

Review

Arboreality, terrestriality and bipedalism

Robin Huw Crompton^{1,*}, William I. Sellers^{2,†}
and Susannah K. S. Thorpe^{3,†}

¹*Primate Evolution and Morphology Research Group, School of Biomedical Sciences, The University of Liverpool, Sherrington Buildings, Ashton Street, Liverpool L69 3GE, UK*

²*Faculty of Life Sciences, The University of Manchester, 3.614 Stopford Building, Oxford Road, Manchester M13 9PT, UK*

³*School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK*

The full publication of *Ardipithecus ramidus* has particular importance for the origins of hominin bipedality, and strengthens the growing case for an arboreal origin. Palaeontological techniques however inevitably concentrate on details of fragmentary postcranial bones and can benefit from a whole-animal perspective. This can be provided by field studies of locomotor behaviour, which provide a real-world perspective of adaptive context, against which conclusions drawn from palaeontology and comparative osteology may be assessed and honed. Increasingly sophisticated dynamic modelling techniques, validated against experimental data for living animals, offer a different perspective where evolutionary and virtual ablation experiments, impossible for living mammals, may be run *in silico*, and these can analyse not only the interactions and behaviour of rigid segments but increasingly the effects of compliance, which are of crucial importance in guiding the evolution of an arboreally derived lineage.

Keywords: bipedalism; biomechanics; evolution; field studies

1. INTRODUCTION

Darwin's (1871) argument on human origins has never appeared stronger than now, when molecular evidence suggests a divergence time of only 5–8 Ma for humans and their extinct relatives (the tribe Hominini), from the chimpanzees and bonobos (tribe Panini; Bradley 2008). But as pointed out by Tuttle *et al.* (1974) in their excellent review, Darwin, while he did not present a detailed model of the last common ancestor of humans and other African apes, made an important point that is too often ignored: that we should not expect the last common ancestor to resemble either living humans or other living apes particularly closely.

2. BIPEDALISM: AN ARBOREAL OR TERRESTRIAL ORIGIN?

In the first four decades of the twentieth century, it was generally accepted that bipedalism had an arboreal origin (e.g. Keith 1903, 1923; Morton 1922; Schultz 1936). But for the last 60 years, since the first field study of mountain gorillas by Schaller (1963), the field studies of chimpanzees by Goodall (1998), and the ensuing recognition (e.g. Zihlman *et al.* 1978) of a special and genetically very close relationship between the hominins (humans and their ancestors)

and the panins (bonobos and common chimpanzees), the prevailing paradigm for the origins of human bipedalism has been the knucklewalking quadrupedalism model (first proposed by Washburn (1967) and reviewed by Tuttle *et al.* (1974)). This model holds that the common ancestor of hominins and panins would have looked much like chimpanzees do today, and so bipedalism would have arisen in an ancestor which was a terrestrial, quadrupedal knucklewalker, like the panins, and the remaining African apes, the gorillines.

This paradigm was developed in some detail by Gebo (1992, 1996), who identified heel-strike plantigrady as a common, shared-acquired character of African apes linked closely to knucklewalking quadrupedalism, and to the hominin acquisition of a terrestrially adapted foot. However, heel-strike plantigrady is not limited to the African apes (Meldrum 1993; Crompton *et al.* 2003); also, heel-strike is actually particularly clearly expressed in an Asian ape, the most arboreal of great apes, the orangutan, subfamily Ponginae (Crompton *et al.* 2003, 2008).

All great apes can and do walk bipedally, and most do so in an arboreal context. Again, it is the most arboreal, the orangutan, which uses bipedal locomotion most often (Thorpe & Crompton 2005, 2006). While bipedal locomotion supported by the hindlimbs alone makes up only about 2 per cent of arboreal locomotion of orangutans, a further 6 per cent consists of bipedalism where one or both forelimbs are used for balance. But this small percentage of locomotor bipedalism (or compressive orthogrady, if preferred) plays an

* Author for correspondence (rhcomp@liv.ac.uk).

† All authors contributed equally to this manuscript.

One contribution of 14 to a Discussion Meeting Issue 'The first four million years of human evolution'.

ecologically crucial role in movement on the fine peripheral branches, where fruits are located. It further allows orangutans to bridge from tree to tree at canopy level, avoiding the very high costs (Thorpe *et al.* 2007a) and predation risk associated with crossing on the ground. It is again the orangutan which of all living apes approaches closest to us in one of the most important of the biomechanical features identified by Alexander (1991) as characteristic of human walking: namely stiff-legged, upright gait. As a consequence of its stiff-legged gait, the orangutan produces, in a fifth of its bipedalism, double-humped vertical ground reaction force curves (vGRF) which, alone among apes, overlap with those produced by human walking (Crompton *et al.* 2003), and which allow a high degree of pendular energy conversion. Our calculations indicate that while in untrained common chimpanzees energy conversion in bipedalism reaches little more than 8 per cent, it approaches some 50 per cent in untrained orangutans, still well short, of course, of the 70 per cent possible in humans (Wang *et al.* 2003). But while it has recently been argued that the elongated, inverted foot of the orangutan does not at all closely resemble our own (Sayers & Lovejoy 2008), orangutan foot function in bipedal walking, expressed in the pattern of foot pressure, is actually very similar (Crompton *et al.* 2008) to that of the bonobo (Vereecke *et al.* 2003), often suggested by others as a model for the common panin–hominin ancestor (e.g. Zihlman *et al.* 1978 and reviewed in Vereecke *et al.* 2003).

It has been apparent for the last few years that a growing number of scientists have found cause to doubt whether firm evidence exists in the fossil record for a knucklewalking origin: see, e.g. Stern & Susman (1983) for *Australopithecus afarensis*; Ward *et al.* (1999) for the South Turkwel handbones and Clarke (1999, 2002) for the StW-573 hand. A range of purported ‘knucklewalking features’, dorsal ridges on the distal aspect of the metacarpals, os centrale–scaphoid fusion or extension of the proximal articular surface of the capitulum onto its dorsum, have been sought in the hominin fossil record, but have either not been found or found only inconsistently. Dainton & Macho (1999) raised doubts about whether knucklewalking was a homologous phenomenon even in chimpanzees and gorillas. However, Richmond & Strait (2000) argued that the distal radial morphology of *Au. afarensis* was evidence for a knucklewalking phase in evolution some time between 3.6 Ma and the commonly accepted 5–8 Ma limits for genetic separation of hominins and panins. It is therefore noteworthy that the morphology plotted by Richmond & Strait (2000) lies well within the orangutan range of variation. Only large male Bornean orangutan make much use of the ground, the Sumatran tiger being a major discouragement to terrestriality on that island, the clouded leopard posing a threat to small or juvenile orangutan on Borneo. Large Bornean males have too much unstable mass above the hip to sustain unassisted bipedalism, and so tend to cross the ground quadrupedally. But when crossing the ground they do not walk on the middle phalanx, as chimpanzees or gorillas do, but on their proximal phalanges or on

the side of their hand. Richmond *et al.* (2001), however, stoutly defended a knucklewalking origin in an extensive review, and Richmond & Jungers (2008) claimed that similarities in curvature of a single phalanx of the late Miocene protohominin *Orrorin* to that in chimpanzees represented evidence of knucklewalking, although *Orrorin* is regarded by its discoverers as arboreally adapted, orthograde and bipedal when moving on the ground (Senut *et al.* 2001). Kivell & Begun (2007) however found no clear functional link between os centrale–scaphoid fusion and knucklewalking and Kivell & Schmitt (2009) argue that there are two functionally distinct modes of knucklewalking in African apes: that in chimpanzees being associated with extended wrist postures in an arboreal environment (directly addressing Richmond & Jungers 2008), and that in gorillas with a neutral wrist posture in a terrestrial environment. Kivell & Schmitt (2009) go on to argue that the purported knucklewalking features of hominins are instead adaptations to arboreality, and thus that bipedalism indeed arose in the arboreal ecological niche common to living apes.

While the absence of purported knucklewalking features in the hand of *Au. afarensis* (e.g. Stern & Susman 1983) leaves little time for hominins to lose any such features after the separation of hominins and panins 5–8 Ma, the publication of a full description of *Ardipithecus ramidus* shows that knucklewalking features, including dorsal distal metacarpal ridges are also absent in *Ar. ramidus* (Lovejoy *et al.* 2009a), with the exception of os centrale–scaphoid fusion. However, recall that Kivell & Begun (2007) found no functional link to knucklewalking for this feature. This extends the lack of evidence for a terrestrial knucklewalking phase in the evolution of human bipedalism to 4.4 Ma. Equally, in linking terrestrial bipedalism to arboreality (Lovejoy *et al.* 2009a,b), publication of *Ar. ramidus* has greatly strengthened the positive case for an arboreal origin for the core hominin adaptation. In doing so, it challenges us to develop a convincing arboreal alternative to a terrestrial knucklewalking model of the origins of human bipedalism.

While still based on the concept that we should look for the origins of human bipedalism among activities of living African apes, the most supported arboreal challenger for the terrestrial knucklewalking model is the ‘vertical climbing’ hypothesis of Fleagle *et al.* (1981). This was derived primarily from electromyographic similarities between hip, buttock and thigh musculature activity of African apes during climbing on large, vertical supports, and that of humans walking bipedally. However, the kinematics of vertical climbing (Isler 2002, 2003; Isler & Thorpe 2003) and knucklewalking (Watson *et al.* 2009) are rather similar, involving highly flexed postures of the hip and knee (Crompton *et al.* 2003), which are quite unlike the extended postures seen in human walking and which underlie its efficiency (Alexander 1991). Running does involve more flexed limb postures, but this is linked to the use of elastic recoil, as the spring-mass mechanism requires substantial elastic energy stores. The most well known of these elastic energy stores, a marked Achilles tendon, is absent in both the African

apes and the orangutan, which all have large distal muscle masses (Thorpe *et al.* 1999; Payne *et al.* 2006a,b), which help the more powerful forelimbs (Thorpe *et al.* 1999; Oishi *et al.* 2009) in climbing but probably also act to tune the limbs to deal with variations in support compliance in an arboreal context. Interestingly, the gibbons and siamangs do have a large Achilles tendon: its mechanical role is currently under investigation in our laboratory (Channon *et al.* 2009).

