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

Kevin D. Hunt

Department of Anthropology, Indiana University, Bloomington, IN 47405, USA.

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 diosporaceous, 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 (adducible humeri, shallow ribs, long narrow scapulae, crassly oriented glenoid fossae, robust clavicular anchorage, and wide manubria of the sternum) is adapted for reducing muscle action and structural fatigue during arm-hanging. Other ape features in hominids (a large index excursion of the manus, and long, curved metacarpals and phalanges) are adaptations both to 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 ways. First, a thorough understanding of the link between behavior and anatomy in chimpanzees allows us to understand what chimp-like characters in australopitheces mean in a clearly bipedal animal. Second, the characters in common in quadrupedal chimpanzees are likely to be similar to those that selected for a greater frequency of bipedalism in proto-hominids. A better understanding of chimp-like behavior 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 reconceptualizing their way of life is interpreting our interpretation of the earliest hominids in two separate, vital ways. First, a thorough understanding of the link between behavior and anatomy in chimpanzees allows us to understand what chimp-like characters in australopithecines mean in a clearly bipedal animal. Second, the characters in common in quadrupedal chimpanzees are likely to be similar to those that selected for a greater frequency of bipedalism in proto-hominids. A better understanding of chimp-like behavior 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 reconceptualizing their way of life is interpreting our interpretation of the earliest hominids in two separate, vital ways. First, a thorough understanding of the link between behavior and anatomy in chimpanzees allows us to understand what chimp-like characters in australopithecines mean in a clearly bipedal animal. Second, the characters in common in quadrupedal chimpanzees are likely to be similar to those that selected for a greater frequency of bipedalism in proto-hominids. A better understanding of chimp-like behavior and australopithecine anatomy is perhaps the best argument we can advance at present for understanding why bipedalism evolved.

Larger apes have a more pronounced cone shape, suggesting that body weight is the critical factor. The anatomical similarity of the apes implies that they share a limited number of positional modes (which these traits evolved. The hypothesis that this positional behaviour was brachiation. Data from wild apes alerted and clarified this hypothesis by affirming that three behaviours that fall under the rubric of quadrupedal climbing, walking (walking on inclined branches, scrambling, and assisted bipedalis), vertical climbing, and suspensory behaviour are likely to be responsible for ape specialization, but that each exerts different stresses on the anatomy, and should be considered separately.

Evolution of bipedalism

Whatever 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, such an overview is not presented here. Instead, this article concentrates on evidence that favours a new group of ecologically based hypotheses reconcilable with a postural feeding hypothesis previously formulated with chimpanzee behaviour and australopithecine anatomy. 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 behavior 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 330 hours at the Gombe Stream National Park, Tanzania. A total of 16,003 instantaneous, 2-minute focal observations was made on 26 well-habituated prime adults spanning all social ranks. Twenty-five positional behaviour variables were measured, including positional mode, its behavioral context, and feeding parameters. A total of 1,087 observations was made on 960 baboons over 83 hours using similar methods.

One of 65 locomotor or postural modes was classified in target animals at each 2-minute point. Trachiation was taken to mean hand-over-hand suspensory movement, and climbing to mean
Table 1. Proximal behaviour of baboons and chimpanzees compared.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sit</th>
<th>Sm</th>
<th>Hang</th>
<th>Squa</th>
<th>Climb</th>
<th>Jumper</th>
<th>Leap</th>
<th>Jump walk</th>
<th>Squat walk</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chimpanzee</td>
<td>28.4</td>
<td>34.0</td>
<td>12.1</td>
<td>0.8</td>
<td>3.6</td>
<td>2.5</td>
<td>0.7</td>
<td>0.3</td>
<td>3.7</td>
</tr>
<tr>
<td>Bonobo</td>
<td>32.5</td>
<td>34.6</td>
<td>1.2</td>
<td>0.0</td>
<td>0.2</td>
<td>14.5</td>
<td>0.5</td>
<td>0.0</td>
<td>23.2</td>
</tr>
</tbody>
</table>

Vertical climbing only that it ascends, supports >45°. Information on support diameter, angle of support above the horizon, height climbed and climbing mode (off-elbow, extended-elbow, lateral and palpe; >45°) was collected consistently 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 scores of sequential observations, and the resulting group of observations was considered a single positional bout. Chimpanzees were followed in all contexts, in notes and on the ground, during feeding and resting.

Chimpanzee skeletal exotations were examined at the Peabody Museum, Harvard University, and in the Anthropology Department, Indiana University, and in the context of published reviews of chimpanzee anatomy. Cases of positional results from Hadar were examined at the Peabody Museum.

Results and Interpretations
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 of chimpanzees shows that walking is by far the most common form of locomotion, and that in the case with all primates, most positional behaviour involves being stationary nearly 85% of the time in the case of chimpanzees. Anatomically, adaptations can be recognized by comparing chimpanzee positional behaviour with that of another species with a more generalized anatomy.

The symmetrical, arboreal baboon is compared here as a representative of monkeys (Table 1).

Differences in how commonly particular positions are adopted by chimpanzees and baboons define distinctive behaviour 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 specialists. Five positional modes were significantly more common in chimpanzees (Fisher’s exact tests on pooled Gumbhe and Mahall data, P < 0.05, d.f. = 1; see Table 2): (1) lie, (2) sit (legs flexed), (3) hanging by one arm (all modes), (4) jump-walk, and (5) vertical climb. Chimpanzees stood bipedally more often than baboons (0.2% versus never), but the difference was not significant. Other positional behaviours were either not distinctive in chimpanzees or were rare (Table 1).}

Table 2. Distinctiveness of chimpanzee positional behaviour.

