

REVIEW

Acquisition of bipedalism: the Miocene hominoid record and modern analogues for bipedal protohominids

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Abstract

The well-known fossil hominoid *Proconsul* from the Early Miocene of Kenya was a non-specialized arboreal quadruped with strong pollicial/hallucial assisted grasping capability. It lacked most of the suspensory specializations acquired in living hominoids. *Nacholapithecus*, however, from the Middle Miocene of Kenya, although in part sharing with *Proconsul* the common primitive anatomical body design, was more specialized for orthograde climbing, 'hoisting' and bridging, with the glenoid fossae of the scapula probably being cranially orientated, the forelimbs proportionally large, and very long toes. Its tail loss suggests relatively slow movement, although tail loss may already have occurred in *Proconsul*. *Nacholapithecus*-like positional behaviour might thus have been a basis for development of more suspensory specialized positional behaviour in later hominoids. Unfortunately, after 13 Ma, there is a gap in the hominoid postcranial record in Africa until 6 Ma. Due to this gap, a scenario for later locomotor evolution prior to the divergence of *Homo* and *Pan* cannot be determined with certainty. The time gap also causes difficulties when we seek to determine polarities of morphological traits in very early hominids. Interpretation of the form–function relationships of postcranial features in incipient hominids will be difficult because it is predicted that they had incorporated bipedalism only moderately into their total positional repertoires. However, Japanese macaques, which are trained in traditional bipedal performance, may provide useful hints about bipedal adaptation in the protohominids. Kinematic analyses revealed that these macaques walked bipedally with a longer stride and lower stride frequency than used by ordinary macaques, owing to a more extended posture of the hindlimb joints. The body centre of gravity rises during the single-support phase of stance. Energetic studies of locomotion in these bipedal macaques revealed that energetic expenditure was 20–30% higher in bipedalism than in quadrupedalism, regardless of walking velocity.

Key words bipedal adaptation; functional anatomy; hominoids; locomotion; Miocene.

Introduction

Since 2000, a series of very early hominids have been discovered from the latest Miocene of Africa (Haile-Selassie, 2001; Senut et al. 2001; Brunet et al. 2002). However, most aspects of the origins of human bipedalism (such as date, location, environment, proximate causes, phylogenetic background and gait) are still poorly known. Furthermore, with regard to the fossil

record of human ancestry, a wide gap exists between these earliest hominids and hominoids from the Middle Miocene of Africa (e.g. *Otavipithecus namibiensis*, *Kenyapithecus wickeri*, *K. africanus* and *Nacholapithecus kerioi*: 13–16 Ma). Although *Samburupithecus kiptalami* (9.5 Ma) is a (single) stepping-stone in the middle of the gap, the only specimen attributed to this species is a maxilla and its locomotor behaviour is therefore totally unknown (Ishida & Pickford, 1997). The gap in the fossil record poses further difficulties in deciding polarities of morphological traits in Late Miocene hominids (Pickford et al. 2002). Ironically, as more of these very early hominid materials are discovered, it has become increasingly clear that form–function relationships are not easily interpreted. As we go further back in time, the number of specialized traits will be fewer and their

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degree of expression less. Without a clear understanding of morphological polarities, diverse opinions easily arise about functional interpretations of fossil traits.

Ultimately, an increase in fossil material will resolve such diversified and contradictory interpretations. However, neontological studies may also play a role in resolving questions regarding form–function relationships, such as how capable less human-like animals are in bipedalism, and what skeletal features are good indicators of frequent bipedalism.

Although such questions are similarly difficult to answer in the absence of any living non-human primate that frequently adopts bipedalism in the wild, a series of experimental studies has been used to address them. Japanese macaques (*Macaca fuscata*), which are trained for the traditional Japanese bipedal monkey performance, acquire amazing capabilities for bipedalism (Hayama et al. 1992; Nakatsukasa & Hayama, 2003). Several researchers have focused anatomical, kinesiological and physiological studies on these macaques. It takes years of training to induce behavioural shifts towards bipedalism in these macaques. This process is an excellent ‘experiment’ by which to investigate the potential for bipedalism in non-human primates, skeletal features related to bipedal behaviour and the process of ontogenetic adaptation for bipedality. Because the anatomy of the macaque is dissimilar to that of the presumed last common ancestor of *Homo* and *Pan*, they are of course not a perfect model for the hypothetical protohominids (*sensu* Rose, 1991). However, it is possible partially to analogize between these macaques and the protohominids. The first part of this paper reviews positional behaviour in Miocene hominoids in Africa and discusses a probable scenario of its evolution prior to the human–chimpanzee divergence. The later half deals with studies of the bipedally performing macaques, particularly with respect to their locomotor kinematics and energetics, in order to provide better understanding of functional anatomy and biomechanics related to bipedal behaviour, and hence insights concerning the early stages of evolution of human bipedality.

The hominoid fossil record from the Miocene of Africa

Early Miocene

Nearly 20 genera of ‘hominoids’ are currently known from the Miocene of Africa (Fleagle, 1999); but taxonomy of

Hominoidea is controversial (see, e.g. Harrison, 2002, for a different perspective). Among Early Miocene hominoids, the anatomy of the postcranium is best known in the 17–20 Ma genus *Proconsul*, owing to the existence of several partial skeletons as well as many isolated specimens (Napier & Davis, 1959; Harrison, 1982; Walker & Pickford, 1983; Beard et al. 1986; Senut, 1986; Gebo et al. 1988; Ward et al. 1991, 1993, 1995; Begun et al. 1994).

Table 1 summarizes the major postcranial features of *Proconsul*. Most of them are obtained from two species of *Proconsul*, a smaller species, *P. heseloni* and a larger, *P. nyanzae*. The thoracic cage is transversely narrow as in most mammals (Ward, 1993). Living apes, however, have a transversely wide thorax, an important adaptation for suspension or climbing (Schultz, 1961; Erikson, 1963; Gebo, 1996). Lumbar vertebrae have a moderately long centrum (Ward et al. 1993) and their transverse processes arise from the body at the pedicle roots (Ward et al. 1993). This condition differs from that in living apes, in which the transverse process arises from the pedicle (Sanders & Bodenbender, 1994). The lumbar region is reduced in extant suspensory specialized primates, even in some New World monkeys (Schultz, 1961; Erikson, 1963). The lumbar vertebrae number six or more in *Proconsul* (Ward et al. 1993), greater than in living apes (in which it is mostly 3–5). Thus, the lumbar region of *Proconsul* is long, like that of Old World monkeys. It is arguable whether or not *Proconsul* had lost the tail (positive assessments in Ward et al. 1991, 1999; negative in Harrison, 1998). However, a recent analysis supports tail loss (M. Nakatsukasa et al., unpubl. data). The pelvis is narrow, as is the thorax (Ward, 1993) and *Proconsul* lacked ischial tuberosities (Ward et al. 1993) unlike Old World monkeys and gibbons (Rose, 1974). Neither forelimb nor forearm is very long (Napier & Davis, 1959). The humerus does not have medial torsion of the head (Walker, 1997), and although it is unclear whether the proximal humeral shaft is curved or not, sharp deltopectoral and delto-triceps crests are developed as in the humeri of Old World monkeys (Napier & Davis, 1959). The humeral trochlea is not truly trochleiform, although the lateral trochlear keel is relatively well developed in *P. heseloni* (Napier & Davis, 1959; Senut, 1986). The ulna articulates with the triquetral and pisiform (Napier & Davis, 1959; Beard et al. 1986). The pollex and hallux are well developed (Harrison, 1982; Begun et al. 1994) unlike in living hominoids in which they are diminutive. However, phalanges lack a pronounced curvature (Napier & Davis,

