The postural feeding hypothesis: an ecological model for the evolution of bipedalism

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Chimpanzee ecology and australopithecine functional morphology suggest a combined terrestrial and arboreal postural feeding origin for hominid bipedalism. Field research has shown that chimpanzees are bipedal most often when they feed on the small fruits of diminutive, open-forest trees. They feed from such trees either by reaching up to pick fruits while standing on the ground, or by balancing on branches in trees, stabilizing themselves by grasping an overhead branch in a semi-arm-hanging posture. Some australopithecine anatomy shared with apes (abductible humeri, shallow ribcages, long narrow scapulae, cranially orientated glenoid fossae, robust clavicular anchors and wide manubria of the sterna) is adapted for reducing muscle action and structural fatigue during arm-hanging. Other ape features in hominids (a large ulnar excursion of the manus, and long, curved metacarpals and phalanges) are adaptations to both vertical climbing and arm-hanging. Australopithecine hip and hindlimb anatomy indicates habitual bipedal locomotion when on the ground, but compared to modern humans their movement was less efficient and generated greater stresses in the hip. Hominid bipedalism may have originated as a feeding posture, with arboreal arm-hanging, arm-hanging/bipedalism, and vertical climbing as vital gathering modes, that was only later refined into an efficient locomotor adaptation.

As the closest living relatives of humans, chimpanzees inform our interpretation of the earliest hominids in two separate, vital areas. First, a thorough understanding of the link between behaviour and anatomy in chimpanzees allows us to understand what chimp-like characters[1-4] in australopithecines mean in a clearly bipedal animal. Second, situations that elicit bipedalism in quadrupedal chimpanzees are likely to be similar to those that selected for a greater frequency of bipedalism in proto-hominids. A hypothesis consistent with both chimpanzee behaviour and australopithecine anatomy is perhaps the best argument we can advance at present for understanding why bipedalism evolved.

Chimpanzee anatomy

Because australopithecines have some features shared with apes, the first step in reconstructing their way of life is interpreting ape anatomy in terms of function. Chimpanzees share with other apes high intermembral indices, long, curved fingers (both metacarpals and phalanges), mobile shoulders (i.e. a fully abductible humerus), adductible wrists, cranially orientated glenoid fossae (an upward tilted shoulder joint), a wide manubrium of the sternum (large breast-bone), an anteroposteriorly flattened torso (shallow chest) with concomitantly long clavicles (collarbones), a reduced number of lumbar (lower back) vertebrae, the lack of a tail, a distinctive pelvic floor[5-8] and a predominance of muscles that flex the elbow and raise (abduct or protract) the upper arm.[9,10] Most apes have mediolaterally reduced and axially elongated scapulae (i.e. oblong shoulder blades; orangs and gorillas display this least). Apes have cone-shaped ribcages, and

larger apes have a more pronounced cone shape,[11,12] suggesting that body weight is the critical factor. The anatomical similarity of the apes implies that they share a limited number of positional* modes for which these traits evolved. The hypothesis that this positional behaviour was brachiation[5,10] (i.e. hand-over-hand locomotion beneath branches) foundered on evidence that it occurs rarely among wild great apes.[13-16] Quadrumanous climbing replaced brachiation as the presumed shared hominoid positional adaptation.[17-19] Data from wild apes altered and clarified this hypothesis by affirming that three behaviours that fall under the rubric of quadrumanous climbing, walking (walking on inclined boughs, scrambling, and assisted bipedalism), vertical climbing, and suspensory behaviour are likely to be responsible for ape specializations, but that each exerts different stresses on the anatomy, and should be considered separately.[20,21]

Evolution of bipedalism

Whichever behaviour(s) ape morphology is linked to, interpreting australopithecine anatomy is less than straightforward, since ape-like, human-like and unique features are all found in early hominids. Because hypotheses of the evolution of bipedalism have been the topic of two particularly thorough reviews recently,[22,23] such an overview is not presented here. Instead, this article concentrates on evidence that favours a narrow group of ecologically based hypotheses[24-29] reconcilable with a postural feeding hypothesis that conforms best with chimpanzee behaviour and australopithecine anatomy.[30] Each of these scenarios emphasizes the importance of feeding behaviours over such activities as predator avoidance, intraspecific agonism and long distance travel. In particular, data on chimpanzee positional behaviour are related to anatomy to show that arm-hanging and vertical climbing are the principal positional specializations of these animals. Consideration of the chimp-like, human-like and unique features of early hominids, when viewed in the light of the chimpanzee's bipedalism, strongly supports the postural feeding hypothesis.

Methods

Chimpanzees were observed for 571 hours at the Mahale Mountains National Park and for 130 hours at the Gombe Stream National Park, Tanzania. A total of 16 303 instantaneous, 2-minute focal observations was made on 26 well-habituated prime adults spanning all social ranks. Twenty-five positional behaviour variables were monitored, including positional mode, its behavioural context, and feeding parameters. A total of 2 087 observations was made on Gombe baboons over 83 hours using identical methods.

One of 65 locomotor or postural modes was identified in target animals at each 2-minute point. Brachiation was taken to mean hand-over-hand suspensory movement, and climbing to mean

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*Positional behaviour is a general term referring to either posture or locomotion.

Table 1. Positional behaviour of baboons and chimpanzees compared.

Species	Sit (in)[2]	Sit (out)[3]	Lie[4]	Arm-hang[5]	AH (supp.)[6]	Stand[7]	Squat[8]	Cling[9]	Bipedal stand[10]	Walk[11]	Vertical climb[12]	Run[13]	Leap[14]	Other susp.[15]	Palm walk[16]	Bipedal walk[17]
									Percentage of positional mode[1]							
Chimpanzee	28.4	34.0	12.1	0.8	3.6	2.5	0.7	0.3	0.3	15.7	0.9	0.3	0.0	0.2	0.6	0.1
Baboon	22.5	34.6	3.2	0.0	0.0	14.5	0.5	0.3	0.0	23.2	0.5	0.4	0.2	0.0	0.0	0.0

[1]Derived from 16 303 instantaneous observations of focal chimpanzees, 2 087 observations of focal baboons, standardized for hour of the day; Gombe and Mahale figures averaged. Positional mode descriptions are given in detail in ref. 31. [2]Sitting with knees and hips flexed. [3]Sitting with knees and hips extended. [4]On side, back or stomach. [5]Unimanual suspension with no other support. [6]Arm-hanging (with support): more than half the body weight suspended from a manus; some support from lower limbs or ischia. [7]Quadrupedal or tripedal posture, trunk pronograde. [8]Weight solely on fully flexed hindlimbs. [9]Support from adducted, retracted, flexed forelimbs and fully flexed hindlimb. [10]Bipedal stand: support from hindlimbs with knees extended, hips partly or wholly extended. [11]Quadrupedal, above branch progression on WBS angled at ≤45°, including digitigrade and knuckle-walking. [12]Hand-over-hand ascension or descension on WBS angled at >45°; propulsion provided by hindlimbs and forelimbs. [13]With a period of free flight. [14]Saltatory locomotion with propulsion provided by extension of the spine and hindlimbs. [15]Suspensory locomotion: brachiation, transferring, riding, tree swaying, 'amoebic' movement arm-swinging that involve suspensory locomotion with a fully abducted humerus. [16]Walking with the manus contacting the WBS by the palm, with the manus supinated, and dorsiflexed. [17]Bipedal walk: locomotion involving propulsion solely by the hindlimbs.

vertical climbing only (that is, ascending supports >45°). Information on support diameter, angle of support above the horizontal, height climbed and climbing mode (of flexed-elbow, extended-elbow, ladder and pulse; >45°) was collected continuously whenever a target animal was observed climbing. To minimize the dependence of data points, findings were reduced by pooling sequential observations in which positional mode did not change. Analytical variables were averaged over the series of sequential observations, and the resulting group of observations was considered a single positional bout. Chimpanzees were followed in all contexts, in trees and on the ground, during feeding and resting.

