5 The Origins of Bipedal Locomotion

William E. H. Harcourt-Smith

Abstract

Bipedalism is a highly specialized and unusual form of primate locomotion that is found today only in modern humans. The majority of extinct taxa within the Hominini were bipedal, but the degree to which they were bipedal remains the subject of considerable debate. The significant discoveries of fossil hominin remains in the last 40 years have resulted in this debate becoming increasingly focused on *how* bipedal certain fossil taxa were rather than on the overall process. Although the early hominin fossil record remains poor, evidence points to at least two distinct adaptive shifts. First, there was a shift to habitual bipedalism, as typified by certain members of *Australopithecus*. Such taxa were bipedal, but also retained a number of significant adaptations to arboreal climbing. The second shift was to fully obligate bipedalism, and coincides with the emergence of the genus *Homo*. By the Early Pleistocene, certain members of *Homo* had acquired a postcranial skeleton indicating fully humanlike striding bipedalism. The final part of this chapter reviews why bipedalism was selected for. There have been many theoretical explanations, and the most robust remain those linked to the emergence of more open habitats. Such an environmental shift would have involved strong selection for new behavioral strategies most likely linked to the efficient procurement of food.

5.1   Introduction

Bipedal locomotion sets modern humans apart from all other living primates. We are the only obligate bipeds among well over 200 extant primate species. It therefore stands to reason that this unusual and highly derived form of locomotion has attracted much attention by those who study human evolution. Current evidence points to anatomical traits strongly associated with bipedalism relatively deep in the hominin lineage (Ward et al. 2001) and well before the advent of other "traditional" human traits such as larger brains and tool use. This chapter reviews the current state of thinking on this unique form of primate locomotion.

In order to understand the origins of hominin bipedalism, one first has to understand the mechanisms that make it such an efficient form of locomotion in modern humans. In the first section of this chapter, I will briefly explore the nature of the modern human walking cycle and the associated anatomical traits that facilitate it. I will then explore the fossil evidence for the origins of bipedalism and speculate on the likely locomotor behaviors that preceded it. Finally, I will discuss some of the theories surrounding why bipedal locomotion was selected for.

5.2 Locomotor differences between modern humans and great apes

Modern humans are fully obligate bipeds. After the first few years of life, it is the sole form of locomotion in all healthy individuals. By comparison, the great apes do not have any one form of specialized locomotion. *Pongo* is almost exclusively arboreal, but its locomotor behavior is taken up by clambering, vertical climbing, brachiation, terrestrial fist-walking, arboreal quadrupedalism, and even some above-branch assisted bipedalism. Orangutans are particularly well known to have a predilection for suspensory postures (Tuttle 1968). Clambering, which accounts for over 50% of observed locomotor behavior, mainly consists of forelimb suspension and hindlimb support and suspension (Tuttle 1968; Cant 1987). In this respect *Pongo* can be considered to be an arboreal specialist.

The most important aspect of the African apes is that, unlike *Pongo* and modern humans, their specialization lies not in their tendency to be *either* arboreal or terrestrial specialists but rather on having a mosaic of different locomotor modes that suit different environments and situations. Field observations have shown that all three taxa of African ape spend considerable time in both the trees and on the ground. The principal form of terrestrial locomotion is fast and slow knuckle-walking, where the legs do most of the propulsive work, and a significant degree of body weight is borne by the upper limbs through the knuckles (Tuttle 1970). African apes spend a small degree of time walking bipedally, but only for relatively short periods (Tuttle 1970; Hunt 1994). *Pan* also spends a proportion of its time standing bipedally, mainly to collect fruit in tall bushes, but it is important to note that even when doing so individuals are partially supporting themselves with their upper limbs, which are grasping onto branches (Hunt 1994; Doran and Hunt 1995). When in the trees, *Pan troglodytes* has a particular predilection for using knuckle-walking to move along large branches (Tuttle 1970).

5.2.1   The walking cycle

The modern human walking cycle is characterized by two distinct phases: the *stance phase*, when the leg is on the ground, and the *swing phase*, when it is off the ground. The stance phase begins with *heel-strike*, as the foot strikes the ground. The knee is fully extended and the foot dorsiflexed, which results in the heel striking the ground well before the rest of the foot. The foot then plantar flexes, and typically force is transmitted through to the substrate along its lateral border. The point when the body is directly over the weight-bearing foot is known as the *midstance phase*. The body then carries its forward momentum over the leg, at which point force moves medially over to the ball of the foot. At this point, strong muscular contraction of the plantar-flexors results in the ball of the foot pushing against the ground and eventually lifting away from it as the body continues to move forward. This action finishes with a final push-off of the big toe, known as *toe-off*. The leg is now off the ground and in the swing phase, with the knee and hip both bent so as to keep the leg off the ground as it swings forward to make the next heel-strike.

   When chimpanzees walk bipedally there are considerable differences. The knees and hips remain bent throughout the stance phase, and the foot is less dorsiflexed at heel-strike. This results in a gait that is an awkward "shuffling" movement, with marked mediolateral swaying of the body from step to step, which is often referred to as a "bent-knee, bent-hip" (BKBH) gait. Heel-strike itself is at best weak and is often almost immediately followed by much of the rest of the foot making contact with the ground. There is little in the way of the lateral-to-medial shift in force transmission to the substrate during the late stance phase, and often three or more toes leave the ground at the same time (Elftman and Manter 1935).

5.2.2   Associated anatomical differences between humans and great apes

A large number of anatomical features are functionally related to bipedal loco-motion, and it is the combination of these traits that allows this to be the sole form of locomotion in modern humans. Naturally, it is sometimes hard to determine which traits specifically *facilitate* bipedal locomotion and which are instead a *result* of it, but in terms of determining the locomotor affinities of fossil remains it is fair to assume that, either way, many of these traits certainly *indicate* bipedal locomotion to a lesser or greater degree. ❯ *Table 5.1* summarizes the major anatomical features associated with human bipedal locomotion, but a

◘ Table 5.1

Some of the important anatomical features specifically related to bipedal locomotion in modern humans

Trait	*Homo sapiens*	African apes	Functional significance in *H. sapiens*
Foramen magnum orientation	Perpendicular to orbital plane	More vertically inclined	Related to vertical positioning of spine
Shape of spine	S curve with lumbar lordosis	C curve with no lumbar lordosis	More efficient balance and support of upright trunk
Intermembral index	Low (~72)	High (103–115)	Longer stride lengths
Size of vertebral bodies	Larger, especially L1-5	Smaller	Increased load of vertical trunk
Shape of iliac blades	Short, wide, and curved	Long, narrow, and flat	Support for vertical trunk
Orientation of iliac blades	Mediolaterally	Anteroposteriorly	Support for vertical trunk
Relative distance from hip to sacroiliac joints	Small	Large	More efficient transfer of weight from spine to hip
Size of acetabulum	Large	Small	Increase in weight-transfer through hip joint
Anterior inferior iliac spine	Present	Absent/Weak	Attachment site for strong iliofemoral ligament—helps maintain balance by preventing thigh from hyperextending
Femoral head size	Large	Small	Increase in weight-transfer through hip joint
Cortical bone distribution in femoral neck	Thicker inferiorly	Even all around	Increase in weight-transfer through hip joint
Bicondylar angle of femur	Valgus	Absent/Varus	Placement of lower leg closer to midline of body
Relative lengths of articular surfaces of femoral condyles	Medial condyle longer	Similar in length	Aids medial rotation of femur and locking of knee joint at heel-strike
Inclination of talar facet on distal tibia	Perpendicular to long axis of tibia	More laterally inclined	Allows perpendicular passage of leg over foot
Plantar tuberosity on calcaneus	Two	One	Facilitates stable heel-strike
Longitudinal arches in foot	Two present—one medial and one lateral	Absent	Acts as "shock absorber" and maintains structural rigidity in foot throughout stance phase
Hallux opposability	Absent	Present	Facilitation of efficient toe-off and loss of arboreal grasp
Relative tarsus length	Long	Short	Increases power arm length in foot—leads to more efficient leverage in foot
Relative lengths of rays II–V	Short	Long	Decreases level arm length in foot—leads to more efficient leverage in foot
Metatarsal robusticity pattern	1 > 5 > 4 > 3 > 2	1 > 3 > 2 > 4 > 5	Reflects increased transfer of weight along lateral edge of foot
Phalangeal curvature	Flat	Curved	Loss of arboreal grasp

Some descriptions adapted from Aiello and Dean (1990).

number of them warrant further discussion. In some cases, where particular traits relate to particular fossil specimens, there is further discussion in ❯ Section 5.3.

Some of the most radical morphological adaptations in the human skeleton that relate to bipedalism are found within the pelvis and lower limb. Compared to apes, the entire lower-limb complex in humans has become highly remodeled to cope with the intricate dynamics of balancing an upright trunk while efficiently moving the body forward. Balance is a particularly important factor as, at any point during the walking cycle, only one limb is actually in contact with the ground, and has to bear the entire weight of the body and balance it accordingly. The minimizing of mediolateral swaying of the body during walking is therefore critical, as it acts to stabilize the body over the supporting leg and reduce energy expenditure. Consequently, many of the traits associated with bipedal locomotion relate to two major factors: balancing the body as a whole, and keeping the downward transmission of force as close to the midline of the body as possible.

In modern humans, the foramen magnum is anteriorly situated and horizontally orientated (i.e., perpendicular to the orbital plane). This is a reflection of the vertical positioning of the spine. The spine itself has a distinct "S" shape, caused by marked lordosis in the lumbar region, which helps to bring the center of the trunk's mass anteriorly (Fleagle 1999). The lower limb is considerably longer in modern humans than in great apes. *H. sapiens* has a low intermembral index (~72), whereas for *Pan* (103–106), *Gorilla* (~115), and *Pongo* (~139), it is far higher, reflecting their relatively shorter lower limbs and longer upper limbs. The longer lower limb in humans directly facilitates a longer stride length. The modern human pelvis is very different in shape to that of all other primates, including the great apes. The iliac blades are short and wide, the ischium extends posteriorly, and the sacrum is relatively wide. These features greatly facilitate support of the upright trunk, place the trunk's center of gravity closer to the hip joint, and allow the lesser gluteal muscles to be positioned at the side of the pelvis (Napier 1967; Aiello and Dean 1990). This last feature is important, as contraction of these muscles during walking tilts the trunk toward the leg in contact with the ground, providing greater stability and balance. Humans also have a large acetabulum to accommodate a large femoral head, reflecting the relative increase in body weight passing through the hip during locomotion. The modern human femur has a valgus bicondylar angle, resulting in the knee being situated far closer to the midline of the body than the femoral head is. This greatly reduces the lateral deviation of body weight during walking, and it is argued by many to be an important feature related to habitual bipedal locomotion. However, modern humans who are unable to walk from birth do not develop a valgus bicondylar angle (Tardieu and Trinkaus 1994), and so this trait is best considered as epigenetic, even though its presence indicates habitual bipedal behavior.

The human knee has the unique ability to lock when in full extension, which greatly facilitates upright walking by keeping the leg straight and enabling the efficient downward passage of the body's weight through to the ankle. This locking action is facilitated in humans by a relatively longer medial femoral condyle and different attachment sites of the femoral posterior cruciate ligament (Aiello and Dean 1990). The distal tibia has a particularly important feature linked to bipedal locomotion worth noting. The talar articular surface is orientated perpendicular to the long axis of the bone, resulting in a less arcuate passage of the leg over the foot (Latimer et al. 1987). This allows more efficient weight-transfer through to the foot. The modern human foot is particularly specialized for the requirements of bipedal locomotion. The African ape foot can be considered a grasping organ with some terrestrial adaptations, whereas that of humans is essentially a propulsive platform. Modern humans are the only living primates to have lost the ability to oppose the hallux, which is in line with the remaining toes. Human toes are relatively short and straight, and the tarsus relatively long, with an elongated calcaneal tuberosity. This allows for a more efficient lever-arm to power-arm ratio, which facilitates efficient propulsion during the stance phase. A combination of bony architecture and strong plantar ligaments results in the human foot being arched longitudinally on both the medial and lateral sides. By comparison, the ape foot is weight-bearing through the midfoot, and this is reflected in the enlarged medial tuberosity on the navicular. This longitudinal arching combined with the unique locking morphology of the calcaneo-cuboid joint allows the human foot to not only act as an efficient shock absorber, but also stay rigid during weight-transfer to the ground.