Table 1 Major postcranial features in *Proconsul*

Thoracic cage is mediolaterally narrow (Ward, 1993)
Lumbar vertebrae have a long centrum (Ward et al. 1993; Rose et al. 1996); small cranial/caudal articular surfaces (Harrison & Sanders, 1999; Nakatsukasa & Hirose, 2002) and transverse processes arising from the body at the pedicle roots (Ward et al. 1993). Lumbar vertebrae number six or more (Ward et al. 1993)
Tail loss controversial (positive: Ward et al. 1991, 1999; negative: Harrison, 1998)
Narrow ilium and sacrum; no ischial tuberosities (Ward, 1993)
Neither forelimb nor forearm is elongated (Napier & Davis, 1959; Walker & Pickford, 1983)
No strong humeral head torsion (Walker, 1997)
Developed deltopectoral/deltotriceps crests (Napier & Davis, 1959)
Humeral trochlea is not truly trochleiform, lacking a developed lateral keel (Napier & Davis, 1959; Senut, 1986)
Ulna articulates with the triquetral and pisiform (Napier & Davis, 1959; Beard et al. 1986)
Well-developed pollex and hallux; phalangeal curvature is not pronounced; II–V phalanges are generally similar between hand and foot (Napier & Davis, 1959; Harrison, 1982; Begun et al. 1994)

1959; Harrison, 1982; Begun et al. 1994). Hand and foot phalanges cannot be distinguished easily (Begun et al. 1994; Nakatsukasa et al. 2003a). In summary, *Proconsul* lacks most of the postcranial specializations for suspensory positional behaviour, which are observed in living apes (see Larson, 1998).

Therefore, *Proconsul* is referred to as a non-specialized arboreal quadruped, somewhat like the howlers (*Alouatta*) in the Neotropics (Fleagle, 1983; Walker & Pickford, 1983; Rose, 1993, 1994; Ward, 1993; Begun et al. 1994). Its hand and foot anatomy suggests strong pollicial/hallucial assisted grasping capability (Begun et al. 1994). Its movements were probably relatively slow or cautious (Begun et al. 1994; but see Harrison, 1982), but researchers agree that frequent suspension was unlikely though not totally absent.

Middle and Late Miocene

During the early phase of the Middle Miocene, roughly between 13 and 15 Ma, several new hominoid species appeared in Africa, such as *Nacholapithecus*, *Kenyapithecus* and *Otavipithecus* (Le Gros Clark & Leakey, 1951; Leakey, 1962; Pickford, 1985; Conroy et al. 1992; McCrossin, 1994; Ishida et al. 1999). The genus *Kenyapithecus* includes two species, *wickeri* and *africanus* (Pickford, 1985; McCrossin, 1994; McCrossin & Benefit, 1997) but there is a proposal to move the latter into a different genus, *Equatorius* (Ward et al. 1999a,b). Although this proposal is not fully accepted, it is becoming apparent that there was a large diversity of medium-to-large hominoids from southern to eastern Africa during this period (S. Ward et al. 1999).

Recently, plenty of *Nacholapithecus* specimens have been excavated from Nachola in northern Kenya

(Nakatsukasa et al. 1998, 2000; Ishida et al. 1999, 2004). The holotype of *Nacholapithecus* KNM-BG 35250 (Fig. 1) is one of the most complete hominoid skeletons ever found (Ishida et al. 2004). Thanks to the excavations at Nachola, the postcranial anatomy of *Nacholapithecus* is now the best known among African fossil hominoids.

Nacholapithecus is a medium-sized hominoid. Body mass in males has been estimated as less than 20 kg, from femoral head size (Nakatsukasa et al. 2000). However, from its large forelimb bones relative to the hindlimb a weight closer to 22 kg has been suggested (Ishida et al. 2004). This would make it about half the size of a common chimpanzee.

Table 2 lists the major postcranial traits of *Nacholapithecus*. The clavicle is very long: for example, the clavicle of KNM-BG 35250 is about 84 mm long (Sent et al. 2004; Fig. 2). Even if it lacks only the sternal end, the original length would be a minimum of 100 mm. With a body mass that is about a half of that of a common chimpanzee and equivalent to that of a male yellow baboon (Smith & Jungers, 1997), this bone is naturally extremely long: the average length of the clavicle in a male chimpanzee is about 125 mm (Senut et al. 2004). A long clavicle suggests either a laterally projecting glenoid fossa of the scapula (= a wide thoracic cage) or an extremely cranially angled clavicle (= a cranially facing glenoid surface) as is in orang-utans (Fig. 3). Because marked medial torsion of the humeral head does not exist in *Nacholapithecus* (M. Nakatsukasa, personal observation), the latter interpretation is more probable. If so, this is most likely an adaptation for climbing.

Morphology of the lumbar vertebrae is generally similar to that in *Proconsul*: for example, non-pedicular origin of the transverse processes, moderate centrum length, vertebral number 6–7 (Rose et al. 1996; Nakatsukasa



Fig. 1 Holotype of *Nacholapithecus kerioi* (KNM-BG 35250).

Table 2 Major postcranial features in *Nacholapithecus*

Very long clavicle (Senut et al. 2004)
Cranially orientated glenoid
Lumbar vertebrae have a long centrum, small centrum articular surfaces and transverse processes arising from the body at the pedicle roots. Lumbar vertebrae number six or more (Rose et al. 1996; Nakatsukasa et al. 1998, 2000, 2003b; Ishida et al. 2004)
Tail-loss (Nakatsukasa et al. 2003c)
Forelimb is large relative to hindlimbs (Nakatsukasa et al. 2000; Ishida et al. 2004)
No strong humeral head torsion (M. Nakatsukasa, personal observation)
Developed deltopectoral/deltotriceps crests (Takano et al. 2003)
Humeral trochlea is not truly trochleiform (Nakatsukasa et al. 1998; Takano et al. 2003; Ishida et al. 2004)
Markedly developed lateral wall of the olecranon-fossa (Nakatsukasa et al. 1998; Takano et al. 2003; Ishida et al. 2004)
Large and globular humeral capitulum (Takano et al. 2003; Ishida et al. 2004)
Ulna articulates with the triquetral and pisiform (Nakatsukasa et al. 2000; Ishida et al. 2004)
Large and robust pollex and hallux. Pedal phalanges are long relative to body mass (Nakatsukasa et al. 2003a)
Pedal and manual phalanges are more easily discriminated than in <i>Proconsul</i> (Nakatsukasa et al. 2003a)

et al. 1998, 2003b). Curiously, *Nacholapithecus* has small lumbar vertebral bodies relative to body mass (Nakatsukasa et al. 2003b). If a lumbar vertebra of KNM-BG 35250 is compared with the fourth lumbar vertebra of a male yellow baboon whose femur is equivalent in size to that of KNM-BG 35250, it is evident that the *Nacholapithecus* vertebra is much smaller (Fig. 4). A similar tendency is observed in *Proconsul* and may be related to a common and unique locomotor pattern in those hominoids (Nakatsukasa & Hirose, 2003).

Although the axial skeleton of *Nacholapithecus* lacks most of the derived features observed in living apes, at least one derived feature may be identified with confidence: *Nacholapithecus* did not have a tail (Nakatsukasa et al. 2003c). Recently, a first coccygeal vertebra of *Nacholapithecus* was discovered (KNM-BG 40949). This is an almost complete bone despite the erosion of the distal tip (Fig. 5). Although it is slightly elongated compared with that of living hominoids, it shares several important functional features with coccygeal bones of living hominoids, such as the complete absence of



Fig. 2 Limb bones of KNM-BG 35250 (casts) compared with those of a male *Pan troglodytes schweinfurthii*. Note great size of the forelimb bones relative to hindlimb bones in KNM-BG 35250. Scale bar = 5 cm.

vertebral foramina, reduced transverse processes and dorsoventral compression. These features indicate a diminution of voluntary ability to control more caudal elements, a reduction of tail muscles and reduced mobility at the sacrococcygeal joint. The reason for the tail loss was probably slow locomotion coupled with enhanced cheiridial grasping capability (Nakatsukasa et al. 2003a). The overall morphological similarity of the coccyx with that in living apes may suggest that incipient formation of a pelvic floor of the type seen in living apes (Abitbol, 1988) existed in *Nacholapithecus*, as an adaptation for orthograde postural and locomotor behaviour.

