are made almost every year, so our current account likely has many gaps and current understanding will alter as new fossils are found.

Fig. 4 gives an overview of currently known hominins. The figure also illustrates the deduced habitual locomotor mode - based most often on anatomical features other than the foot, e.g. the knee, hip and the position of the foramen magnum, and foot bones when they are known.

Here, we will briefly present the known species, in approximate chronological order. We concentrate on the species for which foot bones are known and list the primitive (ape-like) and modern (human-like) features of their feet.

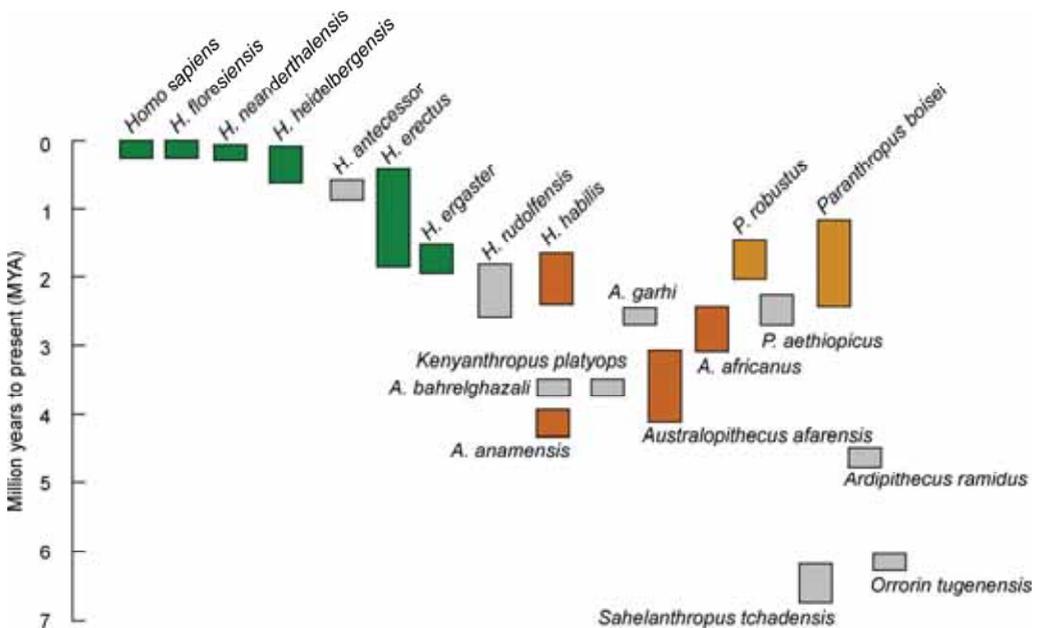


Figure 4: Overview of currently known hominins. Green (dark) bars indicate habitual bipeds, orange (medium grey) bars indicate species that were likely to be either habitual or facultative bipeds.

Sahelanthropus tchadensis (Brunet et al., 2002)

This species, nicknamed “Toumai”, is the oldest hominin (as claimed by the authors), being from the Upper Miocene, and was dated at 6-7 MYA. Interestingly, specimens (of different individuals) were found in Tchad but not further eastwards, in the Rift valley, where old hominins are typically discovered. There is discussion whether it is hominin or not (Wolpoff et al., 2002) although recent new findings (Brunet et al., 2005; Zollikofer et al., 2005) add to arguments that its systematic position must have been close to the common ancestor of *Pan* and *Homo*, but clearly on the hominin branch.

Brunet et al. (2002) state that, even though there is insufficient reliable information, it would not be unreasonable to consider *Sahelanthropus* as a habitual biped. Still, they present only one, indirect argument for bipedalism, i.e. the position of the foramen magnum (Begun, 2004), which may not be sufficient proof. No postcranial elements were found, so we lack foot bones for the species.

Orrorin tugenensis (Senut et al., 2001)

The fossils assigned to this species were dated approximately 6 MYA and were found in Kenya.

Orrorin might have been bipedal (Senut et al., 2001; Pickford et al., 2002), but the evidence is ambiguous, so whether this species was a habitual biped is far from established.

