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Article

Postcranial evidence of late Miocene hominin bipedalism in Chad

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Bipedal locomotion is one of the key adaptations defining the hominin clade. Evidence of bipedalism is known from postcranial remains of late Miocene hominins as early as 6 Ma in eastern Africa¹⁻⁴. Bipedality of *Sahelanthropus tchadensis* was hitherto inferred at circa 7 Ma in central Africa (Chad) based on cranial evidence⁵⁻⁷. Here we present the first postcranial evidence of the locomotor behavior of *S. tchadensis* with new insights on bipedalism at the early stage of hominin evolutionary history. The original material was discovered at locality TM 266 (Toros-Menalla fossiliferous area), and consists of one left femur and two, right and left, ulnae. The morphology of the femur is most parsimonious with habitual bipedality, and the ulnae preserve evidence of substantial arboreal behavior. Thus, taken together, the new findings suggest that hominins were already bipeds at circa 7 Ma but also suggest that arboreal clambering was probably a significant part of their locomotor repertoire.

Discoveries in Chad by the Mission Paleoanthropologique Franco-Tchadienne (MPFT) have substantially contributed to our understanding of early human evolution in Africa. The localities TM 247, TM 266, TM 292 in the Toros-Menalla fossiliferous area in the Lake Chad Basin yielded, among hundreds of vertebrate remains, a nearly complete cranium (TM 266-01-60-1), three mandibles, and several isolated teeth representing a minimum of four adult individuals assigned to the hominin *Sahelanthropus tchadensis*^{5,8}. The fossils were found in the TM Anthracotheriid Unit with biochronological estimates and radiochronological age at circa 7 Ma^{7,9}. Environmental indicators at Toros-Menalla localities suggested a lacustrine fringe, in a desert vicinity, where open areas with dry and humid grasslands coexisted with arboreal cover⁹.

Three other hominin fossil remains were discovered at TM 266 in 2001 by the MPFT: one left femoral shaft (TM 266-01-063, unearthed in July 2001), and two right and left ulnae (respectively TM 266-01-050, unearthed in July 2001 and TM 266-01-358, unearthed in November 2001, see Supplementary Note 1). Although none of these limb bones can be reliably ascribed to any hominin craniodental specimen found at TM 266, the most parsimonious hypothesis is to assign these postcranial remains to the sole hominin species so far identified in this locality, *S. tchadensis*.

The femur

The hindlimb is represented by a left femoral shaft (TM 266-01-063) about 242 mm long (Fig. 1, Extended Data 1 and see description in Supplementary Note 2, Supplementary Table S1), lacking the distal epiphysis and most of the proximal one. The specimen is curved anteroposteriorly as in *Australopithecus* and *Orrorin tugenensis* (BAR 1002'00 and BAR 1003'00; circa 6 Ma from Lukeino, Kenya)¹⁻² and slightly more heavily built than BAR 1003'00 specimen (see also Extended Data 2-3). The two major axes of the proximal and distal diaphyseal portions indicate that the neck was anteverted as in fossil hominins¹⁰ (Extended Data 4), correlated with an antetorsion of the long axis of the shaft¹¹. Femoral antetorsion is also reported in archaic fossil apes such as *Ekembo* but is absent in the putative arboreal biped *Danuvius guggenmosi*^{12,13}. The femur exhibits proximal platymeria just distal to the lesser trochanter (Fig. 2a, see Extended Data 5, Supplementary Note 3

for figure comments and see description in Supplementary Note 2), a trait observed in *Or. tugenensis* and later hominins and suggested to correlate with neck elongation, an indicator of hominin bipedalism^{3,4,11}. The neck is compressed anteroposteriorly as in the Miocene ape *D. guggenmosi*¹² and hominins²⁻⁴ (but see¹⁴ for *Dryopithecus fontani* and *Hispanopithecus laietanus*; Fig. 1f, h-i).

A small but sharp relief, indicative of a lateral and vertical gluteal tuberosity, continues into a rugose surface distally and blends with the lateral component of a broad ‘proto-*linea aspera*’³ (Fig. 1b,d,e,g; 12.2 mm in its narrowest width). In posterior view, the lateral lip of the *linea* forms a well-marked sigmoid line. Similarly, the medial lip of the *linea aspera* is well-marked. The spiral line for the insertion of the *vastus medialis* is linear and merges distally with the medial lip of the *linea aspera*. Such a configuration is also observed in *Or. tugenensis* and *Ardipithecus ramidus*^{2,4,15} albeit with a more salient ‘proto-*linea aspera*’ in TM 266-01-063, but differing from modern humans in which a pilaster develops coincident with the posteromedial translation of the *m. gluteus maximus*³ (see Fig. 2b, see Supplementary Note 3 for figure comments). Overall, the external morphology of TM 266-01-063 does not differ from *Or. tugenensis* and both are similar to the condition seen in later hominins.

Functionally, the anteroposteriorly compressed neck and the subtrochanteric platymeria reflect a hip subjected to high mediolateral bending moments, assumed to be counterbalanced by the gluteal muscles, which is consistent with the presence of a distinct gluteal tuberosity in TM 266-01-063⁴. This array of features is compatible with habitual bipedalism in *S. tchadensis*^{3,4,11}, considered here as a behavioral response repeated under comparable situations¹⁶, and then potentially offering a selective advantage.

The cortical thickness distribution pattern of the femoral shaft is characterized by three relative reinforcement areas corresponding respectively to the proximomedial, lateral and posterior portions of the diaphysis (Fig. 3, see also Supplementary Note 3 for Fig. 3 comments; Extended Data 6 for TM 266-01-063 cortical thickness and bone cross-sectional geometries). Compared to extant hominoids (except gibbons), TM 266-01-063 most resembles the typical *Homo sapiens* condition, especially regarding its posterior and lateral aspects¹⁷ (Fig. 3). Comparative data are, to our knowledge, not available for *Ardipithecus*; and high resolution microCT-scan data are probably needed to assess precisely the cortical thickness in BAR 1002’00/1003’00 (*Or. tugenensis*)^{18,19}. Available CT-scan data shows that *S. tchadensis* and *Or. tugenensis* share an oblique (antero-medial to postero-distal) extension of bone thickening²⁰. Yet, *Or. tugenensis* does not show the posterior thickening nor the expanded lateral thickening seen in TM 266-01-063 and *Homo sapiens*.

