

Reply

Reply to Sarmiento E. “Australopithecine Taxonomy and Phylogeny and the Savanna Hypothesis; Comment on Vaneechoutte et al. Have We Been Barking up the Wrong Ancestral Tree? Australopithecines Are Probably Not Our Ancestors. *Nat. Anthropol.* 2023, 2, 10007”

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Received: 6 May 2024; Accepted: 14 May 2024; Available online: 17 May 2024



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We would like to thank Prof. Sarmiento for his comments [1] on our paper [2].

We appreciate his support for our basic premise that (some) australopithecines may have been ancestral or more closely related to the *Gorilla* and *Pan* lineages and that possibly none were human ancestors. We agree with his view that “the need to find human ancestors has led paleoanthropologists to make baseless claims of human bipedality in australopithecines in order to justify inclusion of their finds into an exclusive human lineage”, and sincerely hope that our paper will encourage others to reconsider the rarely questioned hominin status of *Australopithecus* and associated genera from East and South Africa.

We largely agree with Sarmiento [1] when he writes: “Because it has never been shown that australopithecines are exclusive members of the human lineage or even habitual/obligate or striding bipeds they are not relevant for refuting the savanna hypothesis for human bipedal origins.”

We paid attention to the savanna, however, precisely because australopithecine bipedalism is generally held up as a precursor to human striding bipedalism, and the adaptation to living in open areas is often put forward as the incentive to evolve from quadrupedal locomotion or arboreal/facultative bipedalism to habitual/obligate bipedalism in our putative australopithecine ancestors.

While Sarmiento [1] agrees that it is possible that none of the australopithecines are hominins, he disapproves our dismissal of the savanna hypothesis as the explanation for human striding bipedalism. We first want to point out that dismissal of the savanna hypothesis was not the primary objective of our paper. Our reason for mentioning the savanna hypothesis was to emphasize that it was never a solid hypothesis on which to base the origin of hominid bipedalism, whether it be in the form of australopithecine or human bipedalism. We offered several arguments to indicate that bipedalism or at least orthograde is probably a primitive characteristic of all hominoids (apes), including the hylobatids.

The statement by Sarmiento [1] that “Grassland savannas need not be expanding in Africa to explain the presumed australopithecine adaptations to savannas. There only needs to be the existence of savanna habitats for such adaptations to appear”, denies the fact that it was forced adaptation to increasing savanna (and dwindling forest) that was the main argument of the savanna hypothesis from the beginning as an attempt to explain the odd obligate bipedalism of our genus.

We fail, moreover, to understand how bipedalism can be proposed as an adaptation to open country, especially since the several primate species (such as baboons and patas monkeys) that do live in open country are among the most quadrupedal. We further find a comparison with the evolution of horses as a robust indication of an open country origin of human bipedalism, as put forward by De Vos et al. [3], not really applicable or convincing. (We were unable to check

the arguments made by Osborn [4].) Our point of view was recently reinforced by the finding that bipedalism of Issa savanna chimpanzees is not associated with open country: “Bipedalism (postural and locomotor) at Issa occurred primarily on arboreal substrates (as opposed to terrestrial, ...) and, moreover, primarily during a foraging context (as opposed to other behaviors, ...)” [5]. This confirms the observations of Hunt [6,7], regarding chimpanzee bipedality.

We clearly disagree with Sarmiento’s statement that the savanna hypothesis is “very robust” [1]. First, there is nothing in human physiology that supports an existence in hot, dry, open conditions [8–11]. For example, our bodies simply lose too much water and salt in too short a time and our ancestors would have been especially vulnerable as naked, non-cursorial primates if they had spent any significant time in the open savanna.

On the other hand, a case might be made that the loss of sub-tropical forest, the advent of open spaces and an increase in seasonal wetlands may have played a role in our ancestors’ transition from orthograde climbing and facultative bipedalism towards a more habitual form of locomotion via the form of frequent wading for food acquisition. However, these ecological changes appear to have first occurred in mid-late Miocene Europe rather than Pliocene Africa. Although Böhme et al. [12,13] propose that it might have been the European savanna that led to incipient bipedalism in hominid ancestors, we suggest that climatic changes during the Vallesian forced a transition from arboreal foraging to waterside/shallow water foraging, and it was this that led to a more sustained form of bipedal locomotion in the common (European) ancestor of African great apes, *Australopithecus* and humans.

