



New femoral remains of *Nacholapithecus kerioi*: Implications for intraspecific variation and Miocene hominoid evolution

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1 New femoral remains of *Nacholapithecus kerioi*: implications for intraspecific variation
2 and Miocene hominoid evolution

3

4 **Abstract**

5 The middle Miocene stem kenyapithecine, *Nacholapithecus kerioi* (16–15 Ma; Nachola,
6 Kenya), is represented by a large number of isolated fossil remains and one of the most
7 complete skeletons in the hominoid fossil record (KNM-BG 35250). Multiple fieldwork
8 seasons performed by Japanese-Kenyan teams during the last part of the 20th century
9 resulted in the discovery of a large sample of *Nacholapithecus* fossils. Here, we
10 describe new femoral remains of *Nacholapithecus*. In well-preserved specimens, we
11 evaluate sex differences and within-species variation using both qualitative and
12 quantitative traits. We use these data to determine whether these specimens are
13 morphologically similar to the species holotype KNM-BG 35250 (which shows some
14 plastic deformation), and to compare *Nacholapithecus* with other Miocene hominoids
15 and extant anthropoids to evaluate the distinctiveness of its femur. The new fossil
16 evidence reaffirms previously reported descriptions of some distal femoral traits,
17 namely the morphology of the patellar groove. However, results also show that relative
18 femoral head size in *Nacholapithecus* is smaller, relative neck length is longer, and
19 neck-shaft angle is lower than previously reported for KNM-BG 35250. These traits
20 have a strong functional signal related to the hip joint kinematics, suggesting that the
21 morphology of the proximal femur in *Nacholapithecus* might be functionally related to
22 quadrupedal-like behaviors instead of more derived antipronograde locomotor modes.
23 Results further demonstrate that other African Miocene apes (with the exception of
24 *Turkanapithecus kalakolensis*) generally fall within the *Nacholapithecus* range of
25 variation, whose overall femoral shape resembles that of *Ekembo* spp. and *Equatorius*

26 *africanus*. Our results accord with the previously inferred locomotor repertoire of
27 *Nacholapithecus*, indicating a combination of generalized arboreal quadrupedalism
28 combined with other antipronograde behaviors (e.g., vertical climbing).

29

30 **Keywords:** Miocene hominoids; Femur; Functional morphology; Positional behavior

31

32 **1. Introduction**

33 *Nacholapithecus kerioi* is an extinct hominoid (subfamily Kenyapithecinae, tribe
34 Equatorini) known from the middle Miocene of Kenya (Ishida et al., 1999). Fossil
35 remains belonging to this taxon were found within the Aka Aitheputh Formation
36 (Samburu County, Kenya) in Nachola (Fig. 1), that have been dated at 16–15 Ma
37 (Nakatsukasa et al., 1998; Sawada et al., 1998; Ishida et al., 1999; Nakatsukasa and
38 Kunimatsu, 2009). Originally, the material found in this area was attributed to the genus
39 *Kenyapithecus*, either as *Kenyapithecus* sp. or *Kenyapithecus* cf. *africanus*, by several
40 authors (Ishida et al., 1984; Rose et al., 1996; Nakatsukasa et al., 1998). Later, Ishida
41 and colleagues (1999) erected the new genus and species *Nacholapithecus kerioi* with
42 sufficient evidence to differentiate this taxon from other fossil hominoids.

43 Initial studies of the postcranial anatomy of *Nacholapithecus* were based on two
44 dozen isolated fossil remains collected in the 1980s (most described by Rose et al.,
45 1996) and a partial skeleton (holotype, KNM-BG 35250), as well as some other
46 specimens recovered in the 1990s (Rose et al., 1996; Nakatsukasa et al., 1998, 2003a, b,
47 2007a, b, 2012; Ishida et al., 2004; Senut et al., 2004; Nakatsukasa and Kunimatsu,
48 2009; Pina et al., 2018; Takano et al., 2018, 2020). The basic body plan of
49 *Nacholapithecus* (e.g., narrow thorax and long lumbar spine) is similar to that of
50 *Ekembo* spp., which are considered arboreal quadrupeds engaging in cautious climbing

51 and clambering (Ward, 2015). However, *Nacholapithecus* also shows more derived
52 features, such as longer pedal digits, an anterior projection of the ulnar coronoid
53 process, a more mobile humeroradial joint, and a higher femoral neck-shaft angle
54 (Nakatsukasa et al., 1998, 2004, 2007a; Ishida et al., 2004; Takano et al., 2018, 2020).
55 These derived features provide insights into the positional behavior of *Nacholapithecus*,
56 which includes some of the earliest evidence of forelimb-dominated behaviors with the
57 enhancement of vertical climbing capabilities. No specific adaptations for below-branch
58 suspension have been identified, although this positional behavior cannot be completely
59 discarded on the basis of the current evidence (Nakatsukasa and Kunimatsu, 2009;
60 Takano et al., 2018, 2020).

61 Fortunately, the Nachola area is very rich in fossil remains, and excavations
62 since 2000 have unearthed a large number of fossils attributed to *Nacholapithecus*,
63 resulting in an impressive and unusual collection in comparison with those of other
64 Miocene hominoid taxa. The *Nacholapithecus* fossil collection comprises several fossils
65 representing the same anatomical element, providing an opportunity to assess
66 intraspecific morphological variation, which is rare within the hominoid fossil record.
67 During the past decade, a number of studies have published on these specimens
68 (Kikuchi et al., 2012, 2015, 2016, 2018; Ogihara et al., 2016; Takano et al., 2020).

69 An initial body mass of 20–23 kg was estimated for *Nacholapithecus* males
70 (Rose et al., 1996; Ishida et al., 2004; Nakatsukasa and Kunimatsu, 2009). Recently,
71 Kikuchi et al. (2018) estimated body mass from femoral head dimensions obtained from
72 12 fragments (see Kikuchi et al., 2018: Table 2). These authors reported the presence of
73 marked sexual dimorphism in *Nacholapithecus*' body mass, with males estimated at an
74 average of two times the body mass of females (see also Ishida et al., 1991 for sexual
75 dimorphism estimated from the canines). They assigned six femora of the sample to

76 males (larger) and six to females (smaller) based on their body mass results. Kikuchi et
77 al. (2018) briefly described the femoral specimens, but their focus was on investigating
78 sexual dimorphism. In addition, they were highly selective and did not use specimens
79 with damaged femoral heads. Thus, femoral anatomical features and their functional
80 implications have not been thoroughly addressed.

81 This study focuses on reporting and describing femoral remains attributed to
82 *Nacholapithecus*, as well as investigating the range of intraspecific variation and sex
83 differences in this taxon using a combination of qualitative and quantitative traits. We
84 use these data to determine the extent to which the well-preserved *Nacholapithecus*
85 femora are similar to those of the holotype (whose distorted nature has been reported
86 elsewhere; e.g., Nakatsukasa et al., 2012). We further compare *Nacholapithecus* with
87 other African and Eurasian Miocene hominoids and extant anthropoids. Collectively,
88 these comparisons and analyses allow us to review the *Nacholapithecus* species
89 diagnosis and morphology in detail, and to evaluate the distinctiveness of its femur. A
90 well-defined femoral morphology diagnosis will contribute to a better understanding of
91 the *Nacholapithecus* positional behavior and its role within the locomotor evolution of
92 the Hominoidea.

93

94 **2. Materials and methods**

95 *2.1. Samples*

96 The femoral material from the Nachola fossil sites housed at the National
97 Museums of Kenya (Nairobi) labeled as '*Nacholapithecus*', '*Kenyapithecus* sp.', and
98 'Hominoidea' was reviewed to evaluate its taxonomic diagnosis at the species level. A
99 total of 28 femoral remains was available for *Nacholapithecus* (Table 1).

100 Owing to taphonomic damage (described in detail below), morphometric
101 comparisons are limited and only possible for a reduced number of femoral fragments
102 (see Table 1). When possible (exclusively in nondistorted, nondamaged
103 specimens/regions), selected measurements were taken and then used to quantitatively
104 compare *Nacholapithecus* with other African and Eurasian Miocene hominoids and a
105 wide range of extant anthropoid primates, including platyrrhines, colobines,
106 cercopithecines and hominoids (Fig. 2; Table 2). The Miocene hominoid sample (Fig. 3;
107 taxonomy after Alba, 2012) includes: the afropithecid *Morotopithecus bishopi* (UMP
108 MORII 94'80; MacLatchy et al., 2000); the proconsulids *Proconsul major* (combination
109 of NAP IX 46'99, NAP IX B 64, NAP IX 65 P. 67 fragments; Gommery et al., 1998,
110 2002; Senut et al., 2000), *Turkanapithecus kalakolensis* (KNM-WK 16950I; Leakey et
111 al., 1988), *Ekembo nyanzae* (KNM-MW 13142A and KNM-RU 5527; Harrison, 1982;
112 Ward et al., 1993), the kenyapithecine *Equatorius africanus* (BMNH M.16331; BMNH
113 M.16332-3 is used for qualitative comparisons only; Le Gros Clark and Leakey, 1951;
114 McCrossin, 1994), and the dryopithecines *Dryopithecus fontani* (IPS 41724; Moyà-Solà
115 et al., 2009; Pina et al., 2019) and *Hispanopithecus laietanus* (IPS 18800.29; Moyà-Solà
116 and Köhler, 1996; Pina et al., 2012).

117

118 2.2. Measurements

119 Linear measurements of the proximal femur were taken to the nearest 0.1 mm
120 using digital calipers (Fig. 2). Superoinferior heights of the femoral head (SIH) and
121 femoral neck (SIN), and anteroposterior depth (APN) of the femoral neck were used to
122 create an index of the relative size of the head: $SIH/(\sqrt{SIN*APN})$. Relative length of the
123 femoral neck (relative NL) was estimated by dividing neck length by the total
124 mediolateral width of the proximal end of the femur (TotW; relative NL = NL/TotW x

125 100). Neck-shaft angle (NSangle) was measured from photographs of femora in anterior
126 view using Fiji version 2.0 (Schindelin et al., 2012). The SIH/(ÖSIN*APN) and the
127 NSangle have been traditionally associated with range of hip excursion and joint
128 mobility (the larger the relative size of the head and the NSangle, the greater the motion
129 of the joint), whereas relative NL has been related to the actions of the gluteal muscles
130 during locomotion (the longer the length, the greater the length of the moment arm of
131 the muscles and bending forces supported; Fleagle and Meldrum, 1988; Ruff, 1988;
132 Aiello and Dean, 1990; Lovejoy et al., 2002; Harmon, 2007).

133

134 2.3. Analyses

135 Descriptive statistics (sample sizes, means, standard deviations and ranges) were
136 computed for the SIH/(ÖSIN*APN), relative NL, and NSangle in *Nacholapithecus*
137 (Table 3; see also Table 1 for *Nacholapithecus* raw data and Supplementary Online
138 Material [SOM] Table S1). Boxplots were used to visualize the range of within-species
139 variation and to examine whether *Nacholapithecus* femoral morphology is distinctive
140 from that of other African and European Miocene hominoids.

