

Comment

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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Vaneechoutte et al. 2023 [1] are fully justified in questioning the taxonomy and relationships of the australopithecines. As they emphasized in one of their subtitle headings, “If australopithecines are hominins, where are the fossils of extant African apes?”. The absence of African ape ancestors from the Plio-Pleistocene of Africa appears impossible, given that African apes are autochthonous to Africa and are presently widely distributed throughout the tropics of sub-saharan Africa, with living populations occurring as close as 500 km to the known australopithecine fossil sites (*cf* Lodwar, Kenya to Budongo, Uganda). It is thus more than likely that the African Plio-Pleistocene record contains African ape ancestors which have yet to be identified among the fossils attributed to australopithecines (a well sampled extinct subfamily from the African Plio-Pleistocene universally recognized as being phylogenetically closest to both humans and African apes; but see Pickford 2012 [2]). It is more than just a coincidence that the presence of gracile australopithecines in the Plio-Pleistocene roughly brackets a 4.2 Ma to 2.5 Ma time span that closely overlaps a human/African ape divergence date of 5 Ma to 3 Ma ago, as calculated by 60 years of biomolecular studies [3–8]. Because some australopithecines do not possess all the shared human/African ape characters, a divergence from the common human/African ape stock prior to human and African ape divergence is also likely for some members of this subfamily [9,10]. Considering that other australopithecines may document the Human/African ape divergence it may not be possible to confidently assign these fossils exclusively to anyone of the living lineages both because of their recent divergence and their fragmentary nature. While still other geologically younger australopithecines may prove to be members of an exclusive human lineage, it is nothing short of absurd to refer all australopithecines to an exclusive human lineage postdating the human/African ape divergence without delineating the characters that diagnose each and every individual as such. It is noteworthy that the debunking of Piltdown man by Weiner et al. 1953 [11] led immediately to the acceptance of australopithecines as exclusive human ancestors, underscoring humanity’s strong need to identify and possess human fossil ancestors irrespective of whether their ancestorship was demonstrated or even tested [12]. The acceptance of australopithecines was achieved without any credible phylogenetic and taxonomic studies that tested the polarity and lability of the shared australopithecine/human characters that were claimed to be diagnostic of an exclusive human lineage (mainly a canine that does not project beyond the dental occlusal plane and the absence of a canine-premolar honing complex, see Le Gros Clark, 1950, 1951 [13,14]). Given the current state of knowledge in both comparative studies and the fossil record, it is probably best to envisage australopithecines as an evolutionary radiation that gave rise not only to humans but also to extant African apes, and that this subfamily is likely to contain the earliest ancestors of each of the modern lineages of hominini i.e., *Homo*, *Pan* and *Gorilla*. The non-projecting canine and non-honing premolar that hallowed australopithecines as exclusive human ancestors are more than likely primitive for humans and African apes and are too labile within apes to be the sole basis of a human/African ape phylogeny [15].

Vaneechoutte et al. 2023 [1], are not as well justified in using australopithecines to refute the savanna hypothesis for the origin of human bipedalism. Principally, given their phylogenetic relationship to humans and African apes,

australopithecines as a group do not show evidence that they are habitual/striding bipeds and lack characters that show they engaged in bipedal behaviors more frequently than the non-human hominoids. Their comparatively short fingers and toes, short lower limbs, gracile vertebral bodies and very mild or absent lumbar lordoses and sacral kyphoses suggests they were most likely terrestrial quadrupeds, which probably engaged occasionally in bipedal behaviors and postures, but mainly moved on all fours especially when speed was at a premium [16,17]. Over the years 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. Any skeletal character australopithecines were perceived to share with humans has been claimed to be diagnostic of human-like habitual or striding bipedality without presenting evidence of an exclusive mechanical association of that character to bipedality [18]. This has hallowed the australopithecine femoral bicondylar angle values, lumbar curvature, pelvic and sacral shape, position and orientation of foramen magnum, and terrestrial characters in their feet as diagnostic of habitual and or striding bipedality without comparisons to either humans or non-human primates [12,17,19]. Comparisons to non-human primates is especially important when testing if the claimed bipedal characters also satisfy other non-bipedal behaviors and may thus be seen in non-habitual bipeds or terrestrial quadrupeds. 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. *Homo*, a habitual striding biped [20] is, therefore, the relevant taxon to test the savanna hypothesis. That, shortly after *Homo*'s earliest appearance in East Africa the genus can be found just south of the Caucasus in Dmanisi separated from the East African early *Homo* localities by thousands of kilometers of desert and grassland only serves to strongly support the savanna hypothesis for bipedal origins. Based on analogies among different orders of living mammals that have emigrated from more closed environments to open ones, the savanna hypothesis is very robust [21,22]. As such, it is highly unlikely that fossil remains with an uncertain taxonomy and unresolved behaviors will falsify it.

