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2 **Article**

3 **Postcranial evidence of late Miocene hominin bipedalism in Chad.**

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43 **Terrestrial bipedal locomotion is one of the key adaptations defining the hominin**
44 **clade. Evidences of undisputed bipedalism are known from postcranial remains of**
45 **late Miocene hominins as soon as 6 Ma in eastern Africa. Bipedality of**
46 ***Sahelanthropus tchadensis* was hitherto documented at 7 Ma in central Africa**
47 **(Chad) by cranial evidence. Here, we present the first postcranial evidence of the**
48 **locomotor behavior of the Chadian hominin with new insights on bipedalism at the**
49 **early stage of our evolutionary history. The original material was discovered at**
50 **locality TM 266 (Toros-Menalla fossiliferous area), and consists in one left femur**
51 **and two antimeric ulnae. These new findings confirm that hominins were already**
52 **terrestrial biped relatively soon after the human-chimpanzee divergence but also**
53 **suggest that careful climbing arboreal behaviors was still a significant part of their**
54 **locomotor repertoire.**

55
56 Discoveries in Chad by the Mission Paleoanthropological Franco-Tchadienne (MPFT)
57 have substantially contributed to our understanding of early human evolution in Africa.
58 The locality TM 266 (Extended data 1) in the Toros-Menalla fossiliferous area in the
59 Mega-Chad basin yielded, among hundreds of vertebrate remains, a nearly complete
60 cranium (TM 266-01-60-1), three mandibles, and several isolated teeth depicting a
61 minimum of three adult individuals assigned to *Sahelanthropus tchadensis*^{1,2}. TM 266
62 fossils were found in the Anthracotheriid Unit with biochronological estimates and
63 radiochronological age at ca. 7 Ma^{3,4}. Environmental indicators at Toros-Menalla
64 localities, at the time, suggested a lacustrine fringe, in a desert vicinity, where open
65 areas with dry and humid grasslands coexisted with arboreal cover^{5,6}.

66 Three other hominin fossil remains were discovered at TM 266 in 2001 by the
67 MPFT: one left femoral shaft (TM 266-01-063, unearthed in July 2001), and two right
68 and left ulnae (respectively TM 266-01-358, unearthed in November 2001 and TM 266-
69 01-050, unearthed in July 2001; Supplementary notes). Despite none of these limb
70 bones can be reliably ascribed to any hominin craniodental specimen found at TM 266,
71 the most parsimonious hypothesis is that these postcranial remains belong to the sole
72 hominin species present in this locality. Hence, we favor a conservative attribution of
73 these specimens to *Sahelanthropus tchadensis*.

74 The hindlimb is documented by a left femoral shaft (TM 266-01-063) of about 242 mm
75 long (Fig. 1 and Supporting table 1, Extended data 2), lacking the distal epiphysis and
76 most of the proximal one. The specimen is curved anteroposteriorly as in
77 *Australopithecus*⁷⁻⁹ and *Orrorin tugenensis* (BAR 1002'00 and BAR 1003'00) but more
78 heavily built. The two major mediolateral axes of the proximal and distal diaphyseal
79 portions clearly indicate that the neck must have been anteverted as in fossil hominins<sup>9-
80 11</sup> (Extended data 3). The presence of a groove on the postero-superior surface of the

81 neck for the *obturator internus* and *m. gemelli* supports this interpretation. Resulting in
82 head/neck torsion relative to the long axis of the shaft¹². This condition is also reported in
83 archaic fossil apes such as *Nacholapithecus* and *Ekembo* but is absent in the arboreal
84 biped *Danuvius*¹³. The femur exhibits proximal platymeria just distal to the lesser
85 trochanter (Supplementary notes), a trait encountered in *O. tugenensis* and later
86 hominins and suggested to correlate with neck elongation, a reliable indicator of hominin
87 bipedalism^{9,14-16} (but see ^{8,17}). Concurrently, the neck is compressed antero-posteriorly
88 as in the Miocene ape *Danuvius guggenmosi*¹³ and hominins^{8-9,18} (but see ¹⁹ for
89 *Dryopithecus fontani* and *Hispanopithecus laietanus*; Fig. 1). This array of features
90 agrees with habitual bipedalism in *S. tchadensis*.

91 A small but sharp relief, indicative of the third trochanter, continues into a rugose
92 surface distally and blends with the lateral component of a broad 'proto-*linea aspera*'¹⁷
93 (12.2mm in its narrowest width). The lateral lip of the *linea* forms a well-marked sigmoid
94 line. Similarly, the medial lip of the *linea aspera* is well-marked. The spiral line for the
95 insertion of the *vastus medialis* consists in a straight line, which confounds distally with
96 the medial lip of the *linea aspera*. Such configuration is also observed in *O. tugenensis*
97 and *Ardipithecus ramidus*^{8,16,18} albeit with a more salient 'proto-*linea aspera*' in TM 266-
98 01-063, but differs from modern humans where a pilaster develops. Such an overall
99 pattern is consistent with bipedalism albeit suggesting a less-developed quadriceps
100 system relative to the hamstring compared to modern human-like pattern¹⁷.

101 The femoral shaft exhibits thick cortical bone in cross-section (Fig. 2). Cortical
102 thickness distribution pattern describes a posterior and lateral thickening of the diaphysis
103 relative to an anterior and medial thinning (Fig. 3). Posterior thickening of the cortical
104 bone occurs at the level of the nutrient foramen, where the 'proto-*linea aspera*' is the
105 narrowest. Conversely, extant apes share a posterior thickening on proximal half of the
106 shaft and a relative thinning on distal half²⁰ (see also Supporting Information in ²¹).
107 Lateral thickening can be traced on the major part of the shaft in TM 266-01-063 except
108 in its most distal portion. African apes do not display extended lateral thickening but
109 instead, a circumscribed thickening corresponding to the lateral spiral pilaster. In these
110 aspects, TM 266-01-063 most resembles extant humans. Comparative data are, to our
111 knowledge, inexistent for *Ardipithecus*. Besides, cortical thickness data reported for BAR
112 1002'00 (*O. tugenensis*) rely on CT-scan data whose reliability is questionable²²⁻²⁴.

113 Cortical area and second moment of area (I_x/I_y and I_{max}/I_{min}) are biomechanical
114 parameters frequently used to infer habitual locomotor functions in primates, as they
115 reflect loads undergone by long bones during growth (but see ²⁵). The cortical area of
116 the diaphyseal cross-section is a measure of resistance of the bone to axial compression
117 or tension, while second moment of area measures the resistance to bending loads. In
118 TM 266-01-063, percent of cortical area is 66.5 % at the level of the nutrient foramen
119 (see Methods) and slightly increase proximally. It is within the range of extant and fossil
120 apes (75 % \pm 3.6 in extant humans; 63.3 % \pm 7.6 in chimpanzees; 70 % \pm 3.9 in gorillas;

121 Supporting Information in ²¹) and above the value reported for AL 288-1 femur (59.9 %)
122 at midshaft²⁶. Response to bending loads endured by the femur from TM 266 is
123 assessed at the level of the nutrient foramen using second moment of area^{26,27}. Results
124 for I_{max}/I_{min} and I_x/I_y are respectively 1.31 and 0.81 (Extended data 4). The Chadian femur
125 approaches the chimpanzee/extant human condition in its I_{max}/I_{min} ratio (measured at
126 midshaft^{28,29}; humans, $I_{max}/I_{min}=1.6 \pm 0.36$; chimpanzees, $I_{max}/I_{min}=1.4 \pm 0.2$) whereas
127 it departs from gorillas²⁸ ($I_{max}/I_{min}=1.9 \pm 0.3$). The I_x/I_y of TM 266-01-063 is close to values
128 reported for chimpanzees (chimpanzee³⁰: $I_x/I_y=0.75 \pm 0.08$), early *Homo*³¹⁻³³ and early to
129 Middle Pleistocene hominins³⁴. It departs from extant humans in which a posterior
130 pilaster develops²⁹ ($I_x/I_y = 1.52 \pm 0.39$). Whereas midshaft cross-section of TM 266-01-
131 063 resembles in its overall aspect to AL 288-1, the Chadian specimen present higher
132 I_{max}/I_{min} and lower I_x/I_y values than its younger eastern-African relative (*A. afarensis*: AL
133 288-1²⁶, $I_x/I_y=0.98$ and $I_{max}/I_{min}=1.07$; see also ³⁵ for AL 333-61, $I_x/I_y=1.16$ and
134 $I_{max}/I_{min}=1.16$).

