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► **To cite this version:**

Guillaume Daver, Franck Guy, Hassane Taïssou Mackaye, Andossa Likius, Jean-Renaud Boisserie, et al.. Postcranial evidence of late Miocene hominin bipedalism in Chad. *Nature*, 2022, 609, pp.94-100. 10.1038/s41586-022-04901-z . hal-03760282

HAL Id: hal-03760282

<https://hal.science/hal-03760282>

Submitted on 21 Nov 2022

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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 Africa¹⁻⁴. Bipedality of *Sahelanthropus tchadensis* was hitherto inferred at circa 7 Ma**
40 **in central Africa (Chad) based on cranial evidence⁵⁻⁷. 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*^{5,8}. The fossils were found in the TM Anthracotheriid Unit
55 with biochronological estimates and radiochronological age at circa 7 Ma^{7,9}. 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 cover⁹.

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)¹⁻² 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 hominins¹⁰ (Extended Data 4), correlated with an antetorsion of the long
74 axis of the shaft¹¹. Femoral antetorsion is also reported in archaic fossil apes such as *Ekembo* but
75 is absent in the putative arboreal biped *Danuvius guggenmosi*^{12,13}. 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^{3,4,11}. The neck is compressed anteroposteriorly as in the Miocene ape *D.*
80 *guggenmosi*¹² and hominins²⁻⁴ (but see¹⁴ 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*’³ (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*^{2,4,15}
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*³ (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 01-063⁴. This array of features is compatible with habitual bipedalism in *S. tchadensis*^{3,4,11},
97 considered here as a behavioral response repeated under comparable situations¹⁶, 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 aspects¹⁷ (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*)^{18,19}.
107 Available CT-scan data shows that *S. tchadensis* and *Or. tugenensis* share an oblique (antero-
108 medial to postero-distal) extension of bone thickening²⁰. 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 stimuli²¹, 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 (see¹¹). 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 distribution²². 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 by²³ on anteroposterior and mediolateral
136 subtrochanteric and midshaft femoral dimensions (Supplementary Table S1) yield values from
137 43.5 to 49.4 kg (but see²⁴). 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 in⁴⁰; but see²⁵
140 for estimation of 47.7-50.1 kg) and *Ardipithecus ramidus* (ARA-VP-6/500, 51 kg²⁶).
141 Unsurprisingly, body mass estimates for *S. tchadensis* remain close to the average body mass of
142 *P. troglodytes*, the earliest hominins and australopiths²⁷. 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^{4,11}.

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 1003'00²⁸), early hominins such as *A. afarensis* with

157 MAK-VP-1/1²⁹ and modern humans^{30,31} 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^{28,31}.
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*³² (ALA-VP 2/101) and
179 later hominins (e.g., L 40-19 and OH 36) as well as in African apes^{10,33-35} [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 conditions¹². A recent ulnar curvature analysis³³
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^{35,36}. 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^{35,37}.

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 primates³⁸⁻³⁹. Compared to chimpanzees
198 and orangutans, which tend to grow more bone anteroposteriorly⁴⁰, 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 pronation-supination abilities, indicative
206 of habitual arboreal behaviors, including climbing and/or 'cautious climbing'⁴¹⁻⁴², rather than
207 terrestrial quadrupedalism^{38,41,43}.

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

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. 288-1t⁴⁶.
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*⁴⁶. 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*)^{34,46}. Such a configuration was reported on *D.*
228 *guggenmosi*¹² and is typical of the arboreal large apes that integrate climbing and suspension in
229 their locomotor repertoire⁴⁶ 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 mode⁴⁶. 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*¹², *A. afarensis*⁴⁶, and *A. prometheus*¹⁰. 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^{12,46}.

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^{45,47}. 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 phase⁴⁸. 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^{41,42,49}, and also
251 compatible with the ‘careful climbing’ described in previous studies for *Ar. ramidus*⁴⁵.