Chimpanzee skeletons were examined at the Peabody Museum, Harvard University, and in the Anthropology Department, Indiana University, and considered in the context of published reviews of chimpanzee anatomy. Casts of postcranial fossils from Hadar were examined at the Peabody Museum.

Results and interpretation

Chimpanzee specializations

Positional profiles were calculated for chimpanzees and baboons (Table 1). Such a profile records the incidence of each positional mode for all contexts, for all hours of the day. This representation of behaviour is more accurate for interpreting anatomy than one that includes only locomotor behaviour, or that considers only behaviour in a single context such as feeding. The positional profile[31] of chimpanzees shows that walking is by far the most common form of locomotion, and that, as is the case with all primates, most positional behaviour involves being stationary (nearly 85% of the time in the case of chimps). Anatomical adaptations can be recognized by comparing chimpanzee positional behaviour with that of another species with a more generalized anatomy. The sympatric, similar-sized baboon is compared here as a representative of monkeys (Table 1).

Differences in how commonly particular positions are adopted by chimpanzees and baboons define the distinctive behaviours for these animals (Table 2). In general, if a behaviour is significantly more common in one species than another, adaptations to that behaviour might reasonably be expected in the anatomy of the specialist.[32] Five positional modes were significantly more common in chimpanzees (Fisher's exact tests on pooled Gombe and Mahale data, $P < 0.05$, d.f. = 1; see Table 2): (1) lie, (2) sit (legs flexed), (3) hanging by one arm (all modes), (4) palm-walk

and (5) vertical climb. Chimpanzees stood bipedally more often than baboons (0.3% versus never), but the difference was not significant. Other positional behaviours were either not distinctive in chimpanzees or were rare (Table 1), and therefore cannot be responsible for the anatomical adaptations of chimpanzees. Note that chimpanzees stood (tripedally or quadrupedally) and walked significantly less frequently than baboons. Modes were defined differently by Doran,[33] but her results broadly confirm those presented here and in more detail elsewhere.[31] Other methods of determining distinctiveness yield results quite similar to these[31] and are consistent with conclusions arrived at here.

Table 2. Distinctiveness of chimpanzee positional behaviours.

Positional behaviour	Chimp-baboon difference (in %)
Lie[1]	**8.9**
Sit in	**5.9**
Arm-hang	**4.4**
Palm-walk	**0.6**
Vertical climb	**0.4**
Bipedal stand	0.3
Squat	0.2
Susp. locomotion	0.2
Bipedal walk	0.1
Cling[2]	0.0
Sit out	−0.6
Walk	−7.5
Run	−0.1
Leap	−0.2
Stand	−12.5

[1] Positional modes in bold face are significantly more common in chimpanzees ($P < 0.05$; Fisher's exact test on data reduced on positional behaviour). [2] Modes below the horizontal line are less common in chimpanzees than baboons and therefore cannot be responsible for chimpanzee anatomical specializations.

Interpreting anatomy

Evolutionary anatomy views morphology as the result of conflicting selective pressures — the need to conserve energy, to prevent injury and disease, to provide optimal access to resources, and to avoid predation. The perspective of MacConnaill and Basmajian[34] informs this field of enquiry best. Anatomy is viewed as adapted to 'muscle-sparing', not only via operating efficiently during locomotion, but by shunting body weight support off muscles and onto skeleton and ligaments whenever possible. In so doing, the energy necessary for muscle action is conserved. Accordingly, distinctive behaviours are expected to select for anatomy that allows the performance of behaviours with minimum muscle action. The more often a behaviour is engaged in, the greater the potential energy savings it offers. Although two behaviours may be equally distinctive, musculoskeletal adaptations to them may not offer equal evolutionary rewards (energy-savings, injury prevention, resource optimization and predator avoidance). Distinctiveness must be considered in the light of these pressures in order to interpret anatomical specializations. Likewise, if behaviours do not stress the body, adaptations for maintaining anatomical integrity during other, more vigorous activity such as high-speed locomotion are likely to have exapted the body for the nonstressful behaviours. In sum, we expect to find anatomical adaptations to a behaviour only when the activity is distinctive in the species, and then only if the behaviour is common and/or stressful as well.

Anatomical adaptations to lying, sitting and walking

Lying was both common and distinctive in the chimpanzee (Tables 1 and 2), but adaptations to locomotion are likely to have exapted the body for lying. Sitting may have some anatomical correlates. During sitting, body weight is concentrated on the ischia and the soles of the feet. Chimpanzees have glabrous pads over their ischia as adaptations to sitting, but these are no more extensive than those in baboons. Chimpanzees might be expected as well to have ligamentous adaptations that hold the upper body in a sitting posture with the least stress on the anatomy and with minimal muscle action. Chimpanzees keep their backs straight when sitting compared with many Old World monkeys, in which the upper spine may be found at a 90° angle to the lower back. The capacity of monkeys to flex their spine strongly ventrally allows a longer application of force to the upper body during leaping, allowing greater acceleration and a longer leap. Monkeys leap more than chimpanzees.[35] The straight backs of chimpanzees may reduce tensile strain on muscles and ligaments on the back of the spine during sitting, but other adaptations to this relatively nonstressful behaviour are unlikely.

Palm-walking (0.6%) was significantly more common among chimpanzees than among baboons (Fisher's exact test, $P < 0.002$; $\chi^2 = 10.0$, d.f. = 1), and knucklewalking is unique to the apes. Chimpanzees supinate their hands during palm-walking, and therefore the animal's rotatable wrist may be partly an adaptation to such arboreal activity. An adaptation allowing dorsiflexion with supination, but not with pronation, is suggested. Note that the distinctiveness of palm-walking is quite small compared to that of arm-hanging, and therefore wrist and hand adaptations to suspensory behaviour must dictate wrist flexibility. The hands and wrists of chimpanzees have distinctive knuckling adaptations[36] which are not present in monkeys and hominids. Chimpanzee walking specializations, however, are not expected outside the manus and carpus, because walking was less common among chimpanzees than baboons (Fisher's exact test, $P < 0.0001$, d.f. = 1; see Table 1), making baboons, not chimps, the walking specialists.

Table 3. Percentage of climbing bouts by WBS diameter.[1]

n	≤ 2	$>2-4$	$>4-6$	$>6-8$	$>8-10$	$>10-20$	>20
			WBS diameter (cm)				
189	14.1	37.9	19.6	9.2	6.1	8.4	5.0

[1]Average of Gombe and Mahale values. Data from ref. 46.

Anatomical adaptations to vertical climbing

Vertical climbing was significantly more common among chimpanzees than baboons (Fisher's exact test, $P < 0.03$, d.f. = 1). It is a relatively stressful activity, since it requires lifting body weight directly against the force of gravity. Its high incidence, distinctiveness and physically demanding nature support previous postulations that this behaviour has important anatomical adaptations. A corollary large-support-climbing hypothesis,[13,14,37-45] however, finds no support in these data. 'Extended-elbow climbing', that is, utilizing a leaning back stance to increase friction on the pes, represented only 0.06% of all chimpanzee positional behaviour.[31] Furthermore, 87% of all climbing was on small supports (≤10 cm) easily gripped by the foot (Table 3; $n = 189$). Mahale and Gombe chimpanzees live in forests where stem diameters are smaller on average and tree heights are lower than in other forests where chimpanzees are found, leaving open the possibility that large-support climbing is more important for rainforest chimpanzees.* There was no significant difference between the diameters of supports used by chimpanzees and baboons while climbing, even though baboons are smaller (Mann-Whitney U test, $U = 5163$, $P = 0.08$), suggesting that chimpanzees do not use their long arms to gain access to resources that baboons could not reach. The high P-value of this test suggests that some difference may be found, however, with more observation.

