REVIEW

Fossils, feet and the evolution of human bipedal locomotion

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Abstract

We review the evolution of human bipedal locomotion with a particular emphasis on the evolution of the foot. We begin in the early twentieth century and focus particularly on hypotheses of an ape-like ancestor for humans and human bipedal locomotion put forward by a succession of Gregory, Keith, Morton and Schultz. We give consideration to Morton's (1935) synthesis of foot evolution, in which he argues that the foot of the common ancestor of modern humans and the African apes would be intermediate between the foot of *Pan* and *Hylobates* whereas the foot of a hypothetical early hominin would be intermediate between that of a gorilla and a modern human. From this base rooted in comparative anatomy of living primates we trace changing ideas about the evolution of human bipedalism as increasing amounts of postcranial fossil material were discovered. Attention is given to the work of John Napier and John Robinson who were pioneers in the interpretation of Plio-Pleistocene hominin skeletons in the 1960s. This is the period when the wealth of evidence from the southern African australopithecine sites was beginning to be appreciated and Olduvai Gorge was revealing its first evidence for *Homo habilis*. In more recent years, the discovery of the Laetoli footprint trail, the AL 288-1 (*A. afarensis*) skeleton, the wealth of postcranial material from Koobi Fora, the Nariokotome *Homo ergaster* skeleton, Little Foot (Stw 573) from Sterkfontein in South Africa, and more recently tantalizing material assigned to the new and very early taxa *Orrorin tugenensis*, *Ardipithecus ramidus* and *Sahelanthropus tchadensis* has fuelled debate and speculation. The varying interpretations based on this material, together with changing theoretical insights and analytical approaches, is discussed and assessed in the context of new three-dimensional morphometric analyses of australopithecine and *Homo* foot bones, suggesting that there may have been greater diversity in human bipedalism in the earlier phases of our evolutionary history than previously suspected.

Key words *Australopithecus*; bipedal locomotion; evolution of the foot; *Homo*; human evolution.

Introduction

In terms of human evolution in the broader context, it is now generally considered that the development of obligate bipedal locomotion was one of the most significant adaptations to occur within the hominin lineage. There is a considerable literature on the subject, and with that literature comes considerable debate. Most of this debate can be divided into three distinct parts. First, there is debate surrounding the likely locomotor repertoire that preceded bipedalism (e.g. Richmond & Strait, 2000; Dainton, 2001; Richmond et al. 2001). Secondly, there is the more theoretical debate over the ecological/behavioural reasons as to why bipedalism evolved (e.g. Chaplin et al. 1994; Wheeler, 1988, 1994; Wood, 1993; Hunt, 1994). Lastly, and this is where the majority of studies have focused, there has been debate over the degree to which certain hominin taxa were obligate bipeds (e.g. Le Gros Clark, 1947; Leakey & Hay, 1979; Susman & Stern, 1982, 1991; Stern & Susman,

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1983; Senut & Tardieu, 1985; Susman et al. 1985; Latimer et al. 1987; White & Suwa, 1987; Latimer & Lovejoy, 1989; Gebo, 1992; Spoor et al. 1994; Clarke & Tobias, 1995).

Of all extant primates, humans are the only obligate bipeds. Highly specialized postcranial adaptations, especially in the lower limb, characterize this unique form of locomotion. The foot is particularly specialized in both its anatomy and its function. This makes perfect sense, because in developing bipedal locomotion, the foot becomes the only structure that directly interfaces with the ground, and subsequently is under strong selection pressure to deal with both balance and propulsion in a highly efficient way. Even in the more arboreal great apes, the lower limb is always the principal limb of locomotion. Increased knowledge therefore about the relationship between structure and function in the foot bones of our hominin ancestors, as well as extant primates, is central to our understanding of the origins and evolution of bipedalism.

Fossil hominin foot bones

There has been a considerable degree of debate surrounding locomotor affinities inferred from fossil hominin foot bones. It is well known that geologically more 'recent' hominin species, such as *Homo antecessor*, *H. heidelbergensis, H. neanderthalensis* and anatomically modern *H. sapiens* were fully bipedal (Trinkaus, 1983; Aiello & Dean, 1990; Lorenzo et al. 1999) (Fig. 1). Their feet reflect this bipedalism, although certain aspects of the pedal morphology of *H. antecessor*, *H. heidelbergensis* and

H. neanderthalensis differ from that of modern humans (Aiello & Dean, 1990; Lorenzo et al. 1999). The functional implications of these differences are currently unknown. Although there are no associated foot bones for one of the earliest members of the genus *Homo*, *H. ergaster* (*c.* 1.8 Ma) we do know from the rest of the postcranial skeleton that this taxon was also fully bipedal (Ruff & Walker, 1993). For other hominins, there is still a large degree of disagreement. The OH 8 *H. habilis* foot (at 1.8 Ma) was originally suggested to reflect a fully developed bipedal adaptation (Day & Napier, 1964; Leakey et al. 1964) but others have argued that it still retains evidence of an arboreal adaptation (Lewis, 1980b; Oxnard & Lisowski, 1980; Kidd et al. 1996; McHenry & Berger, 1998a; Wood & Collard, 1999). This is consistent with some recent interpretations of other aspects of *H. habilis* skeletal morphology (e.g. Hartwig-Scherer & Martin, 1991; McHenry & Berger, 1998a; Wood & Collard, 1999).

Similar controversy surrounds the *Australopithecus afarensis* foot bones from Hadar, Ethiopia (*c.* 3.0–3.4 Ma) that are described by some as being compliant with full bipedal locomotion (Latimer & Lovejoy, 1982, 1989, 1990a,b; Latimer et al. 1987), whereas others have suggested that the same fossils show traits that indicate a mosaic of terrestrial and arboreal locomotion (Susman & Stern, 1982, 1991; Stern & Susman, 1983, 1991; Susman, 1983; Susman et al. 1985; Duncan et al. 1994; Berillon, 1998, 1999, 2000). Both sides of this controversy can also be supported by the analysis of other aspects of postcranial anatomy (e.g. Stern & Susman, 1983; Lovejoy et al. 2002).