The pattern and magnitude of bone distribution in organisms stem from a complex interplay between heredity and mechanical stimuli²¹, and early ontogenetic stages may display inherited patterns. With the locomotor autonomy, patterns of bone distribution record the individual activity level and the loadings experienced during ontogeny and adulthood. Hence, in the case of *S. tchadensis*, the hominin-like condition of the femoral bone distribution may retain an evolutionary signal but more likely support individual locomotor activity pattern that includes bipedalism.

Cortical area and second moment of area (I_x/I_y and I_{\max}/I_{\min}) are biomechanical parameters frequently used to infer habitual locomotor functions in primates, as they partly reflect how long bones resist loads, and have been used to infer how they grow in response to habitual loading (see¹¹). The cortical area of the diaphyseal cross-section is a measure of resistance of the bone to axial compression or tension, while the second moment of area measures the resistance to bending and twisting loads.

In all cases, cross-sectional cortical area and second moment of area values for TM 266-01-063 fall within fossil hominin distribution (Supplementary Table S2 and references therein, Extended Data 6-7, see Supplementary Note 4 for comments). The cross-sectional geometric properties (CSGP) of the femoral shaft of TM 266 results, when considered along with shape analyses of the femoral cross-sections at 80% and 50% levels (see Methods *Geometric morphometrics* and Fig. 2 and Extended Data 5), describe a hominin-like pattern, and do not support morphological affinities of *S. tchadensis* with extant gorillas in most analyses, nor with extant and Miocene apes overall.

Many factors such as stature, body mass, muscle attachment sites, positional behavior, ontogeny and sexual dimorphism may contribute to femoral bone mass distribution²². Considering size, values derived from the shape analysis of the femoral cross-section at 80% (centroid size, Extended Data 5) indicate that the *S. tchadensis* femur is in the range of hominin variation, apart from all other extant hominoids but *Homo sapiens*. Additionally, preliminary estimation of the body mass of *S. tchadensis* through univariate regressions provided by²³ on anteroposterior and mediolateral subtrochanteric and midshaft femoral dimensions (Supplementary Table S1) yield values from 43.5 to 49.4 kg (but see²⁴). These results are in the range of values derived from the same metrics reported for australopith and early *Homo*. *Sahelanthropus* body estimates fall between those estimated for *Or. tugenensis* (from 39.9 to 45.7 kg; see Supplementary information in⁴⁰; but see²⁵ for estimation of 47.7-50.1 kg) and *Ardipithecus ramidus* (ARA-VP-6/500, 51 kg²⁶). Unsurprisingly, body mass estimates for *S. tchadensis* remain close to the average body mass of *P. troglodytes*, the earliest hominins and australopiths²⁷. Functionally, the geometric properties of the femoral shaft of TM 266-01-063 indicate a greatest resistance to mediolateral bending stress. This condition seen in A.L. 288-1 and African and Asian early *Homo* is suggested to indicate a more lateral position of the body during the stance phase of gait in association with an increase in femoral neck length and biacetabular breadth^{4,11}.

Functional interpretations remain difficult to formulate given the paucity of early hominin comparative data and the state of preservation of the TM 266 femur. Nevertheless, in the proximal portion of TM 266-01-063, a structure formed by dense cancellous bone, consisting in an array of oblique trabeculae, is clearly identifiable in both transversal and parasagittal planes (Extended Data 8). In the parasagittal plane, this oblique structure originates posteriorly at the level of the distal base of the neck and ends anteriorly on the endosteal surface around the level of the distal portion of the lesser trochanter. In the transverse plane, the structure forms a spur originating from the postero-medial endosteal surface and extending toward the antero-lateral endosteal surface. This structure corresponds to the presence of a *calcar femorale* (CF) in TM 266-01-063. The CF is also documented in *Orrorin tugenensis* (BAR 1003'00²⁸), early hominins such as *A. afarensis* with

MAK-VP-1/1²⁹ and modern humans^{30,31} and is interpreted as a mechanical support in load distribution within the proximal femur in relation to habitual bipedal locomotion. In terrestrial bipeds, it facilitates compressive loads dispelling in the proximal femur by decreasing the stress in the posterior and medial aspects and increasing the stress in the anterior and lateral aspects^{28,31}. TM 266 01-063 and BAR 1003'00 present both an oriented trabecular bundle, of columnar aspect, in cross-section set in parasagittal plane – a morphology recalling the human condition (Extended Data 9), and a similar proximodistal extension of the structure. Nevertheless, the CF is seemingly shorter and appears denser, with a tightened trabecular network, in the transverse cross-sections in BAR 1003'00. The observed differences might be potentially due to the different states of preservation and/or CT-image acquisition settings in TM 266 01-063 and BAR 1003'00. A well-developed *calcar femorale* in TM 266-01-063 might represents a morphological adaptation for terrestrial bipedalism, which is strongly supported by the other lines of evidence derived from the femoral external shape and structural analyses.

Ulnae

The forearm bones attributed to *Sahelanthropus tchadensis* consist of two partial left and right ulnae lacking the distal epiphyses (Supplementary Note 2). Similarity in size and shape for these ulnae could suggest they are from the same individual, but no definitive evidence supports this inference. TM 266-01-050 is a left ulnar diaphysis of 239 mm long (Fig. 4e-h, Supplementary Table S1) with eroded proximal epiphysis. The right ulna (TM 266-01-358; Fig. 4a-d) is a proximal-half shaft that is 155 mm long with a partially preserved epiphysis. The shafts are curved in profile. Similar anteroposterior curvature is observed in *Ar. kadabba*³² (ALA-VP 2/101) and later hominins (e.g., L 40-19 and OH 36) as well as in African apes^{10,33-35} [see comparative views in Extended Data 10]. This curvature contrasts with the straight ulnar shaft of *D. guggenmosi*, but this lack of curvature is likely due to pathological conditions¹². A recent ulnar curvature analysis³³ places the Chadian ulna (TM 266-01-050) within the fossil hominin variation, close to the African apes in morphological space, not differing in this regard from OH 36 and L 40-19 (presumably *Paranthropus*), U.W. 101-499 (*Homo naledi*), and to a lesser extent StW 573 (*Australopithecus prometheus*). In primates, such ulnar curvature is due to habitual loads exerted by the action of *m. brachialis* in order to maintain elbow flexion during arboreal climbing, which in turn involves the action of a powerful antagonistic forearm musculature, including *m. anconeus*, wrist and fingers extensors and flexors^{35,36}. In this context, ulnar curvature is also suggested to be associated with arboreal behaviors in large-bodied primates, especially climbing and to some extent suspensory activities, for instance in facilitating prono-supination and in countering habitual loads due to body weight and the action of digital and carpal flexors^{35,37}.