Unfortunately, in attempting to refute the savanna hypothesis and the human ancestral status of australopithecines, Vaneechoutte et al. 2023 [1] have embraced false facts, baseless claims and misconceptions found in the paleoanthropological literature. Too numerous to review here, only the following are treated. Contrary to Vaneechoutte et al. 2023 [1], 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. It is non-sectorial premolars and non-honing canines that project past the occlusal plane of the teeth that are the "human-like dental characters" likely to be primitive for hominoids [15]. 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 [12,23,24]. "Lucy" AL 288-1 does not preserve the foramen magnum, hence its position and orientation is unknown. Sts 5 a gracile australopithecine which does preserve the position and orientation of the foramen magnum shows values that do not differ from non-human hominoids [12,25,26]. 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* [12,27]. Moreover, there is no evidence that AL 288-1 had curved feet. Given its comparatively short length, the sole curved proximal pedal phalanx of AL 288-1 more precisely reflects flexed toe postures than arboreality. *Lucy's* foot bones, a talus, and a proximal and middle phalanx, do not provide any relevant information as to its degree of hallucal abduction. Contra the Zihlman et al. 1978 citation [28], it is unknown whether Sts 5 had postcranial dimensions comparable to *P. paniscus*. Sts 5 is known only from a skull without a mandible and does not preserve any postcranial dimensions. Nevertheless, specimens of gracile australopithecines that do preserve postcrania show that they had shorter upper limbs and feet, much shorter hands and a lower intermembral index than *P. paniscus* [29]. Moreover, metacarpal length and manual phalangeal length are considerably greater in *P. paniscus* than in any known australopithecine. There is no evidence that *Sahelanthropus*, *Ardipithecus* or *Orrorin* were bipeds or orthograde. *Ardipithecus* was clearly a palmigrade quadruped with a variably fused os centrale [27,30]. Given its hominoid pedigree *Ardipithecus* must have occasionally engaged in bipedal postures, but not more than any other ape [27]. Although the *Sahelanthropus* femoral diaphysis is suggestive of a quadruped, and the ulna has a degree of curvature seen in the knuckle-walking African apes, the fragmentary nature of its remains do not permit confident diagnosis of its locomotor behaviors [31,32] (see Sarmiento, 1995 [33] on diagnosing knuckle walking based on non-manual characters). The same applies to *Orrorin*, a fossil with a postcranium known only from a fragmentary distal humeral diaphysis, three proximal femoral diaphyses (one preserving the proximal epiphysis), a distal pollical phalanx and a proximal manual phalanx [34].

On a more general note, there is no convincing evidence as stated by Vaneechoutte et al. 2023 [1] that knuckle walking evolved independently in gorillas and chimpanzees. Although gorilla knuckle walking is clearly different from chimpanzee knuckle walking and the differences between the two behaviors correspond to differences in hand and wrist structure, the more derived gorilla knuckle walking could have easily evolved from the more generalized chimpanzee behavior [17,35,36]. In closely related forms it is nearly impossible to disentangle parallelisms from shared derived characters. In this regard, it is relevant that all hominoids including humans can assume knuckle-walking postures, so that the propensity to assume these postures appears to be a trait shared by all hominoids [35]. 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. Furthermore, the arguments of Vaneechoutte et al. 2023 [1], underscore the misconception that traits reflecting adaptations have no phylogenetic value. While function/adaptation may play an important role in evaluating the weight of characters in phylogenetic analyses [36], all characters, including those dependent wholly on environmental feedback for their development, may have phylogenetic value at different hierarchical levels and can contribute to unravelling phylogenies. Finally, the absence of retrovirus (PTVER1) 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. Because both Asian macaques and African baboons show the PTVER1 integrations occurring around 2 Ma ago the retrovirus also seems to have been present in Asia [37]. 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.

In summary, Vaneechoutte et al.'s 2023 [1] arguments that australopithecines could be ancestral to African apes or could totally lack any living descendants is well taken. However, the employment of australopithecines to argue that savanna habitats have nothing to do with the origin of humanlike bipedality confuses the postural or occasional bipedality seen in all hominoids with the obligate striding bipedality that is unique to humans. More importantly, it is contradictory for Vaneechoutte et al. 2023 [1] to argue that australopithecines are not human ancestors and at the same time to cite australopithecine habitats to refute the savanna hypothesis for the origin of human bipedality. Vaneechoutte et al. 2023 [1], could have profited from a more critical review of what is known of australopithecines and human evolution.

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