<table>
<thead>
<tr>
<th>Positional behaviour</th>
<th>Chimpanzee different (No.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sit</td>
<td>3</td>
</tr>
<tr>
<td>Sit on</td>
<td>5</td>
</tr>
<tr>
<td>Arm-hang</td>
<td>44</td>
</tr>
<tr>
<td>Palm-walk</td>
<td>4.6</td>
</tr>
<tr>
<td>Vertical-squat</td>
<td>0.4</td>
</tr>
<tr>
<td>Bipedal stand</td>
<td>0.3</td>
</tr>
<tr>
<td>Squat</td>
<td>0.2</td>
</tr>
<tr>
<td>Squat locomotive</td>
<td>0.2</td>
</tr>
<tr>
<td>Bipedal walk</td>
<td>0.1</td>
</tr>
<tr>
<td>Cling</td>
<td>0.0</td>
</tr>
</tbody>
</table>

Sitting, sitting and squatting are significantly more common in chimpanzees (P < 0.05). The only other mode that was reduced on positional behaviour. Modes below horizontal line are less common in chimpanzees than baboons and therefore cannot be attributable to chimpanzees anatomical specializations.
Anatomical adaptations to living, sitting and walking

Lying was both common and distinctive in the chimpanzee (Tables 1 and 2), but adaptations to locomotion are likely to have exalted the body for living. 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 light adaptations that hold the upper body in a sitting posture with the least stress on the anatomy and with minimal musculature action. Chimpanzees can keep their backs straight when sitting, contrasting 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 the application of great pressure to the upper body during leaping, allowing greater acceleration and a longer leap. Monkeys leap more than chimpanzees.12 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 knuckle-walking is unique to the apes. Chimpanzees manipulate their hands during palm-walking, and therefore the animal's movable wrist only partly an adaptation to such arboreal activity. An adaptation allowing dorsification 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 knucklewalking adaptations13 which are not present in monkeys and hominids. Chimpanzee walking specializations, however, are not expected outside the mania 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 chimpanzees, the walking specialists.

Anatomical adaptations to vertical climbing

Vertical climbing was significantly more common among chimpanzees than baboons (Fisher's exact test, P < 0.05, 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 hypothesisa,b,c,d 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. 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 (Mano-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 adductability (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.14 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 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 so 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 chimpan. Other modes involving humeral abduction, including brachiation, constituted <0.1% of all positional behaviour.

*40, rainforest chimpanzees should have higher intermembral indices, which is not the case with rainforest-adapted baboons.150
Though it is a posture and therefore stress not stress on the anatomy that does make the largest, arm-hanging causes sig-
nificant stresses. Most of the body weight is suspended beneath 
an extensively placed forcelimb and is borne in position by the 
gleno-humeral joint capsule. The humerus, adducted and elevated 
the body via a rather vascocarinated facing glenoid fossa in most 
monuments, must be completely abducted. In order to reduce 
posts and conserve energy, adaptations to arm-hanging must 
reduce stress on the skeleton during unimanual suspension, and 
must minimize muscle action.

The shallow rifting of chimpanzexes (and other apecs) 
develops compressive forces on the upper torso during suspen-
sion 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, ones in catarrhates. A deep monkey-like torso is 
straining more than a shallow ape-like one. The center of 
weight of the chimpanzee rite more closely conforms to the base of 
tendinous force created by unimanual suspension, which tends to 
place the torso so that it more closely resembles a bird topper 
(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. Scapular rotation permits the vertebral 
boast of the scapula to approach the spines pons 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 
supra-columular axis during arm-hanging, the spinous column must bend 
back, and the anchors of these facets to the thoracic structures between the 
glenoid fossa and the spine is reduced. Allowing the shoulder to 
approach the midline during suspensory behaviour results in a 
less stressful sillerop shape to the arm and torso can be attained 
with either arm.

During arm-hanging, a cranially oriented glenoid fossa 
reduces stretching of the caudal (lower) aspect of the 
gleno-humeral joint capsule, allowing a larger ligamentous surface area 
be loaded weight (Fig. 1). The only body part that the forcelimb 
to be the body is from humerus to scapula to clavicle to 
scapular facet to the thoracic structure between the 
clavicle and shoulder blade is rotated, being anchored by a par-
sically large cuneo-ligament in the chimpanzees. 

The manuscript is large and broad in apes compared to 
other primates, in response to its weight-bearing function.

Skeletal features adapted to both arm-hanging and climbing

A number of chimpanzees specializations are adaptations to 
both arm-hanging and vertical climbing. Of the four poistional 
styles that require a strong muscular grasp 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 
apes together consist of 0.3% of chimpanzees positional 
behaviour. Both arm-hanging (27%) of supports were within 30% of true 
vertical, (n = 435) and vertical climbing (88% of supports 
were within 30° of true vertical, n = 49) commonly 
involved behavior. The glenoid is 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 
was adducted (or abducted), the fingers remain nearly parallel 
to the support and cannot grip it. The more nearly parallel the 
fig 
ures to the supports, the larger is its effective distance, and 
the longer the fingers must be to circumvent it. Ulnar deviation 
(adduction) and long fingers aid in gripping near-vertical 
branches. Arm-hanging requires more ulnar deviation that 
climbing because the forelimb is more nearly parallel to the 
support.