5.3   Fossil evidence

The precise number and nature of the derived traits characterizing stem hominins are difficult to determine and likely to remain so. It has recently been pointed out that, in its entirety, bipedality requires a combination of many complex anatomical traits and so cannot necessarily be classed as a dichotomous character (Haile-Selassie et al. 2004). However, it is reasonable to assume that strong evidence of bipedal locomotion is the key in determining whether fossil material warrants inclusion within the hominin clade. Perhaps the best way to consider such evidence is to ask whether fossil hominin material indicates *habitual* or *obligate* bipedalism, rather than merely the *occasional* bipedalism, which we see in most extant species of great apes (Rose 1991). In that context, it is clear evidence of a shift from occasional to habitual bipedalism, which is important when considering early hominin remains, and habitual to obligate bipedalism

when considering relatively later hominin remains. Thus, when considering the hominin fossil record, this chapter will consider *occasional* bipeds to be those animals with a bipedal component of their locomotor repertoire similar to that of modern-day chimpanzees. By contrast, *habitual* bipeds are those taxa that had a significantly increased bipedal component but were by no means exclusively bipedal and would have retained an arboreal component to their locomotor repertoire. *Obligate* bipeds are considered as taxa that were exclusively bipedal and had lost all other forms of terrestrial and arboreal locomotor behaviors.

5.3.1 Precursors of bipedalism

There is a significant literature about the likely locomotor mode that directly preceded hominin bipedalism (see reviews by Richmond et al. 2001; Harcourt-Smith and Aiello 2004). In the absence of fossil evidence, early models relied heavily on observed extant primate locomotor behaviors and phylogenetic hypotheses. Arguably, the prevailing view was that a brachiating, hylobatid-like ancestor evolved into a larger-bodied African apelike ancestor capable of orthograde climbing and terrestrial knuckle-walking, which in turn evolved into a bipedal hominin (Keith 1903, 1923; Gregory 1916, 1928; Morton 1924, 1935). Minor variants of these models existed among authors, with Morton (1924, 1935) arguing for a more terrestrial "gorilloid" prehuman locomotor mode, while Gregory (1916, 1927) and Keith (1903, 1923) favored a more "troglodytian" hominin precursor. Others argued for a very deep tarsoid ancestry for humans and bipedalism (Wood Jones 1916, 1929) or for an arboreal quadruped ancestry of monkeylike above-branch locomotion (Straus 1949).

Despite the elegance of some of these early models, the central factor in understanding the evolution of bipedalism lies in the reconstruction of Late Miocene large hominoid locomotor behaviors. The advent of fossil evidence and molecular dating methods has effectively precluded some of these early theories from consideration. Based on molecular data, the last common ancestor of modern humans and chimpanzees is likely to have lived between 5 and 7 Ma (Gagneux and Varki 2000; Page and Goodman 2001), and most Miocene hominoid remains do not show a strong adaptation to brachiation (Napier and Davis 1959; Avis 1962; Rose 1991; Moyà-Solà and Köhler 1996), although the hylobatian model is still argued by some (Tuttle 1974, 1975, 1981). A number of alternatives have replaced these earlier theories in the recent literature. Perhaps the best-known recent theory is a suggested knuckle-walking ancestry for hominins (Washburn 1967; Richmond and Strait 2000; Richmond et al. 2001), which draws heavily on the specialized knuckle-walking behavior of chimpanzees and

gorillas as a model, and argues for a retention of traits associated with knuckle-walking in the wrists of *A. afarensis* and *A. anamensis* (Richmond and Strait 2000). However, this theory is disputed (Tuttle and Basmajian 1974; Dainton 1991; Lovejoy et al. 2001), and although certain Middle Miocene hominoid remains show an increased capacity for terrestriality, no large fossil hominoid taxa from the Middle or Late Miocene show adaptations for knuckle-walking behavior (Stringer and Andrews 2005). Alternative contemporary theories include those suggesting an arboreal climbing ancestor (either large-bodied or small-bodied) (Tuttle and Basmajian 1974; Stern 1975; Tuttle 1975, 1981; Prost 1980; Fleagle et al. 1981; Hunt 1996), a terrestrial quadruped ancestor (Gebo 1992, 1996; Sarmiento 1994, 1998), a *Pongo*-like pronograde-clambering ancestor (Crompton et al. 2003; Thorpe and Crompton 2005), and even an ancestor that practiced a type of terrestrial "tripedalism" with one limb always free to carry objects (Kelly 2001).

A universal theme that links both the older and the more recent hypotheses is the choice of a single specific locomotor mode as the dominant "precursor" to hominin bipedalism. As Rose (1991) points out, apart from humans, most primates usually use several different types of locomotor activity as part of their daily locomotor repertoire. Within the hominoid clade, *Pongo* and particularly *Hylobates* are traditionally considered rather derived and specialized in their locomotor behavior, while *Pan* and *Gorilla* are considered more generalized. However, the great specialization of *Pan* and *Gorilla* in fact lies in their particularly mosaic and versatile locomotor repertoire, especially in the case of the smaller-bodied *Pan*. Both genera regularly engage in terrestrial knuckle-walking, occasional bipedalism, vertical climbing, and orthograde clambering as part of their daily activities. It is quite possible that some of these behaviors, for instance knuckle-walking, may have been independently acquired in *Pan* and *Gorilla* (Begun 2004). Their locomotor behavior and associated anatomy, however, combined with our current knowledge of the Late Miocene fossil record, suggests that the immediate precursors to the very first hominins are likely to have been rather generalized hominoids (McHenry 2002) capable of a suite of different locomotor behaviors. In that context, it is perhaps rather limited to single out one particular locomotor mode as the likely "precursor" to habitual hominin bipedalism.

5.3.2 Evidence for habitual bipedalism outside the hominin clade

Although there is little current evidence to suggest that fossil hominoid taxa existing prior to the Hominini—Panini split had any significant degree of

bipedalism in their locomotor repertoire, the possible locomotor affinities of one specific taxon are worth noting. There has been the suggestion that the Late Miocene European hominoid *Oreopithecus bambolii* was partially bipedal (Köhler and Moyà-Solà 1997; Rook et al. 1999). However, that assertion remains highly controversial. Although the iliac blades of *Oreopithecus* are reduced in length, it also has a suite of postcranial features that indicate adaptations to vertical climbing and forelimb suspension, including longer forelimbs than hindlimbs, a flexible shoulder joint, and a strong grasping foot (Harrison 1987, 1991).

5.3.3   Earliest hominin evidence

The earliest fossil evidence for potential hominin bipedalism comes from recently discovered Late Miocene cranial remains from Chad, dated to almost 7 Ma and assigned to the species *Sahelanthropus tchadensis* (Brunet et al. 2002). Virtual reconstruction of the distorted TM266 cranium is argued to show a foramen magnum that is more anteriorly positioned than in *Pan* and *Gorilla* and, more importantly, orientated almost perpendicular to the orbital plane (Zollikofer et al. 2005). This is a trait shared by modern humans and australopiths and indicates a more vertically orientated spinal column that is associated with bipedal locomotion. Currently, there are no known postcranial remains of *S. tchadensis*, precluding any further speculation on its locomotor behavior.

The femoral remains from the Lukeino formation in Kenya ascribed to a new putative hominin taxon *Orrorin tugenensis* (Senut et al. 2001) are also argued to indicate bipedal behavior. The material is dated to between 5.7 and 6 Ma (Pickford and Senut 2001; Sawada et al. 2002), and it is reported that there are anatomical features (specifically on the BAR 1002′00 proximal femur) that indicate habitual bipedal locomotion. The cortical bone of the inferior section of the femoral neck is argued to be relatively thick, and there is an "intertrochanteric groove" for the tendon of the obturator externus muscle on the posterior surface (Pickford et al. 2002; Galik et al. 2004). Thick cortical bone on the inferior section of the femoral neck is argued by some to imply habitual bipedalism (Pauwels 1980; Lovejoy 1988; Ohman et al. 1997), but others have noted that similar patterns of cortical distribution are found in many other primate species and that only apes and atelines differ in having relatively even distribution around the whole neck (Stern and Susman 1991; Rafferty 1998; Stern 2000). There is also debate as to whether the presence of the *m. obturator externus* tendon groove is reliable for inferring bipedalism. This feature, originally described by Day (1969), is argued to imply regular full extension of the thigh during bipedal locomotion

(Day 1969; Robinson 1972; Lovejoy 1978). Others argue that it is not a diagnostic trait of habitual bipedalism (Stern and Susman 1991) and that it can even be found in quadrupedal cercopithecoids (Bacon 1997). Most recently Lovejoy et al. (2002) claim that while the trait is completely absent in large samples of *Pan* and *Gorilla* and present in australopiths and 60% of modern humans, it does not specifically imply bipedality but merely habitual extension of the femur. Finally, described upper limb morphology of *O. tugenensis* includes a curved proximal manual phalanx and a humeral shaft with a straight lateral crest for *m. brachioradialis* (Senut et al. 2001), both seen as adaptations for arboreal locomotor behavior (Senut 1981a, b, 1989; Stern and Susman 1983, 1991).

The only other hominin remains from the Late Miocene/Early Pliocene that possibly indicate bipedalism belong to the genus *Ardipithecus* from the Middle Awash, Ethiopia (White et al. 1995). The 4.4-Ma *Ardipithecus ramidus* was originally reported to have an anteriorly positioned foramen magnum (White et al. 1994), a trait that may indicate bipedal locomotor behavior (Lovejoy 1981). Older remains (5.6–5.8 Ma) recently ascribed to *Ardipithecus kadabba* include one proximal fourth pedal phalanx that is described as having strong plantar curvature, but also a dorsally inclined proximal articular surface similar to that of *A. afarensis* (Haile-Selassie et al. 2004). This latter trait is argued to show that *A. afarensis* could dorsiflex its foot in a similar way to modern humans (Latimer and Lovejoy 1990b). However, it has also been argued that this feature in *A. afarensis* is in fact intermediate between modern humans and great apes (Duncan et al. 1994).

In summary, the extremely meagre and fragmentary fossil record for early hominins precludes any serious speculation on how bipedal these taxa were. The horizontal orientation of the *Sahelanthropus tchadensis* foramen magnum certainly indicates that this taxon was likely to have spent more time engaging in bipedal behaviors than either *Pan* or *Gorilla* do, but only the discovery of postcranial remains will further strengthen this argument. A combination of independent study and further postcranial finds are also needed to determine whether *O. tugenensis* was anything more than an occasional biped. However, further postcranial remains of *Ardipithecus* are currently under description (White 2002) and are likely to provide much needed insight into the locomotor repertoire of these early hominins.

5.3.4 The first habitual bipeds

Perhaps the first concrete evidence for habitual bipedalism comes with the earliest *Australopithecus* remains from the Kanapoi and Allia Bay localities at Lake

Turkana, Kenya. Assigned to *A. anamensis*, the remains include a large and well-preserved distal and proximal tibia of one individual, and are dated to between 3.9 and 4.2 Ma (Leakey et al. 1995, 1998). Crucially, the distal end of the tibia has a horizontal talar surface relative to the long axis of the shaft, implying that the *A. anamensis* knee would have passed directly over the foot, as in later hominins and modern humans (Ward et al. 1999, 2001). In *Pan and Gorilla*, the talar surface is sharply inclined, which results in the knee passing over the foot more laterally during plantigrade locomotion (Latimer et al. 1987).

Following the *A. anamensis* remains, the record becomes far richer and starts with what is arguably one of the best-known and strongest lines of evidence: the Laetoli footprint trail. Laetoli, Tanzania, is the type locality for *A. afarensis* (see below) and has produced a number of hominin fossils assigned to this taxon. However, it is perhaps best known for its extraordinary series of preserved animal tracks, first discovered in 1976. Excavation through 1977 to 1979 revealed at least two (and probably three) trails of unmistakably bipedal hominin footprints preserved in a volcanic ash-fall layer that had become wet from rainfall (Leakey and Hay 1979; Leakey and Harris 1987; White and Suwa 1987). The footprints are dated between 3.5 and 3.7 Ma (Hay and Leakey 1982; Drake and Curtis 1987). The most distinctly hominid tracks are those from Site G, where there are two trails (and a possible third overprinted on the larger G-2 tracks). There is also a putative hominin track at Site A, although that has been argued by Tuttle et al. (1991) to have possibly belonged to an ursid.

Most researchers agree that the G-1 and G-2 series of tracks are very human-like, with no evidence of any type of forelimb support. The best-preserved prints show a strong heel-strike and toe-off and indicate a transmission of body weight through the stance-phase of walking similar to that of modern humans. In accordance with this, there is evidence of longitudinal arching, and the hallux is in line with the remaining toes (Day and Wickens 1980; Robbins 1987; Tuttle 1987; White and Suwa 1987). Stern and Susman (1983) argue that the footprints show a "transitional" morphology between apes and modern humans, but the prevailing view remains that they are very human-like. Most recently, Schmid (2004) has argued that although the prints were made by habitual bipeds, there is some evidence of increased rotational movement of the upper body reflecting a more ape-like morphology of the trunk. Schmid argues that this implies an ambling gait-pattern inconsistent with the ability to run.

