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**REVIEW**

# Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor

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## Abstract

Based on our knowledge of locomotor biomechanics and ecology we predict the locomotion and posture of the last common ancestors of (a) great and lesser apes and their close fossil relatives (hominoids); (b) chimpanzees, bonobos and modern humans (hominines); and (c) modern humans and their fossil relatives (hominins). We evaluate our propositions against the fossil record in the context of a broader review of evolution of the locomotor system from the earliest hominoids of modern aspect (crown hominoids) to early modern *Homo sapiens.* While some early East African stem hominoids were pronograde, it appears that the adaptations which best characterize the crown hominoids are orthogrady and an ability to abduct the arm above the shoulder – rather than, as is often thought, manual suspension *sensu stricto*. At 7–9 Ma (not much earlier than the likely 4–8 Ma divergence date for panins and hominins, see Bradley, 2008) there were crown hominoids in southern Europe which were adapted to moving in an orthograde posture, supported primarily on the hindlimb, in an arboreal, and possibly for *Oreopithecus*, a terrestrial context. By 7 Ma, *Sahelanthropus* provides evidence of a Central African hominin, panin or possibly gorilline adapted to orthogrady, and both orthogrady and habitually highly extended postures of the hip are evident in the arboreal East African protohominin *Orrorin* at 6 Ma. If the traditional idea that hominins passed through a terrestrial 'knuckle-walking' phase is correct, not only does it have to be explained how a quadrupedal gait typified by flexed postures of the hindlimb could have preadapted the body for the hominin acquisition of straight-legged erect bipedality, but we would have to accept a transition from stem-hominoid pronogrady to crown hominoid orthogrady, back again to pronogrady in the African apes and then back to orthogrady in hominins. Hand-assisted arboreal bipedality, which is part of a continuum of orthograde behaviours, is used by modern orangutans to forage among the small branches at the periphery of trees where the core hominoid dietary resource, ripe fruit, is most often to be found. Derivation of habitual terrestrial bipedality from arboreal hand-assisted bipedality requires fewer transitions, and is also kinematically and kinetically more parsimonious.

**Key words** biomechanics; ecology; fossils; hominins; hominoids; locomotion; posture.

## Introduction

It has long been held (e.g. see Keith, 1923) and taught (e.g. see Fleagle, 1998) that the living apes share, and are best defined by, a set of functional characteristics related to the trunk and upper limb. These features (e.g. see Ward, 2007) include a stiff lumbar spine; a broad, flattened ribcage into which the spine is ventrally 'embedded'; a matching broad pelvis; a scapula located on the back of the ribcage, and a shoulder joint adapted to allow extensive abduction (Rose, 1993, 1997; Larson, 1998). Keith (1923) and most following him considered that such characteristics are linked to 'brachiation': forelimb-suspensory under-branch locomotion. However, as we shall show below, both locomotor ecology and recent fossil evidence suggests that suspensory locomotion may have been acquired independently by several hominoid lineages. Rather, it is actually upright (orthograde) truncal posture which is their common inheritance from their last common ancestor. Upright posture is found not only in suspension, but in the climbing, clambering [in which the forelimbs support the majority of body mass, but the hindlimbs may contribute in either abducted (suspensory) or extended (compressive)

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**R.H.C. and S.K.S.T. dedicate this paper to our mentor Neill Alexander.**

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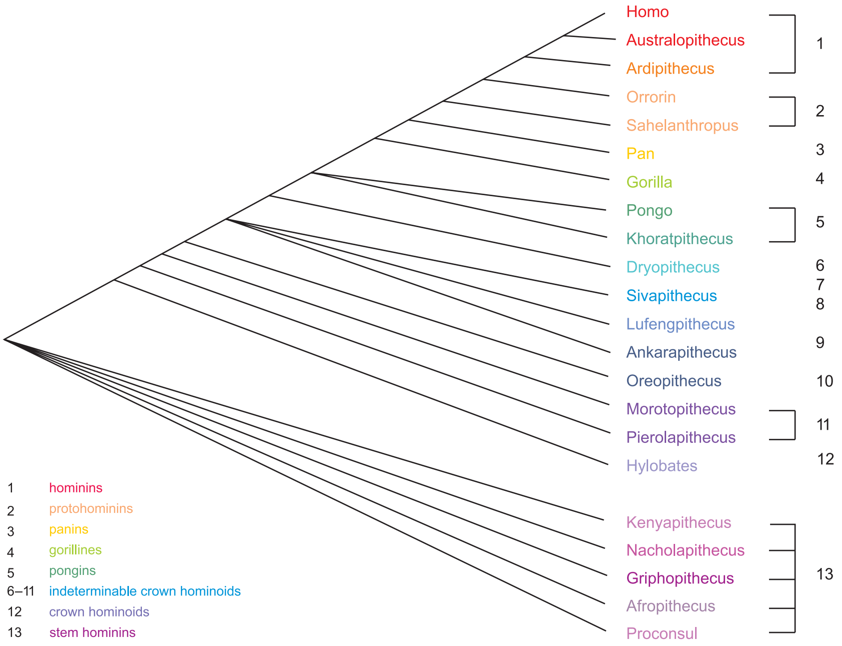

**Fig. 1** Ad hoc and purely heuristic diagram of possible relationships of some hominoid genera included in this review.

postures (Hunt et al. 1996)] and occasional bipedal locomotion shared by all living apes.

All living apes fall into the superfamily Hominoidea. Hominoidea may reasonably be held (e.g. see Wood & Richmond, 2000) to comprise two families, Hylobatidae (gibbons and siamangs) and Hominidae, the latter in turn comprising the subfamilies Ponginae (orangutans), Gorillinae (gorillas) and Homininae. Within the Homininae are tribes Panini (chimpanzees and bonobos) and Hominini (modern humans and their immediate fossil relatives). Despite a substantial pronograde component, of arboreal quadrupedalism (as in orangutans) and terrestrial knuckle-walking in their locomotor repertoire, panins and gorillines share (as indicated above) the characteristic features of truncal morphology found in all other living apes: pongines, hylobatids and hominins.

However, our perception of hominin, as well as hominoid, locomotor evolution has probably been coloured by the fact that one of the largest and most diverse groups of ape-like fossils, while dentally and cranially ‘ape-like’ shows little postcranial similarity to living apes. This group generally referred to as the proconsulids, comes from the ‘cradle of mankind’, East Africa, and dates to 12–19 Ma. A certain degree of locomotor diversity has recently been established, including, for example, some evidence suggesting terrestrial knuckle-walking in *Kenyapithecus*, and perhaps some degree of forelimb-powered suspensory quadrupedalism in *Nacholapithecus*. Nevertheless, proconsulid postcranials, if anything, tend to resemble those of branch-walking monkeys. Thus, they have a mobile lumbar spine, suspending below it an anteroposteriorly deep thorax, in distinction to the case in all living apes. Over the last decade, an increasing number of workers (e.g. Larson, 1998; Begun, 2002; Harrison, 2002; Finarelli & Clyde, 2004; MacLatchy, 2004; Young & MacLatchy, 2004) have suggested that they should therefore be regarded as a ‘stem’ or ‘archaic’ hominoid radiation, not closely related to the ancestry of living hominoids and their fossil affines, the crown hominoids, also called euhominoids.

A methodological difficulty exists in any analysis of the locomotor and postural evolution of the hominoids. The number of dentocranial fossils far outweighs that of postcranial fossils, so that dentocranial remains are usually central to phylogenetic analysis of the fossil record. Yet, it appears not only that living apes are best characterized by their postcranial adaptations, but fossil postcranials attributed to apes show less homoplasy than dentocranial remains (Finarelli & Clyde, 2004), making them in this one case better suited for phylogenetic analysis. While aware of the circularity this creates, we shall use a working hypothesis of generic relationships (Fig. 1) adapted ad hoc from features of the most parsimonious morphologically based phylogenies obtained by Finarelli & Clyde (2004) and Young & MacLatchy (2004). Both separate proconsulids and their affines as stem hominoids.

The aim of this paper* is two-fold, first to provide a single (and thus necessarily non-exhaustive) source of data on hominoid and hominin locomotor evolution, aimed at Honours/senior year undergraduate and beginning postgraduate students, and secondly further to explore our hypothesis (Thorpe et al. 2007a,b; Crompton & Thorpe, 2007; and see also Crompton et al. 2003) that modern human obligate terrestrial bipedality is ultimately derived from facultative arboreal bipedality in an orthograde last common ancestor (LCA) of crown hominoids. We are by no means the first to have proposed an arboreal origin for hominin bipedality: Senut (e.g. 2003, 2006) and Pickford (e.g. 2006) in particular have pointed to an increasing

**Table 1** Predicted features of the last common ancestors (LCAs)*

| | |
|---|---|
| LCA of living crown hominoids | |
| Positional behaviour | Habitually arboreal and orthograde, with some stabilization of lumbar spine and at least gibbon-like thoracic shape. Scapula dorsally placed with elongated vertebral border. Locomotion primarily orthograde clambering, including hand-assisted bipedality. Some quadrupedalism on large branches, suspensory locomotion questionable. |
| Forelimb | Long forelimb, capable of extensive abduction, grasping hand with relatively, but not extremely long fingers. Not necessarily adapted for suspensory posture or locomotion. |
| Hindlimb | Hindlimb relatively but not extremely short, capable of deep extension at hip and knee, and also widely abductable at hip. Foot grasping, used in inverted but plantigrade posture. *Heel-strike appears in LCA of great apes.* |
| LCA of Panini and Hominini | |
| Positional behaviour | Predominantly arboreal, orthograde, extensive stabilization of lumbar spine, scapula dorsally placed with elongated vertebral border. Locomotion primarily orthograde clambering, including hand-assisted bipedality, but vertical climbing present and some unassisted terrestrial bipedalism. |
| Forelimb | Long armed, some suspension with curved fingers of moderate length. |
| Hindlimb | Legs relatively short, with long curved toes. Hip and knee able to transmit force in a very extended posture, but hip joint still capable of a high degree of abduction.<br>Foot plantigrade, with heel-strike, used in a predominantly mid-prone/inverted posture. Mid-tarsal break evident. Achilles' tendon absent or poorly marked. |
| LCA of Hominini | |
| Positional behaviour | Orthograde terrestrial biped with extended hip and knee postures, with some climbing in smaller trees. |
| Forelimb | Long arms and enhanced grasp in hands. |
| Hindlimb | Lower limb relatively short. Hip showing reduced abduction, possibly as a result of pelvic shortening and iliac flare. Knee lacking locking mechanism, bicondylar angle develops with bipedalism. Talocrural joint adapted for parasagittal motion of the tibia over the foot. Stabilization of mid-foot, increased inversion and pronation evident, with a nascent medial arch. Relatively forwards position of centre of pressure at onset of acceleration. Extensive metatarsophalangeal dorsiflexion possible, providing greater force at toe-off. Achilles' tendon probably absent or poorly marked. |

*Predictions are based on our hypothesis of the role of bipedalism and generalised orthogrady in the locomotor repertoire of the apes (see text for further discussion).

weight of evidence from the hominin and protohominin fossil record, and associated palaeoenvironmental evidence pointing in this direction, and both Pickford (e.g. 2003) and Clarke (e.g. 2003) have interpreted the origin of human anatomical features in this context.

The locomotor ecology and biomechanics of the living apes remain a surprisingly underutilized resource – even when several of our hominoid cousins are in immediate danger of extinction in the wild.

We begin with a brief comparison of hominoid locomotor mechanics and foot morphology that identifies the uniqueness of modern human bipedalism, and then discuss those models which have dominated the discussion of the evolution of hominin bipedality over recent decades, using comparative biomechanics of ape locomotion, and locomotor ecology, to identify the behaviour most likely to be preadaptive for obligate bipedality. We suggest that our hypothesis provides a simpler, more parsimonious model for the origins of hominin bipedality than the currently dominant models (particularly the 'knuckle-walking' hypothesis and strict interpretations of the 'vertical climbing' hypothesis) and present its predictions (Table 1) for the locomotor and postural adaptations of the LCAs: (1) of crown hominoids, (2) of Panini and Hominini and (3) of Hominini. We then review the fossil record for the evolution of the hominoid and hominin locomotor system [excluding *Limnopithecus*, *Simiolus*, *Dendropithecus* and *Pliopithecus* as the consensus view is that they are stem *catarrhines*, not even stem hominoids (e.g. see Ciochon & Corruccini, 1977; Szalay & Delson, 1979; Harrison, 2002)] and ending with archaic *Homo sapiens* and *H. neanderthalensis*. The fossils are arranged as far as possible in the standard groupings used elsewhere in this issue, and to facilitate assessment of our propositions for LCAs. Then, in the Discussion, we assess and reconsider our propositions for the three LCAs in the light of the fossil record, and summarize major locomotor trends in the panins, gorillines and early hominins, before discussing the transition to the modern body form seen in genus *Homo* and finally trends within genus *Homo* itself.

## The uniqueness of modern human bipedalism

### (a) Mechanics of locomotion

As observed by Alexander (1991, 2004), modern human bipedalism is mechanically unique primarily in its utilization

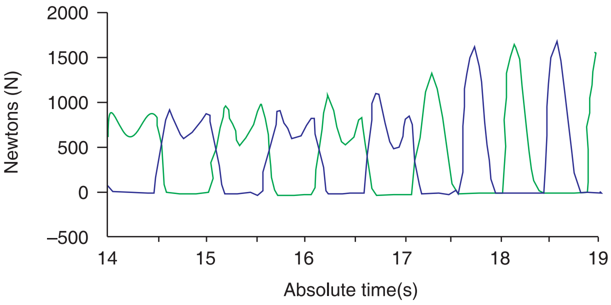

**Fig. 2** Graph showing the vertical ground reaction forces (*n*) under the right (blue) and left foot (green) as a function of time (s) for human walking and running. Human walking produces double-humped vertical ground reaction force curves, and has a period of double-support where heel-strike of one leg overlaps toe-off of the other (left curves). At about 2.2 m s$^{-1}$ we change gaits to running, which gives single-humped ground reaction force curves, lacks a period of double support, and typically has a 'floating' phase when neither foot is in contact with the ground (spaces between right curves).

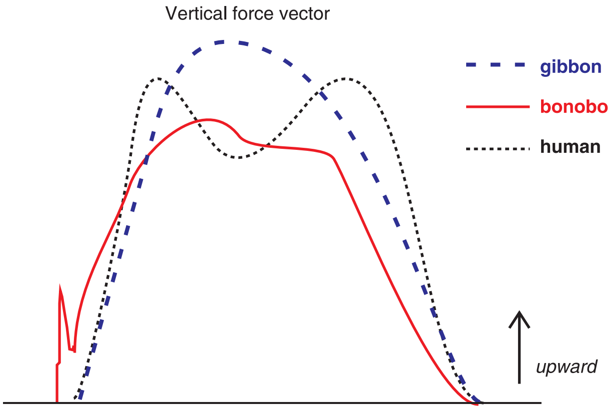

**Fig. 3** Graph showing the average vertical ground reaction force (scaled to body weight) for human (dotted line), bonobo (bold line) and gibbon (dashed line) bipedalism. Ninety per cent of voluntary bipedal walking by bonobos produces a single-humped vertical ground reaction force curve, 10% gives a mildly double-humped form. Gibbon bipedal running produces a single-humped curve, but unlike human running there is usually no floating phase. Note that gibbons do not show a heel-strike transient, which appears to be a great-ape feature. Also note the abrupt drop in vertical force prior to toe-off in humans, and the more gradual decrease in vertical force in both apes.

of extended, or stiff postures of the hip and knee joints during walking. When running, however, we adopt relatively flexed (or compliant) postures of the hip and knee – as most vertebrates do whether walking or running.

In living humans, efficient walking depends on extended postures of the hip and knee, producing a characteristic double-humped vertical ground reaction force curve (Fig. 2) and out-of-phase oscillations of the potential and kinetic energies of the body centre of gravity (CoG). As in an inverted pendulum, when the CoG is highest (mid-stance) and its potential energy is therefore greatest, its forwards velocity and hence kinetic energy are lowest – and vice versa both at heel-strike and toe-off. The extended postures of the hip and knee, and consequent out-of-phase oscillations of kinetic and potential energies of the CoG, permit 50–70% [depending on mode of calculation (Wang et al. 2003a)] of the energy expended in one stride to be exchanged/converted and hence conserved for the next. Heel-strike of one leg overlaps with toe-off in the next, so that there is a phase of double support. At about 2.2 m s$^{-1}$ (Fig. 2) modern humans switch to a running gait, which depends for its efficiency on the elastic storage of energy (comparable with a bouncing ball) in tissues such as the plantar aponeurosis, spring ligament and Achilles' tendon. Human running has no period of double support, but has a floating (i.e. entirely airborne) phase, the higher acceleration needed to lift the body off the ground being substantially paid back by elastic recoil. Running shows a single-humped ground reaction force curve, as the CoG is lower during midstance (Alexander, 2004) and kinetic and potential energies of the CoG are in phase. A third modern human gait exists (Minetti, 1998) in children and interestingly also in simulations which are allowed to develop their own optimal gaits (e.g. see Sellers et al. 2005): skipping is a high-speed bipedal gait in which one foot has both stance and swing phases, followed with a small double stance phase, then by a stance and swing phase of the opposite foot.

In contrast, among the other extant apes, only gibbons can sustain prolonged bipedalism. They are able to attain absolute speeds of 3.5 m s$^{-1}$, well above the modern human walk/run transition speed, and normally adopt a bouncing, flexed-hip-and-knee 'running' gait at all speeds. Unlike modern human running this gait generally (but not always) lacks a floating phase (Vereecke et al. 2006a,b). The vertical force profile during hylobatid bipedalism is nearly always single-humped (Kimura et al. 1977, 1983; Okada et al. 1983; Vereecke et al. 2005, and see Fig. 3). The potential and kinetic energy always fluctuate in-phase, indicating that a spring-mass mechanism is used at all speeds and that a clear-cut gait transition (like the modern human walk–run transition shown in Fig. 2) is absent, although, at low speeds, gibbons occasionally adopt an inverted-pendulum-like gait (Vereecke et al. 2006b).

## (b) Foot morphology

While most of the gross anatomy of the locomotor system of the great apes (including modern humans) is similar (Thorpe et al. 1999; Payne et al. 2006a,b), the human foot is unique in several aspects (e.g. see Klenerman & Wood, 2006) and deserves special attention. The complexity of the higher primate foot, however, with 22 bones arranged in a three-dimensional lattice of tendons, ligaments and connective tissue, has made it particularly resistant to functional analysis. While we can measure the external forces it exerts, and reconstruct its overall action, its internal mechanics remain largely unknown, and so the few partial feet, and greater number of isolated bones, preserved in the fossil record are difficult to analyse other than morphometrically. We know that the modern human foot changes from a compliant, shock-absorbing, supinated organ just before heel-strike to a near-rigid, pronated lever at toe-off. Peak pressure propagates from the heel, along the lateral arch, medially across the dorsiflexing metatarsophalangeal (MTP) joints and distally to the hallux. Coupling of rotation of the tibia/fibula to rotation of the talus, and of talus rotation to rotation of the more distal tarsals, has long been recognized (reviewed in Wolf et al. 2004). This functional arrangement is known as the torque-converter mechanism, or closed kinematic chain, of the foot.

In contrast to this modern human condition, the grasping feet of other apes are traditionally regarded (see e.g. Aiello & Dean, 1990) as flexing in the mid-foot (mid-tarsal break) rather than at the MTP joints (metatarsal break). Propulsive force is thus exerted in the mid-foot rather than by the toes (compare Fig. 5A,B with Fig. 5C) and the torque-converter mechanism and medial-to-lateral transfer of the CoP across the metatarsal heads are therefore absent. The key events marking hominin acquisition of habitual bipedality thus include enlargement of the calcaneal tuberosity, stabilization of the calcaneocuboid and talonavicular joints and formation of a medial longitudinal arch (e.g. see Harcourt-Smith & Aiello, 2004).

## Models of locomotion and posture in the LCA of panins and hominins: the origins of bipedalism

### (a) The hylobatian model

The development of ideas on the evolution of hominoid locomotion has been heavily influenced by the early work of Keith (1923) who first proposed a scenario where pronograde, arboreal, catarrhine monkey-like primates gave rise to small-bodied 'brachiating' arboreal orthograde gibbon-like primates, the 'hylobatians'. From these, Keith argues, arose larger-bodied arboreal orthograde apes with a similar body design, the 'troglodytians', some of which became adapted to terrestrial bipedalism – the human or 'plantigrade' stage. The common suite of hominoid adaptations in the trunk and upper limb appeared almost in full in the 'hylobatians', while the transition from troglodytian to human involved changes confined almost entirely to the lower limbs (see Tuttle et al. 1974).

While several authors have presented scenarios (see below) for the origin of bipedalism based on the 'troglodytians' in large-bodied apes, or to the knuckle-walking behaviour of modern panins and gorillines, Tuttle (e.g. 1969, 1981, et al. 1974) proposes rather that bipedalism arose on the basis of the 'hylobatian' stage. In the 1981 version of his model, he envisions 9–13.5-kg hylobatians, using vertical climbing on tree trunks and vines and bipedalism on horizontal boughs. His hylobatians would have stood bipedally for foraging or display, and engaged in 'short bursts of bipedal running and hindlimb-propelled leaps' (Tuttle, 1981, p. 90) to capture insects and small vertebrates. Anatomically, they would have followed the common hominoid pattern except that they would have had 'long, extensible hindlimbs' with powerful gluteal, quadriceps and triceps surae muscles. The lumbar spine would not have been shortened and would have been laterally flexible to aid vertical climbing. At this stage 'arm-swinging along branches was quite rare and richochetal arm-swinging was not practised at all' (Tuttle, 1981, p. 91), even though the model is identified with the generic name of modern gibbons.

We have seen that walking and running are biomechanically different in modern humans, depending on entirely different mechanical principles for their efficiency, and that it is modern human walking, not running, which is distinctive. Since gibbon bipedalism is nearly all running, and this running differs mechanically from modern human running in that it lacks a floating phase, it is difficult to see how modern human bipedality, walking or running, could readily be derived from 'hylobatian' hindlimb activity, if the latter is indeed modelled on aspects of gibbon locomotion. However, we acknowledge our debt to Tuttle for his early (1969) suggestion that modern human bipedalism has its origins in arboreal, orthograde activities.