The preservation of TM 266-01-050 allows partial assessment of the cross-sectional cortical bone distributions (see Fig. 4, Extended Data 7, Supplementary Note 4). The cortical bone is predominantly distributed anteroposteriorly as in orangutans and to a lesser extent in chimpanzees. This condition contrasts with that seen in gorillas, which tend to grow more bone mediolaterally. Relative mediolateral expansion is suggested to adjust for increased vertical and mediolateral

forces that apply to the forelimb in terrestrial quadrupedal primates³⁸⁻³⁹. Compared to chimpanzees and orangutans, which tend to grow more bone anteroposteriorly⁴⁰, the morphology of TM 266-01-50 more likely reflects bending loads associated with an array of arboreal locomotor modes. The Chadian ulnar geometry deviates from circularity with a major axis oriented anteroposteriorly at the 80% level and antero-laterally at midshaft level where maximum bone deposition occurs. Such conformation is indicative of habitual loads exerted by the oblique cord/interosseous membrane along with the *m. flexor digitorum profundus* anteriorly and along with the wrist/finger extensors posteriorly. Overall, curvature and cross-sectional geometric properties of the ulna conform to greater anteroposterior resistance and optimized pronosupination abilities, indicative of habitual arboreal behaviors, including climbing and/or 'cautious climbing'⁴¹⁻⁴², rather than terrestrial quadrupedalism^{38,41,43}.

The preserved flat distal portion of the olecranon processes indicate that they were not projecting posteriorly as in African apes⁴⁴. In this regard, the distal portion of the olecranon most resembles the condition in Miocene apes⁴⁴⁻⁴⁵ and in hominins⁴⁶. The proximal epiphyses indicate an anteriorly-facing trochlear notch as in fossil hominins and Miocene apes^{10,12,44-45,47}. Hence, the Toros-Menalla ulnae depart from the typical proximally oriented trochlear notch of the extant great apes^{36,46}. In functional terms, a more anteriorly facing notch, associated with an olecranon aligned with the long axis of the forearm, favors triceps leverage at mid-flexion^{36,45,46}. In *Ar. ramidus* such function has been linked to careful climbing and bridging⁴⁵. Conversely, a more proximally facing notch reflects habitual extended elbow, e.g. during suspension⁴⁷ and quadrupedalism, while a posteriorly projecting olecranon favors triceps leverage in extension and is commonly associated with terrestrial quadrupedal locomotion in anthropoids⁴⁴.

Ulnae from Toros-Menalla display a keeled trochlear notch with a comparatively acute angle relative to later hominins and African apes. The distal keeling angle, measured from TM 266-01-358 (distal keeling angle of 117°), is in the lower range of chimpanzees and *Pongo pygmaeus*, and close to values reported for *Oreopithecus bambolii* and the left *A. afarensis* ulna A.L. 288-1t⁴⁶. Likewise, the proximal angle is acute (proximal keeling angle of 101°), in the lower range of reported values for chimpanzees and gorillas, and close to OH 36 and *O. bambolii*⁴⁶. A pronounced trochlear keel likely augments mediolateral stability of the elbow in response to powerful superficial finger and wrist flexors, and forearm pronator (*mm. flexor digitorum superficialis*, *flexor carpi radialis* and *ulnaris*, and *pronator teres*)^{34,46}. Such a configuration was reported on *D. guggenmosi*¹² and is typical of the arboreal large apes that integrate climbing and suspension in their locomotor repertoire⁴⁶ and is unlikely to reflect habitual terrestrial quadrupedalism. Besides, the two TM 266 ulnae trochlear notches present a morphology close to that of humans and chimpanzees in which the middle portion is mediolaterally narrow relative to the distal half. This waisted configuration is an allometric consequence of size and unrelated to locomotor mode⁴⁶. The distomedial quadrant of TM 266-01-358 is clearly more developed than the concave distolateral one, an intermediate morphology between humans and chimpanzees, close to that of *D. guggenmosi*¹², *A. afarensis*⁴⁶, and *A. prometheus*¹⁰. A developed medial portion of the trochlear notch is an adaptation for maximum joint compression medially, a configuration which could meet

mechanical requirements in various non terrestrial locomotor behaviors^{12,46}.

The TM 266 ulnae lack prominent flexor apparatus entheses as in orangutans, *Ar. ramidus* and later hominins. In this respect, it differs from the condition seen in Miocene apes and extant quadrupedal apes/monkeys^{45,47}. A medially prominent flexor apparatus entheses is assumed, through the activity/passive tension of the flexor muscles, to limit the palmar dorsiflexion and to stabilize the forelimb during quadrupedal stance phase⁴⁸. Its absence in *S. tchadensis* ulnae contribute to preclude terrestrial quadrupedalism as the primary locomotor behavior of the Toros-Menalla hominins.

In sum, the ulnae of *S. tchadensis* exhibit a combination of traits commonly seen in apes engaged in habitual arboreal activities. Especially, the ulnar morphology reflects habitual flexed forearm-arm postures, a stabilized elbow in flexion/extension, and powerful wrist/finger flexors along maintained capacities for prono-supination. Such functional pattern is indicative of a form of arboreal locomotion compatible with prono- and orthograde clambering (Supplementary Note 5), probably involving some degree of sure grasp and erratic limb excursion^{41,42,49}, and also compatible with the ‘careful climbing’ described in previous studies for *Ar. ramidus*⁴⁵.

Overall assessment

Given the combination of hominin-like traits identified in this study (as compared with Miocene apes and extant non-human apes), the most parsimonious hypothesis remains that postcranial morphology of *Sahelanthropus* is indicative of bipedality and that any other hypothesis would have less explanatory power for the set of features expressed by the Chadian material. The multiplicity of attested/presumptive bipedalities currently proposed for several phylogenetically distinct hominoid taxa (e.g., *Orrorin*, *Ardipithecus*, *Australopithecus*, and *Danuvius*, *Oreopithecus*) strongly suggests that seeking for unique defining trait of bipedalism is hazardous (‘magic trait’ sensu⁵⁰). Rather, seeking for specific functional complexes for inferring past postural and locomotor behaviors should be favored.