There is much more debate over the taxonomic assignation of these trails. Most researchers accept that *A. afarensis* is likely to have made them, given that the type specimens for that taxon come from Laetoli and are roughly contemporary with the footprints. However, most noticeably, Tuttle and colleagues (1981, 1987, 1990, 1991) have argued that the prints are so human-like that they are

incompatible with the known *A. afarensis* remains from Hadar, which have long and curved pedal phalanges. They argue that another, as yet undiscovered, hominin must have made the tracks. This would have had feet far more human-like than the Hadar *A. afarensis* specimens. White and Suwa (1987) addressed this issue with a large study in which they reconstructed a hypothetical *A. afarensis* foot using an amalgam of Hadar bones and the *Homo habilis* foot complex from Olduvai, OH 8. They argued that this reconstruction perfectly matched the Site G footprints. However, at 1.76 Ma, OH 8 is almost 2 Myr younger than the Laetoli trails, and has a very different combination of morphologies to the Hadar remains (Napier and Davis 1964; Kidd et al. 1996; Harcourt-Smith 2002), and recent research has shown that the Hadar *A. afarensis* are unlikely to have had longitudinal arching in the foot, as seen in the Laetoli prints (Berillon 2000, 2003; Harcourt-Smith 2002; Harcourt-Smith and Hilton 2005). There are also a number of Hadar tarsal remains, including calcanei, two naviculars, and two tali that would be well suited to making a reconstruction of the *A. afarensis* foot based on the Hadar remains alone. Despite all this debate, what is certain is that the footprints provide an excellent temporal benchmark in terms of the origins of bipedalism. They mark a distinct behavioral event in time, which fossils can never do. In that context we can be sure that at least one line of hominins was practicing habitual bipedalism by at least 3.6 Ma, which implies that the shift from occasional to habitual bipedalism occurred some time before that, and probably well before 4 Ma.

5.3.4.1 Locomotion in *A. afarensis* and *A. africanus*

There has probably been more debate over the locomotor affinities of these members of the genus *Australopithecus* than over any other taxa. This is partially due to the fact that there is a relatively rich postcranial record for this genus. However, the main reason is that these remains show intriguing combinations of primitive and derived traits relating to both terrestrial and arboreal locomotor behaviors. Historically, the South African *A. africanus* remains provided the major focus of work through to the early 1970s, perhaps culminating in Robinson's seminal treatise *Early Hominid Posture and Locomotion* in 1972. Between the 1970s and the 1990s, the discovery in Ethiopia of extensive postcranial remains assigned to *A. afarensis*, including the famous "Lucy" skeleton, has shifted the debate to East Africa, and back as far as 3.4 Ma. The *A. afarensis* remains are considerably older than those of *A. africanus* and along with Laetoli confirm that bipedal locomotion was likely to have been selected for well before brain expansion and tool-making behavior. In this section, I will review the morphology and associated locomotor behavior of *A. afarensis* and *A. africanus*, in turn.

A. afarensis   This taxon provides the first direct anatomical evidence of a true shift from occasional to habitual bipedalism. However, there has been considerable debate over the precise locomotor affinities of *A. afarensis*, most of which have fallen into two distinct camps. Some researchers argue that *A. afarensis* was almost as proficient a biped as modern humans (Latimer 1991; Lovejoy et al. 2002; Ward 2002). Others argue that in fact this taxon had a significant number of primitive postcranial traits that must have implied an important arboreal component to the locomotor repertoire (Susman et al. 1984; Stern 2000). Both these views are rather polarized, and it is best to consider *A. afarensis* as highly mosaic in its adaptations (see McHenry 1991, for a comprehensive review of primitive and derived traits in the Hadar hominins).

The first specimen of *A. afarensis* to be discovered showing evidence for bipedality was the AL 129 knee, discovered at Hadar, Ethiopia, and consisting of a well-preserved distal femur and associated proximal tibia (Taieb et al. 1974). Crucially, the morphology of the distal femur indicated a bicondylar angle even higher than that of modern humans (Johanson et al. 1976). This implied that the leg of *A. afarensis* would have fallen close to the midline of the body as in humans, which is an important adaptation to bipedal locomotion. Subsequent discoveries at Hadar, including the AL 288 partial skeleton (Lucy) and the extensive AL 333 assemblage, provided further evidence of a strong selection for bipedality. The AL 288 skeleton, approximately 40% complete, included a well-preserved pelvis, ribs, vertebrae, and representative pieces of all major limb elements. In overall morphology, the pelvis of Lucy is far more similar to that of modern humans. The iliac blades are short and wide, which would have allowed the lesser gluteal muscles to be situated laterally and act as pelvic abductors. The wide sacrum situated behind the hip joint would also have kept the center of mass of the trunk close to the hip, allowing efficient transfer of the weight to the lower limb during walking. Finally, there is a prominent anterior inferior iliac spine, indicating the importance of the knee extensor, rectus femoris, and a strong attachment of the iliofemoral ligament, which helps maintain balance by preventing hyperextension of the thigh (Aiello and Dean 1990). It is worth noting that the pelvis of AL 288 is also somewhat unique in being markedly wide, more so than humans, and that its iliac blades are not orientated as anteroposteriorly as they are in humans. This considerable width may well be functionally linked to the more funnel-shaped rib cage of *A. afarensis* (Schmid 1983, 1991). Such a rib cage would have been relatively wider inferiorly than in humans, therefore requiring a wider pelvis to support the resulting wider trunk. However, overall the features in the *A. afarensis* pelvis imply that it was well suited to two of the major requirements of bipedalism: maintaining balance and efficiently transferring weight from the trunk to the leg during walking.

Apart from the high bicondylar angle in *A. afarensis*, it has been argued that its long femoral neck is especially adapted to bipedality. This feature may in fact have made abduction of the hip biomechanically easier than in modern humans (Lovejoy 1973; Lovejoy et al. 1973). However, it is also possible that this feature is a reflection of the wider thorax and pelvis in *A. afarensis*. There are a number of other traits in the lower limb that unequivocally imply habitual bipedality. The mediolateral orientation of the talar surface of the distal tibia is horizontal relative to the long axis of the shaft. As discussed in ❯ *Section 5.2.2*, this is an important feature unique to later hominin bipeds that facilitates efficient transfer of weight from the leg to the foot. In the *A. afarensis* foot, the talus is very humanlike, particularly with respect to the trochlear surface (Latimer et al. 1987). The calcaneus also has a lateral plantar process on the tuberosity, which greatly helps diffuse stress as produced by ground reaction forces at heel-strike (Latimer and Lovejoy 1989). In general, the morphology of the ankle joint and heel in *A. afarensis* is extremely humanlike and would have been well suited to coping with the increased forces through the ankle associated with bipedal locomotion. It is also argued that the *A. afarensis* foot would not have been capable of opposing its hallux (Latimer and Lovejoy 1990a).

Other features present in the postcranium suggest bipedalism but are more open to interpretation. The femoral neck in both the AL 128-1 and Maka femora has thicker cortical bone inferiorly than superiorly (Lovejoy et al. 2002). As discussed earlier in ❯ *Section 5.3.3*, there is disagreement concerning the usefulness of this trait in inferring bipedality. The femoral condyles of larger-bodied members of *A. afarensis* are also more humanlike in proportions and symmetry, but this is not the case for smaller members of the species such as AL 129 (Aiello and Dean 1990). In the foot, it has been argued that *A. afarensis* had more dorsally orientated proximal articular facets on the proximal pedal phalanges, implying a humanlike ability for increased dorsiflexion of this joint in bipedal walking (Latimer and Lovejoy 1990b). However, a more recent metrical study has found that the *A. afarensis* angle actually falls well outside the human range of variation and between humans and the African apes (Duncan et al. 1994). The foot of *A. afarensis* had also been suggested to have had strong longitudinal arching (Latimer and Lovejoy 1989). This assertion is partially related to the assumption that the arched footprint from Laetoli were made by *A. afarensis*. As discussed earlier in ❯ *Section 5.3.4*, this may not be the case, and when assessing the degree of arching in this taxon it is best to assess the fossil remains directly. The markedly enlarged medial tuberosity on two navicular bones from Hadar strongly implies considerable weight-bearing in the midfoot of *A. afarensis* (Sarmiento 2000; Harcourt-Smith et al. 2002; Harcourt-Smith and Hilton 2005). Such morphology is incompatible with longitudinal arching. A recent

architectural analysis of *A. afarensis* pedal material by Berillon (2003) also finds that this taxon was unlikely to have had a longitudinal arch.

There are also a number of more ape-like traits in the *A. afarensis* postcranium, some of which suggest a degree of arboreal climbing ability (Stern 2000). Most noticeably, the manual and pedal proximal phalanges from the AL 288 and AL 333 localities are markedly curved and long and have prominent flexor ridges (Marzke 1983; Stern and Susman 1983; Susman et al. 1985). These features strongly imply an arboreal proficiency not found in later hominins. In the foot, the morphology of a partial medial cuneiform bone from AL 333 also implies that there may have been a degree of hallucial opposability (Harcourt-Smith et al. 2003), although others assert this to not be the case (Latimer and Lovejoy 1980a). Elsewhere, it has been reported that the morphology and function of the *A. afarensis* calcaneo-cuboid joint may have been apelike (Gomberg and Latimer 1984). Analysis of the limb proportions of the AL 288 skeleton show that the femur was relatively short (Jungers 1982; Jungers and Stern 1983), meaning that Lucy would have had a much shorter stride length than modern humans do. The morphology of the tibial plateau indicates that *A. afarensis* would have had a single attachment for the lateral meniscus, as in apes (Senut and Tardieu 1985), although the phylogenetic relevance of this trait has recently been questioned (Holliday and Dugan 2003). In the upper limb, it has been argued that the distal humerus of smaller-bodied *A. afarensis* specimens shows a well-developed lateral trochlear crest, an apelike trait that prevents dislocation of the elbow joint during climbing/suspension (Senut 1981a, b; Senut and Tardieu 1985), and a more cranially orientated glenoid (Stern and Susman 1983). Both these features could have facilitated above-branch climbing behavior. More recently it has been suggested that *A. afarensis* retained features in the wrist consistent with a knuckle-walking ancestry (Richmond and Strait 2000), although the authors do not go so far as to suggest that *A. afarensis* itself had a capacity for knuckle-walking. Others disagree with this assertion (Dainton 2001; Lovejoy et al. 2001), and it is interesting to note that none of the other important morphological traits associated with knuckle-walking (e.g., transverse dorsal ridges and dorsally expanded articular surfaces on the metacarpal heads) are found in *A. afarensis* specimens (Stern and Susman 1983).

It has also been suggested that there is a significant degree of postcranial variation between larger-bodied and smaller-bodied individuals of *A. afarensis*, particularly in the knee and elbow joints as discussed above, but also in the ankle (Stern and Susman 1983; Senut and Tardieu 1985). These differences could imply locomotor differences between the sexes, as Stern and Susman have suggested (1983), but have also been interpreted as suggesting that there were two distinct species of hominin at Hadar (Senut and Tardieu 1985; Tardieu 1985;

Deloison 1999). However, the prevailing view (Harcourt-Smith and Aiello 2004) remains that the Hadar material constitutes a single species, although there continues to be disagreement over the degree of sexual dimorphism in *A. afarensis* (Plavcan et al. 2005; *contra* Reno et al. 2003).

The considerable debate over the locomotor behavior of *A. afarensis* ultimately rests on how one views the relationship between these traits and the process of selection (Ward 2002; Harcourt-Smith and Aiello 2004). One can argue, as Latimer (1991) does, that the derived anatomical adaptations to bipedalism seen in *A. afarensis* demonstrate clear evidence of directional selection toward bipedality. Conversely, one can also argue that the retention of primitive apelike traits present in *A. afarensis* indicates a degree of stabilizing selection for arboreal proficiency (Stern and Susman 1983; Stern 2000), although there have also been suggestions that such features in *A. afarensis* were reflective of efficient terrestrial quadrupedalism (Sarmiento 1994, 1998). Only better understanding of the relationship between many of these traits and epigenetic factors may help to resolve this debate (Lovejoy et al. 2002; Harcourt-Smith and Aiello 2004). Overall, the postcranial skeleton of *A. afarensis* can be best considered as mosaic, showing a combination of derived human-like bipedal traits, primitive ape-like climbing-related traits, and a number of traits that appear to be unique. There is no doubt that *A. afarensis* was a habitual biped and would have spent a significant amount of time engaging in bipedal locomotor behaviors. However, there are also enough arboreal specialties present to imply a degree of climbing ability, and it is not unreasonable to posit that *A. afarensis* could have spent time in trees at night and for predator avoidance.