### (b) The knuckle-walking model

Washburn (1967) was the first of several to have been led by the genetic proximity of hominins and panins to seek a panin/gorilline (i.e. 'troglodytian', Keith 1923) model for the origin of modern human bipedalism, even suggesting that knuckle-walking was more important than manual dexterity in the origins of tool-use and tool-making. Richmond & Strait (2000), Richmond et al. (2001) and most recently Begun et al. (2007) have endeavoured to support the knuckle-walking model both by reference to the fossil record (and we deal with this aspect in our discussion) and by assembling lists of resemblances between the modern human forelimb and that of the knuckle-walking African apes. But a substantial series of resemblances have also been noted between the postcranium of orangutans and that of humans (e.g. reviewed in Schwartz, 2005, and see below). Some proposed 'knuckle-walking' features resemble features of the forelimb of the giant anteater (Orr, 2005). This does suggest functional linkage, but by the same token, a high likelihood of homoplasy. Only a combination of functional, biomechanical analysis and phylogenetic analysis could show whether the purported 'knuckle-walking' features seen in modern humans can indeed be brought

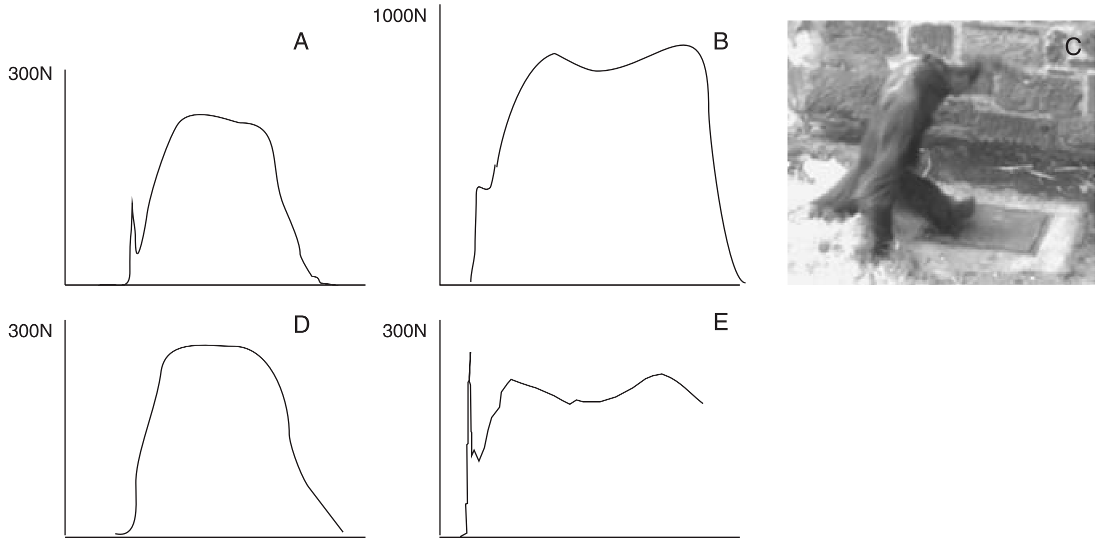

**Fig. 4** Illustration of some vertical ground reaction forces for orangutan (A, ~~D~~, E) and chimpanzee (~~B~~) bipedalism. While most orangutan bipedalism produces a single peak (A) – ignoring the heel-strike transient, seen also in chimpanzee bipedalism (~~B~~), and produced by contact of the calcaneal tuberosity with the ground (see picture C) as in humans – the highly extended hip and knee in voluntary bipedalism of orangutans (C) produce clearly double humped curves in 25% of cases (~~D~~). This gives *c.* 50% energy transformation (depending on method of calculation, e.g. see Wang et al. 2003a), resembling curves in human slow walking and some cases (e.g. E, an incomplete record) even human 'comfortable' walking.

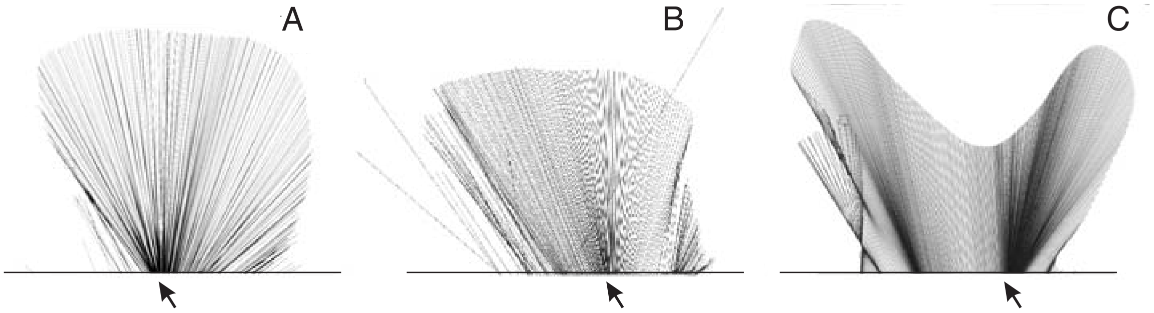

**Fig. 5** Vector (Pedottii) diagrams, showing the force vector over centre of pressure in the sagittal plane from heel-strike (left) to toe-off (right), for untrained chimpanzees (A), orangutans (B) and humans (C). The force vector changes from braking (backwards inclination) to acceleration (forwards inclination) more posteriorly in bipedally walking common chimpanzees (A) than orangutans (B), but most anteriorly in humans (C).

about as adaptations to knuckle-walking alone, and whether they are indeed shared, derived features of the African apes, including hominins.

Lower limb and trunk kinematics of knuckle-walking are very dissimilar to those of modern human bipedalism. In the latter, the angle subtended by the trunk and thigh reaches around 210° at toe-off. In knuckle-walking by common chimpanzees, however, the mean hip extension angle at toe-off is 134° ($n$ = 10, SD = 7.6). In common chimpanzee bipedalism, the hip extends little more than 125° (Jenkins, 1972), so that the stance-phase foot rarely passes behind the hip joint. The consequence of the flexed hip and knee postures which characterize the voluntary bipedalism of untrained common chimpanzees (Li et al. 1996; Alexander, 2004) are flat-topped vertical ground reaction force curves (vGRFs) (Fig. 4B) with kinetic and potential energies nearly in phase, which offer little more than 8% transformation of energy (Wang et al. 2003a). Untrained bonobos usually produce a single-humped curve (Fig. 3), but produce a mildly double-humped vGRF curve in about 10% of voluntary bipedalism (K. D'Août, personal communication). The extended hip and thigh postures adopted by untrained captive-bred orangutans, however, give double-humped vGRFs (Fig. 4D) in about a quarter of cases, similar to those in modern human slow walking, and giving some 50% energy transformation (depending on mode of calculation, see Wang et al. 2003a,b). A few even resemble modern human walking at a 'comfortable' speed (Fig. 4E).

Gebo (1992, 1996) also favours terrestrial quadrupedalism as the precursor for bipedalism. He argues that similarities in the foot structure of the African apes, which he regards as pre-adaptive for the acquisition of bipedalism in hominins,

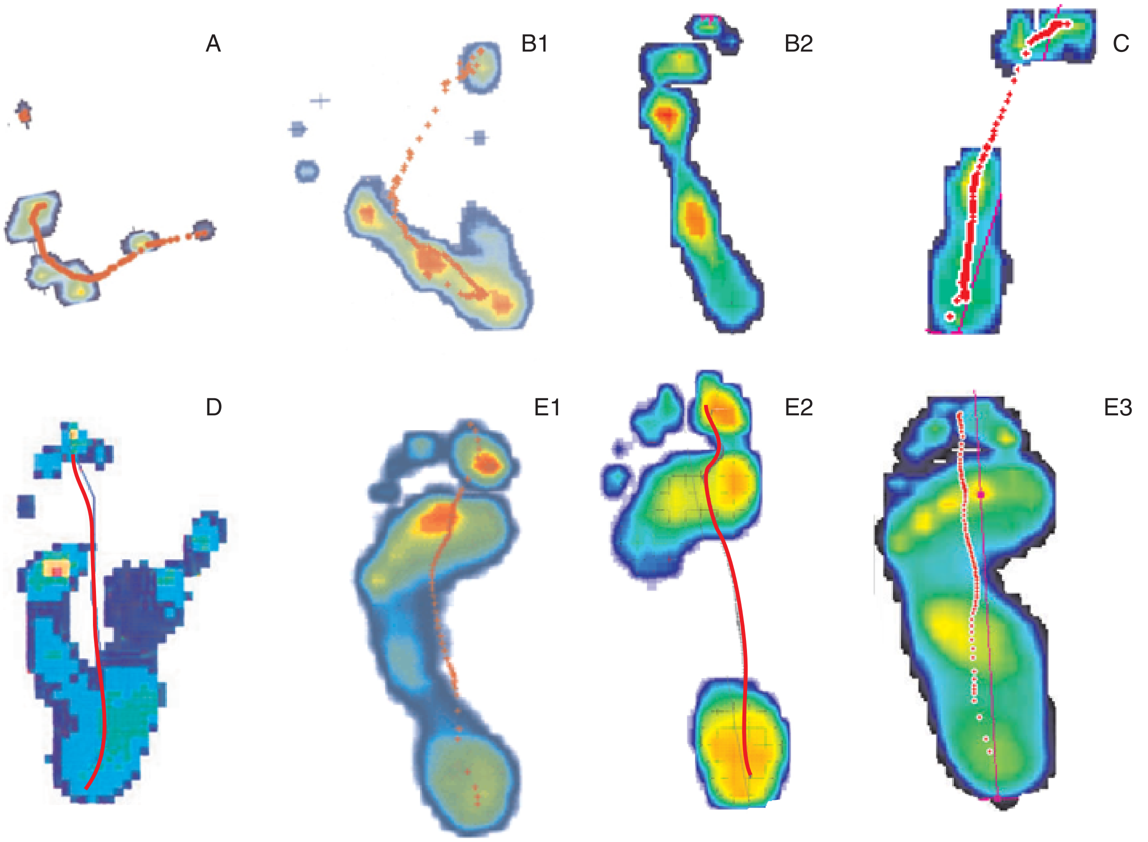

**Fig. 6** Peak plantar pressure maps (high pressures: red, low pressures: blue) during gibbon (A), bonobo (B), orangutan (C), gorilla (D), and human (E) bipedalism. (A) Gibbons lack a heel-strike and the path of the centre of pressure (red line) indicates that the hallux makes first contact. (B) Plantar pressure profiles are variable in bonobos, typically showing a relatively everted foot (B1), but are sometimes quite inverted (B2). Orangutan and gorilla pressure maps are difficult to obtain and hence rare; (C) shows a quite inverted orangutan foot posture (comparable to B2), while the pressure profile of a lowland gorilla shown in (D) displays the most eversion and a directly-forwards path of the centre of pressure (red line). (E) A typical peak pressure map for normal straight-legged human walking (E1) with a typical lateral-to-medial shift of the centre of pressure under the metatarsal heads contrasts with a record for human bent-hip, bent-knee walking (E2), where the trace of the centre of pressure propagates forwards more directly. (E3) In a human showing a pressure peak in the mid-foot, the centre of pressure propagates more or less directly forwards, as it usually does in great apes.

are related to what he terms 'heel-strike plantigrady'. He considers this as a specifically terrestrial, and derived, feature of the great apes, where a specialized heel is the first part of the foot to make ground contact, and then weight is born by the whole plantar surface of the foot. In his 1992 paper he claimed that orangutans, as well as gibbons, lack 'heel-strike plantigrady', i.e. that it is an acquired feature of the African apes. However, Meldrum (1993, p. 380) pointed out that the orangutan 'frequently walks using a plantigrade (i.e. heel-down) foot posture on the ground and on large-diameter supports'. In his 1996 paper, Gebo concedes this point for terrestrial gait only, but argues that since orangutans are predominantly arboreal, they must have developed heel-strike plantigrady in an earlier, terrestrial phase, noting the (then current) arguments that *Sivapithecus* might have been terrestrial. Orangutan bipedalism, however, is not only characterized by heel-strike plantigrady (Crompton et al. 2003), but usually produces a sharp heel-strike transient (Fig. 4A,D,E) which, as Fig. 4C shows, is produced by contact of the calcaneal tuberosity. Vereecke et al. (2005) show that, while gibbons do lack a heel-strike transient, they are, however, clearly plantigrade (Figs 3 and 6A), suggesting that plantigrady is a crown-hominoid characteristic. Heel-strike, however, appears to be a great-ape characteristic, related perhaps to large body size (Vereecke et al. 2005), which in turn may be an adaptation to movement and foraging in the small-branch niche (Larson, 1998; MacLatchy, 2004).

Gebo (1996) argues that the orangutan foot has become specialized for arboreal life, and does not display the weight-bearing features of the African ape foot, which he regards as preadaptive for human bipedalism. It is of course true that the orangutan foot is adapted to arboreal gait, for example in its (usually) inverted posture. However, other functional features of the orangutan foot do resemble those seen in the modern human foot. Figures 5A–C are Pedotti, or 'butterfly' diagrams of the sagittal force vector over the centre of pressure (CoP) under the foot. A forwards position at onset of acceleration increases the power arm of the plantarflexors at push-off. The figures show that a more anterior transition from braking to acceleration may occur in voluntary bipedalism of untrained orangutans (Fig. 5B) than untrained common chimpanzees (Fig. 5A), although still well posterior to the position in adult modern human bipedalism (Fig. 5C). Kimura (1996) found that training chimpanzees in upright bipedalism over several years can result in a more anterior position of the CoP at onset of acceleration, as well as substantial energy transformation. This suggests that our finding is related to the habitually more upright, and extended-leg, posture seen in wild as well as captive orangutans, and may explain how some (but not most) trained chimpanzees may achieve a bipedal gait less costly than their knuckle-walking quadrupedalism (Sockol et al. 2007). But in both Kimura's (1996) trained chimpanzees and our untrained orangutans, substantial transformation of energy only occurs at very slow speeds – some 0.2 m $s^{-1}$ according to Kimura, little more (some 0.3 m $s^{-1}$ ) in orangutans.

Both bonobo (Fig. 6B) and orangutan (Fig. 6C) foot pressure maps show a mid-foot peak indicating a mid-tarsal break, but unquestionably most weight is placed on the lateral side of the foot in the orangutan, and even in the bonobo (Fig. 6B-1). The lowland gorilla (Fig. 6D) seems to show the most everted foot posture, recalling Wang & Crompton's (2004a) model of static loading, which showed that the lowland gorilla has the foot biomechanically best adapted for bipedal standing of the non-human living apes.

Modern humans walking with a 'bent-hip, bent-knee' (BHBK) gait (Fig. 6E-2) produce a substantially more directly-forwards path of the CoP than when using a normal (upright) human gait (Fig. 6E-1), which is characterized by a lateral-to-medial motion of the CoP at late stance. However, as well as patients with Charcot foot, some asymptomatic humans [particularly some basketball players of African origin (personal communication from M. Lafortune of Nike Inc., to J.-P. Wilssens of Footscan)] do produce mid-foot pressure peaks (Fig. 6E-3) and in them it appears the CoP propagates directly forwards, as it does in other apes (e.g. Fig. 6D).

To our knowledge, Gebo is the only supporter of the knuckle-walking hypothesis to have offered a functional argument linking knuckle-walking and the origins of modern human bipedality, but as we have shown, his argument, which is restricted to foot function, is poorly supported by the data. No explanation appears to have been offered of how the characteristic flexed hindlimb postures of knuckle-walking gait could have been pre-adaptive for the extended hindlimb postures of modern human walking, or indeed how the transformation could have occurred. Further, the knuckle-walking hypothesis requires that orthogrady evolved twice: from pronograde simians to the orthograde crown hominoids – and then following an adoption of terrestrial knuckle-walking by the common African ape ancestor to orthograde bipedality in hominins. We prefer the alternative, that knuckle-walking evolved evolved independently in gorillines and panins, as the ontogeny of phalangeal and metacarpal scaling (Inouye, 1992) and of other 'knuckle-walking features' (Dainton & Macho, 1999) is different in panins and gorillines, suggesting that knuckle-walking evolved more than once among the African apes.

### (c) The vertical climbing hypothesis

A second hypothesis relating to Keith's (1923) troglodytian stage and, like the knuckle-walking hypothesis, seeking an origin for modern human bipedalism in the behaviours of panins and gorillines, was first fully elaborated by Prost (1980). He proposed that the locomotor behaviour of the African apes most kinematically similar to modern human bipedalism was not their occasional bipedalism, but their vertical climbing. As interpreted by Prost (and see the definition in Hunt et al. 1996), this term means climbing up and down vertical, or near vertical, supports such as lianas and tree-trunks. Stern (1975) and Stern et al. (1977) had observed that the muscles most prominently used in brachiation (in the sense of arm-swinging) are also used in vertical climbing, and Stern and colleagues suggest that traits previously thought to be adaptive for brachiation were actually adaptive for vertical climbing. Prost (1980) reasons that the transformations required for enhanced climbing presage the adaptive features seen in the australopiths. This view is presented most explicitly by Fleagle et al. (1981), who argue, primarily on the basis of morphological and electromyographic studies, that vertical climbing alone could select for both the features traditionally ascribed to 'brachiation' and for hindlimb features which would be pre-adaptive for bipedalism. They conclude (p. 368) that: 'vertical climbing is the one activity found among non-human primates that would functionally pre-adapt the hindlimb musculature for human-like bipedal walking'.

Indeed, in common chimpanzees, hip extension is greater in vertical climbing than in bipedalism, and in bonobos, hip extension in bipedalism (*c.* 138°) does not greatly exceed values for vertical climbing (132°, $n = 37$) (Crompton et al. 2003). However, it is striking that the knee does not pass behind the hip in the common chimpanzee (Jenkins (1972) or bonobo (D'Août et al. 2002). We (Crompton et al. 2003) have only seen it do so in an unnaturally reared and habitually bipedal common chimpanzee, 'Poko'. In the lowland gorilla, however, the knee *does* pass behind the hip joint: the mean hip extension in bipedalism in this species is 193°. But here, hip extension in bipedalism greatly exceeds that for vertical climbing: 120° for males (*n* = 230) or 133° for females (*n* = 10) (data from Hofstetter & Niemitz, 1998; D'Août, personal communication to R.H.C.; Isler, 2002, 2003; Crompton et al. 2003; Isler and Thorpe, 2003, and unpublished data collected by each). However, it is in the most arboreal genus, *Pongo*, that hip extension overlaps that seen in humans, at 200–215° (*n* = 13, e.g. see Payne, 2001). Here again, however, hip extension in vertical climbing is much less at 120–140° (*n* = 32; Crompton et al. 2003; Isler & Thorpe, 2003, and unpublished data).

### (d) The ancestral orthogrady model, building on Tuttle (1969) and Stern (1975)

Thorpe et al. (2007a,b) have recently shown that the extended postures of the hip and knee, which give rise to high rates of energy transformation in modern human bipedalism and in bouts of voluntary bipedalism by untrained captive orangutans, offer important adaptive advantages to wild Sumatran orangutans. As part of a continuum of orthograde clambering behaviours (see Cant, 1987; Thorpe & Crompton, 2005, 2006), hand-assisted bipedality, with extended hips and knees, is selected for accessing the fine terminal branches in the canopy (Thorpe et al. 2007a), where ripe fruits are to be found and crossings between trees can be made most energy-efficiently (Thorpe et al. 2007b). Remarkably, then, we find bipedal kinematics and kinetics closest to those of modern human bipedalism in the locomotor behaviour of the most arboreal of the great apes (Crompton et al. 2003, Thorpe et al. 2007a,b).

Thus, while vertical climbing elicits orthograde trunk postures similar to those in bipedalism and elicits extended hip postures, we cannot agree with Fleagle and colleagues' view (1981, p. 368) that 'vertical climbing is the one activity found among non-human primates that would functionally pre-adapt the hindlimb musculature for modern human-like bipedal walking'.

Stern (1971, p. 304, quoted in Prost, 1980) argued that 'the hip and thigh musculature of man could be most easily derived from that exemplified by non-running, non-leaping primates which are slow-climbers' and in 1975, Stern noted a series of similarities in the postcranial anatomy of hominins and orangutans, citing Oxnard's (1969) study of the shoulder, and the identification by Lisowski et al. (1974) of a general similarity to the orangutan talus in hominin tali from Kromdraai and Olduvai. Cartmill & Milton (1977, p. 269) also suggest that the structure of the hominoid wrist joint may indicate a 'stage of predominantly orthograde slow suspensory quadrupedalism resembling that of an orangutan'. Other evidence suggesting homoplasies in the locomotor system between orangutans and hominins includes the fact that orangutans are the only great ape in which the bicondylar angle of the femur overlaps the modern human range (Halaczek, 1972) (However, it must be noted that the bicondylar angle is strongly influenced by postnatal development, see below, so this similarity indicates only similar loading regimes). The shape of the proximal femur of modern humans and orangutans is also similar and distinct from that of the knuckle-walking apes (Harmon, 2007).

Schwartz (2007) criticizes our (Thorpe et al. 2007a) paper by drawing attention to Lovejoy et al. (1999) who note that care needs to be exercised in the interpretation of the functional as well as systematic significance of postcranial characters inasmuch as some at least are known to be strongly influenced by genes controlling development (homeobox genes), and mediated at the cellular level by molecules which signal positional information within a limb bud. Thus it is possible, for example, that the shortness of the modern human pelvis, which probably exerts particular influence on the coronal-plane stability of the lower limb [hence enhancing, rather than permitting, both bipedal walking and running (Lovejoy et al. 1999)], may have been brought about by a single random genetic change in homeobox genes, semi-independently or even independently of selective pressures on functional performance. However, Filler (2007) has intriguingly suggested that similar single or plural mutations in homeobox genes governing lumbar vertebra morphology, which would have facilitated habitual orthogrady, may have been present in *Morotopithecus* (see below) and thus by extension in the LCA of crown hominoids.

Some other features (such as the bicondylar angle, and femoral neck-shaft angle), however, seem very strongly influenced by loading during life (Lovejoy et al. 1999). In the case of the pelvis, however, we can be reasonably confident that several changes, some of which may well have been strongly influenced by natural selection on functional performance, were necessary to bring about a fully modern human conformation. As we shall see, this is not even present in KNM-WT 15000, implying that these changes occurred over at least 3 Ma.

We think it highly likely, however, that Darwinian selection for an ability to sustain extended hip and knee postures in the sagittal plane does operate in wild orangutans, whether or not the changes in lumbar spine morphology which underlie non-suspensory orthogrady arose by a mutation in homeobox genes in the common crown-hominoid ancestor, as Filler (2007) suggests. By extension, we propose that such Darwinian selection did operate in the common crown-hominoid ancestor: as untrained captive orangutans still produce more extended-hip and knee, and hence more modern human-like, bipedalism than common chimpanzees raised under training for upright bipedal posture and gait (Crompton et al. 2003).

Stern (1975, p. 67) suggests: 'If we now piece together all the similarities between modern man and living anti-pronograde primates, with one exception they point clearly to an animal that employs its forelimb much as does the living orangutan and its hindlimbs in a somewhat more pronograde quadrupedal manner than does *Pongo*. Such might be the behaviour of a smaller bodied version of the orangutan that had begun to employ its forelimbs extensively in climbing, suspension and other tensile activities, but had not yet reached the size which was to cause it to abandon so completely pronograde quadrupedality.' In fact, Thorpe & Crompton's (2006) review shows that the frequency of pronograde (above-branch) quadrupedalism and tripedalism in the orangutan repertoire is not markedly different from that of panins and gorillines, the orangutan (18%) resembling lowland gorillas (19%) particularly closely in this. Notable quantitative differences between orangutans, on the one hand, and the panins and gorillines, on the other, are in relatively infrequent vertical climbing, but relatively more frequent orthograde clambering and transfer, in orangutans. All great apes engage in brachiation and forelimb swinging in less than 15% of locomotor bouts, while these are of course far more common in gibbons (67%) and siamangs (59%) (Thorpe & Crompton, 2006). The only qualitative difference is the apparent lack in panins and gorillines of torso-pronograde suspensory locomotion, which forms some 4% of orangutan locomotor behaviour.

