Spinopelvic pathways to bipedality: why no hominids ever relied on a bent-hip–bent-knee gait

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Until recently, the last common ancestor of African apes and humans was presumed to resemble living chimpanzees and bonobos. This was frequently extended to their locomotor pattern leading to the presumption that knuckle-walking was a likely ancestral pattern, requiring bipedality to have emerged as a modification of their bent-hip–bent-knee gait used during erect walking. Research on the development and anatomy of the vertebral column, coupled with new revelations from the fossil record (in particular, *Ardipithecus ramidus*), now demonstrate that these presumptions have been in error. Reassessment of the potential pathway to early hominid bipedality now reveals an entirely novel sequence of likely morphological events leading to the emergence of upright walking.

Keywords: *Australopithecus*; bipedality; bent-hip–bent-knee; *Ardipithecus*; human evolution

1. INTRODUCTION

For several decades, largely subsequent to the recovery of A.L.288-1 ('Lucy') (Johanson *et al.* 1982), upright walking in early hominids was argued to have relied on a bent-hip–bent-knee (BHBK) gait (see, e.g. Stern & Susman 1983; Susman *et al.* 1984; Stern 2000). This argument rested on observations of locomotion in chimpanzees and gorillas, coupled with the presumption that the post-cranium of our last common ancestor (LCA) of *Pan* and *Homo* was fundamentally similar to those of extant African apes (but see Filler 1981). Despite the fact that early hominids such as A.L.288-1 (and other members of *Australopithecus afarensis* and *Australopithecus anamensis*) exhibit pelves, knees and feet with highly advanced adaptations to a striding, bipedal gait (Latimer & Lovejoy 1989; Lovejoy 2005a,b, 2007), the BHBK hypothesis has remained largely unchallenged save arguments based on energy consumption (e.g. Crompton *et al.* 1998; Carey & Crompton 2005; Sellers *et al.* 2005).

The BHBK gait of *Pan* and *Gorilla*, however, is *not* a function of limitations imposed by hip or knee anatomy, but is instead a direct consequence of an absence of lumbar spine mobility. African apes are unable to lordose their lumbar spines, and therefore must flex both the hip and knee joints in order to position their centre of mass over the point of ground contact (Lovejoy 2005a). Lumbar immobility in *Pan* and *Gorilla* is a consequence of their possession of only three to four lumbar vertebrae and the 'entrapment' of the most caudal lumbar vertebra(e) between cranially extended ilia (Stevens 2004; Stevens & Lovejoy 2004; Lovejoy 2005a; McCollum *et al.* 2009). Although all three African ape species share these features, there is

now considerable evidence indicating that they have not been retained from the common ancestor shared with the human clade. Instead, a more detailed study of the vertebral formulae and the lumbar column of African apes and early hominids indicates that the LCA of *Pan* and *Homo* most probably possessed a long (six to seven segments) mobile lumbar spine similar in number to those of Old World monkeys (OWMs), *Proconsul* and *Nacholapithecus* (McCollum *et al.* 2009). Because such columns would have been capable of near-full lordosis, these new findings in and of themselves contraindicate pronounced African ape-like BHBK bipedality in early hominids. New revelations about LCA structure provided by *Ardipithecus ramidus* (especially ARA-VP-6/500; Lovejoy *et al.* 2009a–d; White *et al.* 2009) further establish that hominids never displayed any of the numerous African ape-like specializations that have reduced lumbar mobility and thus required an unusually restricted BHBK gait. Here we review this new evidence.

2. THE AXIAL PATTERN OF THE LCA

As is discussed more fully in McCollum *et al.* (2009), it is reasonable to assume that the modal vertebral formula of basal hominoids and the LCA of *Pan* and *Homo* to have been 7-13-6/7-4—one that differs from those of OWMs merely by the addition of a fourth sacral vertebra, and replacement of the external tail by a short coccyx. Two lines of evidence support this view.

First is evidence provided by the vertebral formulae of *Australopithecus* and early *Homo* (Sanders 1995). Although complete axial data are unavailable for any single early hominid specimen, a number of partial specimens, including A.L. 288-1 (complete sacrum) and KNM-WT 15000 (interpretable lumbar column), indicate a pre-coccygeal vertebral formula of 7-12/13-6-4 (Pilbeam 2004; McCollum *et al.* 2009).