It is unlikely that vertical climbing selected for ape humeral abductability (shoulder mobility). Humeral abduction was not observed among vertical climbing chimpanzees; rather, the humerus was protracted (flexed) and the elbow was elevated only to perhaps 10 cm above the shoulder.[46,47] The kinematic of this type of climbing was quite similar to that seen among baboons. When climbing large-diameter trees, chimpanzees abducted the humerus even less. Occasionally, chimpanzees leaned back when climbing large trunks to the extent that the humerus rarely rose even above the shoulder.

The relatively low distinctiveness of vertical climbing, the similarity of chimpanzee vertical climbing to that of baboons, and the occurrence of vertical climbing among other primates suggest that specializations for vertical climbing are no greater, or may even be less, than those for arm-hanging.

Arm-hanging adaptations

Arm-hanging with support (Fisher's exact test, $P < 0.0001$, d.f. = 1), hanging by one hand (Fisher's exact test, $P < 0.0001$, d.f. = 1), and arm-hang/standing (Fisher's exact test, $P < 0.005$, d.f. = 1) were each significantly more common in chimpanzees than baboons; together these modes, each of which required complete abduction of the humerus and suspension of more than half the body weight from an arm, constituted 4.4% of all positional behaviour of chimps. Other modes involving humeral abduction, including brachiation, constituted <0.1% of all positional behaviour.

*If so, rainforest chimpanzees should have higher intermembral indices, which is not the case with rainforest-adapted bonobos.[130]

Though it is a posture and therefore exerts less stress on the anatomy than does a locomotor activity, arm-hanging entails significant stresses. Most of the body weight is suspended beneath an eccentrically placed forelimb and is borne in tension by the glenohumeral joint capsule. The humerus, adducted and attached to the body via a rather ventrolateral facing glenoid fossa in most mammals, must be completely abducted. In order to reduce injury and conserve energy, adaptations to arm-hanging must reduce stress on the skeleton during unimanual suspension, and must minimize muscle action.

The shallow ribcage of chimpanzees (and other apes) decreases compressive forces on the upper torso during suspension by reducing the distance between muscular and bony origins of structures that attach to the humerus, even if suspension is of a hand-foot type seen in orang-utans.[46] A deep monkey-like torso is strained more than a shallow ape-like one. The cone shape of the chimpanzee ribcage more closely conforms to the lines of tensile force created by unimanual suspension, which tends to strain the torso so that it more closely resembles a teardrop shape (Fig. 1).

A narrow scapula allows a wider range of scapular rotation, so that during arm-hanging the shoulder joint can more closely approach the midline.[46] Scapular rotation permits the vertebral border of the scapula to approach the spinous processes of the vertebrae (and attached tissues). In humans a large scapular supraspinous area prevents the degree of rotation possible in chimpanzees (Fig. 1). When the glenoid fossa approximates the spinal column during arm-hanging, the spinal column must bend less, and the amount of shear stress in the structures between the glenoid fossa and the spine is reduced. Allowing the shoulder to approach the midline during suspensory behaviour means that a less stressful teardrop shape to the arm and torso can be attained with either arm.

During arm-hanging, a cranially orientated glenoid fossa reduces stretching of the caudal (lower) aspect of the glenohumeral joint capsule, allowing a larger ligamentous surface area to bear body weight (Fig. 1). The only bony link that the forelimb has to the body is that from humerus to scapula to clavicle to sternum. The acromio-clavicular joint (attachment between collar bone and shoulder blade) is robust, being anchored by a particularly large conoid ligament in the chimpanzee.[48] The manubrium is large and broad in apes compared to other primates,[49] in response to its weight-bearing function.

Skeletal features adapted to both arm-hanging and climbing

A number of chimpanzee specializations are adaptations to both arm-hanging and vertical climbing. Of the four positional modes that require a strong manual grip to support the body weight (various arm-hanging modes, clinging, vertical climbing and suspensory locomotion), only arm-hanging and vertical climbing are common enough to have influenced anatomy. The others together constitute <0.3% of chimpanzee positional behaviour. Both arm-hanging (23% of supports were within 30° of true vertical, $n = 435$) and vertical climbing (88% of supports were within 30° of true vertical, $n = 93$) commonly involved bearing a significant portion of the body weight by gripping near-vertical supports. Because the arm itself is near vertical during these behaviours, the forearm and the branch from which the individual hangs are nearly parallel. In such cases, if the wrist is not adducted (ulnar deviated), the fingers remain nearly parallel to the support and cannot grip it. The more nearly parallel the fingers are to the supports, the larger is its effective diameter, and
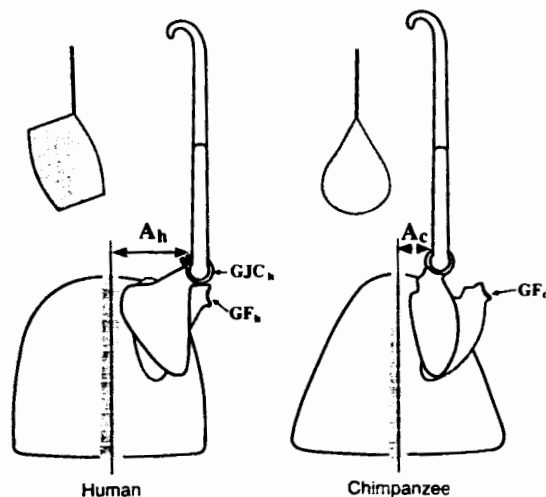

Fig. 1. Schematic human and chimpanzee torsos in posterior view. The 'narrow' scapula and the cone-shaped torso of the chimpanzee allow the scapula to rotate farther towards the midline when the arm is abducted. The distance between the arm and the midline of the torso is greater in humans (A_h) than in chimpanzees (A_c). In chimpanzees the shoulder joint may approach the midline more closely when the arm is abducted. Note that the articulation for the shoulder, the glenoid fossa (black bar labelled GF) is more tilted up (cranially orientated) in the chimpanzee (GF_c) than in the human (GF_h). The glenohumeral joint capsule of humans (GJC_h) is unevenly stretched, causing the lower portion to bear almost all of the body weight during arm-hanging. The glenohumeral joint capsule of the chimpanzee is stretched evenly, thereby allowing more ligament to bear weight. The torso of the chimpanzee is cone-shaped, a form that more closely approximates that of a teardrop, which is the least stressful shape for a voluminous object suspended from a single point. The human torso is more barrel-shaped, causing stress centres that are more prone to fatigue or failure during unimanual arm-hanging (after ref. 46).

the longer the fingers must be to circumduct it. Ulnar deviation (adduction) and long fingers aid in gripping near-vertical branches. Arm-hanging requires more ulnar deviation than climbing because the forearm is more nearly parallel to the support.[46]

Ray curvature serves a muscle sparing function during suspensory behaviour.[50] It also distributes gripping force more evenly around the circumference of the vertical support. Straight phalanges put much of the pressure of the grip on volar tissue near the middle of the phalanx; other tissue is relatively unstressed (Fig. 2). The force of the body weight creates a radial strain on the volar tissue pressed against the support. Other tissue
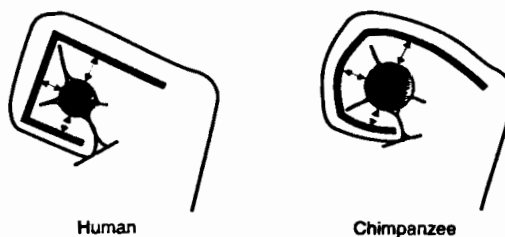

Fig. 2. Schematic gripping statics. Note that with curved phalanges a more uniform distance is maintained between bone (black bars) and a gripped object (stippled area) than with straight phalanges. In a straight-fingered individual, pressure on a branch is higher near the middle of the phalanx where the bone is closer to the branch, whereas in a curved-fingered individual pressure is more uniformly applied along the length of the digit. Note that with curved phalanges the distance between bone and branch remains the same (arrows), but a larger branch may be gripped with fingers of the same length (after ref. 46).

is pulled downwards by the weight of the body, thereby creating torsional strain that may fatigue or damage digital tissue during sustained or repeated arm-hanging. Curved phalanges allow a constant distance between the phalanx and the support along the entire volar aspect of the finger, reducing maximum strain by distributing weight-bearing over a larger area. With straight phalanges, bone near the middle of the phalanx approximates the support more closely than does that near the joints, limiting circumduction; curved phalanges allow fingers of a given length to circumduct larger branches (Fig. 2). Thus, long, curved rays and an adductible wrist may be a functionally related adaptation to permit the strong gripping of vertical or sub-vertical supports during arm-hanging and vertical climbing. Thumbs are reduced in suspensory animals, either absolutely (New World monkeys, African apes) or in relation to hand length (Asian apes[51,52]), though it is not clear why.