The Toros-Menalla femur exhibits several hallmarks of selection for bipedalism as a regular behavior. Results from femoral cross-sectional contours, cross-sectional geometry properties, and cortical bone distribution along a particularly transversally twisted shaft, show that TM 266-01-063 presents distinctive hominin femoral characteristics (Table 1). In addition, a well-developed *calcar femorale* would facilitate the dissipation of compressive loads caused by bipedalism on terrestrial substrates^{28,31}. Although present in some Miocene hominoids, a well-defined proto-*linea aspera*, the presence of a lateral gluteal tuberosity and associated subtrochanteric platymeria without hypotrochanteric or infero-lateral fossae have been traditionally associated with enhanced hip flexion-extension^{3,15}. While they are part of a primitive functional complex^{1-4,15}, they accord with the overall functional pattern seen in habitual hominin bipeds⁵¹ (Supplementary Table S3 and references therein). Hence, based on these multiple lines of evidence, we consider that the Chadian hindlimb bone indicates habitual bipedalism (contra opinion expressed in⁵²), likely on terrestrial substrates.

The Chadian ulnar material displays a suite of morphological features that are consistent with

substantial arboreal behavior, as in *Ar. ramidus*¹⁵ and presumably *Or. tugenensis*¹ and *Ar. kadabba*. All ulnar features, including the shaft curvature, the cross-sectional bone distribution and geometry properties, the trochlear morphology and orientation, converge to rule out terrestrial quadrupedalism (Supplementary Table S3). Instead, the functional pattern, inferred from the ulnae, points to arboreal prono- and orthograde clambering, probably involving some degree of sure grasp and erratic limb excursion^{41, 42, see also 49}, without habitual suspensory activities such as forearm swing and/or suspension. Data from the femur also suggest orthograde clambering in arboreal context, as part of a ‘cautious climbing’ repertoire⁴², that involves weight-bearing functions for the hindlimbs⁴⁹, as described in previous studies for *Ar. ramidus*⁴⁵, and possibly *Or. tugenensis*⁵³. Hitherto, the femur of *Sahelanthropus* supports an early evidence of habitual bipedalism in the hominin clade^{54,55}, confirming previous cranial interpretations based on the relative orientation of the orbital plane and the foramen magnum as well as the nuchal plane orientation and morphology^{6,56-58}. In addition, our postcranial results tend to favor a terrestrial component for the habitual bipedalism in *S. tchadensis*, as shown for penecontemporaneous *Or. tugenensis* and late *Ar. kadabba* (5.2 Ma from Middle Awash, Ethiopia). Altogether, the Chadian postcranial remains suggest that adaptation for bipedalism evolved soon after the human-chimp divergence²⁶, in conjunction with the retention of osteological adaptations for arboreal positional behaviors.

The Toros-Menalla postcranial material adds to previous interpretations of the environmental context of the Miocene hominins from the eastern Africa Miocene so far known. *Or. tugenensis* is associated with open woodland areas with significant tree cover⁵⁹, *Ardipithecus kadabba* (which bipedalism is inferred from foot phalanx AME-VP-1/71 dated to 5.2 Ma³²) is associated with a mixture of woodland combined with wet grassland⁶⁰, *Ar. ramidus* (4.4 Ma from Aramis, Ethiopia) most probably inhabited a ground-water-fed grassy woodland, probably a palm grove^{61,62}.

Taken as a whole, the earliest eastern African hominins share an arboreal component in their environment. Regarding the fossiliferous area of Toros-Menalla, paleoenvironmental proxies suggest a heterogeneous landscape that includes closed forest (probably riparian forests), palm grove and mixed/grassland settings (from woodlands to savannas/aquatic grasslands)^{9,63}. Given the Toros-Menalla surroundings and the inferred locomotor repertoire of *S. tchadensis*, the Chadian hominins were able to exploit both arboreal and terrestrial substrates to forage for food and access water resources. The association between a diverse locomotor repertoire (in trees and on the ground) and wooded habits in mesic context for at least ~2.5 million years suggests that the ecological niche of these early hominins was not necessarily tied to the expansion of relatively dry, open areas. This niche could be depicted as opportunistic in its reliance on terrestrial and arboreal resources.

Based on molecular data, the chimpanzee-human last common ancestor (CHCLA) is estimated to occur in Africa between 10 and 6 Ma^{58,64-66}. Fossil representatives of the panin clade are very scarce⁶⁷⁻⁶⁸ but, at least three hominine taxa have been described in this time interval Ma in Africa: *Samburupithecus*, from Samburu Hills, around 9.5 Ma⁶⁹, *Nakalipithecus* from Nakali, circa 9.8 Ma⁷⁰ and *Chororapithecus* from Chorora, circa 8 Ma^{71,72}. These Miocene taxa are parsimoniously assigned to stem hominines⁷³, even if *Samburupithecus* displays a particularly archaic

morphology⁷³. *Chororapithecus* displays derived dental affinities with *Gorilla*⁷¹. In light of this record and the lack of phylogenetic resolution, the ancestral condition of positional behaviour in African apes and humans will remain elusive until new significant data become available. To date, the identification of the derived traits shared by hominins relies on the analysis of the earliest taxa of the clade. The early hominins *Sahelanthropus*, *Orrorin* and *Ardipithecus* share the same combination of non-honing C-P₃ complex and of features linked to bipedalism. This combination is parsimoniously interpreted as more similar to the condition observed in later hominins than in any other African fossil or extant hominoids⁷⁴. These are currently the only data available for formulating scenarios about the latest Miocene/earliest Pliocene evolution of African hominoids. In the absence of Mio-Pliocene fossils displaying exclusive morphological affinities with *Pan*, cautionary tales about rampant homoplasy and character polarity in this evolutionary sequence⁷⁵ are untestable. Instead, our data support the hypothesis that the combination of a non-honing C-P₃ complex and habitual bipedalism is a synapomorphic signature of the hominin clade.

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Methods

The Chadian postcranial material is curated and conserved by the CNRD (Centre National de Recherche pour le Développement; N'Djamena) in Chad. Access to the Chadian paleontological material collected by the MPFT is regulated by formal agreement between the Université de N'Djamena, the CNRD and the Université de Poitiers and is available for study upon approval from Chadian authorities. Access to the material for loan and/or study of the material, including original 3D microtomographic data, is available upon request to the CNRD, service de paléontologie, at nekoulnc@yahoo.fr.

