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## Postcranial evidence of late Miocene hominin bipedalism in Chad

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1 **Article**

2 **Postcranial evidence of late Miocene hominin bipedalism in Chad**

3  
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37 **Bipedal locomotion is one of the key adaptations defining the hominin clade. Evidence of**  
38 **bipedalism is known from postcranial remains of late Miocene hominins as early as 6 Ma in**  
39 **eastern Africa<sup>1-4</sup>. Bipedality of *Sahelanthropus tchadensis* was hitherto inferred at circa 7 Ma**  
40 **in central Africa (Chad) based on cranial evidence<sup>5-7</sup>. Here we present the first postcranial**  
41 **evidence of the locomotor behavior of *S. tchadensis* with new insights on bipedalism at the**  
42 **early stage of hominin evolutionary history. The original material was discovered at locality**  
43 **TM 266 (Toros-Menalla fossiliferous area), and consists of one left femur and two, right and**  
44 **left, ulnae. The morphology of the femur is most parsimonious with habitual bipedality, and**  
45 **the ulnae preserve evidence of substantial arboreal behavior. Thus, taken together, the new**  
46 **findings suggest that hominins were already bipeds at circa 7 Ma but also suggest that**  
47 **arboreal clambering was probably a significant part of their locomotor repertoire.**

48  
49 Discoveries in Chad by the Mission Paleoanthropological Franco-Tchadienne (MPFT) have  
50 substantially contributed to our understanding of early human evolution in Africa. The localities  
51 TM 247, TM 266, TM 292 in the Toros-Menalla fossiliferous area in the Lake Chad Basin yielded,  
52 among hundreds of vertebrate remains, a nearly complete cranium (TM 266-01-60-1), three  
53 mandibles, and several isolated teeth representing a minimum of four adult individuals assigned to  
54 the hominin *Sahelanthropus tchadensis*<sup>5,8</sup>. The fossils were found in the TM Anthracotheriid Unit  
55 with biochronological estimates and radiochronological age at circa 7 Ma<sup>7,9</sup>. Environmental  
56 indicators at Toros-Menalla localities suggested a lacustrine fringe, in a desert vicinity, where open  
57 areas with dry and humid grasslands coexisted with arboreal cover<sup>9</sup>.

58 Three other hominin fossil remains were discovered at TM 266 in 2001 by the MPFT: one  
59 left femoral shaft (TM 266-01-063, unearthed in July 2001), and two right and left ulnae  
60 (respectively TM 266-01-050, unearthed in July 2001 and TM 266-01-358, unearthed in November  
61 2001, see Supplementary Note 1). Although none of these limb bones can be reliably ascribed to  
62 any hominin craniodental specimen found at TM 266, the most parsimonious hypothesis is to  
63 assign these postcranial remains to the sole hominin species so far identified in this locality, *S.*  
64 *tchadensis*.

65  
66 **The femur**

67 The hindlimb is represented by a left femoral shaft (TM 266-01-063) about 242 mm long (Fig.  
68 1, Extended Data 1 and see description in Supplementary Note 2, Supplementary Table S1),  
69 lacking the distal epiphysis and most of the proximal one. The specimen is curved anteroposteriorly  
70 as in *Australopithecus* and *Orrorin tugenensis* (BAR 1002'00 and BAR 1003'00; circa 6 Ma from  
71 Lukeino, Kenya)<sup>1-2</sup> and slightly more heavily built than BAR 1003'00 specimen (see also Extended  
72 Data 2-3). The two major axes of the proximal and distal diaphyseal portions indicate that the neck  
73 was anteverted as in fossil hominins<sup>10</sup> (Extended Data 4), correlated with an antetorsion of the long  
74 axis of the shaft<sup>11</sup>. Femoral antetorsion is also reported in archaic fossil apes such as *Ekembo* but  
75 is absent in the putative arboreal biped *Danuvius guggenmosi*<sup>12,13</sup>. The femur exhibits proximal  
76 platymeria just distal to the lesser trochanter (Fig. 2a, see Extended Data 5, Supplementary Note 3

77 for figure comments and see description in Supplementary Note 2), a trait observed in *Or.*  
78 *tugenensis* and later hominins and suggested to correlate with neck elongation, an indicator of  
79 hominin bipedalism<sup>3,4,11</sup>. The neck is compressed anteroposteriorly as in the Miocene ape *D.*  
80 *guggenmosi*<sup>12</sup> and hominins<sup>2-4</sup> (but see<sup>14</sup> for *Dryopithecus fontani* and *Hispanopithecus laietanus*;  
81 Fig. 1f, h-i).

82 A small but sharp relief, indicative of a lateral and vertical gluteal tuberosity, continues into a  
83 rugose surface distally and blends with the lateral component of a broad ‘proto-*linea aspera*’<sup>3</sup> (Fig.  
84 1b,d,e,g; 12.2 mm in its narrowest width). In posterior view, the lateral lip of the *linea* forms a  
85 well-marked sigmoid line. Similarly, the medial lip of the *linea aspera* is well-marked. The spiral  
86 line for the insertion of the *vastus medialis* is linear and merges distally with the medial lip of the  
87 *linea aspera*. Such a configuration is also observed in *Or. tugenensis* and *Ardipithecus ramidus*<sup>2,4,15</sup>  
88 albeit with a more salient ‘proto-*linea aspera*’ in TM 266-01-063, but differing from modern  
89 humans in which a pilaster develops coincident with the posteromedial translation of the *m. gluteus*  
90 *maximus*<sup>3</sup> (see Fig. 2b, see Supplementary Note 3 for figure comments). Overall, the external  
91 morphology of TM 266-01-063 does not differ from *Or. tugenensis* and both are similar to the  
92 condition seen in later hominins.

93 Functionally, the anteroposteriorly compressed neck and the subtrochanteric platymeria reflect  
94 a hip subjected to high mediolateral bending moments, assumed to be counterbalanced by the  
95 gluteal muscles, which is consistent with the presence of a distinct gluteal tuberosity in TM 266-  
96 01-063<sup>4</sup>. This array of features is compatible with habitual bipedalism in *S. tchadensis*<sup>3,4,11</sup>,  
97 considered here as a behavioral response repeated under comparable situations<sup>16</sup>, and then  
98 potentially offering a selective advantage.