Even though there is no unanimity, the species is probably hominin (Aiello & Collard, 2001). Some parts of the postcranial skeleton were found (part of a femur) but, unfortunately, no foot bones.

Ardipithecus ramidus

Specimens are attributed to two subspecies: *A. ramidus ramidus* (“*A. ramidus*”, White et al., 1994) and *A. ramidus kaddaba* (Haile-Selassie, 2001). Both were found in Ethiopia, but were dated quite far apart at respectively 4.4 MYA (*A. ramidus ramidus*) and 5.2-5.8 MYA (*A. ramidus kaddaba*).

A. ramidus is considered by many as the oldest reliably diagnosed hominin. The subspecies discovered most recently, *A. ramidus kaddaba*, is particularly interesting in the context of this paper, because a pedal phalanx was preserved (thus, the oldest hominin foot bone). Its features suggest the species may have been bipedal, although this may not be sufficient proof (Begun, 2004). The phalanx is primitive, showing a large plantar curvature and features mosaic between the phalanges of apes and those of *Australopithecus afarensis* (see below) (Haile-Selassie, 2001).

Australopithecus anamensis (Leakey et al., 1995)

Specimens are dated approximately 4 MYA and were discovered in Kenya. *A. anamensis* is undoubtedly hominin.

A largely complete tibia was found, which, interestingly, may be more similar to those from members of the genus *Homo* than to *Australopithecus afarensis*. It shows that *A. anamensis* was bipedal (Ward et al., 2001). Unfortunately, no foot bones are found to date.

Australopithecus afarensis (Johanson & Taieb, 1976; Johanson et al., 1978; Johanson & White, 1979)

This hominin species is best known by the very complete skeleton AL-288-1, known as “Lucy”, found in Hadar, Ethiopia and dated 3.5 MYA. Specimens, including foot bones, attributed to this species were also found in Tanzania and Kenya.

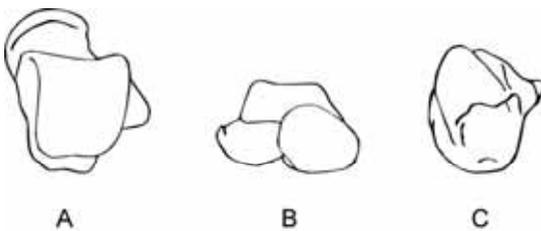
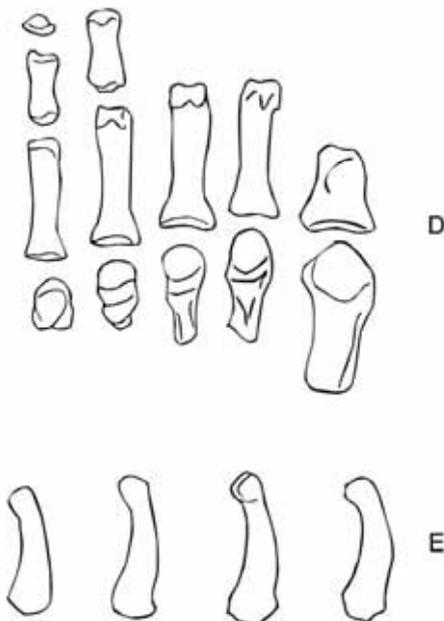


Figure 5:

Australopithecus afarensis. (a) talus, dorsal view (b) talus, anterior view (c) calcaneus, posterior view (d) metatarsals and phalanges, dorsal view (e) proximal phalanges, lateral view (after Johansson et al., 1982, in Aiello & Dean, 1990).



Based on the femur, Lovejoy et al. (2002) stated that this species was fully bipedal, and that its bipedalism differed only trivially from ours. It is generally agreed that *A. afarensis* was habitually bipedal (Lovejoy, 1988). Many authors provide arguments that this would be a different kind of bipedalism than that seen in later *Homo* and modern humans (e.g. Stern and Susman, 1983; Berge, 1994) but recent modeling studies indicate that their gait might have been efficient (Sellers et al., 2005; Nagano et al., 2005).