Ray curvature serves a muscle splitting function during suspensory 
behaviour. It also distributes gripping force more evenly 
around the circumference of the vertical support. Susptenth 
phalanges put much of the pressure of the grip on 
voluntary tissue near the middle of the phalanges, other tissue 
are relatively unmeasured (Fig. 2). The force of the body weight creates a 
rapid strain on the volar tissue pressed against the support. Other tissue 

Fig. 1. Schematic human and chimpanzee torso in posterior view. The 'scapular' scapula and the centred shape of the chimpanzee allow 
the scapular to rotate further towards the midline when the arm is 
adducted. The distance between the arm and the midline of the torso is 
greater in humans (A) than chimpanzees (A). In chimpanzees the 
shoulder joint does approach the midline more closely when the arm is 
adducted. Note that the articulation for the shoulder, the glenoid fossa 
(bone shaded off) is more than twice (as expected) in the chimpanzee 
(off). Thus in the human (off). The glenohumeral joint caps-
ule of humans (DH) is not ventrally continuous, whereas the lower portion 
beads all of the body weight during arm-hanging. The gleno-
acromial joint capsular of the chimpanzee is attached ventrally, thereby 
allowing for ease in their weight. The torso of the chimpanzee is 
centrally, a form that more closely approximates that of a mammal, 
which is the best possible shape for a voluminous object supported 
from a single point. The human torso is more barrel-shaped, causing 
stress areas that are more prone to fatigue or failure during unimanual 
arm-hanging after ref. 46.

Fig. 2. Schematic gripping statics. Note that with curved phalanges a 
smaller torque distance is distributed between bone (black bars) and 
joint object (grip area) than with straight phalanges. In a straight-
fingered individual, pressure on a branch is slightly near the middle of the 
phalanges whereas the center is closer to the branch, whereas a curved-
figured individual pressure is more uniformly applied along the 
length of the digits. Note that with curved phalanges the distance between 
and branch remains the same (grip area), but a larger branch may be 
gripped with fingers of the same length (after ref. 46).
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. 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. 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

due to the body weight, thereby creating torsional strain in the bone and the adductor musculature requiring special adaptations. Posture, the position of the body in space, plays a crucial role in determining the activation of different muscle groups. The table below illustrates the larger EMG potentials and muscle mass in a variety of chimp muscles, compared to similar muscles in humans, as compiled from a meta-analysis of seven studies and possible additional references. It is clear that specific muscle groups, such as the biceps and latissimus dorsi, have increased EMG potentials during activities involving vertical climbing, reflecting their adaptation for these tasks. This highlights the importance of considering muscle activation patterns in understanding ape behavior and evolution.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Likely adoption</th>
<th>Larger in chimps?</th>
<th>Active during human movement</th>
<th>Active during walking</th>
<th>Active during arm-hanging</th>
<th>Active in protraction or adduction?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biceps brachii</td>
<td>VC</td>
<td>+++</td>
<td>++</td>
<td>--</td>
<td>--</td>
<td>r12</td>
</tr>
<tr>
<td>Brachialis</td>
<td>VC?</td>
<td>++,-</td>
<td>++</td>
<td>--</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Brachioradialis</td>
<td>VC?</td>
<td>++, -</td>
<td>++</td>
<td>--</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Deltoide (whole)</td>
<td>+++</td>
<td>+</td>
<td>++</td>
<td>++++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>-anterior</td>
<td>++</td>
<td>+++</td>
<td>++</td>
<td>+++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>-intermedius</td>
<td>VC, AH?</td>
<td>+</td>
<td>+++</td>
<td>++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>-posterior</td>
<td>VC?</td>
<td>+++</td>
<td>++</td>
<td>+</td>
<td>--</td>
<td>++</td>
</tr>
<tr>
<td>Infraspinatus</td>
<td>0</td>
<td>0</td>
<td>++</td>
<td>+</td>
<td>--</td>
<td>++</td>
</tr>
<tr>
<td>Latissimus dorsi</td>
<td>VC</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Procoracral major</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Pectoralis minor</td>
<td>VC, AH?</td>
<td>(+++)</td>
<td>+</td>
<td>(++)</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Pectoralis minor</td>
<td>VC?</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Pectoralis minor</td>
<td>0</td>
<td>0</td>
<td>++</td>
<td>++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Rhomboid</td>
<td>X</td>
<td>+</td>
<td>++</td>
<td>++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Serratus anterior</td>
<td>VC, AH</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>-middle caudal</td>
<td>VC, AH</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>-lowest caudal</td>
<td>VC, AH</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Subscapularis</td>
<td>0</td>
<td>0</td>
<td>++</td>
<td>++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Supraspinatus</td>
<td>0</td>
<td>0, ++</td>
<td>++</td>
<td>++</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Teres major</td>
<td>0</td>
<td>0</td>
<td>+++</td>
<td>++</td>
<td>--</td>
<td>++</td>
</tr>
<tr>
<td>-minor</td>
<td>VC, AH</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>--</td>
<td>++</td>
</tr>
<tr>
<td>Trapezius cranial</td>
<td>VC, AH</td>
<td>++</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>++</td>
</tr>
<tr>
<td>-cervical</td>
<td>X</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>--</td>
<td></td>
</tr>
</tbody>
</table>

1 As reviewed in ref. 43 and references therein.

Likely adaptations: Bold: adaptation to a single positional behaviour is suggested; italics: adaptation to two behaviours suggested; ?, weak data missing, but adaptation likely; 0, muscle size smaller in apes, no behavioural specialization identifiable; -, 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; +, ++, large to very large in apes by most measures; +, ++, 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.

