Kevin D. Hunt

Department of Anthropology, Indiana University, Bloomington, IN 47405, U.S.A.

The evolution of human bipedality: ecology and functional morphology

Contexts that elicit bipedalism in extant apes may provide evidence of the selective pressures that led to hominid bipedalism. Bipedalism was observed most commonly among chimpanzees when they fed on the small fruits of diminutive, open-forest trees. Chimpanzees fed bipedally from such trees either by reaching up to pick fruit while standing on the ground, or from within the tree, in which case bipedalism was frequently stabilized by grasping an overhead branch. The food-gathering function of chimpanzee bipedalism suggests that hominid bipedalism may have evolved in conjunction with arm-hanging as a specialized feeding adaptation that allowed for efficient harvesting of fruits among open-forest or woodland trees. Such evidence is particularly valuable when it is in accord with fossil anatomy. *Australopithecus afarensis* has features of the hand, shoulder and torso that have been related to arm-hanging in chimpanzees. The australopithecine hip and hind limb clearly indicate bipedalism, but also indicate a less than optimal adaptation to bipedal locomotion compared to modern humans. Locomotor inefficiency supports the hypothesis that bipedalism evolved more as a terrestrial feeding posture than as a walking adaptation. A bipedal postural feeding adaptation may have been a preadaptation for the fully realized locomotor bipedalism apparent in *Homo erectus*.

Introduction

Reconstructions of the positional repertoire of the earliest known hominids have ranged from vertical climbing with only facultative bipedal components (Prost, 1980), to terrestrial bipedalism with a substantial arboreal climbing component (and possibly suspension) (Tuttle, 1981; Stern & Susman, 1983), to fully realized, exclusively terrestrial locomotor bipedalism (Johanson & Edey, 1981; Lovejoy, 1981, 1988). The facultative bipedalism perspective has perhaps the fewest adherents. A majority of students of australopithecine anatomy interpret the anatomy of the earliest known fossil hominids as indicating that they were compromised terrestrial bipeds with substantial adaptations to arboreality (Coppens & Senut, 1991; Jouffroy, 1991; Jungers, 1982, 1991; McHenry, 1991; Schmid, 1983, 1991; Senut, 1980; Tardieu, 1983; Tuttle, 1981; Tuttle *et al.*, 1991; Stern & Susman, 1983, 1991). Still, a significant minority present a forceful argument that the principal mode of locomotion for these early hominids was striding terrestrial bipedalism little different from that of modern humans (Johanson & Edey, 1981; Lovejoy, 1981, 1988; Latimer & Lovejoy, 1989, 1990; Latimer, 1991).

The hypothesized selective pressure(s) that led to the evolution of bipedalism are, if anything, more diverse than locomotor interpretations (reviewed in Rose, 1991). Among the most commonly proposed functions of bipedalism are increased viewing distance (Dart, 1959; Day, 1977, 1986), food/tool carriage (Bartholomew & Birdsell, 1953; Etkin, 1954; Hewes, 1961; Washburn, 1967; Isaac, 1978; Lovejoy, 1981), tool use (Washburn, 1960; Ardrey, 1961), more efficient long distance travel in the context of foraging, scavenging or hunting (Shipman, 1986; Sinclair *et al.*, 1986; Carrier, 1984; Rodman & McHenry, 1980), display (Livingstone, 1962; Jablonski & Chaplin, 1993) and thermal radiation avoidance (Wheeler, 1984, 1985, 1991*a,b*, 1992*a,b*, 1993). Tuttle suggested that a significant but low-frequency bipedalism evolved in a gibbon-like suspensory hominoid as an important

large-branch locomotor mode and as an arboreal feeding posture (Tuttle, 1975). The suspensory forelimbs of these proto-hominids were hypothetically poorly suited for quadrupedalism when a more terrestrial gathering strategy emerged, leading first to high-frequency and then exclusive bipedalism (Tuttle, 1975; Stern, 1976). Others have suggested that bipedalism was an adaptation for terrestrial postural gathering of food from grasses, trees or bushes (DuBrul, 1962; Jolly, 1970; Rose, 1976, 1984, 1991; Wrangham, 1980; see also Leuttenegger, 1987). The seed eating hypothesis (Jolly, 1970) focused on the demands of collecting small, evenly distributed resources close to ground level, and its dynamics were little changed by a substitution of small fruits for grass seed (Jolly & Plog, 1987). This latter hypothesis has a locomotor corollary in the observation that bipedal locomotion saves energy by eliminating the action of raising the upper body to feed bipedally after walking between resources in a typical primate quadrupedal fashion (Jolly, 1970; Wrangham, 1980; Jolly & Plog, 1987). These latter hypotheses are straightforwardly synthesized into a Jolly/Rose/Wrangham hypothesis that postulates that bipedalism evolved as a terrestrial feeding posture advantageous for reaching into trees, and that bipedal locomotion evolved to reduce energy costs when traveling between densely packed feeding sites.

Feeding hypotheses are arguably the most supportable (Leuttenegger, 1987) since feeding occupies a greater proportion of the time-budget of a typical primate than any other behavior, often occupying half of the waking day. Even so, the unique combination of arboreal and terrestrial traits in *A. afarensis* is not wholly compatible with any one of the feeding hypotheses presented heretofore. Arboreal hypotheses cannot completely account for the extent to which bipedalism has been perfected, since refinements such as the shock-absorbing nature of the foot would seem to be unnecessary for low-stress branch-walking. Terrestrial hypotheses cannot convincingly explain why arboreal traits persist for over a million years after the adoption of terrestrial bipedalism. Here data on chimpanzee feeding ecology is considered in conjunction with australopithecine skeletal anatomy to suggest an ecologically-based reconstruction of early hominid locomotion and posture that reconciles ape-like upper body features with lower body anatomy indicating habitual but less than optimal bipedal locomotion.

Methods

Twenty-six well habituated healthy young-adult to middle-aged chimpanzees were studied at two sites in Tanzania, resulting in 571 hours of observation at the Mahale Mountains and 130 hours at Gombe. Focal animals were followed for an entire day or for as long as possible. Instantaneous (or time-point) sampling was used; at the two minute mark the target was instantaneously sighted and values were recorded for 25 positional behavior variables. One of 35 possible positional modes was noted (see Hunt, 1989*b*, 1992*a* for more detail). Bipedalism was defined as locomotor or postural modes in which the body weight was supported principally by the hind limbs. During many bouts a forelimb contacted a branch, adding to stability by bearing part of the body weight. For semi-suspensory positional bouts where body weight was supported by hind limbs and a forelimb, the orientation of the forelimb, appearance of the digits and wrist and the depression and orientation of the weight bearing structure (WBS) were used to judge the relative proportion of weight borne by fore- *vs.* hind limbs. Minute movements during food gathering made estimating this datum easier. If the hind limbs were bearing more than half the weight, the posture was judged to be bipedalism. If they were bearing less than half it was labeled arm-hanging; these latter positional bouts