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Figure 1. Probable pathways of lumbar reduction in African apes and hominids as deduced from extant vertebral formulae for each taxon. All axial formulae that exceed 10% of the total sample for each taxon are shown here, along with presumed modal formulae (those of highest probable frequencies) for the LCA and early hominids. A horizontal arrow indicates loss of a body segment (i.e. a reduction in the number of somites contributing to the pre-coccygeal vertebral column). A vertical arrow signifies changes in the positions of the anterior boundaries of *Hox* gene expression domains underlying the indicated transformations of vertebral identities. Note the differences in extant *Pan* species. For details, see McCollum *et al.* (2009). Axial formula data from Pilbeam (2004) and McCollum *et al.* (2009). (© M.A. McCollum).

The second source of evidence is the axial morphology of bonobos (*Pan paniscus*). Unlike chimpanzees (*Pan troglodytes*) and modern humans, whose modal number of pre-coccygeal vertebrae is 29/30, bonobos possess an axial column typically composed of 30/31 vertebrae, identical to that inferred for the basal hominoid. Although it is certainly possible that the long axial column of bonobos re-evolved from an ancestor with an abbreviated column similar to that of chimpanzees and modern humans, such modification has no obvious selective advantage and runs counter to the trend towards axial length reduction observed in all suspensory anthropoids (Benton 1967; McCollum *et al.* 2009). Rather, the long axial column of bonobos, along with the significantly different combinations of sacral, lumbar and thoracic vertebrae that are characteristic of common chimpanzees (seven cervical, 13 thoracic, three to four lumbar, five to six sacral) and bonobos (seven cervical, 13–14 thoracic, four lumbar, six to seven sacral), suggest instead that the two species of *Pan* evolved their short lumbar spines from an ancestor with a long axial column ($n = 30/31$ pre-coccygeal vertebrae) and a long lumbar spine after division from their own LCA. This receives support from data which suggest that lumbar spine reduction in chimpanzees apparently occurred through sacralization of the

caudal-most lumbar vertebrae plus reduction in the number of somites (figure 1). Bonobos, conversely, appear to have reduced their lumbar column purely through transformations of segment identity, i.e. by transforming lumbar vertebrae into sacral and thoracic vertebrae (McCollum *et al.* 2009).

3. THE LOCOMOTOR SKELETON OF *ARDIPITHECUS RAMIDUS*

The *Ar. ramidus* limb skeleton indicates that much of extant African ape locomotor anatomy has been independently derived for vertical climbing, suspension and a feeding habitus that probably included high canopy access in relatively large-bodied hominoids (Lovejoy *et al.* 2009a). While OWMs also frequently climb vertically, they nevertheless retain adaptations that are primarily for more active, above-branch pronograde running and leaping. Such acrobatics appear to have become much more limited in hominoids, presumably *inter alia*, because of their significantly larger body mass (Cartmill 1985).

The locomotor skeleton of *Ar. ramidus* establishes that the LCA, unlike modern apes, retained many OWM-like features sufficiently primitive to assure a primary gait pattern of above-branch pronograde palmigrady (Lovejoy *et al.* 2009a–c). To be sure,

numerous modifications of OWM-like anatomy had become more like that of extant hominoids in the LCA (Lovejoy *et al.* 2009c)—alterations known to have been initiated in likely exemplars of its remote ancestors, especially various species of *Proconsul* (Ward 1991, 1993; Ward *et al.* 1991, 1993; Nakatsukasa *et al.* 2003). However, the *Ar. ramidus* foot still retained a relatively elongated mid-tarsus, a robust *os peroneum* complex and presumably numerous soft tissue features associable with an inherently stiff plantar structure more typical of the above-branch propulsion seen in OWMs. These latter features can be reliably extended to the LCA by parsimony, since they are still present in the feet of modern humans (quadratus plantae, plantaris, *os peroneum*, elongated cuboid, etc.), but have been largely eclipsed by specializations in the feet and ankles of more highly specialized, extant African apes (Desilva 2009; Lovejoy *et al.* 2009a).

Similar observations of the *Ar. ramidus* forelimb suggest that it also shares a number of primitive features with humans. These include a very primitive and unreinforced central joint complex (CJC) (capitate, trapezoid, metacarpals 2 and 3), a relatively substantial pollex, a short metacarpus, a lack of significant Mc4/Mc5–hamulus contact, a narrow trapezoid, a palmarly displaced capitate head and an unmodified, markedly rugose, deltopectoral crest. Each of these has since been modified in extant large-bodied African apes in favour of ones associable with knuckle-walking, suspension and/or vertical climbing (Lovejoy *et al.* 2009c).