Muscular adaptations

Muscles that are distinctively large among apes (Table 4) have higher EMG potentials during vertical climbing than other common positional behaviours, implying that climbing selected for ape muscle mass proportions.[19] New information on positional behaviour adds an increased level of resolution to this perspective. Muscles that are active during important positional modes, that are relatively large, and are not active in any other common behaviour are functionally linked to that positional behaviour.[46] If the same muscles are active in two or more behaviours, each with similar relative importance, large muscle mass is likely to be adapted to all the activity. Two behavioural hypotheses are supported by such data for chimpanzees (Table 4). First, an elbow flexor (biceps brachii) and a major humeral retractor (latissimus dorsi) are unambiguously associated with a pull-up action observed commonly only during vertical climbing. Second, teres minor, middle caudal serratus anterior and cranial

Muscle	Likely adaption	Larger in chimps ?	Active during humeral retraction	Active during walking	Active during arm-hanging	Active in protraction or abduction?
			Table 4. Muscle size and function in chimpanzees.[1]			
Biceps brachii	**VC**	+++	+++	– –	– –	$(-)^2$
Brachialis	VC?	++, –	++	–	– –	
Brachioradialis	VC?	+, –	+++	– –	– –	
Deltoid (whole)		+++			$(- -)^2$	+++
-anterior	VC,AH?		+	+++	– –	++
-intermediate	**AH**	+++	–	++	– –	+++
-posterior	VC?		+++	++	+, – –	– –, ++
Infraspinatus	0	0, –	–	+	++, – –	+++
Latissimus dorsii	**VC**	+++	+++	– –	– –	– –
Pectoralis major		+++				
-clavicular	VC, AH?		$(+++)^2$	+	–	$(+++)^2$
-sternocostal	VC?		++	++	– –	– –
Pectoralis minor	0	0		++		
Rhomboids	X	+	–	+	– –	–
Serratus anterior						
-middle caudal	*VC, AH*	++	–	– –	– –	++
-lowest caudal	*VC, AH*	++	++		++	– –
Subscapularis	0	–	++, –	+	– –	+
Supraspinatus	0	0, ++, – –	++	++	– –	++
Teres -major	0	0	+++	– –	– –	–, +
-minor	*VC, AH*	+	+	–	+, – –	–
Trapezius cranial	*VC, AH*	++	–	– –	– –	+
-caudal	X	++			$(++)^2$	++
Triceps	0	– –	–	+	– –	+

[1] As reviewed in ref. 45 and references therein.
Likely adaptation: Bold, adaptation to a single positional behaviour is suggested; *italics*, adaptation to two behaviours suggested; ?, some data missing, but adaptation likely; 0, muscle size smaller in apes, so no behavioural specialization identifiable; X, too few data, or not distinctive; VC, vertical climbing; AH, reaching during arm-hanging.
Muscle size (when results are contrary more than one value is given): +++, much larger in apes by most measures; ++, larger in apes by most measures or larger in most apes; +, somewhat larger in apes by most measures; 0, no larger in apes or variable according to measure; –, smaller in apes or variably smaller according to measure; – –, much smaller in apes in most studies.
EMG activity: +++, marked in most or all studies; ++, variably high (by study or experiment) or consistently moderate; +, low or variably moderate; –, inactive in most studies or very low activity; – –, inactive in all studies.
[2]EMG data from gibbons.

trapezius are unambiguously associated with arm-raising, a motion observed both during the swing phase of vertical climbing and in reaching out for food while arm-hanging. Intermediate deltoid is active in abduction, not protraction, and is therefore inferred to be an adaptation to reaching out during arm-hanging, not vertical climbing. Other elbow flexors (brachialis and brachioradialis) active during humeral retraction may be adapted to climbing if they are not used during protraction and abduction. Although details on the relative size of cranial and caudal pectoralis major are lacking, the greater size of the entire muscle suggests that both are relatively larger in apes than monkeys. Caudal pectoralis major and pectoralis minor are most active during humeral retraction in the support phase of vertical climbing, and are therefore probably adaptations to it. Lowest serratus anterior is active during both arm-hanging and arm retraction, and may be maintained for both climbing and suspension. Cranial pectoralis is active in rapid non-weight-bearing protraction of the arm during climbing; it may also aid in reaching out during feeding. If posterior deltoid is larger in apes, it is probably an adaptation to vertical climbing.

Large biceps brachii and latissimus dorsi are clear vertical climbing adaptations. The former passes through a deep, well-defined bicipital groove in great apes.[53] The groove is smaller in gibbons. The coracoid process, the origin of biceps brachii, is large in apes.[1]

Anatomical interpretations summarized

Ellefson[54,55] was perhaps the first to warn against interpreting anatomy on the basis of locomotor behaviour to the exclusion of posture, and the first to suggest the pre-eminence of feeding adaptations in explaining morphology. Chimpanzee positional behaviour, mechanics, EMG activity and relative muscle mass all provide strong support for previous contentions that most osteo-ligamentous specializations of the chimpanzee upper body are adaptations to a posture, namely arm-hanging,[56] and that most muscular specializations are adaptations to vertical climbing.[19] Large elbow flexors and humeral retractors are best explained as adaptations to vertical climbing.[19,38] Observations on chimpanzees suggest that large humeral protractors are likely to be adaptations to arm-raising both during vertical climbing and while reaching out to feed during arm-hanging. Humeral abductors probably aid only in reaching out during food gathering while the animal is suspended. Large digital flexors and an iliac origin of latissimus dorsi may aid in both modes. Although the relatively low activity of most muscles during brachiation (*sensu stricto*) precludes a general hominoid muscular brachiating adaptation, skeletal and ligamentous adaptations for suspensory posture may serve similar functions during locomotion while suspended.

Robust clavicular anchors, anteroposteriorly flattened thoraxes (and accompanying strongly curved ribs), mobile, abductible humeri, wide manubria of the sterna and cranially orientated glenoid fossae are postulated to be a functionally related adaptive complex that reduces anatomical strain and therefore fatigue during suspensory posture. Furthermore, among one-handed arm-hanging specialists such as the chimpanzee, cone-shaped rib-cages and long, narrow scapulas further reduce stress. The low frequency of climbing large supports and the fact that both baboons and chimpanzees can climb vertical objects of similar