As we are unconvinced by the argument for a particularly close (i.e. sister taxa) phylogenetic relationship between hominins and pongines (reviewed in Grehan, 2006), given DNA sequencing evidence to the contrary, we must be able to derive an origin for bipedalism from the common African-ape ancestor. This is indeed possible. For example, Hunt (1992, 1994) developed a hypothesis for an origin of hominin bipedalism in postural bipedalism of chimpanzees in Gombe and Mahale, based on his observations of chimpanzees standing bipedally on relatively small (mean 3.9 cm) branches, or on the ground, while taking fruits from overhead, assisted by a second, 'hanging' arm. Further, Stanford (2006) reports considerable amounts (0.73 bouts per observation hour) of arboreal postural bipedalism in feeding contexts in common chimpanzees from the Bwindi Impenetrable Forest, and Stanford & Nkurunungi (2003) report similar arboreal postural bipedalism in lowland gorillas in the same forest.

However, the forces, risks and costs of postural activity are inevitably considerably lower than those in locomotion (even though the duration of postural behaviour may be longer), and it is noteworthy that lowland gorillas in the Democratic Republic of Congo have been filmed for television using hand-assisted bipedal walking on small branches in the deep forest. Crucially, with reference to the lack of quantitative evidence of arboreal bipedal walking in panins and gorillines to match that of orangutans, this walking was flexed-hip, flexed-knee, unlike that of orangutans, and we have filmed similar flexed-knee hand-assisted bipedal walking in captive common chimpanzees (e.g. see fig. 1D in Thorpe et al. 2007a, p. 1329).

The hypothesis that early hominins initially employed bipedality in an arboreal rather than terrestrial environment is also compatible with an increasing volume of evidence linking early hominins to moist or even wet woodland rather than 'savannah' (i.e. Sahel/semi-arid bushlands, Andrews & Humphrey, 1999) environments. Care must be taken in linking the anatomy of individual fossil species to adaptations to the environments in which they happen to be found, for several reasons: firstly, as these may not sample the whole range of environments in which they lived; secondly, in conditions of environmental change and patchiness, because pre-existing changes in morphology probably enabled them to exploit new environments/niches as well as/instead of forcing them to move into new environments. Species diversity in Early Miocene Hominoidea is likely to be a case in point (e.g. see Andrews & Humphrey, 1999; Elton, 2008): diversity appearing to temporally precede environmental change. Character displacement could of course have enhanced the capabilities of given species to exploit given new environments as they appeared, and exploiting new environments would bring new selective pressures to bear on morphology. But partitioning morphological change into enabling or responsive change will not be trivial.

Nevertheless, palaeoenvironmental data suggest that *Ardipithecus* was first associated with 'predominantly wet and closed woodland/forest habitats' with 'open woodland or wooded grassland around lake margins' (*Ar. kadabba*, Wolde Gabriel et al. 2001) but later (*Ar. ramidus*) with seasonally dry forest/closed woodland environments (Andrews & Humphrey, 1999), and *Au. anamensis* and *Au. afarensis* continued to be associated primarily with woodland environments (Andrews & Humphrey, 1999; Ward et al. 1999a,b).

Kingdon (2003) has proposed that in Africa, from the Middle to Late Miocene, fragmentation of closed forest alternated with reclosure and reinvasion of gallery-forest, moist-woodland and rainforest environments, changes also clearly documented by Elton (2008). Within branches of both the *Pan* and the *Gorilla* lineages, the height-range and frequency of vertical climbing locomotion must have increased, suggests Kingdon (2003), to facilitate access to preferred foods in the main and emergent canopy, while permitting travel between trees in broken-canopy woodland on the ground. Middle Miocene crown hominoids, such as *Hispanopithecus* (*Dryopithecus*) *laietanus*, are of a similar size range to living great apes, although undoubtedly male body weights for living great apes exceed estimated values for the Miocene. Thorpe et al. (2007a) thus speculate that the gorillines and panins, independently, became increasingly specialized on forelimb power, to sustain safety and effectiveness of increased vertical climbing, and so tended to adopt similar, extended-elbow, flexed-hip-and-knee kinematics when moving on the ground, hindlimb musculature being unable readily to sustain hip and knee extension and hence a bipedal gait. Hominin ancestors, we speculate, sacrificed continued access to the canopy, and became increasingly ground and small-tree dwellers. Lacking the increased specializations for vertical climbing, they were able to sustain a bipedal gait – and we may add, inasmuch as they were terrestrial, that they could sacrifice coronal-plane mobility, which also characterizes the orangutan, in favour of more effective parasagittal force-production.

Although it might to some seem counter-intuitive, dietary reconstructions for Middle Miocene crown hominoids such as *Sivapithecus* (Nelson, 2003) support the proposition that the dietary range of living great apes is little changed from the Miocene. Indeed, Pilbeam (1996, 2002) notes that the basic niche of hominoids has remained the same through much of their history as tropical-forest ripe-fruit eaters, foraging in the peripheral canopy and hence among fine, unstable branches. The fall-back foods of African apes today, however, are often found on the ground (Pontzer & Wrangham, 2004) and this may be a significant, climate-related shift in adaptation.

Adoption of terrestrial bipedality would have initiated strong selection for increased speed, endurance and possibly carrying ability in early hominins, in particular influencing the talocrural joint, and to some extent the hip, to limit propulsive forces to a parasagittal plane, and of course the foot, to enhance speed and energy return. We shall see from the evidence of the *Au. anamensis* tibia that modification of the talar trochlea to permit the leg to pass directly forwards during mid-stance (Aiello & Dean, 1990) was achieved by one hominin taxon at least relatively early in hominin evolution (by 4.2 Ma at the latest).

## Predicted Features of Last Common Ancestors (LCAS)

To test whether our model offers a parsimonious explanation for hominoid locomotor diversification, we assimilate in Table 1 the hypotheses inherent in the model, to predict the locomotor and postural adaptations of the LCAs of crown hominoids, Panini and Hominini, and of Hominini. These hypotheses focus on (1) a proposition that generalized orthogrady, rather than forelimb suspension exclusively, best describes the core locomotor repertoire of the hominoids and accounts for shared features in the upper limb and trunk. Such positional behaviour enabled relatively large-bodied hominoids to navigate the complex mesh of flexible branches in the forest canopy; (2) a proposition that in locomotor diversification within the African-ape clade during climate-driven forest fragmentation, it was, contrary to traditional belief, the hominins that were conservative and the panins and gorillines that innovated; and (3) a final proposition that selection for terrestrial bipedality did not occur until the appearance of Hominini, at which time the lack of arboreal hand-holds to stabilize a functionally bipedal body initiated the first of many refinements that facilitate efficient terrestrial bipedalism in modern humans.

## The fossil evidence

### (1) Early African and European stem hominoids and crown hominoids, 21–12 Ma *Proconsul* spp.

*Proconsul* species date from the Early and Early Middle Miocene (*c.* 17–20 Ma) and hence considerably antedate the known European hominoids [dating not much earlier than 15 Ma (for *Griphopithecus*)]. According to Andrews & Humphrey (1999) they tend to be associated with evergreen tropical rainforest, or on Rusinga Island, with environments similar to current Kenyan coastal forest. Estimated body weights are about 11 kg for *Proconsul heseloni*, 35.6 kg for *Proconsul nyanzae* and 75 kg for *Proconsul major* (Rafferty et al. 1995; Walker 1997) (Table 2). The large size range, despite the relative homogeneity of known postcranial morphology, surely implies the likelihood of substantially different ecology and behaviour within the genus (Walker, 1997). However, as few postcrania have been described for *P. major*, any ecological distinctions must remain speculative and we follow Rose (1993, 1997) in giving a single composite description for the genus. The skeleton remains best known for *P. heseloni*, for which several partial skeletons exist from Rusinga Island (for a taxonomic and general review see Begun, 1992). Estimates of the intermembral indices of the specimens (Walker & Pickford, 1983; Rose, 1997) resemble those of living cercopithecoids rather than living hominoids. Li et al. (2002) found on the basis of computer modelling that limb proportions of *P. heseloni* (assuming common-chimpanzee-like segment mass distribution) best match the quadrupedal gait of macaques. Ward (1993) was able to demonstrate that the lumbar spine of a partial skeleton of *P. nyanzae*, MW 13142 (Ward et al. 1993), retains six lumbar vertebrae, which are relatively elongated compared with those of living hominoids. They also possess ventrally placed transverse processes, again like those of living cercopithecoids rather than living hominoids [and also the *Morotopithecus* vertebra UMP 67-28, where we shall note that the transverse process is relatively dorsally placed (Ward, 1993) increasing the moment arm of the epaxial muscles which control lumbar flexion]. Ward (1993) interpreted the bony morphology as indicating that the epaxial muscles of *Proconsul* retained the narrow, strap-like form seen in living monkeys, where the lumbar spine is laterally flexible. In living hominoids, by contrast, the broad iliocostalis and quadratus lumborum stiffen the lumbar spine against eccentric bending loads. The narrow, and laterally facing iliac blades (Ward, 1993; Walker, 1997) are consistent with a relatively long, mediolaterally narrow and dorsoventrally deep trunk, unlike that of living hominoids. The scapula must therefore have occupied a lateral rather than dorsal position, implying parasagittal upper limb motion, and hence a primarily pronograde quadrupedal gait (Ward, 1993). A lateral fragment of a clavicle resembles those of

**Table 2** Approximate age ranges of fossil genera and species discussed

| Species | Location | Age (Ma) |
|---|---|---|
| *Proconsul heseloni* | Rusinga Island, Kenya | 17.9–17.0 |
| *Proconsul nyanzae* | Mfangano, Kenya | 17.9 |
| *Morotopithecus bishopi* | Moroto, Uganda | 20.6–15.0 |
| *Pierolapithecus catalaunicus* | Barcelona, Spain | 13.0–12.5 |
| *Nacholapithecus kerioi* | Nachola, Kenya | 15.0–14.0 |
| *Kenyapithecus/Equatorius africanus* | Maboko Island and Tugen Hills, Kenya | 16.0–14.5 |
| *Kenyapithecus wickeri* | Fort Ternan, Kenya | 14.0–114.5 |
| *Hispanopithecus* (*Dryopithecus*) *laietanus* | Can Llobateres, Spain | 9.5 |
| *Paidopithex rhenanus* | Eppelsheim, Germany | |
| *Griphopithecus darwini* | Devinska Nova Ves, Slovakia | 16.0–14.0 |
| *Austriacopithecus/Griphopithecus* | Klein Hadersdorf, Austria | 14.5–14.0 |
| *Dryopithecus brancoi* | Rudabanya, Hungary | 10.0 |
| *Sivapithecus* | Siwaliks, Pakistan | 11.0–9.0 |
| *Oreopithecus bambolii* | Tuscany and Sardinia, Italy | 9.0–7.0 |
| *Sahelanthropus tchadensis* | Toros, Chad | 7.0–6.0 |
| *Orrorin tugenensis* | Tugen Hills, Kenya | 6.2–5.6 |
| *Ardipithecus kadabba* | Middle Awash, Ethiopia | 5.8–5.2 |
| *Ardipithecus ramidus* | Aramis, Middle Awash, Ethiopia | 4.4–3.9 |
| *Australopithecus anamensis* | Allia Bay and Kanapoi, Kenya | 4.2–3.9 |
| | Asa Issie, Ethiopia | 4.2–4.1 |
| *Australopithecus afarensis* | Laetoli, Tanzania | 3.6 |
| | Hadar, Ethiopia | 3.4–3.0 |
| *Australopithecus incertae sedis cf afarensis* | Maka, Middle Awash, Ethiopia | 3.5 |
| | Allia Bay, Kenya | 3.9 |
| | South Turkwel, Kenya | 3.6–3.2 |
| *Australopithecus incertae sedis* | Bouri Hata, Middle Awash, Ethiopia | 2.5 |
| | Omo Shungura, Ethiopia | 2.4–2.2 |
| *Australopithecus incertae sedis cf africanus* | Sterkfontein Member 2, South Africa | 3.5 |
| *Australopithecus africanus* | Sterkfontein Member 1 and 4, S Africa | 3.0–2.4 |
| *Paranthropus robustus* | Swartkrans Member 1, S Africa | 1.9–1.4 |
| | Kromdraai, S Africa | 1.8 |
| *Paranthropus boisei* | Koobi Fora, Kenya | 2.5–1.3 |
| | Olduvai, Tanzania | 2.6–1.4 |
| *Homo incertae sedis* | East Turkana, Kenya | *c.* 2.4–1.6 |
| *Homo habilis incertae sedis cf Paranthropus* | Olduvai Bed I, Tanzania | 1.9–1.6 |
| *Homo habilis* | Olduvai Bed I, Tanzania | 1.9–1.6 |
| | East Turkana, Kenya | |
| *Homo rudolfensis* | East Turkana, Kenya | 2.4–1.6 |
| *Homo erectus* | East Turkana, Kenya | 1.6 |
| | West Turkana, Kenya | |
| | Dmanisi, Georgia | 1.75 |
| | Perning, Java | 1.81 |
| *Homo antecessor* | Gran Dolina, Sierra de Atapuerca, Spain | *c.* 0.8 |
| *Homo heidelbergensis* | Bodo and Broken Hill, Africa | 0.6–0.3 |
| | Mauer, Boxgrove, Arago, Steinheim and Swanscombe, Europe | 0.25–0.5 |
| *Homo neanderthalensis* | | *c.* 0.3– |
| *Homo sapiens* | | *c.* 0.3– |

cercopithecids (Rose, 1997), while a partial scapula recalls those of colobines and large platyrrhines (Rose, 1993). As with *Sivapithecus* (see below) the proximal articular region of the humerus is not available, but (again like *Sivapithecus*) the retroflexion and flat deltoid plane of the humerus resemble the morphology of cercopithecids (Rose, 1993) and show adaptation to forceful motion in the parasagittal plane. Similarly, the distal humerus, as in *Sivapithecus*, suggests a living-hominoid-like elbow joint morphology adapted for use throughout a large range of pronation/supination (Rose, 1993), although *Proconsul* differs from *Sivapithecus* in favouring stabilization in fully prone rather than supine posture (Rose, 1997). Radial and ulnar shafts are robust, and the baboon-like retroflexion of the ulnar olecranon process in *P. nyanzae* has been used to suggest terrestriality (Fleagle, 1983). Rose (1993) argued that the same feature may be interpreted as an adaptation to overhead use of the arm, but later (Rose, 1997) agreed with the inference of terrestriality. A long groove in the triquetral permitting distalwards motion of the ulnar styloid process (Rose, 1997), and a mobile, pulley-shaped metacarpophalangeal joint of the thumb (Rose, 1997) suggest an ability to adduct the hand, and thus resemble the configuration in hominoids rather than cercopithecids (Rose, 1993).

In the hindlimb, the narrow sacrum, small sacroiliac joint and probable absence of a tail (Ward et al. 1991) might be considered hominoid-like features (Rose, 1993). Nevertheless, the hip bone of *P. nyanzae* does not resemble those of hominoids, having short, laterally facing ilia and a narrow pubic region (Ward, 1991). The hip joint does permit increased abduction compared with cercopithecids, and a long ischium increases the lever arm of the hamstrings, as in some hominoids. Mediolaterally broad distal femoral condyles are another hominoid-like feature of *P. nyanzae* (Walker, 1997), but the condyles are small, and a well-marked popliteus groove suggests an ability to resist rotatory motion. The robust fibula resembles that of hominoids rather than cercopithecids (Walker, 1997), but the foot, except for evidence of powerful hallucial grasping, is generally unlike those of hominoids, and like that of colobines (Walker, 1997).

Rose (1993) suggests that the locomotor repertoire of *Proconsul* spp. is likely to have been pronograde quadrupedalism similar to that of cercopithecids, but with a greater component of climbing suggested by adaptations for increased pronation/supination and enhanced pollicial and hallucial grasp. Similarly, Walker (1997) proposes that the morphology of the manual phalanges indicates that *Proconsul* was primarily an above-branch arboreal quadruped, but suggests some tendency to hyperextend the metacarphophalangeal joints on larger branches, while pedal anatomy suggests adaptation for a powerful grasp on narrower branches.

Ward (1993, p. 321) states quite emphatically that: 'KNM-MW 13142 exhibits no obvious derived aspects of torso morphology consistent with ape-like or hylobatid-like arboreal locomotion' and '*Proconsul nyanzae* had not undergone prolonged selection to incorporate locomotor behaviours employing substantial amounts of forelimb abduction-adduction, or increased bending loads about the lower spine, into its positional repertoire. These loading regimes are associated with forelimb dominated climbing, bridging and hanging behaviours in extant hominoids.' Instead, bony anatomy of KNM-MW 13142 and *P. heseloni* support the hypothesis that *Proconsul* species were primarily generalized, arboreal quadrupeds.

Thus, fossil evidence suggests that *Proconsul* shares few of the characteristic postcranial features of all living apes, adaptive for orthogrady, and may be considered a stem hominoid, but not a crown hominoid.

### Morotopithecus bishopi

About the earliest known fossil with recognizably ape-like postcranial bones is *Morotopithecus* (*c*. 20.6–15.0 Ma, but see below) from the early–middle Miocene of Moroto in Uganda. It is classified by Harrison (2002) as Hominoidea *incertae sedis.* Craniodentally, it resembles the larger, but 2.5–4.5 Myr younger (MacLatchy, 2004), proconsuloid *Afropithecus.* Postcranially it is represented by distal and proximal femoral fragments, part of the femoral shaft, the glenoid region of the scapula (although the affinity of this specimen has been questioned by Pickford et al. 1999), phalanges and three vertebrae, of which evidence for the lumbar vertebra UMP 67-28 is best preserved. The date of the holotype is contained by a 20.6 Ma underlying basalt bed (Gebo et al. 1997) and a 14.3 Ma overlying lava. Bishop et al. (1969) and Pickford et al. (1999), however, suggest a middle Miocene date of around 15 Ma for *Morotopithecus* based on faunal correlations. The age of *Morotopithecus* is crucial, as a 20.6 Ma date would exceed the earliest generally accepted molecular date for separation of the hylobatids and great apes (14–18 Ma, Young & MacLatchy 2004). There is unfortunately no comprehensive reconstruction of the palaeoenvironment available.

If lumbar vertebra UMP 67-28 is correctly assigned to *Morotopithecus*, several features of the lumbar spine, such as a caudally directed neural spine and caudally directed transverse processes arising from the pedicles, suggest *Morotopithecus* had a stiff back adapted for use in an upright posture (MacLatchy et al. 2000). The vertebrae bear dorsally placed transverse processes (Ward, 1993), contrasting with the vertebrae of cercopithecids, which are ventrally placed. Dorsal placement serves to increase the moment arm of the epaxial muscles that control lumbar flexion (Ward, 1993) and in *Morotopithecus* both the extent of the dorsal shift and the form of the transverse processes resemble those in gibbons rather than great apes. The glenoid region of *Morotopithecus* possessed a great-ape-like capability to abduct the glenohumeral joint (MacLatchy et al. 2000). All these features suggest that *Morotopithecus* is a crown hominoid, sharing most aspects of the shared postcranial features of living apes. Filler (2007) has argued that features of the lumbar morphology of *Morotopithecus* which facilitate upright trunk posture could have occurred as the consequence of simple mutations in homeobox genes, supporting our suggestion of ancestral orthogrady in the crown hominoids.

The proximal femoral fragments might be considered more monkey-like than great-ape-like, in a restricted capacity for abduction (MacLatchy et al. 2000). However, the distal femoral fragments show a thickened ephiyseal cortex like that of *Pongo.* An apparently enlarged medial condyle is consistent rather with adaptation for bearing body weight, over the hindlimb, perhaps in adducted hindlimb postures, while a marked groove (MacLatchy et al. 2000) for popliteus, a rotator/retractor of the femur over a fixed tibia, suggests a stabilization role in postures where the hindlimb is weight-bearing. Young & MacLatchy's (2004) phylogenetic analysis consistently places *Morotopithecus* within, or as the sister group of a great-ape clade that also includes *Dryopithecus* but excludes *Proconsul*. If the hylobatids did indeed separate from the great apes after *Morotopithecus* then the apparent greater locomotor and anatomical similarities of the rather larger siamangs to living great apes suggest that they may be phyletic dwarfs (Pilbeam, 1996), which have developed small body size and acrobatic suspensory locomotion as an adaptation to permit increased ranging capacity (MacLatchy, 2004).

### Kenyapithecus *and* Equatorius

These two genera will be treated together as descriptions/reconstructions depend to some extent on the genus-assignment of specimens, which differs between authors. Together with one distal humeral fragment of *K. wickeri*, from Fort Ternan (*c.* 14.5 Ma), 28 apparently dissociated postcranial elements of *K. africanus* have been discovered from at least partially disturbed deposits at Maboko island (McCrossin & Benefit, 1997). *Kenyapithecus* tends to be associated with environments similar to current seasonal subtropical forest in India (Andrews & Humphrey, 1999). A partial skeleton of *K. africanus* (KNM-TH 28860) from the Muruyur Middle Miocene beds at Kipsaramon in the Tugen Hills, with a date of 16 Ma, is more or less contemporaneous with *Nacholapithecus kerioi.* With respect to the trunk and hindlimb, Ward (1997) notes that *Kenyapithecus* tends to follow *Proconsul* in its pronograde, monkey-like aspect. McCrossin & Benefit (1997), however, give a series of features of the forelimb of the Maboko specimens which may be indicative of a terrestrial habit, the main feature of locomotor interest. These include: a retroflexed olecranon process and medial humeral epicondyle; a transverse dorsal ridge at the distal end of the metacarpals to resist hyperextension of the metacarpophalangeal joint and robust middle phalanges. On the basis of the KNM-TH 28860 skeleton, Sherwood et al. (2002) add: a deep olecranon fossa; a dorsally extending olecranon process; a retroflexed medial humeral epicondyle; a large radial head; and straight phalanges.

As Corruccini & McHenry (2001) suggest, the distal dorsal ridges on the metacarpals would certainly be regarded as ‘knuckle-walking’ features if they occurred in gorillines, panins or hominins, and their appearance here in a 16 Ma hominoid devoid of the postcranial features of crown hominoids surely increases the likelihood of homoplasy in the ‘knuckle-walking’ features of the living African apes.