4. THORACOABDOMINAL STRUCTURE AND FORELIMB MOBILITY IN THE LCA

At the same time, it is equally clear that the LCA differed fundamentally from its likely ancestors (including *Proconsul*) in several major ways, none more important than the structure of its vertebral column and its position within the thorax (Lovejoy *et al.* 2009c). In comparison with *Proconsul* and OWMs, in which the pectoral girdle is positioned more anteriorly on the thoracic cage, the hominoid pectoral girdle is located more dorsolaterally, in a manner that causes its glenoid fossa to face more laterally than is typical of more primitive taxa (Waterman 1929; Schultz 1961; Erikson 1963; Ward 2007). Such 'posterolateralization' places the girdle into a more favourable position for circumduction, which in turn permits relatively large-bodied primates to successfully negotiate the canopy via clambering, bridging and suspension. What has gone almost entirely unrecognized until the recovery of *Ar. ramidus*, however, is that repositioning of the scapula (so as to make the glenoid face more laterally and less anteriorly) in hominoids was achieved by thoracic reorganization which relied on invagination of the post-cervical spine ventrally into the thorax. This resulted in dorsal repositioning of the lumbar transverse processes (LTPs), a change in bauplan that apparently occurred independently and repeatedly even in some early Miocene hominoid taxa (e.g. in *Morotopithecus* by 17 Ma; MacLatchy *et al.* 2000;

Filler 2007a,b), and was significantly progressing in a number of forms by the Mid-Miocene (e.g. in *Pierolapithecus* by at least 10 Ma; Moya-Sola *et al.* 2004; Almecija *et al.* 2009). This shift appears to have accompanied other forelimb modifications, especially ulnar withdrawal and olecranon abbreviation. These modifications increased potential wrist adduction, enhanced stability during complete elbow extension and greatly increased the forelimb's range of motion at the shoulder girdle (Rose 1988; Lewis 1989). However, as this change in bauplan also resulted in the sacrifice of substantial erector spinae mass (Benton 1967; Lovejoy 2005a), increasing the range of motion of the shoulder came at the expense of dynamic stabilization of the lower back. Consequently, African ape suspension and vertical climbing required compensatory lumbar column reduction—virtually to the point of inherent (i.e. osteological) rather than dynamic (i.e. muscular) rigidity. Thus, LTP position, rather than being the primary target of selection during lumbar column shortening, as has long been argued (e.g. Benton 1967), was instead a product of the fundamental change in the hominoid bauplan that centred about a general restructuring of the thorax.

5. LOCOMOTION IN THE LCA

Features assignable to the LCA, therefore, now point to a pattern of cautious climbing that combined above-branch palmigrady with occasional below-branch suspension, enhanced by a highly mobile, lateralized shoulder girdle in combination with marked wrist adduction (Cartmill & Milton 1977; Lewis 1989) and elbow extension (Rose 1988). Below-branch suspension, however, must not have been so frequently employed (and/or so vigorously performed) as to require emergence of the considerably more advanced metacarpal, carpal, elbow and shoulder modifications seen only extant African apes. This suggests that much of the LCA's activities may have been largely low-canopy, and might have been combined, possibly extensively, with terrestrial travel between food patches (White *et al.* 2009). The latter supposition receives support from the fact that the adaptations to terrestrial travel present in extant African apes (knuckle-walking) and fossil hominids (bipedality) are extensive, fundamentally divergent, and therefore likely to be of substantial antiquity. It is also likely that reliance on terrestrial travel between food patches was driven by increasing competition with radiating OWMs in the Mid-Miocene (Andrews 1981). That the post-crania of *Pongo* and the lesser apes (*Hylobates*, *Symphalangus*) differ substantially from those of the African apes is probably largely due to the absence of a significant terrestrial component in their respective adaptive strategies, and their entirely independent evolution from much more primitive ancestors.

If the above hypothesis is correct, what was the LCA's terrestrial locomotor habitus *prior* to the emergence of either knuckle-walking in apes or bipedality in hominids? One possible pattern 'of choice' might have been a simple extension of its primary arboreal pattern

to ground travel, i.e. palmigrade quadrupedality. In fact, some of the more unusual characters present in *Ar. ramidus* are strongly suggestive that hominids once exhibited such an ancestral gait pattern. These include its primitive intermembral index, relatively short metacarpus, allowance of substantial metacarpal–phalangeal dorsiflexion and especially the strongly palmar positioning of the head of its capitate (Lovejoy *et al.* 2009b). Indeed, the latter can be viewed as being particularly advantageous to palmigrade terrestrial quadrupedality, and this would now seem to be a possible explanation for this unusual peculiarity in *Ar. ramidus*, i.e. it inherited it from a habitually terrestrial palmigrade LCA.