99 The cortical thickness distribution pattern of the femoral shaft is characterized by three relative  
100 reinforcement areas corresponding respectively to the proximomedial, lateral and posterior  
101 portions of the diaphysis (Fig. 3, see also Supplementary Note 3 for Fig. 3 comments; Extended  
102 Data 6 for TM 266-01-063 cortical thickness and bone cross-sectional geometries). Compared to  
103 extant hominoids (except gibbons), TM 266-01-063 most resembles the typical *Homo sapiens*  
104 condition, especially regarding its posterior and lateral aspects<sup>17</sup> (Fig. 3). Comparative data are, to  
105 our knowledge, not available for *Ardipithecus*; and high resolution microCT-scan data are probably  
106 needed to assess precisely the cortical thickness in BAR 1002’00/1003’00 (*Or. tugenensis*)<sup>18,19</sup>.  
107 Available CT-scan data shows that *S. tchadensis* and *Or. tugenensis* share an oblique (antero-  
108 medial to postero-distal) extension of bone thickening<sup>20</sup>. Yet, *Or. tugenensis* does not show the  
109 posterior thickening nor the expanded lateral thickening seen in TM 266-01-063 and *Homo*  
110 *sapiens*.

111 The pattern and magnitude of bone distribution in organisms stem from a complex interplay  
112 between heredity and mechanical stimuli<sup>21</sup>, and early ontogenetic stages may display inherited  
113 patterns. With the locomotor autonomy, patterns of bone distribution record the individual activity  
114 level and the loadings experienced during ontogeny and adulthood. Hence, in the case of *S.*  
115 *tchadensis*, the hominin-like condition of the femoral bone distribution may retain an evolutionary  
116 signal but more likely support individual locomotor activity pattern that includes bipedalism.

117 Cortical area and second moment of area ( $I_x/I_y$  and  $I_{max}/I_{min}$ ) are biomechanical parameters  
118 frequently used to infer habitual locomotor functions in primates, as they partly reflect how long  
119 bones resist loads, and have been used to infer how they grow in response to habitual loading  
120 (see<sup>11</sup>). The cortical area of the diaphyseal cross-section is a measure of resistance of the bone to  
121 axial compression or tension, while the second moment of area measures the resistance to bending  
122 and twisting loads.

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

130 Many factors such as stature, body mass, muscle attachment sites, positional behavior, ontogeny  
131 and sexual dimorphism may contribute to femoral bone mass distribution<sup>22</sup>. Considering size,  
132 values derived from the shape analysis of the femoral cross-section at 80% (centroid size, Extended  
133 Data 5) indicate that the *S. tchadensis* femur is in the range of hominin variation, apart from all  
134 other extant hominoids but *Homo sapiens*. Additionally, preliminary estimation of the body mass  
135 of *S. tchadensis* through univariate regressions provided by<sup>23</sup> on anteroposterior and mediolateral  
136 subtrochanteric and midshaft femoral dimensions (Supplementary Table S1) yield values from  
137 43.5 to 49.4 kg (but see<sup>24</sup>). These results are in the range of values derived from the same metrics  
138 reported for australopith and early *Homo*. *Sahelanthropus* body estimates fall between those  
139 estimated for *Or. tugenensis* (from 39.9 to 45.7 kg; see Supplementary information in<sup>40</sup>; but see<sup>25</sup>  
140 for estimation of 47.7-50.1 kg) and *Ardipithecus ramidus* (ARA-VP-6/500, 51 kg<sup>26</sup>).  
141 Unsurprisingly, body mass estimates for *S. tchadensis* remain close to the average body mass of  
142 *P. troglodytes*, the earliest hominins and australopiths<sup>27</sup>. Functionally, the geometric properties of  
143 the femoral shaft of TM 266-01-063 indicate a greatest resistance to mediolateral bending stress.  
144 This condition seen in A.L. 288-1 and African and Asian early *Homo* is suggested to indicate a  
145 more lateral position of the body during the stance phase of gait in association with an increase in  
146 femoral neck length and biacetabular breadth<sup>4,11</sup>.

147 Functional interpretations remain difficult to formulate given the paucity of early hominin  
148 comparative data and the state of preservation of the TM 266 femur. Nevertheless, in the proximal  
149 portion of TM 266-01-063, a structure formed by dense cancellous bone, consisting in an array of  
150 oblique trabeculae, is clearly identifiable in both transversal and parasagittal planes (Extended Data  
151 8). In the parasagittal plane, this oblique structure originates posteriorly at the level of the distal  
152 base of the neck and ends anteriorly on the endosteal surface around the level of the distal portion  
153 of the lesser trochanter. In the transverse plane, the structure forms a spur originating from the  
154 postero-medial endosteal surface and extending toward the antero-lateral endosteal surface. This  
155 structure corresponds to the presence of a *calcar femorale* (CF) in TM 266-01-063. The CF is also  
156 documented in *Orrorin tugenensis* (BAR 1003'00<sup>28</sup>), early hominins such as *A. afarensis* with

157 MAK-VP-1/1<sup>29</sup> and modern humans<sup>30,31</sup> and is interpreted as a mechanical support in load  
158 distribution within the proximal femur in relation to habitual bipedal locomotion. In terrestrial  
159 bipeds, it facilitates compressive loads dispelling in the proximal femur by decreasing the stress in  
160 the posterior and medial aspects and increasing the stress in the anterior and lateral aspects<sup>28,31</sup>.  
161 TM 266 01-063 and BAR 1003'00 present both an oriented trabecular bundle, of columnar aspect,  
162 in cross-section set in parasagittal plane – a morphology recalling the human condition (Extended  
163 Data 9), and a similar proximodistal extension of the structure. Nevertheless, the CF is seemingly  
164 shorter and appears denser, with a tightened trabecular network, in the transverse cross-sections in  
165 BAR 1003'00. The observed differences might be potentially due to the different states of  
166 preservation and/or CT-image acquisition settings in TM 266 01-063 and BAR 1003'00. A well-  
167 developed *calcar femorale* in TM 266-01-063 might represents a morphological adaptation for  
168 terrestrial bipedalism, which is strongly supported by the other lines of evidence derived from the  
169 femoral external shape and structural analyses.