The original fossil specimens are measured to the nearest 0.1 mm using a Mitutoyo sliding digital caliper.

Comparative samples

The Chadian ulnae and femur were compared to extant and extinct hominoid specimens, including extant apes (humans, common and bonobo chimpanzees, gorillas and orangutans), Miocene apes and fossil hominins representing *Orrorin tugenensis*, australopiths and early *Homo*. Priority has been given to wild caught and non-pathological animals when gathering extant specimens. Comparative sample for fossil hominins and Miocene apes was gathered using published data, high-resolution images, and high-resolution casts when available. We also acquired original data directly from CT-scans, μ CT-scans images and tridimensional meshes as far as possible. In this regard, only CT-data for *Orrorin tugenensis* (BAR 1002'00, BAR 1003'00 and BAR 1215'00) and *Australopithecus prometheus* (StW 573) were kindly shared by the teams in charge of their study. The specimens used in the comparative analysis are listed in Supplementary Table S4.

Computed tomography

High-resolution micro-computed tomography (HR-mCT) images taken from the original femur and ulnae were used to assess the inner morphology of the bones. The material was scanned with EasyTom XL Duo mCT (using a sealed Hamamatsu microfocus x-ray source - 75 W, 150 kV - and an amorphous silicon based detector Varian PaxScan 2520DX, 1536*1920 pixel matrix; 127 mm pixel pitch, 16 bits, CsI conversion screen - from RX-Solutions, France) at Plateforme PLATINA (Arnaud Mazurier, IC2MP - University of Poitiers). For scanning procedures, beam intensity was set at 90 kV and tube current at 333 mA. The TM 266-01-358 ulna was acquired with 3584 projections resulting in 3036 slices of 730*825 pixels using a cone-beam reconstruction algorithm. The isovoxel size was set to 0.0525 mm. The TM 266-01-050 ulna was acquired with 4800 projections resulting in 4051 slices of 589*849 pixels. The isovoxel size was set to 0.0600 mm. The TM 266-01-063 femur was acquired with 5984 projections resulting in 4962 slices of 1162*911 pixels. The isovoxel size was set to 0.0499 mm.

Virtual models processing

Semi-automatic segmentation of the virtual fossil specimens and three-dimensional surfaces

extraction were performed in Avizo Lite 2021 (Thermofisher). Cortical bone thickness distribution for the TM 266 femur was assessed in three dimensions using the *Surface thickness* module in Avizo Lite from the outer surface of the femur to the outer surface of the segmented medullar cavity. All measurements based on 3D virtual models of the fossil specimen were done in Avizo Lite on 3D volumes and Fiji image software⁷⁶ on 2D slices. For comparative purposes, individual cortical bone thickness were divided by their maximal thickness.

Cross-sectional geometric properties (CSGP)

The femur lacks the most part of the epiphyses, which complicates the assessment of its biomechanical length. However, CSGP values in *Homo* and *Pan* do not show significant differences between 45-55 % of the femoral (biomechanical or maximum) length, meaning that various midshaft estimates in this range provide comparable CSGP^{77,78}. In this regard, the nutrient foramen located at the level of the maximum femoral anteroposterior curvature was set to represent the 50% biomechanical level of TM 266-01-063 femur. In addition, the 80% cross-sectional level was set at 10 mm below the distal border of the lesser trochanter as recommended in^{79,80}. Midshaft and subtrochanteric cross-sectional levels were used to infer the total biomechanical length (*circa* 284 mm) of TM 266-01-063 and the positions of the cross-sections set at 65% and 35% respectively. CSGP estimates were computed at midshaft and then, in order to get an assessment of the variation pattern of cortical bone distribution, at 80%, 65% and 35% of the biomechanical length. Surface alteration and fracture prevents from assessing the location of standard cross-sectional levels on TM 266-01-358. Then, CSGP variables were computed solely based on TM 266-01-050. Cross-section at 50% of the biomechanical length was located at the level of the nutrient foramen, whereas the one set at 80% was estimated using similar sized chimpanzee ulna (*P. paniscus*) as analog.

Percentage of cortical area and second moment of area were computed using Fiji image software⁷⁶ and EPMacroJ plugins⁸¹. Comparative data for CSGP in extant and extinct hominoids are provided in Supplementary Table S2 and citations herein for the femur, and come from^{40,82} for the ulna.

The total length of the femur (Supplementary Table S1) was estimated using percentage difference between femoral biomechanical and total length in extant hominoids (*Homo*, *Pan*, *Gorilla* and *Pongo*; n=64). Mean, minimum and maximum reported values are given using the pooled ape sample without *a priori* hypothesis for morphological affinities between TM 266-01-063 and any extant hominoid model.

Geometric morphometrics

Femoral anteroposterior curvature (femur anterior bowing) and shape of the femoral external contours at 80% and 50% were analyzed using 2D geometric morphometrics. Curvature was assessed from the anterior border of the femora, since the development of the pilaster in *Homo sapiens* may affect its estimation. Two landmarks were digitized at the intersection between the anterior border of each aligned femur and the 80% and 35% cross-sectional levels. Between these

two levels, 23 equally spaced semi-landmarks were digitized along the anterior contour. Landmark and semi-landmark coordinates were acquired using TPSDig2 v2.31⁸³. Landmark digitization were performed from the medial view of the oriented 3D virtual model of the femora for all extant and extinct specimens except for one occurrence of *Orrorin tugenensis* (BAR 1002'00) and *Australopithecus prometheus* (StW 573m).

Concerning BAR 1002'00 specimen, the discrepancies between originally described anterior curvature and figured specimens^{1,2,84} and the curvature observed from cast and original CT-scans data (data used in^{20,52}) led us to consider the two alternative reconstructions of BAR 1002'00 femur in our analysis. The medial view of the reconstructed StW 573m femur was obtained from¹⁰.