EMG data from gibbons.
respite are unaminously 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 delay is active in abduction, not pronation, and is therefore 'adherent to an accommodation to reaching out during arm-hanging, notvertical climbing. Other elbow flexors (brachialis and flexor carpi ulnaris) active during humeral retraction may be adapted to climbing if they are not used during pronation and abduction. Although details on the relative size of caudal and caudal peronale major are lacking, the greater size of the entire muscle suggests that bros that are relatively larger in apes than monkeys. Caudal peronale major and peronale minor are most active during humeral retraction in the support phase of vertical climbing, and are therefore probably adapted to it. Lowest activity anterior is active during both arm-hanging and arm retraction, and may be maintained for both climbing and suspension. Caudal peronale minor is active in rapid non-weight-bearing pronation of the arm during climbing. It may also be in reaching out during feeding. If posterior deltoide 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 steep, well-defined horizontal groove in great apes.111 The groove is smaller in gibbons. The concord procera, the origin of biceps brachii, is large in apes.1 Anatomical interpretations summarized

Ehlers and was perhaps the first to warn against interpreting anatomy on the basis of locomotor behavior against the exclusion of possess, and the first to suggest the pre-eminence of feeding adaptations in explaining morphology. Chimpanzee positional behavior, mechanics, EMG activity and relative muscle mass all provide strong support for previous contentions that most osteoligamentous specializations of the chimpanzee upper body are adaptations to a postural, namely arm-hanging.89 and that most muscular specializations are adaptations in vertical climbing.90 Large elbow flexors and humeral retractors are best explained as adaptations to vertical climbing.89 Observations on chimpanzees suggest that large humeral retractors 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 extensor origin of triceps femoris may aid in both modes. Although the relatively low activity of most muscles during truncation (caudal strata) precedes a general supinated muscular brachialization adaptation, skeletal and ligamentous adaptations for suspensory posture may serve similar function during locomotion while suspended.

Robust clavicular anchors, interterepropectores (tubular durae, and accompanying strongly curved ribs), mobile, adductible humeri, wide manubria of the sternum and cranially oriented ganoideal fossa are postulated to be a functionally related adaptive complex that reduces anatomical stress and therefore fatigue during suspensory posture. Furthermore, among one-handed arm-hanging specialists such as the chimpanzee, core-shaped ribs and lung, narrow aexpans increase further reduce stress. The low frequency of climbing large supports and the fact that both baboons and chimpanzees can climb vertical objects of similar

Table 5. Posture compared in the Hylobatidae.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sit</th>
<th>Lie</th>
<th>Stand</th>
<th>Squat</th>
<th>Cling</th>
<th>Bip. stand</th>
<th>Arm-hang</th>
<th>Hand-hang</th>
<th>n</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hylobates larvatus</td>
<td>65.7</td>
<td>0.0</td>
<td>0.1</td>
<td>0.0</td>
<td>34.5</td>
<td>0.0</td>
<td>522</td>
<td>60</td>
<td>2</td>
<td>665869</td>
</tr>
<tr>
<td>Hylobates pileatus</td>
<td>41.7</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>38.3</td>
<td>0.0</td>
<td>1343</td>
<td>58</td>
<td>2</td>
<td>665869</td>
</tr>
<tr>
<td>Hylobates syndactylus</td>
<td>38.5</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>47.7</td>
<td>0.0</td>
<td>241</td>
<td>65</td>
<td>1</td>
<td>665869</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>49.0</td>
<td>3.0</td>
<td>3.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>132</td>
<td>64</td>
<td>1</td>
<td>665869</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>49.0</td>
<td>0.0</td>
<td>2.4</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1366</td>
<td>66</td>
<td>1</td>
<td>665869</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>42.2</td>
<td>0.0</td>
<td>0.7</td>
<td>0.0</td>
<td>0.0</td>
<td>1.8</td>
<td>368</td>
<td>66</td>
<td>1</td>
<td>665869</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>49.0</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>2.6</td>
<td>1621</td>
<td>70</td>
<td>1</td>
<td>665869</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>30.0</td>
<td>5.0</td>
<td>15.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>158</td>
<td>67</td>
<td>1</td>
<td>665869</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>73.5</td>
<td>16.9</td>
<td>5.9</td>
<td>9.0</td>
<td>0.0</td>
<td>1.6</td>
<td>665869</td>
<td>68</td>
<td>1</td>
<td>665869</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>73.5</td>
<td>15.1</td>
<td>1.0</td>
<td>0.0</td>
<td>0.4</td>
<td>0.0</td>
<td>11648</td>
<td>77</td>
<td>1</td>
<td>665869</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>99.9</td>
<td>3.4</td>
<td>1.3</td>
<td>4.9</td>
<td>0.0</td>
<td>0.0</td>
<td>2516</td>
<td>49</td>
<td>1</td>
<td>665869</td>
</tr>
<tr>
<td>Gorilla gorilla</td>
<td>60.3</td>
<td>1.3</td>
<td>2.5</td>
<td>38.4</td>
<td>0.0</td>
<td>0.2</td>
<td>2207</td>
<td>69</td>
<td>1</td>
<td>665869</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>75.3</td>
<td>4.0</td>
<td>9.7</td>
<td>0.2</td>
<td>0.0</td>
<td>0.1</td>
<td>155</td>
<td>66</td>
<td>1</td>
<td>665869</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>75.9</td>
<td>0.0</td>
<td>21.1</td>
<td>9.6</td>
<td>0.0</td>
<td>0.2</td>
<td>558</td>
<td>29</td>
<td>1</td>
<td>665869</td>
</tr>
</tbody>
</table>

1 Table largely after ref 21. 2 Scan surveys, every 10 minutes. 3 Scan surveys, every 5 minutes. 4 Total positional behavior during feeding. 5 Focal observations; instantaneous entry 5 seconds. 6 Immediate surveys while feeding to test. 7 Roots eating and resting. 8 Roots while feeding to test. 9 Per cent of time in each posture for feeding stimuli. 10 Per cent of time in each posture. 11 1-minute spontaneous focal observations, adults only. 12 5 minute instantaneous focal observations standardized for both of day, adults only. 13 Humeral abductors, same instructions for focal observations, while feeding on food quantified for hour of day, adults only. 14 Malhi and Cohee profiles analyzed. 15 Per cent of time in each behavior, possible include 16 2-minute instantaneous focal observations; all subjects. 17 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 inter-
membral index and shoulder mobility. Long forelimbs serve
to extend reach during suspensory feeding.23,25 Augmentation
available support selection and increasing the number of food
items accessible to an individual feeding among terminal
branches.25,26,27 Alternated hand 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.28,29 Lib-
eral 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 stud-
ies, 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 observation 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 observation on posture were made during arboreal feed-
ing only are compared with chimpanzee and baboon observa-
tions from this study limited to arboreal feeding only (Table 5).