141 Quantitative statistical analyses were used to evaluate differences in
142 SIH/(ÖSIN*APN), relative NL, and NSangle between male and female
143 *Nacholapithecus*. Sex assignment follows the classification provided in Kikuchi et al.
144 (2018; Table 1). In addition, comparisons among *Nacholapithecus* (sexes pooled) and
145 extant anthropoids were also carried out to check for potential differences/similarities
146 and defining locomotor affinities. The Shapiro-Wilk test was used to check for
147 normality of the data. The null hypothesis of normally distributed data could not be
148 rejected ($p > 0.05$) for relative NL and NSangle, but the ratio of SIH/(ÖSIN*APN) was
149 not normally distributed ($p < 0.001$). Thus, to evaluate sexual dimorphism, mean

150 differences between male and female *Nacholapithecus* were tested using the two-tailed
151 Student's t-test for NL and NSangle and the nonparametric Mann-Whitney U test for
152 SIH/(ÖSIN*APN). Likewise, for comparisons of relative NL and NSangle between
153 *Nacholapithecus* and extant anthropoids, the parametric analysis of variance (ANOVA)
154 was used along with Student's t-tests for post-hoc comparisons between species,
155 whereas the nonparametric Kruskal-Wallis and Mann-Whitney U tests were used for
156 SIH/(ÖSIN*APN). The Bonferroni method was used to adjust for all multiple pairwise
157 comparisons for every variable. All analyses were performed using the statistical
158 package R v. 3.6 (R Core Group, 2017).

159 In addition to quantitative analyses, some morphological traits of the
160 *Nacholapithecus* femora were also qualitatively compared with those of other Miocene
161 hominoids (including African and Eurasian taxa) to better define the distinctiveness of
162 the *Nacholapithecus* femoral shape.

163

164 **3. Results**

165 *3.1. Morphological descriptions of femoral fragments attributed to Nacholapithecus*
166 KNM-BG 17778 This small head fragment was mentioned previously in Ishida et al.
167 (2004) and Nakatsukasa et al. (2012), but has not been formally described (Fig. 4A–B).
168 It is a half-head fragment with a short portion (ca. 4 mm) of the neck. The position and
169 shape of the fovea capitis suggest that it is an anterior hemi-sphere of a left femoral
170 head. The epiphysis is fused. Its small size (SIH = 17.7 mm) indicates it probably
171 belonged to a female.

172 KNM-BG 40844 A femoral head fragment, probably right (Fig. 4C–D). The fragment
173 bears no epiphyseal line and this, together with its small size (ca. 14 mm

174 anteroposteriorly and ca. 13 mm proximodistally) suggests it belongs to an adult female.
175 The fovea capitis is marked and placed in the distal half of the head.

176 KNM-BG 40964 A right proximal femur missing the neck, the head and part of the
177 greater trochanter (Fig. 4E–F). The whole fragment is compressed anteroposteriorly.
178 The lesser trochanter is damaged. Since juvenile specimens have been recovered in the
179 same locality, the possibility that this femur belonged to an immature individual cannot
180 be precluded. However, its size is consistent with that of adult female specimens.

181 KNM-BG 42757 A left proximal femoral fragment (Fig. 4G–J). Although it preserves
182 all the gross anatomical structures, both the epiphysis and the shaft are severely crushed
183 anteroposteriorly (see Fig. 4I). It likely belonged to a male specimen due to its large size
184 (SIH = 24.8 mm). Despite its deformation, the femoral head shows a circular shape in
185 anterior view and is positioned slightly below the most proximal peak of the greater
186 trochanter. The notch between the greater trochanter and the head appears to be wide
187 and deep.

188 KNM-BG 44953 This specimen includes a right and a left femur and some left hip
189 bone fragments. The right femur (44953A) was described by Kikuchi et al. (2018) and
190 the left counterpart (44953B) is described here (Fig. 4K–M). It is a left proximal femur
191 fragment which lacks most proximal structures, i.e., the head, part of the neck, and the
192 greater trochanter. This fragment is anteroposteriorly compressed. The lesser trochanter
193 is slightly eroded and faces completely posteriorly. However, this morphology is
194 probably a result of deformation (Fig. 4L).

195 KNM-BG 42779 A shaft fragment (ca. 91 mm) probably belonging to the most distal
196 part of the diaphysis, without the distal epiphysis and any diagnostic trait available (Fig.
197 4N–P). It is crushed anteroposteriorly. Due to its large size, this femoral fragment likely
198 belonged to a male.

199 KNM-BG 42738/42756C This proximal femur was recovered from site BG-I west (Fig.
200 5A–C), together with more than 30 other skeletal elements. Although this collection is
201 still being sorted, most of the elements represent a single young adult male. We include
202 this element in our report since it is associated with the KNM-BG 42732 distal femur
203 fragment described below (Fig. 5F–I). A distal femoral shaft of the right counterpart is
204 also described below (KNM-BG 42722; Fig. 5D, E).

205 KNM-BG 42738/42759C is a ca. 51 mm (proximodistally) long proximal
206 portion of a left femur (Fig. 5A–C). Although Kikuchi et al. (2018) described it briefly,
207 we believe this specimen deserves a more detailed description. It comprises two large
208 pieces (the head/neck portion and the shaft/greater trochanter portion) that join
209 perfectly. The tip of the greater trochanter is missing and the lesser trochanter is broken
210 off from the base. The shaft is lost distally from the lesser trochanter base. The
211 epiphyseal line of the head is completely fused and not visible. The head is almost
212 intact, although the cortex is partially worn out on the anterior and posteroinferior
213 aspects. The articular surface is wide anteriorly and posteriorly. In proximal view, the
214 head is offset slightly anteriorly and weakly rotated posteriorly (Fig. 5A). The head and
215 neck surfaces are more confluent in posterior view. However, the center of the head is
216 almost on the central axis of the neck in proximal view. The fovea is lightly weathered
217 and is located in the posteroinferior quarter of the articular surface. The cross-section of
218 the neck is kidney-shaped. It is weakly concave anteriorly, convex posteriorly, and the
219 inferior part is thicker than the superior part. The SIN = 16.5 mm and APN = 12.9 mm.
220 The neck-shaft angle is 121°. The crista trochanterica is present on the neck (Fig. 5C).
221 The posterior bar of the trochanteric fossa is well developed and runs to the base of the
222 lesser trochanter. The posterior cortex of the shaft is badly damaged and displaced to the
223 medullary cavity. The anterior cortex is also fractured, though to a lesser degree, and

224 displaced posteriorly, leaving a wide but shallow depression. The distal part of the great
225 trochanter is protuberant laterally and slightly anteriorly (Fig. 5B, C). Distal and
226 posterior to this protuberance is a small swelling along the distal break. This might be
227 the most proximal part of the lower eminence of the gluteal tuberosity.

228 The shaft is ca. 26.5 mm wide (mediolaterally) and is markedly compressed
229 anteroposteriorly at the distal break point. Despite this compression, the anterior cortex
230 thickness (3.1 mm) is well preserved and not distorted (the posterior thickness is
231 difficult to determine, since the cortex looks affected by the compression).

232 KNM-BG 42722 This specimen is a ca. 61 mm long distal shaft piece of a right femur
233 belonging to the same individual as KNM-BG 42732 and KNM-BG 42738/42756C
234 (Fig. 5). It measures >15 mm mediolaterally, 12.8 mm anteroposteriorly at the proximal
235 break point, and 18.0 mm mediolaterally and 14.1 mm anteroposteriorly at the distal
236 break point. Since the breaks are covered by matrix, cortex is not clearly visible.
237 Surface features are not well developed (Fig. 5D–E). However, two blunt ridges are
238 discernible, which help to identify the anatomical position of this fragment when it is
239 compared with the distal femur of *Eq. africanus* (BNMH M 16332-3; SOM Fig. S1).
240 One of the two ridges, which is sharper at the distal break point, is a continuation from
241 the lateral supra-epicondylar line. The other more rounded ridge divides the shaft
242 surface into the posterior and medial surfaces. The posterior surface is weakly convex
243 mediolaterally. The medial, anterior and lateral surfaces are not clearly differentiated.
244 The shaft cross-section is not symmetrical mediolaterally. Regarding the anteroposterior
245 axis, the medial half is wider than the lateral one.

246

247 KNM-BG 42732 This distal femur is associated with the KNM-BG 42738/42756C
248 proximal femur described by Kikuchi et al. (2018; see above). A distal femoral shaft of
249 the right counterpart is also associated (KNM-BG 42722; see above).

250 This specimen is a ca. 68 mm long distal portion of a left femur (Fig. 5F–I). The
251 epiphyseal line is visible all around where the epiphysis is preserved. It lacks the lateral
252 condyle (and epicondyle). The medial condyle is intact. The width of the medial
253 condyle is 15.6 mm and is visually comparable with that of the left femur (KNM-BG
254 35250J) of the holotype specimen (Ishida et al., 2004). Plastic deformation is minor, as
255 is the distortion (slightly stronger on the lateral side of the shaft). The diaphyseal part
256 suffered notably from erosion. At the level of the proximal break point, which is 45 mm
257 apart from the epiphyseal line on the medial side, the original cortex remains only as a
258 very small (ca. 4 mm wide) portion on the anteromedial surface (Fig. 5I). The break is
259 13.4 mm wide and 12.4 mm thick when the missing outer cortex is not taken into
260 account. Assuming a thickness of the eroded outer layer of cortex of 1 mm (an estimate
261 based on photogrammetry), the original dimension of the break would not exceed 16
262 mm mediolaterally and 15 mm anteroposteriorly. This shaft is rather thin, especially
263 anteroposteriorly when compared with the distal femoral end, probably because it likely
264 belonged to a young adult (note the diaphyseal line in Figure 5F, G). In the femur of *Eq.*
265 *africanus* from Maboko (BNMH M 16332-3: Le Gros Clark and Leakey, 1951), the
266 anteroposterior thickness at an equivalent point is ca. 18 mm (measurement taken from
267 a museum-produced cast). The medial supra-epicondylar ridge is discernible although it
268 is damaged by erosion. The lateral supra-epicondylar ridge (line) is less clear.

269 The distal end is approximately 32 mm anteroposteriorly (in anatomical position
270 and measured at the midpoint of the proximodistal height of the medial condyle). The
271 medial condyle is mediolaterally wide (ca. 15.6 mm) relative to the epiphysis (Fig. 5H).

272 The pit-like insertion for the collateral ligament is well marked on the medial
273 epicondyle. The rim of the medial condyle is posteriorly and distally intact. However,
274 both the anterior part of this rim and the continuing medial rim of the patellar surface is
275 eroded. This damage probably reduced the articular surface width by ~1-2 mm. The
276 lateral patellar surface rim is more eroded than the medial rim. However, the proximal
277 border of the patellar surface is intact and the proximodistal height of both the medial
278 and lateral surface rims are similar, resulting in a quadrilateral shape for the patellar
279 surface. The medial two-thirds of the intercondylar notch is preserved. A round
280 depression is observed on the lateral side of the medial condyle proximally, which is
281 likely the attachment area of the posterior cruciate ligament. Otherwise, there are no
282 remarkable features (e.g., buttresses: MacLatchy et al., 2000) observed.

283 The two specimens described below belong to previously described femoral
284 remains from Nachola, whose former attributions (either anatomical or taxonomic) are
285 revised here:

286 KNM-BG 15533 This fragment was formerly described as a partial femoral head by
287 Rose et al. (1996). However, the articular surface shows an anteroposterior compression
288 that is typical of the humeral head of this taxon (SOM Fig. S2A).

289 KNM-BG 15536 This is a femoral head fragment described by Rose et al. (1996) as
290 belonging to *Nacholapithecus* (then *Kenyapithecus* sp.). However, the morphology
291 around the fovea capitis (shallow and with an irregular articular surface depression
292 adjacent to the fovea, with distinct bone absorptive pits) is not common among the
293 femoral heads of this taxon. This femur fragment may, therefore, belong to another
294 nonprimate mammal (SOM Fig. S2B).