### Nacholapithecus kerioi

*Nacholapithecus kerioi* (Nakatsukasa et al. 1998; Ishida et al. 2004; Nakatsukasa, 2004) is best known from the KNM-BG 35250 skeleton, and dates from the Middle Miocene (*c.* 15 Ma). Like *P. heseloni*, *Nacholapithecus* was a relatively small ape (*c.* 22 kg). It shares with *Proconsul* spp. a long lumbar vertebral column, and lumbar centra are quite small compared with modern hominoids. Like *Proconsul*, *Nacholapithecus* seems to have lost the tail (Nakatsukasa et al. 2003). No evidence of the ribcage survives but the elongated clavicles may suggest a broad thorax and, in the absence of medial torsion of the humeral head, they are interpreted by Nakatsukasa (2004) as supporting cranially orientated glenoid fossae. (It is of course possible that long clavicles here and in other fossil genera indicate a high shoulder position.) *Nacholapithecus* differs markedly from *Proconsul* spp. in having particularly long and large forelimbs. The pedal and manual phalanges are longer and better individuated than in *Proconsul*, showing clear adaptations for a firm grasp in an arboreal context, a feature more confined to the hallux and pollex in *Proconsul.*

Many of the features of *Nacholapithecus* thus indicate a suspensory habit, but the long lumbar vertebral column, with small centra, suggests to us that orthograde clambering, while perhaps more common than in *Proconsul* and *Kenyapithecus*, was less dominant in *Nacholapithecus* than in *Morotopithecus* and later Eurasian Miocene hominoids. It is also possible that *Nacholapithecus* may have independently acquired some type of specialized forelimb-suspensory locomotion. Given evidence that suspension is not a central feature in the locomotor adaptation of living apes or even fossil apes, *Nacholapithecus* should on balance be considered a stem hominoid.

### Pierolapithecus catalaunicus

*Pierolapithecus* is known from a partial skeleton that includes the gnathocranium, fragments of the clavicle, humeri, radius and carpals, metacarpals and phalanges. Two pelvic fragments, femoral shaft fragments, a patella, some pedal phalanges and tarsals, several ribs; and one nearly complete lumbar vertebra and two vertebral fragments (Moyà-Solà et al. 2004) were discovered in a suburb of Barcelona in deposits dating from the Middle Miocene (13.0–12.5 Ma). Body weight is estimated to be similar to *Hispanopithecus* (*Dryopithecus*) *laietanus* (i.e. *c.* 34 kg, see below). The ribs suggest a broad and shallow thorax, although Begun & Ward (2004) suggest the thorax may have been more similar to that of a hylobatid than a modern great ape. The long clavicle suggests a dorsal position of the scapula and/or a high position of the shoulder joint. The mid-lumbar vertebra is described as having a slightly caudally directed neural spine, suggesting a relatively stiff lumbar region, and the transverse processes arise between the pedicle and body as they do in hylobatids; that is, less dorsally than in *Morotopithecus.* Moyà-Solà et al. (2005) dispute this, arguing the reverse; we may conclude that transverse process position is not markedly different to that in *Morotopithecus* or modern hylobatids. The ulna is excluded from participation in the wrist joint as it is in modern hominoids. The manual phalanges indicate relatively short fingers, but the middle phalanges, in particular, display a strong curvature. The total morphological pattern of the postcranials is therefore that of an orthograde crown hominoid with a largely modern wrist joint. Moyà-Solà et al. (2004) and Begun & Ward (2004) dispute the significance of the relatively short phalanges. For the former authors, the shortness of the phalanges suggests that there was no substantial suspensory component to locomotion. On the contrary, the latter authors stress the curvature of the phalanges, and argue that this indicates there was a suspensory component to locomotion. The issue is essentially whether or not *Pierolapithecus* provides any evidence of the dissociation of the suspensory component from the rest of the suite of hominoid postcranial characteristics. If Moyà-Solà et al. (2004) are correct, the *Pierolapithecus* hand is more 'monkey-like' than that of living apes, the orientation of the proximal articular surfaces of the phalanges suggesting that 'vertical-climbing' was accompanied by palmigrade above-branch quadrupedalism, but not by suspension. In that case, the possession by all living apes of one of the generally recognized common suite of postcranial features, a forelimb adapted for suspension, would be homoplastic in some lineages at least (and see Larson, 1998). However, this is not enough, in our view, to reject *Pierolapithecus* as a crown hominoid, as forelimb suspension is not a predominant element of the shared locomotor repertoire, even of living great apes (Thorpe & Crompton, 2006) where it does not exceed 15% of locomotor bouts. Indeed, a preliminary phylogenetic analysis of the *Pierolapithecus* skeleton by Begun & Ward (2004) suggested that *Pierolapithecus* and *Dryopithecus* are sister taxa of the African apes and hominins. However, the identification and selection of characters by Begun & Ward (2004) for their analysis is regarded by Moyà-Solà et al. (2004) as faulty.

### (2) Eurasian stem and crown hominoids, 11–7 Ma

#### Dryopithecus

The possible phylogenetic position of *Dryopithecus* together with *Ouranopithecus* (see Smith et al. 2004), as a sister clade to African apes and hominins (e.g. see Begun, 2002, 2004), makes *Dryopithecus* of particular importance in any consideration of the locomotor and postural biology of LCA of the African apes. Both the middle and the late Miocene hominoids *Griphopithecus* and *Dryopithecus* tend to be associated with seasonal subtropical forest environments similar to those seen in India (Andrews & Humphrey, 1999) with *Griphopithecus* tending to be found in drier, more seasonal variants.

#### Hispanopithecus (Dryopithecus) laietanus

Our best evidence for the postcranial skeleton of *Dryopithecus* comes from one partial skeleton discovered by Moyà-Solà & Köhler (1996) at Can Llobateres, near Sabadell in Spain, in *c.* 9.5 Ma deposits. The skeleton, which in its general limb proportions resembles that of orangutans more than those of other living great apes, represents an adult male of *c.* 34 kg body mass, which is not greatly different from the mean body mass of female Sumatran orangutans (35.6 kg, Smith & Jungers, 1997). The specimen includes a partial skull, partial clavicle, some fragments of ribs, a fragmentary and incomplete humerus, a partial radius and most of an ulna, most metacarpals and phalanges and one triquetral, four partial lumbar, and one partial thoracic vertebrae, two femora, one with a partial diaphysis, one complete as far as the distal epiphysis and the distal third of one tibia. Compared with those of cercopithecoids and *Proconsul*, the lumbar centra are craniocaudally short, with transverse processes arising from the pedicles, as in modern hominoids, and *Oreopithecus* (but probably more dorsally placed than in *Morotopithecus* and *Pierolapithecus*). The authors argue that the dorsally placed costal foveae on the thoracic vertebra imply that the spine was ventrally placed in the ribcage, as in modern great apes, and this, together with a sigmoid clavicle, is strong evidence of a broad but shallow ribcage with a dorsally placed scapula. They further claim that the clavicle would have been more cranially orientated than in African apes, but similar to the condition in *Hylobates* and *Pongo.* Evidence for a reduced stylo-triquetral contact is adduced to argue for a wrist joint similar to that in modern hominoids, with extensive adduction and free pronation/supination, and this is supported by the strongly curved radius, which suggests powerful pronation/supination (Oxnard, 1962). Powerful elbow flexion is suggested by a strongly marked brachialis insertion, and strong, distally placed insertions on the phalanges suggest a powerful power grip. The pollicial metacarpal is particularly robust. In a recent paper, Marzke et al. (2007) argue, however, that one should be cautious with inferring size and functional importance of the digital flexors from the morphology of middle phalanges, as it is demonstrated that size and location of the lateral fossa cannot serve as a reliable predictor. Moyà-Solà & Köhler (1996) comment that the femoral fragments, with their large head, high neck-shaft angle and anteroposteriorly flattened shaft argue for abducted hip postures. They further argue that evidence for a powerful grip in the hand, and relatively longer lumbar vertebrae (hence perhaps less well adapted for axial loading) indicate that the behaviour of *H.* (*D.*) *laietanus* may have included more quadrupedalism than in *Pongo*. Almécija et al. (2007) argue from the hand that palmigrade quadrupedalism is combined with orthogrady: below-branch suspension, arm-swinging, and clambering and postural feeding on slender arboreal supports, enhanced by an orangutan-like double-locking mechanism. However we are more struck by the resemblance to, than dissimilarities with, orangutans, as with *Oreopithecus*, see below, and suggest that *H.* (*D.*) *laietanus* was very probably habitually orthograde, whether above or below branches, although like orangutans, also capable of above and below-branch pronogrady. *H.* (*D.*) *laietanus* is clearly a crown hominoid.

### *Isolated postcranial specimens attributable to* Dryopithecus *and* Griphopithecus

The interpretation of this material is problematic, as even generic attributions have been unstable (see below). While *Dryopithecus* is regarded as a crown hominoid with close relevance to the African apes, *Griphopithecus* has been consistently grouped with stem hominoids. The material is therefore useful to our present purpose in indicating the range of hominoid locomotor anatomy in mid-Miocene Europe, rather than specifically crown hominoid anatomy.

As long ago as 1856, Lartet described a humeral shaft lacking both epiphyses representing *Dryopithecus fontani* from St. Gaudens in France. Slightly more recently, *Paidopithex rhenanus* was described by Pohlig (1892, 1895) on the basis of an intact femur from Eppelsheim in Germany. *Griphopithecus darwini* (Abel, 1902), dated to *c.* 14–15 Ma, was named from a single lower molar (now one of four teeth and two postcranial fragments) from Middle Miocene deposits at Devínska Nová Ves, near Bratislava in Slovakia. A humerus and ulnar shaft from Klein Hadersdorf in Austria have also been referred to this genus by Begun (2002), although Begun (1992) refers to them as *Austriacopithecus* and Szalay & Delson (1979) had referred them to *Sivapithecus darwini*. By far the largest number of finds of *Dryopithecus* come from Rudabanya in Hungary, and these include a distal humerus, proximal radial and ulnar fragments, a talar body, a fragmentary distal first metatarsal and several phalanges (Begun, 1992). Begun (2002) refers most of these to *Dryopithecus brancoi*. According to Begun's (1992) analysis of these isolated bones, the Rudabanya finds (with the exception of some phalanges which he refers to a large pliopithecid, *Anapithecus*) and the St. Gaudens humerus are functionally consistent with each other. Their characters include a humeroulnar joint stabilized throughout a large range of flexion and extension, and a radioulnar joint with a wide range of pronation/supination, quite unlike the radioulnar joint of non-hominoids, which favours stability in a prone and semi-flexed posture. The posterior convexity of the St. Gaudens humerus is attributed to resistance to bending moments in an extended elbow, and to extended and abducted glenohumeral postures. Talus, metatarsal, and pedal and manual phalanges are strongly suggestive of fore- and hindlimb suspension and suspensory locomotion. Begun (1992), however, regards the Klein Hadersdorf material as functionally mosaic, having only a few characteristic hominoid traits of the humeroulnar articulation, and suggesting only limited suspension, while showing signs of adaptation for motion primarily in the parasagittal plane. The radiohumeral articulation, however, suggests a greater mobility in pronation/supination and the bowed shaft and strong supinator crests suggest more powerful pronation/supination than in non-hominoids. The Epplesheim *Paidopithex* femur is lightly built, like that of hylobatids. Begun (1992) attributes the straight diaphysis and large size to 'habitually suspended hindlimb postures' (p. 333) while a high neck-shaft angle may indicate habitually abducted hip postures. Overall similarities to *Pliopithecus* may indicate a similar habit, possibly suspensory quadrupedalism like that seen in *Alouatta*. It is worth noting that, while the evidence of *Dryopithecus* from Rudabanya and St. Gaudens suggests a locomotor repertoire similar to that of *D. laietanus*, Begun (1992) suggests suspensory quadrupedalism was practised by both *D. brancoi* and the Epplesheim ape. Only one living great ape, the orangutan, has been observed to engage in suspensory quadrupedalism: neither the panins nor the gorillines exhibit this behaviour (Thorpe & Crompton, 2006). The absence of such gait in panins and gorillines might, however, be a simple statistical consequence of much more exclusive arboreality in *Pongo.*

### Sivapithecus

Several phylogenetic analyses (e.g. see Finarelli & Clyde, 2004; Begun, 2005, 2007; but *contra* Young & MacLatchy 2004) suggest that both *Sivapithecus* (best known from the Chinji Formation of the Siwaliks in Pakistan) and, especially, *Lufengpithecus* (from Yunnan province in south China) are more closely related to the pongine clade than is *Dryopithecus*, which falls closer to the living African apes (including hominins). No partial skeletons have yet been reported for *Sivapithecus*, but the isolated hind- and forelimb bones referred to this genus sample most regions of the hind- and forelimbs. In particular, Pilbeam et al. (1990) reported humeri from two species of *Sivapithecus* from the Siwaliks (*c.* 9–11 Ma), which potentially cast some doubt on the craniodental evidence for a close relationship between *Sivapithecus* and *Pongo*. The distal part of these bones shows typical hominoid characteristics – namely radiohumeral and ulnohumeral articular morphology which would support the elbow through an extensive range of pronation/supination and flexion/extension, respectively – described above in connection with *Dryopithecus*. However, the proximal shafts of the *Sivapithecus* humeri are curved and retroflexed, which suggested to Pilbeam et al. (1990) a lack of adaptation to forelimb suspension resembling *Proconsul*, *Kenyapithecus* and living cercopithecids, but not the living hominoids. Pilbeam et al. (1990) suggest that this evidence indicates that, if *Pongo* and *Sivapithecus* are sister taxa, suspensory adaptations arose in parallel in African apes and *Pongo*, or that, if they are not sister taxa, the palatal and facial similarities between *Pongo* and *Sivapithecus* must themselves be homoplastic. We have already noted, however, that forelimb suspension is not a predominant locomotor mode of the great apes (Thorpe & Crompton, 2006), and that the fossil evidence for early crown hominoids suggests that it was not a predominant element of the crown-hominoid locomotor niche. Madar et al. (2002) report on a distal femur from the Dhok Pathan Formation, a navicular from the Chinji Formation, and manual and pedal phalanges from the Nagri Formationof the Siwaliks, which have been referred to *Sivapithecus.* They note that whereas the previous postcranial evidence emphasizes quadrupedal rather than suspensory adaptations, a somewhat different, and perhaps unique, locomotor repertoire is suggested by the new material. The femoral diaphysis is distally flattened so as to increase resistance to mediolaterally directed forces, suggesting habitually abducted postures. The medial condyle of the femur is anteroposteriorly longer and mediolaterally wider than the lateral, suggesting, together with a deep groove for popliteus, and a strong marking for the lateral collateral ligament, adaptations to strengthen the knee in medial rotation of the femur on the tibia, and adduction of the tibia on the femur, respectively. Similarly, the patellofemoral joint lacks features associated in cercopithecids with forceful sagittal motion, but shows features adapted to support the knee in rotation. Madar et al. (2002) suggest that these adaptations together would be adaptive in motion on supports orientated in a range of directions above, as well as below, the CoG. The cuboid peg is relatively laterally placed in the calcaneocuboid joint in *Sivapithecus* as it is in *Pongo*, compared with the living African apes, so that any shortening of tibialis posterior would bring about a greater degree of supination for the foot than in the African apes. Evidence from the calcaneal, navicular and hallucial remains of *Sivapithecus* suggests that the hallux was important in grasping instead of relying on the hook-like action of the lateral digits. In these respects, *Sivapithecus* resembles the African apes rather than *Pongo.* Particular features of the manual phalanges, such as dorsoplantar robusticity, and robust flexor-sheath ridges, resemble features in *Gorilla* in particular. Madar et al. (2002) conclude that (p. 746): 'The combination of hindlimb mobility, secure grasping and resistance to loading imposed from various directions is clearly advantageous on supports of various inclinations and diameters. All of these capabilities are most likely to be expressed on arboreal substrates, though none precludes significant terrestriality.' They go on to suggest that the locomotor repertoire of *Sivapithecus* included pronograde clambering on relatively small-sized supports, as well as pronograde quadrupedalism on medium- and large-sized supports. But they note that the hindlimb features are consistent with loading under tension on highly angled or vertical supports, while the proximal humeri indicate that forelimb-suspensory orthogrady was limited.

Madar et al. (2002) propose that flexed-elbow vertical climbing was a substantial part of the locomotor repertoire of *Sivapithecus*, but that this was achieved in a functionally unique way (rather recalling the case in *Nacholapithecus*) so that, instead of being hindlimb-driven, it was stabilized and assisted by a forearm with limited glenohumeral mobility but with a powerful hallucial grasp. They note also that despite a stabilized foot, there are no features of known skeletal elements which suggest a substantial commitment to terrestrial quadrupedalism in the manner of baboons or mountain gorillas. Nevertheless, Begun (2005) cautions that as we do not have fossil evidence for the shoulder joint of *Sivapithecus*, we should not reject the idea that *Sivapithecus* may have been adapted for a 'biomechanically different form of an otherwise similar positional behaviour, antipronograde quadrupedalism' [Begun, 2005, p. 6; ('antipronograde' is a neologism introduced by Stern {1975} to refer to orthograde forelimb-dominated locomotion which is not brachiation *sensu stricto*)]. Given the hindlimb evidence from Madar et al. (2002) – suggesting clambering on supports of different diameters and orientations – the adaptations for tensile loading in *Sivapithecus* limbs could equally suggest that *Sivapithecus* used a form of pronograde suspensory quadrupedalism like that seen in *Pongo* (Thorpe & Crompton, 2006), yet driven by a more anteroposterior motion of the forelimb than is seen in *Pongo*. In either case, the locomotor behaviour of *Sivapithecus* shows some features that are very similar to features of behaviour in *Pongo*, whereas in other respects it is different and possibly more specialized. Such might be expected from a creature at the limits of the pongine climatic/palaeoecological range. Nelson (2003) reconstructed the diet of *Sivapithecus* as a mixture of hard fruit and bark, soft fruit and young leaves – not unlike a living orangutan, chimpanzee or lowland gorilla. The associated palaeoenvironments are described by Andrews & Humphrey (1999) as wet subtropical forest, but by Nelson (2003) as closed tropical forest under a process of fragmentation, with a climate similar to that of southern China today, implying substantial seasonality and a climate outside the range of habitats occupied by living hominoids. Similarly, Middle Miocene palaeoenvironments in the region of discovery of *Lufengpithecus lufengensis*, Yunnan in southern China, would have been more temperate, or at least more seasonal, than the rainforest environments inhabited by both living and Pleistocene *Pongo*.

Pongine-like dental material, initially referred to *Lufengpithecus*, was reported by Chaimanee and colleagues (2003) but from northern Thailand, in deposits from *c.* 10–13.5 Ma. Upon discovery of a 7–9 Ma mandible with similar teeth, but now showing purportedly detailed synapomorphies with living orangutans: *Lufengpithecus* (*Khoratpithecus*) *piriyai*, Chaimanee et al. (2004a,b) described the two finds as forming part of the same lineage, pongine but not directly ancestral to living *Pongo*. If *L.* (*K.*) *chiangmuanensis* and *L.* (*K.) piriyai* are indeed members of the same lineage, then, despite Alpagut et al. (1996), *Ankarapithecus* is unlikely to be ancestral to extant orangutans because of its later date (*c.* 9.5 Ma). Moreover, although the oldest *Sivapithecus* material antecedes *Lufengpithecus* (*Khoratpithecus*) *changmiuanensis*, some doubt would also attach to the proximity of the relationship of *Sivapithecus* to orangutans (and see discussions in Begun & Güleç, 1998; Begun 2004). *L.* (*K.*) *piriyai* at least is associated with a rainforest fauna and flora similar to that which exists today in Thailand, and thus much more similar to modern-day habitats for *Pongo* than the more seasonal tropical forests with which *Sivapithecus* was associated. This suggests that the postcranial peculiarities of *Sivapithecus* might be understood in terms of adaptation to what was becoming marginal habitat for pongines. They might in part reflect the same sort of forelimb-powered pronograde suspension that *Nacholapithecus* might have included in its repertoire, and which is represented today only in *Pongo*.

### Oreopithecus bambolii

Fossils of *Oreopithecus* have been known since before 1872, and the hypodigm now consists of one crushed and distorted but almost complete subadult skeleton, several partial skeletons and dozens of mandibular and cranial specimens (Harrison & Rook, 1997). *Oreopithecus* is thus one of the best-documented fossil higher primate taxa. It is found in *c.* 7–9 Ma deposits, so that while it is much later than *Proconsul* and its affines, it is only slightly younger than *H.* (*D.*) *laietanius* (Köhler & Moyà-Solà, 2003). In view of the phylogenetic and functional interpretations placed on the dental, gnathocranial and postcranial remains, palaeoenvironmental considerations are of considerable interest. Harrison & Harrison (1989) analysed pollen and spores in fossiliferous lignites from Baccinello. Results suggest the palaeoenvironment was lowland mixed mesophytic forest with a rich understorey of small trees and shrubs and a herbaceous ground cover, while abundant aquatic plants, ferns and moisture-loving trees suggest that lowland areas were poorly drained. Upland or montane habitats were located at some distance from the deposits, and rarity of grasses indicate that extensive open country was limited. Harrison and Harrison (1989) infer warm temperate to subtropical conditions with high summer rainfall. The deposits in which *Oreopithecus* is found are predominantly lignites, and associated fauna and flora are thus strongly suggestive of poorly drained humid forest environments (Harrison & Rook, 1997). Köhler & Moyà-Solà (2003), however, stress evidence for a hinterland of drier, more open environments on what were then islands in the Tyrrhenian sea, but now form part of the Italian mainland.

*Oreopithecus* combines, on the one hand: a cranial capacity more like that of extant cercopithecoids rather than extant hominoids, and specialized pre- and post-canine teeth with an abundance of accessory cuspules, with, on the other: a very short face adapted to powerful mastication; a broad thorax; a vertebral column clearly adapted for habitually orthograde posture; femora with a marked bicondylar angulation; hip and knee joints which are adapted for use in highly extended postures; a long forelimb, an elbow joint adapted for a use in an extended posture and an extensive range of pronation/supination; and a glenohumeral articulation adapted for highly abducted postures. The nature of the feet and hands of *Oreopithecus* are disputed. Szalay & Langdon (1986) interpret the foot as adapted to climbing, rather than suspension, but Köhler & Moyà-Solà (1997, 2003) see the foot (which they reconstruct with a hallux even more abducted than in gibbons and siamangs) as primarily adapted to act as a stable base in bipedal standing and slow bipedal walking, as part of a terrestrial-foraging habitus not unlike that proposed by Hunt (1994) for early hominins. While bipedality may well be suggested by the internal architecture of the *Oreopithecus* ilium (Rook et al. 1999), it points most unequivocally to a habitually vertical body posture. Claims for a pollicial precision grip, made by Moyà-Solà et al. (1999), are disputed by Susman (2004) who argues that the hand of *Oreopithecus* is similar to those of arboreal great apes. A majority of researchers would probably now accept that given that some of the dental peculiarities of *Oreopithecus* are also seen in East African Miocene fossils such as *Rangwapithecus*, and occasionally in the teeth of living hominoids (Harrison, 2002), the overwhelming weight of the postcranial evidence points to *Oreopithecus* being a crown hominoid (e.g. see Rose, 1997, but *contra*, for example, Andrews, 1992 and compare phylogenetic analyses by Finarelli & Clyde, 2004 and Young & MacLatchy, 2004).

Interpretations of the overall functional significance of the skeleton differ. Köhler & Moyà-Solà (1997, 2003) argue that *Oreopithecus* was a terrestrial, primarily postural, biped and a slow bipedal walker. In contrast, Jungers (1987) found that the limb proportions of partial skeleton IGF 11788 assigned to *Oreopithecus* most closely resemble those of a female orangutan, suggesting similarity to *Pongo* in locomotor behaviour and support use. Walker et al. (1999) have interpreted some detailed aspects of *Oreopithecus* anatomy as functionally analogous to that of subfossil sloth lemurs. The great-ape-like morphology of the semicircular canals (Rook et al. 2004) suggests, however, that these detailed similarities accurately reflect an extant great-ape-like locomotor repertoire.