Table 1. Contexts of bipedal behavior[1]

| | Arboreal | | Terrestrial | | | |
| | | | | | | |
Context	Unassisted	Assisted	Unassisted	Assisted	Total	%
Feed	11	21	14	11	57	58·8
Feed	?	?	?	?	2	2·1
Move in food patch	1	3	0	0	4	4·1
Eat insects	1	13	1	0	15	15·5
Total feed	13	37	15	11	78	80·4
Beg	0	1	2	1	4	4·1
Play	0	0	2 (1[2])	1	4	4·1
Scan	0	0	2	0	2	2·1
Respond to threat	0	2	0	0	2	2·1
Make bed	1[2]	1	0	0	2	2·1
Respond to calls	0	1	0	0	1	1·0
Dominance display	0	0	1	0	1	1·0
Hold infant	0	0	0	1	1	1·0
Copulate	1	0	0	0	1	1·0
Unknown	0	1	0	0	1	1·0
TOTALS	15	43	23	14	97	100·0

The column header "n" spans the Arboreal and Terrestrial columns.

[1] In unassisted bipedalism the body was not supported by the forelimbs. Assisted bipedalism was that in which half or more of the weight was borne on the hind limbs, but a substantial proportion was borne by a fully abducted forelimb in a semi-suspensory mode.

[2] Bipedal walking.

are not considered in this analysis (see Hunt, 1992a). Casts of *A. afarensis* fossils were examined at the Peabody Museum, Harvard University.

Results

Contexts of bipedalism

Ninety-seven instances of bipedalism among 21 individuals were sampled in 700 hours of observation, no two consecutively. *Ad libitum* observations (i.e., observations on non-target individuals) were used as supplemental evidence. These data show that among chimpanzees, as was the case among baboons (Rose, 1976, 1984, 1991; Hunt, 1989b), bipedalism is a feeding adaptation. Eighty percent of chimpanzee bipedalism was during feeding (86% of all bipedal activity arboreally and 70% terrestrially; see Table 1), and an overwhelming percentage of these bouts were postural (95%, Table 1). During arboreal feeding, arm-hanging and bipedalism were linked. A forelimb oriented in an arm-hanging position stabilized bipedal posture in 93% of observations among terminal branches ($n = 27$, Table 2) and 52% ($n = 23$) of observations in the central portion of a tree. Semi-suspension was less common during terrestrial bipedalism, where only 42·3% of observations ($n = 26$) involved a forelimb. During terrestrial gathering both hands were often used to harvest fruits. Not infrequently one hand was used to pull down and hold an otherwise inaccessible fruit-bearing limb, so that the posture became a terrestrial arm-hanging-bipedalism. A small proportion of terrestrial bouts was locomotor bipedalism when moving between feeding sites in the same tree (4.1%). That is, short-distance within-site shuffling rather than long distance travel was the

Table 2 Food resources utilized during bipedal behavior

Genus	Arboreal Unassisted t.br.[1]	Arboreal Unassisted cent.	Arboreal Assisted[2] t.br.	Arboreal Assisted[2] cent	Terrestrial Unassisted	Terrestrial Assisted	Total n	Tree[3] height	Habitat[4]	Food item diameter
Invert.		1	5	8	1		15	large: 12; small: 1	forest	small
Garcinia		3 (1)[3]	7			1	11	4–8 m[6]	open; open: 2	1–2 cm[6]
Unidentified fruits			3 (1)	1	2	2	8	small	no rec.: 6	no rec.
Leaf	1	2	1		1	1	6	large: 1; small: 5	varied	
Soil, inorg.					5		5	—	forest	
Harungana		1	1		2		4	4–7 m[6]	open	4 mm[6]
Monanthotaxis			1		3		4	shrub	open	7–12 mm[6]
Ficus		1	1		1		3	large: 2; 2 m: 1	varied	large: 1 cm; 1
Grewia		2					2	5 m[6]	open	1 cm[6]
Unidentified fruit		1				1	2	large	forest	1 cm[6]
Not recorded		?			?	2	2	—	forest	—
Shoots/new leaf		?	1				2	small	—	—
Piths						2	2	small	forest	small
Monkey				1		1	2	small: 1; large: 1	open	
Psychotria			(1)	1			2	large: 1	open	5 mm[6]
Landolphia				1	1	1	1	shrub	forest	2–7 cm[7]
Saba			1				1	large	forest	5–6 cm[8]
Pycnanthus	1						1	large	forest	4 cm[9]
Cordia				t			1	large	forest	1 cm[6]
Blossom						1	1	small[6]	open[6]	1 cm[6]
Uapaca			1				1	small	open	small
Parinari			(1)				1	6–10 m[6]	open	1·5–2 cm[6]
Ampelocissus			1				1	13 m[6]	open	2·5 cm[5]
Totals	2	11	25	12	15	11	78	2 m[6]	open	<1 cm[9]

[1] t.br. = Terminal branches, i.e., within 1 meter of the edge of the tree; cent. = central portion of tree.

[2] Assisted = arm-hanging bipedalism.

[3] Trees ≤ 15 m tall were categorized as small, based on personal observation; adults statures given here are taken from Palgrave (1977); > 15 m categorized as "large"; liana fruits were judged by the size of the host as estimated during feeding observations.

[4] Habitat was categorized as forest or open habitat; in all cases except for *Cordia* the author's observations of tree size and habitat coincide with information in *Palgrave* (1977).

[5] Figures in parentheses are locomotor bouts; other values are for posture.

[6] Palgrave (1977); [7] Troupin (1987); [8] Dale & Greenway (1961); [9] White (1962).

most common context for locomotor bipedalism. Such bipedal behaviors as scanning the environment (2·1%) and social display (1%) were quite rare (Table 1).

Ecology of chimpanzee bipedalism

Bipedalism was observed both terrestrially and arboreally when feeding from four fruit trees, *Garcinia huillensis*, *Harungana madagascarensis*, *Monanthotaxis poggei* and *Grewia* sp. Together these four trees constituted 27% of all bipedal feeding episodes, and 48% of the bipedal episodes where the plant material being eaten could be identified (Table 2). Fruits were harvested bipedally terrestrially by reaching up into the trees while standing on the ground. Arboreally fruits were collected with a bipedal posture stabilized by a forelimb oriented in an arm-hanging fashion.