The foot bones are well documented (Harcourt-Smith & Aiello, 2004; Berillon, 2000; Aiello & Dean, 1990; Johanson et al., 1982) and show a mosaic of primitive and modern features. One modern feature is the talocrural joint, which is remarkably human-like (Latimer et al., 1987). Therefore, the leg of *A. afarensis* would move in a sagittal plane in relation to the foot (Aiello & Dean, 1990, Harcourt-Smith, 2002), as it does in humans, but not in apes. Another modern feature is the ability to dorsiflex the toes (Aiello & Dean, 1990) and the calcaneus, also, having a wide tuberosity, seems modern, although it also presents some primitive features (Stern & Susman, 1983; Latimer & Lovejoy, 1989).

Whether *A. afarensis* had a well-developed longitudinal arch (a modern feature) is not yet fully established. Latimer & Lovejoy (1989) suggest that there might have been a strong longitudinal arch, whereas others state it was either not developed or only slightly so (Susman, 1983; Berillon, 2000, 2004). The navicular probably bore substantial weight (Harcourt-Smith & Aiello, 2004, Harcourt-Smith 2005), which also suggests that a fully functional (as in humans) longitudinal arch would not have been present.

A clearly primitive (ape-like) feature of the *A. afarensis* foot is the shape of the phalanges, which are long and curved (Stern & Susman, 1983), the second ray being the longest. These features point to arboreal locomotion, whether as an active mode of locomotion or as a vestigial feature (an issue still under discussion).

Another very important feature of hominin feet, the function of the hallux, points to a primitive situation in *A. afarensis*: the hallux was opposable, as is the case in apes (confirmed by Harcourt-Smith, 2002), but likely to a lesser degree (Berillon, 2000). Specifically, the first metatarso-phalangeal joint has a markedly convex articular facet on the medial cuneiform for the 1st metatarsal (Latimer et al., 1982), a feature resembling the case in apes where the hallux is opposable. Moreover the first metatarsal head is rounded rather than flattened, as in humans (Stern & Susman, 1983; Susman, 1983).

The famous hominin trails found at Laetoli in Tanzania, dated approximately 3.7 MYA (Leakey & Hay, 1979; Leakey & Harris, 1987, Day & Wickens, 1980, Tuttle, 1987) are considered to be made by *A. afarensis* (also found at the Laetoli site), although Harcourt-Smith (2005) states that this was probably not the case and they were made by a species with an almost modern bipedal gait, probably a different species than *A. afarensis* (it is unclear which).

Clearly, more research is needed to establish the link between foot morphology, the dynamics of the foot during gait, and the generation of footprints, to give decisive answers.

Australopithecus africanus (Dart, 1925)

This species was contemporary to *A. afarensis*. Specimens dated more than 3 MYA were found in South Africa.

Like *A. afarensis* and all more recent species (see below) it was clearly bipedal.

One particular specimen, Stw 573 nicknamed "Littlefoot" is particularly interesting as it comprises a good set of foot bones (Clarke & Tobias, 1995) attributed to *A. africanus*. These were studied extensively by Harcourt-Smith (2002). "Littlefoot" is dated approximately 3.6 MYA, although there is recent debate considering its age by some authors (Berger et al., 2002: less than 3 MYA *contra* Clarke, 2002, Pickering et al., 2004: 4 MYA).

As in *A. afarensis*, the foot anatomy of *A. africanus* appears to be a mosaic of primitive and modern features (Clarke & Tobias, 1995), albeit both species represent a quite *different* mosaic. In fact, the *A. africanus* type of mosaic resembles the *H. habilis* foot better than the *A. afarensis* foot. *A. africanus* likely had a primitive talus (Harcourt-Smith, 2002), a mosaic navicular (which was weight bearing, but less so than the *A. afarensis* navicular) and a non opposeable hallux (*contra* Clarke & Tobias, 1995).