Unlike OWMs, quadrupedal terrestrial gait in large-bodied hominoids (including the LCA) may have required a much more compliant wrist, i.e. palmigrady that included more extreme dorsiflexion. Absence of such extreme adaptations in OWMs is likely explicable by their retention of primary above-branch adaptations at the radiocarpal, elbow and shoulder joints. Palmar disposition of the capitate head as seen in *Ar. ramidus* (Lovejoy *et al.* 2009b) may even now serve, given further fossil evidence, as an indicator of palmigrade/plantigrade terrestrial quadrupedality in yet undiscovered, large-bodied, Miocene forms. In combination with the retention of a long mid-tarsus, a robust *os peroneal* complex and other primitive aspects of its foot (retained *M. quadratus plantae*, retained *M. plantaris* and associated dense palmar fascial aponeurosis (see earlier)), palmigrade/plantigrade quadrupedality seems to have been, at the least, a likely terrestrial locomotor habitus in the African ape/hominid LCA (Lovejoy *et al.* 2009c).

6. LOCOMOTOR SPECIALIZATIONS IN EXTANT HOMINIDS

If so, from whence came the relatively highly specialized gait patterns of the LCA's descendants: bipedality in hominids and knuckle-walking in the African apes? The latter is reasonably explicable in these taxa as a relatively facile means of modifying palmigrade/plantigrade terrestrial travel into a form that could be successfully combined with their highly specialized modifications of the pelvis, thorax and limb skeletons for suspension and vertical climbing. Such changes included (independently in each taxon) elongation of the forelimb, abbreviation of the hindlimb, elongation of the metacarpus, stabilization of several major carpal joints either by ligamentous reinforcement or joint enlargement or both (especially in the CJC), major revisions of overall scapular morphology (predominantly in *Pan* as opposed to *Gorilla*), cranial retroflexion of the ulnar trochlear notch, modification of the deltopectoral entheses and especially, virtual fusion of the thorax and pelvis via abbreviation and iliac fixation of the lumbar column (see earlier) (Lovejoy *et al.* 2009c,d). All of the modifications to the forelimb would have reduced its inherent stability and increasingly restricted its energy-dissipating capacity during prolonged terrestrial travel. These difficulties appear to have been

resolved by adoption of knuckle-walking, which permits reliance on substrate-forced dorsiflexion of the wrist that can be eccentrically resisted by powerful wrist flexors as well as both the connective tissue envelopes and contractile components of the long digital flexors. The uniqueness of these long flexors is evidenced by development of a distinctive flexor tubercle on the proximal ulna in both *Pan* and *Gorilla* (Lovejoy *et al.* 2009b).

The most salient question remaining, of course, is the issue of the eventual adoption of bipedality in hominids. Why did hominids exchange palmigrade/plantigrade quadrupedality for upright walking? While there have been many theories advanced for this locomotor shift, most have been made untenable by evidence now provided by *Ar. ramidus* (White *et al.* 2009). The recent suggestion that bipedality is a sequel to an arboreal upright stance stabilized by overhead forelimb grasping (Thorpe *et al.* 2007a,b, 2009) is untenable because the practice has emerged in *Pongo* as a consequence of that taxon's extreme adaptations to suspension, none of which were ever present in hominids or their ancestors (Lovejoy *et al.* 2009c). The most likely explanation for the adoption of terrestrial bipedality, in our view, continues to involve novel adaptations in hominid social structure that required upright locomotion for carrying. These have been discussed extensively elsewhere (Lovejoy 1981, 1993, 2009).

7. SOME ADDITIONAL ANATOMICAL CORRELATES OF BIPEDALITY IN HOMINIDS AND ADVANCED ARBOREALITY IN EXTANT APES

As noted above, still equipped with a mobile lumbar spine, the LCA was probably capable of at least facultative lordosis, sufficient to place its hip and knee either directly below its centre of mass or sufficiently close to that centre so as not to generate excessive ground-reactive torques so large as to require debilitating muscle recruitment during terrestrial travel. While the earliest hominid gait pattern probably required some degree of hip and knee flexion, research on bipedality in OWMs now suggests that it would not have been nearly as excessive as it is in extant apes, so long as the lumbar column remained long and mobile (as it is in OWMs). Studies of OWMs have now greatly illuminated our understanding of its origins in hominids (Nakatsukasa *et al.* 1995, 2004, 2006; Hirasaki *et al.* 2004). Macaques trained to walk bipedally expend less energy than do those in which the behaviour is novel, so much so that the animal's long flexible spine is permissive for convergence with 'human-style' walking in the former. While those using bipedality 'in the wild' exhibit upright gaits that differ kinesiotically from human walking, those exposed to long-term training for bipedality walk 'with longer, less-frequent strides, more extended hindlimb joints, double-phase joint motion at the knee joint, and most importantly, efficient energy transformation by using inverted pendulum mechanics' (Hirasaki *et al.* 2004: 748).

