

Reevaluating bipedalism in *Danuvius*

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Scott A. Williams^{1✉}, Thomas C. Prang², Marc R. Meyer³, Gabrielle A. Russo⁴ & Liza J. Shapiro⁵

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Danuvius guggenmosi is a species of Miocene hominoid from the 11.62-million-year-old site of Hammerschmiede. On the basis of interpretations of its vertebrae and limbs, Böhme and colleagues¹ infer that *Danuvius* exhibited ‘joint positions and loading patterns of both hominin bipedalism that emphasize hindlimb extension and spinal curvatures, and extant great ape suspension’. Although we agree that *Danuvius* was suspensory, we find the functional interpretation of bipedalism to be unfounded on morphological grounds. We therefore call into question the evolutionary scenario for the origin of hominin bipedalism proposed by Böhme and colleagues.

On the basis of differences in the orientation of the spinous process (41°) between purported ‘first’ and ‘lower’ thoracic vertebrae, Böhme and colleagues infer biped-like cervical lordosis and thoracic kyphosis for the upper spine of *Danuvius*. However, their comparative data (drawn from ref.²) are misleading, because they represent a substantially higher thoracic level (T7 in humans and T8 in chimpanzees) than is represented by the *Danuvius* specimen GPIT/MA/10000-16 (described as the ‘penultimate or ante-penultimate [thoracic] position’, in the supplementary information of Böhme et al.¹). When the relevant comparative data² are used, only minor differences in the inclination of the spinous process are found (T1: ante-penultimate thoracic, 8.4° in humans and -0.1° in chimpanzees; T1: penultimate thoracic, 4.2° in humans and 3.2° in chimpanzees). *Danuvius* does not resemble humans or chimpanzees in this metric, although it does overlap with some gorillas and orangutans (Fig. 1). Moreover, in the absence of mid-thoracic or lumbar vertebrae, claims regarding the spinal curvature and lumbar lordosis¹ of *Danuvius* are unsubstantiated.

The interpretation of a long lower back in *Danuvius*¹ is based not on a series of vertebrae, but rather on a single lower thoracic vertebra. On the basis of a well-developed costotransverse facet, Böhme and colleagues¹ argue for ‘a non-ultimate thoracic position for the diaphragmatic vertebra and therefore a functionally longer lower back, as in early hominins, stem-hominoids and cercopithecids.’ Although the last thoracic vertebra in humans lacks costotransverse facets, they are in fact commonly present in great apes (in 30 out of 42 specimens examined; personal observations of S.A.W.) and—in some cases—are large and cranioventrally directed (contra ref.¹) (Fig. 1). Therefore, the presence of a costotransverse facet on a vertebra does not preclude its identification as an ultimate thoracic vertebra (Fig. 1). Moreover, the position of the diaphragmatic vertebra does not directly relate to the length of the lumbar column or to lumbar curvature. All extant hominoid species demonstrate some frequency of cranial displacement of the diaphragmatic vertebra relative to the last thoracic vertebra—approximately 33% of many hominid species, and up to 55% in hylobatids—yet do not have long lumbar columns³. Similarly, atelines, which converge with hominoids on lower back morphology related to suspensory behaviour⁴, exhibit similar frequencies of cranial displacement and possess

short lumbar columns (Fig. 2). Stem hominoids possessed six lumbar vertebrae and cranial displacement by one to two elements and are therefore considered long-backed⁵, whereas *Oreopithecus bambolii* possessed five lumbar vertebrae and demonstrates cranial displacement by at least one element⁶ (Fig. 2). As with *Oreopithecus*⁶, *Danuvius* may have had an ‘intermediate’ lower back similar to that of hylobatids rather than a long, monkey-like lower back or a short lower back that recalls those of the extant great apes (Fig. 2). Regardless, neither the morphology of GPIT/MA/10000-16 nor its potential position in the vertebral column indicate the length of the lumbar column or suggest adaptation to bipedal posture or locomotion.

