How did humans acquire erect bipedal walking?

Tasuku Kimura*1

1The University Museum, The University of Tokyo, Tokyo, Japan

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Abstract  Recent fossil records have suggested that human erect bipedal locomotion started in Africa probably more than 6 million years ago. However, debate continues regarding how locomotion was acquired by our prehuman ancestors. Fossils and the genetic traits of recent humans and animals cannot answer this question directly. Therefore, the present paper reviews acquisition models of human bipedalism and explanations regarding how humans acquired bipedalism based on a comparative kinesiology of contemporary mammal species. Nonhuman primates are adequate models of human bipedal acquisition because of not only the phylogenetically close relationship with humans, but also the trend toward hindlimb dominance and orthograde positional behavior in daily life. Although dissimilar to the erect bipedalism seen in humans, nonhuman primates adopt bipedal positional behavior in the wild. All nonhuman primates use the arboreal environment, but some groups of species utilize the ground predominantly. Compared with relatively terrestrial nonhuman primates, relatively arboreal primates show more similarities with humans in their bipedal locomotion. Comparisons among primate species and between nonhuman primates and nonprimate mammals indicate that human-like bipedal characteristics are strongly related to arboreal life. Our prehuman ancestors likely started and adapted to bipedal locomotion while living in trees; this process is referred to as the generalized arboreal activity model. When humans began terrestrial locomotion, they likely performed proficient bipedalism from the first step. The generalized arboreal activity model presented here does not contradict the fossil records.

Key words: primates, bipedalism, orthograde, hindlimb dominance, arboreal activity

Introduction

Human locomotion is characterized by bipedalism with an orthograde trunk on extended lower limbs. The trunk and spine stand vertically and the hip and knee joints extend greatly. Although many vertebrates, including birds, kangaroos, and some lizards and dinosaurs, have walked or continued to walk bipedally, this is usually done with pronograde trunk orientation and flexed hip joints, similar to quadrupeds. No extant or extinct vertebrates on earth other than humans have acquired habitually erect bipedalism. Erect bipedalism is the one of the most specialized characteristics of humans. Because of the acquisition of bipedalism, human hands became free from locomotion and able to be used for manipulating and carrying tools, food, and infants, even during locomotion. It has been suggested that the large brain and vocal language of present humans were related to the erect bipedalism (Schultz, 1942; Clark and Henneberg, 2017; Xu et al., 2018). When looking at human lineage through the fossil record, bipedalism started at least 4.4 million years ago (Ma) (Lovejoy et al., 2009a), and possibly more than 6 Ma (Senut et al., 2001; Brunet et al., 2002). On the other hand, other specialties of present humans, such as large brains and developed tools, developed relatively more recently. The oldest stone tools discovered appeared around 3 Ma (Harmand et al., 2015), and large brains similar to ours were acquired only a few hundreds of thousand years ago (Henneberg and de Miguel, 2004). Erect bipedal locomotion is the oldest characteristic to distinguish humans from other vertebrates. The acquisition of erect bipedalism is the key to defining hominoid fossils as human ancestors.

When, where, how, and why did our human ancestors acquire bipedal locomotion? In the last few decades, many attempts have been made to answer these questions. The oldest human fossils were discovered from strata of between 4 and 7 Ma in Africa, as described above. The phylogenetically nearest extant animals of human lineage, i.e. African great apes, live in Africa. Human ancestors should have started bipedal locomotion in Africa around this time or a little earlier. Many models have suggested how erect bipedalism may have begun. Fossils are useful for indicating the time and place of evolutionary processes, but locomotion traits should be compared and discussed based on living animals because fossils cannot walk themselves. Explanation of fossil locomotion can be sought only from extant animals. Comparative kinesiology of living nonhuman primates is an important method of analysis to clarify the process of human
bipedal acquisition (Kimura et al., 1979; Schmitt, 2003). Nonhuman primates frequently stand and walk bipedally, and are therefore useful animal models to study human bipedalism, not only because of their phylogenetically close relationship with humans, but also because of their easy and customary bipedalism ability. A comparison between bipedal walking in humans and nonhuman primates may clarify the unique characteristics of human bipedalism. Because locomotion of fossils might not be the same as that of living animals, a simple comparison with one or two living species is not adequate to clarify the problem. Therefore, the present article reviews the models and empirical evidence on the process of human bipedal acquisition based on comparative kinesiology among multiple primate species and between nonhuman primates and nonprimate mammals to present a generalized arboreal activity model.

**Unique positional behavior of nonhuman primates**

Compared with nonprimate terrestrial mammals, which are referred to in the present article as ‘common mammals,’ nonhuman primates have several unique characteristics in terms of their positional behavior.

Measurements of body weight distribution of the fore- and hindlimbs while in the quadrupedal standing position show that in common mammals, the forelimbs are usually dominant, about 60% of body weight (Thompson, 1917; Iwamoto and Tomita, 1966). By contrast, the hindlimbs are usually dominant in nonhuman primates (Krüger, 1943; Iwamoto and Tomita, 1966; Kimura et al., 1979). During quadrupedal locomotion, including asymmetrical high-speed locomotion, in nonhuman adult primates, the hindlimbs mostly put larger foot force components in the vertical, i.e. body supporting, and backward, i.e. accelerating, directions compared with the forelimbs (Kimura et al., 1979; Kimura, 1985, 1992, 2000; Reynolds, 1985; Demes et al., 1994; Schmitt and Hanna, 2004). By contrast, adult common mammals, except the woolly opossum, which is an arboreal marsupial (Schmitt and Lemelin, 2002), usually exhibit larger vertical and backward force components in the forelimbs than in the hindlimbs during quadrupedal walking (Manter, 1938; Barclay, 1953; Björck, 1958; Pratt and O'Connor, 1976; Kimura et al., 1979).