The absence of a medial longitudinal arch (MLA) in the non-human great apes and its reported absence in *Ar. ramidus* (Lovejoy *et al.* 2009a) appears to rule out that possible location of the required mass of elastic tissue. So the existence of one or both of the most likely possible elastic energy stores, a large mass of plantar soft tissue housed within a MLA (Ker *et al.* 1987) or a large Achilles tendon, is required to be demonstrated before a mechanically effective compliant, rather than stiff-legged, gait can reasonably be posited for early hominins.

While energetic efficiency and mechanical performance are by no means the only parameters subject to natural selection (as fieldworkers know better than most), they are very often directly or indirectly important, and can be assessed and predicted relatively readily. Several laboratories, including our own, have therefore used computer simulation to assess the effectiveness of alternative gaits in *Au. afarensis* and other hominins. Independent studies by at least three separate laboratories (Crompton *et al.* 1998; Kramer 1999; Kramer & Eck 2000; Sellers *et al.* 2003, 2004, 2005; Nagano *et al.* 2005) demonstrate that *Au. afarensis* could have been an effective stiff-legged upright biped, particularly over relatively short distances and walking unloaded (Wang & Crompton 2004; Wang *et al.* 2004). Using forwards dynamic modelling, metabolic cost can be predicted. Predicted costs for human models have been verified against experimental values for human adults and come within 10–15% of these values. Predicted values for upright walking by *Au. afarensis* in independent studies by Sellers *et al.* (2004, 2005) and Nagano *et al.* (2005) are in good accord and come quite close to the experimental values for human children of equivalent size. If *Au. afarensis* could thus have been an effective stiff-legged, upright biped, and if moving in a compliant gait would have incurred both substantial increases in the mechanical cost of locomotion (Crompton *et al.* 1998) and physiological costs including increased heat load (Carey & Crompton 2005), an origin for bipedalism in locomotor modes associated with highly flexed limb postures, such as vertical climbing, seems unlikely.

A different objection to the vertical climbing model has recently been raised by DeSilva (2009). He argues that early hominin ankle joint morphology is distinct from that of vertical-climbing African apes, and incompatible with the kinematics required for vertical climbing. Lovejoy *et al.* (2009b) argue that anatomical features of the hand associated with vertical climbing, such as elongated metacarpals, are absent in *Ar. ramidus*, and they follow Thorpe *et al.* (2007b) in proposing that both knucklewalking and a strong

adaptive commitment to vertical climbing were acquired independently in panins, after the divergence from hominins, although Lovejoy *et al.* (2009b) do not appear to make a functional link between the two.

Lovejoy *et al.* (2009a,b,c) identify a number of features in which the hands and feet of *Ardipithecus* resemble those of the root hominoid *Proconsul* and some living arboreal monkeys, rather than living great apes. These include evidence for short hands with an extensive dorsiflexion range in the metacarpophalangeal joints that is absent in living great apes apart from humans (individuals in some human populations, such as the Han Chinese can often dorsiflex to more than 90° when young; personal observation, R. H. Crompton 1982). Following earlier arguments (Moyà-Solà *et al.* 2004) that the presence of the same feature in the Miocene hominoid *Pierolapithecus catalaunicus* suggested that it was an arboreal quadruped, they suggest, although acknowledging that it is a curious combination, that while bipedal on the ground (Lovejoy *et al.* 2009c), *Ar. ramidus* was primarily quadrupedal in the trees (Lovejoy *et al.* 2009b), while using some ‘careful climbing and bridging’, presumably at the periphery of trees (Lovejoy *et al.* 2009b).

The feet of *Ar. ramidus*, like those of monkeys, apparently retained a thick plantar layer of fibrous tissue, and were thus rather stiff when compared with those of the panins, gorillines and pongines (Lovejoy *et al.* 2009a). This implies lesser ability to conform to branch diameter, and thus relatively poor grip for what was apparently a large-bodied (50 kg, Lovejoy *et al.* 2009c) hominin, nearly twice the mass of the largest cercopithecine monkey, the mandrill, and more than 10 kg greater than the largest individuals of the largest monkey, the Sichuan snub-nosed monkey *Rhinopithecus roxellana* (Rowe 1996). It is argued that panins, gorillines and pongines also acquired their compliant feet independently (Lovejoy *et al.* 2009a). With no tail, but equally little pedal gripping power, as well as short hands, there can have been little or no capability to exert balancing counter-torques on the support. Then how did *Ar. ramidus* balance their body mass above branches during pronograde quadrupedalism? Quadrupedal monkeys, lacking the wide and powerful grasp of the living non-human great apes, improve stability by deep flexion of the limbs. Stability in flexion is very often aided by anteflexion of the olecranon process in arboreal monkeys (Fleagle 1998), but there is apparently no evidence of anteflexion of the olecranon in the *Ardipithecus* proximal ulnae (Lovejoy *et al.* 2009b). Further, habitual deep flexion of the limbs as an arboreal quadruped would increase mismatch (in the power capacity of muscles at different joint angles) between the requirements of terrestrial bipedalism and those of arboreal quadrupedalism.

3. THE ARBOREAL ORIGINS OF BIPEDALISM: COMPRESSIVE ORTHOGRADY?

A more parsimonious explanation of the metacarpophalangeal dorsiflexion seen in *Ar. ramidus* is surely desirable. It exists, in part, in consideration of elements of arboreal behaviour of all the great apes,

namely in the use of arboreal hand-assisted bipedalism, or if preferred, compressive orthogrady, both postural and locomotor, to move around the forest canopy. Again, in part, the explanation is to be found in consideration of the similarity, in shared lack of digital elongation and in morphological conservatism, between the human hand and that of *Ar. ramidus*, demonstrated by Lovejoy *et al.* (2009a).

Together with the suggestion of Thorpe *et al.* (2007b) that vertical climbing and knucklewalking were both acquired independently in panins (after the separation from hominins) and in gorillins, and its confirmation by the description of *Ar. ramidus* (Lovejoy *et al.* 2009b,c), there is increasing evidence (e.g. Larson 1998) that suspensory adaptations did not evolve at the same time as other features of orthogrady, but rather homoplastically. While it is difficult to obtain definitive figures from all studies and for all species, table 1 shows that, together, terrestrial knucklewalking quadrupedalism, vertical climbing and forelimb suspension make up some 67 per cent of bonobo locomotion, 93 per cent of common chimpanzee locomotion and 97 per cent of mountain gorilla locomotion, but only 39 per cent of orangutan locomotion. A figure for lowland gorilla knucklewalking versus non-knucklewalking quadrupedalism is more difficult to determine, but based on proportions of arboreal and terrestrial activity, we have assigned a tentative figure which allows a total proportion of novel locomotor modes in the repertoire to be set *pro tempore* at 62 per cent. Thus, from the reported evidence of *Ardipithecus*, the great majority of the panin and gorilline locomotor repertoire employs novel adaptations since the divergence from hominins. This observation has significance for both palaeontologists and fieldworkers, and underlines Darwin's (1871) warning, with which we began this paper, that we should not expect the common ancestor to resemble either humans or living apes particularly closely.

This suggests that what is now the relatively small compressive component of great ape orthograde locomotion may be the oldest, and human locomotion thus relatively conservative. (Whether compressive orthogrady is as old as orthogrady itself, or whether orthograde body posture arose earlier from a random homeotic event (Filler 2007), we currently have no way of knowing). Importantly however, this behaviour offers a reasonable alternative for locomotion in a species not yet in possession of vertical climbing and suspensory adaptations. We suggest that in an arboreal context, hominin species such as *Ar. ramidus* (as well as ourselves) which do not have elongated hands, powerful in suspension, may tend more often to climb upwards (which they must have done relatively frequently if they were exploiting both terrestrial and arboreal niches) by pushing themselves up by pressure of the hands below shoulder level, so that the ulnar four metacarpophalangeal joints pass into deep dorsiflexion. This adds much of the length of the metacarpals to the potential lift. This is of course exactly how humans usually climb large-trunked trees when they lack climbing equipment to help them move on the main trunk, with the human lack of 'vertical climbing' adaptations (primarily very powerful arms; see Thorpe *et al.* 1999; Payne *et al.*

2006a,b; Oishi *et al.* 2009): we climb up bough by bough, further out in the tree. In the absence of climbing aids, humans find it difficult and of course dangerous (Pontzer & Wrangham 2004) to climb up trees where long, naked trunks occur before any side branches. Gorillas and chimpanzees are readily able to do so, using the vertical climbing adaptations, which *Ardipithecus* suggests (Lovejoy *et al.* 2009a,b,c) arose independently and in parallel in the two lineages. Similarly, hand-assisted compressive orthogrady has been shown to allow orangutans to move on very flexible branches at the periphery of tree crowns where the most abundant supply of fruit is generally situated (Thorpe *et al.* 2007b) and it may play a similar role in the behaviour of lowland gorillas (see table 11 in Remis 1994). Analogy with the largest cercopithecine, the mandrill (Lahm 1986), less than 27 kg, and consideration of the behaviour of the largest of all monkeys, Sichuan snub-nosed monkeys *Rhinopithecus roxellana* (Kirkpatrick *et al.* 1999; Li 2001; Li *et al.* 2002), less than 37 kg, suggests that the 50 kg body weight claimed for *Ar. ramidus* (Lovejoy *et al.* 2009c) may exceed mass limits of effective monkey-like arboreal plantigrade quadrupedalism. However, compressive orthogrady is exhibited by similar-sized apes and could facilitate both access into trees and movement within them. Further, Miocene crown-hominoid body weight begins above that of mandrills, and equals or exceeds that of *R. roxellana*: 30–54 kg for *Morotopithecus* (MacLatchy *et al.* 2000), 30 kg for *Pierolapithecus* (Culotta 2004; Moyà-Solà *et al.* 2004), 30–37 kg for *Hispanopithecus* (Moyà-Solà & Köhler 1996) and 32 kg for *Oreopithecus* (Köhler & Moyà-Solà 1997). We suggest that it is unlikely that the consistently larger size of Miocene crown hominoids was not accompanied by a shift from monkey-like arboreal locomotion.