The *Nacholapithecus* elbow exhibits several derived features. Although the humero-ulnar joint is of a primitive cylindrical type, the lateral wall of the olecranon-fossa is markedly developed (Nakatsukasa et al. 1998, 2000; Takano et al. 2003; Ishida et al. 2004). The humeral capitulum is tall and globular. Probably, the elbow joint was adapted for enhanced pronation-supination through the full range of flexion-extension; Takano et al. (2003) suggest use of a wide range of arboreal supports.

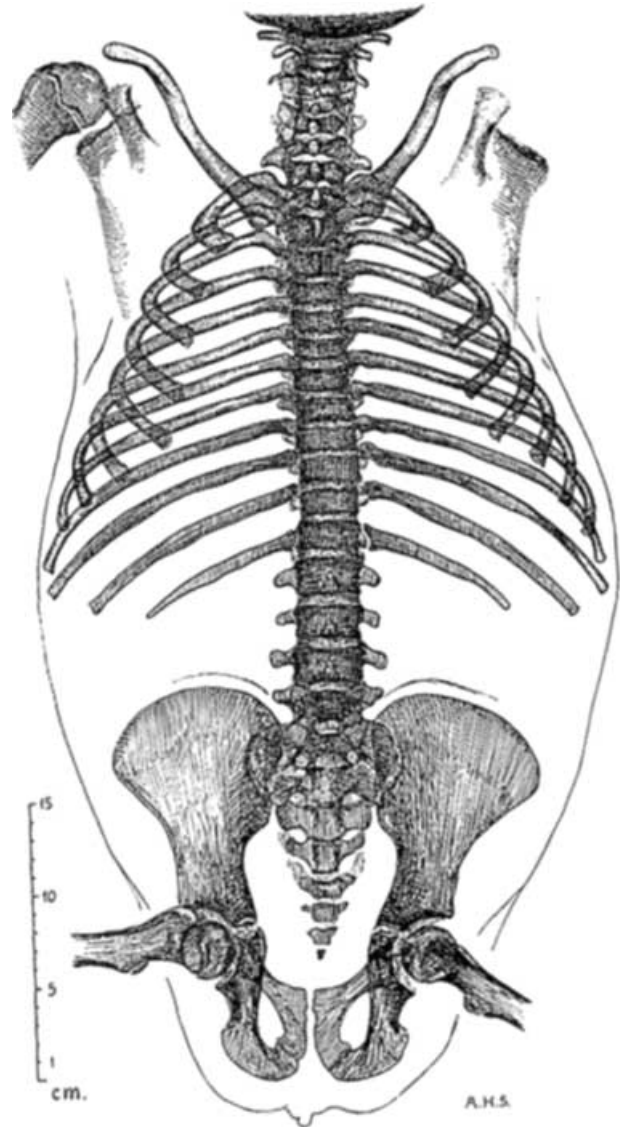


Fig. 3 Tracing of an X-ray photograph of the trunk of a juvenile orang-utan. From Schultz (1961).

The most curious postcranial feature in *Nacholapithecus* is its body proportions. *Nacholapithecus* has forelimb bones that are proportionally large compared with the lumbar vertebrae and hindlimb bones (Nakatsukasa et al. 2000; Ishida et al. 2004). Figure 2 compares limb bones of the *Nacholapithecus* type specimen (KNM-BG 35250) with those of a male chimpanzee. Although the forelimb bones of KNM-BG 35250 are only modestly smaller than in chimpanzees, its hindlimb bones are much smaller. This is apparent in an allometric plot of the distal joint width of the humerus against femoral head diameter (Fig. 6a). Femoral head size is a robust surrogate for body mass prediction,



Fig. 4 Femur and lumbar vertebra of KNM-BG 35250 compared with those of a male baboon (*Papio cynocephalus*). Although the femoral heads are almost identical in size, the lumbar vertebral centrum of this male *Nacholapithecus* is much smaller than that of L4 in this baboon. Also note the left transverse process which arises from the body-pedicle juncture in *Nacholapithecus*. Scale bar = 2 cm.



Fig. 5 First coccygeal/caudal vertebra in short-tailed or tailless primates. Upper (left to right): *Gorilla gorilla*, *Pan troglodytes*, *Hylobates syndactylus*. Lower (left to right): *Macaca nigra*, *Perodicticus potto*, *Nycticebus* sp., *Nacholapithecus*. Note the similarity between *Nacholapithecus* and living hominoids' coccyges. Scale bar = 2 mm.

although it may sometimes yield overestimates of body mass, as it does for example in orang-utans) (Ruff, 1988, 2002). Thus, *Nacholapithecus* has large forelimb bones, not small hindlimb bones, and probably relied on its forelimbs to a greater degree than do other non-suspensory primates. Differentiation of bone structural strength between the fore- and hindlimb bones by locomotor characteristics is noted in various living anthropoids (Ruff, 2002).

Phalanges of *Nacholapithecus* are generally similar to those of *Proconsul* in terms of the absence of specialized features for suspension (Rose et al. 1996; Nakatsukasa et al. 2003a). However, *Nacholapithecus* differs from *Proconsul* in its phalangeal elongation, enhanced robustness of the hallucial phalanges and greater size of manual phalanges relative to corresponding pedal phalanges (Nakatsukasa et al. 2003a). Figure 7 compares hallucial phalanges of KNM-BG 35250 with those

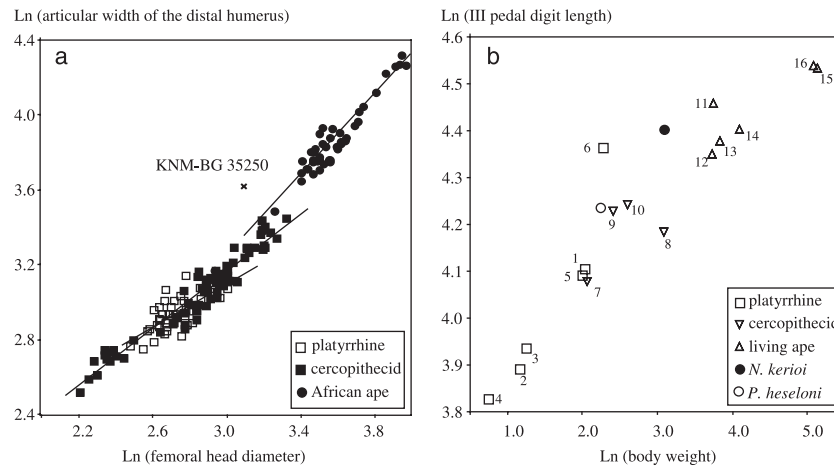


Fig. 6 Allometric scaling of postcranial dimensions. (a) Distal joint width of the humerus against the femoral head diameter with least squares regressions for African apes, cercopithecoids and cebids. (b) Third digit length against body mass. *Nacholapithecus*: KNM-BG 35250AQ-AS. *Proconsul heseloni*: KPS3 ph233, 82, 80. Numeric in the figure corresponds to living taxon as follows. 1: male *Ateles seniculus*, 2: male *Cebus albifrons*, 3: male *Cacajao calvus*, 4: male *Pithecia monachus*, 5: male *Lagothrix lagotricha*, 6: male *Brachyteles arachnoides*, 7: male *Cercopithecus mitis*, 8: male *Papio cynocephalus*, 9: male *Macaca nemestrina*, 10: male *Colobus guereza*, 11: male *Pan troglodytes schweinfurthii*, 12: female *P. t. verus*, 13: male *P. t. verus*, 14: male *P. t. troglodytes*, 15: male *Gorilla gorilla gorilla*, 16: male *G. g. beringei*.

