

The arboreal origins of human bipedalism

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Almost a century and a half ago, Charles Darwin in The Descent of Man (1871: 141) highlighted the evolution of bipedalism as one of the key features of the human lineage, freeing the hands for carrying and for using and making tools. But how did it arise? The famous footprints from Laetoli in Tanzania show that hominin ancestors were walking upright by at least 3.65 million years ago. Recent work, however, suggests a much earlier origin for bipedalism, in a Miocene primate ancestor that was still predominantly tree-dwelling. Here Susannah Thorpe, Juliet McClymont and Robin Crompton set out the evidence for that hypothesis and reject the notion that the common ancestor of great apes and humans was a knuckle-walking terrestrial species, as are gorillas and chimpanzees today. The article is followed by a series of comments, rounded off by a reply from the authors.

Theories regarding the origins of hominin bipedalism have spent some considerable time ‘on the ground’ as a result of the knuckle-walking hypothesis, which postulates that our earliest bipedal ancestor evolved from an ape that knuckle-walked on the ground in a way similar to modern chimpanzees or gorillas. By contrast, we argue that there is compelling and unequivocal evidence that bipedalism has arboreal origins.

The concept of an arboreal origin for habitual human bipedalism was first proposed over a century ago. The arboreal behaviour that was considered to be exaptive (i.e. to have ‘prepared’ the body) for bipedalism has, however, changed fundamentally with the gradual discoveries of new fossil evidence, and with the development of new approaches to reconstructing the ecology and locomotion of extinct species. In particular, study of the ecology and biomechanics of living apes has transformed our understanding of how bipedalism could have evolved. Living apes offer broad models for how the dynamic between habitat and morphology may combine to influence locomotor behaviour. Sir Arthur Keith (1903) was the first to suggest that the arboreal locomotion of apes was important in understanding the process by which upright posture evolved in human ancestors. His studies of primate anatomy and behaviour led to the paradigm that an ape that moved by brachiating (arm-swinging) underneath branches (suspension) later evolved into a habitual biped (e.g. Morton 1922; Keith 1923). Morphological and locomotor observations continued to be proffered in support of this hypothesis for many decades (see Tuttle 1974 for a review). However,

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one of the most important lines of evidence to emerge relatively recently from new fossil discoveries is that adaptations to suspension and arm-swinging must have evolved not once only but convergently, across several millions of years, in multiple fossil ape species (e.g. Almecija *et al.* 2009).

During the 1970s and '80s, Russell H. Tuttle (1974, 1981) proposed that the arboreal ancestor of modern hominins would have been small-bodied—around the size of living gibbons (9–13.5kg)—and would have engaged extensively in vertical climbing (that is, climbing up and down vertical tree trunks with the torso in an upright position), an activity that he considered to be functionally associated with bipedalism. The biomechanical link was defined by Probst (1980) from apparent similarities in the range of joint angles exhibited in vertical climbing by chimpanzees and in human bipedalism, and by Fleagle *et al.* (1981) from joint movements and muscle activity in these behaviours in New World monkeys. But recent work has undermined this hypothesis by showing that gorillas and orangutans have more extended hip joint angles when moving bipedally than when they are using vertical climbing (Crompton *et al.* 2003; Watson *et al.* 2009).

By the early 2000s the fossil record of the Eurasian and East African Miocene (23–5 million years ago (Ma)) was burgeoning and revealing the body form of early 'crown' hominoids ('crown' hominoids being the direct ancestors of all living apes, including humans). These included fossils of species such as *Morotopithecus bishopi* (from approximately 18–22 Ma), *Pierolapithecus catalaunicus* (c. 12 Ma), *Hispanopithecus (Dryopithecus) laietanus* (c. 10 Ma) and *Orrorin tugenensis* (6 Ma). These fossils suggested that, contrary to expectations and fossil evidence from *Proconsul hesoloni* and associated species, the early crown hominoids stood and moved with an orthograde (upright) posture. Thus features such as their broad, shallow trunks; scapulae positioned on the back rather than side of their bodies, and lumbar vertebral bodies that increased in size towards the lower end of the spine all indicated that these species were frequently upright (MacLachy 2004; Moyà-Solà *et al.* 2004; Nakatsukasa *et al.* 2007; reviewed in Crompton *et al.* 2008). In addition, since they are estimated to have weighed between 30 and 50kg, they were also at least as large as adult female great apes (MacLachy 2004; Moyà-Solà *et al.* 2004; Nakatsukasa *et al.* 2007), a finding which casts doubt on the validity of Tuttle's (1981) model of a small-bodied gibbon-like ancestor.

The fact that orthograde (upright) body postures had been evolving and diversifying in our hominoid ancestry for in excess of 15 million years pushed study of the origins of bipedalism back from the Pliocene into the early Miocene. It also challenged the commonly held concept that the acquisition of habitual bipedalism is an appropriate marker of the separation of the hominins from the panins (bonobos and chimpanzees), a separation that is estimated to have occurred only 5–8 million years ago. It pushed the context of bipedal origins back into the forest canopy from the ground (Senut 2011) where it had spent some considerable time as a result of the knuckle-walking hypothesis. This latter paradigm, that has dominated our vision of the evolution of bipedalism since the 1960s, held that because chimpanzees and gorillas move on the ground by quadrupedal horizontal-trunked knuckle-walking, the pre-bipedal ancestor of hominins must also have passed through a terrestrial knuckle-walking phase (e.g. Gebo 1996; Richmond & Strait 2000).

In parallel to the burgeoning fossil record, significant progress was being made in quantifying the locomotor ecology of modern wild apes (i.e. the relative proportions of bipedalism and other forms of movement exhibited by a given species in a given setting). Hunt and colleagues (1996) advocated much-needed uniformity in the language used to describe locomotion across primate clades. They wished primarily to avoid the ubiquitous term ‘climbing’ to describe a wide range of locomotor behaviours that conflated pronograde (horizontal) and orthograde (upright) body postures, and travelling in vertical and horizontal directions. In the event, this has been adhered to more closely by the literature on living primates than that on fossil forms. The significance of the approach was that it allowed comparative quantification of the ecological context of locomotion (how much time a particular species spent in knuckle-walking, brachiating, vertical climbing, etc.; in what kinds of setting—e.g. forest canopy, forest floor, open grassland—and an indication of the stresses different behaviours placed on the body). Thus it made it possible to quantify the adaptive advantages of arboreal behaviours, a factor that was lacking from many earlier studies of locomotion that were restricted to studies of captive animals or qualitative observations of wild-living taxa.