Thus, we argue that a hominin which had not acquired suspensory/vertical climbing features in the forelimb would have accessed the trees and moved within them primarily by palmigrade compressive orthogrady. In the absence of vertical climbing capabilities and a powerful hand grip, access to trees would of course favour use of more stable supports, which can be loaded under compression without excessive deflection. In the absence of suspensory features, hand-assisted bipedalism could have facilitated movement among the finer supports at the periphery of trees, employing strategies similar to those we have reported in the orangutan (Thorpe *et al.* 2007b, 2009). Quadrupedalism would be used when absolutely necessary—as of course it is by ourselves when we no longer trust our balance or stability—but palmigrade hand postures would be inappropriate among finer supports. Many anthropoids are able to employ some degree of suspension, vertical climbing and quadrupedalism regardless of their primary adaptation, although perhaps rarely, and at some additional cost, so suspension is also likely to have been used under certain conditions. It may be argued that this is referential modelling (Sayers & Lovejoy 2008): but at least we are using multiple referents, and we are able to test the predictions of our models by simulation. We predict, for example, that

Table 1. Frequencies of locomotor behaviour in the great apes and 'ballpark estimates' of the per cent of their locomotion that has evolved since divergence from their last common ape ancestor.^a

	knucklewalk/run (terrestrial and arboreal)	other quadrupedal (terrestrial and arboreal)	vertical climb/descent	brachiate	orthograde clamber/transfer	bipedal leap	pronograde scramble	other ^b	% loco evolved since separation ^c
mountain gorilla ^{d,e}	95	<1	<1	0.1	0	0.8	>0	0	≥97
lowland gorilla ^{d,f}	38.5	26.7	19.7	3.6	3.3	6.1	0	1.3	≥62
chimpanzee ^{d,g}	86.1	4.5	6.5	0.8	0.5	0.7	0.2	0.1	≥93
bonobo ^{d,h}	7.8	27.5	50.4	8.9	0	1.5	3.1	0	≥67
orangutan ⁱ	0	8	26	13	22	7	<1	11	≥39

^aNote that all values are ballpark figures as differences in methodology and subject profiles preclude detailed comparison.

^bFor example, tree sway, pronograde suspension.

^cThis value assumes that the common ancestor at all levels was a monkey-like above branch quadruped. The value includes knucklewalking, vertical climb/descent, brachiation and orthograde clamber/transfer.

^dModified after Hunt (2004) and based on data from Turtle & Watts (1985), Doran (1996), Hunt (1992) and Remis (1995).

^eAdapted from Turtle & Watts (1985).

^fKnucklewalking/non-knucklewalking values are not available for lowland gorillas at present. However, 59% of their time is spent terrestrially and 41% arboreally (adapted from Hunt 1996). Consequently, as a rough estimate, we have allocated 51% of quadrupedalism to be terrestrial knucklewalking and the remainder to be arboreal non-knucklewalking quadrupedalism.

^gAdapted from Hunt (1992) following personal communication (K. D. Hunt, 2009).

^hBonobos are more arboreal than chimpanzees but no conclusive data exist, neither for the per cent of time they are arboreal nor for how much of their quadrupedalism is knucklewalking. However, Susman (1984) observed that of 532 bouts of arboreal quadrupedalism, only 20 (3.8%) were knucklewalking and of Susman's (1984) 89 first sightings of bonobos, 17 (19%) were terrestrial. Thus, we have weighted Doran's (1996) frequency data with these values to calculate proportions for knucklewalking and non-knucklewalking quadrupedalism.

ⁱModified from Thorpe & Crompton (2006).

a dynamic model of quadrupedalism in *Ardipithecus* would show that quadrupedalism would be possible, if unstable, and very expensive, if perhaps less so than it would be for longer-legged humans.

A parallel case has very recently been discussed in the literature. *Pierolapithecus* is described by Almécija *et al.* (2009) as orthograde, but as lacking the obvious suspensory adaptations seen in the rather later Iberian crown hominoid, *Hispanopithecus (D.) laietanus*. The metacarpophalangeal joints are described as adapted for use in dorsiflexion in palmigrade postures (Almécija *et al.* 2009). Reference to monkeys would suggest that it was an arboreal quadruped (Moya-Solà *et al.* 2004), but these authors now regard it as orthograde in body plan (Almécija *et al.* 2009) but moving by palmigrade quadrupedalism. The authors also suggest that the description of the Miocene pongine *Sivapithecus* by Madar *et al.* (2002) may suggest similar behaviour. It is very difficult to reconcile an orthograde body plan with quadrupedal locomotion, even when there are no claims that *Pierolapithecus* was a terrestrial biped. The obvious, simple solution is again the one we propose here, that it (and perhaps even *Sivapithecus*) was an orthograde clamberer which, in the absence of marked suspensory adaptations, used hand-compressive climbing techniques below shoulder level, in other words, hand-assisted bipedalism and other components of the compressive-orthograde continuum best exemplified today in orangutans.

4. THE LEGACY OF ARBOREAL ORIGINS FOR HUMAN BIPEDALITY

The arboreal habitat differs markedly in one major mechanical respect from the terrestrial: it is compliant (Alexander 2003) and thus unstable, as it can be set vibrating by imposed forces. Arboreal mammals need to have strategies for dealing with this compliance. Schmitt (1999) has shown that limb flexion (limb compliance) is one such response, but limb flexion requires muscle power to maintain stable flexed postures. For this reason, most probably, muscle masses tend to be higher in arboreal animals (Degabriele & Dawson 1979), while terrestrial cursor limbs have short muscle bellies and long tendons (Alexander 2003). To what extent has this legacy of compliance influenced early hominin evolution?

(a) *A compliant foot?*

Lovejoy *et al.* (2009a) argue that whereas the living non-human great apes have acquired compliant feet, to enable them to grip branches more effectively, and humans have of course acquired a MLA, *Ardipithecus* is again conservative in the plantar foot, lacking a MLA, but retaining a thick and fibrous layer on the plantar aspect of the foot, like that of cercopithecines, contrasting with the loss of such a thick aponeurotic layer in the non-human apes, which gain thereby in foot adaptability to irregular substrates.

Following Bojsen-Møller (1979), it is common in the hominin palaeontology literature (e.g. Lewis 1980; Berillon 2000; Harcourt-Smith & Aiello 2004; Jungers *et al.* 2009) to assess the presence or absence of a MLA by the degree of development and

asymmetry of the cuboid peg for the calcaneus (figure 1a), and Lovejoy *et al.* (2009a) appear to follow this practice. The asymmetry and size of the cuboid peg is not, however, entirely a reliable guide to the existence or absence of a functional MLA: as can be seen in figure 1a, the peg is not overlapped ventrally by the calcaneus. While it is usual to associate this development with loss of the mid-tarsal break (axis of plantarflexion), which is present in other living apes (Lewis 1980), the absence of a mid-tarsal break is not universal in humans. Setting aside conditions such as Charcot foot, where soft-tissue failure arising from diabetes or directly from neurological conditions results in collapse of the lateral midfoot and in some cases a midfoot pressure peak under, or near, the calcaneocuboid joint, figure 1b (unfortunately from uncalibrated pressure plate data, but qualitatively reliable) shows that clinically normal individuals may also show a lateral midfoot pressure peak. It is interesting that this individual also shows absence of a lateral-to-medial path of the centre of pressure and, in figure 1c, a single-peaked vGRF, with a non-human-ape-like slow tailing-off of vGRF at 'toe-off'. While the absence of the mid-tarsal break does seem functionally linked with an extended toe-off, neither are therefore universal features of hominins. Nevertheless, if *Ardipithecus* lacked a human-like cuboid peg, lateral-foot stability would be limited. In both cases, a certain degree of rigidity provided by retention of a thick plantar fibrous layer would improve the capacity of the lateral metatarsals to deliver accelerative force from a more effective, relatively anterior, position.

We (Pataky *et al.* 2008) recently demonstrated a negative correlation of plantar pressure with walking speed in humans, which implies reduced collapse of the MLA, and thus increased stiffness. This may be directly beneficial to force transmission to the ground. It is also important in enabling control of gear ratios, and thus in tuning muscles to enhance performance during constant-speed running by applying pre-tension during landing, while optimizing them also for efficiency or power at toe-off (Carrier *et al.* 1994). Perhaps most importantly, we can optimize muscle properties during rapid changes in speed and changes in incline in both running and walking (Lichtwark & Wilson 2006, 2007, 2008). We have suggested that increased stiffness results from pre-tension applied to the plantar aponeurosis (PA) by heel-strike or early-stance muscle activity (in triceps, tibialis anterior and the digital dorsiflexors; Pataky *et al.* 2008; Caravaggi *et al.* 2009). The windlass mechanism created as the PA wraps round the heads of the metatarsals (figure 1a) is known to contribute to stiffen the foot in late stance (Hicks 1954) by pulling on the calcaneus, causing inversion of the subtalar joint and hence 'locking' the midtarsal joint (Tansey & Briggs 2001). A dynamic model of the plantar foot constructed in our laboratory (Caravaggi *et al.* 2009) however shows that the PA is also pre-tensioned in early stance, from heel-strike onwards, as proposed by Pataky *et al.* (2008), and the tension appears to increase with walking speed. The predicted tension (verified against cadaveric data from Gefen (2003)) increases from lateral to medial, and ranges from 0.47 body weight at