Among the nonhuman primates, monkeys that habitually walk on the ground, such as baboons, Japanese macaques, rhesus macaques, and patas monkeys, do not always exhibit clear hindlimb dominance in terms of foot force. In these animals, the hindlimb force is sometimes equal to or less than the forelimb force. On the other hand, arboreal primates that mainly utilize the arboreal environment, such as chimpanzees, orangutans, spider monkeys, and capuchins, typically show clear hindlimb dominance in terms of foot force (Kimura et al., 1979; Kimura, 1992; Demes et al., 1994; Schmitt and Hanna, 2004). This suggests that hindlimb dominant force distribution is associated with arboreal life.

The footfall order of common mammals during symmetrical quadrupedal walking is usually the sequence RH-RF-LH-LF (Howell, 1944; Hildebrand, 1967; Cartmill et al., 2002), where R is right, L is left, F is forelimb, and H is hindlimb; this is referred to as the lateral sequence (Hildebrand, 1967) or the backward cross type (Iwamoto and Tomita, 1966). By contrast, nonhuman adult primates usually adopt the sequence RH-LH-RF-LF (Prost, 1965; Tomita, 1967; Hildebrand, 1967; Rollinson and Martin, 1981), which is referred to as the diagonal sequence or the forward cross type (Figure 1). In both arboreal and terrestrial environments, forelimbs steer the body during quadrupedal locomotion. During the diagonal sequence, the hindlimb touches down on the substrate at about the same point as that of the forelimb on the same side and nearly under the body’s center of gravity. When the substrate contains large gaps or consists of mechanically weak twigs, which are common traits of the arboreal environment, the diagonal sequence is convenient for the hindlimbs, which mainly support the

![Figure 1. Quadrupedal and bipedal walking. From left to right, a quadrupedal dog representing the common mammal, the quadrupedal and bipedal walking of a chimpanzee, and a bipedal human, respectively. Black circles indicate the center of gravity of the body, which is higher in the bipedal than in the quadrupedal position. The quadrupedal footfall order of nonhuman primates is mainly a diagonal-sequence in which the fore- and hindfoot of the same side touch the substrate at about the same place at successive times. Common mammals mainly adopt the lateral-sequence, where the fore- and hindfoot of the same side touch at quite separate places. Many common mammals touch the substrate mainly with their toes and interdigital pads (digitigrade), but many arboreal nonhuman primates such as chimpanzees support their body with their whole sole (plantigrade), similar to humans. In nonhuman primates, the distal humerus is positioned in front of the shoulder at forefoot touchdown during quadrupedal walking. On the other hand, the excursion of the humerus is not so large in common mammals.](image-url)
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Figure 2. Functional differentiation of the limbs in quadrupedal nonhuman primates. Nonhuman primates show larger acceleration and body supporting force components in the hindlimbs than in the forelimbs during quadruped locomotion. By contrast, common mammals accelerate and support the body mainly using the forelimbs. The steering activity of both groups is situated at the front. Nonhuman primates utilize mainly front-steering/rear-driving locomotion, whereas common mammals utilize mainly front-steering/front-driving locomotion (Kimura et al., 1979).

Primate quadrupedal locomotion is unique in comparison with that of common mammals, showing a more protracted arm and forelimb at the forefoot touchdown of a step (Larson et al., 2000). The distal humerus is positioned in front of the shoulder joint (Figure 1). The total excursion angles of both the humerus and forelimb of nonhuman primates are larger than those of common mammals, except for two arboreal species, the woolly opossum and the koala. Larson et al. (2000) discussed the uniqueness of this characteristic in relation to safe locomotion on and the grasping of small branches. They noted that increased humeral excursion mobility could be accomplished at the expense of joint stability, which may be linked to the relatively small production force by the forelimbs compared with that of the hindlimbs. Larson et al. (2001) demonstrated that the thigh and hindlimb excursions were also larger in primate species than in common mammals. They claimed that large limb excursion could be linked to the ability to increase speed without increasing the step frequency, as well as to greater stability and security on narrow substrates.

Nonhuman primates frequently sit with an orthograde trunk and use the forefoot as a manipulating hand during foraging (Jolly, 1970), social communication, object play, and even tool use. Kawai and Mito (1973) reported that the orthograde posture was assumed for 84% of the day by the Formosan macaque; Morbeck (1975) showed that the guereza’s sitting posture accounts for more than 50% of the total observations; and Hunt (1992) reported that excluding lying in a night nest, sitting was the most common positional behavior, constituting over 61% of the total observations in chimpanzees. Sitting and squatting are the most common postural behaviors in trees for wild adult western lowland gorillas, although there are significant seasonal and sex differences (Remis, 1995). Nonhuman primates often sit while supporting their upper body with their hindlimbs and/or haunches and their forelimbs free. The functional differentiation between the fore- and hindlimbs is clear in the sitting position. The muscles, internal organs, and circulatory organs of the upper body should be accustomed to the orthogonal position (Keith, 1923). Nonhuman primates can easily stand bipedally from their orthograde sitting posture by utilizing their relatively strong hindlimbs.

Extant nonhuman primates have larger limbs than common mammals. The limb bones, especially the hindlimb bones, of primates are relatively longer (Alexander et al., 1979), larger in diameter, and more robust than those of common mammals based on a comparison of body mass control (Kimura, 1991, 1995; see also Polk et al., 2000) (Figure 3). The bones of some arboreal mammals, such as kinkajous, sloths, and possums, are also large (Kimura, 1995). Interestingly, terrestrial humans share the same characteristics with other primates. On the other hand, many nonhuman primates that utilize the ground daily, such as patas monkeys, baboons, and Japanese macaques, share some resemblance with common mammals. The unique hindlimb dominant positional behavior and long and robust limbs of nonhuman primates can be explained by their adaptation to the irregularly discontinuous arboreal space. In such three-dimensional environments, animals travel up and down while maintaining control of gravitational forces. Larger nonhuman primates usually move vertically with an orthogonal trunk and upwardly oriented head, where gravitational forces are mainly supported by the hindlimbs. In the arboreal environment, nonhuman primates use their long forelimbs to forage for foods that are typically found on thin, flexible branches. In such situations, the hindlimbs should support the body on a thicker branch. Long and robust limb bones and large shoulder excursion angles make it possible to reach the food and pass safely over gaps.