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 sensu⁵⁰). 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^{28,31}. 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^{3,15}. While they are part of a primitive functional complex^{1-4,15}, they accord
272 with the overall functional pattern seen in habitual hominin bipeds⁵¹ (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 in⁵²), 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*¹⁵ and presumably *Or. tugenensis*¹ 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^{41, 42, see also 49}, 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’ repertoire⁴², that involves weight-bearing functions for the
285 hindlimbs⁴⁹, as described in previous studies for *Ar. ramidus*⁴⁵, and possibly *Or. tugenensis*⁵³.
286 Hitherto, the femur of *Sahelanthropus* supports an early evidence of habitual bipedalism in the
287 hominin clade^{54,55}, 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^{6,56-58}. 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 divergence²⁶, 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 cover⁵⁹, *Ardipithecus kadabba* (which
297 bipedalism is inferred from foot phalanx AME-VP-1/71 dated to 5.2 Ma³²) is associated with a
298 mixture of woodland combined with wet grassland⁶⁰, *Ar. ramidus* (4.4 Ma from Aramis, Ethiopia)
299 most probably inhabited a ground-water-fed grassy woodland, probably a palm grove^{61,62}.

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)^{9,63}. 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^{58,64-66}. Fossil representatives of the panin clade are very
313 scarce⁶⁷⁻⁶⁸ but, at least three hominine taxa have been described in this time interval Ma in Africa:
314 *Samburupithecus*, from Samburu Hills, around 9.5 Ma⁶⁹, *Nakalipithecus* from Nakali, circa 9.8
315 Ma⁷⁰ and *Chororapithecus* from Chorora, circa 8 Ma^{71,72}. These Miocene taxa are parsimoniously
316 assigned to stem hominines⁷³, even if *Samburupithecus* displays a particularly archaic

317 morphology⁷³. *Chororapithecus* displays derived dental affinities with *Gorilla*⁷¹. 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-P₃ 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 hominoids⁷⁴. 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 sequence⁷⁵
328 are untestable. Instead, our data support the hypothesis that the combination of a non-honing C-P₃
329 complex and habitual bipedalism is a synapomorphic signature of the hominin clade.
330