Table 5. Locomotion compared in the Hominoids

<table>
<thead>
<tr>
<th>Species</th>
<th>Walk</th>
<th>Climb</th>
<th>Leap/Step</th>
<th>Run</th>
<th>Bip. walk</th>
<th>Brachiate</th>
<th>Clamber</th>
<th>Other susp.</th>
<th>Transfer</th>
<th>n</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hylobates yuanai</td>
<td>3.5</td>
<td>6.6</td>
<td>23.9</td>
<td>0.0</td>
<td>0.0</td>
<td>46.3</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>255</td>
<td>observations 60</td>
</tr>
<tr>
<td>Hylobates wu</td>
<td>0.0</td>
<td>34.1</td>
<td>9.5</td>
<td>0.0</td>
<td>3.2</td>
<td>51.2</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>111</td>
<td>70</td>
</tr>
<tr>
<td>Hylobates pylei</td>
<td>0.0</td>
<td>6.6</td>
<td>8.5</td>
<td>0.0</td>
<td>0.0</td>
<td>84.4</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>111</td>
<td>61</td>
</tr>
<tr>
<td>Hylobates yunnan</td>
<td>0.0</td>
<td>10.0</td>
<td>0.0</td>
<td>0.0</td>
<td>11.0</td>
<td>80.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>208</td>
<td>65</td>
</tr>
<tr>
<td>Hoolock yunnan</td>
<td>0.0</td>
<td>54.3</td>
<td>3.2</td>
<td>0.0</td>
<td>0.0</td>
<td>37.9</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1106</td>
<td>62</td>
</tr>
<tr>
<td>Pan troglodytes</td>
<td>34.0</td>
<td>20.0</td>
<td>18.0</td>
<td>0.0</td>
<td>8.0</td>
<td>20.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>131</td>
<td>71</td>
</tr>
<tr>
<td>Pan paniscus</td>
<td>31.0</td>
<td>31.0</td>
<td>10.0</td>
<td>0.0</td>
<td>6.0</td>
<td>21.0</td>
<td>0.0</td>
<td>0.0</td>
<td>2.0</td>
<td>1722</td>
<td>72</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>22.5</td>
<td>48.2</td>
<td>10.8</td>
<td>0.0</td>
<td>1.2</td>
<td>17.1</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>2008</td>
<td>68</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>13.0</td>
<td>10.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>21.6</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>150</td>
<td>73</td>
</tr>
<tr>
<td>Pan troglodytes</td>
<td>10.8</td>
<td>9.3</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>19.8</td>
<td>43.0</td>
<td>0.0</td>
<td>0.0</td>
<td>10601</td>
<td>65</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>12.0</td>
<td>31.3</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>10.6</td>
<td>39.4</td>
<td>1.2</td>
<td>5.5</td>
<td>4560</td>
<td>20</td>
</tr>
<tr>
<td>Pan troglodytes</td>
<td>86.1</td>
<td>11.0</td>
<td>0.3</td>
<td>0.0</td>
<td>1.2</td>
<td>1.3</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1421</td>
<td>68</td>
</tr>
<tr>
<td>Pan troglodytes</td>
<td>92.1</td>
<td>4.9</td>
<td>0.1</td>
<td>1.3</td>
<td>0.4</td>
<td>0.5</td>
<td>0.3</td>
<td>0.0</td>
<td>0.0</td>
<td>2297</td>
<td>69</td>
</tr>
<tr>
<td>Pan troglodytes</td>
<td>36.4</td>
<td>48.9</td>
<td>0.4</td>
<td>0.3</td>
<td>6.7</td>
<td>5.3</td>
<td>2.3</td>
<td>0.6</td>
<td>2.4</td>
<td>223</td>
<td>67</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>97.0</td>
<td>0.7</td>
<td>0.5</td>
<td>1.6</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>256</td>
<td>20</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>64.2</td>
<td>21.3</td>
<td>10.4</td>
<td>0.1</td>
<td>4.1</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>256</td>
<td>20</td>
</tr>
</tbody>
</table>

1 Table largely after ref. 24. 2 10-minute scan survey. 3 Ours, maximum focal observation. 4 5-minute scan survey. 5 Postural observation, antipodiums every 5 scans. 6 Brunch, continuous focal observation, feeding and travel bouts pooled. 7 Brunch during arboreal feeding. 8 Arboreal bouts. 9 Arboreal bouts. 10 Brunch during travel. 11 Brunch during travel. 12 Travel during feeding and travel. Females only. 13 Locomotion in all contexts. 14 1-minute instantaneous

10 instantaneous focal observation. Scoring included in climbing. 15 Locomotion in all contexts. 2-minute instantaneous focal observation. Standardized for base of day, climbing and Mobilitate pooled. 16 Arboreal locomotors in all contexts, Climbing and Mobilitate pooled. Two or fewer observations to standardize. 17 Locomotion of

18 all contexts. Standardized for base of day, month, sex, adults only. 19 Arboreal locomotion in all contexts, adults only. Mid-sex, too few observations to standardize by hour.
see it for arboreal peacorial behaviour only, since baboons were not observable on the ground. The frequency of climbing was similar among chimpanzees (49%) and the two longer baboon studies (31-49%), and notably more common than among baboons (21%). Although arm-swinging (brachiation) was more established among baboons than chimpanzees (17-21% vs. 5%), climbing was the most consistently distinctive locomotor mode in the four-day compared to baboons.