All four of these species are diminutive understory trees (Table 2) found commonly among the more open-forest habitats in the chimpanzee ranges at Gombe and Mahale. The fruits of each species are small (~ 2 cm, 0·4 cm, 1 cm and 1 cm respectively) and are distributed evenly among the terminal branches. Although gathering was not seen *both* arboreally and terrestrially in any other tree, other small trees with small fruits elicited bipedalism either arboreally or terrestrially much more commonly than large trees (Table 2). Although the numbers of chimpanzee plant-feeding observations were similar in small and large trees (1439 *vs.* 1536), bipedal food collecting was significantly more common among small (mature height of $\leqslant 15$ m) trees with small fruits (44 *vs.* 8, Fisher's Exact test, $p < 0·001$, $\chi^2 = 27·8$, d.f. = 1, Table 2), suggesting the fruit diameter and tree height are the critical factors eliciting bipedalism. It is difficult to distinguish between the effects of small trees and small fruits, since all but one small tree also had small ($\leqslant 2$ cm) fruit. Where plant-foods gathered during bipedal bouts were identified, 28 of 33 fruits (85%) were $\leqslant 2$ cm in diameter.

Terrestrial bipedalism allows more fruit to be gathered

Short trees appear to require bipedalism for different reasons terrestrially than arboreally. Terrestrial bipedal foraging in short trees allowed individuals to reach relatively higher into the tree, thereby bringing more fruit within reach, and to use both hands during fruit gathering (cf. Jolly, 1970; Jolly & Plog, 1987). Harvesting with both hands increases the rate at which these small fruits can be put in the mouth (ibid). This is significant because it is the manual gathering component of small-fruit collecting that slows ingestion, not chewing. By using both hands fruit could be gathered more quickly to "keep the mouth busy". This terrestrial gathering mode could not be used when feeding from larger trees because even the lowest branches were too high for the fruit to be reached.

Arboreal bipedalism is a terminal branch feeding posture

The size of the branches on which fruit was found appeared to be a major determinant of whether or not bipedalism was used arboreally. As was the case with arm-hanging (Hunt, 1992a), bipedalism was more common among smaller weight bearing structures (WBS). Assisted bipedalism was observed on significantly smaller branches than other postures (12·2 cm *vs.* 15·0 cm, Mann-Whitney U test, U = 123,620, $p = 0·0001$, $n_{1,2} = 64$, 5375), probably because small trees offer few large WBS stable enough for sitting or unassisted bipedal standing. Small branches are unstable enough that during bipedal standing even minor pressure on the foot to maintain balance results in large excursions of the WBS, which can easily cause the center of gravity to fall outside the small base of support. It is hard to balance on a twig. Among such small branches, extending the hip, fully abducting the arm and

assuming a semi-arm-hanging/bipedal posture maximizes the distance between contact points (hand and the feet), thereby increasing stability. Small WBS and small fruits also encourage an arboreal "shuffling" gathering strategy, since harvesters must move small distances often to complete a meal.

The functional significance of "shuffling"

Short-stride-length arboreal movement and terrestrial bipedal shuffling are advantageous for collecting fine-grained resources such as small evenly distributed fruits in small trees (cf. Jolly, 1970; Jolly & Plog, 1987). Arboreal or terrestrial shuffling is necessitated by a low return at any one feeding site, thereby requiring frequent short distance travel during harvesting (Wrangham, 1980). Small fruits also encourage frequent short-distance movement, since feeding sites are depleted quickly. This means that postures that allow a switch to locomotion with little energy cost are preferred (ibid). As is the case terrestrially, an arboreal sitting posture requires the individual to stand to move. It is not practical for a harvester to avoid the costs of small WBS collecting by breaking off a branch and retreating to a more stable perch, since any one branch contains too little food to constitute a meal. The combination of greater stability and easier movement makes a bipedal collecting strategy practical among smaller trees. The most effective harvesting strategy is to move through the entire "surface" of the tree crown (terminal branches), gathering fruits continually. Chimpanzees achieved such gradual "amoebic" movement by shifting their weight and switching one of the three hand- or footholds commonly used for arm-hanging or bipedalism to a slightly removed support. Such locomotion, with its extremely short stride length, is similar to terrestrial bipedal shuffling. Shifting one contact point, while minutely displacing the body's center of gravity, hardly slows collecting at all.

Shorter trees are preferred by larger chimpanzees

A comparison of large and small chimpanzees revealed that when the effects of social rank were factored out, large individuals utilized shorter trees than smaller individuals. High-ranking individuals gathered terrestrially more than low ranking individuals (Hunt, 1989a, 1992b, in revision). By utilizing shorter trees via bipedal reaching rather than climbing, large chimpanzees reduced the proportion of climbing in their positional repertoire. Vertical climbing is a fatiguing positional activity for a large-bodied hominoid, and despite their climbing proficiency, the relatively great weight of chimpanzees should make reducing the proportion of ascensions in their positional repertoire more important than it would be for smaller animals (Cartmill, 1972; Hunt, 1989b, in revision). Such a tendency suggests that *ceteris paribus* large bodied hominoids will forage from shorter trees and will gather terrestrially rather than arboreally. Whereas in order to fill the day's dietary needs a hominoid must be "upwardly mobile" (Tuttle *et al.*, 1991), an important corollary pressure might be phrased "how low can you go".

Functional interpretation

Chimpanzee functional anatomy

Recent reconsideration of ape functional anatomy (Hunt, 1989b, 1991a,b, 1992a,b) has suggested that a number of features previously associated with vertical climbing may be arm-hanging adaptations. Indeed, the pattern of chimpanzee positional behavior suggests that posture in general has been underestimated in functional interpretations of many ape

specializations in preference to locomotion. Chimpanzees climbed only slightly more often than baboons (0·9% vs. 0·5%) and rarely ascended large-diameter WBS (weight bearing structures); instead they tended to enter trees via lianas or nearby small-diameter trees (Hunt, 1992a). This suggests that large-stratum vertical climbing may not be the principal chimpanzee adaptation.

Consideration of chimpanzee functional morphology supports previous contentions that, crudely, muscular adaptations are related to vertical climbing, whereas osteological commonalities are related to suspensory posture or slow posture-like locomotor modes such as transferring or amoebic suspension (Tuttle & Basmajian, 1977; Hollihn, 1984). Of the chimpanzee muscular specializations that can be either probably or confidently associated with a particular positional mode, six are linked to vertical climbing alone (large humeral retractors and elbow flexors), one to arm-hanging alone (large intermediate deltoid), and six appear to be adaptations for both (large arm flexors and scapular rotators; Hunt, 1991a). Conversely, most osteoligamentous specializations of the chimpanzee upper body appear to be adaptations for posture, specifically unimanual arm-hanging. Long narrow scapulae, cone-shaped ribcages, robust clavicular anchors, anteroposteriorly flattened thoraxes (and accompanying strongly curved ribs), mobile abductible humeri, wide manubria of the sterna, and cranially oriented glenoid fossae in chimpanzees were hypothesized to have evolved to reduce muscular activity and ligamentous and skeletal strain during unimanual suspension (Hunt, 1991a). Many of these features make the chimpanzee torso "pre-stressed" to the shape it tends to assume during unimanual arm-hanging, or they robustly anchor the arm to the body. A narrow scapula allows the shoulder to approach the midline of the torso, thereby allowing the torso to assume a relatively less stressed teardrop shape during arm-hanging. Long, curved fingers and toes were hypothesized as serving three arm-hanging functions; they reduce strain on the phalanges and volar tissue, they increase the diameter of branch that may be circumducted by digits of a given length (Hunt, 1991a) and they reduce muscle action potentials during suspension and climbing (Sarmiento, 1988). Long arms increase reach during arboreal feeding, while short hind limbs allow apes a lower center of gravity during locomotion, a significant advantage in small-branch milieus (Korlandt, 1968; Cartmill & Milton, 1977; Hollihn, 1984; Cant, 1987; Hunt, 1991a).