331 **References**

- 332
- 333 1. Senut, B. *et al.* First hominid from the Miocene (Lukeino formation, Kenya). *C. R. Acad. Sci.*
334 *Paris IIA* **332**, 137-144 (2001).
- 335 2. Pickford, M., Senut, B., Gommery, D., & Treil, J. Bipedalism in *Orrorin tugenensis* revealed by
336 its femora. *C. R. Palevol* **1**, 191-203 (2002).
- 337 3. Almécija, S. *et al.* The femur of *Orrorin tugenensis* exhibits morphometric affinities with both
338 Miocene apes and later hominins. *Nat. Comm.* **4**, 2888 (2013).
- 339 4. Richmond, B. G., & Jungers, W. L. *Orrorin tugenensis* femoral morphology and the evolution
340 of hominin bipedalism. *Science* **319**, 1662-1665 (2008).
- 341 5. Brunet, M. *et al.* A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* **418**,
342 145-151 (2002).
- 343 6. Zollikofer, C. P. *et al.* Virtual cranial reconstruction of *Sahelanthropus tchadensis*. *Nature*, **434**,
344 755-759 (2005).
- 345 7. Lebatard, A. E. *et al.* Cosmogenic nuclide dating of *Sahelanthropus tchadensis* and
346 *Australopithecus bahrelghazali*: Mio-Pliocene hominids from Chad. *Proc. Natl. Acad. Sci. USA*
347 **105**, 3226-3231 (2008).
- 348 8. Brunet, M. *et al.* New material of the earliest hominid from the Upper Miocene of Chad. *Nature*
349 **434**, 752-755 (2005).
- 350 9. Vignaud, P. *et al.* Geology and palaeontology of the Upper Miocene Toros-Menalla hominid
351 locality, Chad. *Nature* **418**, 152-155 (2002).
- 352 10. Heaton, J. L. *et al.* The long limb bones of the StW 573 *Australopithecus* skeleton from
353 Sterkfontein Member 2: Descriptions and proportions. *J. Hum. Evol.* **133**, 167-197 (2019).
- 354 11. Ruff, C. B. Biomechanics of the hip and birth in early *Homo*. *Am. J. Phys. Anthrop.*, **98**(4),
355 527-574 (1995).
- 356 12. Böhme, M. *et al.* A new Miocene ape and locomotion in the ancestor of great apes and humans.
357 *Nature*, **575**, 489-493 (2019).
- 358 13. Williams, S. A. *et al.* Reevaluating bipedalism in *Danuvius*. *Nature*, **586**(7827), E1-E3 (2020).
- 359 14. Pina, M. *Unravelling the positional behaviour of fossil hominoids morphofunctional and*
360 *structural analysis of the primate hindlimb*. Doctoral dissertation, Universitat Autònoma de
361 Barcelona (2016).
- 362 15. Lovejoy, C. O., Suwa, G., Spurlock, L., Asfaw, B., & White, T. D. The pelvis and femur of
363 *Ardipithecus ramidus*: the emergence of upright walking. *Science* **326**, 71e1-71e6 (2009).
- 364 16. Prost, J. H. A definitional system for the classification of primate locomotion. *Am. Anthropol.*,
365 **67**(5), 1198-1214 (1965).
- 366 17. Puymeraill, L. The functionally-related signatures characterizing the endostructural
367 organisation of the femoral shaft in modern humans and chimpanzee. *C. R. Palevol*, **12**(4), 223-
368 231 (2013).
- 369 18. Galik, K. *et al.* External and internal morphology of the BAR 1002'00 *Orrorin tugenensis*
370 femur. *Science* **305**, 1450-1453 (2004).