While lordosis was certainly facilitated by the presence of six to seven lumbar vertebrae in the LCA

Figure 2. Components of sacral breadth in African apes and early hominids. Scatter plot of log total sacral breadth versus log alar breadth. The findings of a strong correlation ($r = 0.901$) between sacral breadth and alar breadth, and an absence of any significant correlation between alar breadth and centrum area (figure 3) indicate that total sacral breadth in African apes and early hominids is largely a consequence of alar breadth. Note especially the exceedingly broad alae in the early hominid specimens. This is consistent with their having mediolaterally expanded the sacrum as an adaptation to free the most caudal lumbar from contact with the iliac crest, and fully accounts for the unusual platypelloidy in A.L.288-1 and Sts-14. Later, a caudally directed gradient of increasing centrum size and interfacet distance (see text) appears in *Homo*, and probably accounts for the unusually large human centrum. Note the much narrower alae in the two African apes compared with those of all hominids.

(most probably six; figure 1), even in most OWMs lordosis is not as complete as it is in five-lumbar humans (Nakatsukasa *et al.* 1995; Hirasaki *et al.* 2004). One probable and very important reason is that complementary motion in the most caudal lumbar vertebra in OWMs is usually restricted by its proximity to the posterosuperior portion of each iliac blade. Such iliac–lumbar propinquity is usually sufficient to probably assure at least some degree of ligamentous restriction of potential motion.

Two characters that are uniquely associated with hominid pelvic adaptations to bipedality are therefore of particular interest: (i) an exceptionally short superoinferior iliac height (coupled with both anterior extension of the anterior inferior iliac spine (AIIS) and development of the greater sciatic notch) and (ii) an extremely wide sacrum generated largely by exceptionally broad sacral alae (figures 2 and 3). Both of these characters eliminate contact between the postermost iliac crest and the most caudal lumbar vertebra, and are therefore likely to have appeared early in hominids as a means of increasing the lordotic capacity of the lumbar spine during terrestrial bipedality. Indeed, these changes are likely to have been the earliest in the evolution of bipedality in hominids,

Figure 3. Components of sacral breadth in African apes and early hominids. Scatter plot of log centrum area (length $\times$ breadth) versus log alar breadth. For discussion, see legend of figure 2.

and largely exaptive for increased abductor capacity during the single-support phase of upright walking (Lovejoy *et al.* 2009c).

Moreover, three features of ape sacra appear to have directly opposite polarity compared with those of hominids (figures 2–4): (i) their strongly *abbreviated* sacral alae, (ii) their reduced lumbar number, and (iii) their greater number of fused sacral elements, the latter almost certainly achieved by progressive sacralization of the most caudal lumbar element(s) (McCollum *et al.* 2009). Alar reduction reduces the space between the two ilia so as to promote contact with the most caudal lumbar vertebra(e). In combination with the additional extension of the ilia superiorly (especially by elongation of the iliac isthmus at least in *Pan*; Lovejoy *et al.* 2009c), the African apes achieved stabilization of the entire lower spine by its fixation to the thorax—creating a rigid pelvithoracic ‘block’ in which the pelvis and thorax are separated by a distance of only a single intercostal space (Schultz 1961). Both mechanisms compensate for the loss of erector spinae mass (see earlier). Thus, both sacral structure and superoinferior iliac length directly reflect hominoid post-cranial natural history. Panids and gorillids independently elongated their ilia, narrowed their bi-iliac spaces and reduced the number of lumbar vertebrae (often by sequestration as additional sacral segments), all mechanisms that stiffened the lower back and eliminated any possibility of lordosis. Hominids, *per contra*, remained almost entirely plesiomorphic, retaining both the primitive number of lumbar (mode = six) and sacral vertebrae (mode = four), and in addition, expanded the sacral alae so as to assure the full independence of the most caudal lumbar, assuring its freedom to participate in lordosis as well.