The dental peculiarities and the small cranial capacity of *Oreopithecus* have been linked to the adoption of folivory (Harrison & Rook, 1997), with a diet of evergreen leaves and possibly seeds from evergreen cones. Such a mixed evergreen-leaf and conifer-seed diet is consistent with a seasonal warm temperate forest palaeoenvironment environment, but also suggests arboreality rather than terrestriality for *Oreopithecus*. In turn, the small cranial capacity of *Oreopithecus* might relate to the depressed metabolic rates of arboreal folivores (e.g. see McNab, 1978; Milton et al. 1979; Degabriele & Dawson, 2004). Köhler & Moyà-Solà (2003), by contrast, lay more stress on the drier bush-woodland component of the reconstructed palaeoenvironment, in relation to their reconstruction of *Oreopithecus* as at least partially terrestrial, taking bush fruits from a bipedal standing posture on the ground, and, in this dietary context, note parallels between the dentition of *Oreopithecus* and that of peccaries.

### (3) Protohominins and protopanins, 7–5 Ma

Sahelanthropus tchadensis

*Sahelanthropus* is perhaps the earliest fossil species with some claim to be a hominin, and it is of some interest that it was found in Chad, 2500 km away from the East African Rift Valley, which had previously held a more or less undisputed claim to be the cradle of humankind (Brunet et al. 1995). Its age of *c.* 6–7 Ma (i.e. within 2–3 Ma of the age of *Oreopithecus*) is based on faunal correlation with the Nawata Formation at Lothagam, Kenya (5.2–7.4 Ma) (Brunet et al. 2002). The flora suggest a palaeoenvironment of peri-lacustrine gallery forest (Vignaud et al. 2002), yet faunal evidence indicates a mosaic of savannah with woodland, and aeolian deposits even suggest desert may have been nearby (Vignaud et al. 2002). Such a palaeoenvironment appears to contrast with the wooded/forested palaeoenvironments with which *Orrorin*, *Ardipithecus* and *Australopithecus anamensis* (see below) are associated. No postcranial specimens had been described at the time of writing, but Zollikofer et al. (2005) claim that the angle between the orbital plane and an anteriorly placed foramen magnum – nearly perpendicular in humans but more acute in *Pan trogylodytes* – suggests that *S. tchadensis* may have been bipedal. Comparison with more frequently orthograde hominoids might, however, have been useful. Wood (2002) notes, of the cranium: 'from the back it looks like a chimpanzee, whereas from the front it could pass for a 1.75-million-year-old advanced australopith' (p. 134). Apart from the face, its main claim to hominin status is the small upper canines, which are worn at the tip. Brunet et al. (2002) note in this context that by comparison the upper canine of *Orrorin* (see below) resembles that of a female chimpanzee. Wolpoff et al. (2002) dispute the significance of both canine size and foramen magnum position and orientation as adequate proof of its hominin status, an argument, not surprisingly, dismissed by Brunet (2002). However, as Wood (2002) observes, it is not likely to be easy to prove hominin or panin status at a time close to the probable separation of the lineages (and see Bradley, 2008).

Orrorin tugenensis

At the time of first reporting (Pickford & Senut, 2001a; Senut et al. 2001 and see Aiello and Collard, 2001), *Orrorin tugenensis* consisted of 13 specimens representing some five individuals, including fragments of the arm, hand and thigh, from the Lukeino Formation (Pickford & Senut, 2001b), and thus dated fairly securely to between 6.2 and 5.6 Ma. Its body mass is estimated at 35–50 kg and stature at least 1.1 m (Nakatsukasa et al. 2007). The palaeoenvironment is described on faunal grounds (Pickford & Senut, 2001b) as 'open woodland' with some denser stands of trees beside streams and a lake, while Pickford (2006) describes the fauna and flora as 'indicative of woodland to forest habitats' (p. 179). *Orrorin*'s adaptations are summarized by Senut and colleagues thus: 'a biped when on the ground, whilst its humerus and manual phalanx show that it possessed some arboreal adaptations' (Senut et al. 2001, p. 137). Specifically, Senut and colleagues adduce curvature of the phalanx as evidence for some degree of arboreality [as in *Au. afarensis* (Stern & Susman, 1983)] and similarly adduce the fact that the humerus bears a strongly salient lateral supracondylar crest, suggesting a considerably more powerful brachioradialis than in modern humans. Senut et al. (2001) claim that the proximal femoral morphology ('femur with a spherical head rotated anteriorly, neck elongated and oval in section, lesser trochanter medially salient with strong muscle insertions, deep digital fossa', p. 139) is more similar to that of *Homo* than is that of *Australopithecus*, suggesting that *Orrorin* is functionally more similar to *Homo* than is *Australopithecus* [and indeed more closely related, although Senut (2006) abandons this view]. *Orrorin*, they argue, was 'already adopted to habitual or perhaps even obligate bipedalism when it was on the ground' (Senut et al. 2001 p. 142). Pickford (2006) further argues that as the femur would have been absolutely longer than that of a chimpanzee, but the humerus would have been the same size, *Orrorin* would have had difficulty walking quadrupedally. Some doubt must attach to this suggestion, however, until more complete postcrania are discovered.

A well-preserved proximal femoral fragment of *Orrorin* (BAR 100'200) shows a clear and strongly marked groove on the dorsal aspect of the neck (see fig. 1 in Pickford et al. 2002). Presence of such a femoral 'intertrochanteric' (obturator externus) groove or line has been associated with frequent bipedalism by Tuttle (1981), Stern & Susman (1983) and Stern et al. (1984). Stern & Susman (1983), however, argue that this marking is not necessarily associated with modern human-like bipedalism, citing its presence in some atelines, pitheciines and *Pongo*, and imply that it may appear for reasons other than hyperextension of the hip. However, atelines, pitheciines and *Pongo* all hyperextend the hip in, for example, bridging and quadrumanous clambering. Day (1969) observes that the obturator externus groove is completely absent in the living African apes, but present in fossils including Spy, Trinil, SK 97 and OH 20, and notes that it would be occupied by the obturator externus tendon in a hyperextended position of the hip joint. Similarly, Galik et al. (2004) note that while absent in a sample of 155 African hominoids, the obturator externus groove is present in the hominins OH20, SK 82 and 97, A.L. 333-95 and 288-1 and MAK-VP-1/1. However, claims by Galik et al. (2004) that CT imaging of BAR 100'200 shows a hominin-like, not panin-like femoral neck cross-section are regarded by Ohman et al. (2005) as insufficiently supported by the evidence.

### Ardipithecus kadabba *and* Ardipithecus ramidus

*Ardipithecus* is referred to the tribe Hominini by White et al. (1994) on the basis of cranial and dental evidence. It now comprises two species, *Ar. kadabba* and *Ar. ramidus* (Haile-Selassie et al. 2004). *Ardipithecus kadabba* (Haile-Selassie, 2001) comes from deposits dated at 5.2–5.8 Ma in the Middle Awash region of Ethiopia, while *Ar. ramidus* comes from higher in the sequence. The palaeoenvironment represented by 5.54–5.77 Ma deposits in the Middle Awash is described by WoldeGabriel et al. (2001) as 'predominantly wet and closed woodland/forest habitats' with 'open woodland or wooded grassland around lake margins' (p. 177). They conclude: 'It therefore seems increasingly likely that early hominids did not frequent open habitats until after 4.4 Ma. Before that, they may have been confined to woodland and forest habitats' (WoldeGabriel et al. 2001). Indeed, Ward et al. (1999a, p. 203) state that *Ar. ramidus* is known from 'relatively high-altitude, closed-canopy woodlands of Ethiopia'. Postcranials assigned to *Ar. kadabba* are generally somewhat larger than the equivalents in *Au. afarensis*, and include a fragment of a robust clavicle, separate from an associated humerus and ulna, a distal humerus, one intermediate, and one proximal manual phalanx. The phalanges not surprisingly resemble those of *Au. afarensis* (see below), showing dorsal convexity and a concave palmar surface providing space for powerful extrinisic flexors. The olecranon fossa of the humerus is less elliptical in shape than in later hominins, while the ulnar shaft is more curved, a feature sometimes associated with powerful pronation (Oxnard, 1962). The proximal pedal phalanx AME-VP-1/71 from Amba dates from later in the succession (*c.* 5.2 Ma), but like that of *Au. afarensis* it shows strong dorsal convexity, suggesting that the flexor musculature was powerful. Mediolateral compression of the proximal shaft and dorsal orientation of the proximal articular surface resemble the case in *Au. afarensis* and are cited as hominin features. This phalanx is described as 'consistent with an early form of terrestrial bipedality' (Haile-Selassie, 2001, p. 180). White et al. (1994) note that the anteriorly placed foramen magnum in the partial *Ar. ramidus* holotype basicranium ARA-VP-6/1 suggests bipedality.

Postcranial material assigned to *Ar. ramidus* is also found in 4.4 Ma deposits at Aramis, Middle Awash. The habitat probably consisted of 'woodland or dry forest growing in a strongly seasonal environment' (Andrews & Humphrey, 1999, p. 294). ARA-VP-7/2 is an associated humerus, radius and ulna, all broken into several fragments. These fossils show a mix of both hominin-like and non-hominin-like features, the latter including a superoposteriorly elongated lateral epicondyle (White et al. 1994) indicating powerful extensors of the wrist and hand. Yet, in modern humans these muscles, particularly brachioradialis, also flex the elbow, especially in midprone position, and a more proximal origin would increase this flexor moment.

## (4) Archaic Hominins, 4.5–2 Ma

### Australopithecus anamensis

Craniodentally, Leakey et al. (1995) and Ward et al. (1999a) attribute differences between *Ar. ramidus* and the somewhat younger (*c.* 3.9–4.2 Ma) *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya, to evolution within a single lineage, a process which may extend to *Au. afarensis.* The palaeoenvironment at Kanapoi is described by Andrews & Humphrey (1999) as 'open woodland with abundant grass' (p. 294). Continuity between *Au. anamensis* and *Au. afarensis* is supported by a recent phylogenetic analysis by Kimbel et al. (2006), but they reject a model of progressive desiccation until after 3 Ma, suggesting that before that date a wide range of habitats was available to these two species over a 2-million-year period. There was local and regional fluctuation in habitat, at least in part corresponding to *c.* 19–23 kyr climatic cycles (Kimbel et al. 2006). The most important postcranial fossil representing *Au. anamensis* (Ward et al. 2001) is a partial tibia from Kanapoi, KNM-KP 29285, that lacks the middle part of the shaft. For the distal tibia of *Au. anamensis*, Ward et al. (2001) concur with the interpretation placed on the *Au. afarensis* distal tibiae by Lovejoy et al. (1982). These researchers suggest that the orientation of the talar facet with respect to the shaft is modern-human-like, permitting the knee to pass vertically over the stance foot. Ward et al. (1999a) conclude that *Au. anamensis* was an habitual biped, as claimed by Lovejoy et al. (1982, and elsewhere) for *Au. afarensis*. Ward et al. (2001, p. 362) summarize the evidence of the tibia as 'showing that habitual terrestrial bipedal locomotion was selectively advantageous for hominins prior to 4.2 Ma'.

Other features indicative of bipedalism include (Leakey et al. 1995) a rectangular proximal (femoral) articular surface with anteroposteriorly elongated, concave condyles, and a small proximal tibiofibular joint. The swollen metaphyses of *Au. anamensis* are interpreted by Ward et al. (2001), following Kunos & Latimer (2000), as a shock-absorbing mechanism to dissipate high impact forces induced at heel-strike. However, the pes anserinus and fascia lata insertions on the tibia are strongly marked, in which respect *Au. anamensis* differs from modern humans, but resembles panins, gorillines and *Au. afarensis* These features could indicate more powerful flexion of a flexed knee, as in gorillines and panins. Perhaps, alternatively, however, they indicate a need for increased muscle action in braking of the swing, and stabilization of the knee in extended/hyperextended postures. These explanations are suggested, respectively, by the roles of gracilis and semitendinosus, and of tensor fasciae latae in humans. The KNM-KP 271 humerus is described by Ward et al. (2001) as lacking the elongated extensor epicondyle seen in *Ar. ramidus*, but this suggestion of reduced flexor power at the elbow, and reduced extensor power more distally, is balanced by cortical robusticity greater than that in living panins and gorillines. Extension of the trochlear surface along the lateral margin of the olecranon fossa [which is tentatively attributed to resisting loads in hyperextension of the elbow (Ward et al. 2001)] is another typical feature of panins and gorillines, linked possibly to knuckle-walking gait, which is lacking in *Au. anamensis*.

A radius (KNM-ER 20419) of a similar age, 3.9 ± 0.1 Ma, was found east of Allia Bay, Kenya (Heinrich et al. 1993), and is now assigned to *Au. anamensis*. It is described by Ward et al. (1999a) as morphologically very similar to that of *Au. afarensis* in all but size: the forearm of the KNM-ER 201419 individual would have been the length of that in a six-foot modern human male. It is considerably longer (*c.* 265–275 mm) than the radii of AL 288-1, and may have come from an individual of *c.* 50 kg in mass (Heinrich et al. 1993). However, the body mass of this individual is estimated at between 47 and 55 kg, somewhat larger than *Au. afarensis* males, but still suggesting that the forearm of this species was absolutely and relatively quite long. A long neck would give substantial mechanical advantage for the biceps, and equally the brachioradialis insertion is marked, indicating powerful elbow flexion with maximum flexor force at the midprone position. The carpals of *Australopithecus* differ from both African apes and modern humans in that the lunate is very broad, almost excluding the scaphoid from contact with the capitate, as is the case with the Kanapoi capitate KNM-KP 31724 (Ward et al. 2001). An extensive lunate–radius contact is present in *Australopithecus*, but in no living African ape, including modern humans. Like AL 288-1, *Pongo* and Hylobatidae, the Allia Bay radius possesses a particularly large radiocarpal facet for the lunate, which may suggest the importance of adducted postures, perhaps in clambering activities. This is the reverse of the condition in panins and gorillines, where a larger scaphoid may assist weight-bearing during knuckle-walking, and in later hominins, where an increase in the relative size of the scaphoid may relate to pollicial dexterity and tool-use. A manual phalanx is described by Ward et al. (2001) as having the same morphology as *Au. afarensis*, with some dorsal convexity and clear flexor ridges.

Ward et al. (2001) note that the radius was adduced by Richmond & Strait (2000) as evidence of knuckle-walking in *Au. anamensis*, but that the feature they identified was an artefact caused by the missing styloid process. Studies by Reno et al. (2000), however, indicate that the proximal radius is not informative as to locomotor habits, and Patel (2005) showed that this result extends to the proximal radius of early hominins, including radius KNM-ER 201419: while the proximal radius does not resemble that of humans or orangutans, similarities to panins and gorillines are present, but equally strong similarities exist to gibbons. He concludes that the proximal radius of early hominins does not show any features which might have supported elbow loads in an hypothetical knuckle-walking ancestor, nor does it rule out such behaviour.

White et al. (2006) reported fossils referable to *Au. anamensis* from Asa Issie, about 10 km from the *Ar. ramidus* site location at Aramis in the Middle Awash. Dating to 4.1–4.2 Ma, 200 kyr later than the latest *Ar. ramidus*, they include a fragmentary femoral shaft (ASI-VP-5/154), a fragmentary metatarsal shaft, an eroded distal foot phalanx, and an intermediate manual phalanx, all resembling those of AL 288-1. This discovery suggests that hominins may have remained in closed-woodland environments in highland Ethiopia well after the time of *Ar. ramidus*.

### Australopithecus afarensis

There has been extensive debate about the significance of the famous one-third-complete 'Lucy' skeleton AL 288-1, and other material from Hadar, since its discovery over 30 years ago. Despite a valgus knee posture, vertical posture of the tibia over the talus, broad ilia, and other features associated with orthogrady and specifically bipedal walking, the diminutive (*c.* 1.05 m, body mass *c.* 29 kg, McHenry & Coffing, 2000) skeleton combines these features with others that resemble the condition in the extant non-human apes. Long forearms, short legs and curved fingers and toes are some of the most striking such features. The derived features of the skeleton, and of a new larger-bodied partial skeleton from Hadar, AL 438-1 (2.94 Ma; male stature is estimated at 1.51 m, male mass 45 kg, McHenry & Coffing, 2000), are shared with modern humans and are sustained across the size range with the exception of a more curved ulna and a suggestion of less manipulative capability in the larger forms (Drapeau et al. 2005). One researcher, Sarmiento (e.g. 1994, 1998), has actually argued that *Au. afarensis* was a palmigrade-plantigrade quadruped, largely on the basis of details of cheiridial anatomy resembling features seen in *Gorilla* [e.g. shorter fingers and toes, a similar configuration for the hamate–triquetral facet, a more palmar direction of the hamulus and pisiform, broad tibialis posterior insertion and large plantar aponeurosis (Sarmiento, 1994)]. Stern & Susman (1983) specifically state that they find no evidence of knuckle-walking features in the AL-333 and AL 333w metacarpals of *Au. afarensis* and mention none, either, in the AL 333 carpals (or the AL 333 phalanges). Instead, they and other researchers concentrate on the nature and effectiveness of *Au. afarensis'* bipedality, and the degree to which the 'ape-like' features represent (retained or acquired) adaptation to arboreality or are simply anachronistic, retentions of no ecological significance. Some have argued that Lucy's bipedal gait would merely have been a different form of bipedality than our own (e.g. Berge & Ponge, 1983; Berge, 1984, 1991, 1994; Berge & Kazmierczak, 1986; Tardieu, 1986a,b, 1999). However, Stern & Susman (e.g. 1983, 1991), Stern (1999, 2000), Schmitt et al. (1996) and Schmitt (2003) have championed the specific argument that, partly as a result of compromise between the demands of arboreal and terrestrial locomotion, Lucy's gait would have been of a 'bent-hip, bent-knee' (BHBK) variety (Stern & Susman, 1983). This 'compliant' gait, they argue, may have delivered benefits in reducing peak loads on the skeleton of an early (and thus supposedly compromised) biped.

In contrast, Latimer et al. (1987), Latimer & Lovejoy (1989) and Latimer (1991) have argued that Lucy would have been an effective, upright, committed terrestrial biped, and that at least some of the adaptations for bipedality expressed in AL-288-1 (such as the talocrural joint configuration, Latimer et al. 1987) would have actually reduced the hominin's effectiveness in arboreal climbing. Ward (2002) argued that evidence from the modern human-like shape of the femoral condyles and from the bicondylar angle of *Au. afarensis* [which is strongly affected by behaviour during ontogeny (Tardieu & Trinkaus, 1994; Duren & Ward 1995; Duren 1999)] suggests that *Au. afarensis* habitually walked bipedally, and did not walk with a BHBK gait. Similar conclusions have been reached in a series of computer modelling studies of *Au. afarensis* gait, which have shown that BHBK gait substantially increases mechanical energy costs and heat load (Crompton et al. 1998; Kramer, 1999; Kramer & Eck, 2000). Experimental studies of the physiological costs of BHBK gait in humans have largely borne out these conclusions (Carey & Crompton, 2005), as have more advanced modelling studies which have predicted metabolic energy costs directly (Sellers et al. 2003, 2004; Nagano et al. 2005). The locomotor costs for *Au. afarensis* walking BHBK would have been some 80% higher, and even taking into account basal metabolic costs, overall costs a third higher, but the increased heat load might have been the greatest disadvantage of BHBK gait, as rest time in excess of 150% activity time would be necessary to control core body temperature.

The case for habitual upright bipedal walking in *Au. afarensis* now seems very strong indeed. The evidence indicates, moreover, that *Au. afarensis* was an habitual terrestrial biped, the lineage of which on the evidence of the *Au. anamensis* KNM-KP 29285 tibia had been the subject of selection for adaptation to terrestrial bipedal walking for at least 0.5 Ma. However, the forelimb evidence for both *Au. anamensis* and *Au. afarensis* remains compatible with some degree of arboreal activity. Perhaps increasing commitment of the hindlimb to bipedalism selected for retention, or even enhancement, of forelimb features which could compensate for reduction of effectiveness of the hindlimb in arboreal contexts. The discovery of the Dikaka partial skeleton (Alemseged et al. 2006) offers new potential for analysis of *Au. afarensis* locomotion, but at present the most indicative component is the curved phalanges and 'gorilla-like' appearance of the scapula, with a rather superiorly orientated glenoid, indicating a high degree of forelimb abduction, despite a rather smaller supraspinous fossa than might then be expected. The environments in the Hadar area vary from deltaic (Alemseged et al. 2006) to, in the '*A. afarensis*-bearing deposits of the Hadar Formation, dry bush/woodland and riparian woodlands in the Sidi Hakoma Member, riverine forests and wetlands in the Denen Dora Member, and dry bush/woodland in the "lower" Kada Hadar Member' (Kimbel et al. 1996, p. 559).

### *Behavioural evidence for the early hominin foot: the Laetoli footprint trails*

The Laetoli footprint trails (see e.g. Leakey and Hay, 1979) remain the most direct behavioural evidence of early hominid bipedality (*c.* 3.5 Ma) and should inform us on the function of the early hominin foot at that time. An immediate question, however, is authorship. The earliest evidence of multiple hominin lineages coexisting in East Africa is the appearance of *Kenyanthropus platyops*, at *c.* 3.5 Ma (Leakey et al. 2001). A partial juvenile skeleton from Laetoli, assigned to *Au. afarensis*, LH-21, shows no marked postcranial differences from other *Au. afarensis* (White, 1980a) and as no adult postcranials have been reported to date, it seems legitimate, for the present, to assume that a locomotor system similar to that of *Au. afarensis* is the most likely maker of the Laetoli footprint trails. Palaeoenvironments in the Laetoli area at the time of the deposition of the Laetolil Beds were earlier regarded as open, but Kovarovic & Andrews' (2007) analysis indicates that at this time the area 'had heavy woodland-bushland cover with some lighter tree and bush cover and grass available' lending 'strong support to recent suggestions that the area was on the more wooded end of the habitat spectrum' (Kovarovic & Andrews, 2007, p. 663) although Andrews & Humphrey (1999) suggest Serengeti-type woodland, although more closed and complex than that seen today.