Shapes of the femoral external contours at 80% and 50% were assessed using 2 landmarks and 46 semi-landmarks. Landmark digitization was performed from the cross-section images issued from 3D virtual model of the femora for most extant and extinct specimens. Specimens, for which 3D data are not available or were not provided, were included based on their published cross-sectional images (Supplementary Table S3). Cross-sectional images were oriented so that the femoral anterior portion faces upward and the femoral medial portion toward the right. Two landmarks were digitized at the anterior and posterior ends of the anteroposterior midline of the cross-sections. Between these two landmarks, 46 equally spaced semi-landmarks were digitized on the femoral outer outline, 23 for each medial and lateral side of the femoral contour. In order to assess replicability, three blinded landmarking sessions were performed independently for TM 266-01-063 at 50% level by GD (n=1) and FG (n=2). Landmark and semi-landmark coordinates were acquired using TPSDig2 v2.31⁸³. In the same manner, two landmarking sessions were performed independently for *Orrorin tugenensis* (BAR 1002'00) at 50% level by GD and FG resulting in two close occurrences in the PC1-2 shape space.

Landmark and semi-landmark coordinates for femoral curvatures and femoral cross-sectional shapes were analyzed using generalized Procrustes superimposition. The analyses were performed using the package Geomorph v4.0.0^{85,86} for R v. 4.0.3⁸⁷. A principal component analyses were performed on Procrustes residuals using Statistica software (Statsoft) with Chadian specimens as a supplementary individuals. Principal component analysis was preferred over between-group principal component analysis⁵², as the later may induce misinterpretations and introduce biases in the case of small sample size^{88,89}.

Femur diaphyseal torsion (antetorsion)

The diaphyseal antetorsion of the TM 266-01-063 femur was assessed between a proximal cross-section taken at the base of the lesser trochanter, and a distal cross-section at 25% of the total biomechanical length. Each cross-section is oriented so that the femoral anterior portion faces upward and the femoral medial portion toward the right, the mediolateral axis being horizontal. The longest axis of each femoral cross-section was assessed by the mean of Feret's diameter, as the longest distance between any two points along the cross-sectional contour, using Fiji image software⁷⁶.

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Author contributions

F.G. and G.D. designed the study, collected and interpreted the data, ran the analyses and interpreted the results. G.D., F.G. and J.-R.B. wrote the manuscript. G.D., F.G., J.-R.B., L.P.,

695 M.H.T., A.L., M.A., P.V. and C.N. discussed the results and revised earlier drafts of the papers.

696
697 **Data and code availability**

698 The Chadian postcranial material is curated and conserved by the CNRD (Centre National de
699 Recherche pour le Développement; N'Djamena) in Chad. Access to the Chadian paleontological
700 material collected by the MPFT is regulated by formal agreement between the Université de
701 N'Djamena, the CNRD and the Université de Poitiers and is available for study upon approval
702 from Chadian authorities. Access to the material for loan and/or study of the material, including
703 original 3D microtomographic data, is available upon request to the CNRD, service de
704 paléontologie, at nekoulnc@yahoo.fr. Data supporting the findings of this study are available
705 within the paper and its supplementary information files.

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710
711 **Correspondence and requests for materials** should be addressed to F.G. and C. N.

Figure legends

Fig. 1 | The femur of *S. tchadensis*. Virtual representation of TM 266-01-063: a, anterior view; b, posterior view; c, medial view; d, lateral view; e, close-up of the proximal portion in lateral view showing the gluteal tuberosity; f, enlarged view of the proximal portion in anterior view; g, transverse microCT-slice at the subtrochanteric level; h, i, oblique microCT-slices of the distal part of the femoral neck. The microCT-slice levels and orientations for g, h, i are shown in e, f. Scale bar for a, b, c, d 50 mm; e, f, 9 mm; g, h, i, 4 mm.

Fig. 2 | Comparative analysis of the subtrochanteric and midshaft cross-sectional contours of the TM 266 femur. a. Principal component analysis of Procrustes coordinates for the subtrochanteric cross-sectional contour (80% of the biomechanical length) in fossil and extant hominoids. Bivariate plot of PC1 and PC2 summarizes 55.3% of the total variation; b. Principal component analysis of Procrustes coordinates for the midshaft cross-sectional contour (50% of the biomechanical length) in fossil and extant hominoids. Bivariate plot of PC1 and PC2 summarizes 69.9% of the total variation. Modern humans, n=12; bonobos, n=12; common chimpanzees, n=18; gorillas, n=9; orangs, n=7; fossil hominins, n=10 (80%), n=13 (50%); Miocene apes, n=3. Cross-sectional contour variation, summarized by the PC₁₋₂ shape space, is illustrated by an outline representation at the extremity of each axis; the red dot is for the anterior portion of the contour, lateral is to the left. Cross-sectional contours of selected fossil specimens are indicated by a black arrow, whereas cross-sectional contour of TM 266-01.063 is represented in the lower left grey box. In the legend, underlined specimen names correspond to individual for which only data for midshaft were collected. Specimens marked by an asterisk correspond to individual for which only data for subtrochanteric contour were collected. See Supplementary Note 3 for comments on the figure.

Fig. 3 | Comparison of cortical thickness distribution between *S. tchadensis* and extant great apes. Panels a, b, c, and d, correspond respectively to anterior, medial, posterior and lateral views. In each panel, from left to right, the femora are TM 266-01-063 (mirrored), modern human, chimpanzee, gorilla and orangutan. The cortical thickness is illustrated for the 80%-35% interval of the femoral biomechanical length using a relative scale (see Methods), this chromatic scale corresponds to the look-up table of cortical thickness, from relatively thin (blue) to relatively thick (red) cortical diaphyseal bone. The extant femora are roughly at the same size, the TM 266-01-063 femur was scaled by aligning its 80-35% biomechanical interval and the corresponding portion in extant hominoids (pooled). See Supplementary Note 3 for comments on the figure.

Fig 4. | Ulnar remains of *S. tchadensis*. TM 266-01-358: a, anterior view; b, posterior view; c, medial view; d, lateral view. TM 266-01-050: e, anterior view; f, posterior view; g, lateral view; h, medial view. Transverse microCT-slices images levels (proximal to distal) are numbered from 1 to 3 (TM 266-01-358) and i to iv (TM 266-01-050) respectively, and are illustrated in the lower

754 left panel. The asterisks mark the location of the nutrient foramina. Ant. for anterior, lat. for lateral
755 and med. for medial. Scale bar a, b, c, d, 20 mm; e, f, g, h, 15 mm; 1, 2, 3, i, ii, iii, iv, 5 mm.
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Table legend

Table 1. List of hominin-like femoral and ulnar traits as reported in the present study, and their conditions in extant and extinct hominoids. Legend is as follow: -, absent; +, intermediate; ++ accentuated; /, variable. The green area emphasizes shared morphology between *Sahelanthropus* and other hominins whereas the light green area underlines uncertainty. Note that *Sahelanthropus* shows a combination of features that more parsimoniously fits with a bipedal hominin condition.