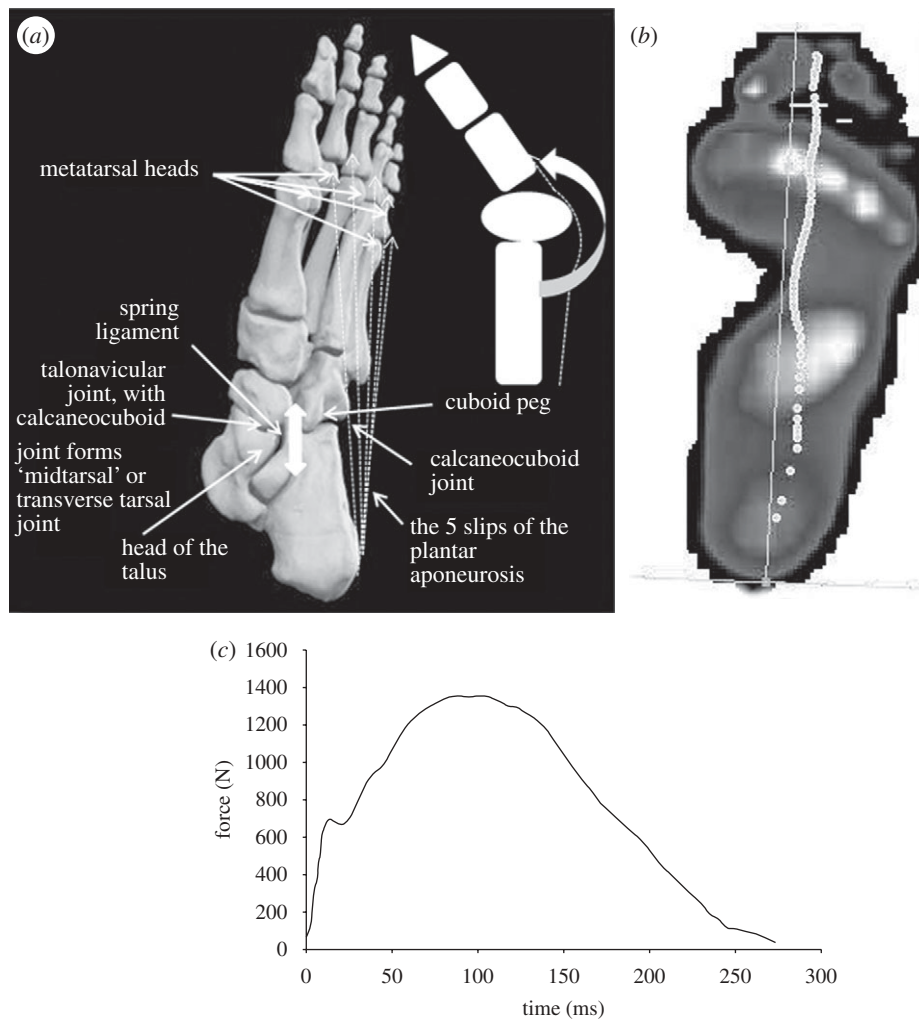


Figure 1. (a) Diagram of the plantar aspect of the human foot, showing the position of the cuboid peg and illustrating the 'windlass mechanism', whereby the five slips of the PA are tensed by the curvature of the metatarsal heads as the metatarsophalangeal joint dorsiflexes. Similarly, the spring ligament is tensed by plantar motion of the head of the talus. Both mechanisms act to stiffen the median longitudinal arch during stance. (Figure modified from image from Primal's 'Anatomy TV'). (b) Peak pressures, in false greyscale, where lighter tone indicates higher pressure, during bipedalism of a clinically normal subject recorded by Nike Inc., courtesy of J.-P. Wilssens of RSscan International. Dots indicate the path of the centre of pressure under the foot. (c) vGRF curve calculated from the same data for the individual featured in (a).

heel-strike to a peak 1.5 BW, generating vertical forces which sustain the MLA and metatarsals. Thus, the MLA is supported through much of stance by soft tissue: stiffening of the PA, as well as bone shape, contributes directly and very substantially to the existence of the MLA. An assumption that lack of a human-like cuboid peg (figure 1a) implies lack of a MLA is unsafe without extensive investigation of the possibility of soft-tissue stiffening. The case of human individuals with a mid-tarsal break suggests that sustained vGRFs and a substantial hallux toe-off depend on stiffening of both the medial and lateral foot by soft-tissue tensioning throughout stance.

It is notable that Vereecke *et al.* (2003) have shown that foot pressure records of human bipedalism are much less variable between strides and between individuals than those of the bipedalism of other hominoids. In humans, forces are applied in a more consistent manner, particularly by the hallux, which plays a limited propulsive role in most non-human apes, and may act more as a balancing structure during bipedalism. If the hallux of *Ardipithecus* is as

abducted as Lovejoy *et al.* (2009a) report, the degree of abduction is comparable to that in living gibbons (e.g. Vereecke *et al.* 2005; Crompton *et al.* 2008) and perhaps *Oreopithecus*. While Moyà-Solà *et al.* (1999) suggested that the extent of hallux abduction in *Oreopithecus* would not have been compatible with other than postural bipedalism, Vereecke *et al.* (2006a,b) have shown that gibbons, despite compliant feet with widely abducted halluces, can sustain running on the ground for some hundred yards and attain absolute speeds equalling the human walk-run transition. Neither do compliant feet prevent the non-human great apes from walking bipedally, terrestrially or arboreally. High robusticity of metatarsals two and three is also a feature of *Ar. ramidus* (Lovejoy *et al.* 2009a) and suggests that these digits may have been more important in applying accelerative parasagittal force than the hallux, while the abducted hallux provided grip on branches. However, even in human bipedal walking, plantar pressure tends to be lower under the hallux, and greater under metatarsal heads two and three, in flat-footed humans or humans who

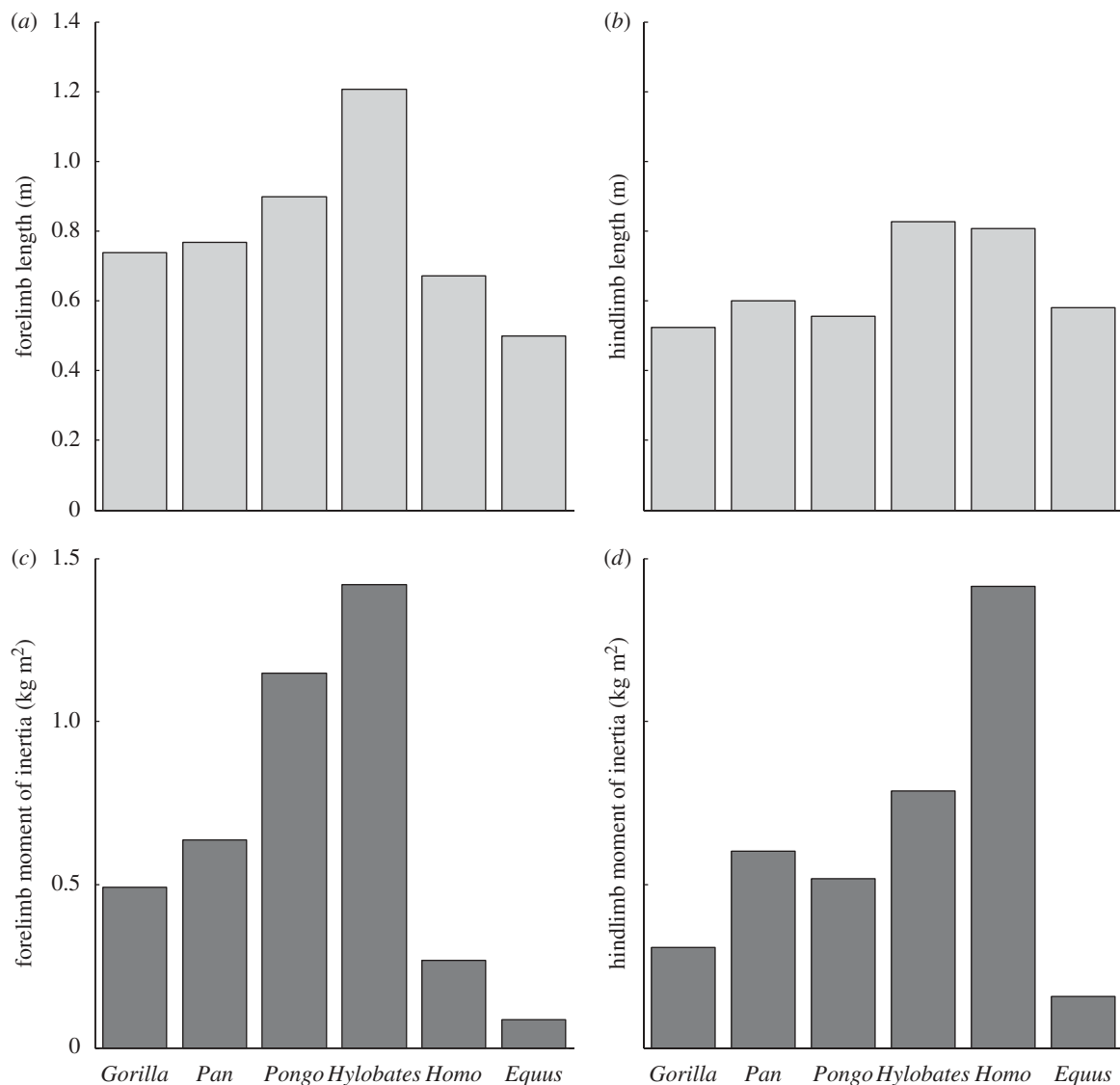


Figure 2. (a,b) Chart showing the limb lengths and (c,d) moments of inertia for hominoids and horse. Forelimb moments of inertia are about the shoulder joint and hindlimb moments of inertia are about the hip joint. Great ape data are from Isler *et al.* (2006), human data are from Winter (1990) using a median male height and weight from the GEBOD database (Cheng *et al.* 1994), horse data from Buchner *et al.* (1997).

have been brought up as barefoot walkers (D'Aouët *et al.* 2009).

Thus, the human foot is less distinct than is often thought from that of other great apes. It has built on the compliant arboreal legacy (whether prior to or after the separation from panins we submit is not yet clear, given the mixed message of *Ardipithecus*; Lovejoy *et al.* 2009a) by becoming a variable-gear organ, able to change its stiffness to accommodate to speed, as well as to support compliance and irregularity.