Humerus-abducted suspensory behaviors (predominantly unimanual arm-hanging) and vertical climbing are the shared, distinctive positional behaviors of all apes (Hunt, 1991b), suggesting that hominoid skeletal synapomorphies are principally adaptations to arm-hanging, and muscular specializations are adaptations to vertical climbing and to a lesser extent arm-hanging.

Australopithecine anatomy

The torso of *A. afarensis* is broad, shallow and cone-shaped* (Fig. 2; Schmid, 1983, 1991), the glenoid fossa cranially oriented (Stern & Susman, 1983), the wrist mobile (McHenry, 1991), the fingers long and ventrally curved (although shorter than those of apes) (Stern & Susman, 1983), the thumb short with ape-like articulation (Tuttle, 1981; McHenry, 1991), arm and leg length proportions intermediate between modern humans and chimpanzees, even when the diminutive stature of the fossils is considered (Jungers, 1982, 1991), the cross sectional areas of the vertebral column quite small (Jungers, 1988; Sanders, 1990; McHenry, 1991), and hand morphology indicative of powerful chimpanzee-like grasping ability (Stern &

*Funnel-shaped in Schmid's terminology. The torso is actually shaped more like a cone than a funnel.
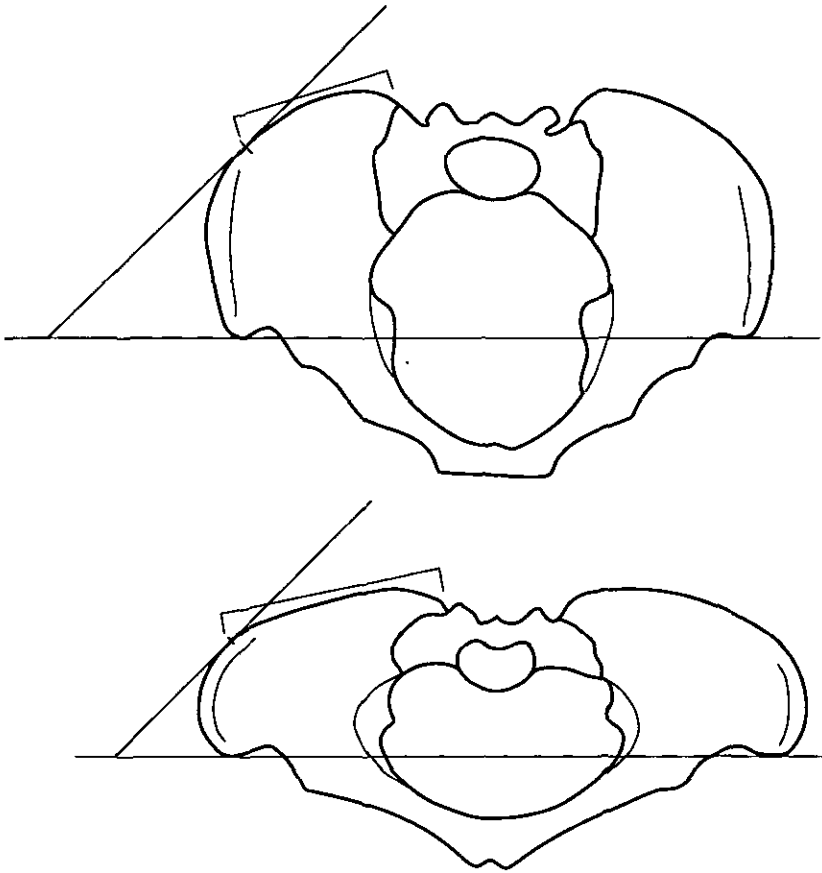
Figure 1. Superior view of pelvis of a modern human female and A.L. 288. Redrawn from Lovejoy, 1988. A coronal plane has been established by drawing a line between the anterior superior iliac spines. A 45° line drawn intersecting this line and the iliac crest roughly divides the pelvis into laterally facing and posteriorly facing planes (brackets). Note that the posteriorly facing plane is approximately twice as long in A.L. 288 as in the modern human female.

Susman, 1983). The presence of six lumbar vertebrae in later hominids (STS 14, Robinson, 1972; Nariokotome) suggests that *A. afarensis* had six lumbar vertebrae as well.

In both general morphology and detail, the pelvis and the lower body morphology of *A. afarensis* unambiguously indicate bipedalism (Johanson & Edey, 1981; Latimer & Lovejoy, 1989, 1990; Lovejoy, 1988; McHenry, 1991). The lumbar vertebrae are lordotic (Abitbol, 1987), the sacral alae are expanded and the pelvis has a very human gestalt (McHenry, 1991). The femur has a deep patellar groove and at least some specimens have an elliptical lateral condyle. The calcaneous is essentially modern (Latimer & Lovejoy, 1989). The great toe is robust and the foot has well developed transverse and longitudinal arches (Latimer & Lovejoy, 1990; Langdon *et al.*, 1991).

A. afarensis deviates from modern humans, however, in exhibiting ape-like features of the medial cuneiform indicating rudimentary first toe abductibility (Stern & Susman, 1983; Deloison, 1991; pers. obs.; *contra* Latimer *et al.*, 1982). *A. afarensis* also has long, curved pedal phalanges (Tuttle, 1981; Stern & Susman, 1983; McHenry, 1991), an antero-posteriorly

short, rounded lateral femoral condyle (for some specimens; Tardieu, 1983; McHenry, 1986, 1991), small joint surfaces from the lumbosacral surface caudad, i.e., waist down, through which the weight of carried objects must pass (Jungers, 1988), short hind limbs (Jungers, 1982, 1991), femoral shaft obliquity even greater than that of modern humans (McHenry, 1986), lack of an iliofemoral ligament (in smaller individuals), and poorly developed sacrotuberous and sacroiliac ligaments (Stern & Susman, 1983). Although the os coxae are human-like in appearance, *A. afarensis* has extraordinarily wide hips (Berge & Kazmierczak, 1986; Rak, 1991), even compared to femoral neck length (therefore indicating a poor mechanical advantage for the lateral stabilization system) (Jungers, 1991). Wide hips are not due simply to highly reflected ilia, but the pelvic inlet is unusually broad as well (Figure 1). Tague & Lovejoy (1986) calculated the pelvic index as the proportion of anterior-posterior minimum dimension, measured from the sacral promontory to the pubic crest, and the transverse breadth (maximum width) of the pelvic inlet, measured at the arcuate line. The index averaged 77·6 for modern human females (ibid) and was 57·6 for A.L. 288-1. That is, the transverse and a-p dimensions of modern human females were subequal, but in Lucy her pelvic width was nearly twice as great as her a-p dimensions. Nor is the wide pelvis of A.L. 288-1 simply a stretched-out modern human pelvis. The posterior-facing aspect of the pelvis is expanded more than the lateral facing aspect. The result is that Lucy has posteriorly oriented ilia (Stern & Susman, 1983; Rak, 1991; McHenry, 1991). This is most apparent in the A.L. 288-1 pelvis if it is divided into two parts, that with a predominantly laterally facing orientation and that oriented posteriorly (Figure 1). Quite different proportions are obvious when compared to a modern pelvis; the posterior facing aspect of Lucy is approximately twice as long as the laterally facing aspect, whereas the two parts are approximately equal in modern humans.