The issue is further complicated by the suggestion that the foot of the important 'Little Foot' specimen (Stw 573), currently assigned to *A. africanus*, and possibly as old as 3.6 Ma, reflects mosaic locomotor affinities (Clarke & Tobias, 1995), however, there is no agreement as to the nature of this mosaic locomotor adaptation (e.g. Berillon, 1999, 2000; Harcourt-Smith, 2002). The oldest currently known hominin foot bone is a left fourth proximal foot phalanx belonging to *Ardipithecus ramidus kadabba* and dating to *c.* 5.2 Ma (Haile-Selassie, 2001). It also shows a mosaic morphology that has features of both apes and *A. afarensis*. The specific nature of the bipedalism reflected in this single bone awaits the discovery of further pedal specimens.

The evolution of hominin bipedal evolution

In the last 80 years or so there have been a number of proposed theories addressing the evolution of hominin
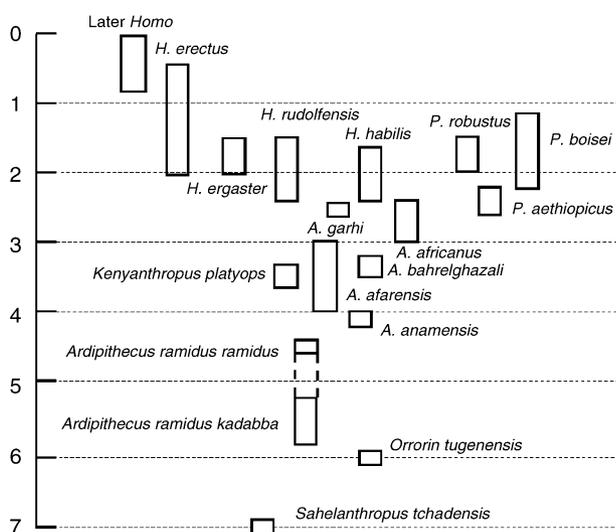

Fig. 1 The temporal distribution of known hominin taxa.

bipedalism from the point of view of comparative anatomy. Historically, these theories can be placed into two categories. First, there are those theories based primarily on observed anatomical differences between extant hominoid taxa, and secondly there are those theories based more on fossil material. Because the vast majority of early hominin fossil remains have been found since the 1960s, theories prior to that date rested almost exclusively on the comparative anatomy of modern humans and the extant primates, particularly the great apes. They addressed the question of the probable post-cranial morphology and associated locomotor repertoire that immediately preceded the appearance of hominin bipedalism. By contrast, ideas about the evolution of hominin bipedalism since the 1960s have tended to be highly influenced by fossil finds and to focus on questions of bipedal evolution within the human clade.

Comparative anatomy and the antecedents of hominid bipedalism

There is an abundance of early literature on the evolution of hominin bipedalism (see Rose, 1991; Richmond et al. 2001). In the 1920s and 1930s arguably the prevailing view (e.g. Gregory, 1916, 1928; Keith, 1923, 1928; Morton, 1924, 1935) was that bipedalism evolved in a relatively linear fashion from a brachiating, hylobatid-like ancestor, passing through a larger-bodied vertical climbing stage, then a terrestrial knuckle-walking stage before finally reaching obligate, plantigrade bipedalism. There were minor differences between the 'brachiationist' theories proposed by these authors and also by Schultz (Schultz, 1930), who favoured a more generalized ape ancestor. They are, however, similar to each other in favouring an ape-like ancestor as the immediate precursor to the hominins and to bipedal locomotion. Other prevailing theories of the time saw either an ancient split of the human lineage and a tarsoid-like ancestor for humans and human bipedalism (Wood Jones, 1929) or a more monkey-like ancestor with an above-branch locomotor pattern similar to modern monkeys (Straus, 1949).

More recently, the concept of a brachiating ancestor has fallen out of fashion (Avis, 1962). This is mainly due to a combination of new fossil evidence, better understanding of the locomotor repertoires of extant great apes, and the introduction of molecular systematics. The first reported significant postcranial remains from the African Miocene ape *Proconsul* (Napier & Davis,

1959) did not show a strong adaptation to brachiation, and this has been confirmed by more recent abundant Miocene fossil material (e.g. Rose, 1991; Tuttle et al. 1991; Moyà-Solà & Köhler, 1996). Furthermore, molecular data confirm the African apes as our closest living relatives and place the common ancestor between modern humans and chimpanzees relatively recently, between 5 and 7 million years ago (Gagneux & Varki, 2000; Page & Goodman, 2001). We know that the African apes spend a considerable time when on the ground engaging in knuckle-walking and when in the trees in arboreal climbing, and do not engage as much in arboreal swinging behaviour. In fact, in place of a brachiating ancestor, a knuckle-walking ancestor was proposed by Washburn (1967) and has recently been championed by Richmond and colleagues (Richmond & Strait, 2000; Richmond et al. 2001) on the basis of the wrist morphology of *A. afarensis* and other early hominins. Tuttle & Basmajian (1974) rejected Washburn's original 'knuckle-walking' hypothesis on the grounds that modern human hands showed no evidence of a knuckle-walking ancestry. Both Dainton (2001) and Lovejoy et al. (2001) have also questioned the modern revival of the hypothesis by offering different interpretations of the *A. afarensis* wrist morphology.

A second current hypothesis for the ape-like locomotor behaviour immediately antecedent to the evolution of bipedalism is the 'climbing hypothesis' involving vertical climbing and orthograde clambering behaviours, but no significant terrestrial locomotion (Fleagle et al. 1981). Tuttle & Basmajian (1974) and Tuttle (1975, 1981) envisage this ancestor as a small-bodied climber and arboreal bipedal whereas others (e.g. Stern, 1975; Prost, 1980; Hunt, 1996) argue for a larger-bodied ancestor who used all four limbs to grasp supports during vertical climbing and suspension. Most recently, Crompton and colleagues (Crompton et al. 2003; Thorpe & Crompton, 2004) have argued on the basis of comparative bipedal kinematics that the antecedent locomotor type would have been more similar to pronograde clambering as observed in modern orang-utans and unknown in extant African apes.