(b) Limb mass proportions

Another likely legacy from a recently arboreal past is the partial retention of arboreal limb mass proportions. A cursorial animal needs to accelerate its limbs rapidly. Rapid acceleration can be achieved with less energy if the moments of inertia are reduced, and this is commonly achieved by a reduction in distal limb elements (Hildebrand 1995). Figure 2 shows a comparison of the inertial properties and limb dimensions of hominoids in comparison with a

dedicated terrestrial cursor (horse). All dimensions have been geometrically scaled to the estimated mass of *Ar. ramidus*, 50 kg, using mass^{1/3} for lengths and mass^{5/3} for moments of inertia. All the arboreal species have longer than expected forelimbs, but, except for humans and gibbons, hindlimb length is not greatly different from that of the specialist cursor. However, when looking at the moments of inertia it can clearly be seen how elongated limbs with heavy autopodia lead to extremely large moments of inertia when compared with the values seen in horses. This has inevitable but complex effects in terms of top speed and efficiency. Long, high-inertia legs are perfectly efficient for the pendular mechanics of slow walking, but the high-speed spring mechanics of running require low moments of inertia to minimize the internal energy lost per step. *Hylobates* seems to some extent to have dealt with the inertial problem of very long legs by reducing distal muscle mass. We suggest, following Channon *et al.* (2009), that several aspects of gibbon anatomy may relate to an unrecognized importance of leaping in the gibbon locomotor repertoire.

However, upper limb–lower limb proportions and the distribution of lengths and mass within limbs also affect their swing frequency. Part of the efficiency of long distance human walking at least depends on a forward swing of the contralateral arm to counteract the horizontal torque applied to the body by the swing leg (e.g. Li *et al.* 2001) which, among other effects, interferes with lateral stability. These swings occur even in short-distance walking of young children of similar stature/mass to *Au. afarensis*, and increase in magnitude with walking speed (Li *et al.* 2001), so they are of relevance to any consideration of early hominin locomotion. Match between the natural pendular period (NPP), and hence swing-time of upper and lower limbs, affects efficiency of all gaits, bipedal and quadrupedal; and distribution of mass within the limb affects the NPP (Isler *et al.* 2006). The distal position of the centre of mass of the forelimb of most great apes, with the exception of the chimpanzee, means that there is a considerable mismatch with forelimb NPP, and segment proportions are thus not well optimized for quadrupedal gaits (Isler *et al.* 2006). Chimpanzees may have modified their limb mass distribution for more efficient quadrupedalism, suggesting that the last common African ape ancestor was not a proficient quadruped (Isler *et al.* 2006). However, experimental work on the oxygen consumption of both bipedal and quadrupedal locomotion in chimpanzees confirms that they are relatively inefficient in both modalities (Sockol *et al.* 2007), compared with both modern humans and quadrupeds of equivalent body size. This may indicate that maximum terrestrial speed, rather than minimal terrestrial energy cost, may be the target of selective pressure for chimpanzees. (By contrast, preliminary data from the same research group suggest that metabolic costs of bipedalism in the orangutan are some of the lowest recorded locomotor costs for the body size; personal communication from H. Pontzer (2009)).

(c) Proportion of mass as tendon

Another area where there is still a considerable legacy from the recent arboreal past is in the amount of tendon in the hindlimbs of hominoids compared with cursorial animals. Figure 3 shows the mass of hindlimb tendon in both hindlimbs as a proportion of body mass. This parameter is informative since its biomechanical interpretation is independent of moment arm data, of which there is very little available for comparison in non-primates. Tendon acts as a simple damped spring during locomotion, so the amount of energy that can be stored depends on the mass. The strain energy storage of tendon is 2500 J kg^{-1} at 8 per cent strain (Vogel 2003), which is therefore the limit of the amount of elastic strain energy that is potentially available per gait cycle—whether for power amplification or energy saving. For the hominoids, tendon mass was estimated using published tendon length and muscle physiological cross-section area data. Tendon cross-section area was estimated by assuming 6 per cent strain at maximal isometric contractile force and muscle contraction stress of 300 kN m^{-2} (Sellers & Manning

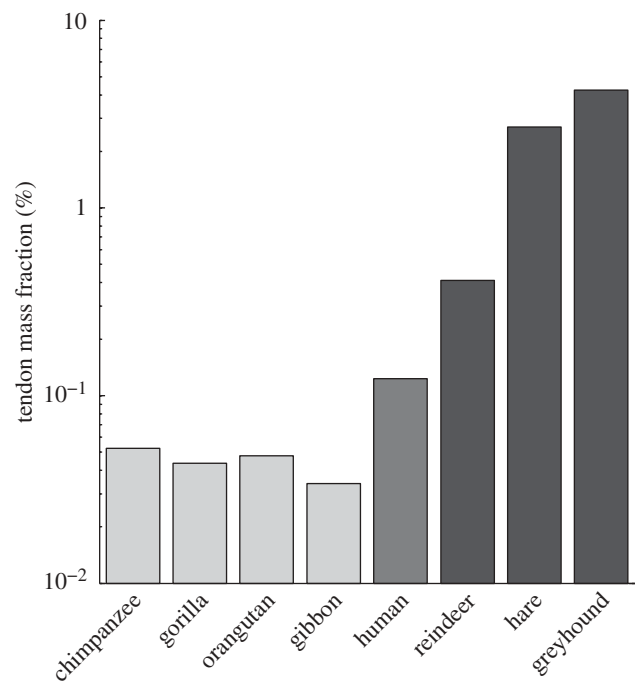


Figure 3. Total tendon in both hindlimbs as a fraction of body mass. Data are based on information from Pierrynowski (1995), Payne *et al.* (2006), Williams *et al.* (2007, 2008) and Wareing *et al.* (submitted).

2007). Resulting volumes were converted to tendon mass using a density of 1100 kg m^{-3} (Watson & Wilson 2007). It is clear that tendon mass is highly variable and more often related to high speed and high acceleration than to efficiency. It is also clear that while humans have appreciably increased their hindlimb tendon proportion when compared with the other apes, they are still a long way from the much higher proportions in more specialized cursorial quadrupeds—particularly those specializing in explosive acceleration rather than long-distance efficiency. This is emphasized if we multiply through by 2500 J kg^{-1} to express elastic storage capacity in terms of energy. Most hominoids have about 1 J kg^{-1} of elastic energy storage, humans nearly three times that, reindeer 10 J kg^{-1} but greyhounds fully 100 J kg^{-1} . Thus, while humans have adjusted tendon mass somewhat to enhance terrestrial running, perhaps retaining a relatively large muscle mass to allow for adjustments to optimize the hindlimb for terrain, speed and support characteristics, the African apes have not. Bonobos and lowland gorillas may not require to do so because of limited terrestriality; mountain gorillas may be protected by size, but chimpanzees may simply have modified mass proportions to match hindlimb–forelimb swing frequencies better, suggesting that the selective pressures associated with movement in an unstable arboreal milieu remain strong.

We can further investigate the role of elasticity in human locomotion by simulation. In recent simulation work (Sellers *et al.* 2010), the role of tendon elasticity was quantified by ‘virtual ablation’. In this paradigm, simulations are repeated with identical anatomical models except for the structure of interest, which is

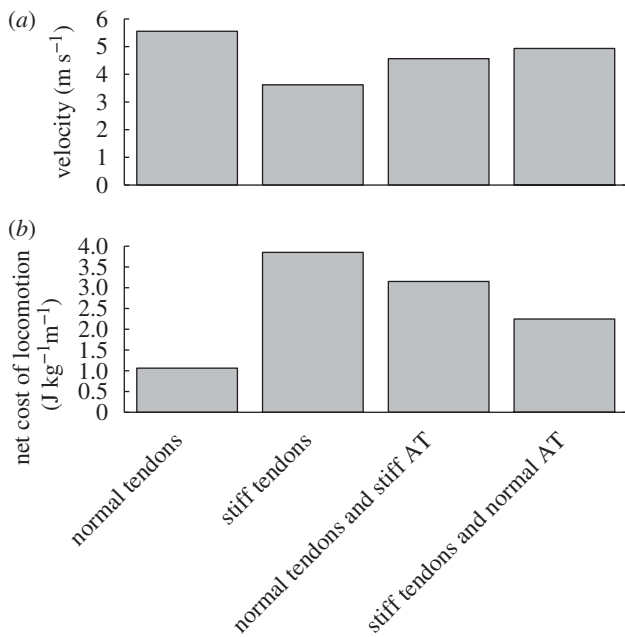


Figure 4. (a) Chart showing the maximum velocity and (b) the cost of locomotion of human running simulations where the elastic properties of the hindlimb tendons are manipulated. AT, Achilles tendon. (Sellers *et al.* 2010).

removed or altered in some versions of the model. This allows the effect of a specific structure to be isolated in much the same way as classical ablation experiments but without the danger of side effects (let alone ethical difficulties) associated with performing such experiments surgically. In this case, the elastic effect of tendons was removed by making them 100 times their normal stiffness, so that the simulated tendons were unable to store appreciable amounts of energy in the simulation. Four experimental conditions were compared: normal hindlimb tendons; all hindlimb tendons stiff; all normal hindlimb tendons except for a stiff Achilles tendon; all tendons stiff except for a normal Achilles tendon. Figure 4 shows that for humans, the presence of tendon has only a moderate effect on the maximum running speed of the simulation but a very marked effect on the net cost of locomotion, and that this effect was mostly produced by the Achilles tendon. This confirms the critical role in efficient, high-performance running of a substantial Achilles tendon, which is missing from all hominoids except humans, gibbons and siamangs. Whether such a structure is present in fossil hominins (and which) is currently unknown but evidence of its presence, perhaps by analysis of calcaneal microstructure, would probably be diagnostic of running ability.