Two kinds of information can be gleaned from footprint trails. Their spacing and size can be used to estimate stride length and speed, while individual prints reflect the pattern of pressure distribution under the foot, and/or peak pressure. Unfortunately, interpretations of the individual prints (up to now only qualitative analyses have been performed) have been as polarized as analyses of the significance of the *Au. afarensis* postcranial skeleton. White (1980b) initially described the Laetoli G tracks (individual footprints) as having a 'total morphological pattern' like that of modern humans, with a well-marked heel-strike, adducted hallux, medial longitudinal arch and with a 'strikingly human' spatial distribution. Similarly, on the basis of stereophotogrammetric reconstruction of depth contours of many of the Laetoli G footprints, Day & Wickens (1980) argued that in addition to hallucial adduction and a modern human-like spread of the lateral toes, the individual tracks indicate a lateral to medial force transfer across the metatarsal heads, a particularly modern human feature. In contrast, Stern & Susman (1983) argued that there is no good evidence in the G1 trail for a pressure concentration on the hallucial metatarsal, and hence for lateral to medial force transfer. They further suggest, primarily on the basis of prints G1/27 and G1/33, that the lateral toes may have been held curled-up off the ground rather as in chimpanzees. They conclude that the Laetoli prints indicate a mode of bipedality different to that seen in modern humans, a view that is consistent with their opinion that *Au. afarensis* was in part arboreal. However, in a detailed response, White & Suwa (1987) argued that Stern & Susman's (1983) evidence for curled lateral toes is the result of post-impression distorting and exfoliation, and argue that although some prints may have only weak markings at the base of the hallux, this may be a consequence of walking in a soft substrate. They presented a new, size-matched reconstruction of the *Au. afarensis* foot and argued that it is consistent both with formation of the G1 trail and with an essentially modern human function of the foot. Susman et al. (1984) maintained that the evidence of the AL 288-1 skeleton itself nevertheless suggests a less efficient gait than that of modern humans, with a short stride and 'bent-hip, bent-knee' posture. Subsequently, Robbins (1987) reaffirmed that the prints indicate a lateral-to-medial force transfer across the metatarsal heads and supported the thesis that the individuals had human-like pedal morphology. Similarly, Tuttle (1987) stated that, if the prints were made by a small species of *Australopithecus*, the species must have had 'virtually human' feet, which 'were used in a manner virtually indistinguishable from those of slowly walking humans'. Tuttle et al. (1991) agree that the Laetoli footprints show a lateral to medial force transfer to the hallucial metatarsal, but suggest that an undiscovered species of *Australopithecus* with feet more similar to modern humans than the Hadar hominid was responsible for the Laetoli prints. Langdon et al. (1991), however, regard the Laetoli prints as entirely consistent with the morphology of the Hadar foot bones, while Deloison (1991) argued that Laetoli print G1/34, which is particularly clear and well preserved, indicates an inverted foot posture and a markedly abducted hallux, more similar to footprints made by bipedally walking common chimpanzees than to those made by modern humans. She argues that the Hadar footbones also indicate an inverted foot posture, hallucial abduction and prehensility. Clarke, who excavated much of the better-known G prints, and provided the cast of G1/34 used by Deloison, earlier regarded them (Clarke, 1979) as generally modern human-like, but considered that they might have been made by a common ancestor for both *Homo* and *Au. africanus.* Most recently, however, Clarke (2003) has strongly endorsed Deloison's interpretation, regarding the prints as consistent with the morphology of the newly discovered *Australopithecus* from Sterkfontein (StW 573). These fossil remains suggest an abducted hallux, inverted foot posture and curled-up lateral toes (Clarke, 2003).

Reconstructions of stride lengths from the Laetoli G trails (Charteris et al. 1982) based on published and well-established relationships between stride length and speed in human adults and children (see, in particular, Grieve & Gear, 1996), lead the authors to suggest that at 0.56 m $s^{-1}$ for trail G1, and 0.72 m $s^{-1}$ for trail G2/3 they corresponded to a 'strolling' gait. A second set of reconstructions based on dynamic scaling, which takes both stature and leg length into consideration, indicated that the gait was in fact equivalent to normal human 'small-town' walking speeds at 0.64 m $s^{-1}$ for G1 and 0.75 m $s^{-1}$ for G2/3 (Alexander, 1984). Sellers et al. (2005) extended their forwards-dynamics evolutionary robotics approach to the analysis of the G1 and G2/3 trails. The model predicts walking speeds of approximately 0.7 and 1.0 m $s^{-1}$, respectively. These estimates substantially exceed those of Charteris et al. (1982) and to a lesser degree Alexander's (1984) estimate. The G2/3 trail consists of overlapping trails most likely made by two adults. Sellers et al.'s (2005) physiological studies of modern humans and forwards-dynamics modelling of modern human and *Au. afarensis* gait found that when compared with predictions for the relationship of stride length, speed and metabolic costs, the predicted speed for G2/3 suggested that the makers were walking at, or near, their energetically optimum speed. Further, they were walking well within the range of predicted speeds for an animal of equivalent body size (cf. Heglund & Taylor, 1988). Modern humans commonly adopt walking speeds between 1.0 and 1.7 m $s^{-1}$, depending on the situation (Bornstein & Bornstein, 1976). Wirtz & Ries (1992) note, however, that young adults most commonly choose to walk at 1.5 m $s^{-1}$; this is near the energetically optimum speed Sellers et al. (2005) recorded for young adult human subjects. Sellers and colleague's (2005) estimate for *Au. afarensis*, although slow compared with a young adult modern human, is nevertheless within the range of absolute values for modern humans, despite the short stature of *Au. afarensis* (about 1.1 m). More recently, Raichlen et al. (2008), using scaling models based on bipedalism of humans and trained chimpanzees, found that the stride-lengths are compatible with those in both erect, or bent-hip, bent-knee (BHBK) bipedalism. Even so (and Raichlen and colleagues' model does not optimize gait for AL 288-1's own proportions) we have noted that Sellers and colleagues (2004) had already shown that optimized BHBK walking for a forwards-dynamic simulant with AL 288-1's likely proportions would have been 32% higher overall, so it is unclear why BHBK gait would have been adopted. Given the substantial sexual dimorphism evident in *Au. afarensis* and the diminutive size of AL 288-1 studies that take into account statures and proportions of males are required. But detailed quantitative analyses of the individual footprints may provide further evidence of the joint kinematics of the Laetoli hominin, but an impression of a 'shuffling' or 'compromise' gait no longer seems sustainable.

### *Fossil evidence for the early hominin foot*

Analyses of available pedal remains for *Au. afarensis*, the most likely maker of the Laetoli footprint trails, have also been subject to controversy and polarization. While Latimer (1983) and Latimer & Lovejoy (1982, 1989, 1990a,b) describe the fossil pedal material from Hadar (from the larger individual, AL 333) as fully compatible with habitual bipedalism, Susman et al. (1984) and Susman & Stern (1991) concentrate on features which suggest arboreality. These may include a powerful ability to flex the hallux, and hence a powerful grip (Deloison, 1991); an 'apelike' navicular (Sarmiento 2000), no lateral plantar tubercle on the calcaneus (Deloison, 1985; Lewis, 1989), and curved phalanges, capable of extensive plantarflexion (Stern & Susman, 1983; Susman, 1983; Duncan et al. 1994). Stern & Susman (1983), Gebo (1992) and Gebo & Schwartz (2006) suggest that the talar morphology indicates that both the subtalar and the transverse tarsal joints were more mobile than in modern humans. Harcourt-Smith & Aiello (2004) draw particular attention to the prominent navicular tuberosity, which they note may indicate increased weight-bearing on the medial side of the foot, and hence no medial longitudinal arch.

However, we have already noted that a good case has been made for the existence of a talar trochlea shaped so as to allow the lower leg to pass over it in a parasagittal plane, as in modern humans, not just in *Au. afarensis* but already in *Au. anamensis.* This indicates that hominins were already adapted to terrestrial bipedality, where parasagittal movement is both feasible and more mechanically effective, for at least half a million years before the Hadar hominins: equally, forelimb bones for *Au. anamensis* suggest that some degree of arboreal activity still took place. The debate over arboreality versus terrestriality may now have run its course.

### *Maka fossils*

A proximal femoral fragment from Maka in the Middle Awash of Ethiopia (Clarke et al. 1984) was assigned a date of 3.5 Ma by faunal correlation (White et al. 1993). It is very similar in morphology to *Au. afarensis* and in the same size range. Features including a marked obturator externus groove, the position of the lesser trochanter and the height of the greater trochanter suggest this individual was an habitual extended-hip biped (Clarke et al. 1984). White et al. (1993) report other material from Maka in the same time bracket, including a mandible strongly resembling the earlier, Laetoli, holotype LH-4. Postcranial remains include a partial shaft and partial distal epiphysis of a humerus (MAK-VP-1/3) which differs from that of AL 288-1, not only in its considerably greater robusticity (8 mm cortical thickness), but in bearing a strong lateral supracondylar ridge for the extensors and for the brachioradialis, retroflexion of the shaft, and a deep insertion for the pectoralis major. It is comparable in size to the *Au. afarensis* humerus AL 137-48 (Kimbel et al. 1996), White et al. (1993) attribute the robusticity to sexual dimorphism, but argue that the shortness of the humerus argues against arboreality.

### *South Turkwel fossils*

Somewhat younger, between 3.2 and 3.58 Ma, are fossils from South Turkwel in northern Kenya (Ward et al. 1999b). They include a metacarpal, capitate, hamate, lunate, a pedal phalanx, mandible, and teeth, and are associated with fauna suggesting a predominance of bushland habitats. Of particular relevance here is the key force-transmitting bone, the capitate, which shows no evidence of adaptation for knuckle-walking (Ward et al. 1999b). The os centrale was probably fused to the scaphoid, however. The lunate does not appear to indicate the particularly high degree of adduction indicated by the extensive facet for the lunate on the Allia Bay KNM-ER 20419 radius. There is evidence for a deeper carpal tunnel and greater mobility of the hypothenar region than in *Au. afarensis*. Ward et al. (1999b), however, draw attention to a parallel in *H. neanderthalensis*, suggesting that the inferred powerful grip does not necessarily imply enhanced climbing or suspensory abilities. Finally, a dorsally positioned proximal articular facet on the proximal pedal phalanx suggests enhanced dorsiflexion of the metatarsophalangeal joint, a characteristic trait for modern humans, as has been noted above for *Ar. kadabba* (Haile-Selassie, 2001). This feature is indicative of habitual bipedality in KNM-WT 22944 (Ward et al. 1999b) and is biomechanically striking, as it suggests that high forces at toe-off during bipedal gait may be have been present as early as 5.2 Ma. An abrupt decline in vertical forces at push-off is one of the clearest remaining differences between human and non-human primate/ape ground reaction forces, as curves in all the other apes tend to tail off slowly.

### *Bouri Hata fossils*

Substantial interest is attached to the material from 2.5 Ma Bouri Hata beds of the Middle Awash (Asfaw et al. 1999). The partial skeleton BOU-VP-12/1 in particular provides more unequivocal assessment of limb proportions than is possible for other early East African hominins, apart from *Au. afarensis* AL-288-1 and the later (*c.* 1.8 Ma) *Homo erectus* KNM WT-15000. There must be some question of whether this taxon should be placed on the *Homo* lineage, or assigned to the contemporaneous *Au. garhi*. BOU-VP-12/1 provides a humeral shaft (unfortunately lacking epiphyses), most of a radius (the distal epiphysis is missing) and most of a femoral shaft, together with a fibular fragment and pedal phalanx. The latter is described as being in most respects similar to that of *Au. afarensis.* The main change in proportions is seen in the femur, which is clearly elongated, relative to the humerus, compared with *Au. afarensis*. This part of Asfaw and colleague's (1999) analysis receives support from both Richmond et al. (2002) and Haeusler & McHenry (2004). These two sets of researchers agree that the humerofemoral index of BOU-VP-12/1 resembles that of WT 15000, while differing from that of *Au. afarensis.* Assuming no corresponding diminution of the length of the tibia and fibula, this would imply an increase in stride length and a proximalwards migration of the centre of mass of the lower limb, reducing its inertial resistance to acceleration. Asfaw et al. (1999) argue, however, that the brachial index, relating upper arm to forearm length, is not greatly dissimilar to that of *Au. afarensis.* If this is the case, anticipating our discussion of *Homo erectus*, hand-carrying capacity and throwing accuracy would not have been as enhanced as they are in hominins. The AL 288-1 radii and the radius of a partial skeleton of *Homo habilis* from Olduvai, OH 62, are too fragmentary to permit confidence in length reconstruction (Richmond et al. 2002). But Aiello et al. (1999) note that a long ulna (L40-19) from the Omo Shungura formation indicates either the presence of a large-bodied hominin, or a hominin with a high brachial index. The Bouri Hata skeleton may thus (Richmond et al. 2002) provide genuine evidence of *Pongo*-like brachial proportions (but not bony morphology) combined with a relatively long hindlimb at 2.5 Ma.

### Australopithecus incertae sedis

A more coherent picture of the arboreal and terrestrial capabilities of hominins prior to *Homo* may yet come when StW-573, a recently discovered associated skeleton from Sterkfontein Member 2, is fully removed from its matrix. StW-573 is dated to *c.* 3.5 Ma (Clarke, 1998) [but see also a date of 4 Ma on the basis of cosmogenic aluminium-26 and beryllium-10 in the matrix (Partridge et al. 2003); another of around 3 Ma based on magnetochronology; a third, *c.* 2–4 Ma based on faunal correlation; and a fourth of *c.* 3.3 Ma using the uranium–lead series (Walker et al. 2006)]. The skeleton appears to be substantially more complete than AL 288-1 and includes hands, feet and complete limb-bones. The upper and lower limbs seem to be subequal in size (Clarke, 2002), and the humerus, radius and ulna fall within the ranges of modern humans and chimpanzees.

Clarke & Tobias (1995) and Clarke (1999, 2003) regard several features of the foot – an abducted hallux, an inverted foot posture, and curled-up lateral toes – as consistent with arboreality. However, Harcourt-Smith (2002) and Harcourt-Smith and Aiello (2004), while describing the talus as ape-like and the navicular as intermediate in form between that in modern humans and that in the apes, regards the hallux as probably unopposable. This view is endorsed by McHenry & Jones (2006), who argue that hallucial convergence is common to all the early hominins that have the relevant morphology preserved. No retained evidence of knuckle-walking features is evident in the hand. The distal pollicial phalanx is spatulate, and seems relatively robust compared with other early hominin material. Clarke (2002) suggests that this Sterkfontein individual combined the ability to climb – using its powerful thumb in a vice-like grip – with bipedality. The relative proportions of the thumb and fingers are modern human-like (Clarke, 1999), as is the case with the *Au. afarensis* hand from AL 333 and AL 333w, according to Alba et al. (2003). This raises the issue of whether modern human-like hand proportions can be attributed to lithic technology (see also Tocheri et al. 2008). But Clarke (2002) suggests that the modern human pollex has its origins in arboreal behaviour (for grasping branches), before it was exploited in more terrestrial hominins for tool-use.

### Australopithecus africanus

This species has been known since the 1920s and the features of individual bones or regions adapted to bipedal gait have been well documented (Robinson, 1972). *Au. africanus* is much more poorly represented with respect to limb proportions than is *Au. afarensis*, but McHenry & Coffing (2000) estimate stature and body weight at 1.38 m and 41 kg (males) and 1.15 m and 30 kg (females). Comparisons of equivalent bones (McHenry, 1986) indicate a generally similar adaptation. When the scapula and proximal humerus of Sts 7 are compared with AL 288-11 and AL288-1m, all show 'ape-like' features such as narrow glenoid fossae, although the *Au. afarensis* material is more *Pan*-like. *Au. afarensis* specimens fall in the range of both *Pongo* and *Homo*. McHenry (1986) compared the pelvic girdle of Sts 14 with that of AL 288-1-an and -1ao, and found that while all are 'reorganized for bipedalism' (p. 183) all showed similar differences with *Homo*, such as small acetabulae and sacral surfaces, and relatively larger pubic bones. These differences, McHenry (1986) suggests, do not imply differences in gait from *Homo*, but differences in the means of achieving that gait. Considering distal femora TM1513 and AL 219-1a, both share the familiar markers of bipedality, such as ellipsoidal condyles, high bicondylar angle, etc. While a multivariate analysis suggested TM 1513 is most similar to the distal femora of modern humans, distances between the fossils were no bigger than between those in the modern human sample. McHenry (1986) concludes that the similarity over space and time of the *Au. afarensis* and *Au. africanus* postcranial skeleton suggest selection for similar locomotion, which differs from that seen in any of the living hominoids (i.e. knuckle-walking, or any other form of quadrupedalism).

McHenry & Berger (1998), including in their sample a recently discovered large-sized partial skeleton of *Au. africanus* (StW 431), found that some body proportions of *Au. afarensis* resemble those of later *Homo* more closely than do those of either *Au. africanus* or *Homo habilis.* They concluded that this may imply a greater degree of arboreality in *Au. africanus* and *H. habilis* and perhaps some homoplasy, although 'arboreal features' may be identified in the upper limb of both *Australopithecus* species.

StW 514 (Berger & Tobias, 1996) consists of proximal and distal tibial fragments including the epiphyses. Several chimpanzee-like features are cited, of which the most remarkable are the strongly convex lateral condyles at the knee joint, the convexity of which appears greatly to exceed those of AL 288-1 laq and matches that seen in the chimpanzee. The detailed morphology of the joint also suggests a single attachment of the lateral meniscus. Both indicate that rotation in the coronal plane was much larger than in modern humans. Berger & Tobias (1996) have raised the possibility that StW 514 is a chimpanzee, but they themselves reject this on account of the close association of the fossil with many other craniodental fossils belonging to *Au. africanus*, including Sts 5 ('Mrs. Ples'). Clarke & White (1994, cited in Berger & Tobias, 1996) have shown that the palaeoenvironment of Member 4 at the time of *Au. africanus* (2.6–2.8 Ma) was tropical woodland or even forest, not bush savannah nor bushland. Together with the fact that this is the only fossil with such a chimpanzee-like morphology, Berger & Tobias (1996) conclude that this fossil specimen represents the extremes of *Au. africanus* adaptation to arboreal/woodland environments.

### Paranthropus robustus *and* P. boisei

Proximal and distal ends of a radius (SKX 3602), thought to be from a single *P. robustus* individual, were reported from Member 1 (*c.* 2 Ma) of Swartkrans by Grine & Susman (1991). The form of the margins of the proximal articular surface suggest enhanced stability against medial displacement in pronation/supination. Prominent dorsal tubercles suggest powerful elbow extension, and a strongly marked brachioradialis crest indicates powerful flexion. Comparison with the Swartkrans *Homo* SK 18b suggests to Grine & Susman (1991) that *Homo* had lost a configuration for elbow stabilization retained by *Paranthropus robustus*, and present in *Australopithecus* species, by 2–2.5 Ma. Hand fossils recovered from Swartkrans Member 1 (Susman, 1989) suggest that *P. robustus* had a precision grip as refined as that in other hominins such as *H. habilis*, and perhaps even modern humans. Relevant features include straight phalanges, a sellar-type carpometacarpal joint, and a prominent apical tuft (see Mittra et al. 2007 for a detailed analysis of primate apical tufts) on the tip of the terminal phalanx of the thumb, with expansions of the flexor insertions probably also present on the distal phalanges of the fingers. Susman (1989) finds that all the features relevant to a precision grip and to tool-making in the OH-7 hand, used by Leakey et al. (1964) to name *Homo habilis*, are also present in Member 1 *Paranthropus.* '*Paranthropus* could well have been a tool-making/using vegetarian' (Susman, 1989, p. 473). The stature and body mass of *Paranthropus robustus* are estimated at 1.32 m and 40 kg (males) and 1.1 m and 32 kg (females), respectively (McHenry & Coffing, 2000). Laetoli hominids LH 36 and L40-19 may possibly represent *Paranthropus boisei* and *P. aethiopicus.* But some researchers consider that *P. boisei* is represented postcranially by KNM-ER 1500, an associated skeleton recovered from the Koobi Fora Formation. The partial skeleton, possibly a female, includes tibial fragments, distal and proximal fragments of a femur, a radius missing its distal epiphysis, a fragmentary ulna, distal fibula, diaphyseal fragments, some pedal elements and a partial glenoid. Stature and body mass are estimated at 1.37 m and 49 kg (males) and 1.24 m and 34 kg (females), respectively (McHenry & Coffing, 2000). Other researchers are less confident that KNM-ER 1500, and the other Koobi Fora postcranial remains linked with *P. boisei* actually belong to that taxon (Wood & Constantino, 2007).

To the extent that proportions can safely be modelled, *P. boisei* shows an intermediate position between *Homo* and the other living great apes in most indices concerning fore- and hindlimb proportions. It lies somewhat closer to *Homo*, differing from *Homo* primarily in having a long and large forelimb when compared with the hindlimb (McHenry, 1978). McHenry (1991) further observes that both the South African and the East African *Paranthropus* would have been small in body size, despite their megadontia, powerful masticatory muscles and robust bones (35% of Swartkrans Member 1 hominins are of a size equivalent to a 28-kg modern human, 22% of a size equivalent to a 43-kg human, and 43% of a size equivalent to a 54-kg human, while the *P. boisei* partial skeleton KNM-ER 1500 has hindlimb joint sizes equivalent to those in a 34–44-kg modern human).

### *The gait of* Paranthropus

Gebo & Schwartz (2006) argue that long trochlear surfaces, and hence a greater range of dorsiflexion/plantarflexion in the Sterkfontein, AL 288-1 and Omo tali, contrast with short talar trochleae in OH 8 and TM 1517. The latter Wood (1974) and Gebo & Schwartz (2006) also assign to *Paranthropus* [although attribution of these fossils to this genus is uncertain; see also Wood & Constantino (2007)], Gebo and Schwartz implying that this genus had a more limited range of plantarflexion/dorsiflexion than *Homo*. Other features common to *Paranthropus*, such as curved medial trochlear rims, suggest to Gebo & Schwartz (2006) greater adduction and a tendency for the tibia to move medially over the foot during the stance phase, and thus a kinematically distinct gait, which they interpret as indicative of some arboreal activity. Susman & Stern (1991), by contrast, argue that *Paranthropus* was predominantly terrestrial. They assign several isolated pedal elements to *Paranthropus robustus.* These include SK 45690 from Swartkrans member 1, *c.* 1.8 Ma. A thickening of the plantar aspect of the base of the SK 45690 proximal hallucial phalanx suggests, according to Susman & Stern (1991), the presence of a plantar aponeurosis, while an open concavity on the dorsal articular surface on the base suggests to them that a modern human-like dorsiflexion was present.

Susman & Brain (1988) report that a hallucial metatarsal from Swartkrans (SKX 5017), while generally resembling that of OH-8 and modern humans, shows little plantar convexity. Moreover, a marked peroneus longus insertion and contact facet for the second metatarsal on its base suggest the hallux was habitually adducted. A robust shaft resembles the condition in KNM-ER 1500, humans and gorillas, and thus suggests habitual terrestriality. The dorsal articular surface, however, is narrow and 'ape-like', suggesting the absence of close-packing in dorsiflexion. Rather than suggesting that either SKX 5017 or OH-8 is misclassified, Susman & Brain (1988) propose that *Homo habilis* may have had a similar gait to *Paranthropus*.

### (5) Transitional hominins, 2–1 Ma

Homo habilis

There is debate about the generic affiliation of material from Olduvai traditionally assigned to *Homo habilis* (Wood & Collard, 1999) and some of this debate revolves around issues in the postcranium. For example, the OH 8 foot has often been described as having 'ape-like' as well as 'human-like' features (see Discussion). Further, *H. habilis* resembles *Au. africanus* more closely than either do *Au. afarensis* in its short legs relative to its forelimbs (McHenry & Berger, 1998). Similarly, forelimb/hindlimb joint size ratios in *H. habilis* and *Au. africanus* resemble each more closely than either ratios do those of *Au. afarensis*, which appear to be more similar to those of later *Homo* (KNM-WT 15000, *Homo erectus*) than either of the former. Homoplasy, and varying degrees of arboreality, may, however, be partly responsible (McHenry & Berger, 1998).