170

## 171 **Ulnae**

172 The forearm bones attributed to *Sahelanthropus tchadensis* consist of two partial left and right  
173 ulnae lacking the distal epiphyses (Supplementary Note 2). Similarity in size and shape for these  
174 ulnae could suggest they are from the same individual, but no definitive evidence supports this  
175 inference. TM 266-01-050 is a left ulnar diaphysis of 239 mm long (Fig. 4e-h, Supplementary  
176 Table S1) with eroded proximal epiphysis. The right ulna (TM 266-01-358; Fig. 4a-d) is a  
177 proximal-half shaft that is 155 mm long with a partially preserved epiphysis. The shafts are curved  
178 in profile. Similar anteroposterior curvature is observed in *Ar. kadabba*<sup>32</sup> (ALA-VP 2/101) and  
179 later hominins (e.g., L 40-19 and OH 36) as well as in African apes<sup>10,33-35</sup> [see comparative views  
180 in Extended Data 10]. This curvature contrasts with the straight ulnar shaft of *D. guggenmosi*, but  
181 this lack of curvature is likely due to pathological conditions<sup>12</sup>. A recent ulnar curvature analysis<sup>33</sup>  
182 places the Chadian ulna (TM 266-01-050) within the fossil hominin variation, close to the African  
183 apes in morphological space, not differing in this regard from OH 36 and L 40-19 (presumably  
184 *Paranthropus*), U.W. 101-499 (*Homo naledi*), and to a lesser extent StW 573 (*Australopithecus*  
185 *prometheus*). In primates, such ulnar curvature is due to habitual loads exerted by the action of *m.*  
186 *brachialis* in order to maintain elbow flexion during arboreal climbing, which in turn involves the  
187 action of a powerful antagonistic forearm musculature, including *m. anconeus*, wrist and fingers  
188 extensors and flexors<sup>35,36</sup>. In this context, ulnar curvature is also suggested to be associated with  
189 arboreal behaviors in large-bodied primates, especially climbing and to some extent suspensory  
190 activities, for instance in facilitating prono-supination and in countering habitual loads due to body  
191 weight and the action of digital and carpal flexors<sup>35,37</sup>.

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

197 forces that apply to the forelimb in terrestrial quadrupedal primates<sup>38-39</sup>. Compared to chimpanzees  
198 and orangutans, which tend to grow more bone anteroposteriorly<sup>40</sup>, the morphology of TM 266-  
199 01-50 more likely reflects bending loads associated with an array of arboreal locomotor modes.  
200 The Chadian ulnar geometry deviates from circularity with a major axis oriented anteroposteriorly  
201 at the 80% level and antero-laterally at midshaft level where maximum bone deposition occurs.  
202 Such conformation is indicative of habitual loads exerted by the oblique cord/interosseous  
203 membrane along with the *m. flexor digitorum profundus* anteriorly and along with the wrist/finger  
204 extensors posteriorly. Overall, curvature and cross-sectional geometric properties of the ulna  
205 conform to greater anteroposterior resistance and optimized prono-supination abilities, indicative  
206 of habitual arboreal behaviors, including climbing and/or 'cautious climbing'<sup>41-42</sup>, rather than  
207 terrestrial quadrupedalism<sup>38,41,43</sup>.

208 The preserved flat distal portion of the olecranon processes indicate that they were not  
209 projecting posteriorly as in African apes<sup>44</sup>. In this regard, the distal portion of the olecranon most  
210 resembles the condition in Miocene apes<sup>44-45</sup> and in hominins<sup>46</sup>. The proximal epiphyses indicate  
211 an anteriorly-facing trochlear notch as in fossil hominins and Miocene apes<sup>10,12,44-45,47</sup>. Hence, the  
212 Toros-Menalla ulnae depart from the typical proximally oriented trochlear notch of the extant great  
213 apes<sup>36,46</sup>. In functional terms, a more anteriorly facing notch, associated with an olecranon aligned  
214 with the long axis of the forearm, favors triceps leverage at mid-flexion<sup>36,45,46</sup>. In *Ar. ramidus* such  
215 function has been linked to careful climbing and bridging<sup>45</sup>. Conversely, a more proximally facing  
216 notch reflects habitual extended elbow, e.g. during suspension<sup>47</sup> and quadrupedalism, while a  
217 posteriorly projecting olecranon favors triceps leverage in extension and is commonly associated  
218 with terrestrial quadrupedal locomotion in anthropoids<sup>44</sup>.

219 Ulnae from Toros-Menalla display a keeled trochlear notch with a comparatively acute angle  
220 relative to later hominins and African apes. The distal keeling angle, measured from TM 266-01-  
221 358 (distal keeling angle of 117°), is in the lower range of chimpanzees and *Pongo pygmaeus*, and  
222 close to values reported for *Oreopithecus bambolii* and the left *A. afarensis* ulna A.L. 288-1t<sup>46</sup>.  
223 Likewise, the proximal angle is acute (proximal keeling angle of 101°), in the lower range of  
224 reported values for chimpanzees and gorillas, and close to OH 36 and *O. bambolii*<sup>46</sup>. A pronounced  
225 trochlear keel likely augments mediolateral stability of the elbow in response to powerful  
226 superficial finger and wrist flexors, and forearm pronator (*mm. flexor digitorum superficialis*,  
227 *flexor carpi radialis* and *ulnaris*, and *pronator teres*)<sup>34,46</sup>. Such a configuration was reported on *D.*  
228 *guggenmosi*<sup>12</sup> and is typical of the arboreal large apes that integrate climbing and suspension in  
229 their locomotor repertoire<sup>46</sup> and is unlikely to reflect habitual terrestrial quadrupedalism. Besides,  
230 the two TM 266 ulnae trochlear notches present a morphology close to that of humans and  
231 chimpanzees in which the middle portion is mediolaterally narrow relative to the distal half. This  
232 waisted configuration is an allometric consequence of size and unrelated to locomotor mode<sup>46</sup>. The  
233 distomedial quadrant of TM 266-01-358 is clearly more developed than the concave distolateral  
234 one, an intermediate morphology between humans and chimpanzees, close to that of *D.*  
235 *guggenmosi*<sup>12</sup>, *A. afarensis*<sup>46</sup>, and *A. prometheus*<sup>10</sup>. A developed medial portion of the trochlear  
236 notch is an adaptation for maximum joint compression medially, a configuration which could meet

237 mechanical requirements in various non terrestrial locomotor behaviors<sup>12,46</sup>.