Based on foot force patterns and bone robustness among nonhuman primates, arboreal species are more hindlimb dominant than terrestrial ones (Kimura et al., 1979; Kimura,
and arboreal non-primate species share a number of similar bone and locomotion patterns with nonhuman primates (Kimura, 1985, 2002). These findings reinforce the arboreal influence on the positional characteristics of nonhuman primates.

Primates who adapt to relatively arboreal environments show strong hindlimb dominance in their quadrupedal posture and locomotion, whereas relatively terrestrial nonhuman primates show weak hindlimb dominance. Arboreal species show large vertical and accelerating foot forces in the hindlimbs and robust hindlimb bones. The hindlimb dominance of primates, which is useful for bipedal walking, is likely acquired in the arboreal environment.

**Bipedal walking in nonhuman primates**

Many nonhuman primates include bipedal locomotion in their daily locomotor repertoires, in spite of having a high center of gravity and the difficulties involved in maintaining balance while in the bipedal compared with the quadrupedal position (Figure 1).

The bipedalism of nonhuman primates, however, contains many characteristics that differ from that of humans. The trunk of bipedal nonhuman primates never stands erect like that of humans, but rather inclines forward (Figure 4). From the side view, the center of gravity in the human body is situated just above the hip joint near the vertebral column while in the bipedal standing position. In nonhuman primates, the center of gravity is situated ventral to the vertebral column at the middle of the belly (Figure 1) (Kimura, 1996). The hip joint in nonhuman primates always flexes during bipedal locomotion, never reaching human-like true hyperextension in which the thigh extends behind the trunk axis (Ishida et al., 1975; Yamazaki et al., 1983; Okada and Kimura, 1985; Okada et al., 1996). The knee joint in nonhuman primates does not fully extend during the stance-phase. To fasten the flexed hip and knee joints against forces such as body weight, both the flexor and extensor muscles work simultaneously during the stance phase, i.e. in the single stance-phase, the center of gravity moves higher, increasing the body's potential energy (Kimura, 1996). Cavagna et al. (1976) and Alexander and Jayes (1978) showed that the high potential energy generated in each single stance-phase compensated for the loss of forward kinetic energy. Part of the kinetic energy that was input during the double stance-phase is recovered by the transformation into gravitational potential energy in the single stance-phase. Thus, the human type of movement of the
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center of gravity economizes energy expenditures. Cavagna et al. (1976) calculated the 'recovery' of this mechanical energy during walking. In chimpanzees, this recovery is sometimes large, but other times small (Kimura, 1996). After touchdown, the flexed knee joint of nonhuman primates flexes much more and the center of gravity moves lower. In chimpanzees during walking, the maximum flexion of the knee during the stance-phase correlates with the height of the hip joint nearby which the center of gravity is situated (Figure 5). When the knee joint stops flexion during the single stance-phase, the center of gravity is kept relatively high and recovery becomes large. When the knee joint is flexed substantially more during the entire single stance-phase, as in the case of bipedal walking in most Japanese macaques, then recovery is small or nearly null. The vertical foot force component in human walking, as measured by a force plate, contains two peaks and a trough, at which time the center of gravity moves higher during the single stance-phase. By contrast, the vertical component in Japanese macaques and many nonhuman primates has only one peak in which the center of gravity moves lower and the potential energy decreases (Kimura, 1985). Chimpanzees, orangutans, and spider monkeys, which are relatively arboreal species, sometimes walk with two peaks and a small trough, and sometimes with a scarce trough (Kimura, 1985, 1996; Pontzer et al., 2014). These animals walk in association with large and sometimes with small recovery. Such irregularities, individual and intraspecific, are one of the main charac-

Figure 4. Stick pictures depicting bipedal walking in a chimpanzee (left) and a human (right) on the sagittal plane. One cycle of walking from a heel-strike to the next heel-strike is shown. The statures of both species are depicted as equal in size. Sticks connect the tragion (ear point), shoulder joint, hip joint, knee joint, ankle joint, and tip of the third toe in the chimpanzee, and the vertex, shoulder joint, hip joint, knee joint, ankle joint, and dorsal surface of the big toe in the human. Points on the head and toe are different between the two species because of the relatively differently shaped body parts. Human walking is characterized by an erect trunk with small angular movements, hyperextended hip joint, fully extended knee during the single stance-phase, and the rocking mechanism of the sole.

Figure 5. Correlation and regression analyses between the knee flexion angle and relative hip height during the stance-phase in chimpanzee bipedal walking. In total, 150 trials of chimpanzee bipedal walking from one year of age to adulthood were analyzed. The relative hip joint height is the highest hip height divided by the sum of the thigh and shank lengths. The knee flexion angle (degree) is obtained at the maximum extension, where 180° means full extension and smaller angles mean larger flexion. The correlation coefficient (0.427) is significant. The less flexed the knee during the stance-phase, the higher the height of the hip joint.

\[ \text{Rel. Hip Height} = 0.609 + 0.003 \times \text{Knee Flexion (deg)}; R^2 = 0.182 \]
teristics of bipedal walking in nonhuman primates, and are in striking contrast to the rhythmic, regular, and constant nature of human walking (Kimura and Yaguramaki, 2009). O’Neill et al. (2015) pointed out that the large intraspecific variance in kinematics would have been important raw material for natural selection.