Comparative anatomy of the foot and the antecedents of bipedalism

Theories in relation to the evolution of the hominin foot evolution have strongly mirrored leading theories of the day on the evolution of bipedalism. Still the most
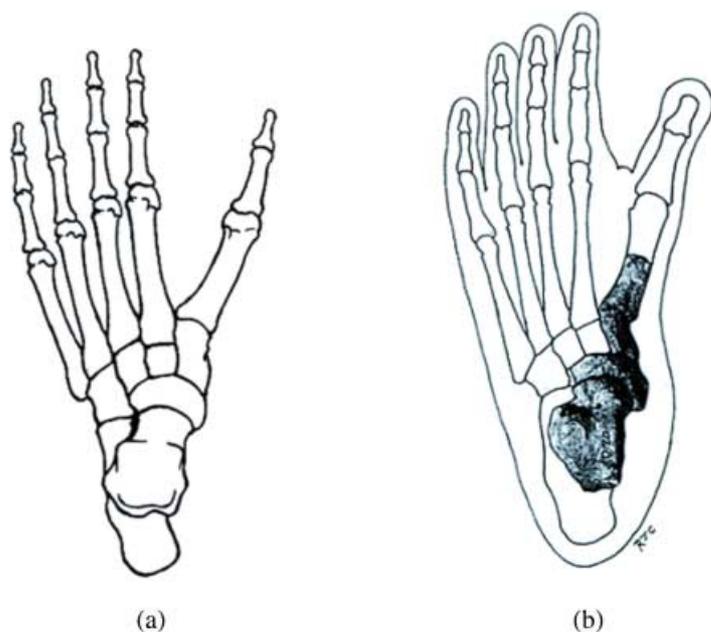
Fig. 2 (a) Dudley Morton's (1935) reconstruction of a 'hypothetical prehuman foot', and (b) Clarke & Tobias's (1995) reconstruction of the Stw 573 specimen 'Little Foot'. (a) Redrawn from Morton (1935); (b) reprinted with permission from RJ Clarke and PV Tobias, *Science* **269**: 521–524 (1995). Copyright 1995 AAAS.

well known model of human foot evolution, is Dudley Morton's 1935 synthesis (Morton, 1935). The culmination of many years work, Morton argued that the foot of the common ancestor of modern humans and the African great apes was that of a 'hypothetical Dryopithecine'. In terms of morphology, it was postulated that it would be intermediate between the foot of *Pan* and of *Hylobates*, with relatively smaller tarsals than for *Pan*, but digits less elongated and curved than for *Hylobates*. Morton also suggested a hypothetical early hominin foot, and postulated that it was intermediate between that of *Gorilla* and modern humans. The reason for this is that he concluded that because *Gorilla* is more terrestrial than *Pan*, then it must be more human-like in its foot, and Morton pointed to a suite of traits in the gorilloid foot that bears this out, such as a longer heel, decreased length of rays 2–5, a slightly less abducted hallux and a decrease in the degree of torsion between the hallux and the remaining metatarsals. The last two observations effectively suggested a reduced grasping potential in *Gorilla*, relative to *Pan*. The hypothetical 'prehuman foot' is suggested by Morton (1935; Fig. 2) to have still been a 'flexible and muscular grasping organ', i.e. with an opposable hallux (although it would be relatively lengthened), but also an enlarged heel for increased weight bearing, shorter toes than *Gorilla*, but no longitudinal arches. It is interesting that the reconstruction of the Stw 573 *A. africanus* ('Little Foot') skeleton (Clarke & Tobias, 1995) is very similar to Morton's (1935) reconstruction.

Morton (1935) therefore suggested that our Plio-Pleistocene ancestors were essentially gorilloid rather than like *Pan*. It is interesting to note that Morton's work was strongly backed up by most other studies of the day. At various times, Weidenreich (1923), Keith (1928) and Gregory (1928) all proposed that the human foot arose in a relatively linear fashion out of a gorilloid terrestrial ancestor. However, Morton took no account of the fact that both *Gorilla* and *Pan* may well be highly derived in their pedal morphology, and that the terrestrial modifications seen in the foot of *Gorilla* (Sarmiento, 1994) could be structural modifications to cope with increased body weight, rather than modifications to becoming more bipedal. The other important fact to consider was that Morton had no fossils to work with, just modern comparative material.

Much more recently, two additional models of pedal evolution have been proposed, one by Lewis (1989) and the other by Kidd (1999). These differ from Morton's model in that both of these refer to the anatomical details of the transformation of an ape-like foot with an opposable hallux to a human-like one in which the great toe is adducted in line with the lateral toes, the tarsal region is stabilized and the foot is modified to act as a propulsive lever. Lewis's model (Lewis, 1980a,b, 1989) challenges what he refers to as the 'traditional' model of how the ape foot remodels to become a human foot. Here the 1st ray adducts to become in line with the functional axis of the foot, and the foot everts so that the sole is flat on the ground. Lewis argues that

the problem with this is that by adducting the hallux, the 1st tarsometatarsal joint becomes unstable, moving from a close packed to a more loosely packed position. Lewis argues that instead, the hallux stayed in its close-packed position, and that the forefoot realigned medially towards this stabilized hallux (see also Aiello & Dean, 1990). Lewis is assuming that the evolutionary changes in the foot would amount to the same changes that occur when an ape adducts its hallux. However, in evolutionary terms, with remodelling of the 1st ray so that it becomes more adducted, one might expect to see remodelling of the actual joint morphology so that maximum congruence (and therefore stability) would be retained between the medial cuneiform and the hallux. In modern humans the joint is essentially in the close-packed position permanently, and has very little ability to either abduct or adduct. The function of the close-packed position is different between apes and humans. In the great apes it is to facilitate a strong grip, whereas in modern humans it is to transfer weight efficiently during toe-off.