Implications for early hominid behavior

Ecological implications for A. afarensis
Although middle to late Miocene habits were drier than those of the early Miocene (Pickford, 1983), recent evidence suggests that the common supposition that australopithecines were grassland adapted is incorrect. Many hominid sites were wetter in the middle-late Miocene than they are today (Bonnefille, 1984). Faunal assemblages suggest a mosaic habitat ranging from bush-savanna to woodland and even to subtropical forest (Rayner *et al.*, 1993; Wesselman, 1984). Although australopithecine habitats are not as tropical and closed as those in which chimpanzees are typically found (Bonnefille, 1984; Pickford, 1983; Vrba, 1985, 1989), they are better described as open-forest or woodland than savanna or bushland. Habitats in which chimpanzees are bipedal, therefore, are probably quite similar to those in which australopithecines were found. An open-forest, small fruit eating adaptation for early hominids also accords well with microwear evidence that australopithecines were frugivores, and made little use of grazing or subterran resources (Walker, 1981; Kay & Grine, 1988; Grine & Kay, 1988).

Functional anatomy: fatigue, power and energy consumption
In determining the extent to which a morphology is highly refined for a particular behavior, at least three different types of optimality must be considered. First, a morphology may minimize the muscular force necessary to perform a behavior. This aspect of optimality

reduces energy consumption, but skeletal elements involved in the behavior may be highly stressed. For example, if a bipedal organism is selected for extraordinarily wide hips, energy consumption can be reduced if the femoral neck (i.e., the biomechanical neck length) and bi-iliac breadth increase proportionally more than hip width. A consequence of this adaptation, however, is that femoral neck bone strain would be much higher than if the hips were narrow.

This energy consumption aspect is partly independent of the second aspect of functional optimality, joint reaction forces. A particular morphology may reduce joint reaction forces, thereby reducing the consequences of high joint loading, such as increased wear or high incidence of stress factors, even though muscular forces remain great and energy consumption therefore high. For example, if both hip width and biomechanical neck length are decreased in the same proportion energy consumption will remain the same, but bone strain and joint reaction forces will decrease.

The third aspect is fatigue. Different individuals may have different amounts of muscle tissue available to power a movement. A lesser amount of muscle tissue means that individual muscle fibers must contract powerfully more often. This does not influence energy consumption, but it still means muscle tissue will fatigue more rapidly. Viewed from another perspective, poor mechanical advantage can be compensated for with a disproportionate increase in muscle mass. If the muscles are large enough, the animal may have extraordinary muscular endurance, yet it may use more energy per step cycle than another with a different configuration—narrower hips, for example.

Often these three types of optimality, lowered energy consumption, lowered bone stress and joint reaction forces and reduced muscular fatigue, are not distinguished. They are important because the lower body anatomy of *A. afarensis* is less than optimal for locomotion in each of these ways. Much of the upper body anatomy of *A. afarensis* may be adapted for two types of optimality, reducing strain and conserving energy during arm-hanging.

Upper body anatomy

With the exception of six lumbar vertebrae, each of the upper body features of *A. afarensis* is functionally related to arm-hanging. The digits of *A. afarensis*, though shorter than those of apes, are just as curved (Stern & Susman, 1983). Ventrally curved fingers and powerful digital flexors are energy saving, stress reducing adaptations to vertical climbing and arm-hanging. Shorter digits are consistent with the smaller supports available among the terminal branches of the smaller trees hypothetically targeted by hominids. A bar/glenoid angle that is not significantly different than that of apes (Stern & Susman, 1983) suggests a substantial armhanging adaptation. The short lumbar region of chimpanzees is hypothesized to be an adaptation to climbing, either to resist buckling strains produced by propulsive forces from the hind limbs (Jungers, 1984) or to allow a more direct link between the lower body and the humerus (Tuttle & Basmajian, 1977). Alternatively (or additionally) a short lumbar region may simply reflect the low frequency of leaping in chimpanzees (Hunt, 1991a). If australopithecines had six lumbar vertebrae, rather than the five of modern humans or the four of chimpanzees they were not likely to have been adapted to vertical climbing or leaping. Neither leaping nor vertical climbing would be required among the short trees hypothesized as protohominid feeding sites. *A. afarensis* may have retained a long back for flexibility; such dexterity would be useful for maximizing the feeding sphere while gathering tree fruits from the ground. Together upper body features of *A. afarensis* suggest that arm-hanging, perhaps in conjunction with bipedalism was an important adaptation for feeding among small, open-forest trees. The intermediate nature of the upper body anatomy of *A. afarensis* suggests that

early hominids engaged in arm-hanging and vertical climbing at frequencies intermediate between those of chimpanzees (4 + % and 1% of the positional repertoire respectively) and modern humans (presumably 0% and 0%).

A. afarensis *lower body anatomy is not optimal for terrestrial bipedal locomotion*
Because the gestalt of the lower body anatomy of *A. afarensis* clearly indicates an organism adapted to locomoting bipedally (Johanson & Edey, 1981; Lovejoy, 1981, 1988; Latimer & Lovejoy, 1989, 1990; Latimer, 1991), it is all the more perplexing that a bipedalism that is not as refined as that of modern humans is apparent. The hips of *A. afarensis* are extraordinarily wide (Figure 1), as wide as those of a modern human despite a stature of perhaps as little as 1 m (Berge & Kazmierczak, 1986; Rak, 1991). It is not certain that this means a greater joint reaction force at the hip. Lovejoy calculates a joint reaction force at the hip joint of 2·4 × body mass, comparable to that of modern human females (Lovejoy, pers. comm.; Lovejoy *et al.*, 1973; Berge & Kazmierczak, 1986). Jungers (1991) produced contrary results in a similar analysis. He found that compared to modern humans, the width of the hips is proportionally greater than the femoral neck length. If this is so, the mechanical advantage of the muscles that prevent the hip from collapsing when one foot is off the ground (the abductors) would be *lower* in *A. afarensis* than in modern humans, not greater. *A. afarensis* therefore would have required greater muscular action potentials of the gluteals than modern humans.