238 The TM 266 ulnae lack prominent flexor apparatus entheses as in orangutans, *Ar. ramidus* and  
239 later hominins. In this respect, it differs from the condition seen in Miocene apes and extant  
240 quadrupedal apes/monkeys<sup>45,47</sup>. A medially prominent flexor apparatus entheses is assumed,  
241 through the activity/passive tension of the flexor muscles, to limit the palmar dorsiflexion and to  
242 stabilize the forelimb during quadrupedal stance phase<sup>48</sup>. Its absence in *S. tchadensis* ulnae  
243 contribute to preclude terrestrial quadrupedalism as the primary locomotor behavior of the Toros-  
244 Menalla hominins.

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

252

### 253 **Overall assessment**

254 Given the combination of hominin-like traits identified in this study (as compared with Miocene  
255 apes and extant non-human apes), the most parsimonious hypothesis remains that postcranial  
256 morphology of *Sahelanthropus* is indicative of bipedality and that any other hypothesis would have  
257 less explanatory power for the set of features expressed by the Chadian material. The multiplicity  
258 of attested/presumptive bipedalities currently proposed for several phylogenetically distinct  
259 hominoid taxa (e.g., *Orrorin*, *Ardipithecus*, *Australopithecus*, and *Danuvius*, *Oreopithecus*)  
260 strongly suggests that seeking for unique defining trait of bipedalism is hazardous (‘magic trait’  
261 sensu<sup>50</sup>). Rather, seeking for specific functional complexes for inferring past postural and  
262 locomotor behaviors should be favored.

263 The Toros-Menalla femur exhibits several hallmarks of selection for bipedalism as a regular  
264 behavior. Results from femoral cross-sectional contours, cross-sectional geometry properties, and  
265 cortical bone distribution along a particularly transversally twisted shaft, show that TM 266-01-  
266 063 presents distinctive hominin femoral characteristics (Table 1). In addition, a well-developed  
267 *calcar femorale* would facilitate the dissipation of compressive loads caused by bipedalism on  
268 terrestrial substrates<sup>28,31</sup>. Although present in some Miocene hominoids, a well-defined proto-*linea*  
269 *aspera*, the presence of a lateral gluteal tuberosity and associated subtrochanteric platymeria  
270 without hypotrochanteric or infero-lateral fossae have been traditionally associated with enhanced  
271 hip flexion-extension<sup>3,15</sup>. While they are part of a primitive functional complex<sup>1-4,15</sup>, they accord  
272 with the overall functional pattern seen in habitual hominin bipeds<sup>51</sup> (Supplementary Table S3 and  
273 references therein). Hence, based on these multiple lines of evidence, we consider that the Chadian  
274 hindlimb bone indicates habitual bipedalism (contra opinion expressed in<sup>52</sup>), likely on terrestrial  
275 substrates.

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

277 substantial arboreal behavior, as in *Ar. ramidus*<sup>15</sup> and presumably *Or. tugenensis*<sup>1</sup> and *Ar. kadabba*.  
278 All ulnar features, including the shaft curvature, the cross-sectional bone distribution and geometry  
279 properties, the trochlear morphology and orientation, converge to rule out terrestrial  
280 quadrupedalism (Supplementary Table S3). Instead, the functional pattern, inferred from the ulnae,  
281 points to arboreal prono- and orthograde clambering, probably involving some degree of sure grasp  
282 and erratic limb excursion<sup>41, 42, see also 49</sup>, without habitual suspensory activities such as forearm  
283 swing and/or suspension. Data from the femur also suggest orthograde clambering in arboreal  
284 context, as part of a ‘cautious climbing’ repertoire<sup>42</sup>, that involves weight-bearing functions for the  
285 hindlimbs<sup>49</sup>, as described in previous studies for *Ar. ramidus*<sup>45</sup>, and possibly *Or. tugenensis*<sup>53</sup>.  
286 Hitherto, the femur of *Sahelanthropus* supports an early evidence of habitual bipedalism in the  
287 hominin clade<sup>54,55</sup>, confirming previous cranial interpretations based on the relative orientation of  
288 the orbital plane and the foramen magnum as well as the nuchal plane orientation and  
289 morphology<sup>6,56-58</sup>. In addition, our postcranial results tend to favor a terrestrial component for the  
290 habitual bipedalism in *S. tchadensis*, as shown for penecontemporaneous *Or. tugenensis* and late  
291 *Ar. kadabba* (5.2 Ma from Middle Awash, Ethiopia). Altogether, the Chadian postcranial remains  
292 suggest that adaptation for bipedalism evolved soon after the human-chimp divergence<sup>26</sup>, in  
293 conjunction with the retention of osteological adaptations for arboreal positional behaviors.

294 The Toros-Menalla postcranial material adds to previous interpretations of the environmental  
295 context of the Miocene hominins from the eastern Africa Miocene so far known. *Or. tugenensis* is  
296 associated with open woodland areas with significant tree cover<sup>59</sup>, *Ardipithecus kadabba* (which  
297 bipedalism is inferred from foot phalanx AME-VP-1/71 dated to 5.2 Ma<sup>32</sup>) is associated with a  
298 mixture of woodland combined with wet grassland<sup>60</sup>, *Ar. ramidus* (4.4 Ma from Aramis, Ethiopia)  
299 most probably inhabited a ground-water-fed grassy woodland, probably a palm grove<sup>61,62</sup>.