- 371 19. Ohman, J. C., Lovejoy, C. O., & White, T. D. Questions about *Orrorin* femur. *Science* **307**,
372 845 (2005).
- 373 20. Puymeraul, L. Caractérisation de l'endostructure et des propriétés biomécaniques de la diaphyse
374 fémorale: la signature de la bipédie et la reconstruction des paléo-répertoires posturaux et
375 locomoteurs des hominines (Paris, Muséum national d'histoire naturelle, 2011).
- 376 21. Wallace, I. J. *et al.* Functional significance of genetic variation underlying limb bone
377 diaphyseal structure. *Am. J. Phys. Anthropol.*, **143**(1), 21-30 (2010).
- 378 22. Lieberman, D. E., Polk, J. D., & Demes, B. Predicting long bone loading from cross-sectional
379 geometry. *Am. J. Phys. Anthropol.* **123**, 156-171 (2004).
- 380 23. Grabowski, M., Hatala, K. G., Jungers, W. L. & Richmond, B. G. Body mass estimates of
381 hominin fossils and the evolution of human body size. *J. Hum. Evol.*, **85**, 75-93 (2015).
- 382 24. Ruff, C. B., Burgess, M. L., Squyres, N., Junno, J. A., & Trinkaus, E. Lower limb articular
383 scaling and body mass estimation in Pliocene and Pleistocene hominins. *J. Hum. Evol.* **115**: 85-
384 111 (2018).
- 385 25. Nakatsukasa, M., Pickford, M., Egi, N., & Senut, B. Femur length, body mass, and stature
386 estimates of *Orrorin tugenensis*, a 6 Ma hominid from Kenya. *Primates*. **48**(3), 171-178 (2007).
- 387 26. Lovejoy, C. O. et al. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last
388 common ancestors with African apes. *Science* **326**, 73-106 (2009).
- 389 27. Jungers, W. L., Grabowski, M., Hatala, K. G., & Richmond, B. G. The evolution of body size
390 and shape in the human career. *Phil. Trans. R. Soc. B*, **371**(1698), 20150247 (2016).
- 391 28. Kuperavage, A., Pokrajac, D., Chavanaves, S. & Eckhardt, R. B. Earliest known hominin
392 *calcar femorale* in *Orrorin tugenensis* provides further internal anatomical evidence for origin of
393 human bipedal locomotion. *Anat. Rec.* **301**, 1834-1839 (2018).
- 394 29. Clark, J. D. *et al.* Palaeoanthropological discoveries in the middle Awash Valley, Ethiopia.
395 *Nature*, **307**, 423-428 (1984).
- 396 30. Hammer, A. The calcar femorale: A new perspective. *J. Orthop. Surg.*, **27**(2),
397 2309499019848778 (2019).
- 398 31. Zhang, Q. *et al.* The role of the *calcar femorale* in stress distribution in the proximal femur.
399 *Orthop. surg.*, **1**, 311-316 (2009).
- 400 32. Haile-Selassie, Y., Suwa, G. & White, T. Hominidae. in *Ardipithecus kadabba*: Late Miocene
401 Evidence From The Middle Awash, Ethiopia (eds. Haile-Selassie, Y., & WoldeGabriel, G.) 159-
402 236 (Univ of California Press, 2009).
- 403 33. Araiza, I., Meyer, M. R., & Williams, S. A. Is ulna curvature in the StW 573 ('Little Foot')
404 *Australopithecus* natural or pathological? *J. Hum. Evol.*, **151**, 102927 (2021).
- 405 34. Drapeau, M. S. M., Ward, C. V., Kimbel, W. H., Johanson, D. C., & Rak, Y. Associated cranial
406 and forelimb remains attributed to *Australopithecus afarensis* from Hadar, Ethiopia. *J. Hum. Evol.*
407 48, 593-642 (2005).
- 408 35. Henderson, K., Pantinople, J., McCabe, K., Richards, H. L. & Milne, N. Forelimb bone
409 curvature in terrestrial and arboreal mammals. *PeerJ*, **5**, e3229 (2017).
- 410 36. Drapeau, M. S. M. Functional anatomy of the olecranon process in hominoids and Plio-

411 Pleistocene hominins. *Am. J. Phys. Anthropol.* **124**, 297-314 (2004).

412 37. Milne, N., & Granatosky, M. C. Ulna Curvature in Arboreal and Terrestrial Primates. *J.*
413 *Mammal. Evol.*, **28**, 897-909 (2021).

414 38. Carlson, K.J. et al. Role of nonbehavioral factors in adjusting long bone diaphyseal structure
415 in free-ranging Pan troglodytes. *Int. J. Primatol.* **29**, 1401-1420 (2008).

416 39. Schmitt, D. Mediolateral reaction forces and forelimb anatomy in quadrupedal primates:
417 implications for interpreting locomotor behavior in fossil primates. *J. Hum. Evol.* **44**, 47-58 (2003).

418 40. Nadell, J. *Ontogeny and Adaptation: A Cross-Sectional Study of Primate Limb Elements.*
419 Doctoral dissertation, Durham University (2017).

420 41. Cartmill, M. & Milton, K. The lorisiform wrist joint and the evolution of “brachiating”
421 adaptations in the Hominoidea. *Am. J. Phys. Anthropol.*, **47**, 249-272 (1977).

422 42. Hunt, K. D., et al. Standardized descriptions of primate locomotor and postural modes.
423 *Primates*, **37**, 363-387 (1996).

424 43. Sarmiento, E. E. Anatomy of the hominoid wrist joint: its evolutionary and functional
425 implications. *Int. J. Primatol.*, **9**, 281-345 (1988).

426 44. Begun, D. R. Phyletic diversity and locomotion in primitive European hominids. *Am. J. Phys.*
427 *Anthropol.* **87**, 311-340 (1992).