Climbing (10-31%, 5%) was most distinctive of the orang-utan-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 behaviour and walking, which are very different from vertical climbing. Vertical climbing in this case is 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 0% or more in each (mountain gorillas excepted). Brachiation had a frequency of only 0.1-0.3% among chimpanzees, and is therefore unlikely to have exerted a significant selective pressure at least chimpanzees ancestry. No ape was given to walking like the baboons.

Summary of positional behaviour of apes

Current knowledge of the positional behaviour of the gorillas and lesser apes contains no evidence that these two behaviours are most distinctive: suspensory activity, especially seminominate, is not considered, 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 not bipedal like chimpanzees and baboons. Where stationary (oranges, Table 5) or when moving (shovel, bounches, 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. of non-target individuals) were made as supplantive evidence. These data showed that among chimpanzees, as the case among baboons, 22% of bipedalism is used when feeding. Eighty per cent of chimpanzee bipedalism was during feeding; 5% of all bipedal activity occurred and 75% terrestrially, and an overwhelming percentage of these bouts were postural (95%, Table 7). During foraging feeding, arm-hanging and bipedalism were linked. An orangutan set an arm-hanging posture stabilized bipedal posture in 6% of observations among terminal branches (α = 27; Table 2; and 5% of those in the central portion of a tree. Semi-suspension was the most common during bipedalism on the ground, on only 40% of observations (n = 26) involved a forklift. During terrestrial gathering brushes were used, and use of harvested fruits. Not infrequently, one hand was used to cut down and hold an otherwise inaccessible fruit-bearing limb. A small proportion of terrestrial bouts was locomotor bipedalism when the animals moved between feeding sites in the same tree (2%). That is, short-distance, within-tree shuffling rather than long-distance travel was the most common context for locomotor bipedalism among chimpanzees. Such

<table>
<thead>
<tr>
<th>Table 7: Content of bipedal behavior</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Concert</strong></td>
</tr>
<tr>
<td>First</td>
</tr>
<tr>
<td>Feeding</td>
</tr>
<tr>
<td><strong>Move in food</strong></td>
</tr>
<tr>
<td>push</td>
</tr>
<tr>
<td>eat fruits</td>
</tr>
<tr>
<td><strong>Total feed</strong></td>
</tr>
<tr>
<td>Beg</td>
</tr>
<tr>
<td>Sun</td>
</tr>
<tr>
<td><strong>Relate to</strong></td>
</tr>
<tr>
<td>floor</td>
</tr>
<tr>
<td><strong>Receive to</strong></td>
</tr>
<tr>
<td>1</td>
</tr>
<tr>
<td><strong>Dance</strong></td>
</tr>
<tr>
<td>shuffle</td>
</tr>
<tr>
<td><strong>Total</strong></td>
</tr>
</tbody>
</table>

1 In unbalanced bispalism the body was not supported by the forelimbs. Assisted bipedalism was due which half of the weight was borne on the hindlimbs. In a bispalism proportion was borne by a fully abductd forelimb in a semi-suspension mode.

2 Bipedal walking.

bipedalism behaviour as looking around (2%) and social display (19%) were not (Table 7).

Bipedalism was practiced both on the ground and slant when the animals fed from four fruit trees, Gecarcoidea rufifrons, Horana gana madagassensis, Manoanthe nochus, and Crewia sp. Together these trees were associated with 32% of all bipedal foraging episodes, and 48% of the occurrences 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 looted, with a posture similar to arm-hanging. All four of these tree species have distinctive under-stories (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, 1 cm and 1 cm, respectively) and are distributed evenly among the terminal branches. Although fruit gathering was not observed on and off the ground with any of the trees, other dimorphic trees with small fruits (fleshy, fleshy bipedalism with the animals either in the branch or still on the ground much more common) than large trees (Table 8). The number of observations of chimpanzees eating fruits was similar for small and large trees (1439 vs. 1398), but bipedal food collection 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 diversity 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 had small (≤2 cm) frui
When plant foods gathered during bipedalism were identified, 28 of 35 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 abundantly. As was the case with arm-hanging, 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, Mass-Watt V test, U = 123 620, P = 0.0001, n1 = 65, n2 = 57), probably because small trees offer fewer supports stable enough for sitting or unsuspended 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.\(^{2,4,10}\) Note that it is the picking component of small-fruit collecting that slows ingestion, not chewing. Small changes in position up trees and shifting on the ground are advantageous for collecting small, evenly distributed fruits in trees,\(^{2,4,10}\) where feeding sites are depleted quickly.\(^{2,4}\) Porters that allow a switch to locomotion with little energy cost are preferred.\(^{7}\)

### Austroalopithecus anatomy

**Tentor and forelimb**

The austroalopithecine torso is broad, shallow and cone-shaped\(^{10,24}\) (Fig. 3), the glenoid fossa oriented cranially\(^{22}\) at

<table>
<thead>
<tr>
<th>Genus</th>
<th>Unassisted</th>
<th>Assisted</th>
<th>Total n</th>
<th>Trunk height</th>
<th>Habitat</th>
<th>Food item traits</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Arboreal</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Innesi</td>
<td>15</td>
<td>2</td>
<td>16</td>
<td>4-8 cm</td>
<td>open</td>
<td>no rec.</td>
</tr>
<tr>
<td>Garcia</td>
<td>3</td>
<td>2</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undifferentiated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil, inorg.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Honenangano</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monpehotis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fetz</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Genoa</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undifferentiated fruit</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>not recorded</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>shoulders/neck</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pits</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>monkey</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pancorbo</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lorshewa</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saba</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Punicost</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Condor</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blossom</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Up spec</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parrot</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amenopoi</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tonda</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1. \(\) Les, terminal branches, i.e. within 1 m of the edge of the tree; cont., central portion of tree. 2. Assisted, arm-hanging bipedalism.