Böhme et al.¹ argue that *Danuvius* had a valgus knee and hominin-like hip abductor mechanics that were associated with extended-limb arboreal bipedalism. They suggested that ‘the more medial position of the lesser trochanter may result in a more exclusively extension function of iliopsoas, particularly if the ilium were rotated laterally on the hip joint’ (supplementary information of Böhme et al.¹). Yet, given its anatomical position, the iliopsoas functions exclusively as a hip flexor and lateral rotator of the thigh, with no contribution to hip extension⁷. Instead, a more medially positioned lesser trochanter may further diminish the ability of the iliopsoas to contribute to lateral rotation of the thigh, which has no clear connection to bipedalism. Additionally, Böhme et al.¹ infer that the ilium was more ‘inferolaterally’ oriented in *Danuvius* on the basis of a high femoral neck-shaft angle and a posterosuperior expansion of the articular surface of the femoral head, implying an increased hip abductor function of the lesser gluteal muscles. However, as shown by Böhme et al.¹, neither of these traits is unique to bipeds. Notably, the *Danuvius* femur appears to lack the elongated femoral neck (figure 1 in ref.¹) that is characteristic of bipeds, and which increases the internal moment arm of the lesser gluteal muscles to counteract external moments at the hip during the single support phase of the gait cycle⁸.

A tibia with a damaged diaphysis (GPIT/MA/10000-15) is central to arguments for an extended lower limb and bipedalism in *Danuvius*, as it purportedly displays a hominin-like, relatively large and anteroposteriorly flattened lateral condyle with a ‘buttressing of the tibial metaphysis’¹, combined with a talocrural joint oriented orthogonally to the diaphyseal long axis. However, the analysis of the tibial condyle shape performed by Böhme et al.¹ is preliminary and includes only eight individuals and seven species, which precludes statistical tests of taxon or locomotor group differences. We agree that the morphology of the proximal tibial metaphysis could reflect knee-joint loading regimes associated with various locomotor and postural modes, but Böhme and colleagues¹ do not provide comparative data to support their claim that the tibial metaphysis of *Danuvius* is expanded relative to those of apes. Moreover, the analysis of the surface area of the tibial plateau relative to tibial length shows *Danuvius* to be most similar to *Pan* and

¹Center for the Study of Human Origins, Department of Anthropology, New York University, New York, NY, USA. ²Department of Anthropology, Texas A&M University, College Station, TX, USA.

³Department of Anthropology, Chaffey College, Rancho Cucamonga, CA, USA. ⁴Department of Anthropology, Stony Brook University, Stony Brook, NY, USA. ⁵Department of Anthropology, The University of Texas at Austin, Austin, TX, USA. ✉e-mail: sawilliams@nyu.edu