Figure 4. Hominid and pongid mechanisms of emancipation or fixation of the most caudal lumbar(s). A human pelvis (left) compared with that of a chimpanzee (right). Note the following numbered characters in each. The iliac isthmus (1) and the ilium itself (3) have both been greatly shortened in the human, so much so that a greater sciatic notch has been created (entirely absent in the chimpanzee), and there is no potential contact between the iliac crest and the most caudal lumbar. In the chimpanzee, the opposite change has occurred, i.e. the iliac isthmus (1) and the iliac blade (3) have both been superoinferiorly elongated, encouraging such contact. In addition, the sacral alae have been greatly broadened in the human and narrowed in the chimpanzee (cf. figure 2). As a consequence, there is now a very substantial horizontal distance between the iliac crest and the most caudal vertebra in the human (2), but a greatly narrowed bi-iliac gulf in the chimpanzee. In combination with (1) and (3), such narrowing in the chimpanzee (via reduced alar breadth; cf. figure 2) results in full restrictive contact between the iliac crest and the most caudal lumbar vertebra(e). In the earliest phases of this morphological shift in hominids, the pelvis became decidedly platypeloid, and the enhanced iliac breadth encouraged a more effective use of the anterior gluteal muscles as abductors during upright gait (Lovejoy 2005a; Lovejoy *et al.* 2009d). The latter was thus an exaptation, rather than the primary adaptation.

8. THE QUESTION OF *OREOPITHECUS*

Delineation of the vertebral evolutionary pattern of African apes and hominids throws considerable new light on the troublesome issue of both the locomotor pattern and phylogeny of perhaps the most enigmatic hominoid of the later Miocene, *Oreopithecus*. Arguments as to its potential phylogenetic relationships and locomotor patterns have been many (reviewed in Harrison 1986, 1991; Kohler & Moya-Sola 1997; Rook *et al.* 1999). However, all have been hampered by its extremely poor condition, largely the consequence of its extreme compression during fossilization. This has frequently led to excessively liberal interpretations of its badly compromised structure.

A case in point is the attribution of a lordotic spine to this taxon based on a sagittal section of specimen BA72, a crushed and compressed amalgam of three lumbar vertebrae (Kohler & Moya-Sola 1997). It seems inconceivable to us that such sectioning can reliably indicate the presence/absence of wedging in centra after they have been compressed to less than one half of their dorsoventral diameter. A far more conservative approach is to rely on more

straightforward morphological characters of greater inherent reliability, and which are more resistant to misinterpretation from crushing defects. Not all of these appear to have been considered.

One of the most important is the vertebral formula of *Oreopithecus*. There is general agreement, based on the '1958 specimen' (IGF 11 778), that *Oreopithecus* had five lumbar vertebrae (Harrison 1986, 1991; Kohler & Moya-Sola 1997; Rook *et al.* 1999). A largely overlooked vital statistic, however, is that it also had six sacral vertebrae (Straus 1963; method of Schultz 1961; for details, see McCollum *et al.* 2009). This can be safely concluded from specimen BA-50, which preserves five sacral foramina on the left side, and at least four on the right. Moreover, the masses of the right and left halves of the sixth sacral vertebra appear to be fully symmetrical (therefore the right side presumably had five full foramina as well). We have demonstrated elsewhere that the basal hominoid column almost certainly exhibited 13 thoracics (among living taxa, only *Homo* and *Pongo* have any significant incidences of fewer). Thus, the *minimum* pre-coccygeal vertebral number in *Oreopithecus* was 31, which, as noted above, is the likely pre-coccygeal vertebral number for basal hominoids and was probably modal for Early and Mid-Miocene apes as well. Except for *P. paniscus*, a modal vertebral number as high as 31 is extremely rare in extant species, occurring in only 2.8 per cent of *P. troglodytes* and 0.06 per cent of *Homo* (McCollum *et al.* 2009).

Much has been made of the putative 'short, broad, ilium' of *Oreopithecus* and of its relatively broad retroauricular segment (Hürzeler 1958). However, a substantial reduction in the size of the post-auricular region of the pelvis appears to have accompanied the spinal invagination underlying scapular relocation in all hominoids (see earlier). That reduction was in turn accompanied by a broadening of the pre-auricular portion of the pelvis and is therefore expected in any clade in which shoulder reorganization occurred (Lovejoy *et al.* 2009c). This same developmental process is likely to have re-occurred a number of times in hominoid evolution, and is almost certainly universally responsible for the dorsal migration of the LTPs. Broadening of the ilium well beyond comparable dimensions in *Proconsul* is therefore fully expected in virtually any large-bodied Miocene hominoid that exhibits posterolateralization of the shoulder.