135 Many aspects such as stature, body mass, muscle attachment sites, positional
136 behavior, ontogeny and sexual dimorphism²⁵ may contribute to femoral bone mass
137 distribution. Yet, geometry of the TM 266-01-063 indicates greatest bending resistance
138 for medio-laterally oriented stresses. This condition seen in AL 288-1 and early African
139 and Asian *Homo* is suggested to relate to a more lateral position of the body during the
140 stance phase of gait in association with an increase in femoral neck length and
141 biacetabular breadth²⁶. Functional interpretations remain difficult to formulate given the
142 paucity of early hominin comparative data and given the state of preservation of the
143 Chadian femur. Nevertheless, the Chadian femoral shaft exhibits a well-developed
144 *calcar femorale* (CF) in its proximal portion (Fig. 4; the CF is 18.80 mm long measured at
145 the level of the lesser trochanter following³⁶), a condition to date only seen in extant
146 humans and reported in *O. tugenensis* (BAR 1003'00). The *calcar femorale* corresponds
147 to a bony wall that originates from the postero-medial endosteal surface at the level of
148 the lesser trochanter and extends laterally toward the greater trochanter. In obligate
149 bipeds, it facilitates compressive loads dispelling in the proximal femur by decreasing the
150 stress in the posterior and medial aspects and increasing the stress in the anterior and
151 lateral aspects^{36,37}. A well-developed *calcar femorale* in TM 266-01-063 represents a
152 morphological requirement for terrestrial bipedalism.

153 The forearm bones attributed to *Sahelanthropus tchadensis* consist in two partial left
154 and right ulnae lacking the distal epiphyses. Similarity in size and shape for the antimeric
155 ulnae could suggest they are from the same individual, even if no definitive evidence
156 supports this assumption. TM 266-01-050 is a left ulnar diaphysis of 239 mm long (Fig.
157 5, Supporting table 1, Extended data 2) showing eroded proximal epiphysis. The right
158 ulna (TM 266-01-358) corresponds to a proximal-half shaft of 155 mm long with partially
159 preserved epiphysis. The shafts are curved in profile. Similar anteroposterior curvature

160 is observed in *Ar. kadabba*³⁸ (ALA-VP 2/101) and later hominins StW 573k and OH 36,
161 as in extant apes^{9,39,40}. This feature contrasts with the straight right ulnar shafts of *D.*
162 *guggenmosi* and *A. prometheus*, but this lack of curvature is likely due to a pathological
163 condition^{9,13}. In primates, such ulnar curvature is due to habitual loads exerted by the
164 action of *m. brachialis* in order to maintain elbow flexion in arboreal context, which in
165 turn involves the antagonistic action of a powerful forearm musculature, including wrist
166 and fingers extensors and flexors^{40,41}.

167 The preserved flat distal portion of the olecranon indicates that they were not
168 projecting posteriorly as in extant African apes⁴². In this regard, the distal portion of the
169 olecranon most resembles the condition seen in Miocene apes⁴²⁻⁴⁴ and in hominins⁴².
170 The proximal epiphyses indicates an anteriorly-facing trochlear notch as in fossil
171 hominins and Miocene apes^{9,13,42-45}. Hence, the Toros-Menalla ulnae depart from the
172 typical proximally oriented trochlear notch in extant great apes^{41,46}. In functional terms, a
173 more anteriorly facing notch, associated with an olecranon aligned with the long axis of
174 the forearm, favors triceps leverage at mid-flexion^{41,46}. In *Ar. ramidus* such function is
175 linked to careful climbing and bridging⁴⁴. Conversely, a more proximally facing notch
176 reflects differential loading during suspension⁴³ while a posteriorly projecting olecranon
177 favors triceps leverage in extension and is commonly associated with terrestrial
178 quadrupedal locomotion in anthropoids⁴².

179 Ulnae from Toros-Menalla display a keeled trochlear notch with a comparatively acute
180 angle relative to later hominins and African apes. The distal keeling angle, measured
181 from TM 266-01-358 (distal keeling angle=109°), is in the lower range of *Pongo*
182 *pygmaeus* and close to the value reported for *Oreopithecus bambolii* and the left ulna AL
183 288-1t in *A. afarensis*⁴⁶. Likewise, the proximal angle is acute (proximal keeling
184 angle=100°), in the lower range of reported values for chimpanzees, and close to OH 36
185 and *Or. bambolii*⁴⁶. A pronounced trochlear keel warrants medio-lateral stability of the
186 elbow in response to powerful superficial finger and wrist flexors, and forearm pronator
187 (*mm flexor digitorum superficialis*, *flexor carpi radialis* and *ulnaris*, and *pronator*
188 *teres*)^{39,46}. Such configuration was supposedly reported on *D. guggenmosi*¹³ and is
189 typical of the arboreal large apes, which integrates climbing, and/or suspension in their
190 locomotor repertoire⁴⁶. It is unlikely to reflect habitual terrestrial quadrupedalism. The TM
191 266 ulnae lack prominent flexor apparatus entheses as in orangutans, *Ar. ramidus* and
192 later hominins. In this respect, it differs from the condition seen in Miocene apes and
193 extant quadrupedal monkeys. Such morphology precludes the possibility of
194 quadrupedalism and, more specifically, of knuckle-walking as primary locomotor
195 behaviors for the Toros-Menalla hominins⁴⁵.

196 Overall, the trochlear notch of TM 266 ulnae present an unusual morphology as the
197 middle portion is mediolaterally narrow relative to the distal half. This waisted aspect of
198 the trochlear notch approaches the condition seen in 'small' apes (humans,

199 chimpanzees and bonobos) and contrasts with that of 'large' apes (orangutans and
200 gorillas). Such configuration is interpreted as locomotor-independent and rather linked to
201 allometry⁴⁶. The disto-medial quadrant of TM 266-01-358 is clearly more developed than
202 the distolateral one, an intermediate morphology between humans and chimpanzees,
203 close to that of *D. guggenmosi*¹³, *A. afarensis*, and *A. prometheus*^{9,46}. A developed
204 medial portion of the trochlear notch is an adaptation for maximum joint compression
205 medially, a configuration which could meet mechanical requirements in various non
206 terrestrial locomotor behaviors^{13,46}.

207 Only limited portions, proximally and distally, of TM 266-01-050 allow assessing
208 cortical bone distribution (see Supplementary notes, Extended data 4). Proximally, the
209 percent of cortical area is 73.4 %, measured at about 70-75 % of the estimated total
210 lengths of the ulna (see methods). At mid-shaft, the percent of cortical area is 81.0 %,
211 falling within the variation of Late Pleistocene hominins (80.1 % \pm 6.6 in *H. sapiens* and
212 82.8 % \pm 7.1 in neandertals)⁴⁷. Besides, I_{max}/I_{min} and I_x/I_y are respectively 2.04/1.62 at 70-
213 75 % level and 1.71/1.13 at midshaft. Values for the Chadian ulna fall outside the
214 reported variation for gorillas⁴⁸ and is within the range of variation in chimpanzees for
215 proximal I_{max}/I_{min} and proximal-midshaft I_x/I_y . Besides, TM 266-01-050 is within the range
216 of variation of Asian non-human apes for all ratios except for the lower measured
217 proximal I_{max}/I_{min} in *Pongo*. The geometry of TM 266-01-050 deviates from circularity in
218 the antero-posterior direction. The cortical bone is predominantly distributed antero-
219 posteriorly as in orangutans and to a lesser extent in chimpanzees. This condition
220 contrasts with the one seen in gorillas, which tend to grow more bone medio-laterally.
221 Relative medio-lateral expansion is suggested to adjust for increased vertical and medio-
222 lateral forces that apply to the forelimb in terrestrial quadrupedal primates^{45,49,50}.
223 Besides, considering comparative data available for chimpanzees and orangutans,
224 which tend to grow more bone antero-posteriorly⁵¹, the Chadian ulna configuration more
225 likely reflects bending loads associated with a wide array of arboreal locomotor modes.
226 Yet, the TM forelimb bones lack any traits typical of suspension or knuckle walking, and
227 exhibit a configuration better seen in apes engaged in careful climbing⁴⁴. However, the
228 possibility that the Chadian hominin was capable of vertical climbing cannot be
229 dismissed given the particularly keeled trochlear notch.