The approach revealed that all great apes occasionally choose to engage in arboreal bipedalism—walking along and between branches on two legs (e.g. Hunt 1992; Remis 1995; Thorpe & Crompton 2005, 2006). It was from this that Hunt (1996) and Stanford (2006) developed the arboreal foraging hypothesis. They showed that in chimpanzees, hand-assisted bipedal posture (as opposed to bipedal locomotion) was associated with arboreal feeding on relatively stable branches >100mm in diameter, and suggested such behaviour might have been exaptive for terrestrial bipedalism. Postures are, however, less energetically demanding to maintain than locomotion, and standing on large-diameter branches does not pose the safety risks that are associated with balancing on thin, flexible branches. In contrast we studied Sumatran orangutans (*Pongo abelii*), as they exhibit strong similarity to humans in the extended-leg bipedal kinematics (joint angles) and kinetics (forces exerted on the ground during locomotion) (Crompton *et al.* 2003; Crompton & Thorpe 2007). Furthermore, they are the only exclusively arboreal great ape. We found that Sumatran orangutans use extended-leg bipedal locomotion on highly flexible branches, <40mm in diameter (Thorpe *et al.* 2007a) (Figure 1). This result countered traditional hypotheses that had suggested that movement along flexible branches should be either via orthograde suspension in which the animal gains stability by hanging with its centre of mass directly under the branch; or by ‘compliant’ quadrupedalism, in which stability is maximised in part by bending the knees and elbows substantially to reduce the movements of the branch caused by the animal’s weight.

We also found that in 75 per cent of our observations of orangutan bipedal locomotion along branches, they used their hands for stabilisation, as do chimpanzees (Hunt 1996; Stanford 2006). Hand assistance ensures maximum safety while the bipedalism enables a free hand to reach out for feeding, weight transfer, or balance in the peripheral branches of trees, where the majority of preferred foods are situated and where primates must cross between tree crowns. Being able to access these peripheral branches effectively is highly advantageous because it allows large-bodied apes to cross more gaps between trees. Crossing rather than circumventing gaps in the canopy can dramatically reduce the energy costs of travel, especially where a change of height would otherwise be required (Thorpe *et al.* 2007b).

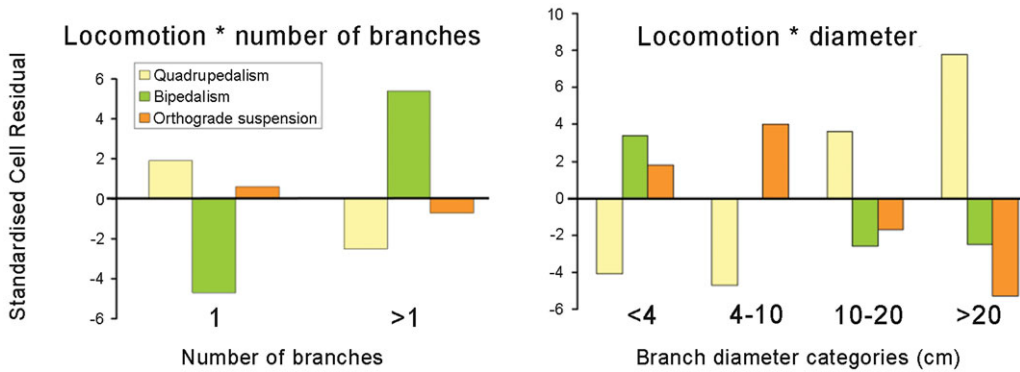


Figure 1. Standardised cell residuals (SCRs) to demonstrate the primary results in the Log linear model of Thorpe et al. 2007a. The left-hand diagram shows the relationship between locomotion and the number of supports used and the right shows the relationship between locomotion and the diameters of the supports used. SCRs indicate by their sign whether an interaction is more (positive values) or less (negative values) common than predicted by the model and, by their size, to what degree. SCRs greater than ± 2.0 indicate a lack of fit. The graphs show that quadrupedalism is strongly associated with locomotion on single, large, stable supports $>200\text{mm}$ in diameter; orthograde suspension is mostly associated with locomotion on supports between $40\text{--}100\text{mm}$ in diameter. In contrast bipedalism is strongly associated with locomotion on multiple supports and those that are $<40\text{mm}$ in diameter.

We concluded that hand-assisted arboreal bipedalism as part of a smooth continuum of orthograde behaviours ranging from suspending underneath branches to standing on top of them confers a major selective advantage on orangutans and argued that arboreal bipedalism would have been equally advantageous for ancestral crown hominoids (Figure 2).

We are convinced that the accumulating evidence for the arboreal origins of human bipedalism is strong. Inevitably, some do not share our conviction. As part of a more general critique on the use of ‘living referential models’ to understand fossil taxa, Sayers and Lovejoy (2008) argued that our use of orangutan data was based on false premises. First, they suggested that we studied bipedal posture and not bipedal locomotion. This indicates that they didn’t read our paper well; even the title alluded to locomotion rather than posture. They also suggested that orangutans are an unsuitable model because they have feet that are highly specialised for gripping, such as very long toes that cannot therefore have been exaptations for bipedality; and that they are rarely terrestrial, and when they are terrestrial they use knuckle- or fist-walking (citing Tuttle & Beck 1972). We agree that the feet of orangutans are highly specialised—but even then our recent work (Bates *et al.* 2013) shows that foot pressures in the bipedalism of orangutans (and bonobos) overlap substantially with those of humans, particularly under the middle of the foot. Nevertheless, orangutan footprint morphology does not need to be exaptive for bipedality for the purposes of our model. We studied Sumatran orangutans because, unlike Bornean orangutans (*Pongo pygmaeus* sp.) and other great apes, they very rarely descend to the ground and should therefore be a good model for arboreal locomotor ecology. If Sumatran orangutans did (hypothetically) descend to the forest floor they probably would move quadrupedally because palmigrade quadrupedalism is strongly associated with travel on broad, stable tree boughs (Figure 1) (Thorpe & Crompton 2006; Thorpe *et al.* 2007a). Furthermore, anecdotal evidence suggests wild Bornean orangutans generally use quadrupedalism when terrestrial. To our knowledge,