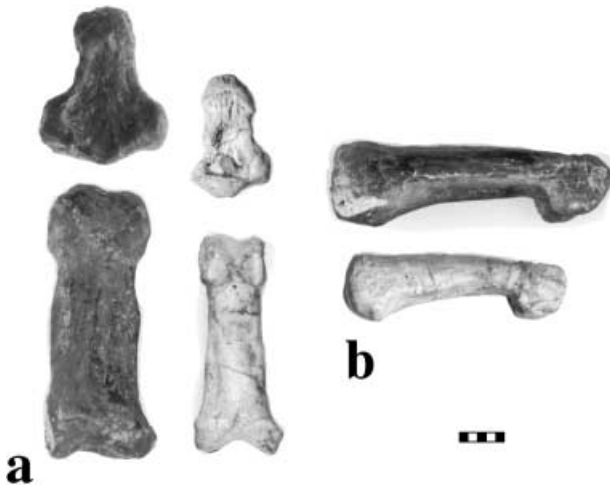


Fig. 7 Right hallucial phalanges of *Nacholapithecus* (KNM-BG 35250) and *Proconsul heseloni* (KNM KPS 3) in plantar (a) and lateral view (b). Scale bar = 5 mm.

of *P. heseloni* (KNM-KPS 3). The wider shaft of the proximal phalanx and the broader base of the terminal phalanx in *Nacholapithecus* are quite distinctive. Figure 6(b) plots pedal third digit length of living anthropoids on body mass bi-logarithmically. A median ray of KNM-BG 35250 is much of a positive outlier as that of the spider monkey (*Ateles*). Although *P. heseloni* also has a long pedal digit compared with most anthropoids, the deviation is less marked in this species.

In summary, the postcranial features suggest that *Nacholapithecus* engaged in orthograde behaviours (e.g. vertical climbing, hoisting, bridging) more frequently than did *Proconsul*; it had developed grasping capability, and moved relatively slowly in the trees (Nakatsukasa et al. 2003a). However, the absence of related features in the shoulder and hand imply that suspensory specialization had not developed by this stage.

Locomotor patterns of other contemporary hominoids are less well known. However, owing to discoveries from Maboko Island, Kenya, of *K. africanus* is an exception. It is proposed that *K. africanus* had forearm and femoral features related to scansorial activities, including a forelimb-dominated positional repertoire (McCrossin et al. 1998). One of the humeral shafts discovered is straight like that of modern apes. Interestingly, it is suggested that the locomotor repertoire of *K. africanus* included a significant terrestrial component (McCrossin, 1994; McCrossin & Benefit, 1997; Sherwood et al. 2002). Benefit & McCrossin (1995) argue that the transition from arboreal life to terrestrial life among African large-bodied hominoids originated at this stage. If so, suspensory specialization occurred later than, or simultaneously with, the terrestrial adaptation in later African hominoids. This scenario needs better justification by discoveries of younger fossil material.

By contrast, apparently suspensorily specialized apes had appeared by 12 Ma in Europe (Moyà-Solà & Köhler,

1996). *Dryopithecus* has long manual phalanges with marked curvature and was apparently adapted for frequent suspension. Slightly older, *Sivapithecus*, from the Siwaliks, shared derived postcranial features with African apes while retaining primitive catarrhine postcranial features (Rose, 1986, 1993, 1994; Pilbeam et al. 1990; Spoor et al. 1991; Ward, 1997; Madar et al. 2002). Its humerus exhibits shaft curvature (Pilbeam et al. 1990; Richmond & Whalen, 2001) and it is unlikely that suspensory behaviour had a large share in its total positional repertoire. Its phalanges exhibit stronger suggestions of arboreal behaviour than do those of *Nacholapithecus* (Nakatsukasa et al. 2003a). But like *Nacholapithecus* it possessed well-developed and large halluces and pollices (Rose, 1994; Madar et al. 2002), which suggests frequent use of a pollex-/hallux-assisted power grip rather than a hook-like hand position. The positional repertoire for *Sivapithecus* advocated by Madar et al. (2002) is very similar to that of *Nacholapithecus*, although *Sivapithecus* was more specialized in many regards. Besides the difference in body size, they probably differed in the proportional contribution of elements of the positional repertoire. However, these two taxa are derived in a similar fashion.

After 13 Ma there is no hominoid postcranial material in Africa until 6 Ma. Probably, suspensorily specialized African hominoid(s) evolved during this period. However, some researchers argue a Eurasian origin of suspensorily adapted hominoids (the 'Return from Eurasia Hypothesis'; see Stewart & Disotell, 1998; Begun, 2001).

Figure 8 presents a scenario of Miocene hominoid locomotor evolution based on the above ideas. It should be stressed, however, that there is no consensus among researchers concerning Middle to Late Miocene hominoid evolution, and that this schema is not necessarily supported by all evidence currently available.

One of the lumbar vertebrae of *Morotopithecus* (UMP 67-28) from Uganda at 20.6 Ma has features like those of modern apes, probably reflecting climbing and/or suspensory activity (Walker & Rose, 1968; Ward, 1993; Sanders & Bodenbender, 1994; MacLachy et al. 2000). The scenario presented relies on the assumption that those modern lumbar features of *Morotopithecus* are homoplastic. However, it is possible that adaptation for suspensory behaviour in hominoids started in the Early Miocene and that most currently known East African fossil hominoids are members of out-groups, relative to *Morotopithecus* and extant apes (Gebo et al. 1997; MacLachy et al. 2000). The similarity between *Nacholapithecus* and *Sivapithecus* in evolutionary trends, as well as a lack of suspensorily specialized hominoids on the likely migration route to Europe (e.g. from Turkey), leads me to favour the first possibility (i.e. a *Sivapithecus*–*Pongo* clade).

Besides the origin(s) of suspensory adaptation, uncertainties remain about the origins of terrestriality/plantigrady in African apes and humans (e.g. Gebo, 1992; Crompton et al. 2003), and knuckle-walking in African apes. Although Richmond & Strait (2000) found wrist bone features of early hominid fossils that suggest

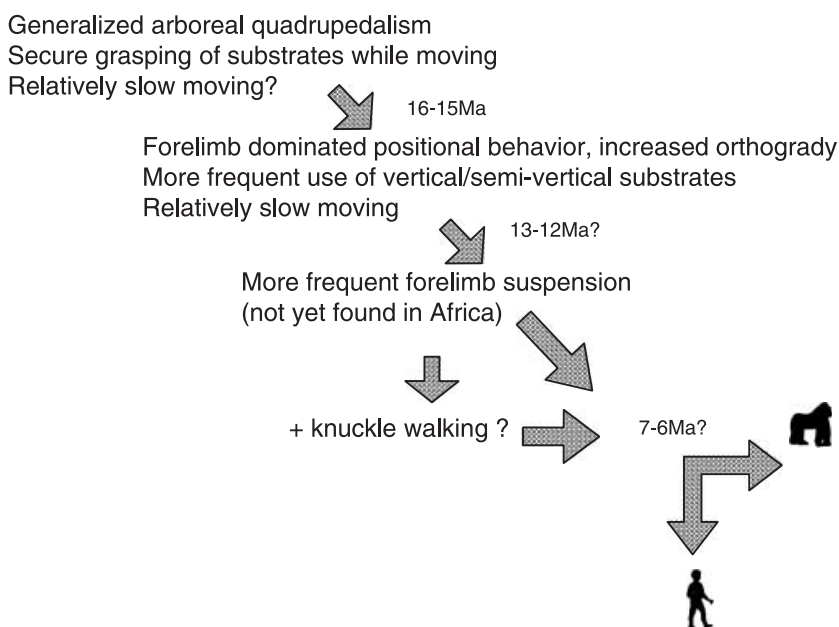


Fig. 8 A hypothetical scenario of Miocene hominoid locomotor/postural evolution.