230 The Toros-Menalla femur exhibits several hallmarks of habitual terrestrial bipedalism.
231 Among them, a well-defined broad proto-*linea aspera*, the presence of a lateral third
232 trochanter and associated subtrochanteric platymeria without hypotrochanteric or infero-
233 lateral fossae, is classically associated with enhanced hip flexion-extension^{16,20,52}, while
234 a particularly developed *calcar femorale* facilitates compressive loads dispelling in
235 terrestrial bipedalism³⁶. These features go with an overall cortical bone distribution
236 pattern and cross-section geometries of the femoral shaft that suggest muscular
237 recruitments and bone loads compatibles with habitual bipedalism. Despite some of the
238 above-mentioned traits are suggested to be the primitive condition in hominins (proximal

239 platymeria or gluteal tuberosity)¹⁷, they are part of a functional complex co-opted for
240 bipedalism. They are routinely considered as such to infer potential bipedal terrestrial
241 locomotion in early eastern African hominins^{7,8,16,18,52,53}. The Chadian hindlimb bone
242 conforms to the overall morphological pattern of Miocene hominin terrestrial bipeds. The
243 forelimbs morphology rules out arboreal specialization for the Chadian material, as in *Ar.*
244 *ramidus*¹⁶ and presumably *O. tugenensis*⁷. Yet, the Chadian postcranial material
245 displays a suite of morphological features that are consistent with substantial non-
246 stereotypical arboreal behaviors, as suggested by ulnar shaft curvature and cross-
247 section geometrical properties, whereas the elbow morphology is potentially indicative of
248 careful climbing⁴⁴, and does not display any evidence of knuckle-walking.

249 Recently, it was suggested that the putative stem hominid *D. guggenmosi* was able to
250 use obligate arboreal bipedalism combined to suspension as early as the late middle
251 Miocene¹³. The authors suggested that hominin terrestrial bipedalism and great ape
252 suspension evolved from such locomotor repertoire¹³. In the lack of evidence supporting
253 a phylogenetic relationship between hominins and Miocene European apes, we cannot
254 infer that hominin terrestrial bipedalism originated from middle Miocene forms in Europe
255 as suggested by¹³. Instead, the Chadian remains described herein reassert African
256 roots. They are the first direct evidence of an obligate terrestrial bipedalism,
257 indistinguishable from that inferred for *O. tugenensis* and *Ar. kadabbalramidus*. They
258 suggest a precocious adaptation to bipedalism after the human-chimp dichotomy⁵⁴. The
259 Chadian remains suggests a conservative evolution of climbing capacities, interpreted as
260 cautious climbing as in stem apes⁵⁴. Hence, cautious climbing modality weakens a
261 potential role of suspension in the emergence of the hominin clade¹³.

262 The Toros-Menalla postcranial material also reasserts the presence of cladistic
263 hominins in the upper Miocene of Chad, within particular environmental settings. Eastern
264 African Miocene hominins are associated with open woodland areas with significant tree
265 cover at ~6 Ma at Lukeino⁵⁵, and a mixture of woodland combined with wet grassland for
266 the earliest postcranial-based bipedalism occurrence in Ethiopia at 5.2 Ma (AME-VP-
267 1/71, *Ardipithecus kadabba*)^{38,56}. At 4.4 Ma, *Ar. ramidus* most probably inhabited a
268 ground-water-fed grassy woodland (probably a palm grove) at Aramis⁵⁷⁻⁵⁸.

269 Taken as a whole, eastern-African early hominins share an arboreal component in
270 their habitat (see^{57,59} for discussion on Aramis). Environmental indicators in Toros-
271 Menalla fossiliferous area suggest heterogeneous landscape types consisting of closed
272 forest formations (probably riparian forests), palm grove formations, and
273 mixed/grassland formations (from woodlands to savannas/aquatic grasslands)^{5,6,60}.
274 Therefore, the Chadian hominins were probably no exception as being reliant on
275 arboreal cover given their potential climbing abilities. As bipeds, they were not exclusive
276 arboreal forest dwellers, because they were able to raid in near open environments for
277 food/water resource harvesting. The association between a polyvalent locomotion
278 (arboreality and bipedal terrestriality), and wooded formations in mesic context during at

279 least ~2.5 million years suggests that the ecological niche of these early hominins was
280 not strongly tied to the expansion of relatively dry, open areas. This niche could be
281 depicted as opportunistic in its reliance on both terrestrial and arboreal resources.

282 Based on molecular data, the chimpanzee-human last common ancestor (CHCLA) is
283 estimated to occur in Africa between 10 and 7 Ma^{61,62}. Indeed, fossil representatives of
284 the panin clade are too scarce and consists in a minimum of three Middle Pleistocene
285 teeth from the Kapthurin formation in Kenya⁶³ and a chimpanzee-like proximal femoral
286 epiphysis of unknown age from the Kikorongo crater in Uganda⁶⁴. However, at least
287 three taxa have been described between 10 Ma and 7 Ma in African deposits:
288 *Samburupithecus*, from Samburu Hills, around 9.5 Ma⁶⁵, *Nakalipithecus* from Nakali,
289 around 9.8 Ma⁶⁶ and *Chororapithecus* from the Middle Awash, around 8 Ma^{62,67}. These
290 Miocene taxa are parsimoniously assigned to stem hominines^{68,69}, even if
291 *Samburupithecus* displays a particularly archaic morphology⁶⁹. *Chororapithecus*
292 displays derived dental affinities with *Gorilla*⁶⁷. In light of this record and of the lack of
293 phylogenetic resolution, the ancestral condition of positional behaviour in African apes
294 and humans will remain elusive until significant new data becomes available. To date,
295 the identification of the derived traits shared by hominins relies on the analysis of the
296 earliest forms of the clade. The early hominins *Sahelanthropus*, *Orrorin* and
297 *Ardipithecus* share the same combination of non-honing C-P3 complex and of features
298 linked to terrestrial bipedalism. This combination is arguably more similar to the
299 condition observed in later hominins than in any other African fossil or extant hominoids.
300 This is currently the only data available for formulating scenarios about the latest
301 Miocene/earliest Pliocene evolution of African hominoids. In absence of Mio-Pliocene
302 fossils displaying exclusive morphological affinities with *Pan*, cautionary tales about
303 rampant homoplasy and character polarity in this evolutionary sequence⁷⁰ are poorly
304 suitable to falsification attempts. Instead, the morphological homogeneity of the
305 purported hominids implies that the interpretation of the combined non-honing C-P3
306 complex-bipedal hindlimb as a synapomorphic signature of early hominids currently
307 remains the most parsimonious hypothesis

308

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310

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476

477 **Methods**

478 The original fossil specimens are measured to the nearest 0.1 mm using a Mitutoyo

479 sliding digital caliper.