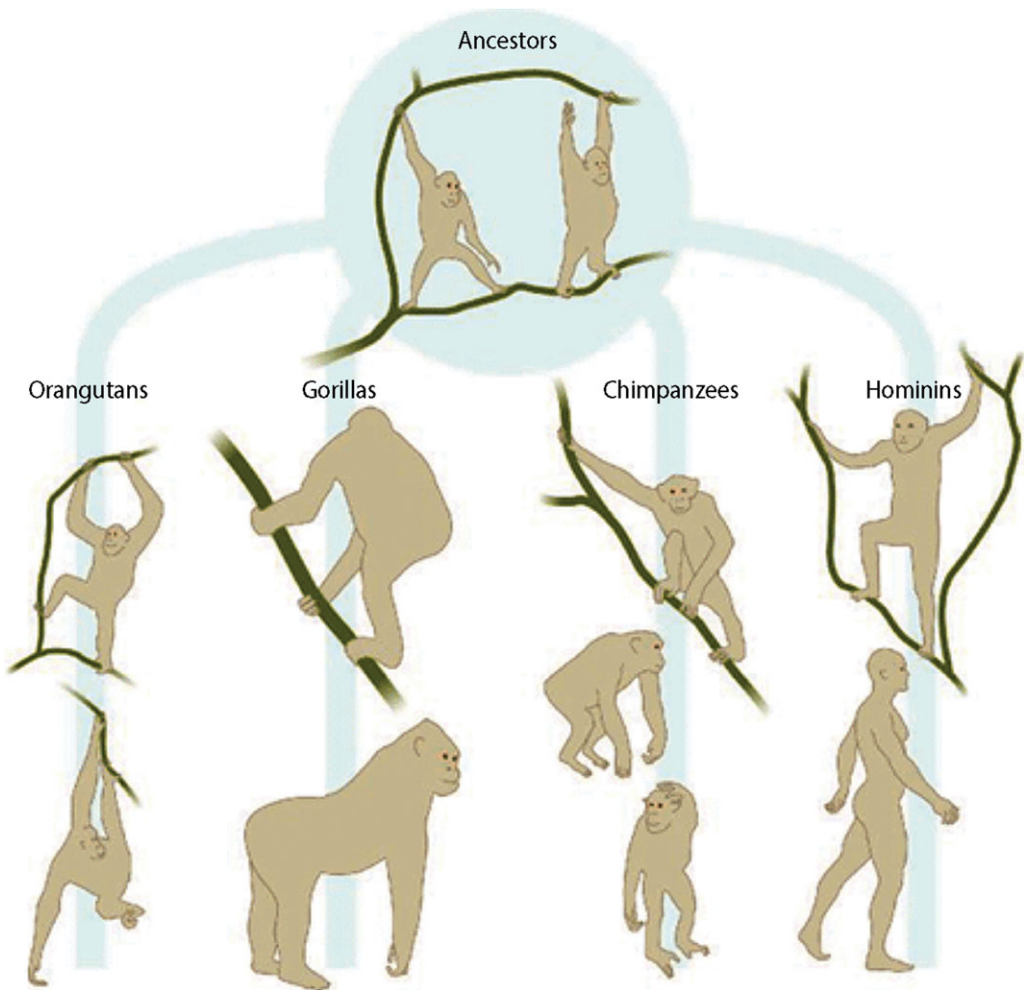


Figure 2. A reconstruction of the arboreal bipedalism hypothesis depicting the evolution of modern great apes including humans from an orthograde ancestral ape, capable of hand-assisted, arboreal bipedalism with extended lower limbs (from O'Higgins & Elton 2007). Orangutan ancestors became arboreal specialists, whereas the ancestors of gorillas and chimpanzees, in response to changing and variable habitats, climbed vertically in and out of trees, and independently acquired knuckle-walking. Hominins retained existing adaptations for extended-limb bipedalism and eventually became committed terrestrial bipeds. Reprinted with permission from AAAS.

however, orangutan hand postures in terrestrial locomotion in the wild have never been quantified because hands are difficult to see in the clutter of the forest floor from the distance required for following orangutans in the wild. The hand postures are likely, however, to be something akin to fist-walking simply because of the length of the digits.

The Tuttle and Beck (1972) paper that Sayers and Lovejoy (2008) reference as evidence for orangutans employing knuckle-walking when terrestrial is based primarily on the mostly postural descriptions of the behaviour of a single, captive, very obese male orangutan called Felix. Tuttle and Beck (1972: 33–34) conclude that “although Felix often places his hands in knuckle-walking postures, he rarely supports a major portion of his body weight on

knuckle-walking hands”. While Sayers and Lovejoy (2008) are entitled to reject the use of referential models, it is then hardly appropriate for them to base their arguments on a referential model based on a single, clearly unhealthy individual whose obesity certainly hampered his locomotor ability. Instead we based our arguments on the behaviours observed in multiple, healthy subjects travelling in a natural habitat.

Overall, Sayers and Lovejoy (2008) fail to grasp the core concepts of our model and perhaps, given their own use of Felix, the concept of referential modelling in general. We suggested that Sumatran orangutans are a useful species to study because they are the only extant great ape to remain in what is generally accepted to be the ancestral great ape niche—the canopy of tropical forest. The value of the model is that Sumatran orangutans employ the behaviour of interest (extended-leg bipedalism) in the appropriate ecological context (the canopy of tropical forest) and therefore can tell us something about that particular behaviour. Whether and how they move on the ground is irrelevant to the model.

Winder *et al.* (2013) also criticised our theory. They proposed that most of the postcranial/locomotor features of modern hominins are attributable to a *single* newly identified driver; adaptation for ‘complex topographies’. With respect to our study among other so-called ‘woodland hypotheses’ they claim “an upright climbing adaptation, evolved within the context of tree-dwelling, would not produce all the features required for effective rapid, long-distance terrestrial bipedalism. Explaining how our ancestors survived a locomotor transition in a relatively dangerous semi-open habitat remains a critical challenge to these hypotheses” (Winder *et al.* 2013: 334). Instead they propose that the acquisition of upright body posture and a broad thorax (chest) (which, currently, can first be identified in the crown hominoid *Morotopithecus* between 18 and 22 Ma (MacLachy 2004)), can be explained as an adaptation to ‘complex topographies’. So equally are: a) the appearance of a foot with functional lateral and medial arches, and adducted hallux (big toe) (currently first evident in the Laetoli G-1 footprint trail at 3.65 Ma; Day & Wickens 1980, Crompton *et al.* 2012); and b) the increase in stature and the shortened upper limb (and the elongated lower limb which seems to accompany it) that are typical of the genus *Homo sensu stricto*. These features currently first appear between 1.8 and 1.95 Ma in *Homo rudolfensis*, or in *Homo ergaster*/Early African *Homo erectus* at *c.* 1.6 Ma (reviewed e.g. in Crompton *et al.* 2008; and Pontzer 2012). It is not at all clear why they consider that exactly the same selective pressure, use of ‘complex topographies’, would lead to these adaptations in such a piecemeal process over millions of years, rather than all at the same time or in a much tighter and linked time frame. Furthermore, in each case they fail to mention the species under discussion, preferring to use the generic term ‘hominins’ to describe all stages. Thus, Winder and colleagues are wrong to suggest that explaining how our ancestors survived in an open habitat is a challenge to our hypothesis. We sought to elucidate the origins of bipedal locomotion, which occurred in a very different environment to later refinements for fast bipedal gait in a (mostly) terrestrial setting. The challenge to their hypothesis however is to explain how their theory fits with the fossil record.