					Percentage of postural behaviour						
Species	Sit	Lie	Stand	Squat	Cling	Bip. stand	Arm-hang	Hand-foot-hang	n	Reference
Hylobates agilis[2]	65.5	0.0	0.0	0.0	0.0	0.0	34.5	0.0	322 bouts	60
Hylobates pileatus[3]	61.7	0.0	0.0	0.0	0.0	0.0	38.3	0.0	655 observations	61
Hylobates syndactylus[4]	38.3	0.0	0.0	0.0	0.0	0.0	61.7	0.0	1376 observations	62
Hylobates syndactylus[5]	47.0	0.0	0.0	0.0	0.0	0.0	53.0	0.0	234 observations	63
Pan paniscus[6]	90.0	3.0	2.0	0.0	0.0	0.0	5.0	0.0	132 observations	64
Pongo pygmaeus[7]	46.0	0.0	24.4	0.0	0.0	0.0	29.7	0.0	5836 bouts	65
Pongo pygmaeus[8]	42.1	0.0	6.7	0.0	0.0	3.8	17.8	30.0	350 bouts	66
Pongo pygmaeus[9]	49.0	0.0	1.0	0.0	0.0	2.0	12.0	36.0	1682 min.	20
Pan troglodytes[10]	80.0	5.0	15.0	0.0	0.0	0.0	0.0	0.0	186 hours	67
Pan troglodytes[11]	75.8	16.9	5.8	0.0	0.0	0.0	1.6	0.0	8658 observations	68
Pan troglodytes[12]	75.2	15.1	3.0	0.8	0.4	0.4	5.3	0.0	11848 observations	This study
Pan troglodytes[13]	80.9	3.4	1.3	1.9	0.3	0.3	12.1	0.0	2518 observations	This study
Gorilla gorilla[14]	60.3	1.3	2.7	35.4	0.0	0.2	0.0	0.0	2300 hours	69
Papio anubis[15]	75.3	4.0	19.7	0.2	0.3	0.1	0.2	0.0	1555 observations	This study
Papio anubis[16]	75.9	0.0	21.1	0.6	1.0	0.2	1.0	0.0	580 observations	This study

Table 5. Posture compared in the Hominoidea.[1]

[1] Table largely after ref. 21. [2] Scan surveys, every 10 minutes. [3] Scan surveys, every 5 minutes. [4] Total positional behaviour during feeding. [5] Focal observations; instantaneous every 5 seconds. [6] Instantaneous surveys while feeding on fruit. [7] Bouts during travel and resting. [8] Bouts while feeding on *Ficus* fruit. [9] Per cent of time in each posture for feeding females. [10] Per cent of time in each posture. [11] 1-minute instantaneous focal observations; adults only. [12] 2-minute instantaneous focal observations standardized for hour of day; adults only. Mahale and Gombe profiles averaged. [13] 2-minute instantaneous focal observations while feeding on fruit standardized for hour of day; adults only. Mahale and Gombe profiles averaged. [14] Per cent of time in each behaviour, juveniles included. [15] 2-minute instantaneous focal observations; all contexts. [16] 2-minute; instantaneous focal observations during feeding bouts.

size in the same way suggests that vertical climbing is not responsible for such chimpanzee specializations as a high intermembral index and shoulder mobility. Long forelimbs serve to extend reach during suspensory feeding,[14,18,20,51] augmenting available support selection and increasing the number of food items accessible to an individual feeding among terminal branches.[20,57,58] Attenuated hind limbs may function both to lighten the lower body and to bring the centre of gravity closer to arboreal supports, thereby decreasing the risk of falling.[20,59] Liberal ulnar deviation of the manus, long, curved metacarpals and phalanges are likely to be adaptations to both vertical climbing and arm-hanging.

Comparisons with other ape posture data

Previous studies of positional behaviour in other apes provide clear evidence that the shared adaptations of apes are suspensory behaviour and vertical climbing. Observations on ape and baboon behaviour are compared in Tables 5 and 6. Positional profiles (see above) could not be established from most ape studies, so posture and locomotion are considered separately. To facilitate comparisons, subsamples of chimpanzee and baboon data were selected from this study to conform to the contexts (e.g. arboreal observations only, feeding data only, etc.) or data collection protocols of other studies, enabling a comparison of three species under similar conditions. Thus, a gibbon study in which observations on posture were made during arboreal feeding only are compared with chimpanzee and baboon observations from this study limited to arboreal feeding only (Table 5).

Hylobatids (gibbons and siamangs) and chimpanzees share a common propensity to arm-hang while feeding (35% of behaviour or more in hylobatids, 12.1% in chimpanzees) compared to baboons (only 1% during feeding). No other behaviour distinguished both members of this dyad from baboons. Arm-hanging (>5%) was the only behaviour that distinguished the bonobo-chimpanzee dyad from baboons. It is the shared posture that most distinguished chimps and orangs from baboons (>11% vs. 0.0%).

Mountain gorillas do not hang from trees, but lowland gorillas do,[74] although less so than chimpanzees. Lowland gorilla morphology is more chimpanzee-like than that of mountain gorillas.[49]

These comparisons show that arm-hanging is the only posture that distinguishes apes from baboons. With the exception of mountain gorillas[69] and one chimpanzee study,[67] all ape studies report a disposition to arm-hanging. No other posture was so uniformly distinctive, and only sitting was more commonly encountered among apes.

Comparisons with ape locomotion data

Brachiation was the most distinctive hylobatid locomotor behaviour, but climbing was the most distinctive locomotor mode among hylobatids and chimpanzees (6–54% and 4.9%, respectively) compared to baboons (0.7%) (Table 6). No other locomotor activity is represented in all studies in both hylobatids and chimpanzees at an incidence higher than 1%.

Bonobos and chimpanzees commonly displayed climbing, brachiation and bipedal walking compared to baboons (compari-

Table 6. Locomotion compared in the Hominoidea.										
Percentage of locomotion behaviour										
Species	Walk	Climb	Leap/Hop	Run	Bip. walk	Brachiate	Clamber	Other susp.	Transfer	n	Reference
Hylobates agilis[2]	3.5	6.3	23.9	0.0	0.0	66.3	0.0	0.0	0.0	255 observations	60
Hylobates lar[3]	0.0	34.1	9.5	0.0	5.2	51.2	0.0	0.0	0.0	211 bouts	70
Hylobates pileatus[4]	0.0	6.0	8.7	0.0	0.9	84.4	0.0	0.0	0.0	218 observations	61
Hylobates synd.[5]	0.0	10.0	0.0	0.0	11.0	80.0	0.0	0.0	0.0	208 observations	63
Hylobates synd.[6]	0.0	54.3	3.2	0.0	4.6	37.9	0.0	0.0	0.0	1206 bouts	62
Pan paniscus[7]	34.0	20.0	18.0	0.0	8.0	20.0	0.0	0.0	0.0	131 bouts	71
Pan paniscus[8]	31.0	31.0	10.0	0.0	6.0	21.0	0.0	0.0	0.0	1722 bouts	72
Pan paniscus[9]	22.5	48.2[8]	10.8	0.0	1.2	17.1	0.0	0.0	0.0	2608 bouts	68
Pongo pygmaeus[10]	13.0	10.0	0.0	0.0	0.0	21.0	41.0	0.0	15.0	219 hours	73
Pongo pygmaeus[11]	10.8	9.8	0.0	0.0	0.0	19.8	43.0	0.0	16.8	10601 bouts	65
Pongo pygmaeus[12]	12.0	31.3	0.0	0.0	0.0	10.6	39.4	1.2	5.6	4360 minutes	20
Pan troglodytes[13]	86.1	11.0	0.3	0.0	1.2	1.3	0.0	0.0	0.0	1421 observations	68
Pan troglodytes[14]	92.1	4.9	0.1	1.3	0.4	0.5	0.3	0.0	0.3	2239 observations	This study
Pan troglodytes[15]	36.4	48.9	0.4	0.3	6.7	5.3	2.3	0.6	2.4	223 observations	This study
Papio anubis[16]	97.0	0.7	0.5	1.6	0.0	0.0	0.0	0.0	0.0	497 observations	This study
Papio anubis[17]	64.2	21.3	10.4	4.1	0.0	0.0	0.0	0.0	0.0	26 observations	This study

[1] Table largely after ref. 21. [2] 10-minute scan surveys. [3] Bouts, continuous focal observation. [4] 5-minute scan surveys. [5] Focal observations; instantaneous every 5 seconds. [6] Bouts, continuous focal observation; feeding and travel bouts pooled. [7] Bouts during arboreal feeding. [8] Arboreal bouts. [9] Arboreal bouts. [10] Bouts during travel. [11] Bouts during travel. [12] Travel distance during feeding and travel. Females only. [13] Locomotion in all contexts. 1-minute instantaneous focal observation. Scrambling included in climbing. [14] Locomotion in all contexts; 2-minute instantaneous focal observation. Standardized for hour of day; Gombe and Mahale pooled. [15] Arboreal locomotion in all contexts; Gombe and Mahale data pooled. Too few observations to standardize. [16] Locomotion in all contexts. Standardized for hour of day; mid-sex, adults only. [17] Arboreal locomotion in all contexts; adults only. Mid-sex; too few observations to standardize by hour.

son is for arboreal positional behaviour only, since bonobos were not observable on the ground). The frequency of climbing was similar among chimpanzees (49%) and the two longer bonobo studies (31–48%), and notably more common than among baboons (21%). Although arm-swinging (brachiation) was more established among bonobos than chimpanzees (17–21% vs. 5%), climbing was the most consistently distinctive locomotor mode in the *Pan* dyad compared to baboons.