The second recent model (Kidd, 1999) is based on a study of the calcaneus, talus, cuboid and navicular of OH 8, the *H. habilis* foot (Kidd, 1995; Kidd et al. 1996). Kidd argues that the talus and navicular of OH 8 are essentially ape-like, but that the calcaneocuboid articulation is markedly human-like. In Kidd's view the medial column of OH 8 is essentially ape-like, with no medial longitudinal arch and an opposable toe, but the lateral column had remodelled to a human-like degree. Kidd (1999) proposes that the lateral side of the hominin foot evolved first, to stabilize mid-tarsal flexibility as an adaptation to increased terrestriality, and that the medial side followed. By the time of *H. habilis* at *c.* 1.8 Ma hominins still had a 'mobile talonavicular joint' and an opposable hallux.

Kidd's conclusions are interesting; however, they are based solely on the analysis of a single fossil specimen. Kidd also argues that the OH 8 foot had an opposable hallux as part of its primitive medial column. However, his study did not include a direct analysis of the OH 8 medial cuneiform, and rather relied on the morphology of the talo-navicular complex as an indicator of hallux abduction. Recent work on the medial cuneiform by other researchers suggests that the hallux of OH 8 was, in fact, adducted and non-opposable (e.g. Berillon, 1999; Harcourt-Smith & Aiello, 1999; Harcourt-Smith, 2002). Finally, Kidd uses just one fossil specimen as the basis of his theory about hominin foot evolution. As we

will see there is considerable variation in postcranial morphology in the hominins that date to earlier periods than does *H. habilis*. Furthermore, the first evidence for the appearance of bipedal locomotion is arguably from *Sahelanthropus tchadensis* dating to *c.* 7 Ma (Brunet et al. 2002), *Orrorin tugenensis* dating to *c.* 6 Ma (Senut et al. 2001) and *Ardipithecus ramidus kadabba* from *c.* 5.2 Ma (Haile-Selassie, 2001). There is no reason to believe that the *H. habilis* foot dating to 1.8 Ma represents the primitive hominin pedal morphology. *H. habilis* is closer to us in evolutionary time than it is to these earlier seemingly bipedal hominins. This model of foot evolution, although possible, can only be considered as an untested hypothesis at this point.

Fossil evidence for bipedal evolution in the human clade

Although emphasis on the likely ancestral locomotor mode of hominins and on the transformation of the ape foot into a human foot may have changed over the years, there is still no current consensus on these issues and there is unlikely to be one in the near future. Furthermore, by its very nature, this approach, which is based on the comparative anatomy of living species and selected fossil evidence, and informed by changing phylogenetic hypotheses, cannot answer essential questions in relation to the pattern of bipedal evolution in the hominin line once it separated from the line leading to the living African apes. What type of bipedalism characterized the various species of early hominin? Was the evolution of bipedal locomotion a slow, gradual, linear process? Was there ever more than one contemporaneous type of bipedalism? Is there any evidence that bipedalism, and the hominin line, evolved more than once from ape-like forebears? The only way to answer these questions is to interrogate the often meagre and fragmentary fossil record.

Anatomical evidence for bipedal locomotion in some of the earlier discovered pre-Neanderthal hominins such as *H. erectus* and the Taung Child (*A. africanus*) played a large part in their ultimate acceptance as hominins. However, the first serious analyses of locomotor mode and variation in the early hominins came as a result of the significant finds in South Africa in the 1930s and 1940s, from the sites of Sterkfontein, Swartkrans and, to a lesser extent, Kromdraai (see Aiello & Andrews, 2000, for an assessable review of the South African hominin fossils). Most notable were two seminal studies published

by Napier (1964) and Robinson (1972). Both authors agreed that *Paranthropus robustus* and *A. africanus* had considerable postcranial adaptations to bipedalism, but that at the same time there were also striking differences in postcranial morphology between them. Napier (1964) argued that the *A. africanus* pelvis (based on Sts 14), relative to *P. robustus* (based on SK 50), was more human-like in having a relatively large acetabulum, a less prominent anterior superior iliac spine, and a relatively shorter ischium (although not to a human-like degree). Based on these features as well as on the morphology of the proximal femur, Napier (1964) concluded that *P. robustus* would have had a far less efficient form of bipedalism that *A. africanus*, with a 'waddling' gait and an inability to transfer body weight from one foot to the other during walking. Napier's explanation for these differences was an ecological one, and he believed that the 'pre-*robustus* stock' had spent considerably more evolutionary time in a woodland savannah setting, whereas the 'pre-*africanus* stock' spent more time in an open savannah setting, thus becoming more human-like in their adaptations to obligate bipedalism. He reasoned that once the two taxa speciated from an unknown common ancestor, their own respective forms of bipedalism evolved separately.

Robinson (1972) agreed with Napier (1964) that *P. robustus* and *A. africanus* (which he calls *H. africanus*) were different in their pelvic and femoral morphology and thus gait, but favoured a more linear scenario akin to the early theories of Keith (1923) and others for the ape precursors of hominin bipedalism. He envisaged a 'stream of evolution' (Robinson, 1972, p. 255) from a hypothetical African variant of the Asian genus *Gigantopithecus* to *P. robustus* with subsequent speciation in *P. robustus* leading to *A. africanus* and ultimately to modern humans.

Any modern debate over the similarities and differences in bipedalism in *A. africanus* (or another taxon of early hominin) and the robust australopithecines continues to be thwarted by the paucity of significant robust postcranial fossils (but see Grausz et al. 1988). In spite of this and beginning with the still continuing discovery of numerous hominin fossil sites in eastern Africa and of new hominin genera and species, the debate in relation to the nature of bipedalism in individual hominin taxa and variation between taxa has intensified. In the past two decades since the early 1980s, the vast majority of literature has focused on the inferred locomotion associated with the prolific

A. afarensis remains found at Hadar and the Middle Awash, Ethiopia, dating to between *c.* 3.0 and 3.6 Ma, and the remarkable footprints from Laetoli, Tanzania (*c.* 3.6–3.75 Ma). In more recent years this literature has been augmented by discussions of new postcranial fossils for older known taxa (e.g. *H. habilis* OH 62, Johanson et al. 1987) and of newer hominin taxa, such as *A. garhi* (*c.* 2.5 Ma, Asfaw et al. 1999), *A. anamensis* (*c.* 3.9–4.2 Ma, Leakey et al. 1995, 1998), *Ardipithecus ramidus ramidus* (*c.* 4.5 Ma, White et al. 1994, 1995), *Ardipithecus ramidus kadabba* (*c.* 5.2–5.6 Ma, Haile-Selassie, 2001), *Orrorin tugenensis* (*c.* 6 Ma, Senut et al. 2001) and *Sahelanthropus tchadensis* (*c.* 7 Ma, Brunet et al. 2002).