The pushing back of bipedal adaptations such as orthograde posture and movement to arboreal early Miocene apes effectively removes the opportunity for a terrestrial knuckle-walking stage in the origins of human bipedalism. The only alternative would be to postulate a transition to orthograde in the crown hominoids (from monkey-like pronograde in the

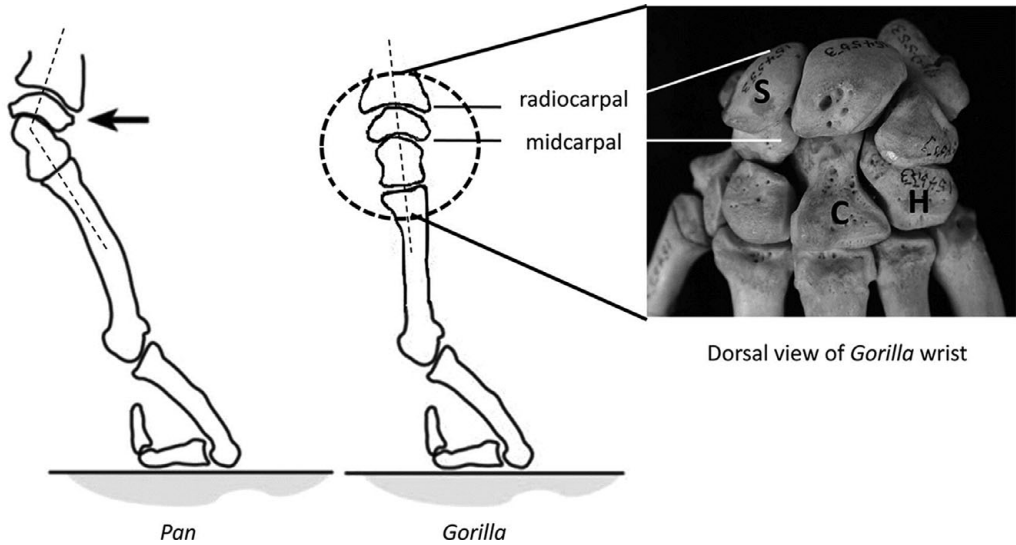


Figure 3. Functional differences in the knuckle-walking hand postures of Pan and Gorilla (from Kivell & Schmitt 2009). In Pan, the wrist (and carpometacarpal) joints are held in an extended posture (dotted line) such that extension-limiting morphological features are required for stability. In contrast, the authors hypothesise that Gorilla use a columnar, neutral wrist and hand posture with axial loading (dotted line). Radiocarpal and midcarpal joints are labelled in lateral and dorsal views of Gorilla carpus. 'S', scaphoid; 'C', capitate; 'H', hamate. © The National Academy of Sciences.

common ancestor of the apes and monkeys), back to pronograde in the African apes and then back again to orthograde in hominins (Crompton *et al.* 2008)). Kivell and Schmitt (2009) further undermined the knuckle-walking hypothesis when they tested the extent to which knuckle-walking adaptations were similar in living chimpanzees and gorillas. Not only did they find clear evidence that modes of knuckle-walking in *Pan* and *Gorilla* were fundamentally different (Figure 3), they also found what had been claimed to be knuckle-walking adaptations in the carpal morphology of a range of non-knuckle-walking monkeys. Of course it is theoretically possible that knuckle-walking did evolve only once in the common ancestor of the African ape and human clade and that these differences evolved after the *Gorilla* and *Pan* lineages split (Kivell & Schmitt 2009). The broad consensus that there is a clear lack of any convincing fossil evidence for knuckle-walking in crown hominoids or early hominins, however, would render it unlikely. Crompton *et al.* (2010) also pointed out that the hindlimb mechanics of vertical climbing and quadrupedal knuckle-walking are rather similar, involving highly flexed postures of the hip and knee, and suggested that it is in fact these locomotor behaviours that are likely to be functionally and ecologically linked.

It has not been possible to reflect all relevant literature in this short debate piece, nor is it necessary as there are many excellent reviews (e.g. Tuttle 1974; Senut 2011). Rather we have focused on selected highlights of the process by which the scientific world has come to view bipedalism as an ancestral arboreal adaptation rather than a recent terrestrial development. Quantitative studies of the biomechanics and locomotor ecology of wild-living primates have been central to 'fleshing-out' the process by which bipedalism could have been selected for. This does not indicate that extinct species should bear any striking similarity to extant taxa; the Miocene and Pliocene fossil record clearly shows variability

in the orthograde and bipedal adaptations of different species. However, analogy to living species facilitates our understanding of the relationship between performance and habitat, which cannot be reconstructed from fossils alone, since the skeleton reflects only a subset of the behaviours that an animal is able to perform. Furthermore, as our own work (Bates *et al.* 2013) demonstrates for human, bonobo and orangutan feet, distinct morphologies do not necessarily imply qualitatively different functions.

Despite the longevity of the paradigm that derived human bipedalism from chimpanzee-like knuckle-walking, we conclude that the arboreal origin of bipedalism is now overwhelmingly supported by the fossil, biomechanical and ecological evidence. The 50-year reign of the knuckle-walking paradigm must be declared over. However, the ancestry of bipedal adaptations; their variability in different species and their piecemeal evolution suggests that their relevance for distinguishing the separation of the hominins from the panins has become substantially blurred.