Other *Australopithecus* and *Kenyanthropus*

Australopithecus bahrelghazali (Brunet et al., 1995, 1996) is represented by a mandible only (dated between 3.0 and 3.5 MYA) and was found in Chad. It is sometimes considered to be *A. afarensis*. Obviously, no information as to the locomotion or foot anatomy of this species is available. *Australopithecus garhi* (Asfaw et al., 1999) was found in Ethiopia and dated 2.0 - 3.0 MYA. It may be an evolutionary link between *Australopithecus* and *Homo*, but unfortunately no foot bones were found. *Kenyanthropus platyops* (Leakey et al., 2001) was discovered recently in Kenya (dated 3.5 - 3.2 MYA), but it is only represented by cranial fragments, mandibles and teeth, not by any postcranial (e.g. foot) bones.

Paranthropus

Formerly considered the "robust Australopithecines", three species are currently known in this genus.

Specimens from *Paranthropus aethiopicus* (Arambourg & Coppens, 1968; Walker et al., 1986) were found in Ethiopia and Kenya, and dated around 2.5 MYA. *Paranthropus boisei* ("*Zinjanthropus boisei*", Leakey, 1959; Leakey & Leakey, 1964) is known from Tanzania, Kenya and Ethiopia and specimens are dated 1.4-2.5 MYA. Foot bones were found for neither of these species.

The third species is *Paranthropus robustus* (Broom, 1938), found in Southern Africa and dated 2.0-1.5 MYA. A few foot bones from *P. robustus* were found, the best being a left Metatarsal I (Sk 5017) (Susman & Brain, 1988). It has some modern (human-like) features (Aiello & Dean, 1990): its proximal articular surface is flat, suggesting that the first ray was alligned with the others, and not abducted (as in apes). Its inferior side is expanded, indicating the presence of well-developed plantar ligaments and thus, likely, a well-developed longitudinal arch. Furthermore, it is robust (indicat-

ing a high imposed load), not torsioned (torsion is associated with grasping in apes) and the articular surface on the head suggests the possibility for good dorsiflexion (as used in humans during bipedal locomotion) even though the joint likely was not as stable (close-packed) as in humans (Susman & Brain, 1988).

P. robustus likely had a striding bipedal gait but with a different weight transfer mechanism than observed in modern humans (Aiello & Dean, 1990). The genus *Paranthropus* is regarded as a sister group of *Homo*, not ancestral to it.

Homo rudolfensis (Alexeev, 1986 in Wood, 1992)

Specimens of *Homo rudolfensis* were found in Kenya and dated to 2.4-1.6 MYA. Wood & Collard (1999 a, b) doubted their membership of the genus *Homo*. Later, it was suggested that *H. rudolfensis* may actually be a *Kenyanthropus* (Leakey et al., 2001). No foot bones attributed to *H. rudolfensis* were found.

Homo habilis (Leakey et al., 1964, Johanson et al., 1987)

This species was first known from Tanzania (dated 1.75 MYA) but was also found in Kenya and South Africa. Wood & Collard (1999 a, b) doubt whether it should be placed in the genus *Homo*.

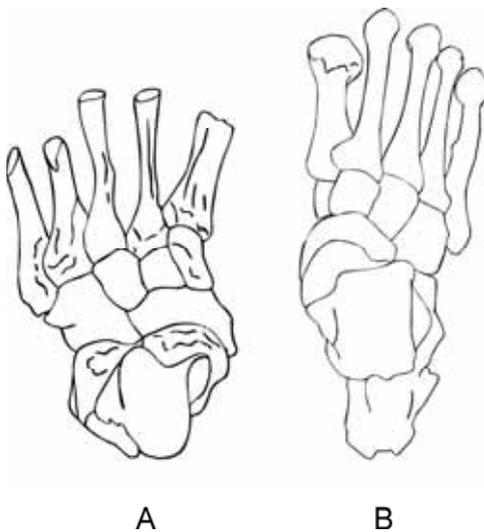


Figure 6:

(a) *Homo habilis*, tarsus and metatarsus (fractured), dorsal view. (after Lewis, 1981, in Aiello & Dean, 1990)

(b) Neanderthaler, tarsus and metatarsus. (after Trinkaus, 1983, in Aiello & Dean, 1990)

It is represented (among numerous other fossils) by a very complete foot skeleton (OH 8; Fig. 6a), of which the midtarsal joint (Kidd et al., 1996; Kidd, 1999; Berillon, 2000) and tarsal bones have been analysed (Harcourt-Smith, 2002; Berillon, 2000). In general, foot characteristics are similar to those of *A. africanus* (but unlike those of *A. afarensis*, which differs from both).