428 45. Lovejoy, C. O., Simpson, S. W., White, T. D., Asfaw, B., & Suwa, G. Careful climbing in the
429 Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. *Science* **326**, 70e1-
430 70e8 (2009).

431 46. Drapeau, M. S. M. Articular morphology of the proximal ulna in extant and fossil hominoids
432 and hominins. *J. Hum. Evol.* **55**, 86-102 (2008).

433 47. Alba, D. M., Almécija, S., Casanovas-Vilar, I., Méndez, J. M., & Moyà-Solà, S. A partial
434 skeleton of the fossil great ape *Hispanopithecus laietanus* from Can Feu and the mosaic evolution
435 of crown-hominoid positional behaviors. *PLoS ONE* **7**, e39617 (2012).

436 48. Tuttle, R. H. Knuckle-walking and the evolution of hominoid hands. *Am. J. Phys. Anthropol.*,
437 **26**, 171-206 (1967).

438 49. Crompton, R. H., Vereecke, E. E., & Thorpe, S. K. Locomotion and posture from the common
439 hominoid ancestor to fully modern hominins, with special reference to the last common
440 panin/hominin ancestor. *J. Anat.*, **212**, 501-543 (2008).

441 50. Stern, J.T., Susman, R.L., 1991. "Total morphological pattern" versus the "magic trait":
442 Conflicting approaches to the study of early hominid bipedalism. in *Origine(s) de la Bipédie chez*
443 *les Hominidés* (eds. Coppens, Y. & Senut, B.) 99-111 (CNRS, Paris, 1991).

444 51. Kozma, E. E. et al. Hip extensor mechanics and the evolution of walking and climbing
445 capabilities in humans, apes, and fossil hominins. *Proc. Natl. Acad. Sci. USA*, **115**, 4134-4139
446 (2018).

447 52. Macchiarelli, R., Bergeret-Medina, A., Marchi, D., & Wood, B. Nature and relationships of
448 *Sahelanthropus tchadensis*. *J. Hum. Evol.*, **149**, 102898 (2020).

449 53. Gommery, D., & Senut, B. The terminal thumb phalanx of *Orrorin tugenensis* (Upper Miocene
450 of Kenya). *Geobios*, **39**, 372-384 (2006).