295

296 3.2. *Within-species variation in Nacholapithecus and sex differences*

297 A summary of the main femoral traits described in this study and discussed in
298 the literature for *Nacholapithecus* can be found in SOM Table S2.

299 In quantitative terms, the range of variation is moderately narrow for
300 $SIH/(\ddot{O}SIN*APN)$ and relative NL in *Nacholapithecus* (Fig. 6A₂B), whereas it is greater
301 for the NSangle (Fig. 6C). Previous authors have noted that the KNM-BG 35250A
302 holotype femur could show some plastic deformation (Fig. 7H). In our results, KNM-
303 BG 35250A falls in an intermediate position within the *Nacholapithecus* range of
304 variation for the relative femoral head size (Fig. 6A). On the other hand, excepting
305 KNM-BG 40826 (whose NSangle value should be considered with caution given the
306 fragmentary nature of this specimen), all the remaining *Nacholapithecus* specimens
307 show NSangle values below KNM-BG 35250A (Fig. 6C). Our quantitative results do
308 not show a clear trend for KNM-BG 35250A within the whole *Nacholapithecus* femora
309 sample that allows us to clearly associate it to plastic deformation issues.

310 Qualitatively, the femoral remains of *Nacholapithecus* display a hemispherical
311 head in all cases and the articular surface is well differentiated from the neck. When
312 preserved, the fovea capitis is generally shallow and is placed on the distal half of the
313 articular surface. Previous authors highlighted the posterior location of the fovea capitis
314 (Nakatsukasa et al., 2012; Kikuchi et al., 2018), but we were unable to confirm the
315 location in these newly described specimens due to their fragmentary nature and/or the
316 poor preservation.

317 Nakatsukasa and colleagues (Nakatsukasa et al., 2012) suggested that the
318 anteversion of the femoral head in KNM-BG 35250A was due to deformation. The
319 newly described specimens shows slight anteversion; the displacement of the femoral
320 head compared to the neck is not marked (Fig. 5A). The configuration observed in the
321 larger femoral sample of *Nacholapithecus* might confirm the view of Nakatsukasa et al.

322 (2012). When the head and the greater trochanter are preserved, the head proximally
323 projects slightly above the greater trochanter (Fig. 7A–C).

324 Due probably to distortion, the neck length could not be measured in KNM-BG
325 35250A; thus, quantitative comparisons are not possible with the holotype. However,
326 qualitative comparisons suggest that the femoral neck of the *Nacholapithecus* holotype
327 is shorter than that of other *Nacholapithecus* femoral remains (e.g., KNM-BG 38391A;
328 Fig. 7A, H).

329 The presence of a lateral flare of the greater trochanter cannot be conclusively
330 added to the morphological suite of features that characterize the *Nacholapithecus*
331 femur. Among the sample, there are specimens with well-defined flaring (e.g., KNM-
332 BG 44954A and KNM-BG 44953A; Fig. 7B), while others are characterized by
333 minimal lateral expansion of this region (e.g., KNM-BG 38391A; Fig. 7A, see also 7C).
334 As previously noted, it seems clear that when the lateral projection is evident, it occurs
335 mainly at the distal part of the greater trochanter (Fig. 7B, F).

336 Previous authors (Ishida et al., 2004; Nakatsukasa et al., 2012; Kikuchi et al.,
337 2018) have noted that the lesser trochanter is placed close to the femoral neck and that it
338 faces posteromedially in *Nacholapithecus*. The best specimen in which to observe this
339 trait is KNM-BG 17816, which perfectly preserves its original form (Fig. 7D, E; Rose et
340 al., 1996). Although not complete, KNM-BG 40800F and KNM-BG 38391A also
341 support this interpretation (Kikuchi et al., 2018; Fig. 7A). The close location of the
342 lesser trochanter to the femoral neck and its posteromedial orientation can be considered
343 diagnostic for *Nacholapithecus* (Fig. 7D, E).

344 Despite variation in size, there were no significant differences between males
345 and females in any of the analyses performed: SIH/(ÖSIN*APN) ($U = 9, p = 0.90$);
346 relative NL ($t = 2.26, df = 3, p = 0.12, \text{)}$, or NSangle ($t = 0.62, df = 3, p = 0.58$; see also

347 Fig. 6). When quantitative comparisons were not possible, the strong sexual
348 dimorphism in body size of *Nacholapithecus* permitted us to tentatively differentiate
349 between male (large) and female (small) specimens on the basis of size (see
350 male/female size differences in Fig. 7A, C; Kikuchi et al., 2018).

351 Due to the distorted nature of the distal femoral fragments attributed to
352 *Nacholapithecus* (KNM-BG 35250B, KNM-BG 35250J, and KNM-BG 42779; KNM-
353 BG 42732 is a young adult individual), only qualitative comparisons could be made for
354 this region (Figs. 4, 5; SOM Table S2). As previously described for the
355 *Nacholapithecus* holotype (KNM-BG 35250B and J; Fig. 7I), the patellar groove is
356 square-shaped, wide, and shallow in the relatively well-preserved juvenile specimen
357 (KNM-BG 42732; Fig. 5F). The intercondylar fossa seems wide in KNM-BG 42732,
358 although it is not possible to verify this trait in the holotype specimen since the remains
359 are highly compressed mediolaterally (KNM-BG 35250B) and anteroposteriorly
360 (KNM-BG 35250J).

361

362 3.3. Comparisons with other Miocene hominoids

363 Previous studies have identified a series of femoral traits that distinguish
364 *Nacholapithecus* from other Miocene hominoids (especially African taxa), mainly
365 focusing on differences with *Ekembo* spp. (Nakatsukasa et al., 1998, 2012; Ishida et al.,
366 2004). Our analysis of the new femora raises questions about the distinctiveness of
367 *Nacholapithecus*, given the overall morphological similarities of the proximal end of the
368 femur to that of *Ek. nyanzae* (e.g., KNM-MW 13142A and KNM-RU 5527; see below).
369 The femoral morphology also shows some resemblance to that of *Eq. africanus* (BNMH
370 M.16331) and *T. kalakolensis* (KNM-WK 16950I), and more clearly differs from *M.*

371 *bishopi* (UMP MORII 94'80), *P. major* (NAP IX 46'99) and the European
372 dryopithecines in general terms (Fig. 3).

373 The femoral head relative size ($SIH/(\overline{OSIN} \cdot APN)$) range of *Nacholapithecus*
374 only overlaps with *Ekembo* and *Equatorius* (Fig. 6A), with the index value of the
375 holotype close to that of *Ekembo* (KNM-MW 13142A; Fig. 3D). *Morotopithecus* (UMP
376 MORII 94'80; Fig. 3A) shows the lowest value (smallest relative femoral head) among
377 fossils; whereas *Hispanopithecus* (IPS 18800.29; Fig. 3H) shows one of the highest
378 values (largest relative femora head) for this index among extinct taxa, slightly below
379 the KNM-BG 38391A *Nacholapithecus* specimen.

380 On the basis of the holotype (KNM-BG 35250A), which is probably plastically
381 deformed (Fig. 7H), it has been suggested that femoral neck length of *Nacholapithecus*
382 is relatively short when compared with *Ekembo* (Fig. 3D–E; Ishida et al., 2004;
383 Nakatsukasa et al., 2012). Kikuchi et al. (2018) subsequently reinforced this suggestion
384 with a larger sample of femoral remains (most of them also included in this study).
385 When quantified, however, our results do not support the characterization of the
386 *Nacholapithecus* femoral neck as relatively short compared with *Ekembo*. The range of
387 variation in neck length is small in *Nacholapithecus* (Fig. 6B) and the *Ekembo* specimen
388 KNM-MW 13142A falls within the range of *Nacholapithecus*; while KNM-RU 5527
389 falls below its lower limit but close to its range of variation. It can be noted that
390 *Turkanapithecus* (KNM-WK 16950I; Fig. 3C) displays a relatively very long femoral
391 neck compared with the Miocene fossil hominoids (as well as the extant anthropoids in
392 our sample; Fig. 6B). The European dryopithecines display relatively shorter necks than
393 *Nacholapithecus*, being *Hispanopithecus* the extinct taxon with the shortest relative
394 neck length (Fig. 6B).

395 When all the available *Nacholapithecus* femora are considered, results show that
396 the NSangle of this taxon is not especially high among the Miocene hominoid taxa
397 (contra Nakatsukasa et al., 2012; Figs. 3 and 6C). All the specimens included in the
398 latter group fall within the range of *Nacholapithecus* except *Turkanapithecus*, whose
399 NSangle value is slightly higher than the uppermost limit of the *Nacholapithecus* range
400 (Fig. 6C).

401 Most of the *Nacholapithecus* specimens display a lateral projection of the
402 greater trochanter but it is not present in all the available femora (e.g., KNM-BG
403 44954A vs. KNM-BG 38291A; see above; Fig. 7A–C; Kikuchi et al., 2018). When it is
404 present, the flare is evident at the base of the greater trochanter (Nakatsukasa et al.,
405 2012; Kikuchi et al., 2018; Fig. 7B). This feature is also present in other Miocene
406 hominoids (Fig. 3; Senut et al., 2000; Bacon, 2001) such as *Ekembo* (KNM-MW
407 13142A), *Turkanapithecus* (KNM-WK 16950I), *Proconsul* (reconstructed specimen
408 from NAP IX), *Equatorius* (BNMH M.16331), and *Hispanopithecus* (IPS 18800.29).
409 Only *Morotopithecus* (UMP MORII 94'80) and *Dryopithecus* (IPS 41724) show a very
410 light lateral protrusion of the greater trochanter (Fig. 3A, G; MacLatchy et al., 2000;
411 Nakatsukasa et al., 2012; Almécija et al., 2013; Pina et al., 2019). Due to the observed
412 variation in the *Nacholapithecus* femora, neither the presence nor the absence of a
413 greater trochanter lateral flare can be considered diagnostic for *Nacholapithecus*.

414 The posteromedial facing and relatively proximal position of the lesser
415 trochanter in *Nacholapithecus* (Fig. 7D, E; e.g., Ishida et al., 2004) not only resembles
416 that observed in *Ekembo* (KNM-MW 13142A; Ward et al., 1993, but see Nakatsukasa
417 et al., 2012) and *Equatorius* (BMNH M16331), but also that described for
418 *Morotopithecus* (UMP MORII 94'80; MacLatchy et al., 2000; Fig. 3A). However, the
419 configuration of the lesser trochanter in *Turkanapithecus* (KNM-WK 16950I; Leakey et

420 al., 1988; Fig. 3C) clearly differs from that defined for *Nacholapithecus* by facing more
421 posteriorly and by being positioned more distally (M. Pina, pers. obs.). This is also the
422 case for *Dryopithecus* (IPS 41724) and *Hispanopithecus* (IPS 18800.29), whose lesser
423 trochanter is placed more distally and facing posteriorly or more medially, respectively
424 (Pina 2016; Pina et al., 2019). In the case of *Proconsul* (reconstructed specimen from
425 NAP IX; Fig. 3B), interpretations of the direction of the lesser trochanter conflict in the
426 literature; Senut et al. (2000) suggested that the lesser trochanter faces posteriorly,
427 whereas Gommery et al. (2002) advocated for a medial direction.