The fifth lumbar vertebra of the '1958 specimen' lies (*in situ*) directly within its bi-iliac space, sharing the same functional position as the trapped (immobilized) L7 of a typical *Presbytis* and the L3 or L4 of *Pan* (see Straus 1963; figure 5). Therefore, *Oreopithecus* exhibits a *maximum* of only four potentially mobile lumbar vertebrae. This is fully consistent with its 'classic' adaptive regimen for suspension as also seen in *Gorilla*, *Pan* and *Pongo*, and with directly opposite polarity compared with their homologues in bipedal hominids in a host of major adaptive characters (table 1). These included transformation of lumbar via their sacralization, direct reduction in lumbar number from the primitive condition and entrapment (immobilization) of at least one lumbar

Figure 5. (a) Sacra of a chimpanzee, (b) A.L. 288-1 and (c) a modern human. Note the extremely narrow sacrum of the chimpanzee compared with the two hominids. Note also the much broader alae in A.L. 288-1 compared with its centrum. Compare this with the similar dimensions in the human specimen (figure 2).

Figure 6. Comparison of interfacet distances in the third lumbar and sacra of African apes and hominids. The drawing on the left demonstrates the comparison being made. In this drawing, the third lumbar has been rotated 180° from its normal anatomical position (its superior zygapophyses now point inferiorly) for comparison with those of the sacrum. Double-headed arrows indicate the interfacet distance in each specimen. (a) chimpanzee; (b) gorilla; (c) A.L. 288-1 and (d) human. Note that in (a) and (b) the interfacet distance is greater in the lumbar vertebra than it is in the sacrum, whereas the opposite is true of the two hominids. The increasing gradient of centrum size and interfacet distance in *Homo* may be an adaptation that facilitated increased lordosis and thereby enabled lumbar column reduction. The opposite gradient in chimpanzees is the likely source of reduction of the bi-iliac space. For discussion, see text. Redrawn from Lovejoy (2005a).

by contact with a posterodorsally extended iliac crest. Given its primitive vertebral number, and a series of others, such as its retention of an anterior keel on its lumbar vertebrae (Straus 1963), *Oreopithecus* appears to have acquired extensive adaptations to suspension entirely independently of other Miocene clades (as did *Nacholapithecus*; Nakatsukasa *et al.* 2007). It is thereby unrelated to hominids, its similarities (which are few; table 1) being largely minor convergences. Any bipedality would have been largely driven by the same context that does so in hylobatids—excessively long forelimbs combined with highly abbreviated hindlimbs (table 1).

One additional supposedly hominid character in *Oreopithecus* is worthy of brief note. The degree of protuberance of its AIIS is *not* unusual for a non-hominid. What distinguishes the AIIS in hominids from those in apes is *not* its protuberance (those of *Gorilla* are often very prominent), but rather its emergence from a novel, separate physis, a hominid adaptation that is almost certainly associated with dramatic expansion of iliac isthmus breadth (Lovejoy *et al.* 2009b). There is no evidence of a similar degree of broadening in *Oreopithecus* (note its relative pelvic breadth in table 1) and certainly none suggesting its origin by means of a separate physis.

Table 1. Principal characters of *Oreopithecus* compared with those of other hominoids.

taxon	no. of sacral vertebra ^a	no. of lumbar vertebra	no. of functional lumbar	forelimb length/body mass ^{(0.35)b}	intermembral index ^b	iliac width/length index (relative iliac breadth) ^c	radius/tibia index ^b	humerus/femur index ^b	medial cuboid length ^b	third Mc length/body mass ^{(0.35)b,d}
<i>Oreopithecus</i>	6 ^e	5 ^e	≤4 ^e	170 ^e	119	80	120	117	very short ^f	20.5
<i>P. troglodytes</i>	5–6	3–4	2–3	160	106	66	111	101	short	24.7
<i>P. paniscus</i>	6–7	4	2–3	159 ^g	101 ^g		107 ^g	108 ^g	short	
<i>Gorilla</i>	5–6	3–4	2–3	152	114	92	113	116	short	18.9
LCA ^h	[4]	[6]	[6]	[131–143]	[87–91]	?	[88–95]	[77–87]	[long]	?
<i>Ar. ramidus</i>	[4]	[6]	[6]	143	89–91	113	95	87	long	?
<i>Au. afarensis</i>	4	6	6	145	84	137	93	84	?	?
<i>H. sapiens</i>	5	5–6	5	135	65–79	125	65	71	very long	15.8
<i>Pongo</i>	5–6	3–4	2–3	192	138	74	147	130	very short	27.6
<i>Hyllobates</i>	4–5	5	4	278	130	49	145	116	short	34.1
<i>Proconsul</i>	[4]	6–7	6	(131–134)	87	50	88	77	[long]	?