The pre-*ergaster* hominin fossils all show variable combinations of human and ape features in their postcranial anatomy. The mosaic nature of the morphology can be typified by the well-known partial skeleton 'Lucy' (Al 288-1, *c.* 3.2 Ma). *A. afarensis*, as represented by 'Lucy', shows some clearly derived bipedal adaptations, with a more human-like pelvis with a short iliac blade and wide sacrum, a human-like bicondylar angle of the femur, and a human-like talo-crural joint (Stern & Susman, 1983). More ape-like postcranial morphologies include a more cranially orientated glenoid, a funnel-shaped thorax, and long and curved pedal and manual phalanges. All these factors might imply an at least partial ability for arboreal climbing, although there is a considerable debate in the literature over the precise nature of *A. afarensis* locomotion (Stern, 2000; Ward, 2002).

This debate surrounds the locomotor significance of the 'primitive' ape-like traits preserved in the fossils. Stern, Susman, Jungers and colleagues (Jungers, 1982; Jungers & Stern, 1983; Stern & Susman, 1983; Rose, 1984, 1991; Susman et al. 1984; Stern, 1999) argue that these traits must have been preserved by selection and therefore have had adaptive significance to *A. afarensis*. Latimer, Lovejoy and Ohman (Latimer et al. 1987; Latimer & Lovejoy, 1989; Latimer, 1991) alternatively emphasize the clear evidence in the skeleton for selection for terrestrial bipedality, which in their view occurred at the expense of arboreal efficiency. They argue that *A. afarensis* was an obligate biped primarily on the grounds that selection did not preserve in these hominins features such as relatively long fingers and toes and the grasping foot that are essential for efficient arboreal locomotion. In Ward's (2002) recent assessment of this controversy she also emphasizes that the two camps are asking different
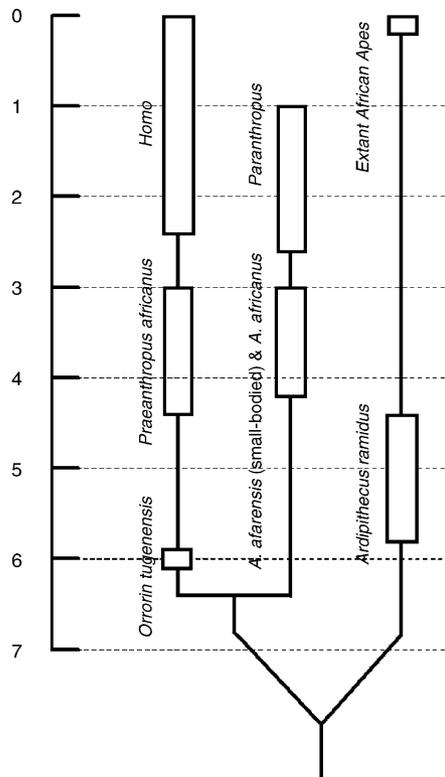
Fig. 3 Hominin phylogeny proposed by Senut et al. (2001). Note that Senut refers some of the *Australopithecus afarensis* collection (the smaller-bodied individuals) to the taxon *A. antiquus* (Ferguson 1984). See text for explanation.

questions. On the one hand Latimer and colleagues are interested in why *A. afarensis* evolved whereas Stern and colleagues are primarily interested in inferring *A. afarensis* behavioural repertoires. Ward, herself, believes that there is clear evidence that *A. afarensis* was a habitual biped and suggests *A. afarensis* climbing behaviour cannot be confidently predicted from primitive traits and can only be convincingly inferred if based on derived traits that reflect selection for arboreal locomotion or through further analysis of epigenetically sensitive traits (traits influenced by function during life) such as perhaps phalangeal curvature or skeletal robusticity.

Analysis of 'Lucy' together with the rest of the large *A. afarensis* postcranial collection has also suggested to some researchers that there is more than one locomotor repertoire represented (e.g. Senut, 1981a,b; Tardieu, 1981, 1983; Stern & Susman, 1983; Senut & Tardieu, 1985). *A. afarensis* is highly sexually size-dimorphic (Richmond & Jungers, 1995) and certain features of the elbow, and lower limb have been interpreted to indicate that the smaller individuals were more efficient climbers and the

larger individuals more efficient bipeds. This indicated locomotor sexual dimorphism to Stern & Susman (1983) and informed Lovejoy's (1981) hypothesis of monogamy and economic division of labour in *A. afarensis*. Senut & Tardieu (1985), and more recently Deloison (1999), have alternatively interpreted this to indicate two separate species of hominin with two different locomotor repertoires. On the assumption of the importance of postcranial features as phylogenetic indicators, Senut (1996) and Senut et al. (2001) posit a clear and deep dichotomy in hominin locomotion (Aiello & Collard, 2001). The smaller, arboreally inclined members of *A. afarensis* (which she places in *A. antiquus*) comprise one lineage of climbers/bipeds together with *A. africanus* and the later robust australopithecines (*Paranthropus aethiopicus, P. robustus* and *P. boisei*). The second lineage characterized by obligate bipedalism includes the 6 Ma *Orrorin tugenensis* (Senut et al. 2001; Pickford et al. 2002), the larger bipedally inclined members of *A. afarensis* together with *A. anamensis* (both of which are referred to as *Praeanthropus africanus*), as well as *Homo* (*rudolfensis, habilis, ergaster, erectus,* and *sapiens*) (Fig. 3).