The bipedal walking practiced among some but not all species of nonhuman primates is relatively similar to that in humans (Kimura et al., 1979). Hamadryas baboons and Japanese macaques walk with strongly flexed hip and knee joints, and their energy recovery is low. Their heels do not usually touch the substrate (digitigrade), similar to their quadrupedal walking (as in Schmitt and Larson, 1995; for an exceptional case involving anubis baboons, see Berillon et al., 2010). These species adapt to the relatively terrestrial environments of their daily lives. Spider monkeys and chimpanzees walk with relatively extended lower limb joints, although not fully extended compared with humans. They usually touch the substrate with their entire soles (plantigrade), probably because they use relatively arboreal environments where they frequently grasp branches with their entire volar surfaces. Their calf muscles work strongly at the take-off phase of walking, somewhat similar to humans (Ishida et al., 1975). Chimpanzees walk with a heel-strike on the substrate and with a toe-off with their smaller toes (Figure 4). They can use the plantigrade rocking mechanism of the foot, similar to human walking, despite the differences in the structure of the foot between chimpanzees and humans; for example, their abducted big toe and lack of a sagittal arch (Holowka et al., 2017). The rocking mechanism of the foot during double stance-phase is thought to help a conversion of downward kinetic energy directly into forward kinetic energy and to prolong step length (Cavagna et al., 1977). Spider monkeys have more flexible feet than chimpanzees, and make touchdown from the lateral forefoot, but attain a suitable posture for grasping by the entire sole (Okada, 1985).

Twisting of the trunk, in which the shoulder and pelvis rotate opposite from each other, is a characteristic of walking in human adults and reduces angular momentum in the trunk. Nonhuman primates have some difficulty twisting the trunk in the same manner (Bramble and Lieberman, 2004; see also Thompson et al., 2015); their whole trunk rotates with the lower limb of the leading side when the step length is long, regardless of whether the trunk twist is large or small.

The metabolic cost of transport for chimpanzees is greater than that for common terrestrial mammals and birds when comparing the same body mass, whereas that for human walking is less costly (Sockol et al., 2007). Among chimpanzees, bipedal walking is not significantly more costly than quadrupedal walking (Taylor and Rowntree, 1973; Sockol et al., 2007; Pontzer et al., 2014). No measurable difference is apparent in the cost of walking on two or four legs for the capuchin monkey (Taylor and Rowntree, 1973). On the other hand, in Japanese macaques, the energy expenditure of bipedal walking is higher than that of quadrupedal walking (Nakatsukasa et al., 2004, 2006). Chimpanzees and capuchins are relatively arboreal primates, whereas Japanese macaques use the terrestrial environment in daily life. The different costs within primate species could be related to the daily use of different environments. For arboreal nonhuman primates, the adoption of bipedal walking would have had only a small effect on walking costs; however, for relatively terrestrial monkeys, the energy cost of bipedal walking would have been high.

**Models of human bipedal acquisition**

Many models on the process of acquiring human bipedalism have been presented.

1. The terrestrial model

Terrestrial locomotion is thought to be a unique human characteristic in comparison with many monkeys and apes that live mostly in arboreal environments. The bipedalism of our human ancestors has been discussed in regard to their debouch into the grassy plains (Senut et al., 2018). Some primates frequently stand bipedally on the ground to look far into the distance or to collect food from the branches of small trees (Rose, 1976; Hunt, 1994). However, terrestrial nonhuman primates cannot extend their hindlimb joints to a large extent because they are limited by the shortness of their muscles, ligaments, and the skin over their joints (Okada and Kimura, 1985; Okada et al., 1996). Strong joint extension is not necessary during quadrupedal locomotion, but is important for efficient bipedal locomotion. Among extant nonhuman primates, bipedal walking in the terrestrial ones differs substantially from that of humans in many regards, such as flexed lower-limb joints, digitigrade touchdown, and weak hindlimb dominance, as previously described. Human bipedal acquisition is therefore difficult to establish from terrestrial quadrupedalism.

2. The knuckle-walking model

The phylogenetically closest living species to humans are African apes, i.e. common chimpanzees, bonobos, and gorillas. When these animals walk quadrupedly, they touch the dorsal side of their flexed fingers on the substrate. This locomotion is referred to as knuckle-walking. Because their forelimbs are longer than their hindlimbs, their shoulders are usually higher than their hips during quadrupedal standing. The knuckle-walking model supposes easy bipedal standing from such apes as a type of positional behavior (Morton, 1922). Quadrupedally walking chimpanzees, however, flex their elbows during the stance-phase, and their shoulders are not always higher than their hips. In the hominoid lineage, gorillas are thought to have branched off before the divergence of humans and chimpanzees/bonobos. It seems more parsimonious to assume that knuckle-walking was acquired by the common ancestors of humans and African apes, after which it was lost by humans after diverging from the chimpanzee/bonobo lineage, than to assume that it developed independently and in parallel in the gorilla and chimpanzee/bonobo lineages after humans diverged from apes. Richmond and Strait (2000) proposed that knuckle-walking traits were apparent in the fossils of early hominids, but their evidence was disputed and not widely accepted (Crompton et al., 2008; White et al., 2015; Semen et al., 2018). The knuckle-walking of the African apes may have developed independently in parallel after diverging from the human lineage (Dainton and Macho, 1999; Kivell and Schmitt, 2009). Lo-
comotion may have been involved because of the adaptations in hand structure in response to suspensory positional behavior (Tuttle, 1969). Suspensory adapted forelimbs and short hindlimbs of extant apes differ much from human limbs in which hindlimbs are much longer than forelimbs (Erikson, 1963).

3. The brachiation model

Brachiation is suspensory locomotion that occurs while hanging onto branches with the forelimbs. Gibbons move frequently by suspensory arm-swinging, including ricochet. The brachiation model has also been referred to as the ‘hylobatian model’ (Keith, 1923). Suspensory locomotion without ricochet was also acquired by the great apes. During brachiation, the trunk orientates vertically. The chests of gibbons are broader transversely than anteroposteriorly, similar to those of humans, but dissimilar to those of common pronograde mammals, where the dorsoventral diameter is large. Gibbons walk bipedally on level ground or on boughs. In bipedal gibbons, the hip and knee joints are extended relatively widely during the stance-phase compared with other nonhuman primates (Ishida et al., 1984). Due to the unique bipedal walking of gibbons, the brachiation model has been proposed to account for pre-habitual bipedal walking (Yamazaki et al., 1983).