5. CONCLUSIONS

We argue that, given the large body mass of *Ar. ramidus*, typical of both living and extinct hominoids, it is more likely that when it moved in the trees it made use of compressive orthogrady, which we suggest may be the oldest crown-hominoid locomotor adaptation, than that it adopted a monkey-like quadrupedalism. This would run counter not only to

expectations from body size but also to *Ar. ramidus*' clear adaptations for one form of compressive orthogrady, terrestrial bipedal walking.

Secondly, we argue that from our arboreal ancestors humans have inherited feet and legs that can adapt to a large variety of terrains, support compliances and speeds. However, at some stage in our evolution we have departed some way from other hominoids in adaptation for energy-efficient running. This combination probably has a lot to do with our ability to outrun horses in trials such as those over 22 miles of hilly mid-Wales or 50 miles of sand-dunes in the United Arab Emirates. But we are not fast runners (see Bramble & Lieberman 2004), and in terms of energy storage have a very long way to go to catch up with dogs bred for hunting. Early human ancestors would clearly have been no match for a cursorial predator, so that it is perhaps fortunate that along with late retention of long forearms (Dunsworth *et al.* 2003), which would improve throwing distance if not accuracy, part of our arboreal inheritance was powerful leg muscles, which remain very helpful for climbing trees!

R.H.C. thanks Alan Walker and Chris Stringer for the invitation to participate in this meeting. We thank the Royal Society, the Leverhulme Trust and the Natural Environment Research Council, the Biotechnology and Biological Sciences Research Council and the Engineering and Physical Sciences Research Council for supporting our research, and Chester and Twycross Zoos for permission to study the hominoids under their care. R.H.C. and W.I.S. also thank the NorthWest Grid and the Science and Technology Facilities Council Daresbury Laboratory for access to high-performance computing facilities.

REFERENCES

- Alexander, R. McN. 1991 Characteristics and advantages of human bipedalism. In *Biomechanics in evolution* (eds J. M. V. Rayner & R. J. Wootton), pp. 225–266. Cambridge, UK: Cambridge University Press.
- Alexander, R. McN. 2003 *Principles of animal locomotion*. Princeton, NJ: Princeton University Press.
- Almécija, A., Alba, D. M. & Moyà-Solà, S. 2009 *Pierolapithecus* and the functional morphology of Miocene ape hand phalanges: paleobiological and evolutionary implications. *J. Hum. Evol.* **57**, 284–297. (doi:10.1016/j.jhevol.2009.02.008)
- Berillon, G. 2000 *Le Pied des Hominoïdes Miocènes et des Hominoïdes Fossiles*. Paris, France: Éditions du CRNS.
- Bojsen-Møller, F. 1979 Calcaneocuboid joint and stability of the longitudinal arch of the foot at high and low gear push off. *J. Anat.* **129**, 165–176.
- Bradley, B. J. 2008 Reconstructing phylogenies and phenotypes: a molecular view of human evolution. *J. Anat.* **212**, 337–353. (doi:10.1111/j.1469-7580.2007.00840.x)
- Bramble, D. M. & Lieberman, D. L. 2004 Endurance running and the evolution of *Homo*. *Nature* **432**, 345–352. (doi:10.1038/nature03052)
- Buchner, H., Savelberg, H., Schamhardt, H. & Barneveld, A. 1997 Inertial properties of Dutch Warmblood horses. *J. Biomech.* **30**, 653–658. (doi:10.1016/S0021-9290(97)00005-5)
- Caravaggi, P., Pataky, T. C., Goulermas, J. Y., Savage, R. & Crompton, R. H. 2009 A dynamic model of the windlass mechanism of the foot: evidence for early stance phase

- preloading of the plantar aponeurosis. *J. Exp. Biol.* **212**, 2491–2499. (doi:10.1242/jeb.025767)
- Carey, T. S. & Crompton, R. H. 2005 The metabolic costs of 'bent hip, bent knee' walking in humans. *J. Hum. Evol.* **48**, 25–44. (doi:10.1016/j.jhevol.2004.10.001)
- Carrier, D. R., Heglund, N. C. & Earls, K. D. 1994 Variable gearing during locomotion in the human musculoskeletal system. *Science* **265**, 651–653. (doi:10.1126/science.8036513)
- Channon, A. J., Günther, M. M., Crompton, R. H. & Vereecke, E. E. 2009 Mechanical constraints on the functional morphology of the gibbon hind limb. *J. Anat.* **215**, 383–400. (doi:10.1111/j.1469-7580.2009.01123.x)
- Cheng, H., Obergefell, L. & Rizer, A. 1994 *Generator of body data (GEBOD) manual*. Report no. AL/CF-TR-1994-0051, Armstrong Lab, Wright-Patterson Air Force Base.
- Clarke, R. J. 1999 Discovery of a complete arm and hand of the 3.3 million-year-old *Australopithecus* skeleton from Sterkfontein. *S. Afr. J. Sci.* **95**, 477–480.
- Clarke, R. J. 2002 Newly revealed information on the Sterkfontein Member 2 *Australopithecus* skeleton from Sterkfontein. *S. Afr. J. Sci.* **98**, 523–526.
- Crompton, R. H., Li, Y., Wang, W., Günther, M. M. & Savage, R. 1998 The mechanical effectiveness of erect and 'bent-hip, bent-knee' bipedal walking in *Australopithecus afarensis*. *J. Hum. Evol.* **35**, 55–74. (doi:10.1006/jhev.1998.0222)
- Crompton, R. H. et al. 2003 The biomechanical evolution of erect bipedality. *Cour. Forsch.-Inst. Senckenberg* **243**, 115–126.
- Crompton, R. H., Vereecke, E. E. & Thorpe, S. K. S. 2008 Locomotion and posture from the common hominoid ancestor to fully modern hominins with special reference to the common panin/hominin ancestor. *J. Anat.* **212**, 501–543. (doi:10.1111/j.1469-7580.2008.00870.x)
- Culotta, E. 2004 Spanish fossil sheds new light on the oldest Great apes. *Science* **306**, 1273–1274.
- Dainton, M. & Macho, G. A. 1999 Did knuckle walking evolve twice? *J. Hum. Evol.* **36**, 171–194. (doi:10.1006/jhev.1998.0265)
- D'Août, K., Pataky, T. C., De Clercq, D. & Aerts, P. 2009 The effects of habitual footwear use: foot shape and function in native barefoot walkers. *Footwear Science* **1**, 81–94.
- Darwin, C. 1871 *The descent of man and selection in relation to sex*. London, UK: John Murray.
- Degabriele, R. & Dawson, T. J. 1979 Metabolism and heat balance in an arboreal marsupial, the koala (*Phascolarctos cinereus*). *J. Comp. Physiol. B* **134**, 293–301. (doi:10.1007/BF00709996)
- DeSilva, J. M. 2009 Functional morphology of the ankle and the likelihood of climbing in early hominins. *Proc. Natl Acad. Sci. USA* **106**, 6567–6572. (doi:10.1073/pnas.0900270106)
- Doran, D. M. 1996 The comparative positional behaviour of the African apes. In *Great ape societies* (eds W. McGrew & T. Nishida), pp. 213–224. Cambridge, UK: Cambridge University Press.
- Dunsworth, H., Challis, J. H. & Walker, A. 2003 Throwing and bipedalism: a new look at an old idea. *Cour. Forsch.-Inst. Senckenberg* **243**, 105–110.
- Filler, A. 2007 Homeotic evolution in the Mammalia: diversification of Therian axial seriation and the morphogenetic basis of human origins. *PLoS ONE* **2**, 10, e1019. (doi:10.1371/journal.pone.0001019)
- Fleagle, J. G. 1998 *Primate adaptation and evolution*. New York, NY: Elsevier.
- Fleagle, J. G., Stern, J. T., Jungers, W. L., Susman, R. L., Vangor, A. K. & Wells, J. P. 1981 Climbing: a biomechanical link with brachiation and with bipedalism. *Symp. Zool. Soc. Lond.* **48**, 359–375.
- Gebo, D. L. 1992 Plantigrady and foot adaptation in African apes: implications for hominid origins. *Am. J. Phys. Anthropol.* **89**, 29–58. (doi:10.1002/ajpa.1330890105)
- Gebo, D. L. 1996 Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. *Am. J. Phys. Anthropol.* **101**, 55–92. (doi:10.1002/(SICI)1096-8644(199609)101:1<55::AID-AJPA5>3.0.CO;2-C)
- Gefen, A. 2003 The *in vivo* elastic properties of the plantar fascia during the contact phase of walking. *Foot Ankle Int.* **24**, 238–244.
- Goodall, J. 1998 *Through a window: my thirty years with the chimpanzees of Gombe*. Boston, MA: Houghton Mifflin.
- Harcourt-Smith, W. E. H. & Aiello, L. C. 2004 Fossils, feet and the evolution of human bipedal locomotion. *J. Anat.* **204**, 403–416. (doi:10.1111/j.0021-8782.2004.00296.x)
- Hicks, J. H. 1954 The mechanics of the foot. II. The plantar aponeurosis and the arch. *J. Anat.* **88**, 25–30.
- Hildebrand, M. 1995 *Analysis of vertebrate structure*. New York, NY: Wiley.
- Hunt, K. D. 1992 Positional behavior of *Pan troglodytes* in the Mahale Mountains and Gombe Stream National Parks, Tanzania. *Am. J. Phys. Anthropol.* **87**, 83–105. (doi:10.1002/ajpa.1330870108)
- Hunt, K. D. 2004 The special demands of great ape locomotion and posture. In *The evolution of thought: evolutionary origins of great ape intelligence* (eds A. E. Russon & D. R. Begun), pp. 172–189. Cambridge, UK: Cambridge University Press.
- Isler, K. 2002 Characteristics of vertical climbing in African apes. *Senckenbergiana Lethaea* **82**, 115–124. (doi:10.1007/BF03043777)
- Isler, K. 2003 Aspects of vertical climbing in gorillas. *Cour. Forsch.-Inst. Senckenberg* **243**, 71–78.
- Isler, K. & Thorpe, S. K. S. 2003 Gait parameters in vertical climbing of captive, rehabilitant and wild Sumatran orang-utans (*Pongo pygmaeus abelii*). *J. Exp. Biol.* **206**, 4081–4096. (doi:10.1242/jeb.00651)
- Isler, K., Payne, R. C., Günther, M. M., Thorpe, S. K. S., Li, Y., Savage, R. & Crompton, R. H. 2006 Inertial properties of hominoid limb segments. *J. Anat.* **209**, 201–218. (doi:10.1111/j.1469-7580.2006.00588.x)
- Jungers, W. L., Harcourt-Smith, W. E. H., Wunderlich, R. E., Tocheri, M. W., Larson, S. G., Sutikna, T., Rhokus Awe Due & Morwood, M. J. 2009 The foot of *Homo floresiensis*. *Nature* **459**, 81–84. (doi:10.1038/nature07989)
- Keith, A. 1903 The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of man and related primates. *J. Anat. Physiol.* **37**, 18–40.
- Keith, A. 1923 Man's posture: its evolution and disorders. *Br. Med. J.* **1**, 451–454, 499–502, 545–548, 587–590, 624–626, 669–672. (doi:10.1136/bmj.1.3246.451)
- Ker, R. F., Bennet, M. B., Bibby, S. R., Kester, R. C. & Alexander, R. McN. 1987 The spring in the arch of the human foot. *Nature* **325**, 147–149. (doi:10.1038/325147a0)
- Kirkpatrick, R. C., Gu, H. J. & Zhou, X. P. 1999 A preliminary report on Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) at Baihe nature reserve. *Folia Primatol.* **70**, 117–120. (doi:10.1159/000021683)
- Kivell, T. L. & Begun, D. R. 2007 Frequency and timing of scaphoid-centrale fusion in hominoids. *J. Hum. Evol.* **52**, 321–340. (doi:10.1016/j.jhevol.2006.10.002)
- Kivell, T. L. & Schmitt, D. 2009 Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. *Proc. Natl Acad. Sci. USA* **106**, 14 241–14 246. (doi:10.1073/pnas.0901280106)

