Reply to: Reevaluating bipedalism in *Danuvius*

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REPLYING TO S. A. Williams et al. https://doi.org/10.1038/s41586-020-2736-4 (2020)

In the accompanying Comment[1], Williams and colleagues question our interpretation of the evolutionary importance of extended limb clambering for the emergence of great ape suspension and hominin bipedalism[2] by casting doubt on the morphological evidence for bipedalism in *Danuvius*. Specifically, they question the hip mechanics, the reported orthogonal set to the distal tibia and the evidence for a functionally elongated lumbar spine by re-interpreting the position of the diaphragmatic vertebra.

Williams et al.[1] discovered a typographical error regarding hip mechanics in the supplementary information of our original paper[2]: iliopsoas is obviously a hip flexor, as Williams et al. state (as well as being an external rotator). However, our inference of the probable orientation of the ilium in *Danuvius* is based on the morphology of the proximal femur, which is consistent with habitual extension and enhanced gluteal abduction at the hip joint.

The main focus of the Comment by Williams et al.[1] is our interpretation of the vertebrae. The GPIT/MA 10000-16 specimen is a transitional (diaphragmatic) vertebra with large, round, anterosuperiorly oriented costotransverse facets and flat articular surfaces (Fig. 1a, b). This indicates articulation with a well-developed, flat and inferiorly oriented coastal rib tubercle, which means that this specimen could not be a last or penultimate thoracic vertebra.

The anatomy of costotransverse joints changes in humans[3] (Fig. 1c) and orangutans according thoracic level. Costotransverse facets of the upper thoracic vertebrae (T1–T7) are anterolaterally oriented, with oval and convex hollows that articulate with the concave tubercle of the sternal ribs and allow rotation and torsional movement of ribs in the pulmonary thorax. In mid-thoracic vertebrae (T8, T9 or T10), both the orientation and shape of the costotransverse facets change (Fig. 1c). The facets are round, flat and oriented anterosuperiorly. They articulate with the posteroinferior rib tubercle (see figure 5 in ref. [4]), which allows the costals of the diaphragmatic thorax a planar gliding movement[5]. The lower thoracic (T11 and T12) vertebrae of humans and orangutans lack costotransverse joints, because the floating ribs have only one articular facet.

The costotransverse facets of the thoracic vertebrae of African apes show less variability. These facets remain anterolaterally oriented at mid-thoracic positions, in which the rib tubercle is convex and posterosuperiorly oriented (figure 5 in ref. [4]). Some gorillas have a caudally shifted transitional vertebra (L1). Here, the last thoracic rib retains a tubercle and the last thoracic (pre-transitional) vertebra (T13) bears a costotransverse facet. This facet resembles the upper- and mid-thoracic costotransverse facets in shape and orientation—for example, in being convex and anterolaterally oriented—and is different from those of *Danuvius* (as visible in figure 1a of Williams et al.[1]). In *Pan*, the lower (transitional) thoracic vertebra always lack costotransverse facets.

In nearly all extant hominoids, the transitional vertebra occurs at the last thoracic level (or first lumbar level in some individuals of *Gorilla*) and lacks costotransverse facets. On the basis of the shape and orientation of the costotransverse facet, we conclude that GPIT/MA 10000-16 represents a mid-thoracic vertebra (a T8, T9 or T10) and would have articulated with the costal ribs. Depending on the number of thoracic vertebrae in *Danuvius*, we expect at least two or three post-transitional thoracic vertebrae, similar to the condition in *Nacholapithecus*, *Ekembo* and cercopithecids[6,7]. Although the number of lumbar vertebrae in *Danuvius* is unknown, the cranial shift of the transitional vertebra is indicative of a functionally elongated lumbar spine, as has recently been reported for *Rudapithecus*[8]. Williams et al.[1] concede that '[a]s with *Oreopithecus*, *Danuvius* may have had an 'intermediate' lower back similar to that of hylobatids ...': recent work on the lower torso of *Oreopithecus* has concluded that it was 'certainly more capable of bipedal positional behaviors than extant great apes'[9]. *Danuvius* and *Oreopithecus* differ in femoral, ulnar and hallucal morphology as well as dentition, but the point remains that an intermediate lower back—which *Danuvius* minimally possessed—predisposed Miocene apes such as *Oreopithecus*, *Rudapithecus* and *Danuvius* to upright postures. As it probably possessed more than five functionally lumbar vertebrae (two or three post-transitional vertebrae, and an unknown number of lumbar vertebrae), lordosis was possible for *Danuvius*. Consistent with our interpretation of GPIT/MA 10000-16 as a mid-thoracic vertebra (a T8, T9 or T10), the data from ref. [10] are appropriate for comparing to the inclination of the spinous process in the thorax of *Danuvius*.