Smooth brachiation with ricochet is difficult for large-bodied animals (Tuttle, 1975). Only infant chimpanzees, but not adults, spend long periods in orthograde suspensory mode (Sarringhaus et al., 2014). The suspensory forelimbs of gibbons are very long, and the body size and proportions of these primates are quite different from those in humans, who have long hindlimbs, relatively short forelimbs, and a relatively large body size. The bipedal walking of gibbons on flat substrates probably resulted from their difficulties in walking quadrupedally owing to their overly long forelimbs compared with their hindlimbs. It is difficult to link brachiation with the development of strong hindlimbs, which are essential for bipedal walking.

4. The vertical climbing model

Prost (1980) demonstrated that the body movement of chimpanzees during vertical climbing was more similar to that during bipedal compared with quadrupedal walking. During vertical climbing, the trunk stands vertically, the hip and knee joints extend strongly, and the ankle joint pushes the body powerfully upwards (Yamazaki and Ishida, 1984). Muscle activity during vertical climbing also shows more resemblance to that during bipedal compared with quadrupedal walking (Stern and Sussman, 1981; Vangor and Wells, 1983). Interestingly, arboreal primates show stronger functional differentiation between the fore- and hindlimbs than relatively terrestrial nonhuman primates during vertical climbing (Hirasaki et al., 2000). Vertical climbing is considered a part of the preadaptation process for bipedalism. However, the locomotion rate involving true vertical climbing—noting that the ascription of locomotor categories ‘climbing’ and other related terms can be problematic because of different definitions given by individual field observers (Fontaine, 1990)—and not including oblique clambering, is relatively small in primates: about 10–16% in wild black-handed spider monkeys (Mittermeier, 1978; Fontaine, 1990), about 12% in wild adult chimpanzees (Doran, 1993b), and about 10–18% in wild adult orangutans (Sugarljito and van Hooff, 1986; Cant, 1987). Vertical climbing could be one of the important preadaptations of the bipedalism, but it is difficult to accept that vertical climbing alone led to the acquisition of bipedal locomotion.

5. The generalized arboreal activity model

Based on comparative kinesiology among extant nonhuman primates, arboreal species such as chimpanzees, orangutans, and spider monkeys show larger functional differentiation between the fore- and hindlimbs during quadrupedal locomotion and greater resemblance to humans in bipedal walking compared with relatively terrestrial species. This resemblance may suggest the pathway via which our prehuman ancestors acquired bipedalism, i.e. preadaptation to arboreal environments (Stern, 1975; Kimura et al., 1979; Crompton et al., 2003, 2008; Thorpe et al., 2014; Senut et al., 2018). Although both brachiators and vertical climbers adapted to arboreal locomotion, it remains difficult to develop bipedal models only from each locomotion pattern, as described above. Stern (1975) proposed that our arboreal ancestors may have employed locomotion similarly to howler monkeys and orangutans, both of which are arboreal activators. Orangutans mainly use arboreal environments with many kinds of positional behaviors. They are able to support their large bodies even with thin lianas with both pronograde and orthograde postures (Cant, 1987; Thorpe et al., 2009; Myatt and Thorpe, 2011). Howler monkeys show particular similarities with humans in their hip and thigh musculature (Stern, 1975). Extant nonhuman primates, however, are not human ancestors and evolved separately for each lineage after diverging from the human lineage (Senut et al., 2018). For instance, the forelimbs are very long compared with the hindlimbs in all apes, in contrast to the relatively long human hindlimbs. The differences in limb length are not large in howler and spider monkeys (Erikson, 1963), like other generalized quadrupedal monkeys, but these species have prehensile tails that are useful for locomotion. It is difficult to develop a model based on only one or two extant nonhuman primate species.

In arboreal environments, primates developed long and robust limbs, orthograde trunks, and strong hindlimbs, which support and drive the body. Hindlimb-supported nearly orthograde locomotion in total, including bipedalism and quadrupedal climbing, and excluding forelimb suspensory, is about 11–26% in wild black-handed spider monkeys (Mittermeier, 1978; Fontaine, 1990). Nearly orthograde locomotion is about 54–59% of arboreal locomotion among wild adult chimpanzees (Doran, 1993b). In wild adult bonobos, nearly orthograde locomotion is about 44–65% of arboreal locomotion (Doran, 1993a). In wild adult orangutans, nearly orthograde locomotion, including quadrupedal clambering, represents around 46–63% of total locomotion in Sumatran orangutans, and about 28–56% in Bornean ones (Sugarljito and van Hooff, 1986; Cant, 1987; Thorpe and Crompton, 2006; Manduell et al., 2012).

The adaptation to arboreal space could therefore be part of the preadaptation process for bipedal locomotion. This model is referred to as the ‘generalized arboreal activity model’ and includes not only single activities, such as orthograde behavior, vertical climbing, or hand-assisted bipedality, but...
focuses on multiple positional behaviors among the three-dimensional discontinuous environments. Kimura and Yaguramaki (2009) suggested the following features of our pre-bipedal ancestors who could easily initiate and continue bipedal locomotion relatively efficiently: relatively erect trunks during locomotion; relatively fixed knee joints; high activity of the triceps surae muscles at push-off; and high potential energy during the single stance-phase. Many of these features are related to the primates associated with arboreal activity among a three-dimensional environment with gaps. In addition, as described and discussed in the previous sections, long and robust limbs, extended lower limb joints, plantigrade soles, and hindlimb dominance can also be related to such arboreal activity. Our human ancestors preadapted in such environments could have started more energy-efficient bipedal walking from the first step they took when they came down to the ground.