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Human bipedalism and the importance of terrestriality

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The paper by Thorpe *et al.* (above) follows on from our own paper (Winder *et al.* 2013); in setting out their view that bipedalism has arboreal origins, they present a critique of our hypothesis, which we address below.

We begin by observing that their views and ours are not in contradiction. We criticised ‘forest hypotheses’ of human evolution, not because we think they are wrong but because we think they are incomplete. In fact we agree with Thorpe *et al.* about the arboreal origin of bipedalism amongst certain groups of apes. What we are interested in, and what they do not address, is a different set of issues: how and why some apes, already perhaps pre-adapted to bipedalism in their anatomy, became committed to a terrestrial (non-arboreal) pattern of existence. We do not argue that upright posture cannot be explained by arboreal selective pressures, rather that such an explanation is not *ipso facto* sufficient to explain all hominin adaptations or produce *all* the features needed to survive on the ground.

We reject their view that our model suggests “a *single* newly identified driver; adaptation for ‘complex topographies’” (Thorpe *et al.* above, p. 911; emphasis in the original). We wrote about *ecologically and structurally complex landscapes*, and used ‘complex’ or ‘rough’ topography as a proxy. Rough terrain is one of several characteristics all complex landscapes might be expected to share and which can be identified (at least to a degree) in the palaeoenvironmental record. We do not suggest that all terrestrial landscapes with rough terrain exert a uniform selective regime on their inhabitants—let alone a single selective pressure—not least because rough landscapes vary considerably in their vegetation cover. We also clearly stated that our model requires no assumptions about the anatomy or behaviour of the last common ancestor. It is thus not in any way incompatible with an arboreal, bipedal ancestry. On the contrary, it adds another layer to such a model, providing a ‘missing link’ between existing theories that work well for the earliest and latest periods of hominin evolution but not for the transition between them.

Thorpe *et al.* also criticise our hypothesis for not explaining why different characteristics of terrestrial bipedalism appeared piecemeal in the fossil record. However, it is a misconception to suppose that we proposed a single, simple selective pressure, which must necessarily act at a specific time in our evolutionary history. In fact, our model specifies a multi-stage trajectory, involving adaptation to complex landscapes as a first stage, and expansion beyond them through tactical use of terrain in a later stage. Central to our hypothesis is the importance of

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spatially and temporally heterogeneous landscapes, in which different hominin populations and species may occupy broadly similar—but not identical—niches.

Our hypothesis thus invokes a mosaic set of niches for early terrestrial hominins, albeit encompassed within a broader ‘complex landscape’ niche, such that different groups might be expected to diverge, adapt to the specific characteristics of differing landscapes, move around, and periodically re-connect with other groups. This would fit well with the mosaic patterning and diversity of hominin anatomical adaptations we see in the fossil record.

Creatures adapted to complex landscapes might move on to specialise in a range of niches, requiring different sorts of locomotory and behavioural adaptations. Our argument is that complex landscapes provided a first step away from dependence on trees, followed by more widespread expansion through tactical use of topographic complexity, offering a *specific* trajectory for hominin evolution.

Finally, Thorpe *et al.* take us to task for failing to link particular environmental features with individual hominin species. We avoided this for two reasons. First, we did not wish to get bogged down in debates about taxonomy, species names and dates. Secondly, a mosaic evolutionary process is inherently complex and hard to reconstruct. Since we cannot identify all the characteristics of the particular complex landscapes that constrained the niches of specific groups, attempting to draw links between the anatomy of individual fossils and the nature of their particular environments is challenging and risky. The specific patterns we see are likely to be *emergent*—the result of chance, contingency and complex interactions—and therefore not predictable.

In conclusion, we emphasise that there is no necessary antagonism between the work of Thorpe *et al.* on the initial origins of bipedalism and our work on the subsequent history of the human lineage and the transition to terrestriality. Whether individual anatomical characters ultimately come to be seen as part of one phase or another is less important than the improvement in our overall understanding of human (and ape) evolution that comes from a consideration of landscape complexity.

Acknowledgements

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Unreasonable expectations

Bernard Wood*

“For every complex problem, there is a simple, easy to understand, incorrect answer”
Attributed to Albert von Szent-Györgyi

Albert von Szent-Györgyi, who won the Nobel Prize in Physiology or Medicine in 1937, is said to have made the observation cited above because he was aware that *in vitro* experiments were unlikely to capture the complexity of *in vivo* reality. This is because the metabolic pathways illustrated as separate entities in textbooks almost certainly interact, so the resultant of a combination of pathways is not readily captured by experiments that are designed to isolate and elucidate a single pathway. I occasionally reflect on Szent-Györgyi’s wise observation, and I have suggested how apt it is in connection with human evolution. The contributions by Winder *et al.* (2013) and Thorpe *et al.* (above) about the origins of hominin bipedalism were a particularly effective reminder.

The two groups of authors ‘seem’ to offer rival and mutually incompatible ‘explanations’ for the evolution of bipedal locomotion in the hominin clade. Winder *et al.* think it was prompted by the need to negotiate the type of uneven ground that has me ‘clambering’ (i.e. searching for places to put my hands to help me balance) rather than walking. Thorpe *et al.* would have us believe that modern human terrestrial bipedalism was an exaptation forged when our ancestors lived in and around the forest canopy. I deliberately write ‘seem’ because it is not entirely clear what Winder *et al.* are seeking to explain. They write that they “focus on the anatomical features associated with locomotion” (2013: 333), and then claim that “complex topography provides a better explanation for the specific anatomical features associated with the human evolutionary trajectory and divergence from other primates” (2013: 333). But they never share with us what these “specific anatomical features” are, although the context suggests that they mean what others refer to as ‘bipedal adaptations’ of the skull, axial skeleton, pelvis and the lower limb.

But at least Winder *et al.*’s claim is a relatively modest one, for all they are suggesting is that the complex topography hypothesis “supplements and complements vegetational and climatic alternatives rather than completely replacing them” (2013: 334). In contrast, Thorpe *et al.* (above) cast modesty to the wind and argue that “there is compelling and *unequivocal* evidence that bipedalism has arboreal origins” (my italics). My point is that both sets of authors, and Thorpe *et al.* in particular, fell into the trap Szent-Györgyi warned us about. They both offer ‘simple’ and ‘easy to understand’ answers to a complex problem, and my instinct is that, as Szent-Györgyi suggests, both answers are incorrect and incomplete.