A partial skeleton (OH 62) from lower Bed I of Olduvai Gorge, dated around 1.8 Ma, provides some information about the limb proportions of *H. habilis* (Johanson et al. 1987) but the incomplete nature of the limb bones, particularly the femora, means that a heavy dependence has to be placed on reconstruction, by use of regression techniques or substitution of missing components from other hominins, and this is a potential source of error. Using these techniques, however, Richmond et al. (2002) conclude that evidence from OH 62 and from KNM-ER 3735 – another partial skeleton assigned to *H. habilis* (Leakey et al. 1989) and dated to 1.88–1.91 Ma – allows proportions to be predicted reliably enough to conclude that *H. habilis* proportions are more similar to those of australopiths than to *Homo erectus* and to the older Bouri Hata skeleton. In fact, if correct, upper limb lengths were longer than lower limb lengths for any species but *Au. africanus* (McHenry & Berger, 1998). This would suggest that *H. habilis* combined arboreal and terrestrial locomotion, which would be supported by palaeoenvironmental evidence suggesting somewhat closed and complex-canopied woodland (Andrews & Humphrey, 1999) but not forest, ranging to more open wooded grassland at the top of Bed I. A new analysis by Haeusler & McHenry (2004) – modelling femur length based on the OH 34 femur rather than on AL 288-1 – however argues that limb proportions of both OH 62 and AL 288-1 fall within the modern human range of variation. OH 62 also falls within the range for chimpanzees, with the larger KNM-ER 3735 falling outside the chimpanzee range, and close to the modern human mean. On the basis of a model based on the OH 34 femur, Haeusler & McHenry (2004) indicate that OH 62 would have had long legs, but a relatively long forearm, as did the Bouri Hata hominin. Statures and body masses are estimated by McHenry & Coffing (2000) at 1.31 m and 37 kg (males) and 1.00 m and 32 kg (females), respectively.

Homo rudolfensis

Within a broad spectrum of material which Wood & Richmond (2000) group as '*Homo habilis* sensu lato' is East African material pre-dating KNM-WT 15000. Some of this material is indeed sometimes referred to *Homo erectus*, and includes a pelvis (KNM-ER 3228, 1.95 Ma) and the KNM-ER 2598 occipital (1.9 Ma). McHenry & Coffing (2000) attribute KNM-ER 3228 and modern-looking femora KNM-ER 1472 and KNM-ER 1481 to *Homo* (*Australopithecus*) *rudolfensis.* KNM-ER 1481 is an associated skeleton that includes proximal and distal tibia and distal fibula. The taxon *H.* (*Au.*) *rudolfensis* is named for cranium KNM-ER 1470, although the postcranials were not found associated with the cranium. McHenry & Coffing (2000) estimate male stature and body mass of *H.* (*Au.*) *rudolfensis* at 1.6 m and 60 kg, and female at 1.5 m and 51 kg, respectively, rather smaller than early *Homo erectus* but markedly greater than earlier hominins. Wood & Richmond (2000) caution, however, that there is no way that we can know that these remains belong to *H.* (*Au.*) *rudolfensis*; they may equally well sample *H. erectus*; and indeed one could remark that only their greater stature seems to militate against attribution to *Homo habilis.*

*Fossil evidence for the foot in transitional hominins*

Various studies have used the OH 8 foot, originally assigned to *Homo habilis*, as a model for the foot in early *Homo*. Day & Napier (1964) described OH 8 as possessing strong longitudinal arches and an unopposable hallux, but the talus as showing a mosaic of human- and ape-like features. However, Kidd (1995, and see Kidd et al. 1996) describes the OH 8 foot very differently, as 'ape-like' medially (no arch, opposable hallux and mobile, unstabilized talonavicular joint) but with a markedly 'human-like' (stabilized) calcaneocuboid joint on the lateral side. McHenry & Jones (2006), by contrast, from a study of the hominin medial cuneiform, suggest that the hallux was unopposable.

Others have questioned directly whether OH 8 is a suitable model for the foot in early *Homo*. Wood (1974) argued that the KNM ER 813 talus (1.7–1.9 Ma, Feibel et al. 1989) is more modern human-like than that of OH 8, suggesting closer affinity of KNM ER 813 to *H. erectus.* Wood regards the talus from the OH 8 foot as best matched by the *P. robustus* talus from Kromdraii (TM-1517). Similarly, Susman & Brain (1988) observed that a hallucial metatarsal from Swartkrans (SKX 5017) resembles that of OH 8. Gebo & Schwartz (2006) agree with Wood (1974) that OH 8 should be assigned to the East African robust australopith, *Au. boisei*, comparing OH 8 to the morphology of a talus (323-76-898) and calcaneus (33-74-896) from the East African Omo Shungura Formation. [The talus, from Member G, dates to 2.2 Ma, but the calcaneus, from Tuff F, is slightly older, 2.36 Ma (Feibel et al. 1989).] Gebo & Schwartz (2006) propose that the Omo talus and calcaneus are a better model for the foot in early *Homo*. The transverse tarsal joint was probably more stable and the plantar aponeurosis insertion more modern human-like in being more posterior. However, the Omo calcaneus resembles that of AL 288-1 in showing greater subtalar mobility than in humans and has a large peroneal tubercle, implying increased power in eversion, perhaps to balance a tendency to invert more readily.

Wang & Crompton (2004a) took a more system-orientated approach to foot function in OH 8, by building a simple biomechanical model of foot function during bipedal standing in the living hominoids. They found that a power arm to load arm ratio around 40% minimizes required muscle force at the talocrural joint; that the presence of a high arch in the modern human foot reduces the forces generated by the plantar musculature; and that the modern human foot has a better distribution of forces in the joints. These results indicate that a 39% power arm/load arm ratio, and a relatively high medial arch, as in modern humans, are indeed better optimized for bipedal standing than the equivalent values in the non-human apes. However, the lever arm ratio is even closer to the 40% optimum, and the arch-height coefficient even greater, in OH 8 than in modern humans. Thus required forces are reduced in the plantar muscles and ligaments, while they are increased relative to those in modern humans in the tibialis anterior. These surprising results may indicate either that the original reconstruction of the OH 8 foot (by M. H. Day and J. R. Napier, unpublished data) is incorrect, or that the OH 8 lever arm ratio and arch-height coefficient help to compensate for unknown functional compromises, resulting in high forces elsewhere in the foot.

### *Homo erectus*

#### Early African *Homo erectus* (*Homo ergaster*)

Compared with the material currently available for *Homo habilis*, the KNM-WT 15000 partial skeleton (Brown et al. 1985; Walker and Leakey, 1993a) provides an unambiguous picture of body form and locomotor adaptation in early *Homo erectus*. The skeleton, almost complete with respect to the limbs, apart from the lack of several hand bones and the absence of feet, dates to 1.51–1.56 Ma (Brown & McDougall, 1993).

Together with partial skeletons KNM-ER 803 and KNM-ER 1808, KNM-WT 15000 provides the most comprehensive information about the postcranial skeleton of *H. erectus* (Anton, 2003), although some question remains about possible pathology in the axial skeleton (e.g. see Ohman et al. 2003). The postcranial skeleton of *Homo erectus* is distinguished from that of *Australopithecus* by features such as: coronal-plane widening; a double attachment of the lateral meniscus [which indicates control of rotation of the knee (see Organ & Ward, 2006, for relevant analyses of australopith tibial condyle morphology)] and probably a modern human-like locking mechanism; a narrower pelvis with marked iliac pillars (perhaps reflecting more extended periods of bipedalism); medial torsion of the ischial tuberosity, enlargement of the pelvic inlet (presumably for obstetric reasons, Ruff & Walker, 1993); and enlarged articular surfaces of long bones; thicker diaphyseal cortex, and a deep intercondylar groove or trochlea of the distal femur (Walker & Leakey, 1993b). However, the most obvious and most biomechanically significant differences are in limb proportions (Ruff & Walker, 1993), with a reduction in upper limb length related to body size, and an elongation of the lower limb. Ruff & Walker (1993) suggest that this kind of body build is typical of modern human Nilotic populations such as Turkana pastoralists, and is associated with hot climates.

The ulnofemoral index, 95% in chimpanzees and 92% in *Au. afarensis* AL 288-1, falls to 85% in *H. erectus* and 80% in modern humans (McHenry & Coffing, 2000). The reduction in forelimb length is thus primarily due to reduction in the length of the forearm, while the humerus remains relatively long. McHenry & Coffing (2000) estimate male stature of East African *H. erectus* to be 1.8 m, and male mass to be 66 kg; female stature to be 1.6 m and female mass to be 56 kg. These are the first hominin values to bear close comparison with modern humans. Compared with the funnel-shaped pelvis often attributed to *Au. afarensis* (e.g. see Schmid, 1991) the *H. erectus* ribcage is mediolaterally narrower inferiorly, and wider superiorly. This 'barrel' shape is most likely primarily linked to the narrower pelvis (Jellema et al. 1993), and would result in an upwards migration of the CoG. The lower part of the vertebral column has relatively small bodies for estimated body mass (Latimer & Ward, 1993) and various other aspects of the anatomy of the lumbar spine differ from modern humans or are problematic [e.g. six lumbar vertebrae have been claimed to be present, as in australopiths (Robinson, 1972), but this has been challenged by Haeusler et al. (2002)]. The larger acetabular size and the narrower pelvis strongly suggest a modern human-like hip mechanism during stance and gait. This would be mechanically different from that in *Australopithecus*, with large forces passing mediolaterally through the hip joint and femoral shaft (although quite possibly equivalent in terms of the external forces exerted against the ground). There is possible evidence of under-foot pressures in *Homo* in footprints reported by Behrensmeyer & Laporte (1981) which require quantitative analysis.

By 1.77 Ma *Homo erectus* material is known from East Africa (KNM-ER 3733), Dmanisi in Georgia and Perning in Java (Anton, 2003), indicating a very rapid dispersal over long distances (and see Roebroeks, 2001). Isolated postcranial elements are known from several sites worldwide (Anton, 2003), including pedal elements from Dmanisi and the Jinnuishan pelvis, but these sample too little of the postcranium to be very informative as to locomotor change.

The two intermediate pedal phalanges found with KNM-ER 803, also belong to the *H. erectus* hypodigm. They are shorter and less curved than those of *Au. afarensis*, suggesting a more modern-human-like pressure distribution under the foot (McHenry & Coffing, 2000). No associated pedal fossils exist for the very complete *Homo erectus* skeleton KNM WT-15000

## (6) Archaic modern hominins, > 0.78 Ma

### *Homo antecessor*

This taxon was established to include fossil material from level TD6 at the Gran Dolina site in the Sierra de Atapuerca, dated to > 0.78 Ma, and it is hence arguably the earliest European hominin material. In addition to the craniodental material which established the taxon as distinct from *Homo erectus sensu lato*, *H. heidelbergensis* and *H. neanderthalensis*, there exist partial vertebrae, fragmentary ribs, partial clavicles and radii (described by Carretero et al. 1999), and incomplete sets of foot and hand bones (described by Lorenzo et al. 1999). Unfortunately for our present purposes, both papers focus on establishing that *H. antecessor* is more similar to *Homo sapiens* than to *H. neanderthalensis*, although possibly ancestral to both, and functional analysis is limited. The pedal remains in general are clearly very similar to those of modern humans, and fall within the modern human range of variation. However, the shapes of the proximal hallucial phalanges are distinguished by more rounded proximal articular surfaces; base, shafts and the midshaft of the other proximal phalanges are wider. The dimensions of the hand bones are similar to those of modern humans, but the marked flexor digitorum superficialis insertions, and insertions for the flexor sheaths indicate a more powerful power grip than in modern humans (Carretero et al. 1999). The other postcranials are unremarkable, and tend to group with *Homo sapiens* rather than *H. neanderthalensis* apart from indications that the length and strong curvature, but relative gracility, of the clavicle (despite its thick cortical bone) resemble that of *H. neanderthalensis* rather than that of *Homo sapiens*, suggesting, in turn, broader shoulders than in modern humans. The radius was probably long compared with most, but not all, modern human populations. *H. antecessor* also lacks the short radial neck of *H. sapiens*, a derived feature compared with most earlier hominins, which indicates reduction of the moment arm of biceps brachii. Similarly, a femoral fragment of *H. antecessor* follows hominins other than *H. sapiens* in possessing a marked hypertrochanteric fossa. Stature estimations of around 1.72 m and features such as a probably high brachial index suggest to Carretero et al. (1999) that *H. antecessor* retained the 'Nilotic' build of earlier African *Homo*.

### *Homo heidelbergensis*

Very little postcranial material exists for this taxon, which includes cranial evidence from sites in Africa dated to 0.6–0.4 Ma such as Bodo and Broken Hill (Kabwe) in Africa, and Mauer, Boxgrove, Arago, Steinheim and Swanscombe in Europe (Rightmire, 1998, Pearson, 2000). Trinkaus et al. (1999) note that the partial tibial shaft from Boxgrove in West Sussex, while having relatively low cortical thickness, retains the mediolaterally wide morphology seen of archaic *Homo* (including KNM-WT 15000). The shaft is robust, like those of *H. neanderthalensis*. Considering three alternative modern human models [a Nilotic; a Neanderthal, i.e. hyperarctic (Holliday, 1997a) and a southern Romano-British (i.e. cold-temperate, to match prevailing climatic conditions)] the authors reject a Nilotic model for reconstructing body build and proportions. Trinkaus et al. (1999) concluded that a hyperarctic model was most appropriate, suggesting that limited ability to buffer climatic conditions culturally favoured a heat-conserving body build.

### *Homo neanderthalensis* and early modern *Homo sapiens*

Although the Neanderthals of Europe, the Near East and western Asia show significant differences in postcranial morphology from both preceding and succeeding populations, these are not such as to suggest that locomotion or posture were qualitatively different (Trinkaus, 1983). They are covered only for completeness, and we rely heavily on Trinkaus' comprehensive review. The differences are primarily in the greater robusticity of the skeleton as a whole, but unfortunately the magnitude of these tends to complicate the identification of features that also indicate functional differences. However, there are inferred differences in the functional grips of the hand; obstetric differences, and differences in limb proportions, notably reduction of the distal limb segments, which are interpreted (Holliday, 1997b) following Allen's rule as cold-adaptive.

The most comprehensive review of the postcranial features of the Neanderthals has been provided by Trinkaus (1983). Compared with those of modern humans, the upper limb shows differences in scapular form which would increase the moment arm of the deltoid, and give greater areas of origin for the rotator cuff muscles and teres major. Similarly, the insertion of pectoralis major on the humerus is particularly well marked, as is the position of the tendinous supinator insertion of biceps brachii in the forearm. A marked pronator quadratus crest, and a strongly curved radius, may both indicate powerful pronation and supination [although note that the presence of a marked pronator quadratus crest in some australopithecines

(AL 438-1a L40-19 and OH 36, Drapeau et al. 2005) has not been clearly linked to a functional requirement for powerful pronation in these species]. In the hand, the moment arms of the thenar and hypothenar muscles are increased by high palmar tuberosities on the scaphoid, hamate and trapezium, and the crest for opponens pollicis is particularly well marked. The proportions of the pollicial phalanges would have increased the thumb's effectiveness in a precision grip, and also increased that of the power grip, perhaps in relation to greater mobility at the pollicial carpometacarpal joint. Some hypertrophy also exists in the hallux. In the lower limb, differences are observable in the greater capability of the longbone diaphyses to resist bending and torsional stresses Similarly, increases in femoral head diameter, and a larger gluteus maximus suggest powerful hip extension. Trinkaus & Hilton (1996) suggest that the mediolaterally broad Neanderthal pedal phalanges may have been a response to extended movement over rough terrrain, and/or a compensation for an inefficient carrying technology that widened the stride while increasing step frequency and thus increased mediolateral forces. Steudel-Numbers & Tilkens (2004) have further calculated that the comparatively short Neanderthal hindlimbs would increase the cost of travel by around 30% compared with modern humans.

Much of Neanderthal locomotion must have been associated with procuring food, predominantly meat, under harsh environmental conditions, and relative inefficiency in locomotion is therefore unlikely unless the Neanderthal life style involved activities in which the greater power conferred by their shorter lower limbs (Smith & Savage, 1955) was of more importance than energetic efficiency (Steudel-Numbers & Tilkens, 2004). It is thus more likely that the Neanderthals were very effective hunters (Sorenson & Leonard, 2001), although the manner of hunting may have differed from succeeding populations. The reduction in forearm length typical of the Neanderthals would not just affect thermoregulation. As Dunsworth et al. (2003) suggested for KNM-WT 15000, it would increase accuracy of throwing, but at the cost of decreasing throwing distance. Churchill (1993), among others, has suggested that Neanderthals may have been close-quarter hunters, using stabbing spears. Together with the prevalence, in Mousterian lithic assemblages, of bifacial points robust in cross-section, over more gracile, lighter points, this suggests that Neanderthals, unlike their successors, may have been 'encounter predators'. Using stabbing spears rather than aerodynamically tuned projectiles would have selected for the forelimb power, combined with robusticity that is typical of Neanderthals (Crompton 1997, 2007). Powerful hind-limbs might also prove very useful in such a context. An alternative explanation of the broad pedal phalanges of Neanderthals is that high mediolateral forces on the foot are likely to have been generated by close-quarter thrusting (Trinkaus & Hilton, 1996). There is some evidence that such close-quarter predation may have extended across the Old World, not just in high latitudes. Yokley & Churchill (2006, p. 614) put it like this: 'the morphological similarity in the proximal ulnae of Neandertals, early modern humans from South Africa (Klaasies River Mouth and Border Cave), and African archaic humans (Baringo) remains enigmatic. Perhaps functional demands for elbow stability in the context of Middle Stone Age/Middle Paleolithic hunting and tool-use behaviors resulted in a shift towards the derived ('archaic' in this context) morphology in populations across the Old World.' In this respect the Kabwe/Broken Hill *H. heidelbergensis* postcranials differ, having a much more modern morphology.

### Early modern *Homo sapiens*

Despite a decrease in robusticity throughout the skeleton (e.g. see Holt, 2003) early anatomically modern *Homo sapiens* still differs from recent European and Near Eastern modern human populations in body proportions, having even higher brachial and crural indices, resembling those of recent North and sub-Saharan African populations. This does not follow expectations from Allen's rule, perhaps suggesting genetic influx from Africa (Holliday, 1997b). From a worldwide perspective, indigenous modern human populations do tend to follow Allen's rule, but local variation between human populations can be marked, so that further generalizations would be unwise.

## Summaries and discussion

### (1) The LCA of living crown hominoids (Table 1)

The fossil evidence for the evolution of the hominoid and hominin locomotor system, when taken in the context of the locomotion of living apes, clearly places the generalized arboreal quadrupeds, i.e. *Proconsul*, *Nacholapithecus* and *Kenyapithecus*, as stem and not crown hominoids. The body size of early crown hominoids is uniformly close to or within the range of living great apes, thus supporting Pilbeam's (1996) and MacLatchy's (2004) suggestion that living hylobatids are phyletic dwarves.

As predicted in Table 1, the crown hominoids are best characterized by adaptations of the lumbar spine and thorax that imply habitual orthograde, rather than forelimb suspensory 'brachiating' locomotion, as traditionally proposed. A mediolaterally broad but anteriorly shallow thorax with a dorsally placed scapula is evident in *Morotopithecus*, *Dryopithecus laietanus* and *Pierolapithecus*, but the thorax of *Pierolapithecus* suggests that only a gibbon-like degree of 'flattening' of the thorax would have been present in the common crown-hominoid ancestor, and the degree of dorsal repositioning of the transverse process may also have been limited to that seen in gibbons. Ward (2007) suggests that some changes in the thorax and spine, such as shortening, may be related to use of the limbs in abducted postures (e.g. a need to control lateral flexion of the spine). This contradicts the prediction of the hylobatian model, which has a laterally mobile lumbar spine. While there is clear evidence in the glenoid of *Morotopithecus* of an ability to use the forelimb in highly abducted postures, the femur of *Morotopithecus* shows features characteristic of limited abduction (compared, for example, with that seen in orangutans) but indicating adaptations of the hip and knee to support the superincumbent, orthograde head, arms and trunk (MacLatchy et al. 2000). Taken together with the lack of convincing evidence of suspensory adaptations in *Morotopithecus*, *Pierolapithecus* and several other Miocene crown hominoids, this suggests that forelimb abduction capacity probably relates more to orthograde clambering than to forelimb suspensory locomotion. This interpretation is supported by the early appearance of a wrist joint similar to that of modern hominoids in *Pierolapithecus*, which would also have had a powerful manual grasp. Evidence in this genus [and in *Hispanopithecus* (*D.*) *laietanus*], for a hand used to some extent in palmigrade, pronograde arboreal quadrupedalism is unsurprising given that such behaviour comprises nearly one-fifth of orangutan locomotion, despite phalangeal curvature.

Forelimb-suspensory locomotion is only very frequent in the hylobatids, and while this is still very much the subject of debate, adaptations for forelimb-suspensory locomotion, where they genuinely exist, may well be homoplastic (cf. Larson, 1998; Begun, 2007; Ward, 2007). The emphasis on bearing the load of the body over the hindlimb but not abduction in the femur of *Morotopithecus* is, however, particularly intriguing and may indicate that clambering in this species was predominantly accompanied by hindlimb support via extended-hip compressive postures, rather than in abducted-hip suspensory postures, such as frequently occurs in orangutans. If so, this may even suggest that the locomotor repertoire of the early crown hominoids utilized extended-hip postures and perhaps bipedalism more than that of the later crown hominoids such as *Hispanopithecus* (the femur of which shows increased adaptations for abduction) and extant orangutans.

Fossil evidence for the foot of the LCA of living crown hominoids is limited and inconclusive, but parallels to the orthograde clambering of the orangutan and lack of heel-strike in modern hylobatids suggest a grasping, inverted but plantigrade foot which lacked heel-strike. The latter is likely to have appeared only in the arboreal common ancestor of living great apes, perhaps as a consequence of bearing a heavy head, arms and trunk on a habitually extended leg. As we have seen, Tuttle (1969, 1974, 1981) was one of the first to elaborate an hypothesis deriving hominin bipedality from arboreal activity, in his 'hylobatian' model, but we have noted that gibbon bipedality is mechanically distinct from both human running and walking. Another difficulty with Tuttle's (1981) hylobatian model is apparent from our review of the fossil record. At 9–13 kg, his hylobatians would be less than half the 34 kg estimated body weight of *Pierolapithecus catalaunicus* or *Hispanopithecus* (*Dryopithecus*) *laeitanus*, and while the position of origin of the transverse processes of *Pierolapithecus catalaunicus* is probably gibbon-like, the rather caudally directed spinous processes suggest a relatively stiff spine more indicative of generalized orthogrady than the laterally mobile spine suggested for the hylobatians. If Moyà-Solà et al. (2004) are right and the relatively short hands of *Pierolapithecus catalaunicus* indicate palmigrady, *Pierolapithecus* could in no way represent the 'hylobatians'.