428 The newly available *Nacholapithecus* femora also confirm other traits formerly
429 highlighted in the literature, e.g., the close proximity of the gluteal tuberosity to the
430 greater trochanter (Fig. 7F, G). This trait differentiates *Nacholapithecus* from *Ekembo*
431 (KNM-MW 13142A) since in *Ekembo*, the gluteal tuberosity is positioned more distally
432 relative to the greater trochanter (Fig. 3D; Nakatsukasa et al., 2012). Although not well
433 preserved, the position of the gluteal tuberosity in *Turkanapithecus* (KNM-WK 16950I)
434 resembles that of *Ekembo* more than that of *Nacholapithecus* (Fig. 3C; Leakey et al.,
435 1988). Only *Dryopithecus* (IPS 41724) displays a marked gluteal tuberosity among the
436 dryopithecines of the sample (Pina et al., 2019). In this case, the gluteal tuberosity is
437 positioned closer to the greater trochanter than in *Ekembo* and resembles the condition
438 of *Nacholapithecus* (Fig. 3G).

439 The patellar groove shape of *Nacholapithecus* is quadrangular and shallow (Fig.
440 5; see also Fig. 7I; SOM Figure S3; SOM 3D Model S1), as in *Turkanapithecus* (KNM-
441 WK 16950I; Fig. 3C; Leakey et al., 1988), *Morotopithecus* (UMP MORII 94'80; Fig.
442 3A; MacLatchy et al., 2000) and probably *Equatorius* (KNM-MB 24727; see
443 McCrossin, 1994:fig. 38 and p. 162). Rose (1983) also noted that the patellar groove of
444 *Ekembo* (e.g., KNM-RU 5527; Fig. 3E) is square-shaped and shallow. Nakatsukasa et

445 al. (2012:238, footnote Fig. 3) highlighted that “the patellar surface is trapezoidal with a
446 more raised lateral rim” in KNM-RU 5527. This trait, together with the asymmetric
447 width of the condyles in KNM-RU 5527, differentiates the *Ekembo* distal femur from
448 that of *Nacholapithecus*. The condyles of KNM-RU 5527 (Nakatsukasa et al., 2012;
449 Fig. 3E), KNM-WK 16950I (Leakey et al., 1988; Fig. 3C) and UMP MORII 94’80
450 (MacLatchy et al., 2000; Fig. 3A) display more asymmetric epicondyles than
451 *Nacholapithecus*.

452 Finally, the asymmetrical cross-section of the distal shaft displayed by
453 *Nacholapithecus* (medial half wider than the lateral one) resembles that of *Equatorius*
454 (BNMH M 16332-3; McCrossin, 1994), although it is much thinner anteroposteriorly in
455 the only available *Nacholapithecus* specimen (KNM-BG 42722), likely reflecting that it
456 is an immature specimen.

457

458 3.4. Comparisons of *Nacholapithecus* femora with those of extant anthropoids

459 *Nacholapithecus*, together with African apes and platyrrhines, shows an
460 intermediate position between cercopithecoids (smaller relative femoral heads) and
461 Asian apes (larger femoral heads) for SIH/(ÖSIN*APN) (Fig. 6A), with some
462 statistically significant differences (Table 4).

463 *Nacholapithecus* displays a long neck (NL) relative to the total mediolateral
464 width of the proximal femur, not significantly different from that of platyrrhines (i.e.,
465 *Cebus apella* and atelids), orangutans, chimpanzees, and gorillas, but significantly
466 different from colobines, cercopithecines, *Hylobates lar* and *Pan paniscus* (Table 4;
467 Fig. 6B; SOM Table S3). We note that variation in relative NL is high in many of the
468 extant anthropoids, particularly in cercopithecines and colobines (whose ranges overlap
469 with those of the other taxa).

470 The neck-shaft angle (NSangle) of *Nacholapithecus* has been described as high,
471 like that of gibbons or *Ateles* (Natasukasa et al., 2012). However, statistically, the
472 *Nacholapithecus* NSangle differs significantly from both *H. lar* and the atelids, as well
473 as *Pongo pygmaeus*, cercopithecines, colobines, *H. lar*, and *P. t. schweinfurthii* (Table
474 4; Fig. 6C; SOM Table S3).

475 Qualitatively, the gluteal tuberosity in the *Nacholapithecus* sample is well
476 marked and situated close to the greater trochanter (Fig. 7F, G), as originally described
477 for the holotype specimen (Nakatsukasa et al., 2012). Among extant hominoids, only
478 gibbons are reported to show a marked gluteal tuberosity (Stern, 1972; Alméjida et al.,
479 2013). As in the case of *Nacholapithecus*, the gluteal tuberosity of gibbons is positioned
480 close to the greater trochanter (Fig. 7K).

481 The distal end of the femur, KNM-BG 42732, which does not suffer from severe
482 distortion, displays an ape-like distal epiphysis, relatively wider medio-laterally than
483 thick antero-posteriorly (Fig. 5H). The patellar groove of *Nacholapithecus* is shallow
484 and more similar in shape to lesser apes (*Hylobates*) than platyrrhines (*Cebus*) (i.e.,
485 with an approximated quadrangular shape); the intercondylar fossa appears wider than
486 in *Cebus* (SOM Figure S3; SOM 3D Models S1–S3).

487

488 **4. Discussion**

489 *4.1 Within species variation in Nacholapithecus*

490 Kikuchi and colleagues (2018; see also Ishida et al., 1991) reported a strong
491 sexual dimorphism for *Nacholapithecus*. Nonetheless, differences in size among the
492 *Nacholapithecus* remains might additionally suggest either 1) the presence of several
493 anthropoid taxa or 2) the presence of two different species of *Nacholapithecus* in the
494 Nachola area.

495 Apart from *Nacholapithecus*, other anthropoid taxa have been recovered in this
496 region, namely *Nyanzapithecus* (Kunimatsu, 1992, 1997) and *Victoriapithecus*
497 (Pickford et al., 1987). It is possible that the smaller femora ascribed to
498 *Nacholapithecus* belong to *Nyanzapithecus*, which might be smaller in overall body size
499 (Kunimatsu, 1992, 1997). Female *Nacholapithecus* and male *Nyanzapithecus* reportedly
500 overlap in size based on dental dimensions (Kunimatsu, 1997). Thus, the smaller femora
501 in our sample could represent male *Nyanzapithecus* remains (see also Kikuchi et al.,
502 2018). Most of the femora included in the current study were collected in the BG-K
503 locality, from which no *Nyanzapithecus* specimens have been formally identified thus
504 far. From the extensive collection of primate fossils (~240 dental specimens) recovered
505 from this locality, only a single fragment of maxilla has been preliminarily catalogued
506 as a non-cercopithecoid small catarrhine (Y. Kunimatsu, unpublished data). This
507 fragment could be potentially accommodated as a nyanzapithecine, but due to its poor
508 preservation, its attribution remains provisional (a formal description has not been
509 published yet). All of the other dental material of *Nyanzapithecus*, as well as material
510 tentatively attributed to this genus as cf. *Nyanzapithecus* (29 specimens including
511 published and unpublished ones), have been collected from another locality (BG-X)
512 together with ca. 190 *Nacholapithecus* dental specimens (Y. Kunimatsu, unpublished
513 data). Only two small femora (KNM-BG 17775 and KNM-BG 17778) were recovered
514 from BG-X. Rose et al. (1996) described nine hominoid postcranial specimens collected
515 from this locality. Other than these two femoral specimens, only one proximal phalanx
516 (KNM-BG 15531: of unknown ray) is considerably smaller than pedal proximal
517 phalanges (median rays) of male *Nacholapithecus* (Nakatsukasa et al., 2003b; see also
518 Nakatsukasa et al., 2012). This proximal phalanx thus could belong to either a female
519 *Nacholapithecus* or a male *Nyanzapithecus*, but it could also be a male *Nacholapithecus*

520 phalanx from a paramedian ray. Although further analysis would help to corroborate
521 this hypothesis, given that *Nyanzapithecus* remains are rare in the area of Nachola, the
522 possibility of currently assigning postcranial remains to non-*Nacholapithecus* taxa is
523 very low (Ishida et al., 1984; Kunimatsu, 1997).

524 The species *Nacholapithecus kerioi* was erected on the basis of the KNM-BG
525 35250 skeleton by Ishida et al. (1999). In their article, these authors included other
526 hominoid specimens discovered from Nachola to the species, although they did not
527 specify catalogued numbers. Subsequent works have underpinned the homogeneity of
528 the dental morphology (regardless the differences in size; e.g. Kunimatsu et al., 2004).
529 The evident differences in size among our femoral sample between the smallest and the
530 largest fragments are not reflected in the femoral morphology. *Nacholapithecus* body
531 mass estimated by Kikuchi et al. (2018), based on the femoral diameter, ranges 8.7–10.8
532 kg for females and 17.3–25.8 kg for males (see their Table 2 BM1 estimates). The
533 largest femur (KNM-BG 40800F) is associated with unpublished dental rows that do
534 not show any diagnostic features to distinguish them from other specimens assigned to
535 *Nacholapithecus* smaller specimens. The same applies for the second largest femur in
536 the Kikuchi et al., (2018) dataset, the subadult KNM-BG 42738/42756C (Y. Kunimatsu,
537 personal observation). These facts lead us to conclude that the femoral sample analyzed
538 here are all attributable to a single species of *Nacholapithecus*.

539 In addition, the sample of femoral fragments attributed to *Nacholapithecus*
540 allows us to shed light on the *Nacholapithecus* holotype and broaden the range of
541 variation for comparison with other species. With the additional femoral remains, we
542 have found that the holotype femora display some quantitative and qualitative
543 differences from other *Nacholapithecus* specimens that might support the idea that the
544 KNM-BG 35250 femora display rather severe deformation. KNM-BG 35250A has been

545 traditionally used to define the femoral diagnostic traits of *Nacholapithecus*, but our
546 results suggest that drawing morphofunctional inferences from the holotype of this
547 taxon would be ill advised (see below).

548

549 4.2. *Functional interpretations and positional behavior in Nacholapithecus*

550 The proximal end of the femur has been the focus of extensive study due to its
551 relation with the functionality of the hip and its potential association with different
552 locomotor modes in primates. Some of the most characteristic traits are found at the
553 head-neck complex. Ruff (1988) suggested that the increase in the femoral head
554 decoupled from that of the neck will result in the enhancement of the hip joint excursion
555 (see also Ward et al., 1993; Harmon, 2007; Hammond, 2014, among others). Likewise,
556 the higher the NSangle, the greater the mobility at the hip (Rose, 1983; Ward et al.,
557 1993; Lovejoy et al., 2002; Hammond, 2014). Thus, a large relative head and a high
558 NSangle enhance the capacity for hip abduction and external rotation of the leg. This
559 configuration also increases the angle of the hind limb related to the midline of the
560 body, which facilitates antipronograde behaviors such as vertical climbing (Stern and
561 Susman, 1981; Rose, 1983; Ward et al., 1993; Harrison, 1986; MacLatchy, 1996;
562 Hammond, 2014). By contrast, quadrupedal monkeys display relatively small heads,
563 short necks, and lower NSangles, which help to resist bending forces and movements of
564 the hind limb preferentially in the parasagittal plane (Fleagle, 1977; Rose, 1983; Fleagle
565 and Meldrum, 1988; Cooke and Tallman, 2012).