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

311 Based on molecular data, the chimpanzee-human last common ancestor (CHCLA) is estimated  
312 to occur in Africa between 10 and 6 Ma<sup>58,64-66</sup>. Fossil representatives of the panin clade are very  
313 scarce<sup>67-68</sup> but, at least three hominine taxa have been described in this time interval Ma in Africa:  
314 *Samburupithecus*, from Samburu Hills, around 9.5 Ma<sup>69</sup>, *Nakalipithecus* from Nakali, circa 9.8  
315 Ma<sup>70</sup> and *Chororapithecus* from Chorora, circa 8 Ma<sup>71,72</sup>. These Miocene taxa are parsimoniously  
316 assigned to stem hominines<sup>73</sup>, even if *Samburupithecus* displays a particularly archaic

317 morphology<sup>73</sup>. *Chororapithecus* displays derived dental affinities with *Gorilla*<sup>71</sup>. In light of this  
318 record and the lack of phylogenetic resolution, the ancestral condition of positional behaviour in  
319 African apes and humans will remain elusive until new significant data become available. To date,  
320 the identification of the derived traits shared by hominins relies on the analysis of the earliest taxa  
321 of the clade. The early hominins *Sahelanthropus*, *Orrorin* and *Ardipithecus* share the same  
322 combination of non-honing C-P<sub>3</sub> complex and of features linked to bipedalism. This combination  
323 is parsimoniously interpreted as more similar to the condition observed in later hominins than in  
324 any other African fossil or extant hominoids<sup>74</sup>. These are currently the only data available for  
325 formulating scenarios about the latest Miocene/earliest Pliocene evolution of African hominoids.  
326 In the absence of Mio-Pliocene fossils displaying exclusive morphological affinities with *Pan*,  
327 cautionary tales about rampant homoplasy and character polarity in this evolutionary sequence<sup>75</sup>  
328 are untestable. Instead, our data support the hypothesis that the combination of a non-honing C-P<sub>3</sub>  
329 complex and habitual bipedalism is a synapomorphic signature of the hominin clade.  
330

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498  
499

500 **Methods**

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

508  
509 The original fossil specimens are measured to the nearest 0.1 mm using a Mitutoyo sliding digital  
510 caliper.

511  
512 ***Comparative samples***

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

523  
524 ***Computed tomography***

525 High-resolution micro-computed tomography (HR-mCT) images taken from the original femur  
526 and ulnae were used to assess the inner morphology of the bones. The material was scanned with  
527 EasyTom XL Duo mCT (using a sealed Hamamatsu microfocus x-ray source - 75 W, 150 kV - and  
528 an amorphous silicon based detector Varian PaxScan 2520DX, 1536\*1920 pixel matrix; 127 mm  
529 pixel pitch, 16 bits, CsI conversion screen - from RX-Solutions, France) at Plateforme PLATINA  
530 (Arnaud Mazurier, IC2MP - University of Poitiers). For scanning procedures, beam intensity was  
531 set at 90 kV and tube current at 333 mA. The TM 266-01-358 ulna was acquired with 3584  
532 projections resulting in 3036 slices of 730\*825 pixels using a cone-beam reconstruction algorithm.  
533 The isovoxel size was set to 0.0525 mm. The TM 266-01-050 ulna was acquired with 4800  
534 projections resulting in 4051 slices of 589\*849 pixels. The isovoxel size was set to 0.0600 mm.  
535 The TM 266-01-063 femur was acquired with 5984 projections resulting in 4962 slices of  
536 1162\*911 pixels. The isovoxel size was set to 0.0499 mm.

537  
538 ***Virtual models processing***

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

540 extraction were performed in Avizo Lite 2021 (Thermofisher). Cortical bone thickness distribution  
541 for the TM 266 femur was assessed in three dimensions using the *Surface thickness* module in  
542 Avizo Lite from the outer surface of the femur to the outer surface of the segmented medullar  
543 cavity. All measurements based on 3D virtual models of the fossil specimen were done in Avizo  
544 Lite on 3D volumes and Fiji image software<sup>76</sup> on 2D slices. For comparative purposes, individual  
545 cortical bone thickness were divided by their maximal thickness.

#### 547 ***Cross-sectional geometric properties (CSGP)***

548 The femur lacks the most part of the epiphyses, which complicates the assessment of its  
549 biomechanical length. However, CSGP values in *Homo* and *Pan* do not show significant  
550 differences between 45-55 % of the femoral (biomechanical or maximum) length, meaning that  
551 various midshaft estimates in this range provide comparable CSGP<sup>77,78</sup>. In this regard, the nutrient  
552 foramen located at the level of the maximum femoral anteroposterior curvature was set to represent  
553 the 50% biomechanical level of TM 266-01-063 femur. In addition, the 80% cross-sectional level  
554 was set at 10 mm below the distal border of the lesser trochanter as recommended in<sup>79,80</sup>. Midshaft  
555 and subtrochanteric cross-sectional levels were used to infer the total biomechanical length (*circa*  
556 284 mm) of TM 266-01-063 and the positions of the cross-sections set at 65% and 35%  
557 respectively. CSGP estimates were computed at midshaft and then, in order to get an assessment  
558 of the variation pattern of cortical bone distribution, at 80%, 65% and 35% of the biomechanical  
559 length. Surface alteration and fracture prevents from assessing the location of standard cross-  
560 sectional levels on TM 266-01-358. Then, CSGP variables were computed solely based on TM  
561 266-01-050. Cross-section at 50% of the biomechanical length was located at the level of the  
562 nutrient foramen, whereas the one set at 80% was estimated using similar sized chimpanzee ulna  
563 (*P. paniscus*) as analog.

564 Percentage of cortical area and second moment of area were computed using Fiji image  
565 software<sup>76</sup> and EPMacroJ plugins<sup>81</sup>. Comparative data for CSGP in extant and extinct hominoids  
566 are provided in Supplementary Table S2 and citations herein for the femur, and come from<sup>40,82</sup> for  
567 the ulna.

568 The total length of the femur (Supplementary Table S1) was estimated using percentage  
569 difference between femoral biomechanical and total length in extant hominoids (*Homo*, *Pan*,  
570 *Gorilla* and *Pongo*; n=64). Mean, minimum and maximum reported values are given using the  
571 pooled ape sample without *a priori* hypothesis for morphological affinities between TM 266-01-  
572 063 and any extant hominoid model.

#### 574 ***Geometric morphometrics***

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

580 two levels, 23 equally spaced semi-landmarks were digitized along the anterior contour. Landmark  
581 and semi-landmark coordinates were acquired using TPSDig2 v2.31<sup>83</sup>. Landmark digitization were  
582 performed from the medial view of the oriented 3D virtual model of the femora for all extant and  
583 extinct specimens except for one occurrence of *Orrorin tugenensis* (BAR 1002'00) and  
584 *Australopithecus prometheus* (StW 573m).