Climbing (10–31%, 5%) was most distinctive of the orangutan-chimpanzee dyad compared to baboons (<1%). It was the only locomotor activity with a high frequency in the one group and low frequency among the other.

In most of these studies climbing encompassed some suspensory behaviours and walking, which are very different from vertical climbing. Vertical climbing is therefore less distinctive than might appear to be the case if 'climbing' and 'vertical climbing' were the same behaviour.

Climbing was the only distinctive locomotor behaviour shared by all apes, constituting 5% or more in each (mountain gorillas excepted). Brachiation had a frequency of only 0.5–1.3% among chimpanzees, and is therefore unlikely to have exerted a significant selective pressure on at least the chimpanzee anatomy. No ape was given to walking like the baboons.

Summary of positional behaviour of apes

Current knowledge of the positional behaviour of the greater and lesser apes constitutes powerful evidence that two behaviours are most distinctive: suspensory activity, especially unimanual arm-hanging, and, perhaps to a lesser extent, vertical climbing. To the extent that the corresponding anatomical features are found in early hominids, they suggest similar behaviour.

Ape bipedalism

Note that apes in closed forest habitats are more bipedal than chimpanzees and baboons, whether stationary (orangs, Table 5) or when moving (gibbons, bonobos, Table 6). This suggests that terrestriality is not necessarily a spur to bipedal behaviour, but the opposite.

Chimpanzee bipedalism

Ninety-seven instances of bipedalism among 21 individuals were sampled in 700 hours of observation, no two consecutively. Random observations (i.e. on non-target individuals) were used as supplemental evidence. These data showed that among chimpanzees, as is the case among baboons,[22,75,76] bipedalism is used when feeding. Eighty per cent of chimpanzee bipedalism was during feeding; 86% of all bipedal activity arboreally and 70% terrestrially, and an overwhelming percentage of these bouts was postural (95%, Table 7). During arboreal feeding, arm-hanging and bipedalism were linked. A forelimb set in an arm-hanging position stabilized bipedal posture in 93% of observations among terminal branches ($n = 27$, Table 2) and 52% ($n = 23$) of those in the central portion of a tree. Semi-suspension was less common during bipedalism on the ground, where only 42% 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. A small proportion of terrestrial bouts was locomotor bipedalism when the animal moved between feeding sites in the same tree (4%). That is, short-distance, within-site shuffling rather than long distance travel was the most common context for locomotor bipedalism among chimpanzees. Such

Context	Arboreal		Terrestrial		Total	%
	Unassisted	Assisted	Unassisted	Assisted		
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

Table 7. Contexts of bipedal behaviour.[1]

[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 hindlimbs, but a substantial proportion was borne by a fully abducted forelimb in a semi-suspensory mode.

[2] Bipedal walking.

bipedal behaviour as looking around (2%) and social display (1%) were rare (Table 7).

Bipedalism was practised both on the ground and aloft when the animals fed from four fruit trees, *Garcinia huillensis, Harungana madagascarensis, Monanthotaxis poggei* and *Grewia* sp. Together these trees were associated with 27% of all bipedal feeding episodes, and 48% of the occasions when the plant material being eaten could be identified (Table 8). Fruits were harvested while the animals reached up into the trees while standing on the ground, or, when aloft, with a posture stabilized by arm-hanging. All four of these tree species have diminutive understories (Table 8) and are 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, 1cm and 1cm, respectively) and are distributed evenly among the terminal branches. Although fruit gathering was not seen both on and off the ground with any other tree, other diminutive trees with small fruits elicited bipedalism with the animals either in the branches or still on the ground much more commonly than large trees (Table 8). The number of observations of chimpanzees eating fruits was similar for small and large trees (1439 vs. 1536), but bipedal food collecting was significantly more common among small (mature height of ≤15 m) trees with small fruits (44 vs. 8, Fisher's exact test, $P < 0.001$, d.f. = 1, Table 8), suggesting that fruit diameter and/or tree height are the critical factors. It is difficult to distinguish between the effects of small trees and small fruits, since all but one small tree also had small (<2 cm) fruit.

Where plant foods gathered during bipedal bouts were identified, 28 of 33 fruits were less than 2 cm in diameter.

The size of the branches bearing fruit appeared to be a major determinant of whether or not bipedalism was used arboreally. As was the case with arm-hanging,[31] bipedalism was more common among smaller weight-bearing structures. Bipedalism was observed more often on relatively small 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 supports stable enough for sitting or unassisted bipedal standing. Small branches are too unstable to allow animals easily to keep their balance bipedally unless they use both hands and feet.

Foraging in short trees with both feet on the ground allowed individuals to reach higher into the tree, thereby bringing more fruit within reach, and to use both hands to maximize the gathering of small fruits.[24,81] Note that it is the picking component of small-fruit collecting that slows ingestion, not chewing.

Small changes in position up trees and shuffling on the ground are advantageous for collecting small, evenly distributed fruits in trees,[24,81] where feeding sites are depleted quickly.[29] Postures that allow a switch to locomotion with little energy cost are preferred.[29]

Australopithecine anatomy

Torso and forelimb

The australopithecine torso is broad, shallow and cone-shaped[82,83,84] (Fig. 3), the glenoid fossa orientated cranially[1,4] at

Table 8. Food resources utilized during bipedal behaviour.

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 diam.
Invert.								large: 12		
		1	5	8	1		15	small: 1	forest	small
Garcinia		3(1)[5]	7				11	4–8 m[6]	open	1–2 cm
Unidentified									open:2	
fruits			3(1)		2	2	8	small	no rec.: 6	no rec.
Leaf								large: 1		
	1	2	1		1	1	6	small: 5	varied	
Soil, inorg.					5		5	–	forest	
Harungana		1			2	1	4	4–7 m[6]	open	4 mm[6]
Monanthotaxis			1		3		4	shrub	open	7–12 mm[6]
Ficus								large: 2	/	large: 1
		2	1				3	2 m: 1	varied	1 cm: 1
Grewia				1		1	2	5 m[6]	open	1 cm[6]
Unidentified fruit						2	2	large	forest	–
not recorded	?	?	?	?	?	?	2	–	–	–
shoots/new leaf		1	1				2	small	forest	small
piths						2	2	–	open	
monkey								small: 1	open	
			(1)	1			2	large: 1	forest	
Psychotria					1	1	2	shrub	forest	5 mm[6]
Landolphia				1			1	large	forest	2–7 cm[7]
Saba			1				1	large	forest	5–6 cm[8]
Pycnanthus	1						1	large	forest	4 cm[9]
Cordia				1			1	small[6]	open[6]	1 cm[6]
Blossom						1	1	small	open	small
Uapaca			1				1	6–10 m[6]	open	1.5–2 cm[6]
Parinari			(1)				1	13 m[6]	open	2.5 cm[6]
Ampelocissus			1				1	2 m[6]	open	◁ cm[9]
Totals	2	11	25	12	15	11	78			