Lewis (1980) described the OH 8 foot as essentially ape-like, but later authors stress the presence of modern features, such as the form of the calcaneocuboid joint

(Kidd et al. 1996), while the talonavicular joint is primitive (resulting in an ape-like motion of the leg over the foot). Further features are mosaic and suggest a diverging first ray (possible pointing to arborealism). Recent analyses, though, provide arguments for modern characteristics such as an unopposable hallux and a medial longitudinal arch (Harcourt-Smith, 2002) and the OH 8 foot may well have belonged to a bipedal individual (Berillon, 2000).

***Homo ergaster* (Groves and Mazák, 1975, in Wood & Richmond, 2000)**

Specimens found in Africa (dated 1.7-1.5 MYA), and attributed to this species, strongly resemble those from Eurasian *H. erectus*. Alternatively, *H. ergaster* may be the same species as *H. habilis* (Wood, 1991).

The species was fully bipedal (Ruff & Walker, 1993), but no foot bones were found.

The intermembral index (arm length relative to leg length) is the same as that of modern humans living in hot, arid regions and the femoral head is as large as that of modern humans. Therefore, it is concluded that *Homo ergaster* was committed to long-range bipedalism (see Wang et al., 2004, for biomechanical evidence and a comparison with *A. afarensis*), and was the first hominin that appears to lack features related to arboreal locomotion (Wood & Richmond, 2000).

Later *Homo*

Five extinct species from the genus *Homo* are known to date. We do not deal with them in detail, because they were all clearly habitual bipeds, whose foot anatomy and gait probably differed from ours only in detail.

Homo erectus ("*Pithecanthropus erectus*", Dubois, 1894) is the first species found outside Africa i.e. on Java and in China), but is also known from Africa (specimens are dated 1.7 - 0.3 MYA). Their limb bones have human-like proportions and the postcranial skeleton clearly points to a habitual bipedalism (Wood & Richmond, 2000) but to our knowledge, no foot bones were found.

Homo antecessor (Bermúdez de Castro et al., 1997) was found in Europe (dated 0.8 MYA) and may be the last common ancestor to *H. neanderthalensis* and *H. sapiens*. Foot bones of this species were found (Lorenzo et al., 1999): they are very similar to those of modern humans, but some subtle differences exist, e.g. the phalanges are shorter and the base of the proximal hallucal phalanx is more rounded.

Homo heidelbergensis (Schoetensack, 1908 in Wood & Richmond, 2000) is found in Europe, Africa and Asia (dated approx 0.1 - 0.6 MYA). Its postcranial skeleton (e.g. limbs) are similar to, but more robust than those of modern humans. It was most likely a long distance walker (Wood & Richmond, 2000). To our knowledge, no *H. heidelbergensis* foot bones were found.

Homo neanderthalensis (King, 1864, in Wood & Richmond, 2000), known from Europe and Asia (approx 150000 - 30000 YA), was sometimes considered a subspe-

cies of *Homo sapiens* (*H. sapiens neanderthalensis*), but molecular evidence separates it a distinct species that, although it coexisted with anatomically modern humans (*H. sapiens*) in Europe, did not contribute to their gene pool (Krings et al., 1997, 1999, Caramelli et al., 2003, Pääbo et al., 2004).

Many Neanderthaler foot bones have been found (Fig. 6b) and the species was fully adapted to bipedal locomotion (Trinkaus, 1983a). Foot anatomy is very similar to modern humans and, in contrast to early claims, the hallux was opposable (Trinkaus, 1983b in Aiello & Dean, 1990). The longitudinal arch was well developed, but was bent slightly medially compared to modern humans (Berillon, 2000). In the forefoot, some anatomical differences with *Homo sapiens* exist however, including a higher robusticity and shorter proximal phalanges with wider diaphyses, pointing to potentially higher loading patterns in Neanderthals when compared to modern humans (Trinkaus & Hilton, 1996).