There is a further important implication of wide hips. Regardless of joint reaction forces at the hip joint or relative femoral neck/pelvic proportions, wide hips cause the moment arm of the body weight of *A. afarensis* to be increased over that of modern humans, increasing the stress on the diaphyseal/femoral neck junction. That is, if all variables remain the same except hip dimensions, wider hips always result in greater stress in the diaphyseal/femoral area.

The relatively small acetabulum/femoral head of australopithecines suggests greater joint reaction forces than in modern humans, though this measure is equivocal. This issue has been clouded somewhat by evidence that the hip joint of Lucy, though smaller proportionally than that of modern humans, falls near a regression line of modern humans extrapolated down to Lucy's size (Ruff, 1988). Recently an analysis using a larger sample size and humans closer to the body weight of *A. afarensis* has apparently resolved this controversy, clearly showing that the *A. afarensis* hip joint is smaller than that of similar-sized modern humans (Jungers, 1991). Even if the hip joint of *A. afarensis* were the size expected of a diminutive human, the capacity of *A. afarensis* for carrying and endurance bipedalism may still be lesser. Ruff (1988:707) makes a plausible case that humans have small joint surfaces because they load their limbs less than other hominoids (including *early* humans), due to decreased activity levels. If this is so, even if the femoral head of *A. afarensis* is the size extrapolated for a scaled down modern human, this would be smaller than expected because *A. afarensis* presumably had a typical hominoid activity level.

Whether the size of the hip results in a modern-human-like stress and function during bipedalism for Lucy or not, it is astounding that *A. afarensis* is not clearly more efficient than moderns. The locomotor disadvantages of Lucy's hips are due partly to a spectacular biacetabular width (Figure 1), for which no functional advantage has been proposed to date. This width is not an obstetric requirement, since cephalopelvic reconstruction of A.L. 288-1 suggests a considerable gap between the fetal head and pelvic inlet walls opposite the acetabula (Tague & Lovejoy, 1986, Fig. 3). Because a broad pelvis carries a high hip joint reaction force, greater stress on the femoral neck and greater muscular activity during walking, a well adapted walker is expected to have hips as narrow as possible (cf. Rak,
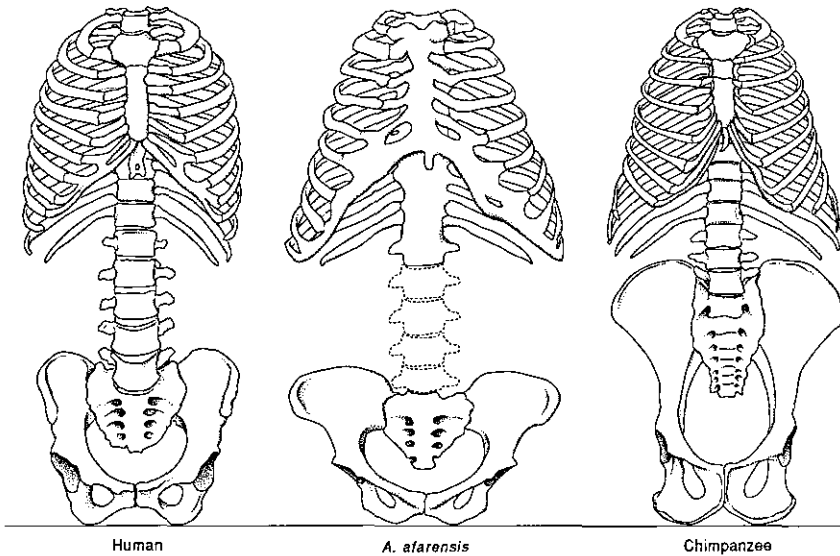
Figure 2. Thoraxes of a modern human, a chimpanzee (after Schultz) and a reconstruction of A.L. 288 compared. Note the similar cone-shape of the ribcages of A.L. 288 and the chimpanzee, hypothesized as functioning in conjunction with a cranially oriented glenoid fossa and an elliptical scapula to allow the shoulder joint to more directly approximate a point over the center of gravity during arm-hanging. Such a configuration may more evenly distribute stress on the thorax and the glenoid capsule, thereby reducing fatigue and obviating muscle action. Thoraxes scaled to same height. Reconstruction after Schmid (1983).

1991), very unlike those of Lucy. Although wide hips are a poor adaptation to locomotor bipedalism, they may be an excellent one for postural bipedalism. In order for static equilibrium to be maintained, the vertical from the center of gravity to the ground must fall in the area of support (Kummer, 1991). Wider hips increase the area of the base of support, increasing the stability of bipedal posture, thereby providing a stable feeding platform on which the gathering upper limbs are mounted (Kummer, 1991). Stresses that wide hips cause during bipedal locomotion do not appear in bipedal posture.

The lumbar vertebrae and lumbosacral articular surface of Lucy and other australo-pithecines are small, whether in proportion to body weight, hip width or nearly any other measure that has been attempted (Jungers, 1988, 1991; McHenry, 1991; Rak, 1991). Since a larger proportion of the *A. afarensis* body weight resides in the torso, during all unassisted bipedal behavior the lumbar vertebrae are under relatively greater stress than is the case in modern humans. When carrying something with the arms the stress would be greater still. High pelvic stresses, a small diameter spine, small joint surfaces below the waist and smaller-than-modern-human sacro-iliac attachments suggest an animal that is less well adapted for sustained bipedal walking or carrying than are modern humans (Jungers, 1988, 1991; Hunt, 1989*b*, 1990). Such an anatomy would be completely appropriate for low-stress bipedalism such as postural gathering, more so since both feet are on the ground often during such gathering, negating the disadvantages of wide hips (Hunt, 1989*b*, 1990).

Taken as a whole, *A. afarensis* joint size and conformation, wider hips that generate greater stresses, and inferred muscular anatomy and limb proportions suggest that compared to modern humans the locomotor apparatus of *A. afarensis* was more prone to fatigue or injurious failure during powerful and sustained bipedal locomotion, and that bipedal locomotion

consumed more energy per unit distance (Jungers, 1988). This anatomy suggests one of three possibilities; that energy consumption is not an important consideration for *A. afarensis*, that *A. afarensis* practiced bipedal locomotion with a low enough frequency that energy loss and/ or structural failure were negligible, or that other kinematic requirements were important enough to counterbalance locomotor energy inefficiency. The former is extremely unlikely (Cant, 1980). The latter two explanations are possible. In either case a lower frequency of bipedal walking is suggested compared to modern humans.