humans evolved from knuckle-walking ancestors, arguments continue (Dainton, 2001; Lovejoy et al. 2001; but see Corruccini & McHenry, 2001; Richmond & Strait, 2001; Richmond et al. 2001). Until timing of these events is defined, many evolutionary scenarios for the antecedents of human bipedality are possible. To test the validity of each scenario, hominoid postcranial material from Africa between 13 and 6 Ma (e.g. Samburu Hills (9.5 Ma), Nakali (9.5 Ma?), Ngeringerwa (9.5–10 Ma) and Ngorora (12.5–10.5 Ma)) would be desirable.

Bipedal macaques as analogues for protohominid bipedality

Research history

The traditional monkey performance has a thousand-year history in Japan and is one of the most popular of traditional attractions. Japanese macaques (*Macaca fuscata*) live at exceptionally high latitude for living non-human primates, are distributed over a large part of the Japanese archipelago and maintain close contacts with the Japanese human population. This is probably one of the reasons why monkey performance has been popular in Japan for such a long time. Unfortunately, the tradition of Japanese monkey performance had disappeared by the early 1960s. In the late 1970s, a group of people endeavoured to revive this tradition, with collaboration of ethnologists, folklorists and primatologists. Since then, primatologists have been aware of the potential of these trained bipeds for studies of the evolution of human bipedality (Hayama et al. 1992).

These macaques, though trained for bipedality (hereafter performing macaques), are not fully bipedal. They spend about 1 h daily in bipedal postural and locomotor behaviour. Otherwise, their behaviour does not differ from that of ordinary Japanese macaques. However, 1 h is sufficiently long to argue that bipedalism is one of the major positional modes in these macaques, and the situation was probably similar in protohominids (Rose, 1991). The training for the bipedal performance begins when the animal is 2–3 years in age. There is no genetic strain from which macaques are chosen for performance. At the very first stage of training, macaques are conditioned, with the assistance of the trainer, to bear the entire body weight on the hindlimbs. About 10–15 min of training is executed several times a day. In training for bipedality,

no restraints are used. Within several days, most of the macaques become able to stand bipedally by themselves for a while (M. Nakatsukasa, personal observation). The trainers pay attention to posture adopted in standing, especially lumbar extension. They do not allow the subjects to walk bipedally until a good (i.e. upright) standing posture is acquired. Only after this step is emphasis placed on bipedal walking. After 1 year's training, the standing posture becomes quite upright (Nakatsukasa & Hayama, 1996). Once ability for stable standing is attained, the macaques may walk quite easily for over 1 km.

Early interest in performing macaques was focused on the marked lumbar lordosis that they developed. Hayama (1986) and Preuschoft et al. (1988) reported lateral X-ray photographs of the lumbar column in the performing macaques. They found that well-trained performing macaques acquired a marked lumbar lordosis (Fig. 9). The lordosis was maintained even in pronograde posture (Fig. 10). A lumbar lordosis should reduce the bending stress on the lumbar column while standing, and increases the leverage of the dorsal musculature. It should help maintain the centre of mass close to the hip and knee joints, thus reducing the moments around the joints. Not surprisingly, the degree of lordosis expressed is related to the length of training. It is significantly greater in the older age groups (trained for more than 3 years) than in younger ones (Hayama, 1986). Nakatsukasa & Hayama (1996) analysed the development of this lordosis cross-sectionally. Through 1 year's training, all the performing macaques show greater development of lordosis and relatively upright posture than do ordinary macaques. However, individual variation exists among the performing macaques, suggesting different potential for bipedal behaviour (Fig. 9).

The performing monkeys cease performance at the age of 11–14 years when they become too large to handle safely. After retirement, they rarely adopt bipedal behaviour. Therefore, it has been unclear what osteological change results from intense daily bipedal behaviour. However, a few performing macaques have died while young from acute infectious diseases. Two skeletons have been examined and several common unique features have been found (Nakatsukasa et al. 1995; Nakatsukasa & Hayama, 2003). The femoral cortex exhibited endosteal bone deposition and thus reduction of the medullary cavity through the proximal-to-middle shaft. The midshaft of the femur is

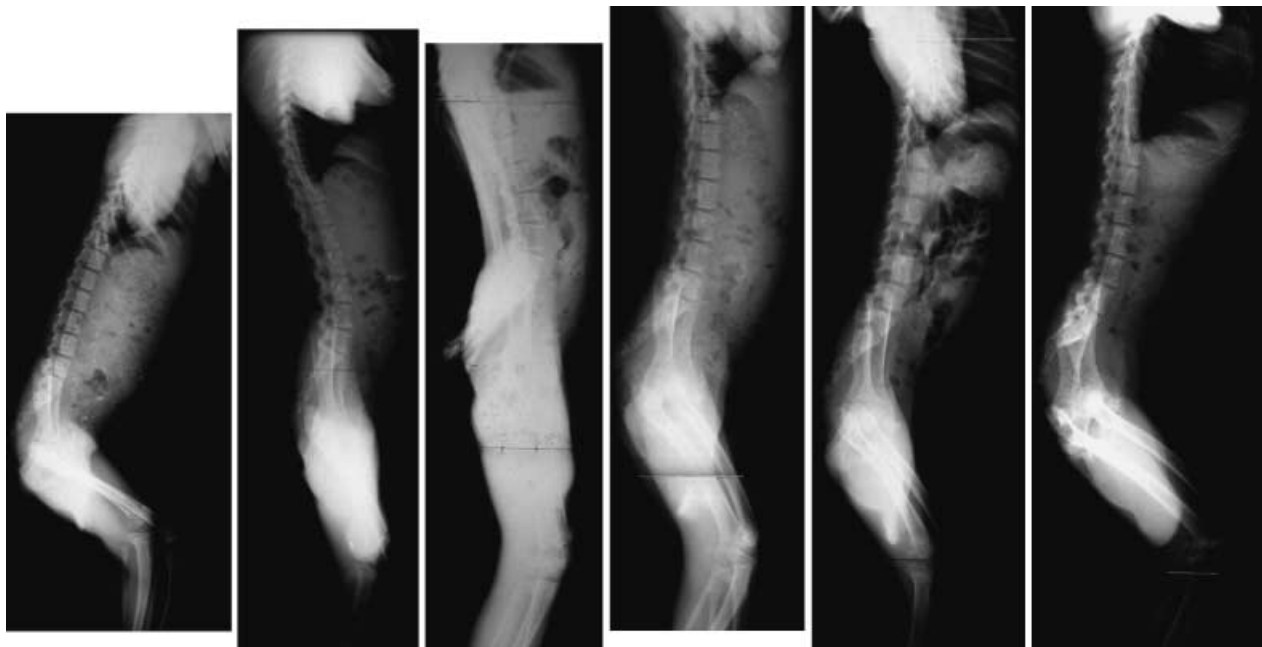


Fig. 9 Lateral X-ray photographs of the lumbar column in performing macaques. One individual, on the left, is a young macaque trained for only a few months. Others have been trained for more than 1 year.

mediolaterally expanded. Although only one individual was examined, the femoral neck of this specimen exhibits marked cortical thickening all round. These results accord with biomechanical predictions from standing posture and walking style (e.g. femoral abduction and lateral rotation together with partial flexion of the hip and knee joints) (Nakatsukasa et al. 1995).

