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

R. H. Crompton<sup>1\*</sup> and S. K. S. Thorpe<sup>2</sup>

Begun *et al.* purport to present technical concerns regarding our case for an arboreal origin for terrestrial bipedalism in early hominins, but merely reiterate their knuckle-walking hypothesis, which lacks support from the fossil record and is highly unparsimonious. The technical concerns are refuted by published studies cited in our study and thus do not affect our original conclusions.

Begun *et al.* (1) question both our recording of hand-assisted bipedality in wild orangutans and the evidence for biomechanical similarities between orangutan and human bipedality that underlies our argument (2). The authors are incorrect in claiming that we confused arboreal hand-assisted bipedality with “foot-assisted forelimb suspension” (i.e., orthograde suspension). The classification used in our orangutan fieldwork (3) is closely based on Hunt and colleagues’ (4) standard classification of primate positional behavior and is grounded on their concept that “weight bearing is...the critical datum when determining into which of two modes a particular behaviour falls.” Evidence of weight bearing can be clearly deduced from the extent to which weight-bearing supports deform, in combination with the position of the extremities relative to the torso (4). Begun *et al.* propose that orangutan bipedality is best considered as a component of quadrumanous (i.e., four-handed) locomotion, but the term “quadrumanous climbing” is unhelpful, because it conflates orthograde and pronograde torso orientations into one positional behavior (4).

Begun *et al.* (1) are also mistaken in claiming that we neither provided nor cited kinematic (movement) data to substantiate our model of arboreal hand-assisted bipedality or to reject the alternative hypothesis that vertical climbing would preadapt hominin ancestors for bipedal postures and locomotion. On the contrary, we did cite a reference providing such data (5) and summarize its findings below. Begun *et al.* argue that a link between vertical climbing and bipedalism is demonstrated because these behaviors resemble each other more than either resembles quadrupedalism. Both vertical climbing and bipedalism are indeed, unlike quadrupedalism, orthograde behaviors, but because

all great apes not only perform vertical climbing but are also facultatively bipedal, Begun and colleagues’ argument requires them to show that the kinematics of nonhuman ape vertical climbing are more similar to human bipedalism than are the kinematics of non-human ape bipedalism. In human bipedalism (5), the hip habitually extends to 210° (measured ventrally as the angle between the trunk and thigh). In common chimpanzees, maximum hip extension is greater in vertical climbing than in bipedalism (85° to 155° versus 125°, respectively), whereas in bonobos, values are similar (136° versus ~138°, respectively). In lowland gorillas, the mean hip extension in bipedalism greatly exceeds that for vertical climbing (193° versus 120° for males or 133° for females) (5). However, it is only in the most arboreal great ape, the orangutan, that hip extension in bipedalism overlaps that seen in humans, at 180° to 215°. Here, though, hip extension in vertical climbing is much less (120° to 140°) (5). Since both facultative bipedalism and vertical climbing are likely to have been present in a generalized orthograde common ancestor, these results suggest that hand-assisted bipedality, not vertical climbing, would best preadapt the hominin body for terrestrial bipedality.

In support of a knuckle-walking origin for human bipedalism, Begun *et al.* cite work by Sockol *et al.* (6) as indicating that the more extended postures seen in bipedal walking of some chimpanzees can be relatively efficient. This study found no statistically significant difference between the metabolic cost of quadrupedal and bipedal walking in a test group of trained chimpanzees, and Begun and colleagues’ claim is based on the performance of only one individual. Our own studies of Poko (5), a common chimpanzee, are equally pertinent. Poko was kept for much of its early life in a parrot cage so narrow-based that at the time of study, the animal could neither readily walk quadrupedally nor climb trees, and instead used terrestrial bipedalism more or less exclusively. The bipedal kinematics it displayed must have been very close to the limits of behavioral plasticity of chimpanzees in

terms of hip and knee extension and truncal uprightness, and even then do not match those of an untrained, naturally raised captive orangutan, Pulu, at The North of England Zoological Society (5). Thus, natural selection in favor of truncal uprightness and hip and knee extension, which in the orangutan give an effective means of accessing fine branches in the peripheral canopy of tropical-forest trees, could similarly have preadapted the ancestors of early hominins for the acquisition of habitual terrestrial bipedalism. Despite the rejection of Richmond and Strait (7) of a fully orthograde ancestor, there is ample fossil evidence that Miocene crown hominoids, including *Pierolapithecus* and *Hesperopithecus* (*Dryopithecus*) *laetanus*, employed levels of orthograde similar to those seen in the living orangutan (8–10). The protohominin *Orrorin* (9) provides additional evidence of habitually highly extended hip postures.

While Begun *et al.* argue [incorrectly (5)] that we have not shown that the pattern of lower limb loading in orangutans in any way resembles our own, we do not know of a single case where purported “knuckle-walking features” have been shown to be biomechanically linked to forces and stresses in the arm or hand during knuckle-walking. Begun himself (11) recently admitted that no functional link could be demonstrated for fusion of the os centrale and scaphoid, a key feature in the knuckle-walking hypothesis. Without such functional evidence, any enumeration of features in which human upper limbs resemble those of other African apes could at best be evidence only of a phylogenetically close relationship.

Richmond and Strait (7) claimed knuckle-walking features in the hands of two early hominins, but flaws in their analysis should be pointed out. The feature headlined in one specimen, the distal radial morphology of KNM-ER 20419, is an artifact of a missing radial styloid process (12), and the wrist morphology of *A. afarensis* fell in the authors’ own plot of orangutan variation (13). In addition, both hominins possess a particularly large radiocarpal facet for the lunate, the reverse of the panin/gorilline condition (14). No knuckle-walking features are evident in the hominin hand bones from South Turkwel (15) or Sterkfontein (StW-573) (16). Another key knuckle-walking feature, dorsal ridges on the distal metacarpals, is absent in humans, but present in *Kenyapithecus* (17), which lacks the postcranial features linking all living apes, and thus cannot be a crown hominoid.

The knuckle-walking hypothesis requires a transition from pronograde in the common root/crown hominoid ancestor, to orthograde in crown hominoids, back to pronograde in the common hominin/panin/gorilline ancestor, and back again to orthograde in Hominini. Derivation of habitual terrestrial bipedality from arboreal hand-assisted bipedalism requires fewer transitions and is kinematically more parsimonious.

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