Their first error is to assume that we have a good enough fossil record, plus good enough contextual information about that fossil record, to ‘know’ where and when bipedal

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locomotion evolved. It seems to me inconceivable that the meagre fossil record we have of the first several million years of hominin evolution captures all there is to know about the tempo and mode of evolutionary change in the hominin clade. There is also a widespread assumption, especially among those who see simplicity in the hominin fossil record, that an upright posture and bipedalism only evolved once. This assumption certainly simplifies the problem, but we do not yet know whether, or to what extent, it over-simplifies it. I am convinced it must do, and in any event there is accumulating morphological evidence that there are at least two types of bipedal adaptations within the hominin clade. And if there are two types, there could be more.

Their second error is to assume the emergence of bipedal locomotion is an ‘event’ in the sense that its time course was relatively short. It might look like that to us, but I suspect that it looks that way because of the paucity of evidence, not because it really was an actual event. In any case, whatever hominin bipedalism ‘is’, it would be sensible to view it as an evolving process rather as a discrete event.

The third error is the assumption, made especially by Thorpe *et al.*, that these events are the result of selection pressures that have a single ‘cause’. The selection pressures that bring about a change in something like locomotor mode are almost certainly multifactorial, and we cannot discount the powerful role of drift and morphological integration, both of which Winder *et al.* (2013) touch on.

My instinct is that the principle Szent-Györgyi alluded to in relation to explanations for physiological phenomena applies in spades to attempts to ‘explain’ morphological changes significant enough to be interpreted, almost certainly erroneously, as ‘events’ in hominin evolution. Consider that the researchers who study living populations of modern humans find it hard enough to ‘explain’ why contemporary hunter-gatherers hunt, or travel in the direction they do. So why should we expect it to be easier to determine the nature of selection pressures that operated several million years ago? And if one insists on using ‘unequivocal’ about a hypothesis that seeks to explain something like hominin bipedalism, or, indeed, anything in palaeoanthropology, then it really is an ‘unreasonable expectation’.

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Ignoring *Ardipithecus* in an origins scenario for bipedality is. . . lame

Tim D. White¹, C. Owen Lovejoy² & Gen Suwa³

Living primates have obvious importance for understanding biodiversity and organismal biology. However, as Thorpe, McClymont and Crompton correctly appreciate (as did Charles Darwin in 1871), “[t]his does not indicate that extinct species should bear any striking similarity to extant taxa” (Thorpe *et al.* above).

Living orangutans are separated from living people by more than 30 Myr (millions of years) of cumulative biological evolution since we separated from our common ancestor with them. Today each genus is highly specialised in its own anatomical, behavioural and physiological ways.

Even without a fossil record, Darwin (1871: 213) added, “[u]nless we wilfully close our eyes we may, with our present knowledge, approximately recognise our parentage. . .”. Ours was an ape ancestry, but there was no way for Darwin and his contemporaries to sketch out the specifics of the common ancestors we hominids once shared with living great apes (here, Hominidae encompasses all species on the human side of our phylogenetic split with the chimpanzee lineage).

Accordingly, as with others of his era, Darwin hoped that fossil evidence would help to better reveal human and ape ancestry. It has. However, even with today’s emergent Middle and Late Miocene fossil records, the still-elusive common ancestors of great apes and humans have yet to be recovered.

Ironically, Thorpe, McClymont and Crompton’s ‘short debate piece’ actually shortchanges the most powerful evidence available to date, which is the 4.4 Myr hominid *Ardipithecus ramidus* and its slightly earlier African relatives. This evidence comes from the depths of the Pliocene, closer than ever to the base of the hominid clade. It bolsters their conclusion that knuckle-walking was *not* an ancestral hominid locomotor mode.

Ardipithecus is situated temporally and cladistically between ancestral apes and later hominids (*Australopithecus* and early *Homo*). *Ardipithecus* primitively retained a widely divergent big toe, along with structures of the lower pelvis and thigh that enabled competent arboreal climbing and clambering. At the same time, this hominid also shared with *Australopithecus* key evolved features of the upper pelvis and lateral foot that allowed it to engage in terrestrial bipedality with extended hips and knees (White *et al.* 2009, forthcoming).

Moreover, in limb proportions and in a suite of functionally relevant hand and foot structures, *Ar. ramidus* shows stronger similarities to Miocene fossil apes that were

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considerably less specialised in their locomotor skeletons than are extant apes. In particular, *Ardipithecus* lacks anatomical specialisations related to below-branch suspension (one- or two-armed hanging) and/or knuckle-walking of living great apes.

Rather, when arboreal, *Ar. ramidus* was probably a relatively slow climber and clamberer compared to more acrobatic extant chimpanzees. This would have involved reliance on both 'pronograde' and 'orthograde' trunk alignments when reaching, bridging and clambering among tree branches. These postures and motions were made possible by its laterally positioned shoulder and other anatomies that enhanced forelimb mobility. Limited forelimb suspension and arboreal bipedality were probably also within its positional repertoire.

The actual emergence(s) of such a versatile arboreal body plan in the Miocene ape ancestors of *Ardipithecus*, a 'bauplan' different and more advanced than that of quadrupedal 'pronograde' seen in monkeys and *Proconsul* (but not yet suspensory-specialised), is obscured by a dearth of sufficiently informative Middle and Late Miocene fossil great apes. However, the recently expanded fossil record increasingly suggests several forms of such parallel derivations across Asia, Europe and Africa. These Miocene apes all lacked the suite of enhanced specialisations for suspensory locomotion exhibited by the more specialised extant great apes (although the insular *Oreopithecus* of the latest Miocene of southern Europe perhaps approximated it).

Thorpe, McClymont and Crompton's assertion that 'orthograde' (and by their inference), suspensory-inclined apes (their Figure 2) were widely represented in the Miocene after *c.* 20 Myr is therefore not supported. Indeed, reviewing the plethora of currently known Miocene apes, we (and others, e.g. Nakatsukasa & Kunitatsu 2009; Alba 2012; Almecija *et al.* 2013) are struck by the conspicuous lack of evidence for suspensory specialisations that characterise all living great apes.

As summarised above, a more generalised ancestral ape is independently suggested by the Pliocene descendant, *Ar. ramidus*, a primate that differs dramatically from living orangutans. Perhaps this is why Thorpe, McClymont and Crompton do not mention it.