We addressed these issues in more detail in a follow up paper by two of the current authors [14]. In it, we refer to evidence that the spread of open grasslands was already well underway in Europe by the mid-Miocene/late Vallesian, and several species, such as *Ouranopithecus macedoniensis* and *Graecopithecus freybergi* seem to have adapted to mosaic conditions of small pockets of sclerophyllous woodland, seasonal grasslands, marshes, swamps and river valleys (Pikermian biome). Perhaps it is not coincidental that both of these species have been proposed as possible ancestors to African great apes and humans, and the latter has been proposed as possibly the first hominin [15]. They are also likely to have been at least facultatively bipedal, if not habitual (wading-climbing) bipeds.

We would further disagree with the statement by Sarmiento [1] that “there is no convincing evidence... that knuckle-walking evolved independently in gorillas and chimpanzees” and we have cited several papers that either support or refute that the latest ancestor of humans and chimpanzees was knuckle walking (Section 3.3 in [2]). In our opinion, the claim by Sarmiento [1] that “all hominoids including humans can assume knuckle-walking postures” or that “the propensity to assume these postures appears to be a trait shared by all hominoids” clearly contradicts the facts that (i) human infants crawl with open palms, (ii) when we lean on a table—we use the flat of our hands or lean on our proximal phalanges rather than on our middle phalanges, and that (iii) even in the rare instances of quadrupedal humans, they walk in a palmigrade manner.

Sarmiento [1] writes that we have “embraced false facts, baseless claims and misconceptions found in the paleoanthropological literature”. To support this claim, he provides the following examples.

1. “Contrary to Vaneechoutte et al. 2023..., the small canines of robust australopithecines and their markedly reduced anterior dentition (both absolutely and relative to the cheek teeth) are derived characters and are not primitive for hominoids.” [1].

We contend that what is considered primitive or derived is largely based on which earlier species are used for comparison. Relatively smaller canines (compared to extant great apes) were apparent in much earlier Miocene apes, such as *Ouranopithecus macedoniensis* [16], as well as in *Anadoluvius turkae* [17], *Graecopithecus freybergi* [15] and *Oreopithecus bamboli* [18], as well as in some African species such as *Sahelanthropus tchadensis* [19] and *Ardipithecus ramidus* [20].

2. “The human foramen magnum is distinguished from those of apes by its forward (anterior) position relative to the cranial base and by its inferior and slightly anterior orientation/inclination relative to the frankfurt plane...” [1].

We outlined in detail the different difficulties with determination and interpretation of the position of the foramen magnum as well as the limitations of its meaning as an indication for bipedalism (Section 3.4.1.6 of [2]).

3. “Contra the Lewin citation, Lucy’s *Pan*-like tree-climbing tendencies cannot be “inferred from her elongated curved feet and hand finger bones. In fact, Lucy has comparatively short fingers and even shorter toes. Its manual and pedal digital proportions are closer to those of baboons (*Papio*) than to those of *Pan* [21,22].” [1].

We can accept that there are contradictory views in the literature regarding the morphology of *A. afarensis*’ manual and pedal digital proportions, as well as its propensity towards bipedalism, mainly due to the lack of available fossils. On the other hand, some fossils attributed to *A. afarensis* complicate the discussion still further. For example, at 3.32

million years old, Dikika (DIK-1-1f) (sometimes referred to as ‘Lucy’s child’), “provides evidence for habitual bipedality combined with some pedal grasping in the juvenile australopiths” [23]. The Burtele foot complicates the picture further as it clearly has a divergent hallux [24].

A number of researchers [25] believe that *A. afarensis* retained climbing adaptations, while others [26] propose it walked like a biped and had lost climbing abilities.