480

481 **Computed tomography**

482 High-resolution micro-computed tomography (HR-mCT) images taken from the
483 original femur and ulnae were used to assess the inner morphology of the bones. The
484 material was scanned with EasyTom XL Duo mCT (using a sealed Hamamatsu
485 microfocus x-ray source - 75 W, 150 kV - and an amorphous silicon based detector
486 Varian PaxScan 2520DX, 1536*1920 pixel matrix; 127 mm pixel pitch, 16 bits, CsI
487 conversion screen - from RX-Solutions, France) at Plateforme PLATINA (University of
488 Poitiers). For scanning procedures, beam intensity was set at 90 kV and tube current at
489 333 mA. The TM 266- 01-358 ulna was acquired with 3584 projections resulting in 3036
490 slices of 730*825 pixels using a cone-beam reconstruction algorithm. The isovoxel size
491 was set to 0.0525 mm. The TM 266-01-050 ulna was acquired with 4800 projections
492 resulting in 4051 slices of 589*849 pixels. The isovoxel size was set to 0.0600 mm. The
493 TM 266-01-063 femur was acquired with 5984 projections resulting in 4962 slices of
494 1162*911 pixels. The isovoxel size was set to 0.0499 mm.

495 **Virtual models processing**

496 Semi-automatic segmentation of the virtual fossil specimens and three-dimensional
497 surfaces extraction were performed in Avizo Lite. Three-dimensional surfaces were
498 prepared and treated using Geomagic Studio. Cortical bone thickness distribution was
499 assessed in three dimensions using the *Surface thickness* module in Avizo Lite from the
500 outer surface of the of the segmented medullar cavity to the outer surface of the femur.
501 All measurements based on 3D virtual models of the fossil specimen were done in Avizo
502 Lite on 3D volumes and Fiji image software⁷¹ on 2D slices.

503 **Cross-sectional geometric properties (CSGP)**

504 The femur lacks the most part of the epiphyses, which prevents from estimating its
505 biomechanical length. However, CSGP values in *Homo* and *Pan* do not show significant
506 differences between 45-55 % of the femoral (biomechanical or maximum) length³¹.
507 Comparison of diaphyseal cross-sectional geometry from fragmentary specimens must
508 be evaluated on a case-by-case basis³¹. Superimposition of the femora BAR 1002'00 (*O.*
509 *tugenensis*) and TM 266-01-063 using the distal base of their lesser trochanter
510 (corresponding to 80 % of the biomechanical length⁷²), show that the nutrient foramen
511 on TM 266-01-063 provides a reliable indicator of the midshaft level. CSGP estimates
512 were computed at nutrient foramen level and then, in order to get an assessment of the
513 variation pattern of cortical bone distribution, at four additional cross-sections, equally
514 spaced from the nutrient foramen to the base of the lesser trochanter. For ulnae, CSGP
515 variables were computed proximally from 35.0 mm below the distal border of the radial
516 notch (and at the level of the nutrient foramen), which corresponds to 70-75 % of the
517 estimated ulna length for TM 266-01-050 (estimated using OMO L40-19 fossil hominin
518 ulna as analog).

519 Percentage of cortical area and second moment of area were computed using Fiji
520 image software⁷¹ and BoneJ plugin⁷³.

521 Comparative data for CSGP with extant and extinct hominoids (Extended data 4)
522 were gathered from ^{19,21,26,28-30,32,33,35,74,75}.

523
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536
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564

565 **Author contributions**

566 G.D. and F. G. designed the study, collected and interpreted the data. G.D., F.G. and J.-
567 R. B. wrote the manuscript. G. D., F. G., J.-R. B., M.H.T., A.L., M.A., P.V. and C.N.
568 discussed the results and revised earlier drafts of the papers.

569

570 **Figure legends**

571

572 **Fig.1 | Femoral remain of *S. tchadensis* from late Miocene at Toros-Menalla 266th**
573 **locality.** Virtual representation of TM 266-01-063: a, anterior view; b, posterior view; c,
574 medial view; d, lateral view; e, enlarged view of the proximal portion: e, lateral view; g,
575 anterior view; microCT-slices at the level of the third trochanter (f); microCT-slices of the
576 distal part of the femoral neck (g, h). The asterisks mark the microCT-slice levels and
577 orientations.

578

579 **Fig.2 | Cross-sectional geometric properties of the TM 266-01-063 femur.** a,
580 microCT-slice levels and corresponding percent of cortical area; b, microCT-slice
581 images; c, interpretive drawings of the cortical thickness at microCT-slice levels,
582 numbers are for the measured cortical thickness anteriorly, posteriorly, medially and
583 laterally (in mm), maximum thickness is in red while minimum thickness is in green. TA,
584 total area in mm²; CA, cortical area in mm²; %, percent of cortical area.

585

586 **Fig.3 | Three-dimensional cortical thickness of TM 266-01-063.** a, anterior view; b,
587 posterior view; c, medial view; d; lateral view. Scale bar is 20 mm. Chromatic scale
588 corresponds to the look-up table of cortical thickness (in mm).

589

590 **Fig.4 | Illustration of the TM 266-01-063 *calcar femorale*.** a, virtual representation of
591 the proximal portion of the femur, posterior view; b, microCT-slice at the lesser
592 trochanter level showing proximo-distal extension of the *calcar femorale* (asterisk); c,
593 virtual representation of the proximal portion of the femur showing microCT-slice levels
594 and orientations; d, e, f, g, h, microCT-slice images for respectively slice levels from 1 to
595 5, showing expression of the *calcar femorale* transversally.

596

597 **Fig.5 | Ulnar remains of *S. tchadensis* from Late Miocene at Toros-Menalla 266**
598 **locality.** TM 266-01-358: a, anterior view; b, posterior view; c, medial view; d, lateral

599 view. TM 266-01-050: e, anterior view; f, posterior view; g, lateral view; h, medial view.
600 MicroCT-slices images levels and orientations are numbered from 1 to 3 and i to iv
601 respectively. The asterisks mark the location of the nutrient foramina.

602
603

604 **Extended data**

605

606 **Extended data 1. Schematic Map of the Republic of Chad and localization of TM 266** 607 **locality.**

608

609 **Extended data 2. Illustration of the postcranial original material from Toros-**
610 **Menalla, Chad.** TM 266-01-063 femur: a, anterior view; b, posterior view; c, lateral view;
611 d, medial view. TM 266-01-358 ulna: e, anterior view; f, posterior view; g, lateral view; h,
612 medial view. TM 266- 01-050 ulna: i, anterior view; j, posterior view; k, lateral view; l,
613 medial view.

614

615 **Extended data 3. Illustration and estimation of the femoral anteversion.** a. view of
616 the femur showing proximal plan; b view of the femur showing the distal plan; c, micro-
617 CT slice showing the major axis of the diaphyseal proximal cross section; d, micro-CT
618 slice showing the major axis of the diaphyseal distal cross section; e, superimposition of
619 the medial and distal axes forming an angle of about 26°.

620

621 **Extended data 4. Comparative CSGP data for TM 266 femur and ulnae.**
622 Comparisons of the TM 266-01-50 ulna and extant hominoid values for a, I_{max}/I_{min} and b,
623 I_x/I_y . Comparisons of the TM 266-01-063 femur and extant hominoid values for c,
624 I_{max}/I_{min} ; d, I_x/I_y and e, %CA (see methods). Circles are for means and whiskers for
625 standard deviations.

626

627 **Supplementary Information**

628

629 1. Supplementary Table

630

631 **Supplementary Table 1.** Morphological state of the main preserved features in *S.*
632 *tchadensis* femur and ulnae and their comparative in the extant and extinct homininae.

633

634 2. Supplementary Notes

635

636 **1. Detailed descriptions of the TM 266 hominin postcranial material**

637

638 ***Left femur (TM 266-01-063)***

639
640 TM 266-01-063 is a left femoral shaft of about 242 mm, lacking the distal epiphysis and
641 its adjoining metaphyseal region, and most of the proximal epiphysis. The femoral shaft
642 is curved antero-posteriorly. The femoral head is missing, the neck being broken about
643 15 mm above the margin, which delineates the lesser trochanter proximally. In proximal
644 view, the neck is compressed antero-posteriorly. The medial border of the neck is
645 oriented proximally, only the medialmost portion of the intertrochanteric line is visible.
646 Lateral to the neck, the greater trochanter and the trochanteric fossa are lacking. The
647 preserved portion of the posterior face of the neck presents a slight depression, which
648 could be evidence of the presence of the *externus obturator*. The lesser trochanter
649 preserves only its basal surface bordered by a prominent margin. It has a raindrop
650 shape, of 25.3 mm long and 16.2 mm wide. Preserved evidences suggest that the lesser
651 trochanter was substantially developed albeit there is no definitive indication on its
652 overall orientation. The lesser trochanter connects to the neck with a slightly concave
653 surface. There is no evidence of an intertrochanteric crest. A linea pectinea, expressed
654 by a bulge, arise from the distal margin that delineates the lesser trochanter. There is no
655 evidence of a hypotrochanteric fossa or lateral pilaster. There is no evidence of
656 superomedial and inferolateral fossae. Just distal to the lesser trochanter location, the
657 diameter of the shaft is 24.0 mm antero-posteriorly and 32.0 mm medio-laterally
658 illustrating subtrochanteric platymery.