A. africanus   Until the discovery of the Hadar remains in the 1970s, the South African *A. africanus* fossils provided the best insight into the locomotor behavior of ancient fossil hominins. This was initiated by the discovery of the Taung Child in the 1920s, and Dart's (1925) description of its foramen magnum as being in a more humanlike position, thus implying upright posture and locomotion. Since then a large number of fossils assigned to *A. africanus* have been discovered, predominantly at the site of Sterkfontein. The specimen most diagnostic of bipedality is the partial skeleton Sts 14, which includes a parts of the pelvis, femur, and vertebral fragments, and has been recently argued to belong to the same individual as the Sts 5 skull (Thackeray et al. 2002). The pelvis is morphologically very similar to that of AL 288, in having wide and short iliac blades and being predominantly more humanlike than ape-like (McHenry 1986). Also like AL 288, the pelvis of *A. africanus* is very wide, with laterally flaring iliac blades, and has a relatively smaller acetabulum and iliosacral joint. This high-pelvic width is confirmed by other *A. africanus* pelvic fragments, including the recently

reconstructed Stw 431 pelvis from Member 4, Sterkfontein (Kibii and Clarke 2003). As for *A. afarensis*, this is argued to have provided a distinct advantage in bipedal walking (Lovejoy 1973). Distal femora from Sterkfontein (TM 1513 and Sts 34) also indicate that *A. africanus* had a high bicondylar angle, as in *A. afarensis* and modern humans. Recently discovered *Australopithecus* postcranial remains from the Jacovec Cavern at Sterkfontein, which may be as old as 4.0 Ma, include a proximal femur (Stw 598) that has a markedly long neck and small head, as for the *Paranthropus* femora from Swartkrans (see ❯ Section 5.3.4.2 below) (Partridge et al. 2003).

Other aspects of *A. africanus* locomotor anatomy have been argued to be more mosaic. McHenry and Berger (1998a, b) argue, mainly based on analysis of the Stw 431 skeleton, that *A. africanus* had relatively large upper limbs and small lower limbs, implying a more primitive climbing-related component of the locomotor repertoire. However, Stw 431 does not have any lower limb remains, only a partial pelvis with a preserved acetabulum and sacroiliac joint, making the scope for comparison limited. It is important to note that this study is often misinterpreted as stating that the limb proportions (e.g., humerofemoral index) of *A. africanus* were primitive. In fact, the study mainly concentrated on measurements taken from the articular surfaces at the ends of limb elements. Full recovery and analysis of the well-preserved Stw 573 skeleton from Sterkfontein Member 2 (Clarke 1998) will prove vital in helping to resolve this debate, as there are complete upper and lower-limb elements preserved. It has also been argued that a proximal tibia from Member 4, Stw 514a, is "chimpanzeelike" in having a more rounded lateral profile of the lateral condyle, thus inferring an apelike range of motion at the knee joint (Berger and Tobias 1996). This may have been so, but it is premature to describe a structure as complex as the proximal tibia as apelike based on one feature alone, and further analysis is needed. The discovery of the 3.3-Ma "Little Foot" partial skeleton (Stw 573) (Clarke and Tobias 1995; Clarke 1998) promises to one of the most important discoveries in the early hominin fossil record. The skeleton is far more complete than that of Lucy, with a complete skull, arm bones in articulation, leg bones, foot bones, ribs, and fragments of vertebrae and the pelvis (Clarke 1999, 2002). Most of these bones await removal from the breccia, but the foot bones were found separately and were initially described as showing a mosaic of adaptations, with a partially opposable hallux capable of some grasping potential but a more humanlike ankle joint (Clarke and Tobias 1995). However, recent metrical analyses of these remains shows that Little Foot could not oppose its hallux, had a navicular distinct from those at Hadar, but did have a more apelike ankle joint, implying that overall the foot was mosaic, but in a different way to that previously suggested (Harcourt-Smith et al. 2003; Harcourt-Smith and Aiello 2004). Finally, analysis of the relative size

of the semicircular canals in the inner ear indicates that *A. africanus* had canals of apelike proportions. The morphology of the semicircular canals is closely linked to locomotor behavior, and while this finding does not preclude *A. africanus* from having been a biped, it is likely that it would have been less competent at complex bipedal behaviors such as running and jumping (Spoor et al. 1994).

Locomotor differences and similarities between *A. africanus* and *A. afarensis*   The postcrania of both *A. afarensis* and *A. africanus* show distinct adaptations for bipedal locomotion. Particularly for *A. afarensis*, however, there is also strong evidence of retained apelike traits indicating a proficiency for arboreal climbing, especially within the upper limb. There is no doubt that both taxa were habitual bipeds, but at the same time they cannot be considered as obligate bipeds, and it is best to treat them as having had degrees of mosaicism in their locomotor repertoires. A number of studies have suggested that *A. africanus* and *A. afarensis* were very similar to each other in their locomotor anatomy (McHenry 1986; Dobson 2005). However, a number of other recent studies show that there is in fact a number of interesting differences between these two taxa. In a major analysis of the Stw 431 skeleton, Haeusler (2001) argues that a number of subtle but significant anatomical differences between the Stw 431 and Al 288 pelves to imply that *A. africanus* may have had a different and more humanlike bipedalism. Recent work on the tarsal bones of australopithecines also shows that the putative Stw 573 *A. africanus* foot may well have been mosaic (see above for details) in a different way to that of *A. afarensis* (Harcourt-Smith 2002; Harcourt-Smith et al. 2003). Given that the Hadar remains and those from Sterkfontein (Member 2) could well be of an approximately similar geological age (Partridge et al. 1999), this suggests that there was perhaps a significant degree of locomotor diversity within *Australopithecus*. *A. afarensis* and *A. africanus* both show significant adaptations for bipedality, but it is entirely possible that they achieved this through different evolutionary pathways (Harcourt-Smith and Aiello 2004).

5.3.4.2 Bipedalism in *Paranthropus*

The majority of available postcranial material from the genus *Paranthropus* come from the South African sites of Swartkrans and Kromdraai, and is assigned to *Paranthropus robustus*. There are no complete long bones for *P. robustus*, but from Swartkrans there are a partial pelvis (SK 50), two proximal femora (SK 82 and 97), and a number of other postcrania including hand and foot bones, while from Kromdraai there is a partial talus (TM 1517). Two major studies on this postcranial material by Napier (1964) and Robinson (1972, 1978) argued that *P. robustus*

had a slightly less derived postcranial skeleton than *A. africanus* and would have had a less efficient type of bipedal gait. The main anatomical arguments for this were a more laterally facing acetabulum and longer ischium in the SK 50 pelvis, smaller femoral heads and a more medially orientated talar neck and head, which has been sometimes linked to hallux opposability (Broom and Schepers 1946; Napier 1964; Robinson 1972). However, the SK 50 pelvis is severely distorted, and it is questionable whether there is enough well-preserved morphology for serious anatomical analysis. The Kromdraai talus, although apelike in some metrical aspects (Wood 1974), also has a relatively flat humanlike trochlear surface (Robinson 1972), and the significance of talar neck orientation for grasping potential has been brought into question by Lewis (1980, 1989). More recent finds assigned to *P. robustus* suggest that it was likely to have been an efficient biped (Susman 1989). In particular, two well-preserved 1st metatarsals from Swartkrans show that *P. robustus* would have had a strong toe-off during walking, which accords with efficient bipedality (Susman and Brain 1988; Susman and de Ruiter 2004).

5.3.5 The rise of obligate bipedalism

In the ❯ Section 5.3.4.1 I discussed locomotor behavior within the genus *Australopithecus*. While there may well have been some diversity in the way that different species of *Australopithecus* were bipedal, what is certain is that they cannot be considered as fully obligate bipeds in the way that modern humans are. Conversely, later species of *Homo*, such as *H. erectus*, *H. antecessor*, and *H. neanderthalensis* were unequivocally obligate bipeds (see ❯ *Figure 5.1* for a summary of which taxa there is agreement and disagreement over concerning bipdalism). There are some subtle anatomical differences in the postcranial skeletons of these taxa when compared to modern humans, but their overall skeletal biology strongly implies fully humanlike bipedal locomotion (Trinkaus 1983; Aiello and Dean 1990; Lorenzo et al. 1999). It seems, then, that the emergence of true obligate bipedal locomotor behavior occurred between about 2.5 and 1.8 Ma. This time period is associated with the emergence of the genus *Homo* with which the emergence of obligate humanlike bipedalism is likely to be strongly associated.

This period is also extremely complex in terms of hominin evolution, and has been the subject of a diverse range of taxonomic interpretations. At least nine widely accepted hominin species have first or last appearances within this time frame, and the fossil record implies that there was considerable overlap in the temporal and geographical distribution of many of these taxa. Determining

■ Figure 5.1
Temporal ranges of known hominin taxa. Solid shading indicates taxa that were unequivocally obligate bipeds. Crosshatching indicates taxa where there is disagreement over the degree to which they were bipedal. No shading relates to those taxa where there is insufficient evidence. Adapted from Wood (2002)
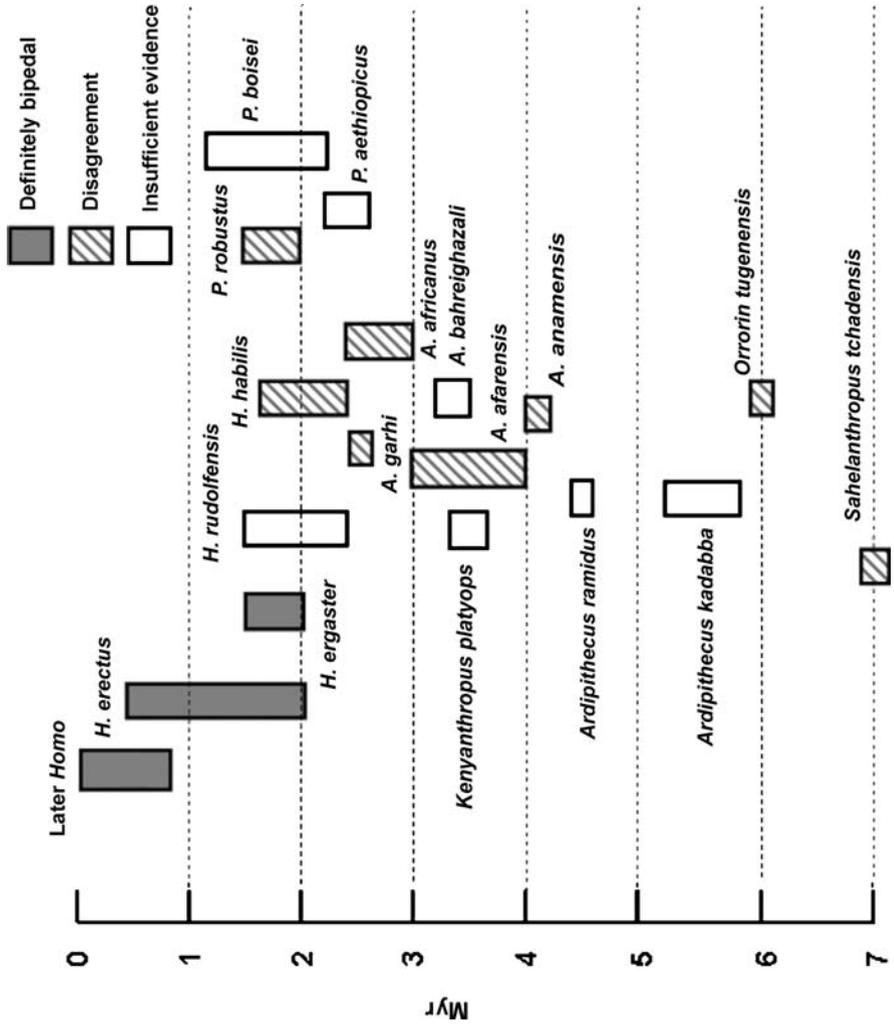
which of these species were fully obligate bipeds and which were not has been hampered by a number of factors. The principal issue is a meagre postcranial fossil record, but even where there are significant numbers of postcranial elements, as at Koobi Fora (Leakey et al. 1978), there are often problems of reliable taxonomic association. However, the 1.8-Ma juvenile *Homo ergaster* skeleton from Nariokotome, Kenya (KNM-WT 15000) is shown to have been fully bipedal. Its postcranial skeleton is remarkably humanlike, with long legs and short arms and all of the derived postcranial traits associated with obligate bipedal locomotion (Ruff and Walker 1993). With such an advanced body plan, it is reasonable to assume that *H. ergaster* and possibly its direct precursors had developed obligate bipedal behavior before 2 Ma. There are also a number of other postcranial remains from Koobi Fora that imply striding bipedalism. In particular, the femora KNM-ER 1472 and 1481A are long and extremely humanlike. However, it is difficult to speculate whether these specimens belonged to *H. rudolfensis*, *H. ergaster*, or even to *P. boisei*.