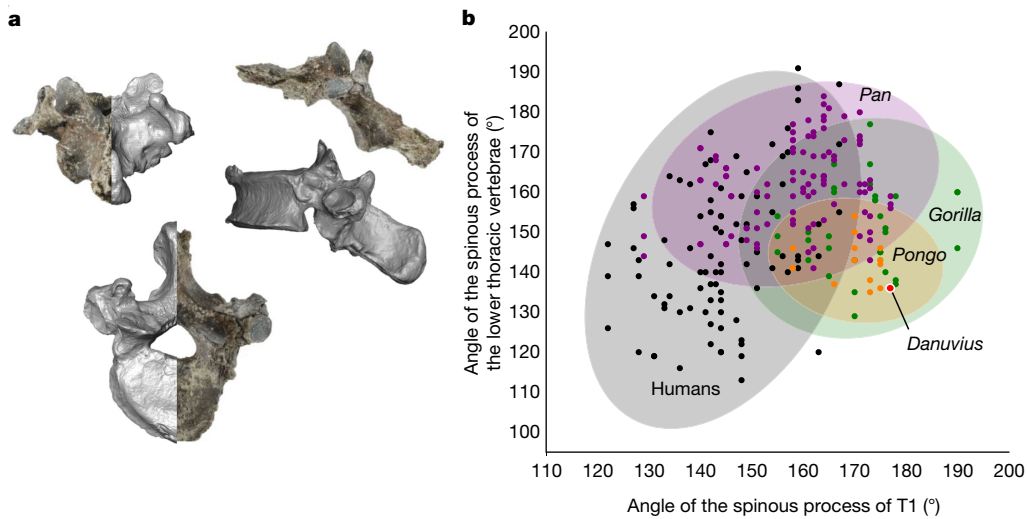


Fig. 1 | Lower thoracic vertebra of *Danuvius* (GPIT/MA/10000-16) in comparative context. a, The cranially oriented costal facets and ‘rod-like’ laminae of GPIT/MA/10000-16 (colour) (from ref. ¹) can be found on the last thoracic vertebrae of great-ape specimens (for example, on a gorilla (grey)) (not to scale). Therefore, the contention that GPIT/MA/10000-16 cannot be the ultimate or penultimate thoracic vertebra on the basis of the presence of these

morphologies is incorrect. **b**, Angles of the spinous process of upper and lower (ultimate, penultimate and ante-penultimate) thoracic vertebrae of a range of hominoids: *Pongo* ($n = 7$), *Gorilla* ($n = 11$), *Pan* ($n = 37$) and modern humans ($n = 30$). *Danuvius* falls near some of the specimens of *Gorilla* and *Pongo*, which indicates that it is neither unique nor humanlike.

Pongo (extended data figure 3 in ref. ¹). The inference that *Danuvius* habitually loaded its proximal tibia in extended-knee bipedalism on the basis of comparisons of proximal tibia morphology is therefore currently unsubstantiated.

As noted by Böhme and colleagues¹, the anteroposteriorly thin patella of *Danuvius* resembles those of extant great apes and Miocene hominoids such as *Pierolapithecus*. The relatively thin patellae of great apes reflect the use of varied knee positions during orthograde climbing and suspension, including extended positions. By contrast, the

thicker patellae of cercopithecoids are associated with the generation of higher-magnitude knee extension moments from more-habitually flexed positions as pronograde quadrupeds⁹. However, patellar thickness does not distinguish among living great apes⁹. Although we agree that the *Danuvius* patella is anteroposteriorly thin and great-ape-like, its morphology cannot therefore support the conclusion that *Danuvius* used ‘slow and deliberate movements, most similar to *Pongo*’ (supplementary information of Böhme et al.¹). In addition, the great-ape-like patella of *Danuvius* reduces the moment arm of the quadriceps at