Solicitation of a uniquely specialised suspensory extant ape such as the living orangutan as either a proxy or model for the far more generalised climbing/clambering Miocene apes from which terrestrially bipedal hominids must have emerged represents a dubious undertaking in light of the currently available Pliocene and Miocene fossil records.

It is also evident that observing the locomotor behaviors of extant relict survivors of the richly divergent Miocene ape radiation will never be as revealing as finding the still-missing remains of the actual last common ancestors we once shared with them during the Miocene. As Darwin also appreciated, such revelations can only come from palaeontology. That is why, even more than a century later, living primates are informative, but more fossils are still urgently needed to clarify the origins and subsequent evolution of Hominidae.

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When the ancestors were arboreal

Brigitte Senut*

Darwin suggested that bipedalism was one of the key features of the human lineage, but more than 60 years earlier, the French naturalist, Lamarck (1809) had suggested that a quadrumanous creature (with all four feet adapted for grasping) living in the trees became bimanous (stopped using its hands as feet, and the big toe ceased to be separated from the other toes) on the ground when the trees disappeared. Lamarck did not know the evolutionary processes involved, but he recognised that bipedalism was an important trait of human evolution and that an arboreal environment was crucial for understanding its origins. To evaluate the possibility of arboreality in human ancestors, most researchers would focus on the African apes (being genetically closer to humans) and would forget orangutans (*Pongo*). We thereby fall into the trap of the specialised locomotor behaviours of African apes, and the pre-conceived idea that the chimpanzee could be considered a good model for our forebears. Was knuckle-walking part of ‘human palaeo-locomotion’? Probably not: it is a highly specialised adaptation and as yet there is no good evidence in the Mio-Plio-Pleistocene fossils for such a mode of locomotion, from the fragmentary bones available. This is why the paper by Thorpe *et al.* (above) taking *Pongo* as the model is stimulating and brings new fuel to the debate.

And the authors are right: there is an accumulation of data which supports a probable arboreal origin for human bipedalism. However, *Pongo* is a highly arboreal animal and the Miocene African fossil hominoid record does not seem to advocate a canopy lifestyle (at least not in the upper layer of the canopy).

Despite the fact that the fossil record is increasing every year, postcranial evidence for several hominoid species remains limited. The fossil record goes back as far as 20 million years with *Ugandapithecus*, an animal the size of a female *Pongo*. It lived in a forested environment as suggested by faunal and floral remains found at Napak (Uganda) (Pickford *et al.* 1999). *Morotopithecus* remains a problem as it has been shown by several authors to be synonymous with *Afropithecus* and the femur has been wrongly reconstructed (Senut 2006). Furthermore its age is still debated, but probably not older than 17.6–18 Ma according to biochronology and new radiometric dates. Two large apes are recognised at Moroto II and

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the lumbar vertebra may not belong to *Afropithecus* (= *Morotopithecus*), but more probably to a younger species of *Ugandapithecus* which was a vertical climber (Gommery *et al.* 2002; Gommery 2006). The first evidence of an erect torso is *Ugandapithecus*. However, was it an ancestral feature or an homoplasy (when two or more taxa converge to share the same trait)? The Lower Miocene *Proconsul* is now considered an arboreal quadruped and must probably be removed from our ancestry. In the Middle Miocene of Africa, few postcranial remains have been found and those do not actually bring a lot to this debate as the record is too scarce. In Europe, however, the skeleton of *Pierolapithecus* suggests an orthograde vertical climbing adaptation but the phalanges seem to be more monkey-like. In the European Upper Miocene, hominoids exhibit arboreal adaptations with long upper limbs compared to short hindlimbs (*Oreopithecus*, *Hispanopithecus*). There may have been an arboreal radiation of hominoids with erect torsos at that time, at least in Europe. In Africa, the record of the earliest human ancestor and the earliest ancestors of African apes is still poor, but the gap is being filled. The known hominoids inhabited arboreal environments, not dry savannah. The first hominid (the word is taken in the restricted sense of the first evidence of human lineage), *Orrorin* at 6 million years ago, is the only taxon for which postcranial elements are reasonably known. It clearly shows a duality of terrestrial and arboreal adaptations (Pickford *et al.* 2002; Senut 2006). Interestingly enough, the same is true for later Australopithecines: *Australopithecus afarensis*, *A. prometheus*, *A. africanus* and *A. sediba*.

In conclusion, the Mio-Pliocene ancestors would hence have been living in trees but probably not in the canopy. The tree was crucial in the environment for providing food and security, and the morphology of our ancestors did not resemble that of modern chimpanzees.

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Adaptive diversity: from the trees to the ground

Sarah Elton*

Bearing in mind that modern humans, with our huge brains, complex cultures and upright walking, seem incredibly different to other living primates, it is surprisingly difficult to identify ‘hominin’ traits at the base of our lineage. Wood (2002) lists only a handful of features that appear to differentiate the earliest hominins from other apes—a relatively small male canine honing only at the tip, proportionately large chewing teeth, slightly larger brains, upright posture and bipedalism. The fundamental importance of bipedalism as a hominin characteristic is one obvious reason why its origins are so hotly debated. However, if reconstructing the evidence in the fossil record is akin to doing a palaeontological jigsaw, for the latest Miocene in Africa, the time period that saw the origins of our lineage, we are missing not only the picture on the box but also most of the pieces. The paucity of fossil remains inevitably makes it hugely challenging to pin down the locomotor behaviour of the hominin ancestor.

Thorpe *et al.* (above) outline their important and compelling case for an arboreal origin of hominin bipedalism. Their theory provides an elegant explanation for the evolution of a suite of characters that make upright standing and walking—whether in the trees or on the ground—possible. The arboreal bipedalism likely to have been present in at least some Miocene apes was an exaptation that facilitated the evolution of terrestrial bipedalism. What remains a conundrum is the sequence of events that led to terrestrial bipedalism. As Paul O’Higgins and I pointed out several years ago (O’Higgins & Elton 2007), we are still some way from having a full picture of the environmental context for the evolution of hominin bipedalism, and none of the ‘prime movers’ or triggers currently proposed for the adoption of terrestrial bipedalism (including feeding, social behaviour and thermoregulation) are entirely satisfactory.