Most of the debate over the locomotor affinities of early members of *Homo* has concentrated on postcranial remains assigned to *Homo habilis* from Olduvai Gorge, Tanzania. Found at site FLK NN, the holotype for this taxon, OH 7, includes a number of predominantly juvenile hand bones. These bones are argued to be mosaic in their overall morphology. The scaphoid is apelike, the proximal and intermediate phalanges are more curved than in modern humans, and the intermediate phalanges have more apelike attachments for *m. flexor digitorum superficialis*, a muscle associated with climbing and suspensory behavior (Susman and Creel 1979; Aiello and Dean 1990). The OH 8 foot, also found at FLK NN, is included as a paratype of *H. habilis*, and provides the best insight into the locomotor behavior of this taxon (Day and Napier 1964; Leakey et al. 1964). Extensive analyses of these bones indicate that the foot had strong longitudinal arches, a locking calcaneo-cuboid joint, a metatarsal robusticity pattern similar to that of modern humans, and perhaps most importantly, a hallux in line with the remaining toes that was wholly incapable of any opposability (Day and Napier 1964; Susman and Stern 1982; Berillon 1999, 2000; Harcourt-Smith and Aiello 1999). The combination of all these features points to an individual capable of efficient bipedal locomotion. However, the talus is less humanlike than the rest of the foot and has a trochlea that is strongly grooved and medially sloping. This is a more-apelike morphology and is consistent more laterally arcuate passage of the leg over the foot during the stance phase (Latimer et al. 1987). The implication of this is that although the OH 8 foot is very humanlike in most critical features, its ankle joint implies less efficient weight-transfer from the leg during walking. There are also the OH 35 distal tibia and fibula, which were found at site FLK (Davis 1964). These are also argued to be humanlike, with a talar facet that is

perpendicular to the long axis of the shaft and predominantly human-like muscle attachments (Davis 1964; Lovejoy 1975; Susman and Stern 1982). It has been argued that OH 35 is likely to have come from the same individual as OH 8 based on morphological similarity (Susman and Stern 1982). Recent metrical comparisons contradict that assertion (Aiello et al. 1998), and indeed the two specimens were found 300 yards apart and in different geological horizons (Davis 1964; Dunsworth and Walker 2002).

The final specimen of interest is the more recently discovered partial skeleton OH 62, found at site FLK and assigned to *H. habilis* based on associated craniodental remains (Johanson et al. 1987). Although OH 62 is extremely fragmentary, it has been argued that its intermembral proportions were more apelike and similar to those of *A. afarensis*. This assertion was based on humerofemoral proportions that relied on an estimate of the femoral length of OH 62 as similar to that of the considerably older AL 288 (Johanson et al. 1987; Hartwig-Scherer and Martin 1991). Based on these findings, it has also been suggested that OH 62 has limb proportions as primitive as those of *A. africanus* (McHenry and Berger 1998a, b). However, the OH 62 femur is incomplete, lacking a considerable part the distal end, and it is impossible to accurately estimate the correct length of this fossil (Korey 1990; Haeusler and McHenry 2004). Furthermore, a recent reconstruction, based on morphological similarity to the younger (1.15–0.8 Ma) and undescribed OH 34 femur from Bed III, yields a far more human-like value, and therefore implies far more human-like limb proportions (Haeusler and McHenry 2004). Given that OH 34 could have been subjected to a degree of postdepositional erosion that may have compromised its morphology (Day and Molleson 1976), this latter finding must also be treated with caution. However, given that the OH 35 tibia and fibula are also relatively long, it is not unreasonable to assume that the limb proportions of *H. habilis* could have been rather more human-like than some have suggested. Until further evidence is uncovered, the evidence is not strong enough to definitively support either scenario.

There are a number of things that can and cannot be said about the locomotor affinities of *H. habilis*. The foot, tibia, and fibula are all very human-like in most critical aspects. There is some degree of uncertainty over whether the limb proportions were more human-like or apelike, but this issue cannot currently be resolved. The hand bones also show a mosaic of human-like and ape-like morphologies that may imply some climbing activity. Therefore, a conservative estimate of the locomotor behavior of *H. habilis* would place it *between* the habitual bipedalism of the australopiths and the obligate bipedalism of *H. ergaster* and later species of *Homo*. These findings imply a type of bipedalism in *H. habilis* more human-like and more efficient than those of either *A. afarensis* or *A. africanus*.

In summary, there is likely to have been some degree of locomotor diversity among different species of early *Homo*. The anatomy of the *Homo ergaster* post-cranial skeleton (mainly based on KNM-WT 15000) is extremely human-like and derived, and it would have been an obligate biped capable of long distance travel (Wang et al. 2004). Recently it has also been suggested that this would have included endurance bipedal running, something that earlier hominins are un-likely to have been able to do (Bramble and Lieberman 2004). On the other hand, there is less certainty concerning *Homo habilis*. Although there is evidence of a distinct shift between the morphology and associated locomotor function of its postcranial remains and those of *Australopithecus*, it would not have been as efficient a biped as *H. ergaster* and is likely to have had a unique pattern of gait. Therefore, while it is certain that by the beginning of the Pleistocene fully obligate bipedalism had developed in some lineages of *Homo*, it cannot be argued that this had occurred in *all* species within that genus. This has been used by some to add weight to the argument that *Homo habilis* should be transferred to the genus *Australopithecus* (Wood and Collard 1999). This may or may not be the case craniodentally, but it cannot be argued postcranially. Further fossil discoveries will undoubtedly help resolve some of these issues. Recently, a number of new postcranial remains have been discovered at the 1.8 Ma site of Dmanisi in Georgia. Analysis of these remains could greatly aid our understanding of the emergence of the modern human body-plan in early *Homo*, as well as the nature of the locomotor anatomy of the first hominins to leave the African continent.

5.3.6   Summary of locomotor behaviors within the hominin clade

As we have seen, there are varying degrees of fossil evidence for the origins of bipedalism. More often than not, we are faced with the problem of being unable to place skeletal remains diagnostic of bipedality within a particular taxonomic hypodigm. Conversely, those fossil specimens which are associated with a partic-ular species often show bewildering combinations of primitive, derived, and unique characteristics. However, on the basis of existing evidence a number of broad conclusions can be made (◉ *Figure 5.2*). It is possible that the earliest hominins, such as *A. ramidus*, *O. tugenensis*, and *S. tchadensis*, show important enough features to imply a slight shift to increased terrestrial bipedality. However, current evidence is extremely meagre, and further finds may show that any shift to bipedality could have been more or even less substantial. Following these taxa, there appear to have been at least two distinct shifts in the development of hominin locomotion. First, between 4.5 and 3 Ma, a number of habitually bipedal

■ Figure 5.2
The degree of bipedality in known fossil hominins relative to time. Only taxa with documented traits relating to bipedal locomotion are included. *Ardipthecus, O. tugenensis,* and *S. tchadensis* are classed as occasional bipeds on the basis of having very few or weak traits related to bipedality. *Australopithecus afarensis* and *africanus* are classed as habitual bipeds on the basis of major anatomical remodeling of structures functionally related to bipedality, but retention of a number of apelike climbing specializations. *H. ergaster, H. erectus,* and later species of *Homo* are classed as obligate bipeds, but there is enough debate over *H. habilis* to place it between habitual and obligate bipedalism
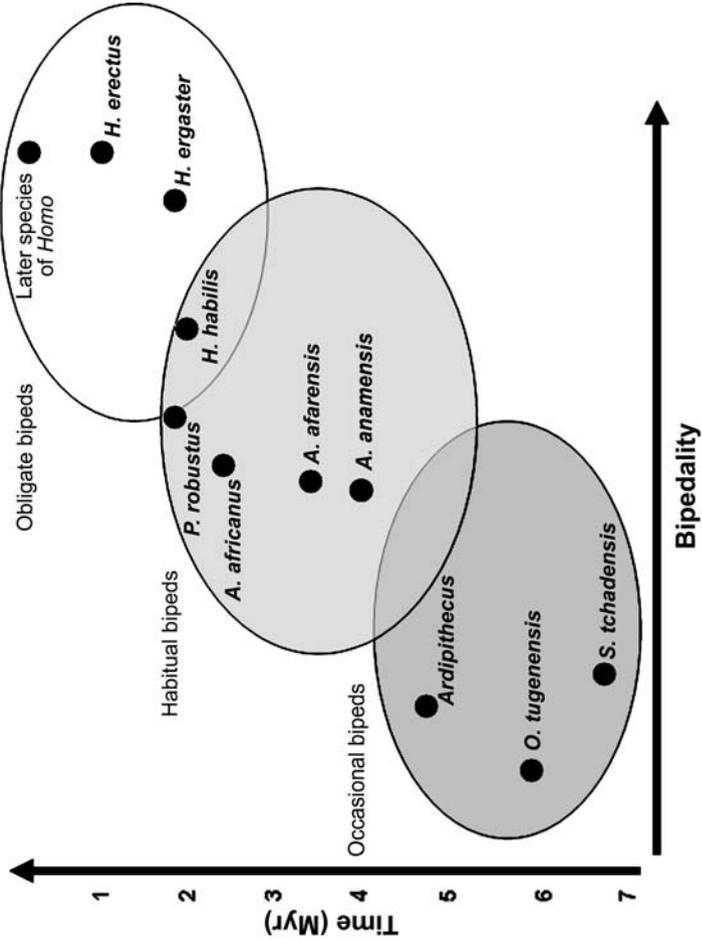
hominin species emerged, as typified by the Laetoli footprints and the extensive postcranial remains from Hadar. Within this time frame it is possible that different species varied in the way that they became bipedal, and that there were several different "types" of bipedalism being practiced. The period between 2.5 and 1.8 Myr heralds a second shift to fully obligate bipedalism. This period coincides with the emergence of the genus *Homo*, and by 1.8 Ma at least some members of this genus (i.e., *H. ergaster*) were fully obligate bipeds with a modern human body plan. Other early species of *Homo*, like *H. habilis*, may well have had a locomotor repertoire that was transitional between that of *Australopithecus* and that of *H. ergaster*. Subsequent to the advent of *H. ergaster* and *H. erectus*, all known hominins were fully obligate bipeds.

5.4   Why was bipedalism selected for?

As has been discussed, much contemporary debate over the origins of bipedalism rests on the locomotor adaptations of particular taxa or individual specimens. This is understandable given that fossils provide concrete evidence. However, it is critical to also ponder why bipedalism was selected for and why it became such a successful form of locomotion for our species. Most early theories as to why humans became bipedal center on the "freeing of the hands" as the principal force of selection. This can be traced back to Darwin, who argued in the *Descent of Man* (1871) that bipedal locomotion must have evolved to allow for the construction and use of hunting weapons. Since that first explanation there has been an abundance of different theoretical explanations, ranging from the plausible to the wholly implausible. When considering these different potential selection pressures, it is important to consider that bipedal locomotion is a highly derived and unique form of primate locomotion. In that context, we have seen that the skeletal modifications associated with bipedality are considerable. Strong selection pressures that specifically required prolonged periods of upright walking that are therefore likely to provide the key as to why bipedalism evolved (Lovejoy 1981; Rose 1991).