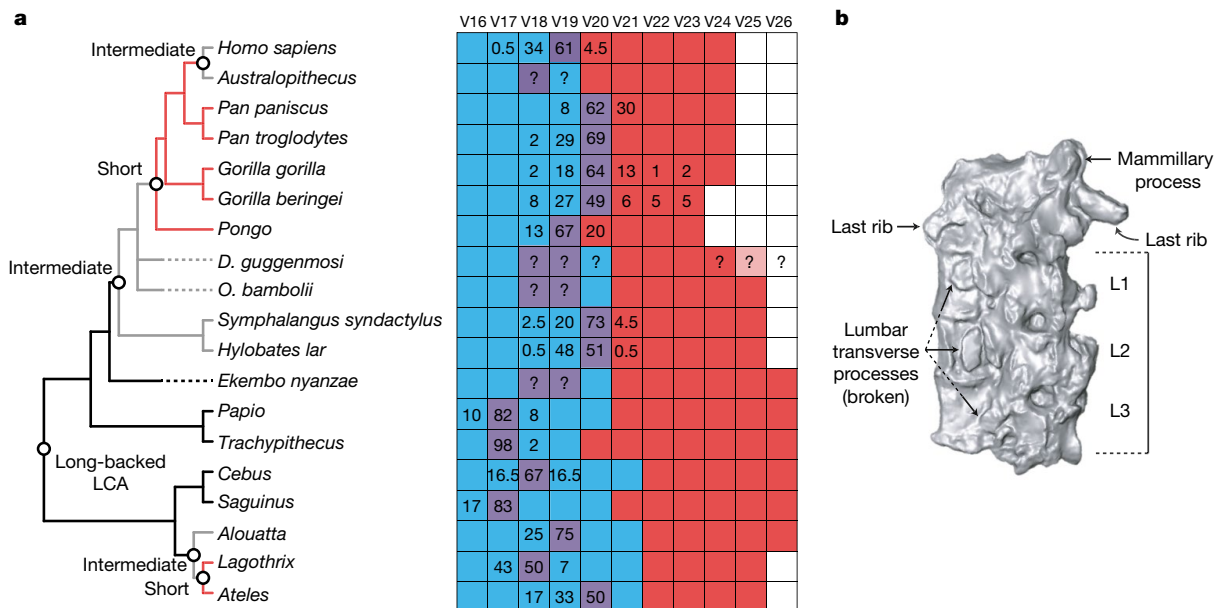


Fig. 2 | Evolution of vertebral formulae in anthropoids. a, Regional numbers of thoracic (blue or purple squares, starting at T9 (vertebra 16)) and lumbar (red squares) vertebrae are shown, along with the modal diaphragmatic vertebra (purple squares, with the frequencies listed). Hypothesized ancestral patterns of lower back (lumbar column) length are indicated. LCA, last common ancestor. **b**, In the IGF11778 *Oreopithecus* skeleton, two additional lumbar

vertebrae (L4 and L5) are entrapped between the iliac blades of the pelvis⁶. Additionally, the last thoracic vertebra is post-diaphragmatic, as evidenced by a cup-shaped, sagittally oriented superior articular facet with a mammillary process lateral to it; this indicates that the specimen is characterized by cranial displacement.

the knee¹⁰, which diminishes the ability of the quadriceps to counteract sagittal-plane moments that flex the knee in the early part of the stance phase of the bipedal gait cycle¹¹. Finally, the damaged tibial diaphysis and distal metaphysis preclude accurate measurement of the tibial diaphysis clearly indicate frontal-plane curvature, particularly along the lateral border of the midshaft and below—potentially resulting in a more obliquely oriented talocrural joint, which is characteristic of African apes¹². The lower limb of *Danuvius* shares morphometric affinities with great apes that are consistent with a positional repertoire that included orthogrady and suspension, but the evidence for bipedalism is equivocal.

In summary, *Danuvius* lacks features associated with bipedal posture and locomotion. Its preserved morphology appears to reflect the increased limb mobility and powerful hallucal grasping that are expected to characterize a relatively large-bodied, tailless arboreal ape¹³. The discovery of *Danuvius* substantially contributes to our understanding of hominoid evolution, but relevant comparative data do not support the hypothesis of Böhme et al.¹ that the last common ancestor of humans and chimpanzees was a long-backed, lordotic and arboreal biped^{3,14,15}.

Reporting summary

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

Data availability

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

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Competing interests The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to S.A.W.

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Reply to: Reevaluating bipedalism in *Danuvius*

<https://doi.org/10.1038/s41586-020-2737-3>

Madelaine Böhme^{1,2✉}, Nikolai Spassov³, Jeremy M. DeSilva⁴ & David R. Begun⁵

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

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In the accompanying Comment¹, Williams and colleagues question our interpretation of the evolutionary importance of extended limb clambering for the emergence of great ape suspension and hominin bipedalism² 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 paper²: 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 humans³ (Fig. 1c) and orangutans according to 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 movement⁵. 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 concert¹¹. 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 posteriosuperior 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 ($91.5 \pm 5^\circ$) and falls clearly outside the ranges of the great apes ($100\text{--}108^\circ$). 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