585 Concerning BAR 1002'00 specimen, the discrepancies between originally described anterior  
586 curvature and figured specimens<sup>1,2,84</sup> and the curvature observed from cast and original CT-scans  
587 data (data used in<sup>20,52</sup>) led us to consider the two alternative reconstructions of BAR 1002'00 femur  
588 in our analysis. The medial view of the reconstructed StW 573m femur was obtained from<sup>10</sup>.

589 Shapes of the femoral external contours at 80% and 50% were assessed using 2 landmarks and 46  
590 semi-landmarks. Landmark digitization was performed from the cross-section images issued from  
591 3D virtual model of the femora for most extant and extinct specimens. Specimens, for which 3D  
592 data are not available or were not provided, were included based on their published cross-sectional  
593 images (Supplementary Table S3). Cross-sectional images were oriented so that the femoral  
594 anterior portion faces upward and the femoral medial portion toward the right. Two landmarks  
595 were digitized at the anterior and posterior ends of the anteroposterior midline of the cross-sections.  
596 Between these two landmarks, 46 equally spaced semi-landmarks were digitized on the femoral  
597 outer outline, 23 for each medial and lateral side of the femoral contour. In order to assess  
598 replicability, three blinded landmarking sessions were performed independently for TM 266-01-  
599 063 at 50% level by GD (n=1) and FG (n=2). Landmark and semi-landmark coordinates were  
600 acquired using TPSDig2 v2.31<sup>83</sup>. In the same manner, two landmarking sessions were performed  
601 independently for *Orrorin tugenensis* (BAR 1002'00) at 50% level by GD and FG resulting in two  
602 close occurrences in the PC1-2 shape space.

603 Landmark and semi-landmark coordinates for femoral curvatures and femoral cross-sectional  
604 shapes were analyzed using generalized Procrustes superimposition. The analyses were performed  
605 using the package Geomorph v4.0.0<sup>85,86</sup> for R v. 4.0.3<sup>87</sup>. A principal component analyses were  
606 performed on Procrustes residuals using Statistica software (Statsoft) with Chadian specimens as  
607 a supplementary individuals. Principal component analysis was preferred over between-group  
608 principal component analysis<sup>52</sup>, as the later may induce misinterpretations and introduce biases in  
609 the case of small sample size<sup>88,89</sup>.

610

### 611 ***Femur diaphyseal torsion (antetorsion)***

612 The diaphyseal antetorsion of the TM 266-01-063 femur was assessed between a proximal cross-  
613 section taken at the base of the lesser trochanter, and a distal cross-section at 25% of the total  
614 biomechanical length. Each cross-section is oriented so that the femoral anterior portion faces  
615 upward and the femoral medial portion toward the right, the mediolateral axis being horizontal.  
616 The longest axis of each femoral cross-section was assessed by the mean of Feret's diameter, as  
617 the longest distance between any two points along the cross-sectional contour, using Fiji image  
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653

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691  
692 **Author contributions**  
693 F.G. and G.D. designed the study, collected and interpreted the data, ran the analyses and  
694 interpreted the results. G.D., F.G. and J.-R.B. wrote the manuscript. G.D., F.G., J.-R.B., L.P.,

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696

697 **Data and code availability**

698 The Chadian postcranial material is curated and conserved by the CNRD (Centre National de  
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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  
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708

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710

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712

713

714 **Figure legends**

715  
716 **Fig. 1 | The femur of *S. tchadensis*.** Virtual representation of TM 266-01-063: a, anterior view; b,  
717 posterior view; c, medial view; d, lateral view; e, close-up of the proximal portion in lateral view  
718 showing the gluteal tuberosity; f, enlarged view of the proximal portion in anterior view; g,  
719 transverse microCT-slice at the subtrochanteric level; h, i, oblique microCT-slices of the distal part  
720 of the femoral neck. The microCT-slice levels and orientations for g, h, i are shown in e, f. Scale  
721 bar for a, b, c, d 50 mm; e, f, 9 mm; g, h, i, 4 mm.

722  
723 **Fig. 2 | Comparative analysis of the subtrochanteric and midshaft cross-sectional contours of**  
724 **the TM 266 femur.** a. Principal component analysis of Procrustes coordinates for the  
725 subtrochanteric cross-sectional contour (80% of the biomechanical length) in fossil and extant  
726 hominoids. Bivariate plot of PC1 and PC2 summarizes 55.3% of the total variation; b. Principal  
727 component analysis of Procrustes coordinates for the midshaft cross-sectional contour (50% of the  
728 biomechanical length) in fossil and extant hominoids. Bivariate plot of PC1 and PC2 summarizes  
729 69.9% of the total variation. Modern humans, n=12; bonobos, n=12; common chimpanzees, n=18;  
730 gorillas, n=9; orangs, n=7; fossil hominins, n=10 (80%), n=13 (50%); Miocene apes, n=3.  
731 Cross-sectional contour variation, summarized by the PC<sub>1-2</sub> shape space, is illustrated by an outline  
732 representation at the extremity of each axis; the red dot is for the anterior portion of the contour,  
733 lateral is to the left. Cross-sectional contours of selected fossil specimens are indicated by a black  
734 arrow, whereas cross-sectional contour of TM 266-01.063 is represented in the lower left grey box.  
735 In the legend, underlined specimen names correspond to individual for which only data for  
736 midshaft were collected. Specimens marked by an asterisk correspond to individual for which only  
737 data for subtrochanteric contour were collected. See Supplementary Note 3 for comments on the  
738 figure.

739  
740 **Fig. 3 | Comparison of cortical thickness distribution between *S. tchadensis* and extant great**  
741 **apes.** Panels a, b, c, and d, correspond respectively to anterior, medial, posterior and lateral views.  
742 In each panel, from left to right, the femora are TM 266-01-063 (mirrored), modern human,  
743 chimpanzee, gorilla and orangutan. The cortical thickness is illustrated for the 80%-35% interval  
744 of the femoral biomechanical length using a relative scale (see Methods), this chromatic scale  
745 corresponds to the look-up table of cortical thickness, from relatively thin (blue) to relatively thick  
746 (red) cortical diaphyseal bone. The extant femora are roughly at the same size, the TM 266-01-063  
747 femur was scaled by aligning its 80-35% biomechanical interval and the corresponding portion in  
748 extant hominoids (pooled). See Supplementary Note 3 for comments on the figure.