Prior to the discovery of the *A. afarensis* remains from Hadar, the orthodox view remained that tools and tool-use were intrinsically involved with the emergence of habitual bipedalism. Echoing Darwin (1871), some argued that tool use itself explained the selection for bipedalism (Washburn 1960), while others suggested that tool-carrying behavior was a more likely explanation (Bartholomew and Birdsell 1953; Washburn 1967). Both these theories are now contradicted by the temporal sequence of events provided by the contemporary fossil and archeological records (Rose 1991). Evidence of bipedal locomotion

currently predates the earliest stone tools by at least 1.5 Myr and probably more, which precludes the involvement of any stone-tool associated behavior in the origins of bipedality. More recent hypotheses have tended to be strongly linked to paleoenvironmental changes from the end of the Miocene through to the beginning of the Pleistocene. The emergence of habitual bipedalism strongly correlates with generally cooler and dryer global conditions, and an associated increase in more open grassland habitats (Van Couvering 2000). Predominantly forested environments were gradually replaced by more mosaic environments made up of different degrees of open grassland, bushland, and open woodland (Reed 1997). To cope with these environmental changes there is no doubt that hominins had to adapt a series of new behavioral strategies. Change in habitat composition would have resulted in a shift in food availability and thus necessitated a shift in food acquisition behaviors (Rose 1991; Foley and Elton 1998). Hominins either had to range further to find food or develop strategies to procure new and different types of food. It is therefore very likely that hominins would have had to have engaged in more terrestrial travel over more open habitats, and it is in this change in activity patterns that we are likely to find the reasons for the emergence of bipedality.

There are a number of more recent theories strongly associated with these selection pressures that warrant discussion. Lovejoy (1981) argues that food carrying and procurement by males was the driving selection pressure. This would tie in with some interpretations of the fossil material from Hadar that suggests that there was a degree of locomotor sexual dimorphism in *A. afarensis* (Stern and Susman 1983). Recent experimental work also supports Lovejoy's (1980) theory in showing that introducing widely distributed "food piles" leads to an increase in chimpanzee and bonobo locomotor bipedality, mainly associated with food carrying (Videan and McGrew 2002). Such a situation could be analogous to the more spread-out concentrations of food sources available to hominins in a more open grassland environment. Increased bipedalism in such a setting would greatly increase the ability to carry food to desired locations. Other theories argue for terrestrial food gathering (Jolly 1970; Wrangham 1980), or even hunting (Carrier 1984; Shipman 1986; Sinclair et al. 1986). Jolly's (1970) model uses the open-savannah gelada baboon as a modern-day analogue to suggest that early hominin bipedalism was linked to rapid seed-collecting behavior. Hunt (1990, 1994, 1996) has argued that chimpanzee postural behaviors may provide the key to our understanding of this issue. Over 80% of chimpanzee bipedalism is related to postural feeding. Using this as a behavioral analogue, Hunt argues that early hominin postcranial adaptations in *Australopithecus* were related to similar postural feeding behaviors and that true bipedal locomotion emerged with the advent of *Homo* (Wood 1993). It is

certainly possible that bipedal postural behavior may have preceded bipedal locomotion, but posture alone is likely to be too weak a selection pressure to have resulted in the significant anatomical remodeling seen in the *A. afarensis* and *A. africanus* pelvis and lower-limb structures (Lovejoy 1981; Rose 1991). It has also been recently suggested that bipedal threat displays may have been an important selective precursor to bipedal locomotion (Jablonski and Chaplin 1993).

One of the most interesting and widely accepted explanations of why hominins became bipedal is the thermoregulatory hypothesis suggested by Wheeler (1984, 1988, 1991, 1993, 1994). This argument rests on strong physiological explanations related to the reduction of thermal stress, and directly relates to the more open habitats that hominins would have been exposed to during the Early to Middle Pliocene. On the open savannah, quadrupedal animals expose considerably more of their body's surface area to the sun. Wheeler calculated that a hominin standing upright would absorb 60% less heat at midday. Furthermore, being upright exposes the subject to any potential breeze, which would have a further cooling effect. These factors would greatly reduce the rate at which hominins would have overheated on open ground, meaning that they could have ranged further without having to have increased water intake. In a more open environment, where food sources were likely to have been more spread out, such an advantage would have greatly enhanced the ability of hominins to successfully collect food. One other physiological explanation for the development of bipedalism warrants comment. Rodman and McHenry (1980) have argued that there is a considerable energetic advantage to become bipedal. However, it has been shown that *Pan* and *Gorilla* locomotion is not any less efficient physiologically than that of modern humans (Steudel 1994).

Perhaps the most interesting point relating to all the above theories is that made by Robinson (1972), who states that there is unlikely to have been *one* specific reason why bipedalism was selected for. It was more likely a combination of several selective factors strongly relating to feeding strategies and reproductive behavior that provided the impetus for this shift in the hominin locomotor repertoire. Furthermore, bipedalism would have not only provided the ability to range further for food and other resources but also have exposed hominins to novel parts of the surrounding landscape, different types of predators, and new food sources. This in turn would have led to new hominin behavioral strategies to cope with such changes. It has also been argued that on the basis of increasingly variable environmental conditions during the Late Miocene and Pliocene, associated behavioral versatility would have been a critical selective factor for early hominins (Potts 1998). In this context, there is little doubt that selection for bipedality would have considerably facilitated such behavioral versatility.

5.5   **Summary and concluding remarks**

There is no doubt that the evolution of bipedalism is a critical issue in the study of human origins. However, as we have seen, there has often been a considerable degree of rather polarized debate and disagreement as to how, when, why, and in whom hominin bipedalism evolved. In particular, the emergence of so many important fossil finds in the last 40 years has resulted in the literature becoming increasingly "fossil driven" in its concentration on *how* bipedal a particular hominin taxon might have been. This has often clouded our understanding of the larger issues at stake surrounding the emergence of this unique form of primate locomotion. As Rose (1991) has pointed out, selection for bipedality was not an event but rather a series of processes. In that context, what can be said about these processes? It is certain that the selection pressures for bipedality must have been strongly linked to reproductive success, and it is therefore likely that such pressures would have been related to the efficient gathering and transport of food and other resources across increasingly open habitats. As discussed earlier in the chapter, the current fossil record points to at least one minor and two major steps in the emergence of obligate, humanlike bipedality. The earliest hominins were little more than occasional bipeds, while the australopiths can certainly be considered as habitual bipeds who still engaged in some arboreal locomotor behaviors. By the emergence of early *Homo*, certain species within that genus were unequivocally obligate bipeds much in the way that we are today. It is perhaps seductive to view such steps as punctuated events, and that may have been the case, but it is also possible that the fragmentary fossil record merely creates the illusion of such steps. Only the recovery and analysis of further fossil remains relating to bipedality, particularly from the Late Miocene hominoid record, will increase our understanding of this complex and unique process.

References

Aiello LC, Dean MC (1990) An introduction to human evolutionary anatomy. Academic, London

Aiello LC, Wood B, Key C, Wood C (1998) Laser scanning and palaeoanthropology: an example from Olduvai Gorge, Tanzania. In: Strasser E, Fleagle J, Rosenberger A, McHenry H (eds) Primate locomotion: recent advances. Plenum Press, New York, pp 223–236

Avis V (1962) Brachiation: the crucial issue for man's ancestry. Southwestern J Anthropol 18: 119–148

Bacon A-M (1997) Presence of an obturator groove in some cercopithecoids and small-sized platyrrhines. Comptes Rendus de l'Academie des Sciences—Serie III, Sciences de la Vie 320(5): 421–425

Bartholomew GA, Birdsell JB (1953) Ecology and the protohominids. Am Anthropol 55: 481–498

Begun DR (2004) Knuckle-walking and the origin of human bipedalism. In: Meldrum DJ, Hilton CE (eds) From biped to strider: the emergence of modern human walking,

running and resource transport. Kluwer Academic/Plenum, New York

Berger LR, Tobias PV (1996) A chimpanzee-like tibia from Sterkfontein, South Africa and its implications for the interpretation of bipedalism in *Australopithecus africanus*. J Hum Evol 30: 343–348

Berillon G (1999) Geometric pattern of the hominoïd hallucal tarsometatarsal complex. Quantifying the degree of hallux abduction in early hominids. Comptes-Rendus de l'Académie des Sciences, Paris, Série IIa 328: 627–633

Berillon G (2000) Le pied des hominoïdes Miocènes et des hominidés fossiles. Architecture, locomotion, évolution. CNRS Editions, Paris, France

Berillon G (2003) Assessing the longitudinal structure of the early hominid foot: a two-dimensional architecture analysis. Hum Evol 18(3–4): 113–122

Broom R, Schepers GWH (1946) The South-African ape-men: the *Australopithecineae*. Transvaal Museum Memoir No. 2, Pretoria, South Africa

Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Ahounta D, et al. (2002) A new hominid from Upper Miocene of Chad, Central Africa. Nature 418: 145–151

Cant JGH (1987) Positional behavior of female Bornean orangutans *Pongo pygmaeus*. Am J Primatol 12: 71–90

Carrier DR (1984) The energetic paradox of human running and hominid evolution. Curr Anthropol 25: 483–495

Chaplin G, Jablonski NG, Cable NT (1994) Physiology, thermoregulation and bipedalism. J Hum Evol 27: 497–510

Clarke RJ (1998) First ever discovery of an associated skull and skeleton of an ape-man. S Afr J Sci 94(10): 460–463

Clarke RJ (1999) Discovery of complete arm and hand of the 3.3 million-year-old *Australopithecus* skeleton from Sterkfontein. S Afr J Sci 95: 477–480

Clarke RJ (2002) Newly revealed information on Sterkfontein Member 2 *Australopithecus* skeleton. S Afr J Sci 98: 523–526

Clarke RJ, Tobias PV (1995) Sterkfontein member 2 foot bones of the oldest South African hominid. Science 269: 521–524

Crompton RH, Li Y, Thorpe SK, Wang WJ, Savage R, Payne R, Carey TC, Aerts P, Van Elsacker L, Hofstetter A, Gunther MM, D'Aout K, De Clerq D (2003) The biomechanical evolution of erect bipedality. Cour Forsch Inst Senckenberg 243: 115–126

Dainton M (2001) Did our ancestors knuckle-walk? Nature 410: 325–326

Dart RA (1925) *Australopithecus africanus*: the ape-man of South Africa. Nature 115: 195–197

Darwin C (1871) The descent of man and selection in relation to sex. Random House, New York

Davis PR (1964) Hominid fossils from Bed I, Olduvai Gorge, Tanganyika. A tibia and fibula. Nature 201: 967–968

Day MH (1969) Femoral fragment of a robust australopithecine from Olduvai Gorge, Tanzania. Nature 232: 383–387

Day MH, Molleson TI (1976) The puzzle from JK2: a femur and a tibial fragment from (OH 34) from Olduvai Gorge, Tanzania. J Hum Evol 5: 455–465

Day MH, Napier JR (1964) Fossils from Bed I, Olduvai Gorge, Tanganyika. Fossil foot bones. Nature 201: 969–970

Day MH, Wickens EH (1980) Laetoli Pliocene hominid footprints and bipedalism. Nature 286: 385–387

Day MH, Wood BA (1968) Functional affinities of the Olduvai Hominid 8 talus. Man 3: 440–455

Day MH, Leakey RE, Walker AC, Wood BA (1976) New hominids from East Turkana, Kenya. Am J Phys Anthropol 45: 369–435

Deloison Y (1999) L'Homme ne descend pas d'un Primate arboricole ! une évidence méconnue. Biom Hum et Anthropol 17: 147–150

Dobson SD (2005) Are the differences between Stw 431 (*Australopithecus africanus*) and AL 288-1 (*A. afarensis*) significant? J Hum Evol 49: 143–154

Doran D, Hunt KD (1995) Comparative locomotor behavior of chimpanzees and bonobos: species and habitat differences. In: Wrangham RW, McGrew WC, de Waal F, Heltne PG (eds) Chimpanzee cultures. Harvard University Press, Cambridge, pp 93–108

Drake R, Curtis GH (1987) K-Ar geochronology of the Laetoli fossil localities. In: Leakey MD, Harris JM (eds) Laetoli: a Pliocene site in Northern Tanzania. Clarendon Press, Oxford, pp 48–52

Duncan AS, Kappelman J, Shapiro LJ (1994) Metatarsophalangeal joint function and positional behavior in *Australopithecus afarensis*. Am J Phys Anthropol 93: 67–81

Dunswoth H, Walker A (2002) Early genus *Homo*. In: Hartwig WC (ed) The primate fossil record. Cambridge University Press, Cambridge, pp 419–435

Elftman H, Manter J (1935) Chimpanzee and human feet in bipedal walking. Am J Phys Anthropol 20: 69–79

Foley RA, Elton S (1998) Time and energy: the ecological context for the evolution of bipedalism. In: Strasser E, Fleagle J, Rosenberger A, McHenry H (eds) Primate locomotion: recent advances. Plenum Press, New York, pp 419–433

Fleagle JG (1999) Primate adaptation and evolution, 2nd edn. Academic Press, New York

Fleagle JG, Stern JT, Jungers WL, Susman RL, Vangor AK, Wells JP (1981) Climbing: a biomechanical link with brachiation and bipedalism. Symp Zoolog Soc (Lond) 48: 359–373