**Fossil evidence**

Does the fossil record agree with the generalized arboreal activity model? *Proconsul sensu lato* is thought to be the common ancestral hominoid of humans and African apes from between 17 and 20 Ma. This species utilized generalized arboreal quadrupedalism with a pronograde posture but not suspension under branches (Walker and Pickford, 1983). Based on the estimated length of the limb bones, their forelimbs were likely slightly shorter than their hindlimbs. Around the same age of between 16 to 18 Ma, *Afropithecus* appears to have had similar locomotion adaptations to *Proconsul sensu lato* (Leakey et al., 1988; Ward, 1998). On the other hand, *Morotopithecus* were arboreal African hominoids from about 20 Ma that are considered to have relied on some orthograde positional behaviors such as forelimb suspension and climbing; however, few parts of its postcranial skeleton have been found (MacLatchy et al., 2000). Following these species, between 14 and 17 Ma, *Nachalopithecus*, which were hominoids that lived in the trees, may have had more developed forelimbs and engaged relatively frequently in orthograde behavior such as vertical climbing; however, no evidence has been found to suggest a suspensory specialization (Nakatsukasa, 2004). All of the above hominoids were arboreal locomotors who basically practiced generalized arboreal quadrupedalism and did not obviously specialize in suspensory locomotion or knuckle-walking, although some hominoids shared traits of orthograde positional behavior. *Equatorius* is an exceptional fossil hominoid that practiced semi-terrestrial quadrupedalism in early and middle Miocene Africa (Sherwood et al., 2002; Patel et al., 2009). No locomotor skeleton fossils from just before and after the divergence of the human lineage from African apes have been found, and fossils of locomotor African ape skeletons after the divergence have rarely been unearthed.

Regarding the human lineage after the divergence, 4.4 Ma, *Ardipithecus* exhibited erect bipedalism on level substrates, but with an abducted big toe that was capable of grasping (Lovejoy et al., 2009a, 2009b; White et al., 2015). This species is thought to have lived in both wooded grasslands and forests. This clearly demonstrates that the bipedality exhibited by this species started in arboreal environments. Its forelimbs were shorter than its hindlimbs, similar to the generalized above-branch quadrupedal monkeys and *Proconsul sensu lato*; furthermore, no traces of knuckle-walking have been found, and no obvious specializations attributed to forelimb dominant suspension and vertical climbing as in extant African apes (Lovejoy et al., 2009b; White et al., 2015).

The next human ancestor, *Australopithecus*, from between 2.5 and 4.2 Ma, lost the abducted big toe, but gained an adducted one for toe-off together with the small toes associated with the rocking mechanism of the foot during bipedal walking, similar to present-day humans (Leakey and Hay, 1979; Masao et al., 2016). However, some arboreal adaptations, such as somewhat long upper limbs and long and ventrally curved hand bones, were retained in its postcranial bones (Susman et al., 1984). Because of the difference in body proportions compared with recent humans, the bipedal patterns of *Australopithecus* could have differed from those of present-day humans. However, bone morphology has confirmed that bipedal walking in *Australopithecus* was not ‘bent-hip, bent-knee’ walking, but rather was performed while relatively erect with extended lower limb joints (Lovejoy et al., 1973; Crompton et al., 1998; Lovejoy, 2007).

At the around same time, bipedal feet with abducted big toes dating from 3.4 and 3.3 Ma have been discovered in Ethiopia (Haile-Selassie et al., 2012) and South Africa (Clarke and Tobias, 1995), respectively. *Ar dipithecus*-like locomotion adaptation (Haile-Selassie et al., 2012) could have persisted for a long time. More detailed discoveries are awaited.

*Homo erectus sensu lato*, which appeared about 1.8 Ma in Africa, had long lower limbs, relatively short upper limbs, and straight and short hand bones (Walker and Leakey, 1993), similar to present-day humans. Their relatively short upper limbs were lighter, and together with their long lower limbs (Steudel-Numbers, 2006), increased efficiency during walking. Their locomotion would be fundamentally similar to that of present-day humans. They migrated out of Africa for the first time in human lineage, likely utilizing their locomotor ability on the ground, including their long-distance gait.

The generalized arboreal activity model of human bipedal acquisition presented here is not fundamentally contradicted by the fossil record. In other words, our human ancestors had already preadapted to erect bipedalism in the arboreal environment and subsequently refined this process in their terrestrial surroundings.

**Terrestrial humans**

The process described in this review attempts to explain how humans acquired erect bipedal locomotion. Comparative studies of extant primates have indicated that arboreal life is crucial for acquiring bipedalism. Our human ancestors were able to progress to bipedalism because humans belong to an order of primates that was generally arboreal in nature. The fossil record to date supports the hypothesis that our early bipedal human ancestors lived in the trees. Therefore, the general arboreal activity model of bipedal acquisition
appears valid.

The final question of why our human ancestor acquired bipedalism remains unanswered. It is still difficult to answer this question based on the evidence. The local environment of *Ardipithecus* from 4.4 Ma is thought to have ranged from the forest to wooded grasslands (White et al., 2009). Other so-called early humans from around 6 to 7 Ma are considered to have lived in environments comprising both grasslands and forests (Pickford and Senut, 2001; Vignaud et al., 2002). Present-day African great apes traverse the ground between the trees mainly using quadrupedal locomotion, probably because they have not developed full bipedalism in the trees. Ancestors of relatively terrestrial quadrupedal extant primates, such as baboons, might have existed in arboreal environments, and could have descended from the trees without acquiring the enough bipedal ability at the time and adapted to the quadrupedal locomotion on the ground afterwards. By contrast, our human ancestors probably already had sufficient bipedal ability in the forest and employed bipedal locomotion from the very first step they took when they came down to the ground. However, whether our human ancestors acquired bipedalism necessarily or contingently remains unclear. If bipedalism was inevitable, why was it necessary? This question should be addressed in future studies.

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References

Alexander R.McN. and Jayes A.S. (1978) Vertical movements in walking and running. Journal of Zoology, 185: 27–40.

Alexander R.McN., Jayes A.S., Maloiy G.M.O., and Wathuta E.M. (1979) Allometry of the limb bones of mammals from shrews (Sorex) to elephant (Loxodonta). Journal of Zoology, 189: 305–314.

Barclay O.R. (1953) Some aspects of the mechanics of mammalian locomotion. Journal of Experimental Biology, 30: 116–120.

Berillon G., Daver G., D’Aouit K., Nicolas G., de la Villenet B., Multon F., Digrandi G., and Dubreuil G. (2010) Bipedal versus quadrupedal hind limb and foot kinematics in a captive sample of *Papio anubis* and *Pongo pygmaeus* and *Loxodonta africana*: setup and preliminary results. International Journal of Primatology, 31: 159–180.