566 Overall, the enlarged sample of *Nacholapithecus* femora suggests that the femur
567 of this taxon is characterized by a relatively small head ($SIH/[ÖSIN*APN]$), a
568 moderately long neck relative to the total mediolateral width of the proximal end of the
569 femur, and an intermediate (or moderate) NSangle, compared with extant anthropoids

570 (Fig. 6). These analyses suggest that previous functional interpretations based on the
571 femoral morphology of KNM-BG 35250, the *Nacholapithecus* holotype (Fig. 7H, I),
572 should be revised. Although KNM-BG 35250A does not always represent an extreme
573 condition in the *Nacholapithecus* sample for the variables analyzed here (Fig. 6),
574 functional inferences based exclusively on this specimen must be considered cautiously
575 due to its plastic deformation. Therefore, as the relative femoral head, neck length and
576 neck-shaft angle have been related to hip mobility and the capability of abduction of the
577 hind limb (Grand, 1968; Fleagle and Meldrum, 1988; Ruff, 1988; Aiello and Dean,
578 1990; Hammond; 2014), our results have important implications regarding locomotor
579 inferences in *Nacholapithecus*, suggesting it might have a less mobile hip joint than
580 previously proposed (e.g., Nakatsukasa et al., 2012).

581 Although quantitative analyses are not possible for the distal femur, the new
582 evidence supports previous descriptions of *Nacholapithecus* as having an apparently
583 shallow and square-shaped patellar groove (Fig. 5F and Fig. 6I; SOM 3D Model S1).
584 The shape of the patellar groove is controversial since some authors have suggested a
585 high degree of intraspecific variation in this feature in *Nacholapithecus*, with some
586 individuals displaying a square shape and others a more trapezoidal outline of the
587 groove (Rose et al., 1996). The shallow patellar groove of the *Nacholapithecus* distal
588 femur accords with its previously described morphology of the patella, which exhibits
589 some living ape-like affinities that probably foretell the specialized patellae of living
590 great apes (Fig. 6L; Ward et al., 1995; Rose et al., 1996; Pina et al., 2014, 2020).
591 *Nacholapithecus* also displays condyles that are subequal in size (Nakatsukasa et al.,
592 2012), a trait typical of quadrupedal anthropoid monkeys in which loadings are equally
593 distributed through the distal end of the femur (Rose, 1983; Georgiou et al., 2018;
594 Sukhdeo et al., 2018).

595 The general evidence found for the *Nacholapithecus* femur suggests that only
596 the patellofemoral articulation might show enhanced range of motion, since this taxon
597 does not display the stabilization traits of this joint characteristic of quadrupedal
598 monkeys (e.g., deep patellar groove at the femur and compartmentalized articular
599 surface of the patella; Harrison, 1986; Ward et al., 1995; DeSilva et al. 2013; Pina et al.,
600 2014, 2020). On the other hand, the hip joint might maintain more restricted movements
601 in the parasagittal plane (also supported by distal femoral condyles and epicondyles
602 similar in size). Although *Nacholapithecus* does not show the whole set of
603 characteristics of the proximal femoral end traditionally related to abduction movements
604 and external rotation of the hip (long neck, low greater trochanter related to the head,
605 relatively large femoral head, among others; Lovejoy et al., 2002; Richmond and
606 Jungers, 2008; Almécija et al., 2013), these movements cannot be completely ruled out
607 from its positional repertoire. This morpho-evolutionary gradation at the femur is also
608 found in *Morotopithecus* (limited hip abduction and less-restricted movements at the
609 knee; MacLatchy et al., 2000) and departs from the femoral evidence observed in
610 *Ekembo*, *Turkanapithecus* and *Equatorius*. The reviewed morphology of the
611 *Nacholapithecus* femur presented in this work is completely compatible with the
612 positional repertoire formerly proposed for this Miocene taxon, which probably
613 combined generalized above-branch quadrupedalism with other antipronograde
614 behaviors, such as vertical climbing (no clear evidence for suspension is found in its
615 femur or elsewhere; Nakatsukasa et al., 2003b, 2012; Ishida et al., 2004; Nakatsukasa
616 and Kunitatsu, 2009; Ogihara et al., 2016; Takano et al., 2018, 2020).

617 Results presented in this work suggest that the *Nacholapithecus* femur resembles
618 those of *Ekembo*, *Turkanapithecus*, and *Equatorius*, showing a general primitive (stem
619 hominoid-like) appearance. In contrast, *Nacholapithecus* differs from those femora

620 showing more derived (living hominoid-like) traits, such as *Morotopithecus* and
621 *Proconsul* in Africa (MacLatchy et al., 2000; Senut et al., 2000; Gommery et al., 2002)
622 and *Sivapithecus* in the late Miocene of Asia (Kelley, 2005; Madar et al., 2002).
623 *Nacholapithecus* is also unlike the younger European hominids. Although also
624 displaying quadrupedal affinities (Moyà-Solà et al., 2009; Pina et al., 2019), our results
625 show that *Nacholapithecus* differs from *Dryopithecus* at the proximal end of the femur
626 and clearly departs from those taxa with well-defined affinities for forelimb-dominated
627 behaviors (i.e., *Hispanopithecus*, *Rudapithecus*, *Danuvius*, and *Oreopithecus*; Straus,
628 1963; Hürzeler, 1968; Harrison, 1986; Jungers, 1987; Begun 1992, 2013; Rose, 1993;
629 Moyà-Solà and Köhler, 1996; Begun and Kordos, 2011; Begun et al., 2012; Pina et al.,
630 2012; Böhme et al., 2019; Ward et al., 2019).

631 When the whole anatomy is taken into account, similarities between
632 *Nacholapithecus* and *Ekembo* are less clear. Although the general body plan in these
633 two taxa is similar (narrow and deep trunk; Ward et al., 1993; Nakatsukasa et al.,
634 2007a), *Nacholapithecus* clearly departs from *Ekembo* regarding forelimb shape. The
635 former displays a series of characteristics more related to the stabilization of the
636 humeroantibrachial complex (e.g., anterior projection of the coronoid process of the
637 ulna and globular humeral capitulum) and enhancement of the pronation-supination
638 movements, as shown in the elbow of living apes (Nakatsukasa and Kunitatsu, 2009;
639 Takano et al., 2018, 2020). As occurs in other Miocene taxa (not only in Africa, but also
640 in Eurasia; see e.g., Pilbeam et al., 1980; Begun, 1992, 2015; Moyà-Solà and Köhler,
641 1996; Madar et al., 2002; Almécija et al., 2013; Ward, 2015; Böhme et al., 2019), the
642 postcranial morphology of *Nacholapithecus* shows a unique combination of primitive
643 and derived features; in general, a more derived forelimb, foot, and lumbar region, and a
644 primitive hind limb compared with *Ekembo* (Ishida et al., 2004; Nakatsukasa and

645 Kunimatsu, 2009). These results are compatible with general inferences made for this
646 taxon, but also for the rest of middle Miocene hominoids included in this work. Overall,
647 these African primates potentially combined general arboreal quadrupedalism with
648 other antipronograde behaviors (Rose, 1983; Nakatsukasa and Kunimatsu, 2009; Alba,
649 2012; Begun, 2012; Ward, 2015). In the case of *Nacholapithecus*, its forelimbs and feet
650 were apparently more derived than its hind limbs and trunk. This fact could suggest the
651 presence of selective pressures on the upper half of the body in Miocene African taxa,
652 underpinning the development of forelimb-dominated behaviors such as vertical
653 climbing and, more recently, below-branch suspension (Nakatsukasa and Kunimatsu,
654 2009). Although no specific traits for the latter locomotor mode or slow-cautious
655 quadrupedalism have been identified in *Nacholapithecus* (Nakatsukasa and Kunimatsu,
656 2009; Takano et al., 2018, 2020), they cannot be entirely ruled out for the positional
657 behavior repertoire of this taxon. Nonetheless, like the other middle Miocene hominoid
658 taxa in this work, *Nacholapithecus* was likely adapted for an arboreal life, and some
659 antipronograde behavior (e.g., vertical climbing, clambering, and/or cautious and
660 eclectic climbing) could have been a component of its locomotor repertoire, though less
661 than in middle and late Miocene Eurasian taxa (Nakatsukasa et al., 2003b; 2007a; 2012;
662 Senut et al., 2000; Takano et al., 2018, 2020).

663

664 **5. Conclusions**

665 The study of a larger sample of femora assigned to *Nacholapithecus* allowed us
666 to review the original description and species diagnostic femoral traits reported for
667 KNM-BG 35250 (holotype). Our results show that the morphology of the better-
668 preserved femora differs in some respects from that of the original description derived
669 from the holotype (mainly at the femoral head and neck). These findings suggest that

670 previous interpretation of the femoral morphology of *Nacholapithecus* may have been
671 influenced by the presence of some distortion and/or deformation in the holotype
672 femora (see also Nakatsukasa et al., 2012). Consequently, in contrast with previous
673 work, we found that the overall femoral morphology in *Nacholapithecus* is more similar
674 to that of early and middle Miocene taxa (mainly *Ekembo* spp. and *Equatorius*) than
675 previously thought. At the same time, the new femoral fragments provide qualitative
676 support for some of the formerly proposed differences with other taxa, such as the
677 relative position of the gluteal tuberosity.

678 In addition, our results highlight the more primitive (stem hominoid-like)
679 appearance of the proximal femur in *Nacholapithecus*, in contrast to the more derived
680 (extant hominoid-like) traits found in its forelimb, which clearly depart from those
681 shown in *Ekembo* spp. Taking into account the whole evidence from *Nacholapithecus*,
682 the mosaic condition of its postcranial skeleton fits well within the positional behavior
683 scenario inferred for the early-middle Miocene of Africa (femoral morphology of
684 *Nacholapithecus* clearly departs from those of the Eurasian Miocene hominoids). Most
685 of the extinct hominoids found thus far would have a positional behavior repertoire that
686 might include frequent use of general arboreal quadrupedalism combined with other
687 ape-like antipronograde behaviors, such as vertical climbing. However,
688 *Nacholapithecus* might have displayed certain enhancement of forelimb-dominated
689 behaviors. Although further evolutionary studies are needed to corroborate this
690 hypothesis, such a unique combination in the *Nacholapithecus* skeleton could be the
691 origin of the more-derived behaviors found in younger Eurasian hominoids.

692

693 **References**

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991

992 **Figure captions**

993 **Figure 1.** Map of the fossil locality of Nachola in Kenya.

994

995 **Figure 2.** Linear measurements taken of the proximal femora for quantitative analyses.
996 A) proximal view; B) posterior view; and C) anterior view. Abbreviations: APN =
997 anteroposterior depth of the femoral neck; SIH = maximum superoinferior height of the
998 femoral head; SIN = minimum superoinferior height of the femoral neck; NL = femoral
999 neck length (between the most lateral edge of the femoral head to the medialmost limit
1000 of the trochanteric crest); NSangle = femoral neck-shaft angle; TotW = total
1001 mediolateral width of the proximal femur from the medialmost point of the femoral
1002 head to the lateralmost point of the greater trochanter. Modified from Pina, 2016.

1003

1004 **Figure 3.** Proximal fossil femoral fragments used for comparisons with
1005 *Nacholapithecus kerioi* (anterior view). When available, the distal portion is also
1006 displayed (anterior view above, posterior view below). A) *Morotopithecus bishopi*
1007 (UMP MORII 94'80); B) *Proconsul major* (combination of NAP IX 46'99, NAP IX B
1008 64, NAP IX 65 P. 67 fragments; reversed); C) *Turkanapithecus kalakolensis* (KNM-
1009 WK 16950I); D) *Ekembo nyanzae* (KNM-MW 13142A); E) *Ekembo nyanzae* (KNM-
1010 RU 5527; reversed); F) *Equatorius africanus* (BMNH M.16331; reversed; pictures from

1011 cast); G) *Dryopithecus fontani* (IPS 41724); and H) *Hispanopithecus laietanus* (IPS
1012 18800.29). Femora are displayed with the same maximum superoinferior height of the
1013 femoral head (SIH) to facilitate morphological comparisons. Dashed lines at the right
1014 bottom of A, C, and E represent the outline of the patellar groove. Scale bars = 20 mm.
1015

1016 **Figure 4.** Fossil femoral fragments belonging to *Nacholapithecus kerioi* described in
1017 this work (A–P). KNM-BG 17778 (A, anterior view; B, posterior view); KNM-BG
1018 40844 (C, anterior view; D, posterior view); KNM-BG 40964 (E, anterior view; F,
1019 posterior view); KNM-BG 42757 (G, proximal; H, anterior; I, medial; and J, posterior
1020 views); KNM-BG 44953B (K, anterior; L, medial; and M, posterior views); and KNM-
1021 BG; 42779 (N, anterior; O, side; and P, posterior views). Scale bar = 20 mm.