Gagneux P, Varki A (2000) Genetic differences between humans and great apes. Mol Phylogenet Evol 18(1): 2–13

Galik K, Senut B, Pickford M, Gommery D, Treil J, Kuperavage AJ, Eckhardt RB (2004) External and internal morphology of the BAR 1002'00 *Orrorin tugenensis* femur. Science 305: 1450–1453

Gebo DL (1992) Plantigrady and foot adaptation in African apes: implications for hominid origins. Am J Phys Anthropol 89: 29–58

Gebo DL (1996) Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. Am J Phys Anthropol 101: 55–92

Gomberg DN, Latimer B (1984) Observations on the transverse tarsal joint of *A. afarensis*, and some comments on the interpretation of behavior from morphology. Am J Phys Anthropol Suppl 63(2): 164

Gregory WK (1916) Studies on the evolution of the primates. Bull Am Museum Natural History 35: 239–355

Gregory WK (1927) Two views on the origin of man. Science 65: 601–605

Gregory WK (1928) The upright posture of man: review of its origin and evolution. Proc Am Philos Soc 67: 339–376

Haeusler MF (2001) New insights into the locomotion of *Australopithecus africanus*: implications of the partial skeleton of Stw 431 (Sterkfontein, South Africa). Ph.D. thesis, University of Zurich

Haesusler MF, McHenry HM (2004) Body proportions of *Homo habilisi* reviewed. J Hum Evol 46: 433–465

Haile-Selassie Y (2001) Late Miocene hominids from the Middle Awash, Ethiopia. Nature 412: 178–181

Haile-Selassie Y, Suwa G, White TD (2004) Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental development. Science 303: 1503–1505

Harcourt-Smith WEH (2002) Form and function in the hominoid tarsal skeleton. Ph.D. thesis, University College London, London

Harcourt-Smith WEH, Aiello LC (1999) An investigation into the degree of hallux abduction of OH 8. Am J Phys Anthropol Suppl 28: 145

Harcourt-Smith WEH, Aiello LC (2004) Fossils, feet and the evolution of bipedal locomotion. J Anat 204: 403–416

Harcourt-Smith WEH, Hilton C (2005) Did *Australopithecus afarensis* make the Laetoli footprint trail? New insights into an old problem. Am J Phys Anthropol 126 (S40): 112

Harcourt-Smith WEH, O'Higgins P, Aiello LC (2002) From Lucy to Littlefoot: a three dimensional analysis of Plio-Pleistocene hominin tarsal remains. Am J Phys Anthropol Suppl 34: 82

Harcourt-Smith WEH, O'Higgins P, Aiello LC (2003) 3D morphometrics and the evolution of bipedality. Am J Phys Anthropol Suppl 36: 109

Harrison T (1987) A reassessment of the phylogenetic relationships of *Oreopithecus bambolii* Gervais. J Hum Evol 15: 541–583

Harrison T (1991) The implications of *Oreopithecus bambolii* for the origins of bipedalism. In: Coppens Y, Senut B (eds) Origine(s) de la bipédie chez les hominidés. Editions du CNRS, Paris, pp 233–244

Hartwig-Scherer S, Martin RD (1991) Was "Lucy" more human than the "child"? Observations on early hominid postcranial skeletons. J Hum Evol 21: 439–449

Hay RL, Leakey MD (1982) The fossil footprints of Laetoli. Sci Am 246: 50–57

Holliday TW, Dugan J (2003) The utility of the lateral meniscal notch in distinguishing taxa of early hominins. Am J Phys Anthropol Suppl 36: 116

Hunt KD (1990) Implications of chimpanzee positional behavior in the Hominoidea. Am J Phys Anthropol 81: 242

Hunt KD (1994) The evolution of human bipedality: ecology and functional morphology. J Hum Evol 26(3): 183–203

Hunt KD (1996) The postural feeding hypothesis: an ecological model for the origin of bipedalism. S Afr J Sci 9: 77–90

Johanson DC, Lovejoy CO, Burnstein AH, Heiple KG (1976) Functional implications of the Afar knee joint. Am J Phys Anthropol 44: 188

Johanson DC, Masao FT, Eck GG, White TD, Walter RC, Kimbel WH, et al. (1987) New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. Nature 327: 205–209

Jolly CJ (1970) The seed-eaters: a new model of hominid differentiation based on a baboon analogy. Man 5(1): 5–26

Jungers WL (1982) Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. Nature 297: 676–678

Jungers WL, Stern JT (1983) Body proportions, skeletal allometry and locomotion in the Hadar hominids: a reply to Wolpoff. J Hum Evol 12: 673–684

Keith A (1903) The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of man and allied primates. J Anat Physiol 37: 18–40

Keith A (1923) Man's posture: its evolution and disorders. BMJ 1: 451–454, 499–502, 545–548, 587–590, 624–626, 669–672

Kelly RE (2001) Tripedal knuckle-walking: a proposal for the evolution of human locomotion and handedness. J Theor Biol 213: 333–358

Kibii JM, Clarke RJ (2003) A reconstruction of the Stw 431 *Australopithecus* pelvis based on newly discovered fragments. S Afr J Sci 99: 225–226

Kidd RS, O'Higgins P, Oxnard CE (1996) The OH8 foot: a reappraisal of the hindfoot utilizing a multivariate analysis. J Hum Evol 31: 269–291

Köhler M, Moyà-Solà S (1997) Ape-like or hominid-like? The positional behavior of *Oreopithecus bambolii* reconsidered. Proc Natl Acad Sci 94: 11747–11750

Korey KA (1990) Deconstructing reconstruction: the OH 62 humerofemoral index. Am J Phys Anthropol 83: 25–33

Latimer B (1991) Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. In: Coppens Y, Senut B (eds) Origine(s) de la bipédie chez les hominidés. Editions du CNRS, Paris, pp 169–176

Latimer B, Lovejoy CO (1989) The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. Am J Phys Anthropol 78: 369–386

Latimer B, Lovejoy CO (1990a) Hallucial tarsometatarsal joint in *Australopithecus afarensis*. Am J Phys Anthropol 82: 125–133

Latimer B, Lovejoy CO (1990b) Metatarsophalangeal joints of *Australopithecus afarensis*. Am J Phys Anthropol 83: 13–23

Latimer B, Ohman JC, Lovejoy CO (1987) Talocrural joint in African hominoids: implications for *Australopithecus afarensis*. Am J Phys Anthropol 74: 155–175

Leakey LSB, Tobias PV, Napier JR (1964) A new species of the genus *Homo* from Olduvai Gorge. Nature 202: 7–9

Leakey MD, Harris JM (1987) Laetoli: a Pliocene site in Northern Tanzania. Clarendon Press, Oxford

Leakey MD, Hay RL (1979) Pliocene footprints in the Laetoli Beds at Laetoli, northern Tanzania. Nature 278: 317–323

Leakey MG, Fiebel CS, McDougall I, Walker AC (1995) New four-million-year-old hominid

species from Kanapoi and Allia Bay, Kenya. Nature 376: 565–571

Leakey MG, Feibel CS, McDougall I, Ward C, Walker A (1998) New specimens and confirmation of an early age for *Australopithecus anamensis*. Nature 393: 62–66

Leakey REF, Leakey MG, Behrensmeyer AK (1978) The hominid catalogue. In: Leakey MG, Leakey RE (eds) Koobi Fora research project. Vol 1: The fossil hominids and an introduction to their context, 1968–1974. Clarendon Press, Oxford

Lewis OJ (1980) The joints of the evolving foot. Part III. The fossil evidence. J Anat 131(2): 275–298

Lewis OJ (1989) Functional morphology of the evolving hand and foot. Clarendon Press, Oxford

Lorenzo C, Arsuaga J-L, Carretero J-M (1999) Hand and foot remains from the Gran Dolina Early Pleistocene site (Sierra de Atapuerca, Spain). J Hum Evol 37: 501–522

Lovejoy CO (1973) The gait of Australopithecines. Yrbk Phys Anthropol 17: 147–161

Lovejoy CO (1978) A biomechanical review of the locomotor diversity of early hominids. In: Jolly CJ (ed) Early hominids of Africa. St Martin's Press, New York, pp 403–429

Lovejoy CO (1981) The origin of man. Science 211: 344–350

Lovejoy CO (1988) Evolution of human walking. Sci Am 259: 82–89

Lovejoy CO, Heiple KG, Burnstein AH (1973) The gait of *Australopithecus africanus*. Am J Phys Anthropol 38: 757–780

Lovejoy CO, Heilpe KG, Meindl RS (2001) Palaeoanthropology: did our ancestors knuckle-walk? Nature 410: 325–326

Lovejoy CO, Meindl RS, Ohman JC, Heilpe KG, White TD (2002) The Maka femur and its bearing on the antiquity of human walking: applying contemporary concepts of morphogenesis to the human fossil record. Am J Phys Anthropol 119(2): 97–133

Marzke MW (1983) Joint function and grips of the *Australopithecus afarensis* hand, with special reference to the region of the capitate. J Hum Evol 12: 197–211

McHenry HM (1986) The first bipeds: a comparison of the *A. afarensis* and *A. africanus* postcranium and implications for the evolution of bipedalism. J Hum Evol 15: 177–191

McHenry HM (1991) First steps? Analyses of the postcranium of early hominids. In: Coppens Y, Senut B (eds) Origine(s) de la bipédie chez les hominidés. Editions du CNRS, Paris, pp 133–141

McHenry HM (2002) Introduction to the fossil record of human ancestry. In: Hartwig WC (ed) The primate fossil record. Cambridge University Press, Cambridge, pp 401–405

McHenry HM, Berger LR (1998a) Body proportions of *Australopithecus afarensis* and *A. africanus* and the origin of the genus *Homo*. J Hum Evol 35: 1–22

McHenry H, Berger LR (1998b) Limb lengths in *Australopithecus* and the origin of the genus *Homo*. S Afr J Sci 94: 447–450

Morton DJ (1924) Evolution of the human foot II. Am J Phys Anthropol 7: 1–52

Morton DJ (1935) The human foot. Its evolution, physiology and functional disorders. Columbia University Press, New York

Moyà- Solà S, Köhler M (1996) A *Dryopithecus* skeleton and the origins of great-ape locomotion. Nature 379: 156–159

Napier JR (1964) The evolution of bipedal walking in the hominids. Arch Biologie (Liege) 75: 673–708

Napier JR (1967) The antiquity of human walking. Sci Am 216(4): 56–66

Napier JR, Davis PR (1959) The forelimb skeleton and associated remains of *Proconsul africanus*. Fossil Mammals Afr 16: 1–69

Ohman JC, Krochta TJ, Lovejoy CO, Mensforth RP, Latimer B (1997) Cortical bone distribution in the femoral neck of hominoids: implications for the locomotion of *Australopithecus afarensis*. Am J Phys Anthropol 104: 117–132

Page SL, Goodman M (2001) Catarrhine phylogeny: noncoding DNA evidence for a diphyletic origin of the Mangebys and a for a Human-Chimpanzee clade. Mol Phylogenet Evol 18(1): 14–25

Partridge TC, Shaw J, Heslop D, Clarke RJ (1999) The new hominid skeleton from Sterkfontein, South Africa: age and preliminary assessment. J Quaternary Sci 14(4): 293–298

Partridge TC, Granger DE, Caffee MW, Clarke RJ (2003) Lower Pliocene hominid remains from Sterkfontein. Science 300: 607–612

Pauwels F (1980) Biomechanics of the locomotor apparatus: contributions on the functional anatomy of the locomotor apparatus. Springer-Verlag, Berlin

Pickford M, Senut B (2001) The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya. Comptes Rendus de l'Académie des Sciences –Series IIA—Earth and Planetary Sciences 332(2): 145–152

Pickford M, Senut B, Gommery D, Treil J (2002) Bipedalism in *Orrorin tugenensis* revealed by its femora. Comptes Rendus Palevol 1(4): 191–255

Plavcan JM, Lockwood CA, Kimbel WH, Lague MR, Harmon EH (2005) Sexual dimorphism in *Australopithecus afarensis* revisited: how strong is the case for a human-like pattern of dimorphism? J Hum Evol 48: 313–320

Potts R (1998) Environmental hypotheses of hominin evolution. Yrbk Phys Anthropol 41: 93–136

Prost JH (1980) Origin of bipedalism. Am J Phys Anthropol 52: 175–189

Rafferty KL (1998) Structural design of the femoral neck in primates. J Hum Evol 34: 361–383

Reed KE (1997) Early hominid evolution and ecological change through the African Plio-Pleistocene. J Hum Evol 32: 289–322