At least some of the anatomical evidence to support significantly different locomotor repertoires in the *A. afarensis* collection, no matter how these differences are interpreted, have been shown to fall within the expected range of intraspecific variation in modern humans and/or have no discriminating power (e.g. Asfaw, 1985; Latimer et al. 1987; Holliday & Dugan, 2003). On this basis and with reference to the degree of sexual size dimorphism as well as craniodental and postcranial compatibility, the majority of anthropologists today would seriously question the hypothesis of multiple locomotor repertoires and/or multiple species justified on the basis of different locomotor repertoires represented in the *A. afarensis* collection. Furthermore, analyses of the limited postcranial material currently available for *A. anamensis* suggest that this species had a locomotor repertoire much like that of other members of the genus *Australopithecus* (Lague & Jungers, 1996; Ward et al. 1999).

There is other evidence, however, that might indicate locomotor diversity among the early hominins. Tuttle et al. (1991; in contrast to White & Suwa, 1987) argue that the extraordinary trail of hominin footprints from Laetoli, Tanzania (*c.* 3.7 Ma), could not have been made by *A. afarensis* because of an incompatibly with *A. afarensis* foot morphology. This would imply the existence of a contemporary hominin biped with compatible pedal morphology.
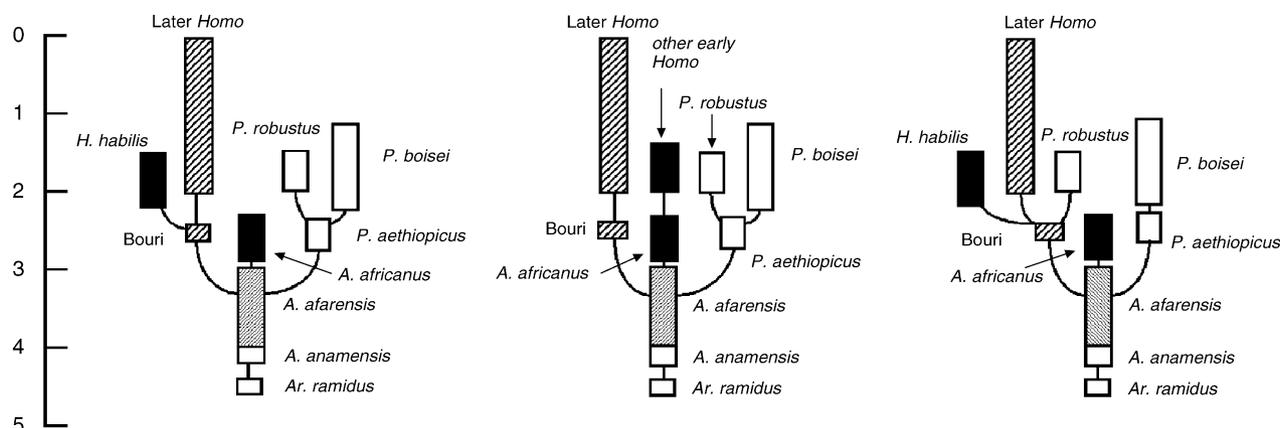
Fig. 4 Three possible scenarios for the evolution of body proportions in the early hominins. These are selected from a large number of possible phylogenies and are presented for illustration only. Note that of the three presented phylogenies only the middle one does not imply homeoplasy. Also, all of these hypothetical scenarios imply that the more ape-like body proportions of *Australopithecus africanus* and *Homo habilis* are dervied in relation to the intermediate proportions of *A. afarensis*. If this ultimately proves to be the case, it would suggest that both *H. habilis* and *A. africanus* were engaged in locomotor behaviours that would have selected for these more ape-like proportions. Black = ape-like humerofemoral proportions, coarse hatching = human-like humerofemoral proportions, fine hatching = intermediate humerofemoral proportions. See text for explanation. Note that these scenarios do not include all known hominin taxa.

Some of the most interesting work on early hominin locomotor diversity centres on the interpretation of hominin body proportions in the few taxa for which we have sufficient evidence (*H. ergaster*, *H. habilis*, *A. africanus*, *A. afarensis* and possibly *A. garhi*) (Hartwig-Scherer & Martin, 1991; Clarke & Tobias, 1995; Berger & Tobias, 1996; McHenry & Berger, 1998a; Asfaw et al. 1999; Richmond et al. 2001). Based on the length of the femur in relation to the length of the humerus (humero-femoral index), the emerging picture is that *H. habilis* has humerofemoral proportions similar to living African apes, *A. afarensis* (represented by AL 288-1 'Lucy') is intermediate between African apes and humans, and *H. ergaster* together with bones that may belong to *A. garhi* (the Bouri Skeleton – BOU-VP 12/1) has human-like humerofemoral proportions (Hartwig-Scherer & Martin, 1991; Asfaw et al. 1999). On the basis of upper and lower limb joint size, *A. africanus* appears to be similar to *H. habilis* and the African apes in its inferred humerofemoral proportions (McHenry & Berger, 1998a,b). A further complication is that in spite of its human-like humerofemoral proportions, the Bouri skeleton has a very long forearm (radius in relation to humerus), reminiscent of a modern orang-utan (Asfaw et al. 1999; Richmond et al. 2001).

Error associated with reconstruction of particularly the *H. habilis* limb lengths render conclusions about humerofemoral proportions less than secure (Korey, 1990; Richmond et al. 2001); however, based on our current assessment of the data there are at least two different postcranial morphologies in roughly contemporaneous hominins at two different periods in the hominin fossil record. *A. africanus* with inferred ape-like intermembral proportions overlaps in time with the Bouri skeleton with inferred human-like intermembral proportions (but orang-utan-like brachial proportions), and *H. habilis* with inferred ape-like intermembral proportions overlaps in time with *H. ergaster* with human-like intermembral proportions (and human-like brachial proportions). *A. afarensis* has intermediate intermembral proportions that differ from those of *H. habilis* to a degree that is almost never seen in humans and is rare in extant great apes (Richmond et al. 2001) and pre-dates these other hominins. This situation implies considerable locomotor diversity that would be difficult to incorporate within a linear evolutionary framework.