¹Department of Geosciences, Eberhard-Karls-Universität Tübingen, Tübingen, Germany. ²Senckenberg Centre for Human Evolution and Palaeoenvironment, Tübingen, Germany. ³National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria. ⁴Department of Anthropology, Dartmouth College, Hanover, NH, USA. ⁵Department of Anthropology, University of Toronto, Toronto, Ontario, Canada. ✉e-mail: m.boehme@ifg.uni-tuebingen.de

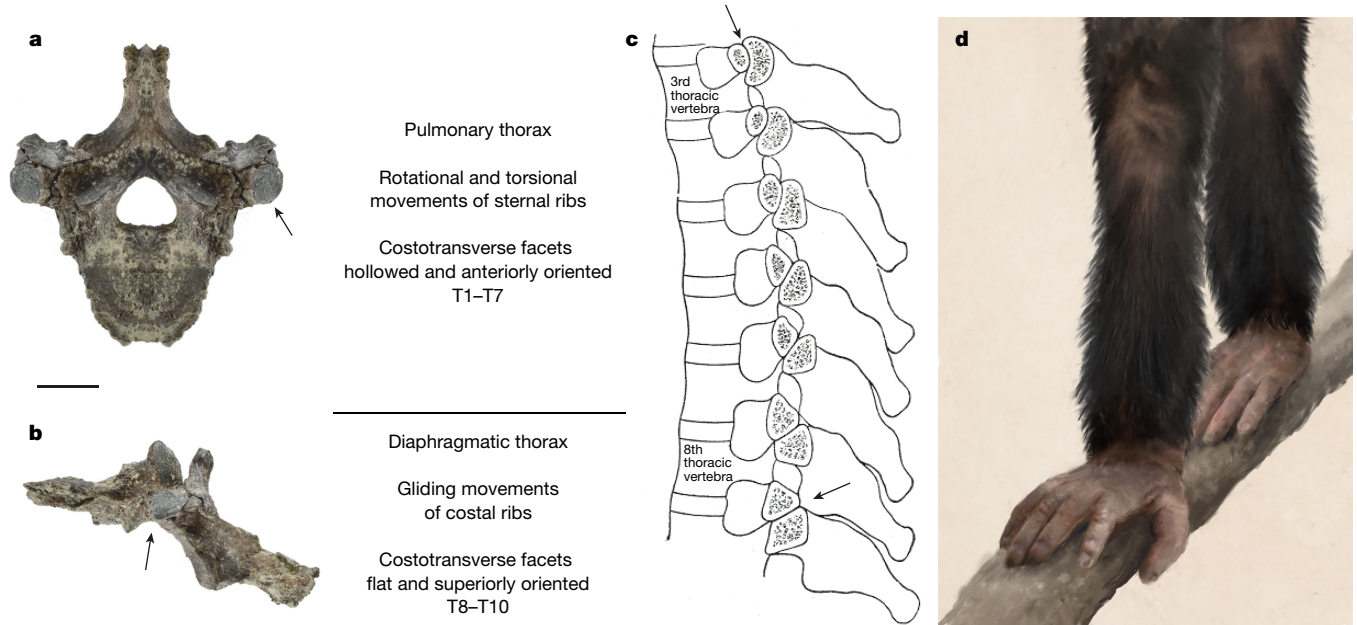


Fig. 1 | Transitional vertebra of *Danuvius guggenmosi*. **a, b**, Specimen GPIT/MA 10000-16 in superior (a) (mirror-imaged) and left lateral view (b). Scale bar, 10 mm. **c**, Human thoracic spine (from ref. ³), showing the shape and orientation of costotransverse facets (indicated by arrows). **d**, 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* ($n = 29$, $104.0 \pm 2.6^\circ$). The set of the ankle joint from the epiphysis alone in *Danuvius* falls between the range of *Pan* ($n = 32$, $100.6 \pm 4.6^\circ$) and *Homo sapiens* ($n = 29$, $91.8 \pm 2.3^\circ$) and is closest in value to that of *Australopithecus* ($n = 9$, $93.4 \pm 2.7^\circ$).

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.

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Correspondence and requests for materials should be addressed to M.B.

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