1022
1023 **Figure 5.** Fossil femoral fragments belonging to *Nacholapithecus kerioi* described in
1024 this study. These remains are associated with the same individual (probably an
1025 immature). A–C) KNM-BG 42738/42756C (proximal fragment); D–E) KNM-BG
1026 42722 (shaft fragment); F–I) KNM-BG 42732 (distal fragment). A, I) proximal views;
1027 B, D, F) anterior views; C, E, G) posterior views; H) distal view. Black arrows denote
1028 (A) the absence of anteversion of the head, (C) the intertrochanteric line, and (F) the
1029 most proximal point of the lateral and medial rims of the patellar groove. Dashed white
1030 lines denote the supracondylar ridges (E). Dashed black line represents the square-
1031 shaped outline of the patellar groove (F). Scale bar = 20 mm.

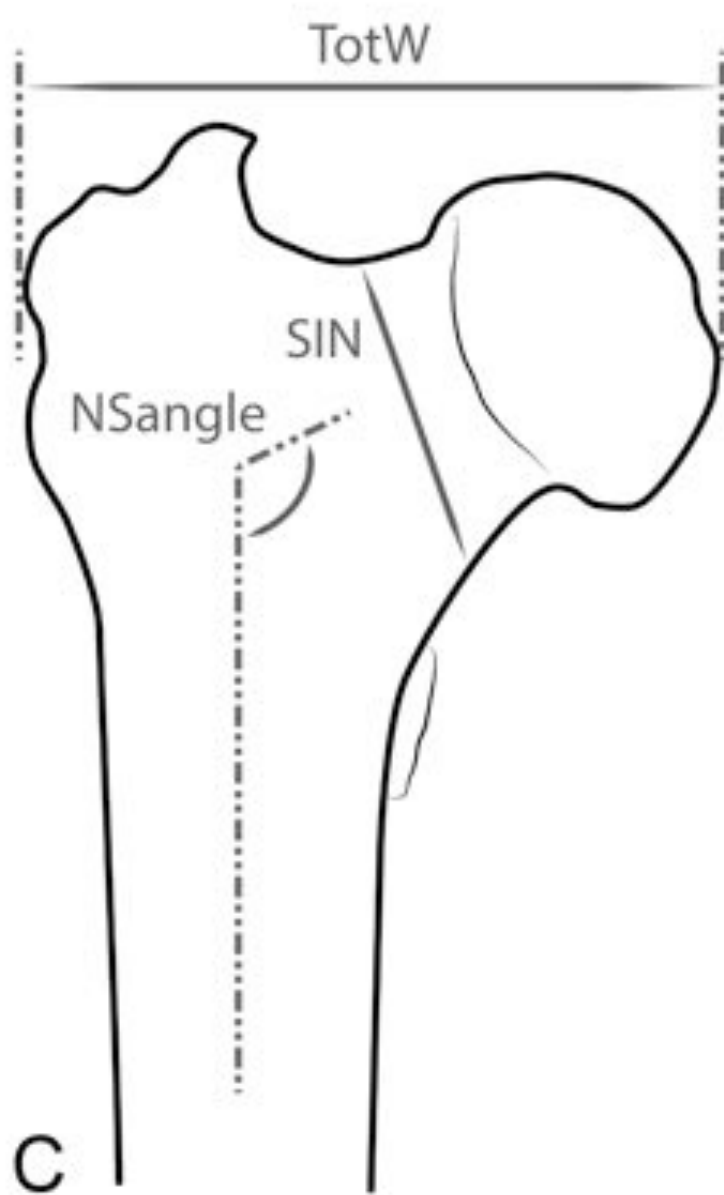
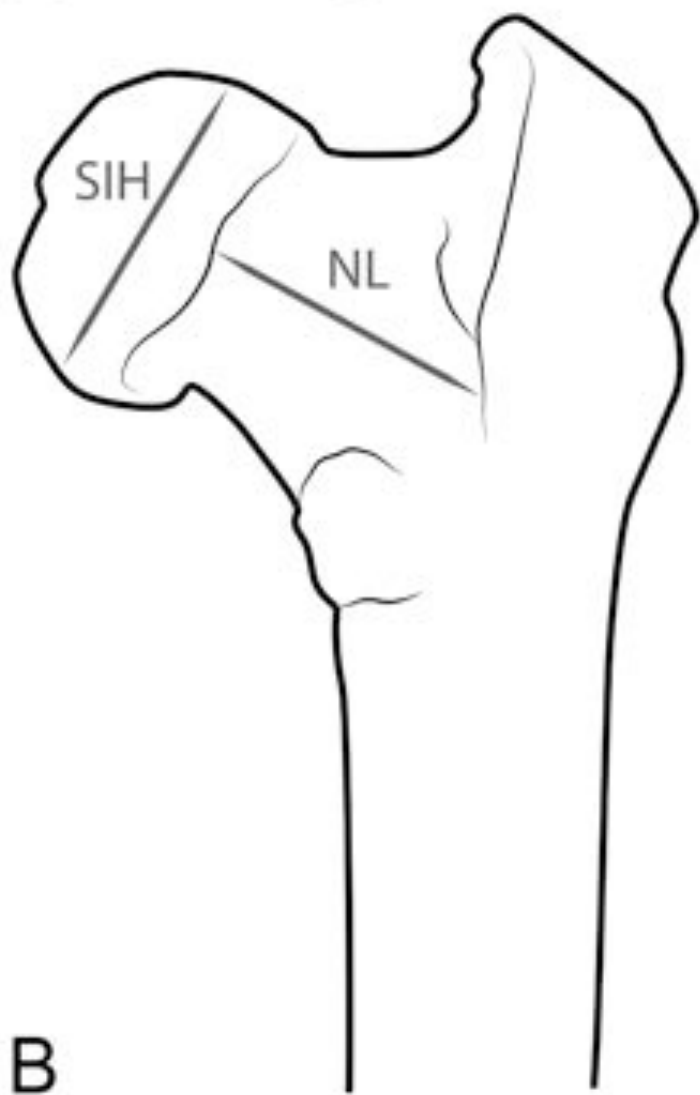
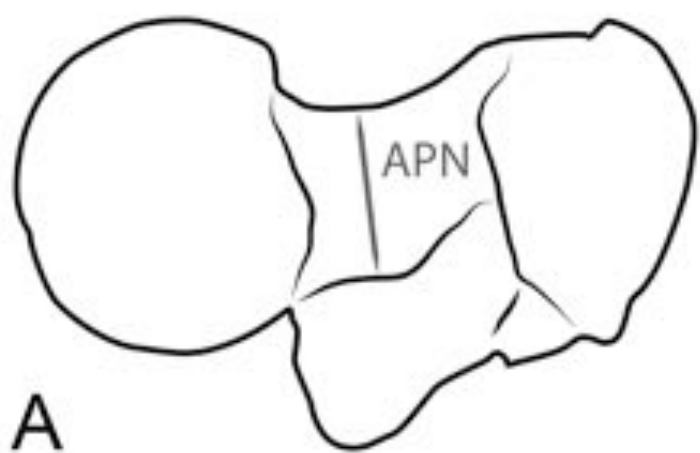
1032
1033 **Figure 6.** Boxplots showing (A) the relative size of the head index: $SIH/(\bar{C}SIN*APN)$
1034 (SIH = superoinferior height of the femoral head; SIN = superoinferior height of the
1035 femoral neck; APN = anteroposterior depth); (B) the relative neck length (RelativeNL);

1036 and (C) neck-shaft angle (NSangle). Vertical lines represent the median, boxes the
1037 interquartile range, IQR (between the 25th and the 75th percentiles), whiskers the
1038 1.5*IQR, and circles the outliers. Colors represent major taxonomic groups: dark green,
1039 African apes; light green, Asian apes; yellow, cercopithecines; orange, colobines; dark
1040 blue, atelids; light blue, cebines (for colors see online version).

1041

1042 **Figure 7.** *Nacholapithecus kerioi* femoral fragments showing some of the anatomical
1043 features discussed in the text. A) KNM-BG 38391A (anterior view); B) KNM-BG
1044 44953A (anterior view); C) KNM-BG 48093 (anterior view); D–E) KNM-BG 17816
1045 (D, anterior view; E, posterior view); F–G) KNM-BG 44954A (F, posterior view; G,
1046 lateral view); H) KNM-BG 35250A (holotype; anterior view); I) KNM-BG 35250J
1047 (holotype; anterior view); J) AMNH 103659, *Macaca fascicularis* (anterior view) ; K)
1048 AMNH 103344, *Hylobates klossi* (anterior view); L) AMNH 86857, *Pan paniscus*
1049 (anterior view). J–L are depicted at the same femoral length (from the head to the distal
1050 end). A–B) differences in greater trochanter lateral flare (fragments scaled to the same
1051 superoinferior height of the femoral head). A, C) sexual dimorphism: C, smallest femur
1052 belonging to a female (Kikuchi et al., 2018); its small size can be compared with A, the
1053 largest male femur (except for H; Kikuchi et al., 2018). A and C femoral fragments are
1054 depicted to the same scale. D–E) lesser trochanter close to the femoral neck; F–G)
1055 marked gluteal tuberosity close to the greater trochanter. I) square-shaped patellar
1056 groove. Black arrows highlight the referenced anatomical traits. Scale bar = 20 mm.