- 451 54. Kirscher, U. et al. Age constraints for the Trachilos footprints from Crete. *Scientific reports*,
452 **11**, 1-9 (2021).
- 453 55. Meldrum, J., & Sarmiento, E. Comments on possible Miocene hominin footprints. *Proc. Geol.*
454 *Assoc.*, **129**, 577-580 (2018).
- 455 56. Guy, F. et al. Morphological affinities of the *Sahelanthropus tchadensis* (late Miocene hominid
456 from Chad) cranium. *Proc. Natl. Acad. Sci.*, **102**, 18836-18841 (2005).
- 457 57. Neaux, D. et al. Relationship between foramen magnum position and locomotion in extant and
458 extinct hominoids. *J. Hum. Evol.*, **113**, 1-9 (2017).
- 459 58. Pilbeam, D. R. & Lieberman, D. E. Reconstructing the last common ancestors of chimpanzees
460 and humans. in *Chimpanzees and Human evolution* (eds Muller, M. N., Wrangham, R. W. &
461 Pilbeam, D. R.) 22-141 (Belknap Harvard, Cambridge, 2017).
- 462 59. Senut, B., Pickford, M., Gommery, D., & Ségalen, L. Palaeoenvironments and the origin of
463 hominid bipedalism. *Hist. Biol.*, **30**, 284-296 (2018).
- 464 60. WoldeGabriel, G. et al. Geology and palaeontology of the late Miocene Middle Awash valley,
465 Afar rift, Ethiopia. *Nature*, **412**, 175-178 (2001).
- 466 61. White, T. D. et al. Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus*
467 *ramidus*. *Science* **326**, 67-93 (2009).
- 468 62. Barboni, D., Ashley, G. M., Bourel, B., Arraiz, H. & Mazur, J. C. Springs, palm groves, and
469 the record of early hominins in Africa. *Rev. Palaeobot. Palynol.* **266**, 23-41 (2019).
- 470 63. Novello, A. et al. Phytoliths indicate significant arboreal cover at *Sahelanthropus* type locality
471 TM266 in northern Chad and a decrease in later sites. *J. Hum. Evol.* **106**, 66-83 (2017).
- 472 64. Steiper, M. E., & Seiffert, E. R. Evidence for a convergent slowdown in primate molecular
473 rates and its implications for the timing of early primate evolution. *Proc. Natl. Acad. Sci.*, **109**,
474 6006-6011 (2012).
- 475 65. Püschel, H. P., Bertrand, O. C., O'reilly, J. E., Bobe, R., & Püschel, T. A. Divergence-time
476 estimates for hominins provide insight into encephalization and body mass trends in human
477 evolution. *Nat. Ecol. Evol.*, **5**, 808-819 (2021).
- 478 66. Besenbacher, S., Hvilsom, C., Marques-Bonet, T., Mailund, T., & Schierup, M. H. Direct
479 estimation of mutations in great apes reconciles phylogenetic dating. *Nat. Ecol. Evol.*, **3**, 286-292
480 (2019).
- 481 67. McBrearty, S. & Jablonski, N. G. First fossil chimpanzee. *Nature* **437**, 105-108 (2005).
- 482 68. DeSilva, J., Shoreman, E. & MacLatchy, L. A fossil hominoid proximal femur from Kikorongo
483 Crater, southwestern Uganda. *J. Hum. Evol.* **50**, 687-695 (2006).
- 484 69. Ishida H. & Pickford M. A new late Miocene hominoid from Kenya: *Samburupithecus*
485 *kiptalami* gen. et sp. nov. *C.R. Acad. Sci. Paris*, **325**, 823-829 (1997).
- 486 70. Kanimatsu, Y. et al. A new Late Miocene great ape from Kenya and its implications for the
487 origins of African great apes and humans. *Proc. Natl Acad. Sci. USA* **104**, 19220-19225 (2007).
- 488 71. Suwa G., Kono R.T., Katoh S., Asfaw B. & Beyene Y. A new species of great ape from the
489 late Miocene epoch in Ethiopia. *Nature* **448**, 921-924 (2007).
- 490 72. Katoh, S. et al. New geological and palaeontological age constraint for the gorilla-human

491 lineage split. *Nature* **530**, 215-218 (2016).
492 73. Begun, D.R. Fossil record of Miocene hominoids in *Handbook of Paleoanthropology*, (eds.
493 Henke, W. & Tattersall, I.) 1261 - 1332 (Springer-Verlag, Berlin Heidelberg, 2015).
494 74. Mongle, C.S., Strait, D.S., Grine, F.E. Expanded character sampling underscores phylogenetic
495 stability of *Ardipithecus ramidus* as a basal hominin. *J. Hum. Evol.*, **131**, 28–39 (2019).
496 75. Wood, B. & Harrison, T. The evolutionary context of the first hominins. *Nature* **470**: 347-352
497 (2011).
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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 nekoulnc@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, μ 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 software⁷⁶ on 2D slices. For comparative purposes, individual
545 cortical bone thickness were divided by their maximal thickness.

546

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^{77,78}. 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^{79,80}. 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 software⁷⁶ and EPMacroJ plugins⁸¹. 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^{40,82} 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.

573

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 v2.31⁸³. 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^{1,2,84} and the curvature observed from cast and original CT-scans
587 data (data used in^{20,52}) 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 from¹⁰.

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 v2.31⁸³. 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^{85,86} for R v. 4.0.3⁸⁷. 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 analysis⁵², as the later may induce misinterpretations and introduce biases in
609 the case of small sample size^{88,89}.