Arboreal adaptations in the A. afarensis *lower body*
A number of ape-like features of the *A. afarensis* lower body have been related to arboreal behavior. A long posterior aspect of the ilia means that a larger proportion of the gluteal muscles is oriented posteriorly, rather than laterally (Figure 1). Although the function of the glutei is not certain in either humans or apes (e.g., Tuttle *et al.*, 1978; Stern & Susman, 1981), such a morphology suggests a greater mass for gluteus maximus, a hip extensor. The posterior orientation of the ilia is an ape-like feature suggesting greater climbing competence compared to modern humans (Stern & Susman, 1983). It also suggests that Lucy has more pelvic musculature dedicated to extending the femur or raising the trunk than for stabilizing the hip during the stance phase of bipedal walking. Such anatomy is particularly significant because the wider hips of *A. afarensis* would seem to require a more powerful lateral stabilization system than in a modern human to achieve an equivalent function. It follows that, energy consumption aside, *A. afarensis* would fatigue during extended bipedal walking more quickly than a modern human, since a smaller amount of muscle tissue would be called on to perform the same function. Climbing and thorax raising suggest arboreal adaptations. Trunk movements might be used during bipedal foraging as the individual reaches out to gather and then returns to an upright position. Whichever function is indicated, climbing or gathering, the relatively high proportion of posteriorly versus laterally oriented glutei suggests a reduced role for locomotor bipedalism in the australopithecine positional repertoire.

A strongly developed fibular groove for the tendon of the peroneal muscle suggests ape-like great-toe flexion (Tuttle, 1981; Deloison, 1991), as might be used to grip branches when standing arboreally or climbing. Alternatively, the arch may be supported by a robust peroneus longus; if so, bipedalism would be that much less energetically efficient, since muscular support would be necessary for toe-off, rather than a non-energy-consuming ligamentous support. A long movement arm for the hamstrings (Stern & Susman, 1983) increases the power of hip extension, implying a better climbing adaptation than in modern humans. A plantar set, or at least greater mobility (Latimer & Lovejoy, 1990), of the ankle allows full plantar-flexion of the foot, common when the toes grip a branch to support body weight with the hind limb in tension (pers. obs.). Curved pedal phalanges (Sarmiento, 1988; Hunt, 1991*b*) and a *third* pedal digit longer than the first or second (Stern & Susman, 1983) are gripping adaptations. Such pedal gripping, especially with the lateral four toes only, is used by chimpanzees during arm-hanging to increase stability among slender terminal branches (pers. obs).

A bipedal postural adaptation
Together, chimpanzee behavioral analogy and australopithecine anatomy suggest that harvesting small fruits from diminutive trees may have resulted in the peculiar combination of compromised bipedalism and arm-hanging morphology found in *A. afarensis*. Bipedal posture augmented with bipedal shuffling is hypothesized to be an efficient solution for

harvesting small, evenly distributed food items available from the ground. An arm-hanging bipedalism is particularly effective for harvesting such fruits arboreally in small trees because it provides maximum support and mobility. Sustained bipedal postures are necessary because small food items are time-consuming to harvest and therefore cannot be picked in bulk and eaten elsewhere. A feed-as-you-go strategy allows the time between picking individual fruits to be used for chewing. Bipedalism is particularly efficient during fine-grained terrestrial harvesting because it reduces "gear change" costs that quadrupedal animals suffer when moving between adjacent feeding sites (Wrangham, 1980; cf. Jolly, 1970; Jolly & Plog, 1987). Relatively inefficient bipedal locomotion and efficient bipedal harvesting posture combined with considerable arboreal competence might be more energetically efficient than a quadrupedal adaptation for harvesting similar resources. Such an origin for bipedalism does not in itself suggest clumsy bipedal locomotion in australopithecines, but does suggest that adaptations for stable, efficient terrestrial postural harvesting might be selected for at the expense of efficient locomotor adaptations.

Even if terrestrial harvesting had the highest energetic return for early hominids, two factors would work against exclusive terrestriality, especially for all individuals in a group. Because climbing is disproportionately expensive in larger animals and manoeuverability and balance are worse (Cartmill, 1972), arboreal harvesting would provide a relatively greater net energy return for smaller animals. Among chimpanzees, females are more arboreal than males because males monopolize terrestrial feeding sites (Hunt, 1989b, 1992c, 1993; Doran, 1993). Even if terrestrial feeding provided the highest energy return for all hominids, higher ranking larger individuals might be expected to monopolize better feeding sites, leaving less optimal arboreal feeding sites to females and juveniles. It is significant that among *A. afarensis* presumed males more commonly have traits associated with terrestriality, whereas females exhibit anatomy associated with arboreality (Senut, 1980; Tardieu, 1983; Stern & Susman, 1983; Susman *et al.*, 1984). This is not to say that males might never have harvested arboreal food resources. During food shortages chimpanzee males are not as selective, and behave more like females (Wrangham, 1975). Arboreal foraging more than doubles the amount of fruit available to a terrestrial frugivore, since only fruit found on the lower 2 m of these 3–15 m tall trees can be harvested from the ground.

Discussion

Either chimpanzee behavior, hominoid functional morphology, or both, are somewhat at odds with previously proposed hypotheses for the evolution of bipedalism. An exclusively terrestrial gathering adaptation should not require morphology linked to arboreality, nor should an arboreal gathering/locomotor adaptation have resulted in striding, human bipedalism. Other behaviors hypothesized to select for bipedalism, e.g., vigilance or social display, are engaged in only rarely by chimpanzees (Table 1) and other primates (pers. obs.), and it is unlikely that the advantages of such behaviors would be great enough to overcome the disadvantages of bipedalism. If display and conflict resolution are consequences of a more open habitat (Jablonski & Chaplin, 1993), one might expect that many open habitat primates would have evolved similar bipedal adaptations. Vigilance and greater viewing distance hypotheses suffer from other disadvantages. It has not been demonstrated that bipedalism actually increases the sight lines in habitats hypothesized for early hominids. Variation in the height of ground cover in woodland areas makes it unlikely that a small

increase in stature would improve viewing distance for a significant proportion of the time. For very low vegetation bipedalism is unnecessary. For tall vegetation the additional half meter of height provides no advantage. In any case it would seem easier to stand up when it is needed than evolve a new mode of locomotion to accommodate such a rare behavior.

It has been suggested that even if human bipedalism is not terribly efficient, it is more efficient than ape quadrupedalism (Rodman & McHenry, 1980). Bipedalism might therefore be an energy-saving adaptation for moving between forest patches. One difficulty with this hypothesis is although human bipedalism may be more efficient than pongid quadrupedalism, the bipedalism of an incipient biped would not have been (Ishida, 1991). Furthermore, the meager energy savings of even fully evolved bipedalism would have been poor compensation for the loss of manoeuverability, speed and arboreal competence that such a change would require (Lovejoy, 1988). A more straightforward alternative would be to evolve a highly efficient cursorial quadrupedal locomotion, a realistic course if protohominids became more terrestrial and therefore had little selective pressure to retain energy-inefficient arboreal adaptations.