Perhaps it is time that we shift focus away from seeking to explain the evolution of hominin bipedalism within polarised discussions of ‘knuckle walking ancestor *versus* other’ to consider the extent of adaptive diversity in locomotor behaviours, postures and postcrania in the Miocene ape radiation more broadly. In doing so, we may be able to consider how bipedalism fits into an array of behaviours that—we assume—are each adaptive in a particular niche and under certain contexts. Of course, this is easier said than done given the patchy nature of the Late Miocene fossil record in Africa, but such an exercise would certainly be possible if the Eurasian species were considered. We need more fine-scaled and detailed studies on how small variations in postcranial morphology relate to locomotion, and how those in turn link to environment.

We may treat the type of terrestrial bipedalism evident in hominins as ‘special’ because of the suite of easily identifiable adaptations to it. But as Thorpe *et al.* state, these adaptations

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evolved later, after a commitment to terrestriality, and were not present in such a distinct form when the behaviour originated. Indeed, taking a broader mammalian perspective, identifying derived traits relating to locomotion in open-habitat terrestrial animals that have evolved from more generalist ancestral forms is not hard—the modern horse is a case in point (Wood *et al.* 2011). Bipedalism is also viewed as ‘special’ as it is one of the few features we can use to identify members of our lineage. Thorpe and colleagues point out that given the probably ancient roots of bipedalism and the variability in arboreal bipeds, it is getting harder to use locomotion as a means of distinguishing the Hominini. By downplaying the ‘special’ status of bipedalism and instead considering it as one of multiple ways in which to exploit a given environment, we may be able to explore ecomorphological adaptation in more nuanced ways, and hence construct plausible scenarios that move bipedalism from the trees to the ground.

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Putting flesh on to hominin bones

Susannah K.S. Thorpe¹, Juliet M. McClymont² & Robin H. Crompton²

In their comment (above), Winder and colleagues refine their original hypothesis (Winder *et al.* 2013) to focus explicitly on the transition from arboreal to terrestrial orthograde. They indicate that they avoided relating their model to the fossil record because they “did not wish to get bogged down in debates” (Winder *et al.* above) about hominin taxonomy and because of the complexity of reconstructing mosaic evolution. We sympathise with this concern, the validity of which is only strengthened by some of the comments made by our palaeontologist colleagues, which we endeavour to address below. However, hypotheses are only useful when tested against the available evidence.

Wood (above) is uncomfortable with our use of the term ‘unequivocal’ for the evidence that bipedalism has arboreal origins. Although some still hold to the alternative knuckle-walking hypothesis, solid evidence exists for arboreal origins for bipedalism, but none for the knuckle-walking hypothesis, and we see no reason to be equivocal about this rather broad

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conclusion. Contrary to Wood's apparent reading, we did not state that we regarded the evolution of bipedalism to be an 'event'; indeed *quite the opposite* (see Crompton *et al.* 2003; Thorpe *et al.* 2007). We agree with Wood that the palaeontological record is constantly changing, and that this leads to uncertainty. Perhaps White, Lovejoy and Suwa (above) might heed Wood's caveat when insisting that *Ardipithecus* (which we mentioned at least 14 times in an earlier review (Crompton *et al.* 2010)) is central to any discussion of the *origins* of bipedalism. However, if current interpretations of the morphology of orthograde adaptations in mid-Miocene apes are even substantially correct then *Ardipithecus* is informative not so much about the *origins* of bipedalism (our topic in Thorpe *et al.* above), but about subsequent locomotor diversification in the common panin/hominin clade. From *Ardipithecus* down to *Paranthropus boisei*, there is clear evidence that the context and nature of bipedalism had multiple forms, that were probably shaped by numerous and varying selective pressures.

We agree that the current fossil and environmental records are not sufficient to reveal the tempo and mode of these evolutionary radiations of bipedal adaptations. This is especially crucial in view of the fragmentary nature of the fossil record. This leads, for example, to the uncertainty highlighted by Senut (above) concerning the nature, content and status of material assigned to *Morotopithecus* by other authors, and perhaps attaches some uncertainty to her interpretations of the ecomorphology of *Ugandapithecus*. The above concerns are of course very strong arguments for making better use of these data by detailed analysis of the functional significance of the morphological features preserved in the fossil record by painstaking, quantitative, biomechanical analysis of regional form-function relationships which encompass the behavioural variation which may be served by given morphological features.

Our piece (Thorpe *et al.* above) was therefore concerned primarily with highlighting the importance of non-palaeontological techniques in reconstructing human evolution. In this piece, we touched on the differences in the language used to describe locomotion between those interpreting the fossil record and those quantifying the locomotion of living primates. The latter can of course be much more specific than the former because it has the luxury of living subjects to study, but the problem it creates is highlighted by White *et al.*'s (above) description of the locomotion of *Ardipithecus*. They describe the species as a "relatively slow climber and clamberer compared to more acrobatic extant chimpanzees" that employed pronograde and orthograde trunk alignments with "limited forelimb suspension and arboreal bipedality". In the generally accepted classification of living primate locomotion (Hunt *et al.* 1996) orthograde clambering is described as a form of suspensory locomotion because the forelimbs support most body weight in tension (stretched between the body and the weight-bearing support) rather than in compression ('squashed' between the body and support, as in bipedalism). Sixty percent of orangutan 'suspension' is actually orthograde clambering (Thorpe & Crompton 2006) and orthograde clambering can, within a single stride, grade into hind-limb assisted orthograde suspension; hand-assisted bipedalism; or even pronograde bridging, pronograde scrambling (which is compressive) or pronograde suspension, depending on subtle variations in the positioning of suitable weight-bearing supports. This is because muscle activity and the mechanical properties of connective tissue smooth the transitions between locomotor behaviours and allow animals to behave in ways to which their skeletons are not overtly adapted. We were not therefore, as White and colleagues claim,

asserting that orthograde suspensory-inclined apes were widely represented in the Miocene or that bipedalism evolved from a suspensory ape; far from it. Rather, we stress the importance of linking palaeontological interpretation of locomotion to the way locomotion is classified for living species, because the differences between species in repertoires of locomotion are much more subtle than analysis of their skeletons is often interpreted to suggest.

Senut (above) notes the extended period of time during which human ancestors exploited both terrestrial and arboreal habitats, and we concur with her suggestion that *early human ancestors* would have been living in trees but probably not in the canopy. This only underlines Elton's comment (above), with which we fully concur, that "we need more fine-scaled and detailed studies on how small variations in postcranial morphology relate to locomotion, and how those in turn link to environment". We conclude that the fullest reconstruction of human evolution can be achieved only through the combination of palaeontology, environmental reconstruction and the use of living species as referential models for regional function, and, where a close enough parallel exists, for specific ecological context.

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