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
618 software⁷⁶.

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620

621 76. Schindelin, J. et al. Fiji: an open-source platform for biological-image analysis. *Nature methods*
622 **9**, 676-682 (2012).

623 77. Mongle, C. S., Wallace, I. J. & Grine, F. E. Cross-sectional structural variation relative to
624 midshaft along hominine diaphyses. II. The hind limb. *Am. J. Phys. Anthropol.* **158**, 398- 407
625 (2015).

626 78. Puymeraul, L. et al. Structural analysis of the Kresna 11 *Homo erectus* femoral shaft (Sangiran,
627 Java). *J. Hum. Evol.* **63**, 741-749 (2012).

628 79. Ruff, C. B., McHenry, H. M., & Thackeray, J. F. Cross-sectional morphology of the SK 82 and
629 97 proximal femora. *Am. J. Phys. Anthropol.*, **109**, 509-521 (1999).

630 80. Ruff, C. B. Long bone articular and diaphyseal structure in Old World monkeys and apes. I:
631 locomotor effects. *Am. J. Phys. Anthropol.* **119**, 305-342 (2002).

632 81. Sládek, J. et al. Effect of deriving periosteal and endosteal contours from microCT scans on
633 computation of cross-sectional properties in non-adults: the femur. *J Anat.* **233**, 381-393 (2018).

634 82. Ruff, C. E., Higgins, R. W., Carlson, K. J. Long bone cross-sectional geometry. in *Hominin*
635 *Postcranial Remains from Sterkfontein, South Africa, 1936-1995* (eds Zipfel, B., Richmond B. G.,
636 Ward, C.) 307-320 (Oxford University Press, 2020).

637 83. Rohlf, F. J. 2005. *tpsDig, digitize landmarks and outlines*, version 2.05. Department of Ecology
638 and Evolution, State University of New York at Stony Brook.

639 84. Senut, B. Bipédie et climat. *C. R. Palevol*, **5**, 89-98 (2006).

640 85. Adams D, Collyer M, Kaliontzopoulou A, Baken E. *Geomorph: Software for geometric*
641 *morphometric analyses*. R package version 4.0. <https://cran.r-project.org/package=geomorph>,
642 (2021).

643 86. Baken, E. K., Collyer, M. L., Kaliontzopoulou, A., & Adams, D. C. Geomorph v4.0 and
644 gmShiny: Enhanced analytics and a new graphical interface for a comprehensive morphometric
645 experience. *Meth. Ecol. Evol.*, **12**, 2355-2363 (2021).

646 87. R Core Team R. A language and environment for statistical computing. R Foundation for
647 Statistical Computing, Vienna, Austria. <https://www.R-project.org> (2021).

648 88. Bookstein, F.L. Pathologies of Between-Groups Principal Components Analysis in Geometric
649 Morphometrics. *Evol. Biol.* **46**, 271–302 (2019)

650 89. Cardini, A., O’Higgins, P. & Rohlf, F. J. Seeing Distinct Groups Where There are None:
651 Spurious Patterns from Between-Group PCA. *Evol. Biol.*, **46**, 303–316 (2019).