[1] t.br., terminal branches, i.e. within 1 metre 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 from ref. 77 listed for small trees; >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 ref. 77.
[5] Figures in parentheses are locomotor bouts; other values are for posture. [6] Ref. 77; [7] ref. 78; [8] ref. 79; [9] ref. 80.
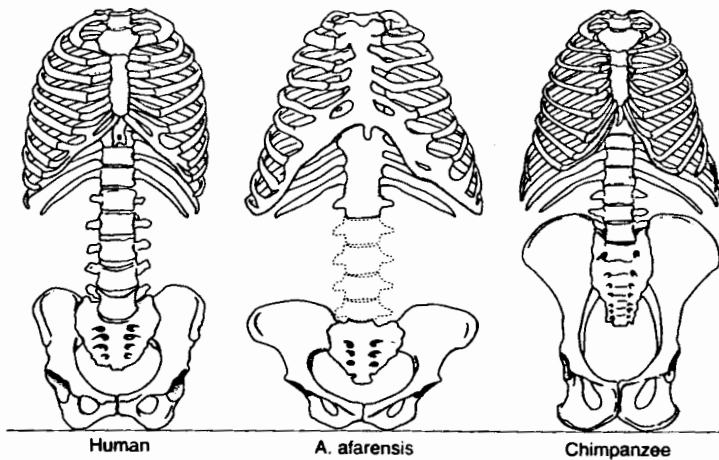
Fig. 3. Thoraxes of a modern human, a chimpanzee (after Schultz) and a reconstruction of AL 288 (after ref. 83). Note the similar cone-shape of the ribcages of AL 288 ('Lucy') and the chimpanzee, postulated as functioning in conjunction with a cranially orientated glenoid fossa and an elliptical scapula to reduce stress during arm-hanging. Such a configuration is hypothesized to distribute stress more evenly on the thorax and the glenoid capsule during unimanual arm-hanging, thereby reducing fatigue and obviating muscle action. Thoraxes scaled to same height (after ref. 30).

Human   A. afarensis   Chimpanzee

an angle intermediate between that of chimpanzees and humans, the cross-sectional area of the vertebral column small and chimpanzee-like,[1,85] and the brachial index is chimpanzee-like.[86] These features are adaptations to arm-hanging,[46] though mostly expressed less than is the case with chimpanzees.

The coracoid process (origin of biceps brachii) is large[1] and the supracondylar ridge (origin of brachioradialis) is huge.[88] These features are adaptations to vertical climbing.[46]

The australopithecine wrist is mobile,[89] the fingers curved (although shorter than those of apes),[3] the thumb short with an ape-like articulation,[3,89] arm and leg length proportions intermediate between modern humans and chimpanzees, even when the diminutive stature of the fossils is considered,[90,91] and hand morphology is indicative of powerful chimpanzee-like grasping ability.[3] The deltoid tuberosity is large and laterally flaring, suggesting a large deltoid.[86,88] These are features functionally related to both arm-hanging and vertical climbing.[46]

The bicipital groove is large,[1,87] but open and shallow,[89] more similar to that of humans than chimpanzees. The function of a large lesser tubercle and therefore a deep (i.e. chimpanzee-like) bicipital goove may be either to increase the lever arm of subscapularis or to prevent bowstringing when the elbow is flexed with the arm above the head. In either case the australopithecine condition indicates a lesser adaptation to vertical climbing in hominids than in chimpanzees. Australopithecines have six lumbar vertebrae[1] (Sts 14), a feature not found in living hominoids, and therefore not likely to be an adaptation to arm-hanging or vertical climbing.

Human-like features of the pelvis and hindlimb

In both general morphology and detail, the pelvis and the lower body morphology of *Australopithecus afarensis* and later hominids unambiguously indicate bipedalism.[89,92–95] The lumbar vertebrae are lordotic,[96] the sacral alae are expanded and the pelvis has a human gestalt.[89,95] The femur has a deep patellar groove and at least some specimens have an elliptical lateral condyle. The calcaneus is essentially modern.[93] The great toe is robust and the foot has well-developed transverse and longitudinal arches.[94,97] Because the gestalt of the lower body anatomy of *A. afarensis* clearly indicates an organism adapted to bipedal locomotion,[92–95,98,99] it is intriguing that it is a bipedalism that is not as refined as that of modern humans (Fig. 4).

Unique features of the pelvis and hindlimb

Although the os coxae are human-like in appearance, the *A. afarensis* pelvis differs from that of modern humans in ways that

suggest less than optimum bipedal locomotor capabilities. *A. afarensis* has smaller sacro-iliac ligaments than those of modern humans.[3] The width of the AL 288 pelvis is proportionally greater than the femoral neck length, suggesting a greater joint reaction force at the hip and a lower mechanical advantage for muscles that prevent the hip from collapsing when one foot is off the ground than in modern humans.[91] A relatively small acetabulum/femoral head in australopithecines compounds the stresses caused by wide hips, creating even more stress in the hip joint. Perhaps most surprising, *A. afarensis* has extremely wide hips. This causes the moment arm of the body weight of *A. afarensis* to be increased greatly over that of modern humans, increasing the stress on the diaphyseal/femoral neck junction when bearing weight.

The extraordinarily wide hips of AL 288[100,101] and Sts 14[1] are due in part to highly reflected ilia, but also to an unusually broad pelvic inlet.[1] The pelvic index averaged 77.6 for a sample of modern human females,[102] but was 57.6 for AL 288-1. The spectacular biacetabular width of australopithecines is particularly at odds with an adaptation for efficient, stress-reduced bipedal
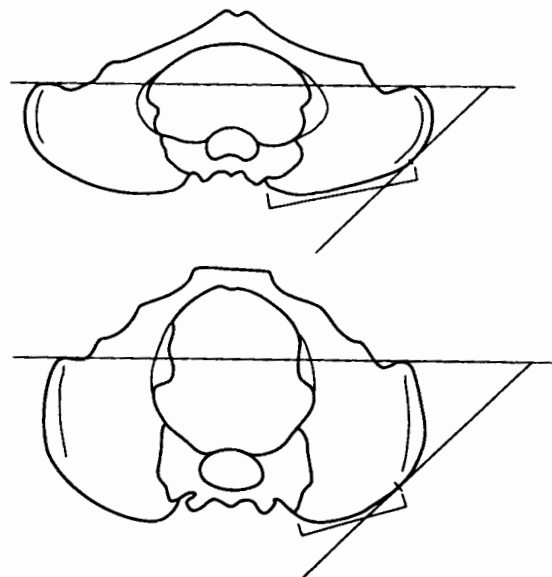

Fig. 4. Superior view of pelves of a modern human female and AL 288. A coronal plane has been established by drawing a line between the anterior superior iliac spines. A 45° line drawn intersecting this line and the iliac crest roughly divides the pelvis into laterally facing and posteriorly facing planes (brackets). Note that the posteriorly facing plane is approximately twice as long in AL 288 as in the modern human female, making AL 288 divergent in the direction of apes. Redrawn from ref. 95.

locomotion. A broad pelvis decreases energetic efficiency by requiring greater muscular activity during walking[91] and produces high stress on the femoral neck.[30] If australopithecines were well-adapted to bipedal walking, they would be expected to have hips as narrow as possible.[101] Although a large biacetabular breadth in modern humans is a necessary adaptation for giving birth to large-headed offspring, cephalopelvic reconstruction of AL 288-1 shows a considerable gap between the foetal head and pelvic inlet walls opposite the acetabula.[102] That is, the pelvis is much broader than could possibly be necessary for parturition.