One advantage of bipedalism is that compared to quadrupedalism it reduces incident solar radiation, puts a greater proportion of the body in a cooler microhabitat and increases convective cooling (Wheeler, 1982 et seq.). This hypothesis suffers from several handicaps. Early australopithecine habitats are not as open as has often been assumed. Furthermore, even hominids in very open habitats need not have foraged in the direct sun. Chimpanzees actively and effectively avoid exposure to the direct sun when it is warm (pers. obs.). The short squat australopithecine physique is also poorly adapted for dissipating heat, compared to later hominids (Wheeler, 1993), and therefore seems to be an unlikely morphology if the animal adopted bipedalism to cope with heat stress. A more significant piece of evidence is the relative inefficiency of early hominid bipedalism. If bipedalism evolved to save energy and lower heat stress, there would be strong selection to make locomotion as efficient as possible, since extra energy consumption means extra heat and a higher water demand.

Tool use hypotheses have not yet demonstrated convincingly that tool use is incompatible with quadrupedalism (Jouffroy, 1991). Most tool use is at least as effective sitting as standing. Nor does tool carriage imply bipedalism. Chimpanzees carry termiting tools in their flexed fingers while walking quadrupedally. They are adept at balancing things on their backs, and when this is ineffective they carry large objects between the hip and thigh by flexing the thigh and walking on three limbs.

Provisioning hypotheses are at least partly inconsistent with primate ecology. Few primate food items (meat is an exception) are nutrient-dense enough to serve as effective provision, and the exception is one that lends itself well to chimpanzee-style carrying. Moreover, cultural innovations such as containers, the canid adaptation of ingestion/regurgitation, or a chimpanzee-like sling-it-over-the-shoulder carrying (Bauer, 1977) would seem to be better solutions to food transport than a complete reorganization of the lower body anatomy and the attendant disadvantages of bipedal locomotion. Carrying in the arms requires that the arm muscles sustain the weight of a load. Arm fatigue is not a factor with other quadrupedal carrying methods. Arm-carrying therefore appears to be an unlikely solution to food provisioning needs. More significantly, small lumbar vertebrae, a small lumbosacral articular surface (through which the weight of carried objects must pass), short legs, wide hips, a lightly articulated pelvis and comparatively gracile joint surface areas of the *A. afarensis* lower body all but exclude the possibility that its anatomy was adapted for carrying or long distance travel (Jungers, 1988, 1991).

It might be argued that arboreal and energy-inefficient features are merely holdovers from a previous, more arboreal adaptation, or that there has been too little time for extensive refinement of the positional anatomy to have occurred. The persistence of most arm-hanging features in *A. africanus* (Robinson, 1972; McHenry, 1986) and still later hominids, including *Homo habilis* (Hartwig-Scherer & Martin, 1991; Rak, 1991; Wheeler, 1993) is contrary to this. Australopithecine arboreal adaptations appear to remain relatively unchanged until the evolution of an essentially modern postcranial morphology, in *Homo erectus* (Day, 1971; Leakey, 1976; Bramble, 1991; Preuschoft & Witte, 1991; Jungers, 1991). Accordingly, scavenging, hunting, provisioning and carrying arguments for the origin of bipedalism (Shipman, 1986; Sinclair *et al.*, 1986; Carrier, 1984; Wheeler, 1984; Lovejoy, 1981; Jungers, 1991) are more convincing explanations for the refinement of locomotor bipedalism in *Homo erectus*, as are heat stress models (Wheeler, 1993). Although the evolution of efficient bipedal locomotion may indeed have coincided with provisioning, carrying and/or the inclusion of more animal protein in the diet, selection for these activities may have had little to do with the origin of bipedalism.

The most reasonable explanation of australopithecine anatomy and chimpanzee bipedal behavior appears to be a synthesis of what are perhaps the two most plausible hypotheses for the evolution of bipedalism, Tuttle's hylobatian hypothesis (1975) and the Jolly/Rose/Wrangham terrestrial feeding hypothesis. Such a synthesis appears to address weaknesses in both hypotheses. Whereas the hylobatian hypothesis maintains that bipedalism evolved as a feeding posture and as a large-branch locomotor mode, chimpanzee bipedalism suggests a protohominid that used bipedal locomotion relatively infrequently, instead engaging in bipedalism as a partly-suspensory feeding posture most useful among small branches. The Jolly/Rose/Wrangham hypothesis does not predict arboreal adaptations, since it proposes terrestrial gathering alone as the impetus for bipedal behavior. Chimpanzee behavior and australopithecine anatomy, however, suggest significant arboreality.

Bipedalism apparently evolved during the Miocene climatic upheaval associated with the opening of the great rift and the uplifting of the Ruwenzori Mountains (Pickford, 1991). An increase in the proportion of drier more open habitat, and a patchier resource distribution (Hill, 1987) left at least two possible niches for African hominoids. In the changing forest, chimpanzees adapted by augmenting their arboreal fruit-gathering suspensory adaptations with adaptations for terrestrial quadrupedal walking between distant food resources (Temerin & Cant, 1983), also allowing them to add a critical food to their diet, terrestrial herbaceous vegetation (Wrangham *et al.*, 1991). Gorillas took this adaptation to its extreme. Protohominids in woodland habitats may have included more food items from increasingly abundant small trees and bushes, eventually evolving into terrestrial *and* arboreal bipeds.

Summary and conclusion

Chimpanzee bipedal behavior and australopithecine anatomy suggest a synthesis of two scenarios for the origin of bipedalism previously viewed as rather contrary, i.e. terrestrial (Jolly & Plog, 1987; Wrangham, 1980; Rose, 1984) and arboreal (Tuttle, 1975, 1981) bipedal postural feeding hypotheses. Arboreal arm-hanging/bipedalism and terrestrial bipedalism during small-fruit collecting may have been the signal adaptation of the earliest hominids. Although bipedalism may have been virtually the only terrestrial locomotor mode in *A. afarensis*, poor bipedal mechanics and compromises that improve arboreal competence suggest a role for locomotor bipedalism that is relatively reduced compared to modern

humans. The small-tree postural feeding hypothesis reconciles the presumed contradiction between bipedal lower body morphology and arboreal upper body anatomy in *A. afarensis*. It also suggests that early hominids may not have been reluctant, half-evolved bipeds, but rather they had a fully evolved, unique adaptation for both terrestrial and arboreal bipedal gathering that was unlike that of any extant species, including humans. The persistence of arm-hanging features in later hominids (Robinson, 1972; Rak, 1991; Wheeler, 1993) suggests that this adaptation may have remained relatively unchanged, even in *Homo habilis* (Hartwig-Scherer & Martin, 1991) until the evolution of a more locomotion-oriented, near-modern postcranial morphology in *Homo erectus* (Day, 1971; Leakey, 1976; Rose, 1984; Bramble, 1991; Jungers, 1991; Preuschoft & Witte, 1991).

Acknowledgements

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