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654

655 **Acknowledgments** We thank for their unreserved support: the Chadian Ministère de
656 l'Enseignement Supérieur, de la Recherche Scientifique et de l'Innovation and Centre National de
657 Recherche pour le Développement (CNRD), the University of N'Djaména, the University of
658 Poitiers, the CNRS, the French Ministère de l'Europe et des affaires étrangères, the Embassy of
659 France to Chad, the region Nouvelle Aquitaine (project AH-HEM, NA2018-195586), as well as
660 the French Army (MAM, Épervier and Barkhane) for its logistic support. We especially thank
661 Mahamoud Youssouf Khayal and Baba Mallah (Director of the CNRD) and for their support.
662 We deeply thank all the MPFT members who participated to the field missions, particularly
663 Ahounta D., Fanoné G. (deceased), Mahamat A., F. Lihoreau and J. Surault.
664 We would like to especially thank M. Brunet, head of the MPFT, for initiating this work and
665 gathering the first comparative data at the basis of the present manuscript. We are very grateful to
666 the following institutions and colleagues who granted M. Brunet and us access to their collections,
667 as well as all the participants who contributed to the field research that collected these specimens:
668 Musée Royal d'Afrique Centrale at Tervuren (E. Gillissen), National Museum of Ethiopia,
669 National Museums of Kenya, Universitair Ziekenhuis at Leuven (W. Coudyzer), University of the
670 Witwatersrand, B. Asfaw (Rift Valley Research Service), Y. Haile-Selassie (Cleveland Museum
671 of Natural History), D. Johanson and W. Kimbel (Institute of Human Origins and Arizona State
672 University at Tempe), C.O. Lovejoy (Kent State University), M. G. Leakey and R. Leakey, D.
673 Pilbeam (Peabody Museum and Harvard University), T. White (University of California at
674 Berkeley) and G. Suwa (University Museum of Tokyo), and B. Zipfel (University of the
675 Witwatersrand) for facilitating access to the South African hominin material, including the StW
676 573m femur. We are most thankful to G. Berillon, J. Braga, K. Carlson, R. Clarke, Quentin
677 Cosnefroy, R. Crompton, J. Heaton, J. Kappelman, F. Marchal, M. Pina, D. Stratford, and M.
678 Tocheri for kindly providing comparative data and valuable comments.
679 We are especially grateful to B. Senut, M. Pickford and D. Gommery for stimulating discussions
680 and granting access to the CT-scan and cast material of *Orrorin tugenensis*. In this regard, we also
681 thank the Orrorin Community Organisation and the Kenya Ministry of Education, Science and
682 Technology. The CT scans were done at the Clinique Pasteur (Mr Jean-Pierre Deymier, Dr Franck
683 Berthoumieu, Georges Larrouy, Sylvie Charreau, Alfred M'Voto and Pascal Roch). Warm
684 acknowledgements are due to Kiptalam Cheboi and the Tugen palaeontology field team.
685 Special thanks to all our colleagues and friends for their help and discussion, and particularly to D.
686 Barboni, A. Mazurier (Plateforme Platina, IC2MP), A. Novello, J. Surault. We also thank S.
687 Riffaut, J. Surault and X. Valentin for technical support. We are most grateful to G. Florent, C.
688 Noël, G. Reynaud, C. Baron, M. Pourade, and L. Painault for administrative guidance. We greatly
689 thank D. Lieberman, C. Ruff and one anonymous reviewer for their valuable comments on the
690 earlier versions of our manuscript.

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.,

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

696

697 **Data and code availability**

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

706

707 **Funding** funding provided by PALEVOPRIM and project AH-HEM (NA2018-195586).

708

709 **Competing interests** The authors declare no competing interests.

710

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

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 PC₁₋₂ 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.

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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^{2,84}), BAR 1002'00
780 (*Or. tugenensis*, acquired from CT-scan data, as published in⁵²), 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 in¹⁰) 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^{2,84}), and BAR 1002'00** (*Or. tugenensis*, acquired from CT-scan data,
788 as appears in⁵²). 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^{2,84}), and BAR 1002'00**
798 (*Or. tugenensis*, acquired from CT-scan data, as appears in⁵²).

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° counterclockwise, relative to mediolateral axis; Ft_2 : 153.2° counterclockwise,
830 relative to mediolateral axis; DT is 38.5°. 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 mm²; %, 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^{40,82}. 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* (following²⁸); 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 from²⁸ 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 from³⁴), ALA-VP-2/101 (modified from³²) and StW 573
926 (modified from¹⁰). Scale bar is 40 mm. F and M are for female and male.

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928