Extended Data

Extended Data 1. Photographs of the postcranial original material from Toros-Menalla, Chad. TM 266-01-063 femur: a, anterior view; b, posterior view; c, lateral view; d, medial view. TM 266-01-358 ulna: e, anterior view; f, posterior view; g, lateral view; h, medial view. TM 266-01-050 ulna: i, anterior view; j, posterior view; k, lateral view; l, medial view. Scale bar 10 mm.

Extended Data 2. Femoral anterior curvature.

Panel a. comparative femoral anteroposterior curvature. The TM 266-01-063 femur (*S. tchadensis*) is compared (from left to right) to BAR 1002'00 (*Or. tugenensis*, as published in^{2,84}), BAR 1002'00 (*Or. tugenensis*, acquired from CT-scan data, as published in⁵²), BAR 1003'00 (*Or. tugenensis*, acquired from CT-scan data, courtesy of B. Senut, M. Pickford and D. Gommery), StW 573 (*A. prometheus*, as published in¹⁰) and A.L. 288-1p (*A. afarensis*, cast). Femora are in medial view. The colored portions for TM 266-01-063, BAR 1002'00, BAR 1003'00 and StW 573 illustrate the interval used for the 2D geometric morphometrics analysis of the femoral antero-posterior curvature (between 80% and 35% of the biomechanical femoral length, this study). Two version of *Or. tugenensis* anterior femoral curvature were included in the analysis, BAR 1002'00* (*Or. tugenensis*, as published in^{2,84}), and BAR 1002'00** (*Or. tugenensis*, acquired from CT-scan data, as appears in⁵²). Femora are about the same scale. Ant. for anterior, dist. for distal.

Panel b. Comparative analysis of the anterior femoral curvature of the TM 266 specimen. Principal component analysis of Procrustes coordinates for the anterior femoral curvature, in medial view, as estimated between 80% and 35% of the femoral biomechanical length in fossil and extant hominoids. Bivariate plot of PC1 and PC2 summarizes 89.3% of the total variation. Anterior femoral curvature variation, summarized by the PC1-2 shape space, is illustrated by an outline representation at the extremity of each axis; the red dot is for the proximal end of the anterior contour. Black solid arrows mark the main anterior convexities, whereas white open arrows are for the main anterior concavities. Two version of *Or. tugenensis* anterior femoral curvature were included in the analysis, BAR 1002'00* (*Or. tugenensis*, as published in^{2,84}), and BAR 1002'00** (*Or. tugenensis*, acquired from CT-scan data, as appears in⁵²).

Distribution of the specimens along PC1 describes the degree of curvature between two morphological femoral shapes; rectilinear (negative values) and anteriorly curved (positive values). Along PC2, distribution of the specimens illustrates additional aspects of the femoral curvature including a transition between proximally (negative values) to distally (positive values) located anterior curvature. Along PC1, extant apes describes a morphological gradient from straight femora in orangs to curved femora in gorilla, chimpanzee and humans being intermediates. Along PC2, humans, gorillas and orangutans present a proximally located anterior curvature while chimpanzees display a relatively more distal anterior curvature. In this pattern, the fossil hominins, apart from BAR 1002'00** and early *Homo*, occupy a central position in the morphospace in having moderately curved femora and a centrally located anterior curvature. TM 266-01-063

presents higher degree of curvature compared to other fossil hominins, within the range of chimpanzees and gorillas along PC1 but close to BAR 1002'00*. Alternative version of BAR 1002'00** falls out of the range of variation for the extant apes in having a relatively straight femoral shaft, clearly differing in this respect from BAR 1002'00*. BAR 1002'00** is in line with early *Homo* along PC1 and is overall closer to KNM-ER 1481 than any other apes.

Extended Data 3. Comparison of TM 266-01-063 with extant African apes and *Or. tugenensis*, illustrating femoral size variation. From left to right: femoral specimens of *Gorilla*, *Pan*, *Homo*, TM 266-01-063, BAR 1003'00, BAR 1002'00. All femora are in posterior view. Scale bar is 50 mm.

Extended Data 4. Illustration and estimation of the TM 266-01-063 diaphyseal antetorsion. a. 3D view of the femur (virtual model) showing the position of the proximal (base of the lesser trochanter) and distal (25% of the total biomechanical length) transverse sections; b. transverse CT-slice cross-sections showing the mediolateral axis (M-L) and the orientation of the longest axis of the diaphyseal sections (proximal, upper panel and distal, lower panel) assessed by the mean of Feret's diameters (Ft_1 and Ft_2 respectively); c., 3D view of the femur (virtual model) showing the femoral antetorsion by the mean of the relative orientation of the proximal and distal Feret's diameters. The white curved arrows mark the diaphyseal torsion angle (DT) measured between Ft_1 and Ft_2 . Ft_1 : 11.7° counterclockwise, relative to mediolateral axis; Ft_2 : 153.2° counterclockwise, relative to mediolateral axis; DT is 38.5°. The right panel d presents an illustration of the variation of the parameter DT, in degrees, in chimpanzee, gorilla and modern human. Box and whiskers are for mean (centre), mean \pm standard deviation (bounds of box) and minimum/maximum (whiskers). In chimpanzee means for *P. paniscus* (Pp, n=6) and *Pan troglodytes* (Pt, n=12) are given. The red dotted line corresponds at the value measured for TM 266-01-063.

Extended Data 5. Bivariate plot of PC1 (33.8%) versus centroid size (Cs). The Cs mean (symbols are for group mean) and its range (whiskers) for the extant and extinct hominoid sample are provided in the left grey panel. Modern humans, n=12; bonobos, n=12; common chimpanzees, n=18; gorillas, n=9; orangutans, n=7; fossil hominins, n=10 (80%), n=13 (50%); Miocene apes, n=3.

Extended Data 6. Cortical bone variation of TM 266-01-063.