749  
750 **Fig 4. | Ulnar remains of *S. tchadensis*.** TM 266-01-358: a, anterior view; b, posterior view; c,  
751 medial view; d, lateral view. TM 266-01-050: e, anterior view; f, posterior view; g, lateral view; h,  
752 medial view. Transverse microCT-slices images levels (proximal to distal) are numbered from 1  
753 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.  
756  
757  
758

759 **Table legend**

760

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

766

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769

770 **Extended Data**

771  
772 **Extended Data 1. Photographs of the postcranial original material from Toros-Menalla,**  
773 **Chad.** TM 266-01-063 femur: a, anterior view; b, posterior view; c, lateral view; d, medial view.  
774 TM 266-01-358 ulna: e, anterior view; f, posterior view; g, lateral view; h, medial view. TM 266-  
775 01-050 ulna: i, anterior view; j, posterior view; k, lateral view; l, medial view. Scale bar 10 mm.

776  
777 **Extended Data 2. Femoral anterior curvature.**

778 Panel a. comparative femoral anteroposterior curvature. The TM 266-01-063 femur (*S. tchadensis*)  
779 is compared (from left to right) to BAR 1002'00 (*Or. tugenensis*, as published in<sup>2,84</sup>), BAR 1002'00  
780 (*Or. tugenensis*, acquired from CT-scan data, as published in<sup>52</sup>), BAR 1003'00 (*Or. tugenensis*,  
781 acquired from CT-scan data, courtesy of B. Senut, M. Pickford and D. Gommery), StW 573 (*A.*  
782 *prometheus*, as published in<sup>10</sup>) and A.L. 288-1p (*A. afarensis*, cast). Femora are in medial view.  
783 The colored portions for TM 266-01-063, BAR 1002'00, BAR 1003'00 and StW 573 illustrate the  
784 interval used for the 2D geometric morphometrics analysis of the femoral antero-posterior  
785 curvature (between 80% and 35% of the biomechanical femoral length, this study). Two version  
786 of *Or. tugenensis* anterior femoral curvature were included in the analysis, BAR 1002'00\* (*Or.*  
787 *tugenensis*, as published in<sup>2,84</sup>), and BAR 1002'00\*\* (*Or. tugenensis*, acquired from CT-scan data,  
788 as appears in<sup>52</sup>). Femora are about the same scale. Ant. for anterior, dist. for distal.

789 Panel b. Comparative analysis of the anterior femoral curvature of the TM 266 specimen. Principal  
790 component analysis of Procrustes coordinates for the anterior femoral curvature, in medial view,  
791 as estimated between 80% and 35% of the femoral biomechanical length in fossil and extant  
792 hominoids. Bivariate plot of PC1 and PC2 summarizes 89.3% of the total variation. Anterior  
793 femoral curvature variation, summarized by the PC1-2 shape space, is illustrated by an outline  
794 representation at the extremity of each axis; the red dot is for the proximal end of the anterior  
795 contour. Black solid arrows mark the main anterior convexities, whereas white open arrows are for  
796 the main anterior concavities. Two version of *Or. tugenensis* anterior femoral curvature were  
797 included in the analysis, BAR 1002'00\* (*Or. tugenensis*, as published in<sup>2,84</sup>), and BAR 1002'00\*\*  
798 (*Or. tugenensis*, acquired from CT-scan data, as appears in<sup>52</sup>).

799  
800 Distribution of the specimens along PC1 describes the degree of curvature between two  
801 morphological femoral shapes; rectilinear (negative values) and anteriorly curved (positive  
802 values). Along PC2, distribution of the specimens illustrates additional aspects of the femoral  
803 curvature including a transition between proximally (negative values) to distally (positive values)  
804 located anterior curvature. Along PC1, extant apes describes a morphological gradient from  
805 straight femora in orangs to curved femora in gorilla, chimpanzee and humans being intermediates.  
806 Along PC2, humans, gorillas and orangutans present a proximally located anterior curvature while  
807 chimpanzees display a relatively more distal anterior curvature. In this pattern, the fossil hominins,  
808 apart from BAR 1002'00\*\* and early *Homo*, occupy a central position in the morphospace in  
809 having moderately curved femora and a centrally located anterior curvature. TM 266-01-063

810 presents higher degree of curvature compared to other fossil hominins, within the range of  
811 chimpanzees and gorillas along PC1 but close to BAR 1002'00\*. Alternative version of BAR  
812 1002'00\*\* falls out of the range of variation for the extant apes in having a relatively straight  
813 femoral shaft, clearly differing in this respect from BAR 1002'00\*. BAR 1002'00\*\* is in line with  
814 early *Homo* along PC1 and is overall closer to KNM-ER 1481 than any other apes.

815  
816 **Extended Data 3. Comparison of TM 266-01-063 with extant African apes and *Or. tugenensis*,**  
817 **illustrating femoral size variation.** From left to right: femoral specimens of *Gorilla*, *Pan*, *Homo*,  
818 TM 266-01-063, BAR 1003'00, BAR 1002'00. All femora are in posterior view. Scale bar is 50  
819 mm.

820  
821 **Extended Data 4. Illustration and estimation of the TM 266-01-063 diaphyseal antetorsion.**  
822 a. 3D view of the femur (virtual model) showing the position of the proximal (base of the lesser  
823 trochanter) and distal (25% of the total biomechanical length) transverse sections; b. transverse  
824 CT-slice cross-sections showing the mediolateral axis (M-L) and the orientation of the longest axis  
825 of the diaphyseal sections (proximal, upper panel and distal, lower panel) assessed by the mean of  
826 Feret's diameters ( $Ft_1$  and  $Ft_2$  respectively); c., 3D view of the femur (virtual model) showing the  
827 femoral antetorsion by the mean of the relative orientation of the proximal and distal Feret's  
828 diameters. The white curved arrows mark the diaphyseal torsion angle (DT) measured between  $Ft_1$   
829 and  $Ft_2$ .  $Ft_1$ :  $11.7^\circ$  counterclockwise, relative to mediolateral axis;  $Ft_2$ :  $153.2^\circ$  counterclockwise,  
830 relative to mediolateral axis; DT is  $38.5^\circ$ . The right panel d presents an illustration of the variation  
831 of the parameter DT, in degrees, in chimpanzee, gorilla and modern human. Box and whiskers are  
832 for mean (centre), mean  $\pm$  standard deviation (bounds of box) and minimum/maximum (whiskers).  
833 In chimpanzee means for *P. paniscus* (Pp, n=6) and *Pan troglodytes* (Pt, n=12) are given. The red  
834 dotted line corresponds at the value measured for TM 266-01-063.