We agree with Williams et al.[1] that *Danuvius* possessed a highly mobile hip joint that is characteristic of arboreal hominoids, and that its femur does not have some of the apomorphies that are typical of the hominin bipeds. However, it is unclear why we might expect *Danuvius* to have possessed the full suite of features of a terrestrial biped (an anteroposteriorly thick patella, elongated femoral neck and so on). Bipedal adaptations evolved piecemeal, as the early hominin fossil record indicates—and as has recently been reinforced by findings that the valgus knee and human-like pelvic drop did not evolve in concert[11]. We emphasize the arboreal adaptations of *Danuvius* and define extended limb clambering as a pattern of arboreal behaviour. At the same time, we draw attention to bipedal attributes in *Danuvius*. The posterosuperior expansion of the articular surface of the femoral head, which is found in many mammals, is nevertheless consistent with enhanced hip extension in *Danuvius*.

Compared with the fossils of other European Miocene apes, the preserved skeletal elements of *Danuvius* are notably complete: the tibia and the ulna are the only complete specimens known from the Neogene hominid record. Even though the distal tibia is detached at the metaphysis, the orthogonal set of the ankle joint relative to the tibial shaft—which is found only in bipeds[12,13]—can be measured with confidence (91.5±5°) and falls clearly outside the ranges of the great apes (100–108°). The orthogonal tibial angle can be inferred from the epiphysis alone. We measured the set of the ankle joint at its midpoint relative to the medial border of the medial malleolus and found a value

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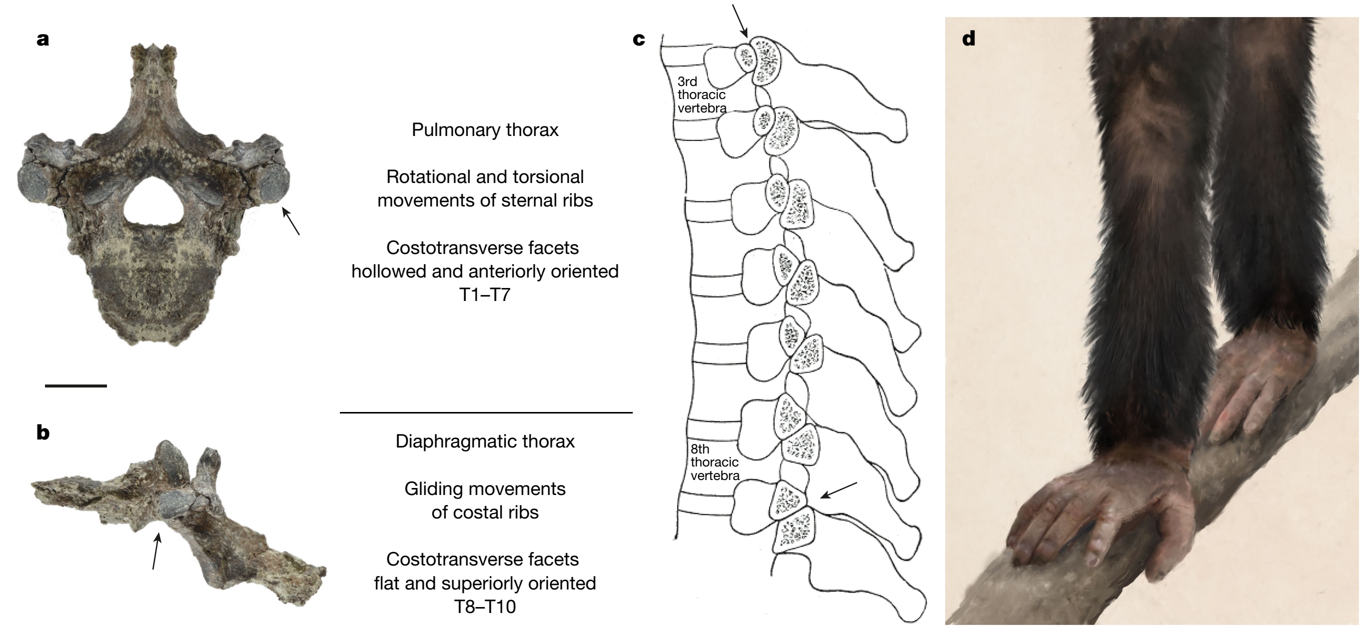

Fig. 1 | Transitional vertebra of *Danuvius guggenmosi*. **a**, **b**, Specimen GPIT/MA 10000-16 in superior (**a**) (mirror-imaged) and left lateral view (**b**). Scale bar, 10 mm. **c**, Human thoracic spine (from ref. [3]), showing the shape and orientation of costotransverse facets (indicated by arrows). **d**, Artist's reconstruction (by V. Simeonovski, according to scientific instructions of the authors) of the foot and knee postures of *D. guggenmosi* during deliberate bipedal walks on horizontal arboreal branches.

of 95.5° for *Danuvius*, which is well outside the range of the tibiae from other Miocene apes (*Hispanopithecus*, *Sivapithecus* and *Ekembo*, 104.0–107.3°) and *Gorilla* (n = 29, 104.0±2.6°). The set of the ankle joint from the epiphysis alone in *Danuvius* falls between the range of *Pan* (n = 32, 100.6±4.6°) and *Homo sapiens* (n = 29, 91.8±2.3°) and is closest in value to that of *Australopithecus* (n = 9, 93.4±2.7°).