What we do observe, however, is that evidence of arboreal tendencies in *Australopithecus* tend to increase over time, while evidence of morphologies indicative of bipedalism tend to decrease in later species.

Green et al. [27] concluded that the more recent *A. africanus* was more ape-like than *A. afarensis*: “These results strongly support the hypothesis that *A. africanus* possessed more apelike limb-size proportions than *A. afarensis*, suggesting that *A. africanus* either evolved from a more postcranially primitive ancestor than *A. afarensis* or that the more apelike limb-size proportions of *A. africanus* were secondarily derived from an *A. afarensis*-like ancestor. Among the extant taxa, limb-size proportions correspond with observed levels of forelimb- and hindlimb-dominated positional behaviors. In conjunction with detailed anatomical features linked to arboreality, these results suggest that arboreal posture and locomotion may have been more important components of the *A. africanus* behavioral repertoire relative to that of *A. afarensis*.”

Our position is that *A. afarensis* represents either an arboreal species investing in some form of bipedal foraging (wading) or that it was a terrestrial species that may have spent some time in the trees. Whether its combined mixture of features are more “apelike” or more “humanlike” does not help us understand the direction of evolution.

This is something we hope to address in more detail in a future paper.

Finally, Sarmiento [1], citing Yohn et al. [28], correctly points out that Asian macaques were infected with PtERV retroviruses as well. However, his conclusion that “the absence of retrovirus (PTERV1) insertions in humans that are present in African apes, fails to provide evidence that our ancestors were in Asia and were not present in Africa between 4 and 3 Ma”, is not correct, as we did not claim that our ancestors were in Asia at that time. We consider the absence of these insertions only as a strong indication that our ancestors were not in Africa.

Further, he [1] states: “Because both Asian macaques and African baboons show the PTERV1 integrations occurring around 2 Ma ago the retrovirus also seems to have been present in Asia [28]. The latter refutes the notion that humans would have escaped infection in Asia and suggests that our ancestors must have developed resistance to the virus.”

This ignores the fact that several attempts to show that humans have developed resistance to the virus have been unsuccessful. Polavarapu et al. [29] were successful only in “effectively eliminating the possibility that the elements were once present in humans but subsequently excised.” Additional investigation by Perez-Caballero et al. [30] showed that—contra to expectation—the antiviral protein TRIM5a “did not play a prominent role in the inactivation of, or limit the cross-species transmission of these primate gammaretroviruses.”

Yohn et al. [28] ruled out four possible scenarios that might have accounted for why humans lacked copies of PtERV1 and finally concluded: “Another scenario may be that the lineage that ultimately gave rise to humans did not occupy the same *habitat* as the ancestral chimpanzee and gorilla lineages. An excursion by early hominids to Eurasia during the time that PtERV1 infected African great apes and then a return to Africa would explain this phylogenetic inconsistency”.

There is no evidence, however, that australopithecines ever left the African continent, as is apparent from the lack of their fossils outside of Africa. Indeed, Böhme et al. [31] suggest that there were no faunal migrations out of Africa during the Pliocene. Our more recent follow-up paper details our view on where our proto-*Homo* ancestors might have been during the Pliocene [14]. This view concurs with the most parsimonious explanation for the current distribution of the hominoids [32].

Yohn et al. [28] found retroviral sequences in Asian macaques, but they also concluded that this infection took place approximately 1.5 Ma, long after the PtERV infection wave that infected all African primates, approx. 4-3 Ma. At first sight, it is intriguing that human ancestors were not infected, but in fact, none of the Eurasian hominoids (pongids and hylobatids) were infected either. Since different hominoid lineages (*Hylobates*, *Pongo*, ancestors of *Homo*) remained virus-free, the ‘not-in-Africa’ explanation is more parsimonious than assuming the presence of innate immunity in three separate lineages against a virus that could infect all African primates. Taken together, the absence of PtERV retroviral genes from the genomes of humans is most parsimoniously explained as the result of the absence of hominin ancestors in Africa approx. 4-3 Ma.

We thank Prof. Sarmiento for his comments and look forward to reading his forthcoming paper.

Author Contributions

All authors contributed equally to this reply.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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