Little quantitative research on the kinematics and kinetics of bipedal locomotion in the performing macaques has been done until recently (but see Ishida, 1991). However, recent experiments have found an amazing capacity of the performing macaques for sustained bipedal behaviour (Hirasaki et al. 2002). The performing macaques walk with longer stride length (when standardized by hindlimb length) and lower stride frequency compared with ordinary macaques. The hip and knee joints exhibit greater extension. The knee joint displays a human-like 'double knee action' so that the body centre of mass (CM) rises during the single-support phase of stance. The trajectory of the hip joint displays the inverted pendulum motion seen in humans, forming an upward convex curve during stance, compared with the concave curve seen in ordinary macaques. This feature suggests exchange of potential and kinetic energies of the CM (Hirasaki et al. 2002). Many such characteristics of human bipedal

walking are understood as energy-saving mechanisms (e.g. Cavagna et al. 1977). Therefore, the similarity of kinematic features in the performing macaques to those in humans may suggest increased locomotor efficiency in the bipedality of the performing macaques. This hypothesis may ultimately be tested by studies of locomotor energetics. Additionally, energetic studies on the performing macaques will enable us to investigate whether those characters unique to human bipedal walking really contribute to energy-saving, as theoretical prediction suggests. Not all such studies are in hand, but some progress has been attained in recent years.

Locomotor energetics of macaque bipedalism

Experiments of locomotor energetics in non-human subjects involve difficulties in terms of the training of subjects. In particular, it is very difficult to elicit unusual gait patterns (e.g. bipedalism). Thus, it is not surprising that only one study has dealt with the energetics of bipedalism in non-human primates (Taylor & Rowntree, 1973) before the present studies on performing macaques. Taylor and Rowntree trained two chimpanzees and capuchin monkeys for bipedal and quadrupedal walking on a treadmill and measured oxygen consumption during locomotion. Results showed no

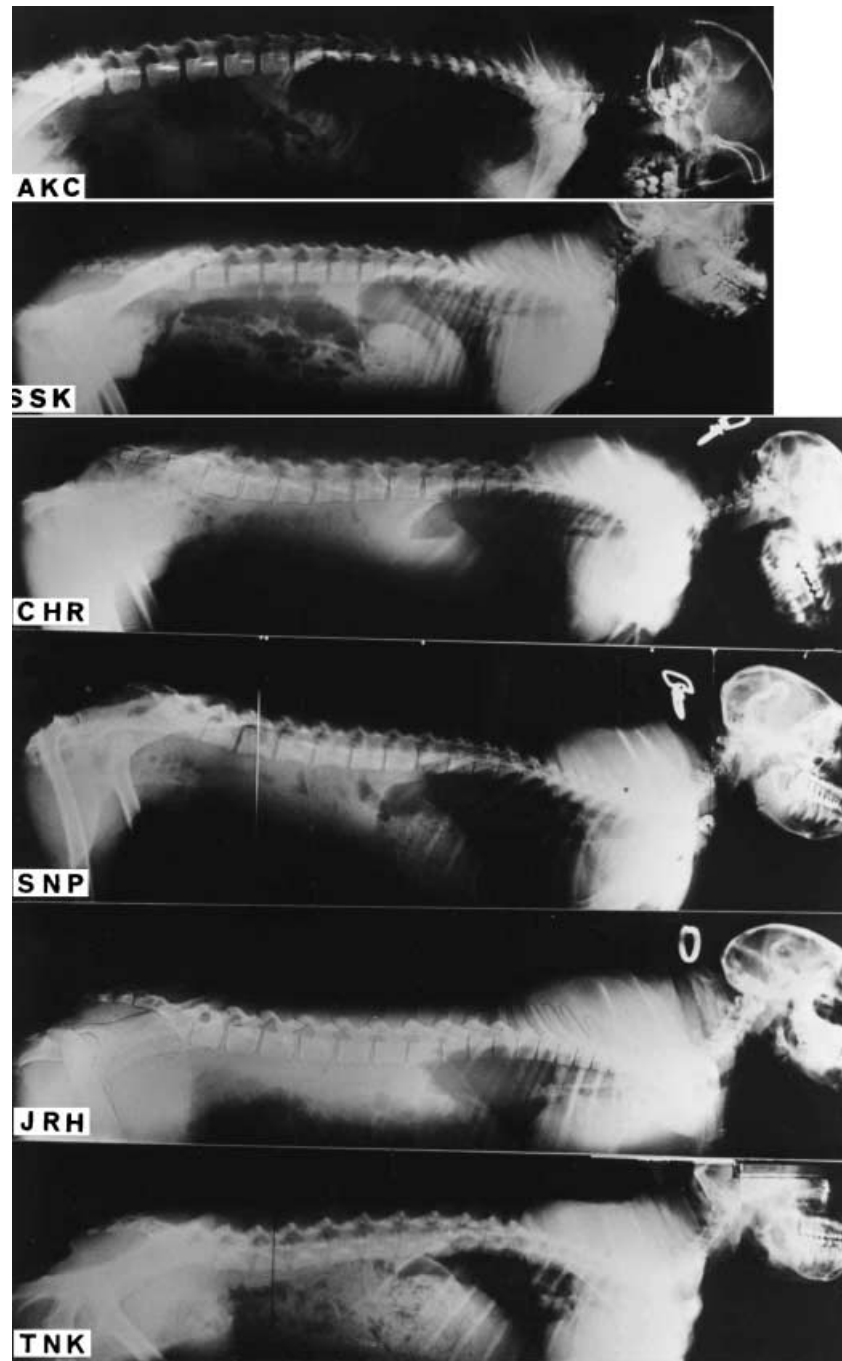


Fig. 10 Lateral X-ray photographs of the lumbar column in performing macaques while standing quadrupedally. The top two are young macaques trained for only less than 3 months. Modified from Hayama (1986).

difference in the costs of bipedal and quadrupedal walking. Because kinematic records were not made, it is impossible to know the characteristics of the bipedalism displayed. It would be interesting therefore to know if a similar finding applies to the trained Japanese macaques. We may make several alternative predictions: (1) if the energetic cost of bipedal and quadrupedal walking is identical in ordinary Japanese macaques, the energetic cost of bipedalism should be

lower than that of quadrupedal walking in the performing macaques; (2) the energetic costs for bipedalism and quadrupedalism may be identical in the performing macaques (suggesting the subjects of Taylor & Rowntree's (1973) study were as good bipeds as performing macaques); or (3) the energetic cost of bipedalism may be higher than that of quadrupedalism in performing (and ordinary) macaques. To identify the correct alternative, we measured relative locomotor

costs of bipedal walking compared with quadrupedal walking in performing macaques. Experimental details are published in Nakatsukasa et al. (2004), but the conditions differ from the standard techniques (for the latter, see, e.g. Taylor et al. 1982). Thus, it is appropriate to summarize the points of difference, potential criticisms and our response to them. Further, additional experiments have been conducted to support the conclusions of Nakatsukasa et al. (2004) and these data are also presented.