Extended limb clambering should not be confused with striding terrestrial bipedalism, which represents another form of positional behaviour. Just as knuckle-walkers are also suspensory, extended limb clamberers incorporate bipedalism into their positional repertoire. This does not make them human bipeds: *Danuvius* has attributes that we interpret as functionally enabling arboreal bipedalism, but not striding terrestrial bipedalism. Very few of the morphologies we describe and quantify are identical to the corresponding hominin features related to terrestrial striding bipedalism. One of these differences is indeed in the patella, as Williams et al.[1] note. However, the flat patellar surface in *Danuvius* is suggestive of slow, deliberate orangutan-like movements[14,15].

The ability of *Danuvius* to walk bipedally on branches is an apomorphic behaviour that was enabled by the suite of unique morphological adaptations that characterize extended limb clambering. Besides the spinal and tibial characters, the strongly developed cruciate ligaments and the hinge-like morphology of the talocrural joint are consistent with extended limb clambering in *Danuvius*. Together with a laterally torqued and robust opposable hallux, these features—which are not present in this combination in striding terrestrial bipeds or any extant apes—contributed to increased foot and knee stability during slow and careful bipedal walks on narrow arboreal supports (Fig. 1d).

Reporting summary

Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

The datasets generated during and/or analysed in this article are available from the corresponding author on reasonable request.

1. Williams, S. A., Prang, T. C., Meyer, M. R., Russo, G. A. & Shapiro, L. J. Reevaluting bipedalism in *Danuvius*. *Nature* https://doi.org/10.1038/s41586-020-2736-4 (2020).
2. Böhme, M. et al. A new Miocene ape and locomotion in the ancestor of great apes and humans. *Nature* **575**, 489–493 (2019).
3. Gray, H. *Anatomy of the Human Body* (Lea & Febiger, 1918).
4. Schmid, P. et al. Mosaic morphology in the thorax of *Australopithecus sediba*. *Science* **340**, 1234598 (2013).
5. Ward, M. & Macklem, P. in *The Thorax* (ed. Roussos C. J. & Macklem, P. T.) 515–533 (Marcel Dekker, 1995).
6. Ward, C. V., Walker, A., Teaford, M. F. & Odhiambo, I. Partial skeleton of *Proconsul nyanzae* from Mfangano island, Kenya. *Am. J. Phys. Anthropol.* **90**, 77–111 (1993).
7. Nakatsukasa, M. & Kunimatsu, Y. *Nacholapithecus* and its importance for understanding hominoid evolution. *Evol. Anthropol.* **18**, 103–119 (2009).
8. Ward, C. V., Hammond, A. S., Plavcan, J. M. & Begun, D. R. A late Miocene hominid partial pelvis from Hungary. *J. Hum. Evol.* **136**, 102645 (2019).
9. Hammond, A. S. et al. Insights into the lower torso in late Miocene hominoid *Oreopithecus bambolii*. *Proc. Natl Acad. Sci. USA* **117**, 278–284 (2020).
10. Latimer, B. & Ward, C. in *The Nariokotome* Homo erectus *Skeleton* (eds. Walker, A. & Leakey, R.) 266–293 (Cambridge Univ. Press, 1993).
11. Kikel, M., Gecelter, R. & Thompson, N. E. Is step width decoupled from pelvic motion in human evolution? *Sci. Rep.* **10**, 7806 (2020).
12. Latimer, B., Ohman, J. C. & Lovejoy, C. O. Talocrural joint in African hominoids: implications for *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* **74**, 155–175 (1987).
13. DeSilva, J. M. Functional morphology of the ankle and the likelihood of climbing in early hominins. *Proc. Natl Acad. Sci. USA* **106**, 6567–6572 (2009).
14. Thorpe, S. K. & Crompton, R. H. Orangutan positional behavior and the nature of arboreal locomotion in Hominoidea. *Am. J. Phys. Anthropol.* **131**, 384–401 (2006).
15. Thorpe, S. K., Holder, R. L. & Crompton, R. H. Origin of human bipedalism as an adaptation for locomotion on flexible branches. *Science* **316**, 1328–1331 (2007).

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Competing interests The authors declare no competing interests.

Additional information
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