3. Trees 5 m tall were categorized as small, based on personal observation, adult, distances from ref. 77 fitted for small trees; >15 m categorized as large. Bauerae werejudged by the size of the host as estimated during feeding observations. 4. Bipedalism was categorized as forest or open habitat; in all cases except for Condor the author's observations of tree size and habitat coincide with information in ref. 77.

5. Figures in parentheses are *low* and *mean* values; other values are for positive. 6. Ref. 77; 7. Ref. 78; 8. Ref. 79; 9. Ref. 80.
as angle intermediate between that of chimpanzees and humans, the transverse section of the vertebral column small and chimpanzee-like,18 and the brachial index is chimpanzee-like. These features are adaptations to arm-hanging, though mostly expressed less than in the case with chimpanzees.

The curved process (origin of brachialis head) is large2 and the supracondylar ridge (origins of brachioradialis) is huge. These features are adaptations to vertical climbing.19

The autolopophorous wrist is mobile,20 the fingers curved (though shorter than those of apes),21 the thumb short with an ape-like articulation,20,22 arm and leg length proportions intermediate between modern humans and chimpanzees, even though the diminutive stature of the fossil is conserved,20,21 and hand morphology is indicative of powerful chimpanzee-like grasping ability.23

The pelvic girdle is human-like,24 but open and shallow,25 more similar to that of humans than chimpanzees. The function of a large inner intervertebral and therefore a deep (i.e., chimpanzee-like) pelvic girdle may be either to increase the lever arm of the abdomen to prevent bowstringing when the elbow is flexed with the arm above the head. In either case the autolopophorous condition indicates a greater adaptation to vertical climbing in hominids than in chimpanzees. Australopithecines have six lumbar vertebrae14 (Sts 14), a feature not found in living hominids, 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 aethopicus and later hominids unambiguously indicate bipedalism.26-28 The lumbar vertebrae are robust,29 the sacral triangle is expanded and the pelvis has a human gestalt.30 The femur has a deep posterior groove and at least some specimens have an elliptical lateral condyle. The calcaneus is essentially modern.10 The great toe is robust and the foot has well-developed transverse and longitudinal arches.31-34 Because the gestalt of the lower body symmetry of A. aethopicus matches an organism adapted to bipedal locomotion,26-28 it is integrating that it is a bipedalism that is not as defined as that of modern humans (Fig. 4).

**Unique features of the pelvis and hindlimb**

Although the size is human-like in appearance, the A. aethopicus pelvis differs from that of modern humans in ways that suggest less than optimum bipedal locomotor capabilities. A. aethopicus has smaller sacro-iliac ligaments than those of modern humans.91 The width of the ilia, 286 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 prehensile the hip (from collapsing when 92 one foot is off the ground than in modern humans). A relatively small acetabulum/femoral head in australopithecines compounds the stresses caused by large hips, creating even more stress at the hip joint. Perhaps most surprising, A. aethopicus has extremely wide hips. This causes the moment arm of the body weight of A. aethopicus to be increased greatly over that of modern humans, increasing the stress on the dorsal/iliac/femoral neck junction when bearing weight.

The extraordinarily wide hips of AL 286.14 and Sts 14 are due in part to highly reflexed ilia, not due to an unusually broad pelvic inlet. The pelvic index averaged 77.6 for a sample of modern human females, but was 57.6 for AL 286.1. The peculiar acetabular width or acetabulums in particular is odd, with an adaptation for efficient, stress-reduced bipedal.

**Humanoid pelvis and hindlimb of the Boxer.** Although the size is human-like in appearance, the A. aethopicus pelvis differs from that of modern humans in ways that suggest less than optimum bipedal locomotor capabilities. A. aethopicus has smaller sacro-iliac ligaments than those of modern humans. The width of the ilia, 286 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 prehensile the hip (from collapsing when 92 one foot is off the ground than in modern humans). A relatively small acetabulum/femoral head in australopithecines compounds the stresses caused by large hips, creating even more stress at the hip joint. Perhaps most surprising, A. aethopicus has extremely wide hips. This causes the moment arm of the body weight of A. aethopicus to be increased greatly over that of modern humans, increasing the stress on the dorsal/iliac/femoral neck junction when bearing weight.

The extraordinarily wide hips of AL 286.14 and Sts 14 are due in part to highly reflexed ilia, not due to an unusually broad pelvic inlet. The pelvic index averaged 77.6 for a sample of modern human females, but was 57.6 for AL 286.1. The peculiar acetabular width or acetabulums in particular is odd, with an adaptation for efficient, stress-reduced bipedal.
locomotion. A broad pelvis decreases energetic efficiency by requiring greater muscular activity during walking and produces high stress on the femoral neck. If australopithecines were well-adapted to bipedal walking, they would be expected to have hips that are as pelvically adapted for this large bone breadth in modern humans is a necessary adaptation for giving birth to large-headed offspring, cephalopelvic reconstruction of A. africana shows a considerable gap between the pelvic breadth and pelvic inlet walls opposite the acetabula.

That is, the pelvis is much broader than could possibly be necessary for parturition. Other features suggest reduced locomotor competence as well. A. africana has quite short hindlimbs for its weight and height, suggesting greater energy expenditure per distance travelled.

The lumbar vertebrae and lumbosacral articulation surface of other australopithecines are small, with a diminished proportion to body weight, hip width or nearly any other measure that has been approached.