Panels a, b, c. Cross-sectional geometric properties of the TM 266-01-063 femur. a, Location of transverse microCT-slices at the distal margin of the lesser trochanter (1) and at standard levels of biomechanical length (2-5). Corresponding percent of cortical area (i.e., $CA/TA \times 100$) is given at 80%, 65%, 50% and 35%; b, microCT-slice images of the selected transverse sections; c, interpretive drawings of the cortical thickness for selected microCT-slice sections, numbers are for the measured cortical thickness anteriorly, posteriorly, medially and laterally (in mm), maximum thickness is in red while minimum thickness is in green. TA, total area in mm^2 ; CA, cortical area

in mm²; %, percent of cortical area. Med. is for medial and Lat. is for lateral. Scale bar is (a) 10 mm; (b) 6 mm.

Panel d. Three-dimensional cortical thickness of TM 266-01-063. From left to right, anterior, posterior, medial and lateral view. Scale bar is 25 mm. Chromatic scale corresponds to the look-up table of cortical thickness, from relatively thin (blue) to relatively thick (red) cortical diaphyseal bone.

Posterior thickening of the cortical bone occurs at about the level of the nutrient foramen, where the ‘proto-linea aspera’ is the narrowest. The femoral cortical thickness distribution is also characterized by an anterior thinning, with a proximo-distal gradient. The lateral reinforcement pattern appears to parallel an insertion area including the *mm. vastus lateralis* and *gluteus maximus* proximally, and the attachment zone of the *m. vastus intermedius* distally. In medial view, the relative cortical thickening is restricted to the proximal portion of the femoral shaft, corresponding to the attachment of the *m. vastus medialis*. The third reinforcement occurs posteriorly at about 35-55% of the biomechanical length and corresponds to an insertion area delineated by the two *mm. vasti* and comprising the hip adductor and extensor (*m. biceps femoris*) muscles.

Extended Data 7. Comparative CSGP data for the Chadian femur and ulna.

a., b., c., Cross-sectional geometric properties at 80% of the femoral biomechanical length including percentage of cortical area (a, %CA.), second moments of area (b., I_x/I_y , and c., I_{max}/I_{min}). d., e., f., Cross-sectional geometric properties at 50% of the femoral biomechanical length including percent of cortical area (d, %CA.), second moments of area (e., I_x/I_y , and f., I_{max}/I_{min}). g., h., Second moments of area (g., I_{max}/I_{min} and h., I_x/I_y) at 50% of the ulna biomechanical length (TM 266-01-050). Extant apes are represented by mean (circle) and standard deviation (whiskers), whereas isolated circles represent individual values for fossil specimens. See Supplementary Table S2 specimen list. Ulnar data are from^{40,82}. The yellowish frame encompasses the early hominin range of variation whereas the red dotted lines mark the mean values for *Pan* and extant *Homo* within each panel. For the femur: modern humans, n=40; chimpanzees, n=20; gorillas, n=23; orangutans, n=23; Miocene hominoids, n=3; Miocene hominins, n=3; australopiths, n=5; early *Homo*, n=6; neandertals, n=9. For the ulna: modern humans, n= 19; chimpanzees, n=17; gorillas, n=14; orangutans, n=14; gibbons, n=16, Australopiths, n=3.

Extended Data 8. Illustration of the *calcar femorale* of TM 266-01-063. a, virtual representation of the proximal portion of the femur in posterior view, the asterisk marks the position of the parasagittal microCT-slice passing through the lesser trochanter; b, microCT-slice image of the parasagittal section showing the proximo-distal extension of the *calcar femorale* (cf) and b’, corresponding binarized image enhancing the *calcar femorale*; c, microCT-slice image of the parasagittal section in BAR 1003’00 femur (*Or. tugenensis*) showing the proximo-distal extension of the *calcar femoral*, and c’, corresponding binarized image; d, virtual representation of the proximal portion of the femur in posterior view showing transversal levels (i-vi) used for imaging

the development of the *calcar femorale* (following²⁸); e, microCT- slice images of the sections (i-vi as in TM 266-01-063) showing expression of the *calcar femorale* transversally (medial to the right and anterior to the top), and f, corresponding binarized version; g, microCT- slice images of the sections (i-vi) showing expression of the *calcar femorale* transversally in BAR 1003'00 (acquired from CT-scan data, this study). Scale bar for a, d, 10 mm; b, 6 mm; e, f, 4 mm.

Extended Data 9. Calcar femorale morphology in extant hominines.

The selected individuals corresponds to morphological extrema, i.e., the minimal and maximal degrees of expression of the *calcar femorale*, in our comparative sample (wild caught specimens). The boxes are for a, modern humans; b, chimpanzees (*Pan paniscus*); c, chimpanzees (*Pan troglodytes*); d, gorillas. For each box, parasagittal views are on the left (taken at the maximal possible degree of expression of the *calcar femorale*, around mid-width of the lesser trochanter, see lower right panel); transversal views are on the right (taken at the maximal possible degree of expression of the *calcar femorale*, ca at the proximal border of the lesser trochanter, see lower right panel). The asterisk marks an evidence of a *calcar femorale*.

The *calcar femorale* is present in all modern humans of our sample; in parasagittal view, its expression displays a columnar aspect with an oblique orientation. The trabecular bundle forming the CF shows various degree of densification and thickness, from loose (e.g., third specimen from the top) to tightened (e.g., first and fourth specimens from the top). In transversal view, the CF forms a rather short spur originating from the thickened medial cortical bone.

By contrast, most of our sampled non-human apes do not show any evidence of a columnar and oblique trabecular bundle. At best, a thin, curved, cancellous bone densification is identifiable in parasagittal view. In transversal view, the CF, when present, corresponds to a thin ray composed of few or single trabeculae, contrasting in this aspect with the modern human condition. Besides, the degree of development of the CF is associated with a relative thickening of the antero-medial cortical bone, but with a less extent in non-human apes than in modern humans. In modern humans, the thickening tends to be more medial than antero-medial. This configuration potentially enlightens the results from²⁸ showing a lengthened CF in modern humans compared to non-human apes, as the absolute CF length was measured from the tip of the CF to the exterior cortical boundary.

Extended Data 10. Ulnar comparison of *S. tchadensis* and extinct and extant hominines.

a., lateral view; b., anterior view; c., medial view; d. posterior view. All ulnae are from 3D virtual models, except for A.L. 438-1 (modified from³⁴), ALA-VP-2/101 (modified from³²) and StW 573 (modified from¹⁰). Scale bar is 40 mm. F and M are for female and male.