Björck G. (1958) Studies on the draught force of horses. Acta Agriculturae Scandinavica, Supplement 4: 1–109.

Bramble D.M. and Lieberman D.E. (2004) Endurance running and the evolution of *Homo*. Nature, 432: 345–352.

Brunet M., Guy F., Pilbeam D., Mackaye H.T., Likis A., Ahunta D., Beauvilain A., Bloncle C., Bocherens H., Boissiere J.R., De Bonis L., Coppons Y., Dejean J., Denys C., Düringer P., Eisenmann V., Fanone G., Fronty P., Geraads D., Lehmann T., Lilkoaru F., Louchart A., Mahamat A., Mercreon G., Mouchelin G., Otero O., Pelaez Camponanes P., Ponce De Leon M., Rage J.C., Sapanet M., Schuster M., Sudre J., Tassy P., Valentijn X., Vignaud P., Viriot L., Zazzo A., and Zolliker C. (2002) A new hominin from the Upper Miocene of Chad, Central Africa. Nature, 418: 145–151.
Holowka N.B., O’Neill M.C., Thompson N.E., and Demes B. (2017) Chimpanzee and human midfoot motion during bipedal walking and the evolution of the longitudinal arch of the foot. Journal of Human Evolution, 104: 23–31.

Howell A.B. (1944) Speed in Animals. Hafner, New York (1965 facsimile of 1944 edition).

Hunt K.D. (1992) Positional behavior of Pan troglodytes in the Mahale Mountains and Gombe Stream National Parks, Tanzania. American Journal of Physical Anthropology, 87: 83–105.

Hunt K.D. (1994) The evolution of human bipedality: ecology and functional morphology. Journal of Human Evolution, 26: 183–202.

Ishida H., Kimura T., and Okada M. (1975) Patterns of bipedal walking in anthropoid primates. In: Kondo S., Kawai M., Ethara A., and Kawamura S. (eds.), Proceedings from the Symposium of the Fifth Congress of the International Primatological Society, Japan Science Press, Tokyo, pp. 287–301.

Ishida H., Kimura T., Okada M., and Yamazaki N. (1984) Kinesiological aspects of bipedal walking in gibbons. In: Preuschoft H., Chivers D.J., Brockelman W.Y., and Creel N. (eds.), The Lesser Apes: Evolutionary and Behavioural Biology. Edinburgh University Press, Edinburgh, pp. 135–145.

Iwamoto M. and Torita M. (1966) On the movement order of four limbs while walking and the body weight distribution to fore and hind limbs while standing on all fours in monkeys. Journal of the Anthropological Society of Nippon, 74: 228–231.

Jolly C.J. (1970) The seed-eaters: a new model of hominid differentiation based on a baboon analogy. Man, New Series, 5: 5–26.

Kawai M. and Mito U. (1973) Quantitative study of activity patterns and postures of Formosan monkeys by the radiotelemetrical technique. Primates, 14: 179–194.

Keith A. (1923) Man’s posture: its evolution and disorders. British Medical Journal, 3246: 451–454, 3247: 499–502, 3248: 545–548, 3249: 587–590, 3250: 624–626, 3251: 669–672.

Kimura T. (1985) Bipedal and quadrupedal walking of primates: comparative dynamics. In: Kondo S., Ishida H., Kimura T., Okada M., Yamazaki N., and Prost J.H. (eds.), Primate Morphophysiology, Locomotor Analyses and Human Bipedalism. University of Tokyo Press, Tokyo, pp. 81–104.

Kimura T. (1991) Long and robust limb bones of primates. In: Ethara A., Kimura T., Takenaka O., and Iwamoto M. (eds.), Primatology Today, Elsevier, New York, pp. 495–498.

Kimura T. (1992) Hindlimb dominance during primate high-speed locomotion. Primates, 33: 465–476.

Kimura T. (1995) Long bone characteristics of primates. Zeitschrift für Morphologie und Anthropologie, 80: 265–280.

Kimura T. (1996) Centre of gravity of the body during the ontogeny of chimpanzee bipedal walking. Folia Primatologica, 66: 126–136.

Kimura T. (2000) Development of quadrupedal locomotion on level surfaces in Japanese macaques. Folia Primatologica, 71: 323–333.

Kimura T. (2002) Primate limb bones and locomotor types in arboreal or terrestrial environments. Zeitschrift für Morphologie und Anthropologie, 83: 201–219.

Kimura T. (2003) Differentiation between fore- and hindlimb bones and locomotor behaviour in primates. Folia Primatologica, 74: 17–32.

Kimura T. and Yaguramaki N. (2009) Development of bipedal walking in humans and chimpanzees: a comparative study. Folia Primatologica, 80: 45–62.

Kimura T., Okada M., and Ishida H. (1979) Kinesiological characteristics of primate walking: its significance in human walking. In: Morbeck M.E., Preuschoft H., and Gomberg N. (eds.), Environment, Behavior, and Morphology: Dynamic Interactions in Primates, Gustav Fischer, New York, pp. 297–311.

Kivell T.L. and Schmitt D. (2009) Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. Proceedings of the National Academy of Sciences of the United States of America, 106: 14241–14246.

Krüger W. (1943) Ueber die Beziehungen zwischen Schwerpunktslage und Stärke der Substantia compacta einzelner Gliedmassenknöchern bei vierfussigene Säugetieren. Morphologisches Jahrbuch, 88: 377–396.

Larson S.G., Schmitt D., Lemelin P., and Hamrick M. (2000) Uniqueness of primate forelimb posture during quadrupedal locomotion. American Journal of Physical Anthropology, 112: 87–101.

Larson S.G., Schmitt D., Lemelin P., and Hamrick M., (2001) Limb excursion during quadrupedal walking: how do primates compare to other mammals? Journal of Zoology, 255: 353–365.

Leacey M.D. and Hay R.L. (1979) Pliocene footprints in the Laetoli Beds at Laetoli, northern Tanzania. Nature, 278: 317–323.