659 Lateral to the lesser trochanter level, the insertion of the *gluteus maximus* left a small but
660 sharp relief, indicative of the third trochanter, continuing into a rugose surface distally.
661 This rugose surface blends with the lateral component of the *linea aspera* distally.
662 Medially to the lesser trochanter runs the spirale line for the insertion of the *vastus*
663 *medialis*. It consists in a straight line, which confounds distally with the medial border of
664 the spirale line. The linea spirale delimits posteriorly a medial shallow fossa.

665 The lateral border of the *linea aspera* forms a well-marked, sigmoid, and continuous line
666 from the gluteal ridge to approximately 37.5 mm to the distalmost end of the shaft. It
667 curves medially at about 20 mm distal to the nutrient foramen. The medial and lateral
668 borders of the *linea aspera* do not form a pilaster. The distance between medial and
669 lateral borders of the *linea aspera* is 12.2 mm in its minimum. The anterior face of the
670 proximal end bears a large slightly concave surface, with no discernable relief except a
671 restricted rugose surface located on the proximal border. There is no evidence of the
672 femoral tubercle.

673 Enlargement of the diaphysis start soon after mid-shaft. Distally, there is no anatomical
674 evidence to estimate the location of the metaphyseal region. The medial and lateral
675 borders of the *linea aspera* diverge at about the distal fifth of the shaft length. In anterior
676 view, no patellar fossa is visible. No reliable indicator allows estimating the length of the
677 missing distal portion of the femur.

678

679 Inner structure: The medullar cavity is almost completely filled by sediment and no
680 trabecular network is preserved except at proximal end with limited evidences close to
681 the cortical bone. At this level, the lesser trochanter is strengthened internally by a spur
682 of bone, also called *calcar femorale*, projecting out superiorly from the cortex into central
683 cancellous bone. Precise location of the midshaft is uncertain, but there is a distinct
684 nutrient foramen located posteriorly at about the maximum of curvature of the shaft.
685 Overall preservation of the bone and taphonomic aspects prevents from having exact
686 estimation of the average cortical thickness. Nevertheless, linear measurements
687 obtained from micro-CT slice orthogonal to the long axis of the shaft, at nutrient foramen
688 show thickest cortical bone laterally and thinnest anteriorly. The outline of the bone at
689 the same level of the shaft is subcircular with a posterior flattened portion corresponding
690 to the space between the lateral and medial margins of the *linea aspera* (diameters are
691 27.6 mm mediolaterally and 25.3 mm anteroposteriorly).

692

693 ***Right ulna (TM 266-01-358)***

694

695 It is a half proximal portion of a right ulna, of about 155 mm, preserving most of the
696 proximal epiphysis. The trochlear notch is almost complete but the anteroproximal end of
697 the anconeal process and most part of the posteroproximal portion of the olecranon. At
698 the level of the coronoid process, the preserved posterior portion of the ulna suggests
699 olecranon does not project posteriorly. The trochlear notch is keeled, narrow in its middle
700 portion, and enlarging distally. In anterior view, the trochlear notch axis defined by the
701 anconeal and coronoid processes is in line with shaft axis. In medial/lateral view, the
702 trochlear notch faces anteriorly. The distomedial portion of the trochlear notch is weakly
703 concave and is proportionally large mediolaterally when compared with its lateral
704 counterpart.

705 The articular surface of the radial notch is not preserved but its outline shows that it was
706 not rounded but rather subrectangular with 16.2 mm wide anteroposteriorly and 12.6 mm
707 long proximodistally. The radial notch is on a promontory. In proximal view, the plan of
708 the radial notch makes an acute angle ($\sim 30^\circ$) with the major axis (as defined by the
709 keeling axis) of the trochlear notch. In the coronal plan, the radial notch should have not
710 been vertical but slightly oblique distally. Distally, the supinator crest emerges directly
711 from the posterior border of the radial notch and run distally for about 40 mm, the distal
712 end being difficult to estimate due to taphonomic alterations.

713 Posteriorly to the supinator crest, a wide and concave fossa for the *anconeus* is
714 posteriorly delimited by a sharp crest running from the base of the olecranon process to
715 15 mm distally to the level of the distal border of the radial fossa and then become
716 smooth. Distally, the shaft is subtriangular in section. It is defined by an anterior edge
717 due to the insertion of the interosseous membrane, this later separates medially the face
718 for the *flexor digitorum profundus*, and laterally the face for the *extensor ulnaris carpi*.

719 The posterior border is delimited laterally by the crest delimiting the *anconeus*
720 attachment and medially by the edge for the insertion of the *flexor ulnaris carpi*. The
721 proximal portion dedicated for the attachment of the *flexor digitorum profundus*
722 corresponds to a large and shallow depression. The shaft is curved in profile and twists
723 transversally, the insertion of the interosseous membrane deviating laterally.

724

725 **Left ulna (TM 266-01-050)**

726

727 TM 266-01-050 consists in a left ulnar diaphysis of 239 mm long as preserved. The
728 proximal epiphysis is badly damaged. In anterior view, the trochlear notch is eroded
729 preserving only a small distal portion of the *anconeus* process. Most part of the
730 olecranon is missing but its preserved posterodistal portion indicates olecranon does not
731 project posteriorly.

732 In overall shape, the trochlear notch is narrow in its middle portion. The coronoid
733 process is unpreserved, making impossible any reliable estimation of the trochlear notch
734 angle. The fossa for the *brachialis* is located anteriorly, in line with the estimated
735 trochlear notch axis (as defined by the anconeal-coronoid processes) and is 15-16 mm
736 long.

737 The articular surface of the radial notch is lacking. The radial notch is on a promontory
738 which outline is comparable in shape to the right ulna. Distally, the supinator crest
739 emerges directly from the posterior border of the radial notch, and despite taphonomic
740 damage shows comparable condition to the right ulna.

741 Posteriorly to the supinator crest, a wide and concave fossa for the *anconeus* is
742 posteriorly delimited by a sharp crest running distally from the base of the olecranon
743 process to the level of the radial fossa and then fades into a rounded margin. At
744 midshaft, the ulna is subtriangular in section, in the same configuration of the right ulna
745 and becomes oval distally. As for TM 266-01-358, the posterior face of the ulna is
746 bordered laterally by the crest delimiting the *anconeus* attachment and medially by the
747 insertion edge for the *flexor ulnaris carpi*, forming a noticeable flat surface. The proximal
748 portion dedicated for the attachment of the *flexor digitorum profundus* corresponds to a
749 large and shallow depression. There is no medial protuberance for the attachment of the
750 *flexor digitorum profundus*. The shaft is curved in profile, sigmoid coronally and twists
751 transversally, the insertion of the interosseous membrane deviating laterally. Distally, the
752 shaft is likely broken proximal to the quadratus pronator attachment.

753 The nutrient foramen is located at 92 mm from the anteroproximal surface of the lateral
754 quadrant of the trochlear notch.