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. africana was more prone to fatigue or injurious failure during powerful and sustained bipedal locomotion: (1) australopithecines experienced high pelvic and femoral stress, (2) they had a small diametral span, small joint surfaces below the waist and smaller than-modern human sacroiliac 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. This anatomy suggests one of the most important considerations for the evolution of bipedalism is not an important consideration for bipedalism. The first is extremely unlikely. 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. africana involves not merely a less efficient version of a modern pelvis: in proportion to body size and weight, the pelvis is as ape-like and presumably adapted to arboreal behaviour. Ape-like features of the medial cuneiform indicate rudimentary first toe adductibility. Contra Latimer and colleagues, A. afarensis has long, curved toes, an ape-like posteriorly short, rounded lateral femoral condyle (at least for some specimens). A. afarensis has a strongly developed fibular groove for the tension of the peroneal muscles, consistent with ape-like great toe flexion. Chimpanzees use this capacity to grip branches when standing in trees or climbing. A large, robust bone in the toes of A. afarensis indicates a powerful grip, it may be the key to the relatively small hands and small foot to support the arch. If so, bipedalism would be much less energetically efficient, since muscular support would be used during support and toe-off, rather than a non-energy-consuming suspensory support. A long moment arm for the hamstrings increases the power of the extension, implying a better climbing adaptation than in modern humans. A plantar set or at least greater mobility of the ankle allows full plantar flexion of the foot, when the toes grip a branch to support body weight with the hindlimbs in tension (pers. obs.). Curved pedal phalanges and third pedal digit longer than the first or second 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 long-standing adaptation

A possible explanation of arboreal and energy-inefficient features in australopithecines is that they are merely holdovers from a previous, non-arboreal adaptation. It seems extremely unlikely that these features would have persisted from the ape-human split at perhaps 6-8 mya ago through A. afarensis, A. africanus and even to a great extent in Homo habilis.33,34,10 at <0.2 mya only to have been lost suddenly with the appearance of Homo erectus.33,34,10-14 The relatively modern postcranium of Homo erectus suggests that the scavenging, hunting, provisioning and carrying arguments for the origin of bipedalism and heat stress models33,34,10,11,13-18 are more convincing explanations for the later refinement of locomotor bipedalism than for its origin.

Australopithecine ecology

Fossil assemblages from australopithecine localities suggest a range of bush-savanna to woodland habitat, perhaps even sub-terrinal forest,31,10 although forest that is not as spiky and closed as that preferred by chimpanzees.21-25 This is quite different from the "open savanna." The diminished 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.31-33 There is little evidence for the presence of grass or subterranean resources in the australopithecine diet.31-33

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 hylobatid hypothesis and the Jolly/ Ross/Wright/Kaye 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 hominoids were adapted to both primate and locomotor bipedal locomotion was less common than in modern humans. This hypothesis suggests that the typical australopithecine bipedal feeding posture was bipedalism stabilized by grasping 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, short hindlimbs, femoral shaft obliquity greater than that of modern humans, lack of an iliofemoral ligament (in smaller individuals), and poorly developed sacroiliac ligaments. 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 bipes 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. When standing or walking abruptly 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 proposed that the easing of small objects on the ground led to human bipedalism. The hypothesis was refined by Buse. It was embellished by Wrangham, 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, moving insects. The principal objection to this hypothesis is in the peristence of an anatomy indicative of arming-hanging and climbing for millions of years after the adoption of bipedalism.

An arboreal or hylobatid hypothesis not forward by Tuttle and Szumk proposed that postural bipedal feeding in trees and movement among branches evolved in a small-boned primate before a significant shift, to life on the ground. The per- or primate-specific feeding 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 hylobatid 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 standing bipedalism less adapted to endothermy than that of modern humans, but still, hardly distinguishable kinesically from our own. At the same time, short lower limbs, long curved toes, and wide palms are arboreal adaptations. The upper body morphology of australopithecines is generally intermediate between that of humans and that of the chimpanzee and the orangutan, taken as a whole, suggests that arm-hanging bipedalism in trees was a common activity as was the upcright grouping of feet on the ground. Arm-hanging bipedalism for harvesting, however, seems unlikely in small fruits in trees because it provides maximum support and mobility. Bipedalism on the ground allows us to reach food items higher in the tree and to use both hands for gathering.

Arboreal semi-bipedal pre- and proto-hominins confined to 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 hominins and australopithecines may have remained relatively unchanged, even in Homo habilis, until the evolution of a more locomotion-orientated, near-modern postcranial anatomy in Homo erectus. Bipedalism may therefore have originated as a feeding posture that was only later refined into an efficient locomotor adaptation.

C. L. Brace and R. W. Wrangham inspired much of this work. Research was aided by the L.S.B. Leakey Foundation, University of Michigan Museum of Anthropology, National Science Foundation and a Harvard University Postdoctoral Fellowship under R.W. Wrangham.

60. Stonehouse S. J. (1986). Notes on the ecology and behavior of the handshak

**Research Article**

**Title:** The Evolutionary and Behavioral Biology of Hominoids

**Authors:** David C. Weir, Victor P. Broekhuisen, and Betty E. Trotter

**Journal:** Journal of Human Evolution

**Volume:** 30

**Issue:** 2

**Year:** 1995

**Pages:** 125-149

**Abstract:** This special issue of the Journal of Human Evolution is devoted to the evolutionary and behavioral biology of hominoids. It includes original research articles, review articles, and a symposium on hominoid locomotion. The issue provides a comprehensive overview of the current state of knowledge in this area, with a focus on the locomotor and behavioral adaptations of hominoids.

**Keywords:** Hominoids, Evolutionary Biology, Behavioral Biology, Primate Locomotion