- Köhler, M. & Moyà-Solà, S. 1997 Ape-like or hominid-like? The positional behavior of *Oreopithecus bambolii* reconsidered. *Proc. Natl Acad. Sci. USA* **94**, 11 747–11 750. (doi:10.1073/pnas.94.21.11747)
- Kramer, P. A. 1999 Modeling the locomotor energetics of extinct hominids. *J. Exp. Biol.* **202**, 2807–2818.
- Kramer, P. A. & Eck, G. G. 2000 Locomotor energetics and leg length in hominid bipedality. *J. Hum. Evol.* **38**, 651–666. (doi:10.1006/jhev.1999.0375)
- Lahm, A. A. 1986 Diet and habitat preference of *Mandrillus sphinx* in Gabon: implications of foraging strategy. *Am. J. Primatol.* **11**, 9–26. (doi:10.1002/ajp.1350110103)
- Larson, S. G. 1998 Parallel evolution in the hominoid trunk and forelimb. *Evol. Anthropol.* **6**, 87–89. (doi:10.1002/(SICI)1520-6505(1998)6:3<87::AID-EVAN3>3.0.CO;2-T)
- Lewis, O. J. 1980 The joints of the evolving foot part II, the intrinsic joints. *J. Anat.* **131**, 275–298.
- Li, Y. 2001 The seasonal diet of the Sichuan snub-nosed monkey (*Pygathrix roxellana*) in Shennongjia Nature Reserve, China. *Folia Primatol.* **72**, 40–43. (doi:10.1159/000049919)
- Li, Y., Wang, W., Crompton, R. H. & Gunther, M. M. 2001 Free vertical moments and transverse forces in human walking and their role in relation to arm-swing. *J. Exp. Biol.* **204**, 47–58.
- Li, Y., Stanford, C. B. & Yang, Y. 2002 Winter feeding tree choice in Sichuan snub-nosed monkeys (*Rhinopithecus roxellanae*) in Shennongjia Nature Reserve, China. *Int. J. Primatol.* **23**, 657–675.
- Lichtwark, G. A. & Wilson, A. M. 2006 Interactions between the human gastrocnemius muscle and the Achilles tendon during incline, level and decline locomotion. *J. Exp. Biol.* **209**, 4379–4388. (doi:10.1242/jeb.02434)
- Lichtwark, G. A. & Wilson, A. M. 2007 Is Achilles tendon compliance optimised for maximum muscle efficiency during locomotion? *J. Biomech.* **40**, 1768–1775. (doi:10.1016/j.jbiomech.2006.07.025)
- Lichtwark, G. A. & Wilson, A. M. 2008 Optimal muscle fascicle length and tendon stiffness for maximising gastrocnemius efficiency during human walking and running. *J. Theor. Biol.* **252**, 662–673. (doi:10.1016/j.jtbi.2008.01.018)
- Lovejoy, C. O., Latimer, B., Suwa, G., Asfaw, B. & White, T. D. 2009a Combining prehension and propulsion: the foot of *Ardipithecus ramidus*. *Science* **326**, 72e1–72e8. (doi:10.1126/science.1175832)
- Lovejoy, C. O., Simpson, S. W., White, T. D., Asfaw, B. & Suwa, G. 2009b Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. *Science* **326**, 70e1–70e8. (doi:10.1126/science.1175827)
- Lovejoy, C. O., Suwa, G., Simpson, S. W., Matternes, J. H. & White, T. D. 2009c The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. *Science* **326**, 100–106. (doi:10.1126/science.1175833)
- MacLatchy, L., Gebo, D., Kityo, R. & Pilbeam, D. 2000 Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion. *J. Hum. Evol.* **39**, 159–183. (doi:10.1006/jhev.2000.0407)
- Madar, S. I., Rose, M. D., Kelley, J., MacLatchy, L. & Pilbeam, D. 2002 New *Sivapithecus* postcranial specimens from the Siwaliks of Pakistan. *J. Hum. Evol.* **42**, 705–752. (doi:10.1006/jhev.2002.0554)
- Meldrum, D. J. 1993 On plantigrady and quadrupedalism. *Am. J. Phys. Anthropol.* **91**, 379–385. (doi:10.1002/ajpa.1330910310)
- Morton, D. J. 1922 Evolution of the human foot I. *Am. J. Phys. Anthropol.* **5**, 305–336. (doi:10.1002/ajpa.1330050409)
- Moyà-Solà, S. & Köhler, M. 1996 The first *Dryopithecus* skeleton: origins of great-ape locomotion. *Nature* **379**, 156–159. (doi:10.1038/379156a0)
- Moyà-Solà, S., Köhler, M. & Rook, L. 1999 Evidence of a hominid-like precision grip capability in the hand of the Miocene ape *Oreopithecus*. *Proc. Natl Acad. Sci. USA* **96**, 313–317. (doi:10.1073/pnas.96.1.313)
- Moyà-Solà, S., Köhler, M., Alba, D. M., Casanovas-Vilar, I. & Galindo, J. 2004 *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. *Science* **306**, 1339–1344. (doi:10.1126/science.1103094)
- Nagano, A., Umberger, B. R., Marzke, M. W. & Gerritsen, K. G. M. 2005 Neuromusculoskeletal computer modeling and simulation of upright, straight-legged, bipedal locomotion of *Australopithecus afarensis* (A.L. 288-1). *Am. J. Phys. Anthropol.* **126**, 2–13. (doi:10.1002/ajpa.10408)
- Oishi, M., Ogihara, N., Endo, H., Ichihara, N. & Asari, M. 2009 Dimensions of forelimb muscles in orangutans and chimpanzees. *J. Anat.* **215**, 373–382. (doi:10.1111/j.1469-7580.2009.01125.x)
- Pataky, T. C., Caravaggi, P., Savage, R., Parker, D., Goulermas, J. Y., Sellers, W. I. & Crompton, R. H. 2008 New insights into the plantar pressure correlates of walking speed using pedobarographic statistical parametric mapping (pSPM). *J. Biomech.* **41**, 1987–1994. (doi:10.1016/j.jbiomech.2008.03.034)
- Payne, R. C., Crompton, R. H., Isler, K., Savage, R., Vereecke, E. E., Günther, M. M., Thorpe, S. K. S. & D'Août, K. 2006a Morphological analysis of the hindlimb in apes and humans. I. Muscle architecture. *J. Anat.* **208**, 709–724. (doi:10.1111/j.1469-7580.2006.00563.x)
- Payne, R. C., Crompton, R. H., Isler, K., Savage, R., Vereecke, E. E., Günther, M. M., Thorpe, S. K. S. & D'Août, K. 2006b Morphological analysis of the hindlimb in apes and humans. II. Moment arms. *J. Anat.* **208**, 725–742. (doi:10.1111/j.1469-7580.2006.00564.x)
- Pierrynowski, M. R. 1995 Analytical representation of muscle line of action and geometry. In *Three-dimensional analysis of human movement* (eds P. Allard, I. A. F. Stokes & J. P. Blanch), pp. 215–256. Champaign, IL: Human Kinetic Publishers.
- Pontzer, H. & Wrangham, R. W. 2004 Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. *J. Hum. Evol.* **46**, 315–333. (doi:10.1016/j.jhevol.2003.12.006)
- Remis, M. 1994 Feeding ecology and positional behavior of western lowland gorillas (*Gorilla gorilla gorilla*) in the Central African Republic. PhD thesis, Yale University, New Haven, CT.
- Remis, M. 1995 Effects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. *Am. J. Phys. Anthropol.* **97**, 413–433. (doi:10.1002/ajpa.1330970408)
- Richmond, B. G. & Strait, D. S. 2000 Evidence that humans evolved from a knuckle-walking ancestor. *Nature* **404**, 382–385. (doi:10.1038/35006045)
- Richmond, B. G. & Jungers, W. L. 2008 *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. *Science* **319**, 1662–1665. (doi:10.1126/science.1154197)
- Richmond, B. G., Begun, D. R. & Strait, D. S. 2001 Origin of human bipedalism: the knuckle-walking hypothesis revisited. *Yrbk. Phys. Anthropol.* **44**, 70–105.