755

756

757 **2.2. Context of the discoveries**

758

759 The Mission Paléontologique Franco-Tchadienne (MPFT, directed by Michel Brunet) has
760 conducted field missions in the Djurab desert since 1994. Its first major discovery was a
761 partial mandible attributed to a new species, *Australopithecus bahrelghazali*^{1,2}, found in
762 the fossiliferous sector of Koro Toro (upper Pliocene). In 1997, Brunet led an exploratory
763 team in the western part of the Djurab and discovered a new fossiliferous sector
764 dominated by upper Miocene outcrops (Toros-Menalla, TM). From 1997 to 2001, the
765 MPFT documented the full extension of this large area (ca. 100 km along an East-West
766 axis) and initiated its systematic survey. In July 2001, a technical team of four MPFT
767 members¹ performed a recognition survey at TM and reached a particularly rich area
768 (locality TM 266), at that time a ca. 1.5 km² surface more or less clear of sand
769 accumulations. The team collected an abundant sample of fossil specimens and
770 documented photographically the work, but did not performed precise recording of
771 specimen positions relative to each other within the locality. The partial cranium TM 266-
772 01-060-1 proposed as holotype specimen for *Sahelanthropus tchadensis* by ³, the femur
773 TM 266-01-063 and one of the ulnae (TM 266-01-050) were among the collected
774 specimens. The participants to this mission reported conflicting information regarding the
775 precise locations within the locality TM 266 of the various fossil remains collected during
776 this mission. Pictures used to discuss the original position of the femur and cranium⁴ do
777 not include the ulna TM 266-01-050, and do not present contextual elements allowing
778 identifying the location and timing of their shooting. Most specimens observed on these
779 pictures, also including various craniodental and postcranial remains of other
780 vertebrates, do not display the dust and sand coverage usually observed on surface
781 finds in the Djurab desert: they were therefore photographed after handling. This
782 corroborates claims by Chadian team members that these pictures did not record the
783 initial position of the fossils and that they were shot after the fossils were gathered from
784 the surroundings. Given the minimum number of hominin individuals calculated for TM
785 266 (six, among which three adults⁵), suggestions that TM 266-01-060-1 and any of the
786 newly described postcranial elements belong to the same individual remain highly
787 hypothetical.

788 In Ndjamena, the team roughly sorted the 561 specimens collected during the mission
789 (141 for TM 266) by high-level taxonomic ranks and eventually stored most of the
790 postcranial specimens as an “indet.” group. This was the case for the femur TM 266-01-
791 063 and the ulna TM 266-01-050. The material then waited for examination by skilled
792 anatomists, which did not happen during the two following years. At the time, the MPFT
793 gave the highest priority to other tasks. First, the study of the craniodental material and
794 the initial characterization of the TM 266 faunal assemblage occupied all the research
795 time and resulted in their first description in *Nature* a year after TM 266 discovery^{6,7}.
796 Second, several field missions aimed at unearthing further specimens at TM 266 and
797 adjacent areas in the context of quickly increasing cover of the hominin locality by eolian
798 sands and of extreme sand-blast erosion of surface specimens. From 2001 to 2003,

799 despite the low density of fossil remains in Djurab fossil-bearing localities, the MPFT
800 collected more than 7,000 specimens at TM, including new craniodental specimens
801 attributed to *Sahelanthropus* and described by ⁵.

802 In early 2004, prior to careful examination by skilled paleontologists, various postcranial
803 remains discovered in July 2001 were selected for the training of a master student in
804 taphonomy, including TM 266-01-063. Seeking an identification, the student handed this
805 specimen to Roberto Macchiarelli⁸, not a member of the MPFT. Macchiarelli correctly
806 identified the femur to be that of a hominin⁸. In parallel, the MPFT identified the ulnar
807 remains. Later, the existence of a hominin femur from TM 266 leaked to the public prior
808 to its formal description, damaging the ability of the MPFT to preserve the novelty of its
809 disclosure for a formal scientific publication. Since 2004, the MPFT attempted
810 discovering further remains documenting the postcranial anatomy of the TM hominins, to
811 date unsuccessfully.

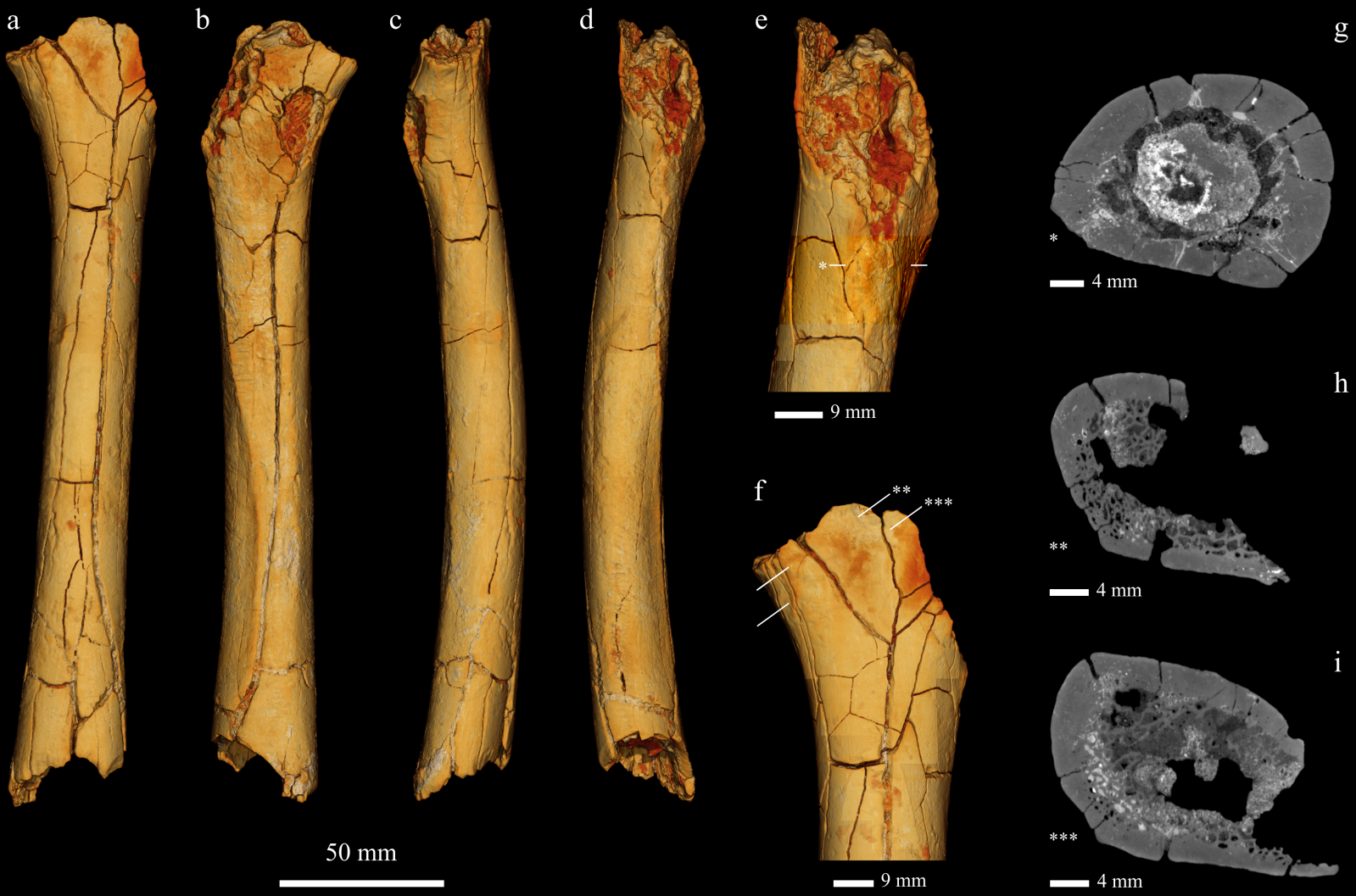
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813 ¹ Including three Chadian technicians of the Centre National d'Appui à la Recherche
814 (CNAR, now CNRD) led by one "cooperation assistant" from the Embassy of France to
815 Chad.