KNM-BG 17778



A

B

KNM-BG 40844



C

D

KNM-BG 40964



E

F

KNM-BG 42757



G



H

I

J

KNM-BG 42779



N

O

P

KNM-BG 44953B



K

L

M



KNM-BG 42738/42756C

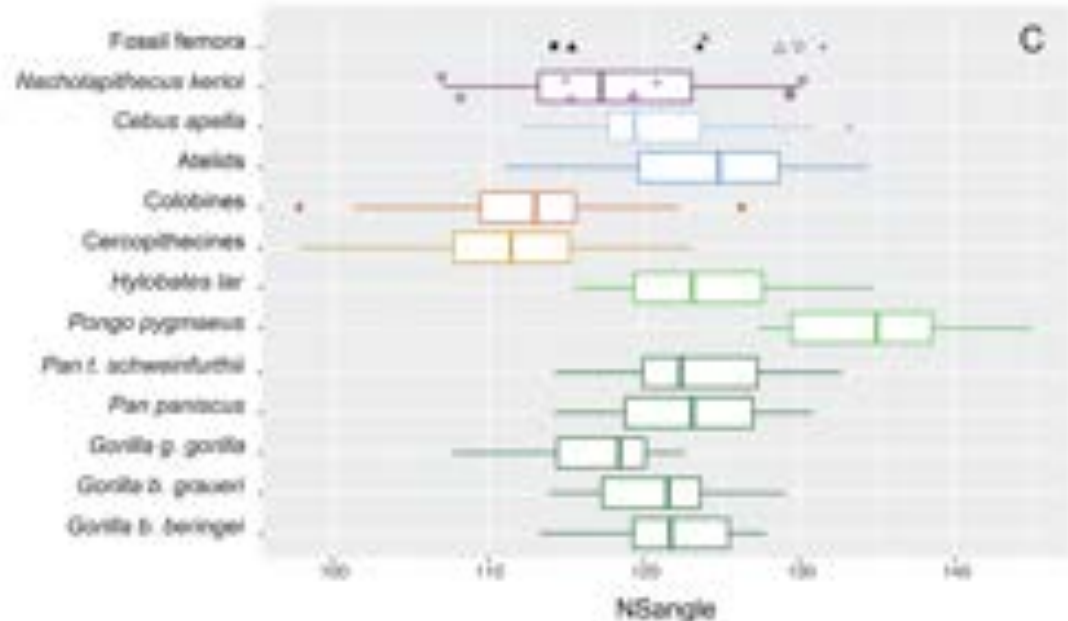
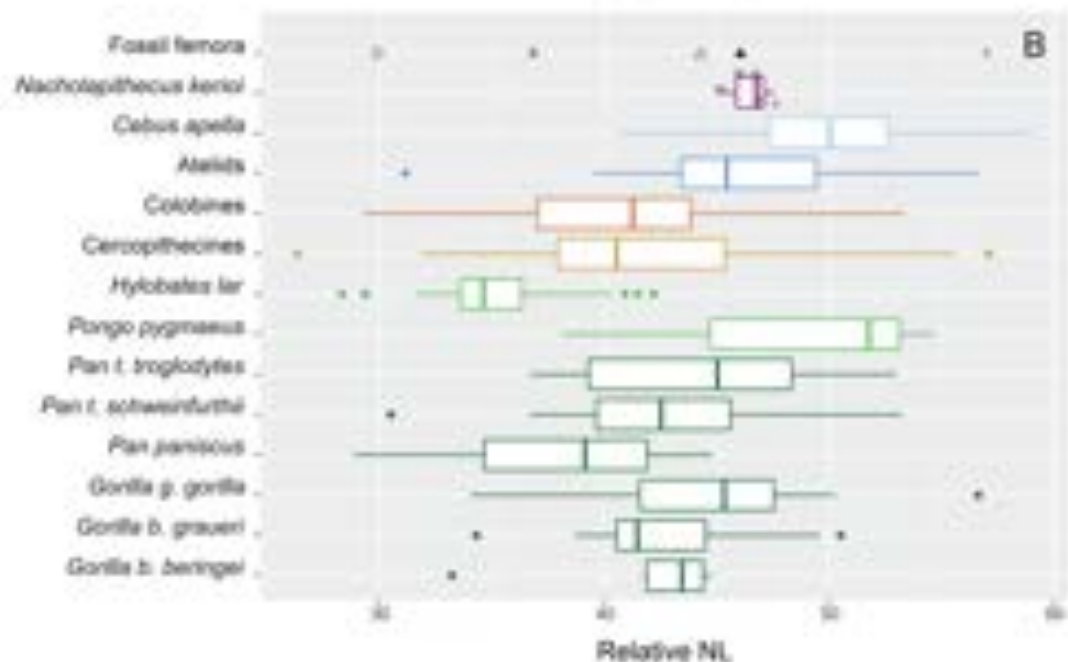
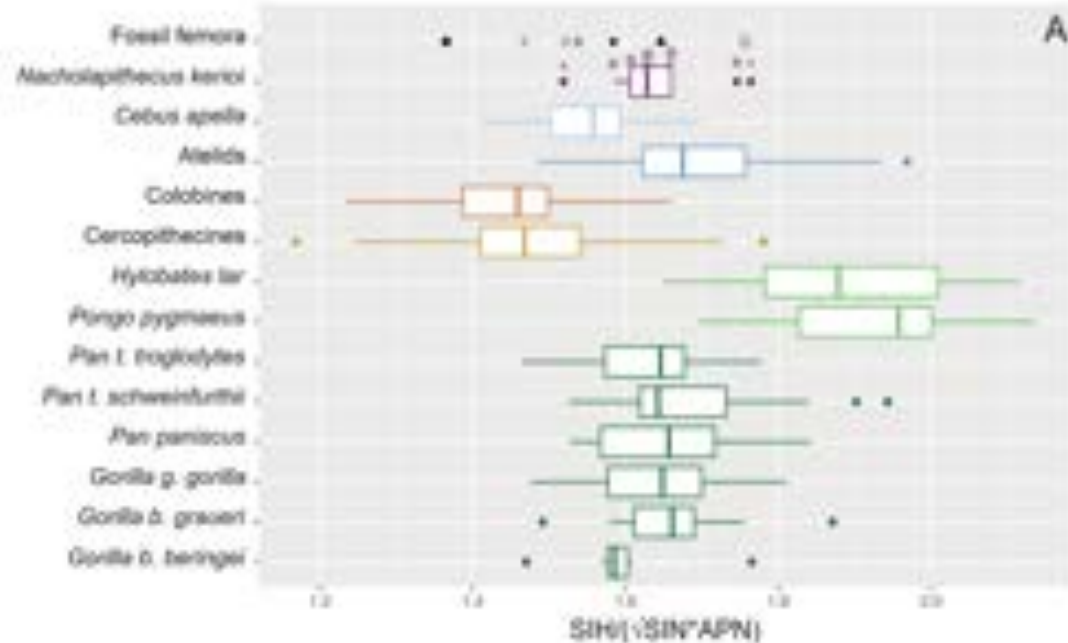


KNM-BG 42722



KNM-BG 42732





- *N. kerioi* (KNM-BG 35250A)
- *Eg. africanus* (BMNH M16331)
- *P. major* (JMP IX 46790)
- *N. kerioi* females
- ▲ *Ek. ryanzae* (KNM-BG 13142A)
- *M. dachopi* (JMP MORR 94780)
- ▲ *N. kerioi* males
- △ *Ek. ryanzae* (KNM-RU 5537)
- × *D. fontani* (IPS 41724)
- *T. kalakolensis* (KNM-WK 16950)
- *H. heisterius* (IPS 16800.29)

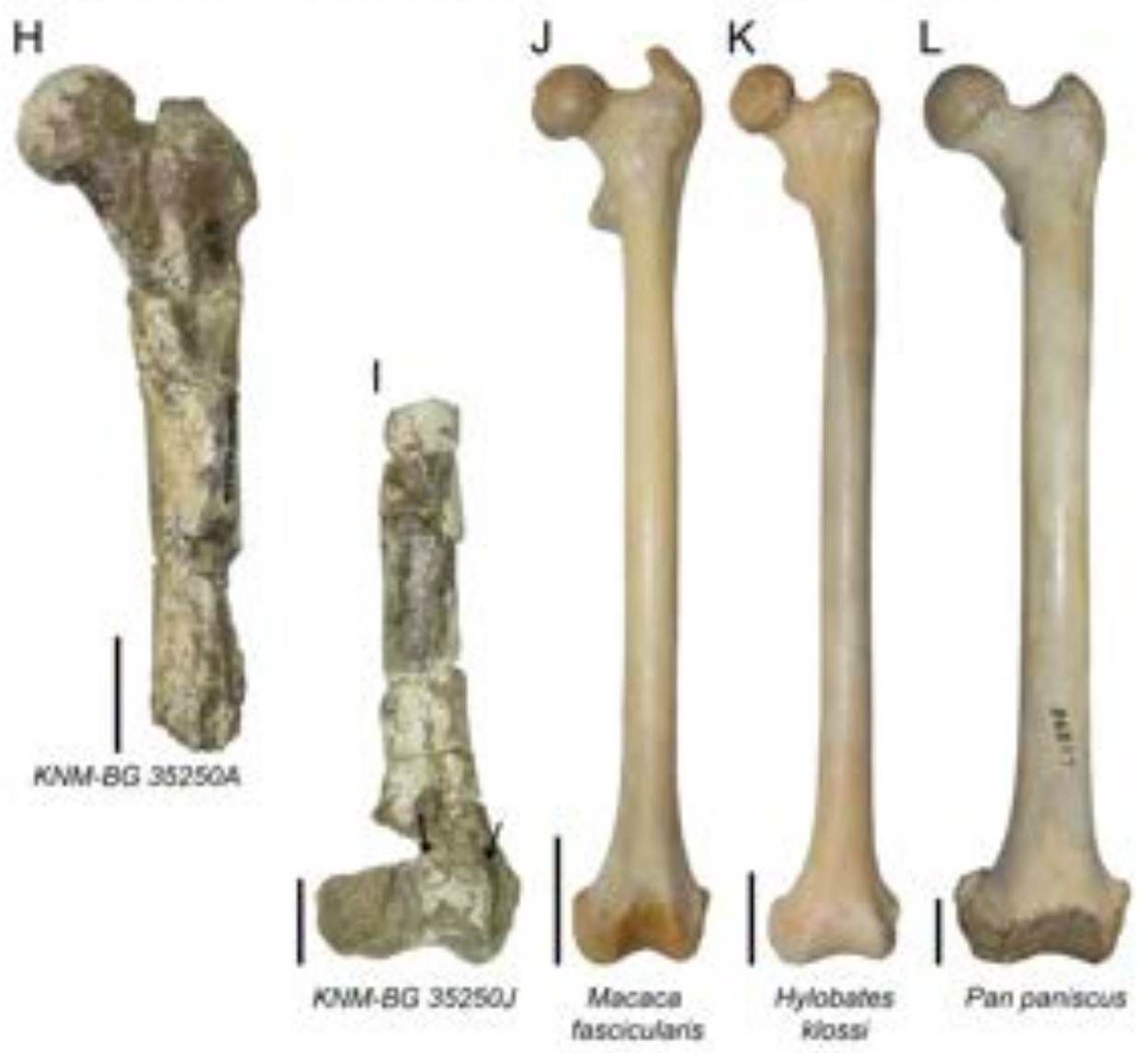


Table 1

Femoral remains attributed to *Nacholapithecus kerioi*. Sex is provided for those specimens included in the sexual dimorphism analysis in Kikuchi et al. (2018).^a

Accession number	Description	Side	Sex	Locality	First reference	APN	SIH	SIN	NL	TotW	NSangle
KNM-BG 17775	Head with neck	?		BG-X	Rose et al. (1996)						
KNM-BG 17778	Head	?L		BG-X	This study ^b						
KNM-BG 17816	Proximal shaft, including LT	R		BG-I	Rose et al. (1996)						
KNM-BG 17819	Head with neck	R		BG-I	Rose et al. (1996)						
KNM-BG 17820	Proximal fragment	L		BG-I	Rose et al. (1996)						
KNM-BG 17821	Head with neck	?		BG-I	Rose et al. (1996)						
KNM-BG 35250A	Proximal half	R	M	BG-K	Nakatsukasa et al. (1998) ^c	12.1	22.3	15.5			129.4
KNM-BG 35250B	Distal fragment	R		BG-K	Nakatsukasa et al. (1998)						
KNM-BG 35250D	Proximal fragment	L		BG-K	Nakatsukasa et al. (1998)						
KNM-BG 35250J	Shaft and distal end	L		BG-K	Nakatsukasa et al. (1998)						
KNM-BG 35250U	Proximal fragment	L		BG-K	Nakatsukasa et al. (1998)						
KNM-BG 38391A	Proximal fragment	L	M	BG-K	Kikuchi et al. (2018) ^c	9.6	22.0	16.2	23.4	49.7	115.3
KNM-BG 40794A	Head with neck	R	F	BG-K	Kikuchi et al. (2018) ^c	7.8	18.5	14.5			