Other features suggest reduced locomotor competence as well. A. afarensis has quite short hindlimbs for its weight and height, suggesting greater energy expenditure per distance travelled.[91] The lumbar vertebrae and lumbosacral articular surface of other australopithecines are small, whether in proportion to body weight, hip width or nearly any other measure that has been attempted.[1,85,89,91,101] This suggests greater stress on the lumbar vertebrae during bipedal locomotion, with proportionally greater stress during arm-carrying.

Taken as a whole, then, three observations 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: (1) australopithecines experienced high pelvic and femoral stresses, (2) they had a small diameter spine, small joint surfaces below the waist and smaller-than-modern-human sacro-iliac attachments, and (3) their wide hips and short legs required more energy per unit distance to operate. In short, australopithecines were less well-adapted for sustained bipedal walking and/or carrying than are modern humans.[30,85,91]. This anatomy suggests one of three possibilities; that energy consumption is not an important consideration for A. afarensis, that it practised 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 first is extremely unlikely.[103] The last two explanations are possible. In either case a lower frequency of bipedal walking is suggested compared to modern humans.

Ape-like features of the pelvis and hindlimb

The locomotor anatomy of A. afarensis involves not merely a less efficient version of a modern pelvis; a number of features are ape-like, and presumably adaptations to arboreal behaviour. Ape-like features of the medial cuneiform indicate rudimentary first toe abductibility[3,104] contra Latimer and colleagues.[105] A. afarensis also has long, curved toes,[2,3] an antero-posteriorly short, rounded lateral femoral condyle (at least for some specimens[89,106,107]). A strongly developed fibular groove for the tendon of the peroneal muscle is consistent with ape-like great-toe flexion.[2,104] Chimpanzees use this capacity to grip branches when standing in trees or climbing. A large peroneus longus indicative of a powerful grip, it may be large in early hominids to help support the arch. If so, bipedalism would be that much less energetically efficient, since muscular support would be used during support and toe-off, rather than a non-energy-consuming ligamentous support. A long moment arm for the hamstrings[3] increases the power of hip extension, implying a better climbing adaptation than in modern humans. A plantar set or at least greater mobility[89,94] of the ankle allows full plantar-flexion of the foot, common when the toes grip a branch to support body weight with the hindlimb in tension (pers. obs.). Curved pedal phalanges[21,108] and a third pedal digit longer than the first or

second[3] 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 longstanding adaptation

A possible explanation of arboreal and energy-inefficient features in australopithecines is that they are merely holdovers from a previous, more arboreal adaptation. It seems extremely unlikely that these features would have persisted from the ape-human split at perhaps 6 Myr ago through to A. afarensis, A. africanus and even to a great extent in Homo habilis[101,109,110] at <2.0 Myr only to have been lost suddenly with the appearance of Homo erectus.[91,111-114] The relatively modern postcranium of Homo erectus suggests that the scavenging, hunting, provisioning and carrying arguments for the origin of bipedalism and heat stress models[91,98,110,115-118] are more convincing explanations for the later refinement of locomotor bipedalism than for its origin.

Australopithecine ecology

Faunal assemblages from australopithecine localities suggest a range of bush-savanna to woodland habitat, perhaps even subtropical forest,[119,120] although forest that is not as tropical and closed as that preferred by chimpanzees.[121-125] This is quite different from the 'open savanna'. The diminutive trees at which chimpanzees feed bipedally are found in the most open habitats in their ranges, locations quite similar to those which australopithecines are believed to have occupied. A frugivorous adaptation for australopithecines is suggested by tooth microwear evidence.[126-128] There is little evidence for the presence of graze or subterranean resources in the australopithecine diet.[126-128]

The bipedal postural feeding hypothesis

The best reconciliation of australopithecine functional morphology and chimpanzee bipedal behaviour is a synthesis of what are perhaps the two most plausible postulates for the evolution of bipedalism, Tuttle's hylobatian hypothesis[25] and the Jolly/Rose/Wrangham[27,29,81] terrestrial feeding hypothesis. The postural feeding hypothesis proposes that, compared to modern humans, australopithecines occupied a more postural, more arboreal bipedal fruit-gathering niche. Whereas early hominids were adapted to both postural and locomotor bipedalism, bipedal locomotion was less common than in modern humans. This hypothesis suggests that the typical australopithecine arboreal feeding posture was bipedalism stabilized by gripping an overhead branch, that they reached up into trees to feed while standing on the ground, and that they walked upright in search of food, but less efficiently than can modern humans.

Among the features of australopithecines that are consistent with the postural feeding hypothesis, and inconsistent with the idea of long-distance locomotion or carrying ability, are small joint surfaces from the lumbosacral surface down, through which the weight of carried objects must pass,[85] short hindlimbs,[1,90] femoral shaft obliquity greater than that of modern humans,[1,107] lack of an iliofemoral ligament (in smaller individuals), and poorly developed sacrotuberous and sacroiliac ligaments.[3] These features are poor adaptations to walking upright, but are wholly consistent with bipedal postural gathering, both in trees and on the ground. Wide hips are less disadvantageous for postural bipeds because stresses that wide hips cause when walking do not arise when simply standing. Wide hips lower the centre of

gravity, and make it easier to maintain balance in trees.[129] When standing or walking bipedally in trees, such an adaptation is preferable to the high centre of gravity that narrow hips, long legs and wide shoulders give modern humans. The postural feeding hypothesis reconciles the seeming contradictions between australopithecine anatomy that at once suggests arboreality, bipedality and locomotor inefficiency.

Summary and conclusion

Thirty-five years ago Jolly[24] proposed that the eating of small objects on the ground led to human bipedalism. The hypothesis was refined by Rose.[26] It was embellished by Wrangham,[29] who suggested that a significant advantage of habitual bipedalism is that it reduces 'gear change' costs that quadrupedal animals suffer when moving between adjacent feeding sites in the search for small grains to eat. The principal objection to this hypothesis is the persistence of an anatomy indicative of arm-hanging and climbing for millions of years after the adoption of bipedalism.

An arboreal or hylobatian hypothesis put forward by Tuttle[25] and Stern[28] proposed that postural bipedal feeding in trees and movement among branches evolved in a small-bodied protohominid before a significant shift to life on the ground. The pre- or protohominid forelimb anatomy was poorly adapted for quadrupedalism, favouring habitual bipedalism in an animal already practising it. Discovery of a gibbon-like common ancestor for chimps and humans would be strong confirmation of this hypothesis. Even if the ancestor is not gibbon-like, poor quadrupedal mechanics still may have provided a significant impetus towards bipedalism.

Although the 'small object feeding' and hylobatian hypotheses are typically perceived as contradictory, chimpanzee ecology and australopithecine anatomy support a synthesis of the two into a bipedal 'postural feeding hypothesis'. Australopithecine anatomy of the lower body suggests a striding bipedalism less adapted to endurance than that of modern humans, but still hardly distinguishable kinematically from our own. At the same time, short lower limbs, long curved toes, and wide pelves are arboreal adaptations. The upper body morphology of australopithecines is generally intermediate between that of humans and that of chimpanzees. Australopithecine anatomy, taken as a whole, suggests that arm-hanging bipedalism in trees was a common activity as was the upright gathering of food on the ground. Arm-hanging bipedalism is particularly effective for harvesting small fruits in trees because it provides maximum support and mobility. Bipedalism on the ground allows an individual to reach food items higher in the tree and to use both hands for gathering.[81] Arboreal semi-bipedal pre- and protohominids confronted with a more open forest may have found bipedal feeding and bipedal shuffling the most energy-efficient terrestrial positional behaviour, leading gradually to more committed bipedalism as they became more terrestrial.

The persistence of arm-hanging features in later hominids[1,101,110] suggests that this adaptation may have remained relatively unchanged, even in *Homo habilis*,[109] until the evolution of a more locomotion-orientated, near-modern postcranial anatomy in *Homo erectus*.[27,91,111-114] Bipedalism may therefore have originated as a feeding posture that was only later refined into an efficient locomotor adaptation.

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