835  
836 **Extended Data 5.** Bivariate plot of PC1 (33.8%) versus centroid size (Cs). The Cs mean (symbols  
837 are for group mean) and its range (whiskers) for the extant and extinct hominoid sample are  
838 provided in the left grey panel. Modern humans, n=12; bonobos, n=12; common chimpanzees,  
839 n=18; gorillas, n=9; orangutans, n=7; fossil hominins, n=10 (80%), n=13 (50%); Miocene apes,  
840 n=3.

841  
842 **Extended Data 6. Cortical bone variation of TM 266-01-063.**  
843 Panels a, b, c. Cross-sectional geometric properties of the TM 266-01-063 femur. a, Location of  
844 transverse microCT-slices at the distal margin of the lesser trochanter (1) and at standard levels of  
845 biomechanical length (2-5). Corresponding percent of cortical area (i.e.,  $CA/TA*100$ ) is given at  
846 80%, 65%, 50% and 35%; b, microCT-slice images of the selected transverse sections; c,  
847 interpretive drawings of the cortical thickness for selected microCT-slice sections, numbers are for  
848 the measured cortical thickness anteriorly, posteriorly, medially and laterally (in mm), maximum  
849 thickness is in red while minimum thickness is in green. TA, total area in  $mm^2$ ; CA, cortical area

850 in mm<sup>2</sup>; %, percent of cortical area. Med. is for medial and Lat. is for lateral. Scale bar is (a) 10  
851 mm; (b) 6 mm.

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

856  
857 Posterior thickening of the cortical bone occurs at about the level of the nutrient foramen, where  
858 the ‘proto-linea aspera’ is the narrowest. The femoral cortical thickness distribution is also  
859 characterized by an anterior thinning, with a proximo-distal gradient. The lateral reinforcement  
860 pattern appears to parallel an insertion area including the *mm. vastus lateralis* and *gluteus maximus*  
861 proximally, and the attachment zone of the *m. vastus intermedius* distally. In medial view, the  
862 relative cortical thickening is restricted to the proximal portion of the femoral shaft, corresponding  
863 to the attachment of the *m. vastus medialis*. The third reinforcement occurs posteriorly at about 35-  
864 55% of the biomechanical length and corresponds to an insertion area delineated by the two *mm.*  
865 *vasti* and comprising the hip adductor and extensor (*m. biceps femoris*) muscles.

866  
867 **Extended Data 7. Comparative CSGP data for the Chadian femur and ulna.**

868 a., b., c., Cross-sectional geometric properties at 80% of the femoral biomechanical length  
869 including percentage of cortical area (a, %CA.), second moments of area (b.,  $I_x/I_y$ , and c.,  $I_{max}/I_{min}$ ).  
870 d., e., f., Cross-sectional geometric properties at 50% of the femoral biomechanical length  
871 including percent of cortical area (d, %CA.), second moments of area (e.,  $I_x/I_y$ , and f.,  $I_{max}/I_{min}$ ). g.,  
872 h., Second moments of area (g.,  $I_{max}/I_{min}$  and h.,  $I_x/I_y$ ) at 50% of the ulna biomechanical length (TM  
873 266-01-050). Extant apes are represented by mean (circle) and standard deviation (whiskers),  
874 whereas isolated circles represent individual values for fossil specimens. See Supplementary Table  
875 S2 specimen list. Ulnar data are from<sup>40,82</sup>. The yellowish frame encompasses the early hominin  
876 range of variation whereas the red dotted lines mark the mean values for *Pan* and extant *Homo*  
877 within each panel. For the femur: modern humans, n=40; chimpanzees, n=20; gorillas, n=23;  
878 orangutans, n=23; Miocene hominoids, n=3; Miocene hominins, n=3; australopiths, n=5; early  
879 *Homo*, n=6; neandertals, n=9. For the ulna: modern humans, n= 19; chimpanzees, n=17; gorillas,  
880 n=14; orangutans, n=14; gibbons, n=16, Australopiths, n=3.

881

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

890 the development of the *calcar femorale* (following<sup>28</sup>); e, microCT- slice images of the sections (i-  
891 vi as in TM 266-01-063) showing expression of the *calcar femorale* transversally (medial to the  
892 right and anterior to the top), and f, corresponding binarized version; g, microCT- slice images of  
893 the sections (i-vi) showing expression of the *calcar femorale* transversally in BAR 1003'00  
894 (acquired from CT-scan data, this study). Scale bar for a, d, 10 mm; b, 6 mm; e, f, 4 mm.

895  
896

#### 897 **Extended Data 9. Calcar femorale morphology in extant hominines.**

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

906

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

912 By contrast, most of our sampled non-human apes do not show any evidence of a columnar and  
913 oblique trabecular bundle. At best, a thin, curved, cancellous bone densification is identifiable in  
914 parasagittal view. In transversal view, the CF, when present, corresponds to a thin ray composed  
915 of few or single trabeculae, contrasting in this aspect with the modern human condition. Besides,  
916 the degree of development of the CF is associated with a relative thickening of the antero-medial  
917 cortical bone, but with a less extent in non-human apes than in modern humans. In modern humans,  
918 the thickening tends to be more medial than antero-medial. This configuration potentially  
919 enlightens the results from<sup>28</sup> showing a lengthened CF in modern humans compared to non-human  
920 apes, as the absolute CF length was measured from the tip of the CF to the exterior cortical  
921 boundary.

922

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

924 a., lateral view; b., anterior view; c., medial view; d. posterior view. All ulnae are from 3D virtual  
925 models, except for A.L. 438-1 (modified from<sup>34</sup>), ALA-VP-2/101 (modified from<sup>32</sup>) and StW 573  
926 (modified from<sup>10</sup>). Scale bar is 40 mm. F and M are for female and male.

927  
928