Homo floresiensis, nicknamed the “Hobbit” is a recent discovery from Flores (Indonesia). The species lived probably from 95 000 - 12 000 years ago (Morwood et al., 2004, 2005). Its status as a separate species is currently still debated.

Homo sapiens includes fossil specimens (e.g. those from the Cro-magnon shelter) and modern humans, and first appeared approximately 120 000 years ago. For details of foot morphology in modern humans, a comparison with extant apes and gait characteristics, we refer to subsequent papers in this volume (Vereecke & Van Sint Jan, 2008, Sobczak et al., 2008).

How did the hominin foot evolve?

From the overview presented above, it becomes clear that the very oldest species cannot provide us with good information regarding the evolution of bipedal locomotion and foot anatomy, either because their phylogenetic position as hominin is disputed, because their mode of locomotion is disputed, or because crucial skeletal remains are lacking. The most interesting species that can provide us with insight about the acquisition of habitual bipedalism and the corresponding foot anatomy are those from the Pliocene and early Pleistocene.

Foot specimens from these species show both primitive and modern features. The modern (human-like) features include: (1) loss of hallux opposeability (2) a long and well-developed calcaneal tubercle with a long Achilles tendon (3) the proportions of the foot, with relatively short phalanges, making it a more effective lever (4) a well-developed, passively stabilised, plantar arch (5) a closely-packed calcaneo-cuboid joint (6) a talocrural joint permitting the leg to pivot over the foot in a sagittal plane during stance (Aiello & Dean, 1990; Bramble & Lieberman, 2004).

No single unequivocal evolutionary sequence links the known Plio-Pleistocene species and several hypotheses have been proposed with regard to the consecutive events in the evolution of the hominin foot (i.e. Morton, 1935; Lewis, 1989 and Kidd, 1999). Harcourt-Smith & Aiello (2004) presented a scenario that seems most

compatible with the fossil material available to date. In this scenario, an ancestor with an arboreal lifestyle and a grasping foot function (with associated primitive foot features as mentioned above) would give rise to a bipedal *Australopithecus africanus*. The latter would then in turn give rise to *Homo habilis* and consequently, to later *Homo*. With respect to this scenario, a sequence including *A. afarensis* as an evolutionary intermediate would seem more parsimonious (despite the fact that it is often, but not always, considered ancestral to *Homo*).

In any case, it is certain that the ancestral condition was some kind of arboreal locomotion, leading via some intermediate steps which may have been brachiation, vertical climbing (Fleagle et al., 1981), terrestrial quadrupedalism (Gebo, 1992, 1996) or orthograde scrambling (Crompton et al., 2003; , Thorpe et al., 2007). The characteristics of the modern foot are all adaptations for bipedalism, and are associated with changes in paleo-environment and in behaviour, with arboreal locomotion losing importance and bipedal locomotion gaining importance, maybe as early as 7 MYA. The highly efficient, “stiff-legged” walking of modern humans was likely secondarily acquired over the course of hominin evolution.

The modern features mentioned above are typically associated with bipedal endurance walking, but recently it has been argued that the modern foot is also well-adapted for bipedal standing (Wang & Crompton, 2004) and for endurance running (Bramble & Lieberman, 2004). The latter locomotion might have been important in the later *Homo* species. In fact, endurance running for hunting purposes may have played a role in hominin evolution (Carrier, 1984). Most modern foot features are adaptive for all three functions (standing, walking, running). Most likely, early hominin feet still had grasping functions, combined with some adaptations for bipedalism. Later, hominins gradually lost the grasping possibilities and became fully adapted to bipedal posture and locomotion (efficient walking), having a “lever” foot (these functions likely involving Australopithecines and early *Homo*). Still later, the lever function of the foot was optimised, as we see it in modern human feet. When exactly the characteristics typical of a “bipedal” foot were developed is unknown, but most likely it was early in hominin evolution (Berillon, 2000).