Reno PL, Meindl RS, McCollum MA, Lovejoy CO (2003) Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. Proc Natl Acad Sci 100: 9404–9409

Richmond BG, Strait DS (2000) Evidence that humans evolved from a knuckle-walking ancestor. Nature 404: 382–385

Richmond BG, Begun DR, Strait DS (2001) Origin of human bipedalism: the knuckle-walking hypothesis revisited. Yrbk Phys Anthropol 44 (Suppl 33): 71–105

Robbins LM (1987) Hominid footprints from site G. In: Leakey MD, Harris JM (eds) Laetoli: a Pliocene site in Northern Tanzania. Clarendon Press, Oxford, pp 497–502

Robinson JT (1972) Early hominid posture and locomotion. University of Chicago Press, Chicago

Robinson JT (1978) Evidence for locomotor differences between gracile and robust early hominids from South Africa. In: Jolly C (ed) Early hominids of Africa. pp 441–457

Rodman PS, McHenry HM (1980) Bioenergetics and the origin of hominid bipedalism. Am J Phys Anthropol 52: 103–106

Rook L, Bondioli L, Köhler M, Moyà-Solà S, Macchiarelli R (1999) *Oreopithecus* was a bipedal ape after all: evidence from the iliac cancellous architecture. Proc Natl Acad Sci 96: 8795–8799

Rose MD (1984) A hominine hip bone, KNM-ER 3228 from East Lake Turkana, Kenya. Am J Phys Anthropol 63: 371–378

Rose MD (1991) The process of bipedalization in hominids. In: Coppens Y, Senut B (eds) Origine(s) de la bipédie chez les hominidés. Editions du CNRS, Paris, pp 37–48

Ruff CB, Walker AC (1993) Body size and body shape. In: Walker AC, Leakey RE (eds) The Nariokotome homo erectus skeleton. Harvard Press, Cambridge MA, pp 234–265

Sarmiento EE (1994) Terrestrial traits in the hands and feet of gorillas. Am Mus Nov 3091: 1–56

Sarmiento EE (1998) Generalized quadrupeds, committed bipeds and the shift to open habitats: an evolutionary model of hominid divergence. Am Mus Nov 3250: 1–78

Sarmiento EE (2000) The Os navicular of humans, great apes, OH 8, Hadar, and Oreopithecus: function, phylogeny, and multivariate analyses. Am Mus Nov 3288: 2–38

Schmid P (1983) Eine rekonstruktion des skelettes von AL 288-1 (Hadar) und deren konsequenzen. Folia Primatol 40: 283–306

Schmid P (1991) The trunk of the australopithecines. In: Coppens Y, Senut B (eds) Origine(s) de la bipédie chez les hominidés. Editions du CNRS, Paris, pp 225–234

Schmid P (2004) Functional interpretations of the Laetoli footprints. In: Meldrum DJ, Hilton CE (eds) From biped to strider: the emergence of modern human walking,

running and resource transport. Kluwer Academic/Plenum, New York

Schultz AH (1930) The skeleton of the trunk and limbs of higher primates. Hum Biol 2: 303–438

Senut B (1981a) Humeral outlines in some hominoid primates and the Plio-Pleistocene hominids. Am J Phys Anthropol 56: 275–283

Senut B (1981b) L'humerus et ses articulations chez les hominides Plio-Pleistocenes. Cahiers de Paleontologie (Paleoanthropologie). Editions du CNRS, Paris

Senut B (1989) Climbing as a crucial preadaptation to for human bipedalism. Ossa, 14: 35–44

Senut B, Tardieu C (1985) Functional aspects of Plio-Pleistocene hominid limb bones: implications for taxonomy and phylogeny. In: Delson E (ed) Ancestors: the hard evidence. Alan R. Liss, Inc., New York, pp 193–201

Senut B, Pickford M, Gommery D, Mein P, Cheboi K, Coppens Y (2001) First hominid from the Miocene (Lukeino formation, Kenya). Comptes Rendus de l'Académie des Sciences–Series IIA–Earth and Planetary Sciences 332(2): 137–144

Shipman P (1986) Scavenging or hunting in early hominids: theoretical framework and tests. Am Anthrop 88: 27–43

Sinclair ARE, Leakey MD, Norton- Griffiths M (1986) Migration and hominid bipedalism. Nature 324: 307–308

Spoor F, Wood BA, Zonneveld F (1994) Implications of early hominid labyrinth morphology for evolution of human bipedal locomotion. Nature 369: 645–648

Stern JT (1975) Before bipedality. Yrbk Phys Anthropol 19: 59–68

Stern JT (2000) Climbing to the top: a personal memoir of *Australopithecus afarensis*. Evol Anthropol 9(3): 113–133

Stern JT, Susman RL (1983) The locomotor anatomy of *Australopithecus afarensis*. Am J Phys Anthropol 60: 279–317

Stern JT, Susman RL (1991) "Total morphologocal pattern" versus the "magic trait": conflicting approaches to the study of early hominid bipedalism. In: Coppens Y, Senut B (eds) Origine(s) de la bipédie chez leshominidés. Editions du CNRS, Paris, pp 99–111

Steudel KL (1994) Locomotor energetics and hominid evolution. Evol Anthropol 3: 42–48

Straus WL (1949) The riddle of man's ancestry. Q Rev Biol 24: 200–223

Stringer C, Andrews P (2005) The complete world of human evolution. Thames and Hudson, London

Susman RL (1989) New hominid fossils from the Swartkrans Formation (1979–1986 excavations): postcranial specimens. Am J Phys Anthropol 79: 451–474

Susman RL, Brain TM (1988) New first metatarsal (SKX 5017) from Swartkrans and the gait of *Paranthropus robustus*. Am J Phys Anthropol 77: 7–15

Susman RL, Creel N (1979) Functional and morphological affinities of the subadult hand (OH 7) from Olduvai Gorge. Am J Phys Anthropol 51: 211–332

Susman RL, de Ruiter DJ (2004) New hominin first metatarsal (SK 1813) from Swartkrans. J Hum Evol 47: 171–181

Susman RL, Stern JT (1982) Functional morphology of *Homo habilis*. Science 217: 931–934

Susman RL, Stern JT, Jungers WL (1984) Arboreality and bipedality in the Hadar hominids. Folia Primatol 43: 283–306

Susman RL, Stern JT, Jungers WL (1985) Locomotor adaptations in the Hadar hominids. In: Delson E (ed) Ancestors: the hard evidence. Alan R Liss, New York, pp 184–192

Taieb M, Johanson DC, Coppens Y, Bonnefille R, Kalb J (1974) Découverte d'hominidés dans le séries Plio-Pleistocénes d'Hadar (Bassin de l'Awash; Afar, Ethiopia). CR Acad Sci Paris 279: 735–738

Tardieu C, Trinkaus E (1994) Early ontogeny of the human femoral bicondylar angle. Am J Phys Anthropol 95: 183–195

Thackeray F, Gommery D, Braga J (2002) Australopithecine postcrania (Sts 14) from the Sterkfontein Caves, South Africa: the skeleton of "Mrs Ples"? S Afr J Sci 98: 211–212

Thorpe SK, Crompton RH (2005) The locomotor ecology of wild orangutans (*Pongo pygmaeus abelii*) in the Gunung Leuser ecosystem, Sumatra, Indonesia: a multivariate

analysis using log-linear modeling. Am J Phys Anthropol 127: 58–78

Trinkaus E (1983) Functional aspects of Neanderthal pedal remains. Foot Ankle 3(6): 377–390

Tuttle RH (1968) Propulsive and prehensile capabilities in the hands and feet of the great apes: a preliminary report. VIIIth Congress of Anthropological and Ethnological Sciences, Tokyo, pp 31–32

Tuttle RH (1970) Postural, propulsive, and prehensile capabilities in the cheiridia of chimpanzees and other great apes. In: The chimpanzee, vol 2. Karger, Basel/New York, pp 167–253

Tuttle RH (1974) Darwin's apes, dental apes, and the descent of man: normal science in evolutionary anthropology. Curr Anthropol 15: 389–398

Tuttle RH (1975) Knuckle-walking and knuckle-walkers: a commentary on some recent perspectives in Hominoid evolution. In: Tuttle RH (ed) Primate functional morphology and evolution. Mouton, The Hague, pp 203–212

Tuttle RH (1981) Evolution of hominid bipedalism and prehensile capabilities. Philos Trans R Soc Lond Ser B 292: 89–94

Tuttle RH (1987) Kinesiological inferences and evolutionary implications from Laetoli bipedal trails G-1, G-2/3 and A. In: Leakey MD, Harris JM (eds) Laetoli: a Pliocene site in Northern Tanzania. Clarendon Press, Oxford, pp 497–502

Tuttle RH, Basmajian JV (1974) Electromyography of forearm musculature in Gorilla and problems related to knuckle-walking. In: Jenkins FA (ed) Primate locomotion. Academic, New York, pp 293–348

Tuttle RH, Webb D, Weidl E, Baksh M (1990) Further progress on the Laetoli trails. J Archaeol Sci 17: 347–362

Tuttle RH, Webb DM, Tuttle NI (1991) Laetoli footprint trails and the evolution of hominid bipedalism. In: Coppens Y, Senut B (eds) Origine(s) de la bipédie chez les hominidés. Editions du CNRS, Paris, pp 187–198

Van Couvering JA (2000) The Pliocene. In: Delson E, Tattersall I, Van Couvering JA, Brooks AS (eds) Encylopedia of human evolution and prehistory, 2nd edn. Garland, New York, pp 574–576

Videan EN, McGrew WC (2002) Bipedality in chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*): testing hypotheses on the evolution of bipedalism. Am J Phys Anthropol 118: 184–190

Wang W, Crompton RH, Carey TS, Gunther MM, Li Y, Savage R, Sellers WI (2004) Comparison of inverse-dynamics musculo-skeletal models of AL 288-1 *Australopithecus afarensis* and KNM-WT 15000 *Homo ergaster* to modern humans, with implications for the evolution of bipedalism. J Hum Evol 47: 453–478

Ward CV (2002) Interpreting the posture and locomotion of Australopithecus afarensis: where do we stand? Yrbk Phys Anthropol Suppl 35: 185–215

Ward CV, Walker A, Leakey MG (1999) The new species *Australopithecus anamensis*. Evol Anthropol 7: 197–205

Ward CV, Leakey MG, Walker A (2001) Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. J Hum Evol 41: 255–368

Washburn SL (1960) Tools and human evolution. Sci Am 203: 63–75

Washburn SL (1967) Behavior and the origin of man. Proc R Anthropol Inst GB/Ireland 3: 21–27

Wheeler PE (1984) The evolution of bipedality and loss of functional body hair in hominids. J Hum Evol 13: 91–98

Wheeler PE (1988) Stand tall and stay cool. New Sci 118(1613): 62–65

Wheeler PE (1991) The influence of bipedalism on the energy and water budgets of early hominids. J Hum Evol 21: 117–136

Wheeler PE (1993) The influence of stature and body form on hominid energy and water budgets: a comparison of *Australopithecus* and early *Homo* physiques. J Hum Evol 24: 13–28

Wheeler PE (1994) The foraging times of bipedal and quadrupedal hominids in open equatorial environments (a reply to Chaplin, Jablonski, and Cable 1994). J Hum Evol 27: 511–517

White TD (2002) Earliest hominids. In: Hartwig WC (ed) The primate fossil record. Cambridge University Press, Cambridge, pp 407–417

White TD, Suwa G (1987) Hominid footprints at Laetoli: facts and interpretations. Am J Phys Anthropol 72: 485–514

White TD, Suwa G, Asfaw B (1994) *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. Nature 371: 306–312

White TD, Suwa G, Asfaw B (1995) *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia—a corrigendum. Nature 375: 88

Wood BA (1974) A *Homo* talus from East Rudolf, Kenya. J Anat 117: 203–204

Wood BA (1993) Four legs good, two legs better. Nature 363: 587–588

Wood BA (2002) Palaeoanthropology: hominid revelations from Chad. Nature 418: 133–135

Wood BA, Collard M (1999) The human genus. Science 284: 65–71

Wood Jones F (1916) Arboreal man. Edward Arnold, London

Wood Jones F (1929) Man's place among the mammals. Edward Arnold, London

Wrangham RW (1980) Bipedal locomotion as a feeding adaptation in Gelada Baboons, and its implications for hominid evolution. J Hum Evol 9: 329–331

Zollikofer CPE, Ponce de León MS, Lieberman DE, Guy F, Pilbeam D, Likius A, Mackaye HT, Vignaud P, Brunet M (2005) Virtual reconstruction of *Sahelanthropus tchadensis*. Nature 434: 755–759