In Nakatsukasa et al. (2004), experiments conducted had two major limitations. Because the experiments were made with the collaboration of a professional monkey performance organization, available time for research was limited. Thus, a closed chamber system was adopted, avoiding the need to accustom subjects to a gas mask for breath sampling. Because the subjects would not walk without a trainer, a large chamber was constructed in which the subject and a trainer could stay together. The trainer breathed through a tube extending to the outside. The large chamber size meant that oxygen concentration changes were too small to be measured accurately using standard oxygen sensors. Therefore, carbon dioxide concentration, which can be monitored under these conditions, was recorded instead. (Standard carbon dioxide sensors are much more sensitive than oxygen sensors, reflecting the composition of the atmosphere.) Production of carbon dioxide can be converted into consumption of oxygen if the respiratory quotient (the ratio of produced carbon dioxide to oxygen intake) is known. This means that if the respiratory quotient is constant or not significantly variable under experimental sessions, the consumption of oxygen (the universal measure of energy consumption) will be proportional to the production of carbon dioxide. Hence, the relative cost of bipedal walking can be estimated for each subject.

The second limitation was the experimental duration. When the subject stopped stable walking, experimental measurements also ceased because continuous, steady walking is required to measure the total production of carbon dioxide in each session (see below). Although the trained monkeys can walk over quite long distances outside the laboratory, they do not like monotonous tasks, and experimental duration was performed short: average duration was 2.5 min (range 2–6 min). This means that the measured energetic cost includes the presteady-state cost, which is higher than that of the steady-state period (Taylor

et al. 1982). To avoid this problem, in the standard experimental protocol subjects are required to walk for more than 15 min. However, because the primary purpose of our study was to measure the 'relative cost' of bipedalism, and because energetic costs of bipedal and quadrupedal walking were measured under identical conditions (including the presteady-state cost), the relative costs can be estimated.

Nakatsukasa et al. (2004) used two performing macaques. The mean experimental duration was about 2 min in both bipedal and quadrupedal sessions. The concentration of carbon dioxide was monitored every 10 s. To allow air mixing, the first 30 s of data after the chamber was closed were discarded. The concentration of carbon dioxide was plotted against elapsed time and the least-squares regression was calculated (Fig. 11). The correlation was highly significant in all sessions ($r^2 > 0.98$). The energetic cost of locomotion is conveniently given by the rate of carbon dioxide concentration increase standardized by body mass (p.p.m. $s^{-1} kg^{-1}$). The slope of the line was therefore standardized by body mass and employed as a convenient measure of locomotor cost. Figure 12 summarizes the results of our experiments, showing least-squares regression lines of

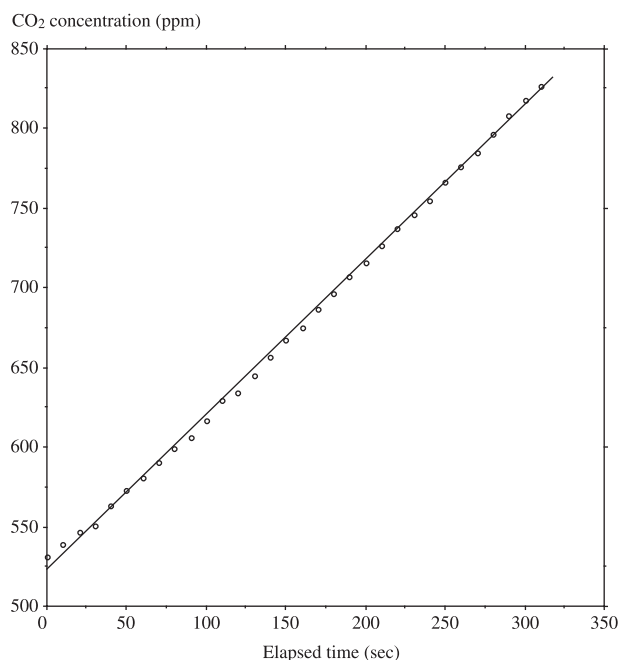


Fig. 11 Change of carbon dioxide concentration (p.p.m.) within the chamber against elapsed time (s) during an experimental session. Concentration (y) is linearly correlated with elapsed time (x). The least-squares regression: $y = 0.97x + 523.2$ ($r^2 = 0.999$).

Fig. 12 Standardized carbon dioxide concentration increase rates (p.p.m. s^{-1} $kg^{-1} \times 10^{-2}$) in bipedal and quadrupedal walking with various velocities (km h^{-1}). values are given as mean \pm SD. Diagonal lines are least-squares regression trajectories: $y = 1.961x + 2.156$ ($r^2 = 0.957$) in bipedal walking and $y = 1.504x + 1.582$ ($r^2 = 0.927$) in quadrupedal walking in Subject 1; $y = 1.65x + 4.68$ ($r^2 = 0.901$) for bipedal walking and $y = 1.486x + 3.34$ ($r^2 = 0.960$) for quadrupedal walking in Subject 2. From Nakatsukasa et al. (2004).

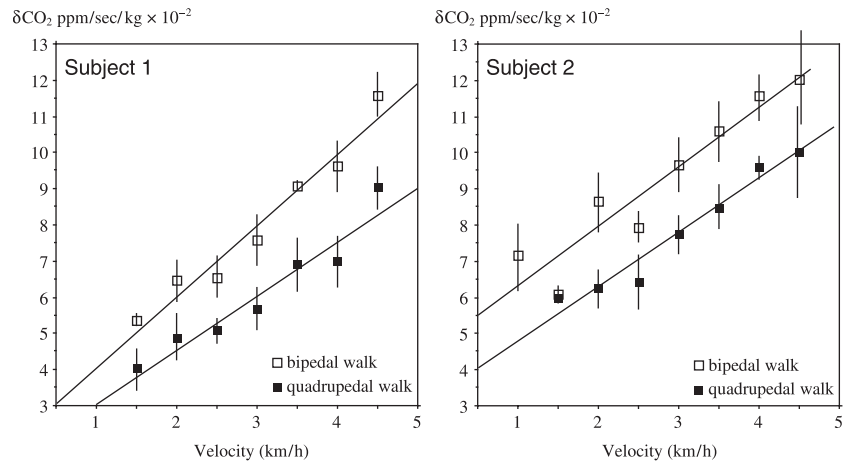


Table 3 Energetic costs (carbon dioxide concentration increase rates (p.p.m. s^{-1} $kg^{-1} \times 10^{-2}$)) in bipedal and quadrupedal walking by Subject 1. From Nakatsukasa et al. (2004)

	Walking velocity (km h^{-1})						
	1.5	2.0	2.5	3.0	3.5	4.0	4.5
Bipedalism							
Mean	5.37	6.48	6.55	7.60	9.06	9.62	11.59
SD	0.09	0.54	0.56	0.70	0.13	0.71	0.59
n	5	6	5	9	5	6	3
Quadrupedalism							
Mean	4.05	4.87	5.10	5.67	6.93	6.98	9.05
SD	0.54	0.62	0.36	0.55	0.76	0.73	0.56
n	5	6	4	10	5	10	3
B/Q ratio*	1.33	1.33	1.29	1.34	1.31	1.38	1.28

*Bipedal/quadrupedal ratio.

energetic cost on walking speed. Locomotor cost is correlated with walking velocity both in quadrupedal and in bipedal walking. No significant difference was found between slopes of the bipedal and quadrupedal regression lines in either subject, but the regression line for bipedalism is displaced upwards with respect to that of quadrupedal walking. These results mean that bipedal walking incurs a proportionally greater energetic cost. Tables 3 and 4 compare the relative energetic cost of bipedal walking with that of quadrupedal walking for each velocity. The ratio is around 1.3 in one subject (Table 3) and 1.25 in the other (Table 4). (Although the costs of bipedalism and quadrupedalism are almost the same at a velocity of 1.5 km h^{-1} in one subject, this velocity is too slow for stable walking.) Apparently, bipedal walking does require more energy than quadrupedal walking in the performing macaques.