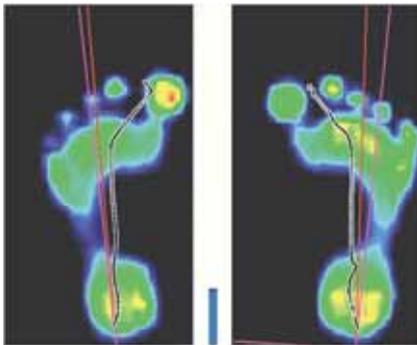
Footwear

So far, we have considered the evolution from the Crossopterygian fin to the anatomically modern foot. Is this the foot we see in everyday scientific and clinical practice? Maybe not – there are good arguments that the feet of Western populations, typically represented in scientific and clinical studies, are deformed due to the habitual use of footwear.

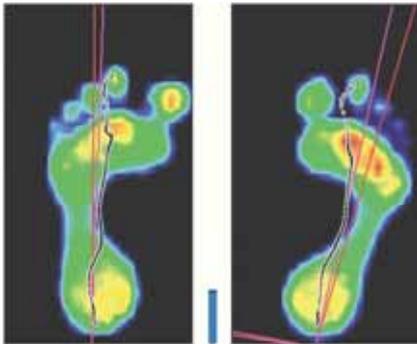
The fact that the foot is a phenotypically highly plastic structure that can be morphologically influenced by constricting footwear, is demonstrated to the extreme in traditional Chinese foot binding (Cummings et al., 1997). Less extreme cases are described as well, e.g. in rock climbers wearing tight shoes (Killian et al., 1998). But

even everyday shoes likely deform feet. This can be seen in clinical cases, but has already been observed in a medieval population (i.e., hallux valgus due to narrow pointed shoes, Mays, 2005). More arguments why Western feet are likely to be deformed due to footwear can be seen in the foot shape of modern people who have never worn footwear. Only a few studies have analysed feet of such people. The ones that do exist, though, show that they have foot shapes different from habitually shod

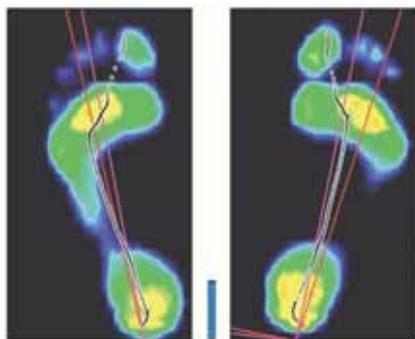
Westerners, e.g. they are often more fan-shaped and morphological flat feet are common but asymptomatic (Kusumoto et al., 1996; Ashizawa et al., 1997, east Asian people). Fig. 7 illustrates typical foot shape differences between a habitually barefoot Indian, a habitually shod Indian, and a Western subject by means of pressure profiles, made using a portable pressure plate (RSscan footscan® USB system).



A



B



C

Figure 7:

Example footscan® images of (a) a habitually walking Indian (b) an Indian habitually using footwear (c) a European. Note that the fan-shape of the toes, most pronounced in the barefoot walker.

Arch height has been found to be influenced by footwear in a few studies (Rao & Joseph, 1992; Sachithanandam & Joseph, 1995 for Indian people; Echarri & Forriol, 2003 for African children).

The habit of wearing some form of (constraining) footwear is very recent in human evolution. The first indications (rock paintings in Spanish caves) date back to approximately 15 000 years ago, and the oldest footwear ever found dates back to approximately 8 300 years ago (Kuttruff et al., 1998). Thus, footwear appeared long after the fully anatomically modern foot had evolved and has not played a role in shaping the biologically normal, modern human foot.

Summary

The origin of the human foot can be traced back to the fins of lobe-finned fishes. These were modified into a pentadactyl structure in early reptiles which already had the basic bony elements of the human foot. In early mammalian feet, all modern human foot bones were already present. The function of the foot shifted to a grasping function, needed for arboreal locomotion, in primates. Such a structure was retained in the ancestors of the hominins. During hominin evolution, arboreal locomotion shifted quite rapidly to terrestrial bipedalism. This involved a whole suite of adaptations in the foot and the rest of the skeleton. The foot was modified from a flexible structure with a grasping function, to a rigid structure with a lever function. Such a highly specialised foot was already present in the later *Homo* species, long before the invention of footwear, and may be found today in modern people who don't wear shoes.

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