Leacey R.E., Leakey M.G., and Walker A.C. (1988) Morphology of Afropithecus turkanensis from Kenya. American Journal of Physical Anthropology, 76: 289–307.

Lovejoy C.O. (2007) The natural history of human gait and posture. Part 3. The knee. Gait & Posture, 25: 325–341.

Lovejoy C.O., Heiple K.G., and Burstein A.H. (1973) The gait of Australopithecus. American Journal of Physical Anthropology, 38: 757–779.

Lovejoy C.O., Latimer B., Suwa G., Asfaw B., and White T.D. (2009a) Combining prehension and propulsion: the foot of Ardipithecus ramidus. Science, 326: 72e1–72e8.

Lovejoy C.O., Suwa G., Simpson S.W., Maternes J.H., and White T.D. (2009b) The great divides: Ardipithecus ramidus reveals the posteriama of our last common ancestors with African apes. Science, 326: 100–106.

MacLatchy L., Gebo D., Kityo R., and Pilbeam D. (2000) Postcranial functional morphology of Morotopithecus bishopi, with implications for the evolution of modern ape locomotion. Journal of Human Evolution, 39: 159–183.

Manduell K.L., Harrison M.E., and Thorpe S.K.S. (2012) Forest structure and support availability influence orangutan locomotion in Sumatra and Borneo. American Journal of Primatology, 74: 1128–1142.

Manter J.T. (1938) The dynamics of quadrupedal walking. Journal of Experimental Biology, 15: 522–540.

Masao F.T., Ichimbabi E.B., Cherin M., Barili A., Boschian G., Iurino D.A., Menconero S., Moggi-Cecchi J., and Manzi G. (2016) New footprints from Laetoli (Tanzania) provide evidence for marked body size variation in early hominins. eLife, 5: e19568.

Mittermeier R.A. (1978) Locomotion and posture in Ateles geoffroyi and Ateles paniscus. Folia Primatologica, 30: 161–193.

Morbeck M.E. (1975) Positional behavior in Colobus guereza: a preliminary quantitative analysis. In: Kondo S., Kawai M., Ethara A., and Kawamura S. (eds.), Proceedings from the Symposium of the Fifth Congress of the International Primatological Society, Japan Science Press, Tokyo, pp. 331–343.

Morton D.J. (1922) Evolution of the human foot. American Journal of Physical Anthropology, 5: 305–336.

Myatt J.P. and Thorpe S.K.S. (2011) Postural strategies employed by orangutans (Pongo abelli) during feeding in the terminal branch niche. American Journal of Physical Anthropology, 146: 73–82.

Nakatsukasa M. (2004) Acquisition of bipedalism: the Miocene hominoid record and modern analogues for bipedal hominoids. Journal of Anatomy, 204: 385–402.

Nakatsukasa M., Ogihara N., Hamada Y., Goto Y., Yamada M., Hirakawa T., and Hirasaki E. (2004) Energetic costs of bipedal and quadrupedal walking in Japanese macaque. American Journal of Physical Anthropology, 124: 248–256.

Nakatsukasa M., Hirasaki E., and Ogihara N. (2006) Energy expenditure of bipedal walking is higher than that of quadrupedal walking in Japanese macaques. American Journal of Physi-
Vignaud P., Düringer P., Mackaye H.T., Likiu A., Blondel C., Boissière J.R., De Bonis L., Eisenmann V., Etienne M.E., Geraads D., Guy F., Lehmann T., Lihoreau F., Lopez-Martinez N., Mourer-Chauviré C., Otero O., Rage J.C., Schuster M., Viriot L., Zazzo A., and Brunet M. (2002) Geology and palaeo-ontology of the Upper Miocene Toros-Menalla hominin locality, Chad. Nature, 418: 152–155.

Walker A. and Leakey R. (eds.) (1993) The Nariokotome Homo Erectus Skeleton. Springer-Verlag, Berlin.

Walker A.C. and Pickford M. (1983) New postcranial fossils of Proconsul africanus and Proconsul nyanzae. In: Ciochon R.L. and Corruccini R.S. (eds.), New Interpretations of Ape and Human Ancestry. Plenum, New York, pp. 325–351.

Ward C.V. (1998) Afropithecus, Proconsul, and the primitive hominoid skeleton. In: Strasser E., Fleagle J., Rosenberger A., and McHenry H. (eds.), Primate Locomotion: Recent Advances. Plenum Press, New York, pp. 337–352.

White T.D., Ambrose S.H., Suwa G., Su D.F., DeGusta D., Bernor R.L., Boissière J.R., Brunet M., Delson E., Frost S., Garcia N., Giourtsakis I.X., Haile-Selassie Y., Howell F.C., Lehmann T., Likiu A., Pehlevan C., Saegusa H., Semprebon G., Teaford M., and Vrba E. (2009) Macrovertebrate paleontology and the Pliocene habitat of Ardipithecus ramidus. Science, 326: 87–93.

White T.D., Lovejoy C.O., Asfaw B., Carlson J.P., and Suwa G. (2015) Neither chimpanzee nor human, Ardipithecus reveals the surprising ancestry of both. Proceedings of the National Academy of Sciences of the United States of America, 112: 4877–4884.

Xu S., Liu P., Chen Y., Chen Y., Zhang W., Zhao H., Cao Y., Wang F., Jiang N., Lin S., Li B., Zhang Z., Wei Z., Fan Y., Jin Y., He L., Zhou R., Dekker J.D., Tucker H.O., Fisher S.E., Yao Z., Liu Q., Xia X., and Guo X. (2018) Foxp2 regulates anatomical features that may be relevant for vocal behaviors and bipedal locomotion. Proceedings of the National Academy of Sciences of the United States of America, 115: 8799–8804.

Yamazaki N. and Ishida H. (1984) A biomechanical study of vertical climbing and bipedal walking in gibbons. Journal of Human Evolution, 13: 563–571.

Yamazaki N., Ishida H., Okada M., Kimura T., and Kondo S. (1983) Biomechanical evaluation of evolutionary models for prehabitual bipedalism. Annales des Sciences Naturelles, Zoologie, 5: 159–168.