Figure 4 indicates three out of a theoretically large number of phylogenetically possible scenarios for the evolution of body proportions in the early hominins. Because of the considerable uncertainy in hominin phylogenetic relationships (e.g. Strait et al. 1997; Asfaw et al. 1999), it is currently impossible to conclude more than that there is growing evidence for postcranial diversity and inferred locomotor diversity in the early hominin fossil record. The situation is even more complicated when the one very fragmentary and

poorly preserved associated skeleton of *P. boisei* is taken into consideration. This skeleton may have more human-like limb proportions than either *H. habilis* or *A. afarensis* and be similar to the Bouri skeleton in this respect (Leakey, 1973; Day et al. 1976; Leakey et al. 1978; Grausz et al. 1988; Ward, 2002).

Evidence from the foot for locomotor diversity

The degree of diversity in the body proportions of the early bipedal hominins implies that there might also be significant differences in their modes of bipedal locomotion. The analysis of hominin fossil foot bones offers a means to test this hypothesis. The *H. habilis* foot (OH 8) has been pivotal to the understanding of hominin pedal diversity.

Day & Napier (1964) argued that whereas the OH 8 foot as a whole belonged to a fully bipedal individual (with strong longitudinal arches and a hallux that could not be opposed), its talus was the least human-like of its tarsals, and may have had a mosaic of ape-like and human-like features. They observed that the talar neck and neck-torsion angles were similar to those of the Kromdraai talus TM 1517 (assigned to *Paranthropus robustus*), that the length and breadth measurements approached those of modern humans, but that the morphology of the trochlear surface was unlike that of modern humans. Metrical analysis by Lisowski (1967) confirmed that the neck and neck-torsion angles of the OH 8 talus were similar to those of Kromdraai, and that the OH 8 talus was significantly different to that of modern humans, being essentially ape-like. Oxnard (1972) re-examined Day & Wood's (1968) multivariate analysis of the data and concluded that the OH 8 talus was equally different to both human and ape tali, but was similar to the talus from Kromdraai (and that of *Proconsul*). The culmination of these and many other studies was that the OH 8 talus is unique in its morphology and function, but is the least human-like of the OH 8 pedal assemblage. However, crucially, using multivariate analyses, Wood (1973, 1974) carried out a broader comparison and noted that the talus KNM-ER 813, from Koobi Fora, Kenya, and of a similar age to OH 8, was far more human-like than OH 8. This implies that there were different hominin ankle morphologies existing at a similar point in time. *H. habilis* and *P. robustus* have a similar talar morphology and KNM-ER 813 (*H. ergaster*?) has a different and more modern morphology.

Much more recently, the discovery of the *A. africanus* pedal assemblage, Stw 573 (or 'Little Foot'), currently referred to *A. africanus*, found in Member 2 at Sterkfontein, South Africa (Clarke & Tobias, 1995), has brought foot bones back into the debate on the origins of bipedalism. The preliminary study accompanying the original description suggests, mainly from visual appraisal, that the Stw 573 foot was mosaic in its affinities, having an essentially human-like talus, a mosaic navicular and an 'intermediate' hallux capable of a significant degree of grasping (Clarke & Tobias, 1995). Importantly, Clarke & Tobias (1995) argue that the foot of *A. africanus* is different to that of *H. habilis*, in that *A. africanus* still had an opposable hallux and a mobile mid-tarsal joint. However, if they are right, because the consensus view is that the younger OH 8 (and by inference *P. robustus*) has a more ape-like talus, and the talus of *A. africanus* is more human-like, short of reversals, it is likely that *A. africanus* and *H. habilis*, with different combinations of foot morphologies (but with similar body proportions), represent different types of bipedalism likely to have arisen from different lineages.

The issue is further complicated by the *A. afarensis* foot bones from Hadar, Ethiopia. These are contemporary in age to the Stw 573 foot bones (Walter, 1994; Partridge et al. 1999), and yet show a number of differences in morphology. The consensus view of *A. afarensis* is that it has a very human-like talus, with a flat trochlea with lateral and medial margins that are of a similar elevation to each other (which allows the leg to pass over the foot in an efficient, human-like way; Latimer et al. 1987). Clarke & Tobias (1995) describe the Stw 573 talus as being human-like, and so this would make the *A. afarensis* and *A. africanus* tali essentially similar in morphology and inferred function. However, the *A. afarensis* foot is also described as having the derived human-like traits of an unopposable hallux (Latimer & Lovejoy, 1990a) and strong longitudinal arches (Latimer & Lovejoy, 1989). Clarke & Tobias (1995) clearly stated that Stw 573 had retained an ability at least partially to oppose the hallux (Fig. 2). Such a finding highlights that contemporary *A. africanus* and *A. afarensis* pedal assemblages were mosaic in distinctly different ways.

Some studies provide alternative interpretations for these remains. *A. afarensis* may have retained a degree of hallux opposability, strong great-toe flexion and therefore gripping (Tuttle, 1981; Deloison, 1991), a more ape-like navicular (Sarmiento, 2000), a mobile talonavicular

joint (Gomberg & Latimer, 1984), an ape-like talo-crural joint (Susman, 1983), an absent lateral plantar tubercle on the calcaneus (Deloison, 1985; Lewis, 1989), a lack of longitudinal arches (Berillon, 1998; Harcourt-Smith, 2002) and curved phalanges more capable of ape-like plantar flexion (Stern & Susman, 1983; Susman, 1983; Duncan et al. 1994). Perhaps the most striking aspect of the *A. afarensis* foot is one that has been strangely neglected: the morphology of the navicular tuberosity, which is, relative to modern humans, extremely large and prominent proximo-distally (Sarmiento, 2000; Harcourt-Smith, 2002). A prominent navicular tuberosity has been shown to be indicative of an increased degree of weight-bearing on the medial side of the foot, and would thus be indicative of the absense of a medial longitudinal arch (Elftman & Manter, 1935; Sarmiento, 2000). Harcourt-Smith (2002) has shown that *Gorilla* has a relatively enlarged tuberosity compared with *Pan* and *Pongo*. This is supported by the fact that *Gorilla* is known to be considerably more terrestrial than either *Pan* or *Pongo* (Tuttle, 1968) and also to transfer considerable force through the navicular into the ground throughout the stance phase (Elftman & Manter, 1935; Morton, 1935). Based on these findings, it is likely that the *A. afarensis* foot lacked a human-like medial longitudinal arch, and therefore could not transfer weight as efficiently through the foot during the stance phase. In this respect, this assertion strongly supports the findings of several other recent studies that reached similar conclusions (Berillon, 1998, 2000; Sarmiento, 2000).