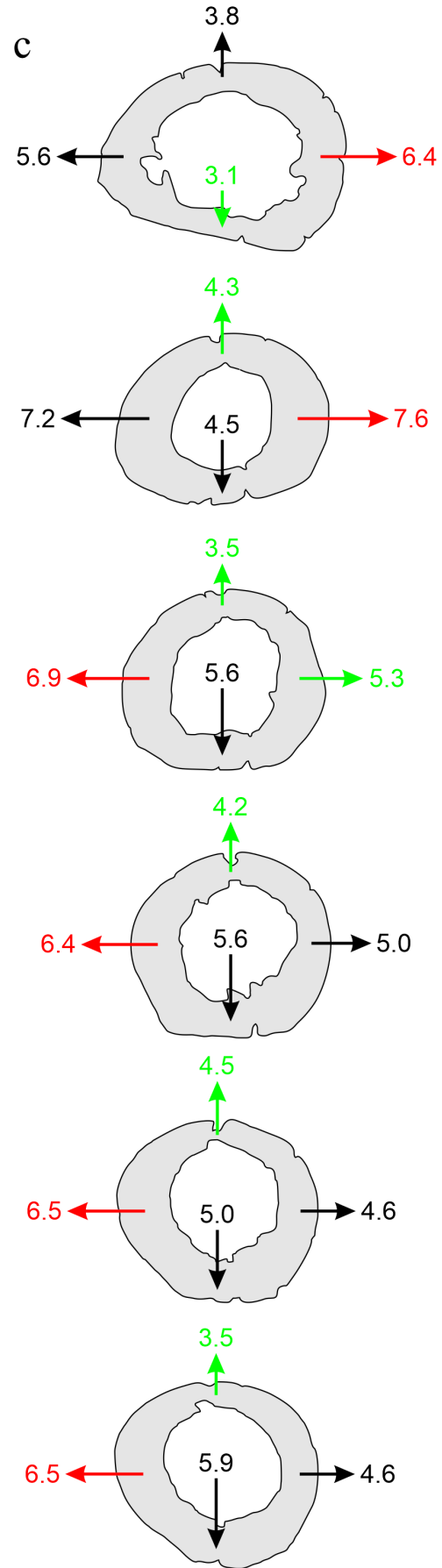
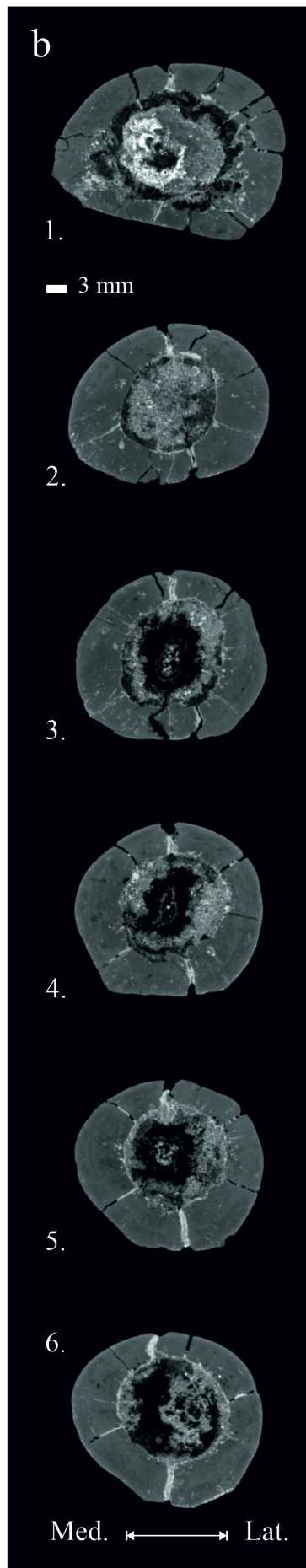
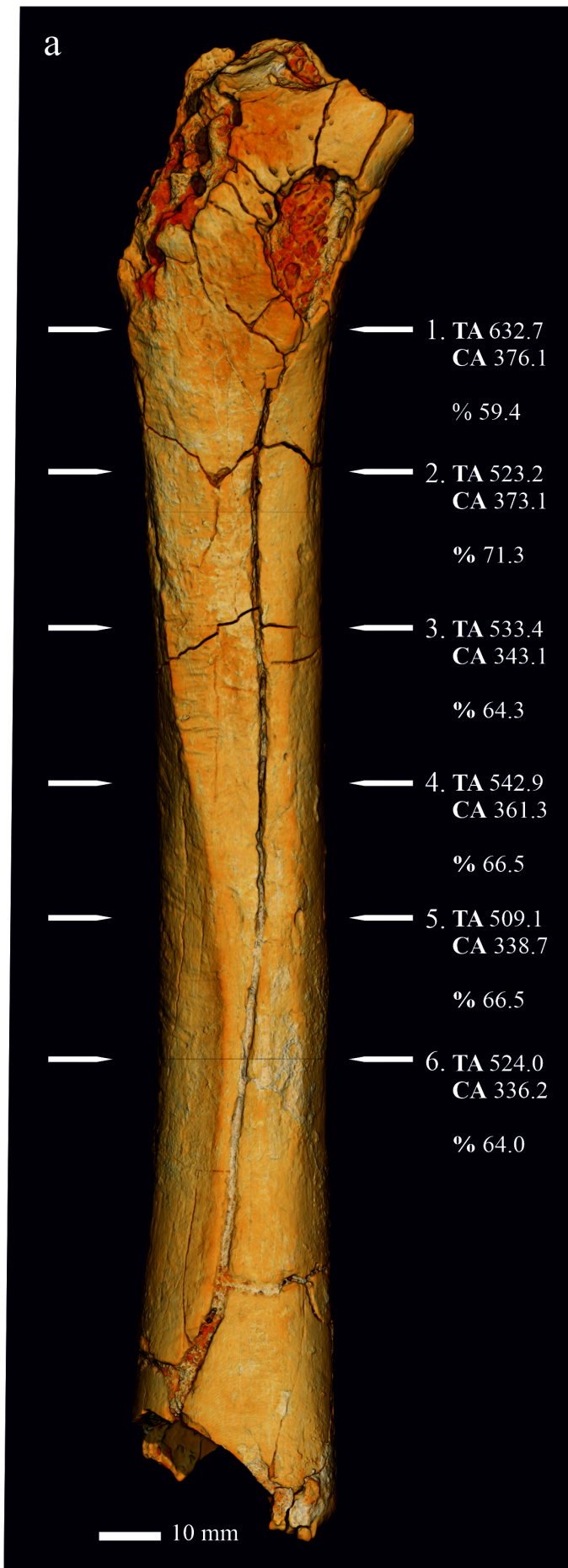
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818 **References**