- Rowe, N. 1996 *The pictorial guide to the living primates*. Charlestown, RI: Pogonias Press.
- Sayers, K. & Lovejoy, C. O. 2008 The chimpanzee has no clothes. *Curr. Anthropol.* **49**, 87–114. (doi:10.1086/523675)
- Schaller, G. B. 1963 *The mountain gorilla*. Chicago, IL: University of Chicago Press.
- Schmitt, D. 1999 Compliant walking in primates. *J. Zool. (Lond.)* **248**, 149–160. (doi:10.1111/j.1469-7998.1999.tb01191.x)
- Schultz, A. H. 1936 Characters common to higher primates and characters specific for man. *Quart. Rev. Biol.* **11**, 259–283, 425–455.
- Sellers, W. I. & Manning, P. L. 2007 Estimating dinosaur maximum running speeds using evolutionary robotics. *Proc. R. Soc. B* **274**, 2711–2716. (doi:10.1098/rspb.2007.0846)
- Sellers, W. I., Dennis, L. A. & Crompton, R. H. 2003 Predicting the metabolic energy costs of bipedalism using evolutionary robotics. *J. Exp. Biol.* **206**, 1127–1136. (doi:10.1242/jeb.00205)
- Sellers, W. I., Dennis, L. A., Wang, W. & Crompton, R. H. 2004 Evaluating alternative gait strategies using evolutionary robotics. *J. Anat.* **204**, 343–351. (doi:10.1111/j.0021-8782.2004.00294.x)
- Sellers, W. I., Cain, G., Wang, W. J. & Crompton, R. H. 2005 Stride lengths, speed and energy costs in walking of *Australopithecus afarensis*: using evolutionary robotics to predict locomotion of early human ancestors. *J. R. Soc. Interface* **2**, 431–442. (doi:10.1098/rsif.2005.0060)
- Sellers, W. I., Pataky, T. C., Caravaggi, P. & Crompton, R. H. 2010 Evolutionary robotic approaches in primate gait analysis. *Int. J. Primatol.* **31**, 321–338. (doi:10.1007/s10764-010-9396-4)
- Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K. & Coppens, Y. 2001 First hominid from the Miocene (Lukeino formation, Kenya). *CR. Acad. Sci. Paris Ser. IIA* **332**, 137–144.
- Sokol, M. D., Raichlen, A. & Pontzer, H. 2007 Chimpanzee locomotor energetics and the origin of bipedalism. *Proc. Natl Acad. Sci. USA* **104**, 12 265–12 266. (doi:10.1073/pnas.0703267104)
- Stern, J. T. & Susman, R. L. 1993 The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* **60**, 279–317. (doi:10.1002/ajpa.1330600302)
- Susman, R. L. 1984 The locomotor behavior of *Pan paniscus* in the Lomako forest. In *The Pygmy Chimpanzee* (ed. R. L. Susman), pp. 369–394. New York, NY: Plenum Press.
- Tansey, P. A. & Briggs, P. J. 2001 Active and passive mechanisms in the control of heel supination. *Foot Ankle Surg.* **7**, 131–136. (doi:10.1046/j.1460-9584.2001.00264.x)
- Thorpe, S. K. S. & Crompton, R. H. 2005 The locomotor ecology of wild orangutans (*Pongo pygmaeus abelii*) in the Gunung Leuser Ecosystem, Sumatra, Indonesia: a multivariate analysis using log-linear modelling. *Am. J. Phys. Anthropol.* **127**, 58–78. (doi:10.1002/ajpa.20151)
- Thorpe, S. K. S. & Crompton, R. H. 2006 Orang-utan positional behavior and the nature of arboreal locomotion in Hominoidea. *Am. J. Phys. Anthropol.* **131**, 384–401. (doi:10.1002/ajpa.20422)
- Thorpe, S. K. S., Crompton, R. H., Gunther, M. M., Ker, R. F. & Alexander, R. M. cN. 1999 Dimensions and moment arms of the hind- and forelimb muscles of common chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthropol.* **110**, 179–199. (doi:10.1002/(SICI)1096-8644(199910)110:2<179::AID-AJPA5>3.0.CO;2-Z)
- Thorpe, S. K. S., Crompton, R. H. & Alexander, R. M. cN. 2007a Orangutans use compliant branches to lower the energetic cost of locomotion. *Biol. Lett.* **3**, 253–256. (doi:10.1098/rsbl.2007.0049)
- Thorpe, S. K. S., Holder, R. L. & Crompton, R. H. 2007b Origin of human bipedalism as an adaptation for locomotion on flexible branches. *Science* **316**, 1328–1331. (doi:10.1126/science.1140799)
- Thorpe, S. K. S., Hodder, R. & Crompton, R. H. 2009 Orangutans employ unique strategies to control branch flexibility. *Proc. Natl Acad. Sci. USA* **106**, 12 646–12 651. (doi:10.1073/pnas.0811537106)
- Tuttle, R. H. & Watts, D. P. 1985 The positional behavior and adaptive complexes of *Pan gorilla*. In *Primate morphophysiology, locomotor analysis and human bipedalism* (ed. S. Kondo), pp. 261–288. Tokyo, Japan: Tokyo University Press.
- Tuttle, R. H., Butzer, K. W. & Blumenberg, B. 1974 Darwin's apes, dental apes, and the descent of man: normal science in evolutionary anthropology. *Curr. Anthropol.* **15**, 389–426. (doi:10.1086/201494)
- Vereecke, E. E., D'Aout, K., De Clercq, D., Van Elsacker, L. & Aerts, P. 2003 Dynamic plantar pressure distribution during terrestrial locomotion of Bonobos (*Pan paniscus*). *Am. J. Phys. Anthropol.* **120**, 373–383. (doi:10.1002/ajpa.10163)
- Vereecke, E. E., D'Aout, K., De Clercq, D., Van Elsacker, L. & Aerts, P. 2005 Functional analysis of the gibbon foot during terrestrial bipedal walking: plantar pressure distributions and 3D ground reaction forces. *Am. J. Phys. Anthropol.* **128**, 659–669. (doi:10.1002/ajpa.20158)
- Vereecke, E. E., D'Aout, K. & Aerts, P. 2006a Speed modulation in hylobatid bipedalism: a kinematical analysis. *J. Hum. Evol.* **51**, 513–526. (doi:10.1016/j.jhevol.2006.07.005)
- Vereecke, E. E., D'Aout, K. & Aerts, P. 2006b The dynamics of hylobatid bipedalism: evidence for an energy-saving mechanism? *J. Exp. Biol.* **209**, 2829–2838. (doi:10.1242/jeb.02316)
- Vogel, S. 2003 *Comparative biomechanics, life's physical world*. Princeton, NJ: Princeton University Press.
- Wang, W. J. & Crompton, R. H. 2004 The role of load-carrying in the evolution of modern body proportions. *J. Anat.* **204**, 417–430. (doi:10.1111/j.0021-8782.2004.00295.x)
- Wang, W. J., Crompton, R. H., Li, Y. & Günther, M. M. 2003 Energy transformation during erect and bent-hip-bent-knee walking by humans with implications for the evolution of bipedalism. *J. Hum. Evol.* **44**, 563–580. (doi:10.1016/S0047-2484(03)00045-9)
- Wang, W. J., Crompton, R. H., Carey, T. C., Günther, M. M., Li, Y., Savage, R. & Sellers, W. I. 2004 Comparison of inverse-dynamics musculo-skeletal models of AL 288-1 *Australopithecus afarensis* and KNM-WT 15000 *Homo ergaster* to modern humans, with implications for the evolution of bipedalism. *J. Hum. Evol.* **47**, 453–478. (doi:10.1016/j.jhevol.2004.08.007)
- Ward, C. V., Leakey, M. G., Brown, B., Brown, F., Harris, H. & Walker, A. 1999 South Turkwel: a new Pliocene hominid site in Kenya. *J. Hum. Evol.* **36**, 69–95. (doi:10.1006/jhev.1998.0262)
- Washburn, S. L. 1967 Behaviour and the origin of man (The Huxley Memorial Lecture 1967). *Proc. Roy. Anthropol. Inst. Great Brit. Ireland*, pp. 21–27.
- Watson, J. C. & Wilson, A. M. 2007 Muscle architecture of biceps brachii, triceps brachii and supraspinatus in the horse. *J. Anat.* **210**, 32–40. (doi:10.1111/j.1469-7580.2006.00669.x)
- Watson, J., Payne, R., Chamberlain, A., Jones, R. & Sellers, W. I. 2009 The kinematics of load carrying in humans

- and great apes: implications for the evolution of human bipedalism. *Folia Primatol.* **80**, 309–328. (doi:10.1159/000258646)
- Wareing, K., Tickle, P. G., Stokkan, K.-A., Codd, J. R. & Sellers, W. I. Submitted. The musculoskeletal anatomy of the reindeer (*Rangifer tarandus*): fore- and hindlimb.
- Williams, S. B., Payne, R. C. & Wilson, A. M. 2007 Functional specialisation of the pelvic limb of the hare (*Lepus europeus*). *J. Anat.* **210**, 472–490. (doi:10.1111/j.1469-7580.2007.00704.x)
- Williams, S. B., Wilson, A. M., Rhodes, L., Andrews, J. & Payne, R. C. 2008 Functional anatomy and muscle moment arm of the pelvic limb of an elite sprinting athlete, the racing greyhound (*Canis familiaris*). *J. Anat.* **213**, 361–372. (doi:10.1111/j.1469-7580.2008.00961.x)
- Winter, D. A. 1990 *Biomechanics and motor control of human movement*. New York, NY: John Wiley and Sons.
- Zihlman, A. L., Cronin, J. E., Cramer, D. L. & Sarich, V. M. 1978 Pygmy chimpanzee as a possible prototype for the common ancestor of humans, chimpanzees and gorillas. *Nature* **275**, 744–746. (doi:10.1038/275744a0)