^aMethod of Schultz (1961).^bData from sample described in Lovejoy *et al.* (2009c) or additional sources therein unless otherwise noted.^cData from Straus (1963), except for *Proconsul*, *Ar. ramidus* and *Au. afarensis*, which were obtained from casts.^dData for *Oreopithecus* from Susman (2004).^e*Oreopithecus* data from Straus (1963) and examination of BA-50; other data from Pilbeam (2004) and McCollum *et al.* (2009).^fSee Kohler & Moya-Sola (1997).^gData from Morbeck & Zihlman (1989).^hData in brackets hypothesized for LCA of African apes and humans and/or *Proconsul* based on *Ar. ramidus* and living hominoids.

9. A NOTE ON POTENTIAL MECHANISMS IN LUMBAR COLUMN MODIFICATION

In considering the anatomy of the lumbosacral spine, it is of some interest that whereas in humans both the overall size of the centrum and the distances separating the articular facets (zygapophyses) increase in each successively more caudal lumbar vertebrae, centrum size and interfacet distances in extant African apes instead *decrease* caudally (Latimer & Ward 1993; figure 6). Lumbar centrum dimensions do not appear to differ substantially in the only column that permits their observation in *Australopithecus* (Sts-14; Robinson 1972). There is, however, an increase in the interfacet distance between the putative L3 and sacrum of A.L. 288-1 (Lovejoy 2005a). The latter findings suggest that the progressive caudal expansion of both the interfacet distances and centrum dimensions evident in *Homo*, but only partially adumbrated in *Australopithecus* (i.e. no increase in lumbar centrum dimensions, a retention of six lumbar vertebrae, but a partial increase in interfacet distance), may be an adaptation that permits a more intense lordosis in humans, ultimately enhancing lumbar column stability by allowing a reduction in total lumbar number. If so, emergence of this gradient must have postdated *Homo erectus* at 1.6 ma, since the lumbar column in KNM-WT-15000 still numbers six with four sacral vertebrae (Latimer & Ward 1993; Pilbeam 2004; McCollum *et al.* 2009).

10. SUMMARY AND CONCLUSIONS

New evidence from the fossil record and from observations of extant hominoid skeletal anatomy leads to several conclusions. Among the most important is that hominids never acquired the numerous specializations seen in extant apes for vertical climbing, suspension or knuckle-walking. This demonstrable divergence between the natural histories of hominids and those of all living apes renders most observations of locomotor behaviour in the latter, whether conducted in the laboratory or observed in the wild, no longer directly relevant to the reconstruction of the earliest locomotion of hominids. Bipedality in hominids can instead now be seen to have emerged from a predominantly primitive locomotor skeleton with a long lumbar spine capable of at least partial lordosis, and one never restrictively modified for suspension, vertical climbing or knuckle-walking.

Suspension (e.g. *Pongo*, *Hylobates*) and vertical climbing (e.g. extant African apes) have repeatedly induced a rigid lower spine, especially as body mass increased. This has been accomplished in a variety of taxa in several ways, but always by a combination of reduction in lumbar number (by reduction in somite vertebral number and/or transformation of lumbar identity) via modification of *hox* regulation and further entrapment of a portion of the remaining lumbar vertebrae by narrowing of the bi-iliac space. The latter has been accomplished either by sacral narrowing or dorsal extension of the iliac crest (e.g. *Pan* and *Gorilla*), or both. The failure of hylobatids (but not symphalangids (i.e. modal lumbar number = 4) to achieve the extreme lumbar column reductions seen

in African apes is probably a product of their modest body size and the unique nature of suspension in these lesser apes.

The earliest hominids were able to functionally achieve bipedality because they had never rigidified their lumbar spines. Instead, they evolved an opposite morphology—a *reduction* in iliac height and a *broadening* of the sacrum, both of which assured sufficient lordosis to reduce and eventually eliminate what were probably only moderate vertical moments about the knee and hip. Were hominids to have first engaged in African ape-like behaviours, the ‘Rubicon’ to bipedality may have become too great to cross. Our decades-long assumption that the abducent capacity of the early hominid pelvis was its *primary* selective agent (e.g. Lovejoy *et al.* 1973) was, in retrospect, entirely misdirected. The favourable position of the anterior gluteal muscles in hominids that allows them to control pelvic tilt during single support can now be seen to have been largely a refinement that *followed* the initial primary adoption of a lordotic spine with an emancipated caudal-most lumbar vertebra. The generalized structure of earliest hominids that permitted this sequence of events is almost certainly extendable to the LCA. At least initially in pre-divergence hominids, it now suggests a combination of cautious, palmigrade, plantigrade climbing with a long flexible back during arboreal travel, and possibly, palmigrade quadrupedality during terrestrial travel as well.

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