Recent multivariate analyses of the Stw 573 tarsal bones (medial cuneiform, navicular and talus) using geometric morphometric techniques demonstrate that this fossil had a very ape-like talus, a navicular that was intermediate between apes and modern humans, and a human-like medial cuneiform inferring a lack of any hallux opposability (Harcourt-Smith, 2002). This finding contrasts with the findings of Clarke & Tobias (1995), but is does not change the fact that Stw 573 would still have a different combination of morphologies in the foot than does *A. afarensis*. This scenario would, conversely, give the Stw 573 foot a similar type of mosaicism to the OH 8 foot, and single out the *A. afarensis* as being different. Interestingly, although the OH 8 foot is over 1.4 million years younger than the Hadar remains, a combination of consensus views shows that OH 8 still had a more ape-like talus than *A. afarensis*. Again, short of a reversal, this would imply, within the foot at least, two distinct paths of adaptation to the requirements of bipedalism (Fig. 5).
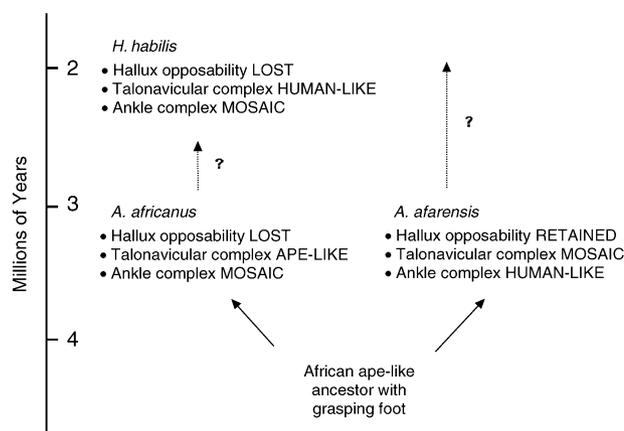

Fig. 5 One possible scenario for the evolution of the hominin foot. Note that this scenario posits that *Homo habilis* is more similar in its foot morphology to *Australopithecus africanus* than it is to *A. afarensis*. The only difference between the *A. africanus* foot and the *H. habilis* foot is that the talonavicular complex has changed from an ape-like morphology to a human-like morphology (Harcourt-Smith, 2002). This pattern is reminiscent of the similarity in the humerofemoral proportions in these hominins.

In summary, there are a number of different scenarios for the evolution of the hominin foot, and these largely depend on which interpretations one prefers. However, what emerges is that the overall picture is highly complex, and implies that different taxa living in different parts of Africa, but at a similar point in time, were most likely to have had feet that represent a mosaic of human-like and ape-like morphologies, but that these mosaics were different to each other, implying qualitatively different modes of bipedalism. Depending on the interpretation, this most probably suggests a spectrum of hominin bipedal adaptation from species incorporating a greater or lesser degree of arboreal climbing behaviour with terrestrial bipedalism, to full obligate bipedalism.

Conclusions

Recent discoveries of taxa such as *Kenyanthropus platyops*, *Sahelanthropus tchadensis*, *Orrorin tugenensis* and *Ardipithecus ramidus kadabba* suggest a far wider degree of taxonomic diversity in the African fossil hominin record than had previously been thought (Fig. 1) (Haile-Selassie, 2001; Leakey et al. 2001; Senut et al. 2001; Brunet et al. 2002; Wood, 2002). At present, craniodental remains almost exclusively support the evidence for this diversity. Based on this inferred diversity and supported by the existing evidence for postcranial diversity, it is not unreasonable to assume that there was also a

considerable degree of locomotor diversity in the early hominins. As has been shown, the prevailing view in the earlier literature on the evolution of bipedalism has been a particularly linear one, with the usual pattern being a neat series of steps from arboreal quadruped to obligate biped. As more fossil evidence accumulated, some researchers entertained the possibility of locomotor diversity in contemporary early hominins (e.g. Napier, 1964), but this view was far from prevalent. Furthermore, many of the more recent studies, informed by the growing collection of hominin postcranial fossils, have focused on the degree to which particular skeletal elements imply one type of locomotion or another.

The central point is that contemporary fossil taxa may well have been mosaic in their adaptations, but, critically, may have been mosaic in different ways to each other. This has recently been shown to be the case for the feet of *A. afarensis* and the new and similarly aged *A. africanus* specimen 'Little Foot' (Harcourt-Smith, 2002). Further analyses of other skeletal elements are needed to reinforce this interpretation. If correct, this would imply that there was more locomotor diversity in the fossil record than has been suggested, and raises questions over whether there was a single origin for bipedalism or not. At the very least, if bipedalism appeared only once in the hominin radiation and is therefore monophyletic, such evidence would suggest that there were multiple evolutionary pathways responding to that selection pressure. It is currently difficult to determine primitive from derived morphologies in the hominins because of the problem of homoplasy and resulting phylogenetic uncertainty. Although perhaps controversial, it is important that when considering such a unique adaptation as bipedalism, we do not allow that uniqueness to imply that there was ever only one successful mode of bipedalism in our hominin ancestry. In light of the richness of recent findings in the hominin fossil record, it is important to ask the question of whether the evolution of bipedalism was a more complex affair than has previously been suggested.

Acknowledgements

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