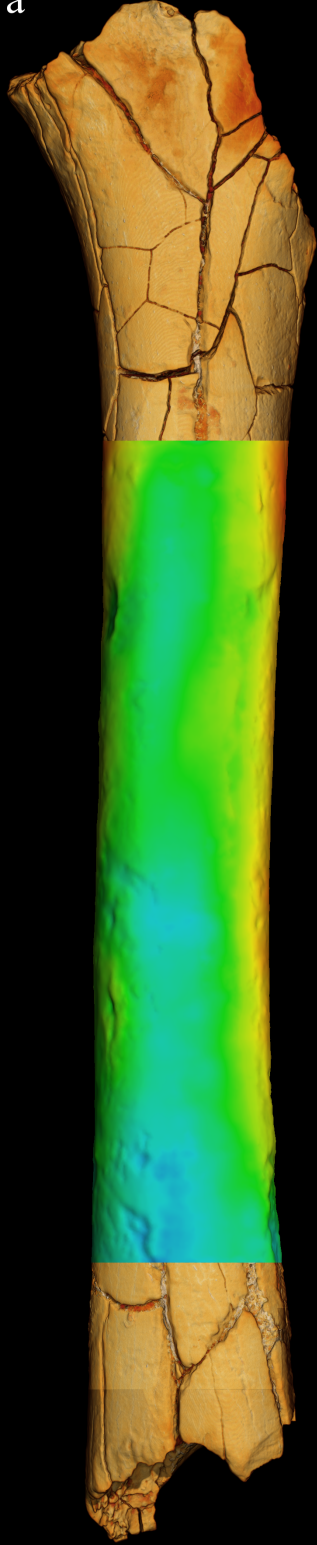
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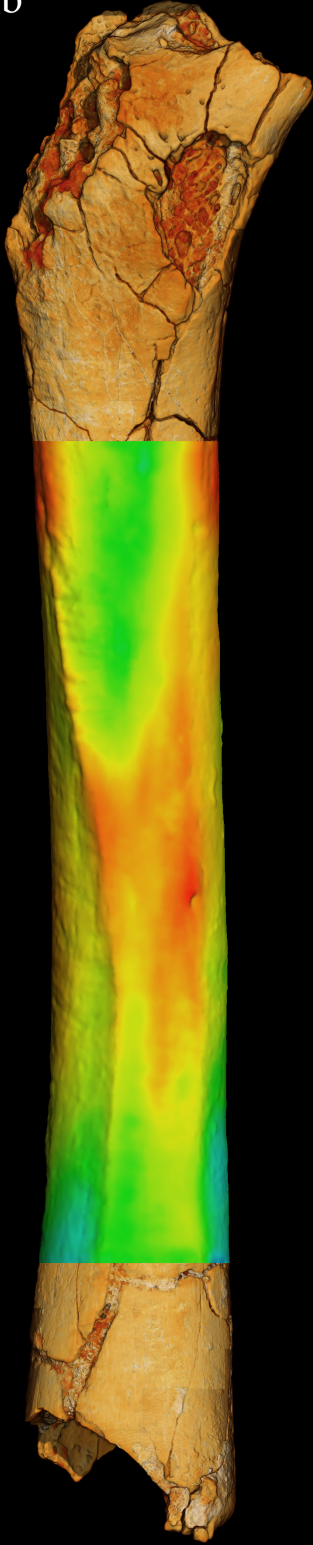




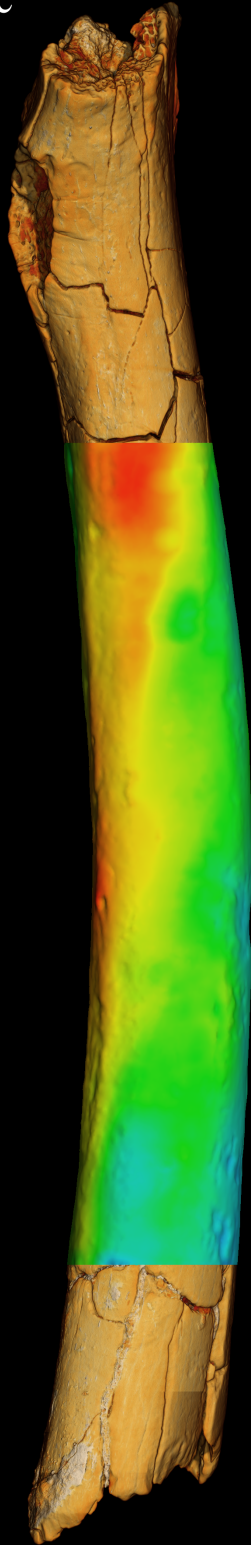
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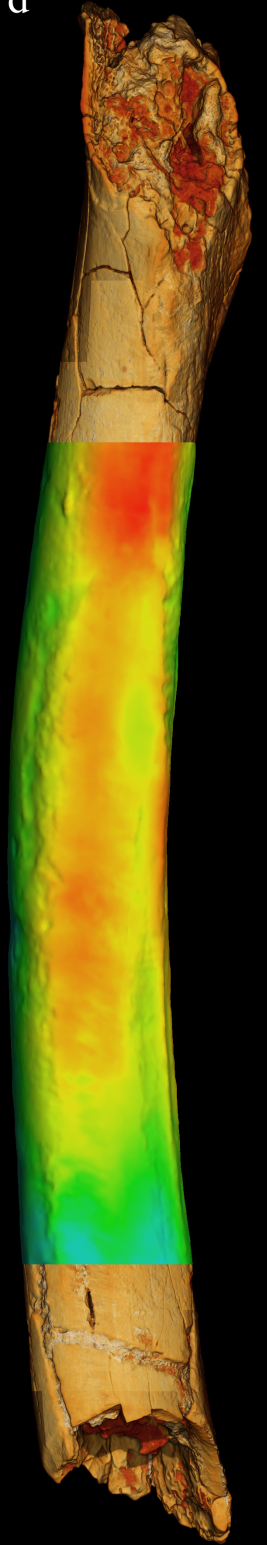
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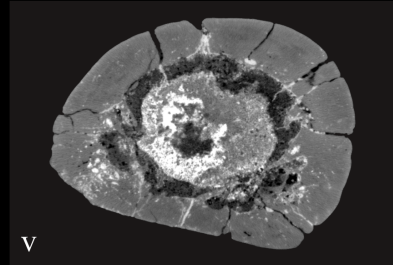
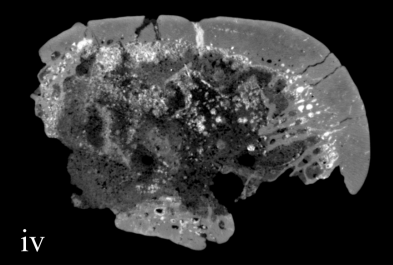
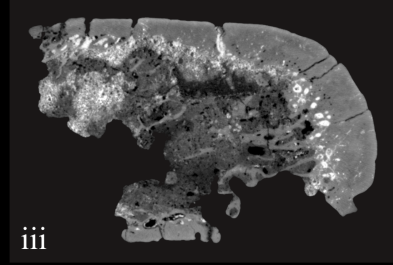
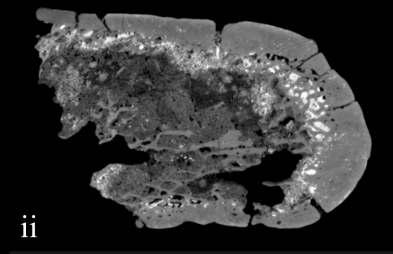
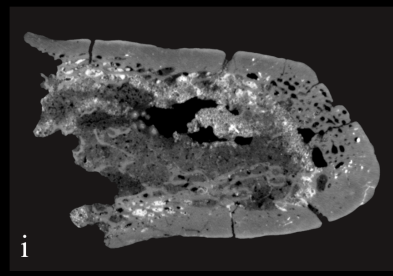
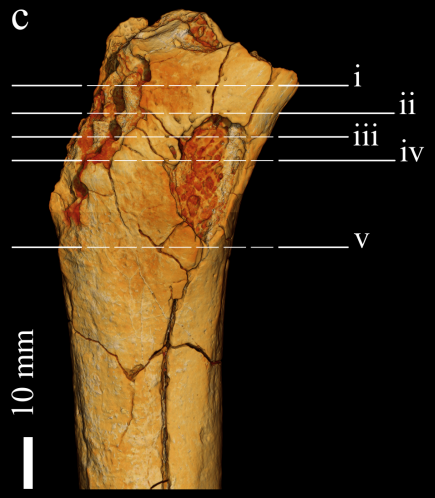
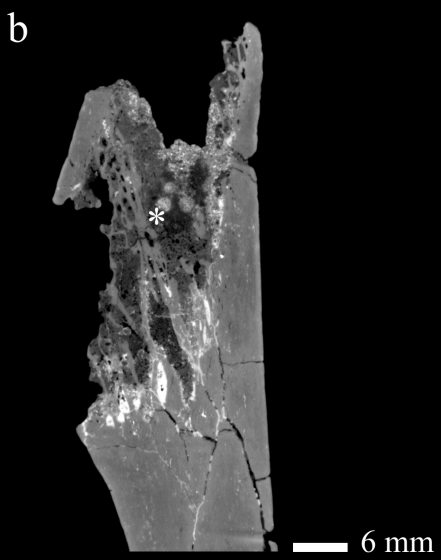


Thick



Thin





4 mm

med.
post.