The basic niche of hominoids, as tropical forest ripe-fruit eaters foraging in the peripheral canopy (Pilbeam, 1996), suggests that the crown-hominoid suite of postcranial characteristics would have arisen as an adaptation to foraging in the large trees of closed woodland or forest, much as does the living orangutan. *Hispanopithecus* (*Dryopithecus*) *laietanus*, while possibly more often quadrupedal than are orangutans, is nonetheless more similar to orangutans than anything else and, with particular reference to the hylobatian model, has notably short hindlimbs. *Morotopithecus*, at 36–47 kg, is even further out of the hylobatian size range and also had a stiff lower back. Much later in time, *Orrorin* would also have had short hindlimbs, and so, as we have seen, do early hominins.

### (2) The LCA of Panini and Hominini (Table 1)

Crown hominoids almost certainly evolved from a pronograde simian stock. The existence of clear adaptations for orthogrady in the crown hominoid *Morotopithecus*/*Ugandapithecus* at 16–21 Ma thus implies one change from pronogrady to orthogrady prior to this date. The prime issue is whether the panin–hominin LCA (at a molecular date of some 4–8 Ma, see Bradley, 2008) would have been chimpanzee-like, as suggested by Pilbeam (1996) and many others, and hence a knuckle-walker, in its postcranial adaptations. However, if one assumes our prediction for the LCA of crown hominoids is correct, the knuckle-walking hypothesis would require a change back to pronogrady in the lineage leading to the common hominine–gorilline stock, and then a second change to orthogrady in the hominins clade. The early date (6–6.5 Ma) of the unquestionably arboreal, orthograde, and quite probably bipedal *Orrorin* leaves little time for this reversal to occur. Further, as our review indicates, the knuckle-walking hypothesis has long suffered from the weakness that no early hominin has been shown to retain the various anatomical features of the hand that have been proposed to be associated with this behaviour [e.g. see Stern & Susman (1983) for *Au. afarensis*; McHenry (1983) for the capitate and indeed forelimb of *Au. afarensis* and *Au. africanus*; Ward et al. (1999b) for the metacarpals, capitate, hamate, and lunate from South Turkwel; and Clarke (2002) for the StW-573 hand]. These features include, variously: fusion of the os centrale with the scaphoid, extension of the proximal articular surface of the capitulum onto the dorsum, and a ridge at the proximodorsal margin of the distal articular surface of the metacarpals to support the proximal phalanx in hyperextension. The latter feature, absent of course in modern humans, is reported by McCrossin & Benefit (1997) in *Kenyapithecus*, which is not a likely crown hominoid and not apparently proposed by McCrossin and Benefit as a knuckle-walker (they seem to use the feature simply as evidence of terrestriality). Lewis (1972, 1974) found no evidence of features of the wrist of African apes adaptive for knuckle-walking. He argued that features of African-ape wrists such as 'waisting' of the capitate were, instead, related to forelimb suspension. However, Jenkins & Fleagle (1975), using radiography of passively manipulated wrists of anaesthetized apes, did identify features of common chimpanzees which would limit wrist extension in a knuckle-walking posture. One of the best known 'knuckle-walking features', fusion of the os centrale (Corrucini & McHenry, 2001) – like other alleged 'knuckle-walking' features of the hand – is variable in expression (Susman, 1979), sometimes being present in *Pongo*. It occurs quite often also in *Avahi* and *Hapalemur* (Kivell & Begun, 2007), lemurs from two separate families, but both broadly specialized for leaping. Neither orangutans nor the two strepsirrhines of course are knuckle-walkers. While an argument might still be made that fusion of the os centrale is a synapomophy of the living African apes (modern humans, chimpanzees, bonobos and gorillas), Kivell & Begun (2007) found no clear kinematic or biomechanical evidence to link fusion of the os centrale and scaphoid with mid-carpal stability in knuckle-walking and conclude that it is a feature under primarily phylogenetic influence, in which case its presence in modern humans, chimpanzees, bonobos and gorillas might signify only that they are closely related. By contrast, its frequent occurrence in two strepsirhines which both leap and climb, but when leaping habitually land hindlimb first, suggests that a powerful manual grasp (as required in branch grasping but also in lithic technology) may also lead to fusion of the os centrale.

Richmond & Strait (2000) claim to have found morphometric evidence of retention of derived knuckle-walking features in the distal radius of *Au. afarensis* AL 288-1 and *Au. anamensis* radius KNM-ER 20419. However, Richmond & Strait (2000) made their measurements on a cast of KNM-ER 20419 without making allowance for a missing styloid process, and their headline canonical variates plot (p. 382) shows that the distal radial morphology of AL 288-1 lies within the overlap between the ranges of *Gorilla* and *Pongo.* However, Richmond & Strait (2001) replied to a similar criticism of Dainton (2001) by claiming that additional statistics do support a separation of AL 288-1 and KNM-ER 20419. *Pongo* does not show any knuckle-walking features in its postcrania, with the possible exception of occasional fusion of the os centrale with the scaphoid (but see above) and it usually fist-walks during terrestrial quadrupedalism observed in captivity (Corrucini & McHenry, 2001). Heinrich et al. (1993) also observed that like AL 288-1, *Pongo* and the hylobatids, the KNM-ER 20419 radius possesses a particularly large radiocarpal facet for the lunate, suggesting importance of adducted wrist postures, perhaps in climbing, and the reverse of the condition in panins and gorillines.

As we noted above, *Kenyapithecus* exhibits at least one knuckle-walking adaptation, yet both Finarelli & Clyde (2004) and Young & MacLatchy (2004) found that *Kenyapithecus* is more distantly related to modern humans than the living *Hylobates* and *Pongo*, or a range of fossil genera including *Hesperopithecus* and *Oreopithecus*. Both the latter fossil genera as well as the two living genera are well enough known postcranially that we can be confident that they lack knuckle-walking adaptations.

Further, Drapeau & Ward (2007, p.327) cast doubt on the value of *Pan* as a good model for the hand of the LCA of panins and hominins: '*Pan* species are unique in having long metacarpals relative to ulnar length, demonstrating that they probably differ from the common human–chimp ancestor'. We thus concur with the conclusion of Dainton & Macho (1999) from ontogenetic evidence (see also Inouye, 1992) that knuckle-walking probably evolved in parallel in *Gorilla* and *Pan* (as pressures to stabilize the metacarpophalangeal, midcarpal and radiocarpal joints would have been intense under loads exerted in knuckle-walking). *Pan*, we suggest, cannot be regarded as a model for the ancestral condition of the forelimb in African apes.

At 9–11 Ma *Oreopithecus* is not now thought to be a hominin, but was unquestionably habitually orthograde, and perhaps even habitually bipedal. From its cranium *Sahelanthropus* was quite probably orthograde, and either a panin, gorillin or hominin at 7.5 Ma. *Orrorin* at 6.5 Ma is certainly a hominine and quite probably a hominin. It shows adaptations for arboreality, orthogrady and habitually extended hip postures (at least as frequent as in orangutans, which usually lack the obturator externus groove) prior or close to molecular dates for chimpanzee–human divergence. At the time this paper was going to press, Richmond and Jungers (2008) reported evidence from multivariate morphometry that proximal femoral morphology in *Orrorin* follows the pattern seen in *Australopithecus*, consistent with a substantial component of locomotor bipedalism. However, while acknowledging that the morphology of the humerus and proximal phalanx in *Orrorin* suggests substantial 'arboreal climbing' (most commonly interpreted as forelimb-dominated suspensory behaviour), Richmond and Jungers further assert that the claimed similarity in curvature of this (single) phalanx to the levels of curvature seen in chimpanzees is evidence of a knucklewalking origin for bipedality. Unless *Orrorin* somehow combined terrestrial knucklewalking (and thus habitually flexed hips) with terrestrial and/or arboreal bipedalism (and thus habitually extended hips), their argument implies that even at 6.5 Ma. (compared with Bradley's [2008] 4–8 Ma. estimate for the chimpanzee–human divergence) the protohominin postcranial skeleton bore anachronistic features inherited from an unknown knuckle-walking ancestor. It seems more likely that Richmond and Jungers place rather too much faith in their ability to reconstruct locomotor repertoire from the degree of curvature of a incomplete phalanx, from an immature individual, and that the balance of the current fossil evidence supports our proposition that the LCA of modern humans and chimpanzees, rather like *Orrorin* in many respects, was a predominantly arboreal, orthograde, short-legged but long-armed great ape, with long, curved fingers and toes. In this common ancestor we suggest that the foot would have been used in a predominantly mid-prone posture when walking on branches, and a relatively inverted posture even when walking on the ground. The bipedal gait of the LCA of panins and hominins would have a clear heel-strike, as this appears to be a genuine great-ape synapomorphy but a functional mid-tarsal break would have been evident, as it is in orangutans, bonobos and common chimpanzees and even (if usually pathologically, e.g. in Charcot foot) sometimes in modern humans. In the absence of any evidence from the calcaneus of a marked Achilles' tendon in *A. afarensis*, and its apparent weakness of expression in great apes apart from *Homo* it remains most likely that the Achilles' tendon was not well developed.

We regard our predictions for the LCA of panins and hominins as better sustained by the fossil record than those of the knuckle-walking hypothesis. We acknowledge again our debt to both Tuttle, for his identification of the arboreal origins of bipedalism, and to Stern, whose earlier versions of what became the 'vertical climbing hypothesis' have much in common with our own hypothesis, unlike the strict version espoused by Prost.

### (3) Trends in panins, hominins and gorillines: the origins of terrestrial bipedality and knuckle-walking

We speculate that the adoption of terrestrial bipedalism by early hominins was driven by the same climate-driven fragmentation of woodland which led to an increase in vertical climbing in panins and gorillines. This meant that panins and gorillines could ensure continued access to canopy fruits, while enabling access to fall-back foods on the ground. Increased commitment to vertical climbing in panins and gorillines implies an increased commitment to flexed-hip, flexed-knee kinematics, which would have favoured knuckle-walking being adopted on the ground. We argue further that adoption of terrestrial bipedalism in hominins, combined with some limited arboreality in the smaller trees, arose as a different response to the same pressures, and a means of more efficient access to (given more committed specialization on) the same fall-back foods on the ground. Hominins sacrificed access to the canopy for an increased commitment to the bipedal element of the common hominoid locomotor repertoire.

### (4) The LCA of Hominini

The hominin and bipedal status of *Ardipithecus* must remain in some doubt, until more extensive discovery and publication of the postcranials in particular; the early evidence for extensive metatarsophalangeal dorsiflexion is, however, tantalizing. The earliest undoubted hominin, *Au. anamensis*, already shows a talocrural joint adapted for parasagittal motion of the tibia over the foot, and this is only compatible with a considerable degree of terrestrial bipedalism, despite evidence that their palaeoenvironment was riparian woodland (Kenyan sites) or closed woodland/forested (Ethiopian sites). Such early changes in lower-limb morphology would have reduced hindlimb effectiveness in arboreal contexts, favouring retention of the long forearms, to facilitate balance in arboreal bipedalism, and also favouring retention of a low CoG, and hence short legs. Any degree of terrestriality is likely to have reduced the need for the hip abduction capabilities seen in living arboreal great apes, which enhance stability in the three-dimensional arboreal environment, and hence favoured adaptations for, or mutations producing, lateral stability, and hence changes in pelvic anatomy however these originated. There is no clear evidence for a knee locking mechanism until *Homo erectus* (e.g. see Organ & Ward, 2006), but ontogenetic changes in the bicondylar angle would reduce forces required to maintain the CoG over the knee.

Any degree of terrestriality would have tended to favour increased pronation of the foot and some degree of mid-foot stabilization, at the expense of the hallucial grasp. A more powerful pollicial grasp may thus have been selected for so as to compensate for reduced arboreal performance in the foot, and enhanced hand-grips may have facilitated the adoption of early (e.g. hard-hammer) stone-tool knapping techniques (cf. Clarke, 2002). Or, of course, the two pressures could have acted concurrently.

*Fossil exemplars of the LCAs of living crown hominoids; Panini and Hominini and of Hominini*

We tentatively identify the following as the best available fossil exemplars for the state of the postcranium in each LCA: *Pierolapithecus catalaunicus* for the crown hominoids – despite its late date, until the nature of *Morotopithecus* is clarified; *Hispanopithecus* (*Dryopithecus*) *laeitanus* for the LCA of great apes only; *Orrorin tugenensis* for panins and hominins; and *Au. anamensis* for hominins. This should not be taken as implying that we regard these fossils as LCAs: some or all may belong to daughter lineages.

### (5) Trends in early hominins

The adoption of a increasingly terrestrial lifestyle, as a consequence of the spread of open and grassland environments that is well documented in East Africa from 2 Ma, would have led to increased lower limb length, reduced forelimb length and reduced trunk length, all of which enhance carrying capacity and endurance walking. Inversion and pronation-capacity of the foot was a likely exaption for a functional medial longitudinal arch, which in turn probably implies loss of the mid-tarsal break to permit more efficient leverage about an already anteriorly shifted CoP. This would have permitted greater vertical forces at push-off, both in walking and in running. Were these acquired very early, as suggested by the *Ardipithecus* metatarsal? Acquisition of modern dimensions and configuration of the semicircular canals in early African *Homo erectus* (Spoor, 2003), absent in *Australopithecus* and earlier hominins, would have facilitated running, whereas enhanced capacity for efficient/fast running would have required acquisition of a large Achilles' tendon and/or other compliant energy-stores such as a plantar aponeurosis. It is likely, but not certain, that all these were in place by the time of early African *Homo erectus*, e.g. KNM-WT 15000.

### (6) Transition in body form between australopiths and early *Homo*

While it is not clear that foot function changed dramatically between australopiths and *Homo erectus*, overall body proportions unquestionably did. What drove these changes in body form? Aiello & Wells (2002) show how the increase in body size and in brain size, which began with evolution of the genus *Homo*, would have led to both an absolute increase in energy requirements and a shift of requirements away from the gut (as occurs in long-distance running) but in this case towards the brain, because of the very high energy demands of both the brain and the liver. An increase in brain size would bring about particularly increased metabolic costs during a longer pregnancy. These increases in energy requirements would have demanded increased daily ranging distances to obtain high-quality food, which in turn would have permitted a change in body build de-emphasizing gut volume. A need for high-quality food may have driven a more predatory lifestyle, and Anton et al. (2002) estimate that with a moderate increase in consumption of meat – driven itself partly by progressive increase in grasslands and reduction in biodiversity – *Homo erectus* would have required home range areas ten times the size of those of australopiths. This, in turn, they argue, drove the dispersal of early *Homo*. It does need to be borne in mind, however, that the spread of grasslands substantially preceded the changes in bipedalism (Ségalen et al. 2007) just as the appearance of substantial areas of $C_4$ grasslands in East Africa substantially preceded the appearance of habitual bipedalism: hominins were exploiting grasslands rather than being forced into them.

Some suggest a direct relationship between increased predation and the changes in limb proportions witnessed in KNM-WT 15000. For example, Dunsworth et al. (1993) point out that an increase in stature increases the distance over which projectiles can be thrown, or permits flatness of trajectory, and hence reduces flight time and the chances of escaping the projectile. Further, whereas a reduction in forearm length will reduce the throwing distance and the 'launch window', it will increase accuracy. Dunsworth et al. (1993) suggest that as animal consumption increased, accuracy became more important, and short forelimbs were selected for. Further, Bramble & Lieberman (2004) suggest that selection for endurance running (ER), quite likely in the context of pursuit predation, can account for most of the differences in anatomy between *Australopithecus* and *Homo.* This is not so much a new hypothesis as a revision of a similar proposal originally developed by Carrier (1984) for hominins as a whole. In the light of more recent knowledge of the body form of *Au. afarensis*, Bramble & Lieberman (2004) apply the ER hypothesis to the transition from *Australopithecus* to *Homo.* While the ER hypothesis is in many respects an attractive idea, Bramble & Lieberman (2004) depended heavily on the OH 8 foot as their evidence for changes in the foot from australopiths to *Homo*, and OH 8, as we have seen, may well actually represent *Paranthropus*, not *H. habilis*. Further, their claim that selection for endurance running was solely accountable for features of the new trunk shape which help control rotations induced by hip-joint motion, is not sustained by experimental evidence which show that these counter-rotations occur also during walking (Witte et al. 2004). Similarly, although elastic energy storage is more important in running than in walking, it does occur during walking, particularly in the plantar soft tissue of the foot. It is not likely therefore that the evolution of ER alone can explain the changes in body form between *Australopithecus* and *Homo*: changes in the nature of walking must also be implicated.

Indeed, the changes in body proportions between australopiths and *Homo erectus can* also be explained as an adaptation to load-carrying and long-distance walking. Wang et al. (2003b) and Wang and Crompton (2004b) used a mathematical model to investigate the effect of limb proportions on swing-symmetry of the upper and lower limbs, a major condition of efficient long-distance walking, with respect to hand-carrying of a load. They found that AL 288-1 could only have carried loads equivalent to 15–50% of upper limb weight while maintaining swing symmetry, but KNM-WT 15000 and modern humans could both carry loads three times heavier than the upper limb while maintaining swing symmetry. Modern human intermembral indices are optimized for hand-carrying of loads. Using musculoskeletal models of modern humans, KNM-WT 15000 and AL 288-1, Wang et al. (2004) also showed that the distance-specific cost of walking, in terms of muscle power and stress requirements, is higher for AL 288-1 than for either modern humans or KNM-WT15000. From this it follows that the greater the distance walked, the more advantage accrues to the modern human type of body build. A further inverse dynamic model (Wang & Crompton, 2004b) where the mechanical costs of carrying loads of different masses on the back were compared, showed that KNM-WT 15000 could have carried loads of 10–15% body mass for less cost, relative to body size, than AL 288-1 walking erect but unloaded, and loads of 40% body mass for the same cost. WT 15000 would have had better mechanical effectiveness in bearing light loads on the back than the modern Chinese male adults who were the study subjects, although the latter would be more effective in load carrying than KNM-WT 15000 for loads over 33% body weight. The contrast between KNM-WT 15000 and modern humans might have been different, if Nilotic subjects had been used as the example of modern humans.

There is direct evidence for increase in long-distance transport (whether in single journeys or additively) at the time of appearance of *H. erectus*. The Oldowan industries associated with australopiths at Olduvai Bed I (Leakey, 1971; Hay, 1976) document transport of the raw material for stone tool manufacture over distances of 3–12 km from the outcrops of origin, and distances of up to 20 km can similarly be documented at East Turkana (Harriss & Herbich, 1978). However, in Acheulean sites, which are associated rather with *Homo erectus*, evidence suggests that transport occurs more often, and over much greater distances. At Olorgesailie, Isaac (1977) recorded cases where quartz was brought over 40 km. At Kilombe, similarly, two obsidian bifaces appear among many hundreds made from local lavas, implying that long-distance transport occurred (Gowlett, 1982). At Gadeb, in eastern Ethiopia (*c.* 1.5 Ma), several obsidian bifaces document a transport distance of over 100 km (Clark, 1980). Any hypothesis which seeks to explain the dramatic shift in postcranial anatomy with the appearance of *H. erectus* needs to address how it facilitated long-distance travel and load-bearing.

### (7) Trends in genus *Homo*

Later evolution of gait within *Homo* is marked particularly by selection for increased robusticity that appears to have evolved in connection with effective close-quarter predation. This may have been a phenomenon in both high and low latitudes in the Old World (Yokley & Churchill, 2006). In high latitudes, reduced distal limb segments in 'Classic' Neanderthalers may be more directly related to thermoregulation (Holliday, 1997b) following Allen's rule, and changes in hunting practice may have been accelerated by an increased need for high-quality food under cold conditions. This was followed by a return to gracility. Increased gracility appears to be an overall biomechanical trend in hominin evolution, and minimizes the power required for motion (Wang & Crompton, 2003). Equally, populations in high latitudes returned to more elongated distal segments as cultural thermoregulation became more effective in *Homo sapiens*. Gene flow from low-latitude populations, less affected by glaciation, is likely to have accelerated these reversals. A return to longer distal segments may possibly have led to further fine-tuning of forelimb and hindlimb swing cycles in *H. sapiens* to enhance hand-carrying of small loads.

### (8) Time of appearance of a functionally modern foot

The *Au. anamensis* tibia implies an advanced, parasagittal motion of the leg over the foot, and hence habitual, but not obligate, terrestrial bipedality by 4.2 Ma. The evidence of the AL 333 foot-bones and the Laetoli footprints is so far inconclusive concerning whether a habitually pronated foot, with a well-formed medial longitudinal arch, had appeared by 3.6 Ma. Our understanding of the relationship between joint shape and joint kinematics in the foot is not yet good enough to resolve this issue. But although we cannot yet reliably diagnose differences in the kinematics of gait, or habitat differences between lineages, there seems to be good evidence that even as late as 1.8 Ma, the function of the mid-foot differed between at least the *Paranthropus* and *Homo* lineages, and these lineages may also have differed in presence or absence of a toe-off mechanism, possibly indicating greater arboreality in either one of these. An entirely modern foot may thus not have been in place until well after the appearance of early *Homo.*

## Conclusion

The fossil evidence is compatible with each of the three LCAs (i.e. crown hominoids, panins and hominines, and hominins): hypotheses we constructed primarily on the basis of our own expertise, locomotor ecology and biomechanics. We believe that a strong enough case now exists for ancestral orthogrady, and thus an arboreal origin, for facultative bipedality, that it merits serious attention. Many issues remain to be clarified: these include the extent of homoplasy in (and significance of) the acquisition of suspensory adaptations both by stem hominoids such as *Nacholapithecus*, and each of the various crown hominoids; the nature of *Sivapi-thecus* and its relationship (if any) to the origin of the pongines; the identity and locomotor evolution of the lineage which gave rise to the hominins; and as we have just indicated, the mechanical evolution of the hominin foot. Broader issues are raised, and one of the most challenging is the nature of the interplay between developmental genes, environmental change and natural selection. Is the common pattern in hominoid evolution for developmental genes to mutate, facilitating locomotor diversification, when and if environmental change occurs, and then for natural selection to act to optimize or at least enhance performance in the new environment? We suspect that much circumspection will be necessary to address this complex relationship, beset as it is by Hopeful Monsters, Spandrels and the like.

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## Note

*Like Topsy, this contribution 'just grew'. In the first instance Sarah Elton and Bernard Wood kindly invited R.H.C. to their Oxford symposium both to review locomotor evolution in the Hominoidea, and to attempt to reconstruct the locomotion of the last common ancestor of modern humans and chimpanzees/bonobos, largely as a one-stop-shop resource for student dissertations or term papers. A more senior colleague was unable to commit himself to do the same for posture, and so R.H.C.'s presentation accrued that aspect. Bernard then suggested R.H.C. also discuss locomotor evolution in the hominin line, until the appearance of an essentially fully modern morphology. At the writing-up stage, it seemed wise to recruit younger and more energetic spirits as co-authors. The core of our argument concerning the origins of hominin bipedalism can be found in Thorpe & Crompton (2006), Thorpe et al. (2007a,b) and Crompton & Thorpe (2007). However, we hope that while our remit here is primarily didactic, colleagues may also find some of what we have to say of interest, as this format allows us to set out more of the details in support of our ancestral orthogrady hypothesis, structured in the 'hypothetico-deductive' format suggested by one reviewer.

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