However, criticisms may still be made of the experimental design, with respect to constancy of the respi-

ratory quotient and to measurement of cost presteady state. Therefore, an additional experiment has now been conducted to eliminate these methodological problems. Experimental settings were the same as in the previous study, but the conditions were modified. The experimental duration was 10 min and the subject switched locomotor mode 5 min from the beginning. Both sequences were adopted (i.e. bipedalism first, and quadrupedalism first). The walking velocity was 2 km h^{-1} . Three trials were made for each sequence using a single macaque (subject 2 in the previous experiment). Table 5 summarizes the results. Because the energetic costs (carbon dioxide concentration increase rates: here given by p.p.m. s^{-1}) were measured continuously in a single session, the issue of constant respiratory quotient is resolved. The energetic costs during the first 5 min were probably measured at a presteady state. However, regardless of the sequence, energetic costs of bipedal walk remain higher than those of quadrupedal

Table 4 Energetic costs (p.p.m. s⁻¹ kg⁻¹ × 10⁻²) in bipedal and quadrupedal walking by Subject 2. From Nakatsukasa et al. (2004)

	Walking velocity (km h ⁻¹)						
	1.5	2.0	2.5	3.0	3.5	4.0	4.5
Bipedalism							
Mean	6.08	8.65	7.94	9.66	10.61	11.56	12.04
SD	0.22	0.77	0.42	0.72	0.80	0.59	1.31
<i>n</i>	4	4	6	9	6	5	2
Quadrupedalism							
Mean	5.98	6.28	6.45	7.75	8.50	9.61	10.01
SD	0.11	0.50	0.72	0.53	1.08	0.25	1.24
<i>n</i>	3	5	4	6	4	3	2
B/Q ratio*	1.02	1.38	1.23	1.25	1.25	1.20	1.20

*Bipedal/quadrupedal ratio.

Locomotor sequence	Carbon dioxide concentration increase rate (p.p.m. s ⁻¹)		Locomotor cost of bipedal walk relative to quadrupedal walk
	First 5 min	Last 5 min	
Bipedal to quadrupedal average			
	1.206	0.988	1.22
	1.204	0.936	1.29
	1.149	0.947	1.21
	1.186	0.957	1.24
Quadrupedal to bipedal average			
	0.924	1.092	1.18
	0.968	1.118	1.15
	0.967	1.183	1.22
	0.953	1.131	1.19

Table 5 Energetic costs of bipedal and quadrupedal walking measured in single contiguous sessions (p.p.m. s⁻¹)

walking, by about 20%. The additional experiment thus confirms the conclusion of Nakatsukasa et al. (2004).

Thus, bipedal walking requires more energetic cost than does quadrupedalism even in highly trained Japanese macaques, which have acquired some 'human-like' features of bipedal gait. It is unclear why our result differs from that of Taylor & Rowntree (1973). Japanese macaques may have only low potential for efficient bipedal walking compared with other anthropoid primates (see Yamazaki, 1985); their anatomical specialization for semiterrestrial cursorial locomotion may hence entail greater energetic expenditure in bipedalism. If this is true, the same would apply to many cercopithecoid monkeys because characters related to semiterrestriality are ubiquitous among cercopithecoids, as a consequence of phylogenetic inertia (see, e.g. Nakatsukasa, 1994). More, and comparative, studies are necessary.

We are particularly interested to discover the relative efficiency of bipedal walking in the performing macaques, compared with that in ordinary macaques. This is a difficult task, but we are currently planning experiments to address this question (see below).

Prespectives for future study

What inferences can be obtained from these performing macaques? How useful are these macaques for understanding the origins of human bipedalism? The macaques are genetically/anatomically specialized for pronograde leaping-quadrupedal type locomotion, with anatomical features such as a long lumbar region, restriction of joint motion ranges, and digitigrade hands and feet. These anatomical features certainly did not exist in the last common ancestor of *Homo* and *Pan*. Nevertheless, several implications have emerged

for functional anatomy and biomechanics of bipedalism and for the early evolution of human bipedality.

For example, functional anatomists have long considered that human lumbar lordosis is an adaptation for bipedalism because lordosis is theoretically expected to reduce bending stresses on the lumbar spine. The existence of an acquired lumbar lordosis in performing macaques is clear evidence for such a link between bipedal posture and lumbar lordosis, and suggests that lordosis would have evolved at a very early stage of human bipedal evolution.

It is also interesting to note that the 'human-like' kinetic features of bipedalism in the performing macaques were the results of an autonomic process: what trainers modified in the performing macaques were rather degrees of trunk erection and hip joint extension in standing. The parallel development of some gait characteristics may suggest the presence of a common (or similar) mechanism of gait regulation in humans and macaques.

Nakatsukasa & Hayama (2003) compared gaits of these artificially 'tuned' bipeds with those of wild born macaques that, because of injuries, displayed a high degree of bipedalism. They reported bipedal gaits of a wild, young adult Japanese macaque that had lost its forearms from a congenital malformation. Its trunk was more inclined and the hip and knee joints were less extended (Nakatsukasa & Hayama, 2003) with respect to the trained performing macaques. The trajectory of the hip joint did not display inverted pendulum motion (N. Ogihara, personal communication). Thus, adoption of bipedal locomotion may not of itself lead to ontogenesis of 'human-like' bipedalism. Probably, the contrast in kinematics reflects a difference in the processes by which bipedal walking was developed. Hayama et al. (1992) identified an important role of postural habituation in the training of the performing macaques. By contrast, the wild-born macaque had not 'learned' upright standing posture before it started to walk. Postural adaptation thus significantly affects the efficiency of bipedal locomotion. This difference may at least partly support the postural adaptation hypothesis of the origins of human bipedalism (e.g. Hunt, 1996).

One of the most important future requirements is comparison of energetic costs of bipedal walking between performing macaques and other macaques. Measuring energetic costs in ordinary macaques will be impossible using the closed chamber system. However, it will be possible, over time, to accustom young laboratory

monkeys to a gas mask. Alternatively, it is possible to investigate variation of kinematics, kinetics and energy consumption among performing macaques: Hirasaki et al. (2002) recognized differences in kinematics of bipedalism (see also Fig. 8 for variation in bipedal standing posture). Likewise, there was a difference in the relative energetic cost of bipedal walking between our two subjects (Tables 3 and 4). We plan to investigate how much the 'human-like' kinematic features we have identified account for energy saving in bipedal locomotion. Integration of locomotor energetic and kinesiological studies of individuals has not yet been achieved for non-human primates. However, kinematic data for bipedal walking in the performing macaques show high regularity within individuals. Longitudinal analyses, from the onset of training, will also provide more opportunities for study, and are also a useful way to check predictions from theoretical biomechanical studies (e.g. inverse dynamics). Although it is only cursorily treated here, studies of *in vivo* bone remodelling in the performing macaques will be valuable for a better understanding of the bone response invoked by mechanical stress. Besides cortical bone distribution, trabecular structure is significantly altered in the performing macaques (Macchiarelli et al. 2001).

The protohominids probably incorporated bipedalism into their total positional repertoire as one of a few major positional modes (Rose, 1991). Palaeoenvironments of early hominids do not contradict this prediction (WoldeGabriel et al. 1994; Pickford & Senut, 2001). If the initial behavioural shift was subtle, associated signs might be faint in the skeletal system. The sensitivity of response in trabecular architecture to frequently repeated stresses is well known (Lanyon, 1974; Radin et al. 1982; Carter et al. 1989; Biewener et al. 1996). Currently, trabecular architectures in the pelvis, the knee and in lumbar vertebral bodies are being investigated in a few performing macaque skeletons, and will provide a sounder basis for fossil interpretation in future.

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