Comment on “Origin of Human Bipedalism As an Adaptation for Locomotion on Flexible Branches”

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Thorpe et al. (Reports, 1 June 2007, p. 1328) concluded that human bipedalism evolved from a type of bipedal posture they observed in extant orangutans with seemingly human-like extended knees. However, humans share knuckle-walking characters with African apes that are absent in orangutans. These are most parsimoniously explained by positing a knuckle-walking precursor to human bipedalism.

Thorpe et al.’s interpretation of orangutan kinematics (i.e., movement) is also problematic. The nature of the loading and movement of the lower limb in Pongo “hand-assisted arboreal bipedalism” is so different from hominin bipedalism that it raises the question as to whether these modes of locomotion are homologous. Indeed, it is not even clear that the behaviors observed by Thorpe et al. (1) can be truly called bipedalism. Orangutans, by nature, extend their lower limbs when suspending from their hands even when their feet hang freely (see figure 1 in (1)). Thorpe et al. have not distinguished the relative weight support borne by forelimbs versus hindlimbs, so they cannot determine whether orangutans employ true “hand-assisted arboreal bipedalism” or whether their behavior is better described as “foot-assisted forelimb suspension.” The fact that orangutans practice this behavior more frequently on smaller supports suggests that they are predominantly supporting themselves with their forelimbs. Furthermore, the observation that Pongo may more frequently fully extend their knees when adopting “bipedal” postures on small, compliant supports compared with Pan probably reflects the tremendous mobility of the lower limb in Pongo, which in turn is related, as Thorpe et al. suggest, to the need to distribute a large body mass across as many supports as possible. All large primates use this strategy to varying degrees (9). Pongo excels in this behavior and has long been called quadrumanous (four-handed), given the handle-like morphology of their feet. The behavior observed by Thorpe et al. (1) is perhaps best considered a component of this locomotor repertoire. Moreover, Pongo does not load the lower limbs in a manner even approaching the human condition (with extended lower limbs positioned beneath the center of mass, knees in sagittal plane, feet fully plantigrade) and, not surprisingly, lacks all of the unique features of the human lower limb that are related to load-bearing and joint motion essential for committed bipedalism.

Key to the argument of Thorpe et al. (1) is their claim that orangutans use human-like extended hindlimbs when they are bipedal and that orangutans differ from the African apes in this respect. Indeed, for orangutans to serve as a better model for the origin of hominin bipedalism, they would need to walk bipedally more like humans than do African apes. However, Thorpe et al. do not provide or cite quantitative kinematic data. Previous studies have reported that orangutans, chimpanzees, and gibbons all use flexed hindlimbs during bipedal walking (10). These studies indicate that orangutans may walk with slightly more extended knees compared with chimpanzees, but they still walk bipedally with partly flexed knees, unlike humans. Recent studies of chimpanzee bipedalism found considerable variability in limb kinetics, with some individuals using more extended lower limbs and, like humans and trained macaques (11), enjoying energy benefits (12). Moreover, hip and knee extension are not the only important kinematic criteria. Orangutans are awkward bipeds, using partly abducted hips, with their knees facing laterally, and walking on the sides of their feet. In these respects, chimpanzees and bonobos appear to be better bipeds.

Thorpe et al. (1) reject the broadly accepted hypothesis that vertical climbing provides an important biomechanical link to hominin bipedalism, despite the fact that multiple studies show that both kinematics and muscle recruitment during terrestrial bipedalism and vertical climbing are more similar to each other than either is to quadrupedal locomotion (10, 13, 14). Nothing in the knuckle-walking hypothesis precludes a suspensory, vertically postured arboreal ancestry for all great apes and humans or the importance of orthograde and vertical climbing adaptations in the origin of hominin bipedalism (3, 4).

Finally, Thorpe et al. cite “recent paleontological evidence” in support of their hypothesis, but this evidence merely states that some Miocene apes were orthograde and that early hominins lived in wooded habitats and were bipeds that retained some suspensory characteristics. As previously noted (3), all of this evidence is also consistent with a knuckle-walking ancestry for hominins. After all, African apes are arboreal orthograde, suspensory, and forest-dwelling, while also having knuckle-walking adaptations to move on the ground.

We applaud Thorpe et al.’s field observations and statistical analysis of Pongo positional behavior, which adds to our understanding of this fascinating and highly endangered large, very arboreal, and extremely specialized great ape. However, we question whether these observations are relevant to understanding the origins of human bipedalism, especially in light of the large body of evidence for a climbing and knuckle-walking ancestry. We agree with long-standing evidence that orthograde and probably vertical climbing (10, 13) adaptations of the last common ancestor of chimpanzees and humans made possible the origin of hominin bipedalism but suggest that this ancestor employed terrestrial...
knuckle-walking behaviors as part of its locomotor repertoire. Why bipedalism was favored over knuckle-walking in the hominin clade remains an open question.

References

13 June 2007; accepted 4 October 2007
10.1126/science.1146446
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Science 318 (5853), 1066. [doi: 10.1126/science.1146446]