KNM-BG 40826	Proximal fragment	R	F	BG-K	Kikuchi et al. (2018) ^c	8.9	17.3	13.4			130.1
KNM-BG 40844	Head	?R		BG-K	This study						
KNM-BG 40933	Head with neck	L	M	BG-K	Kikuchi et al. (2018) ^c	12.3	21.9	16.9			
KNM-BG 40964	Proximal fragment without head and neck	R		BG-K	This study						
KNM-BG 42713A	Proximal half	L	F	BG-K	Kikuchi et al. (2018) ^c						
KNM-BG 42722	Shaft fragment	R		BG-I	This study						
KNM-BG 42732	Distal fragment	L		BG-I	This study						
KNM-BG 42738/42756C	Proximal fragment	L	M	BG-I West	Kikuchi et al. (2018) ^c	12.9	24.2	16.5	25.8	54.2	121.0
KNM-BG 42757	Proximal fragment	L		BG-K	This study ^b						114.9
KNM-BG 42779	Shaft fragment (distal)	L		BG-K	This study						
KNM-BG 44953A	Proximal fragment	R	F	BG-K	Kikuchi et al. (2018) ^c	8.1	17.1	13.1	17.3	37.7	108.3
KNM-BG 44953B	Proximal fragment without head and neck	L		BG-K	This study						
KNM-BG 44954A	Proximal fragment	L	M	BG-K	Kikuchi et al. (2018) ^c						
KNM-BG 48092A	Proximal fragment	R	F	BG-K	Kikuchi et al. (2018) ^c	9.1	18.0	13.8	18.0	38.5	119.2
KNM-BG 48093	Proximal fragment	L	F	BG-K	Kikuchi et al. (2018) ^c	8.2	17.0	13.3	17.3	38.3	107.1

Abbreviations: APN = anteroposterior depth of the femoral neck (mm); BG = Baragoi; F = female; L = left; LT = lesser trochanter; M = male; NL = neck length (mm); NSangle = neck-shaft angle (degrees); R = right; SIH = superoinferior height of the femoral head (mm); SIN = superoinferior height of the femoral neck (mm); TotW = total mediolateral width of the proximal femur from the medialmost point of the femoral head to the lateral-most point of the greater trochanter (mm); ? = uncertain.

^aThese femoral fragments are fully open access for further analytical studies.

^bUsed for comparative purposes (Ishida et al., 2004; Nakatsukasa et al., 2012), but never formally described.

^cFragment included in the quantitative analyses.

Table 2

Extant anthropoid taxa included in the analyses. Number of females/males/unknown sex in parentheses.^a

Species	<i>n</i>		
	SIH/(ÖSIN*APN)	Relative NL	NSangle
<i>Cebus apella</i>	33 (13/20/-)	27 (12/15/-)	27 (12/15/-)
<i>Ateles</i> sp.	8 (5/2/1)	8 (2/2/4)	8 (2/2/4)
<i>Alouatta</i> sp.	45 (22/19/4)	28 (15/8/5)	30 (14/10/6)
<i>Presbytis</i> sp.	34 (20/14/-)	25 (14/11/-)	33 (16/17/-)
<i>Colobus</i> sp.	28 (13/15/-)	32 (12/18/2)	27 (12/14/1)
<i>Nasalis larvatus</i>	25 (12/13/-)	25 (12/13/-)	25 (12/13/-)
<i>Chlorocebus</i> sp.	16 (6/8/2)	10 (4/5/1)	—
<i>Cercopithecus</i> sp.	49 (19/30/-)	37 (11/20/6)	14 (5/8/1)
<i>Macaca</i> sp.	30 (15/15/-)	27 (13/14/-)	26 (13/13/-)
<i>Lophocebus</i> sp.	15 (2/12/1)	7 (1/5/1)	—
<i>Mandrillus</i> sp.	13 (4/8/1)	10 (3/6/1)	10 (3/6/1)
<i>Papio</i> sp.	25 (5/11/9)	18 (2/8/8)	20 (4/9/7)
<i>Hylobates lar</i>	26 (13/13/-)	25 (12/13/-)	26 (13/13/-)
<i>Pongo pygmaeus</i>	12 (4/5/3)	11 (5/4/2)	12 (4/5/3)
<i>Pan t. troglodytes</i>	29 (14/15/-)	17 (4/9/4)	—
<i>Pan t. schweinfurthii</i>	25 (8/17/-)	21 (7/10/4)	26 (8/16/2)
<i>Pan paniscus</i>	20 (11/9/-)	20 (11/9/-)	20 (11/9/-)
<i>Gorilla g. gorilla</i>	31 (13/18/-)	20 (10/10/-)	26 (13/13/-)
<i>Gorilla b. graueri</i>	21 (8/13/-)	22 (8/14/-)	21 (8/13/-)
<i>Gorilla b. beringei</i>	10 (5/5/-)	7 (4/3/-)	8 (4/4/-)

Abbreviations: APN = anteroposterior depth of the femoral neck; n = sample size; NL = neck length; NSangle = neck-shaft angle; SIH = superoinferior height of the femoral head; SIN = superoinferior height of the femoral neck.

^a Data for these femora were collected at the American Museum of Natural History, New York (AMNH, USA), the Museum of Comparative Zoology, Harvard University (MCZ, USA), Peabody Museum of Archaeology and Ethnology, Harvard University (PBMA, USA), and the Royal Museum of Central Africa (RMCA, Belgium).

Table 3

Descriptive statistics for the $SIH/(\overline{OSIN} * APN)$ index, relative NL, and NSangle variables in the *Nacholapithecus kerioi* sample.

	<i>n</i>	Mean	SD	Min	Max
$SIH/(\overline{OSIN} * APN)$	9	1.644	0.076	1.519	1.764
Relative NL	5	46.50	0.969	45.17	47.60
NSangle	8	118.2	8.587	107.1	130.1

Abbreviations: APN = anteroposterior neck depth; *n* = sample size; Max = maximum value; Min = minimum value; NL = neck length; NSangle = neck-shaft angle; SIH = superoinferior height of the femoral head; SIN = superoinferior height of the femoral neck; SD = standard deviation.

Table 4

Post-hoc pairwise comparisons between *Nacholapithecus kerioi* and extant anthropoids for the SIH/($\sqrt{\text{SIN} \cdot \text{APN}}$) index, relative NL, and NSangle.^a

	<i>Nacholapithecus kerioi</i>		
	SIH/($\sqrt{\text{SIN} \cdot \text{APN}}$)	Relative NL	NSangle
<i>Cebus apella</i>	NS	NS	NS
Atelids	NS	NS	**
Colobines	***	*	*
Cercopithecines	**	*	**
<i>Hylobates lar</i>	***	***	*
<i>Pongo pygmaeus</i>	*	NS	***
<i>Pan troglodytes troglodytes</i>	NS	NS	—
<i>Pan troglodytes schweinfurthii</i>	NS	NS	*
<i>Pan paniscus</i>	NS	**	NS
<i>Gorilla gorilla gorilla</i>	NS	NS	NS
<i>Gorilla beringei graueri</i>	NS	NS	NS
<i>Gorilla beringei beringei</i>	NS	NS	NS

Abbreviations: SIH/($\sqrt{\text{SIN} \cdot \text{APN}}$) = relative size of the femoral head (APN = anteroposterior neck depth; SIH = superoinferior height of the femoral head; SIN = superoinferior height of the femoral neck); Relative NL = neck length divided by total mediolateral width of the proximal femur multiplied by 100; NSangle = neck-shaft angle of the femur.

^a NS, no significant differences; *, $p < 0.05$; **, $p < 0.005$; ***, $p < 0.001$.

Supplementary Online Material (SOM):

New femoral remains of *Nacholapithecus kerioi*: Implications for intraspecific variation and Miocene hominoid evolution

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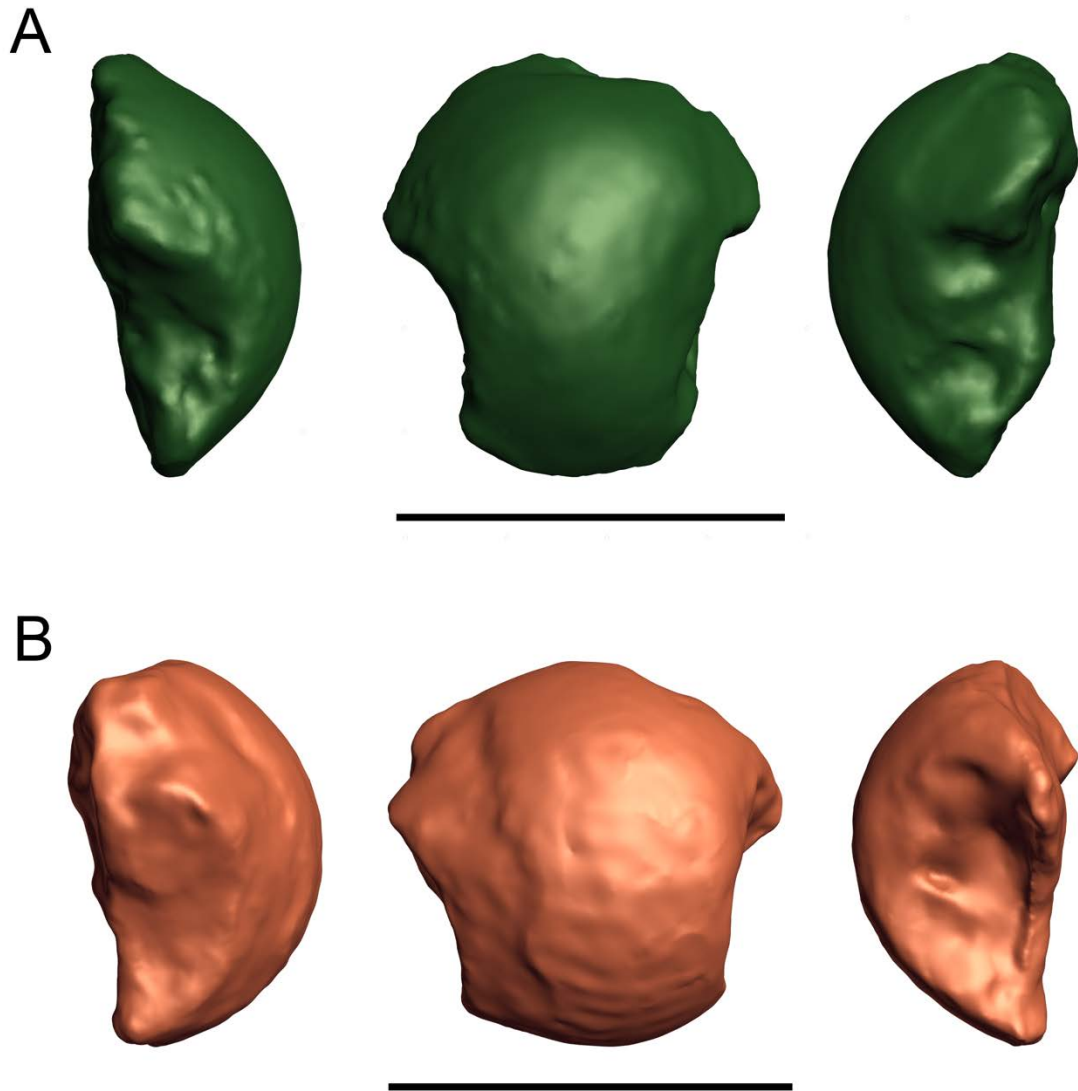
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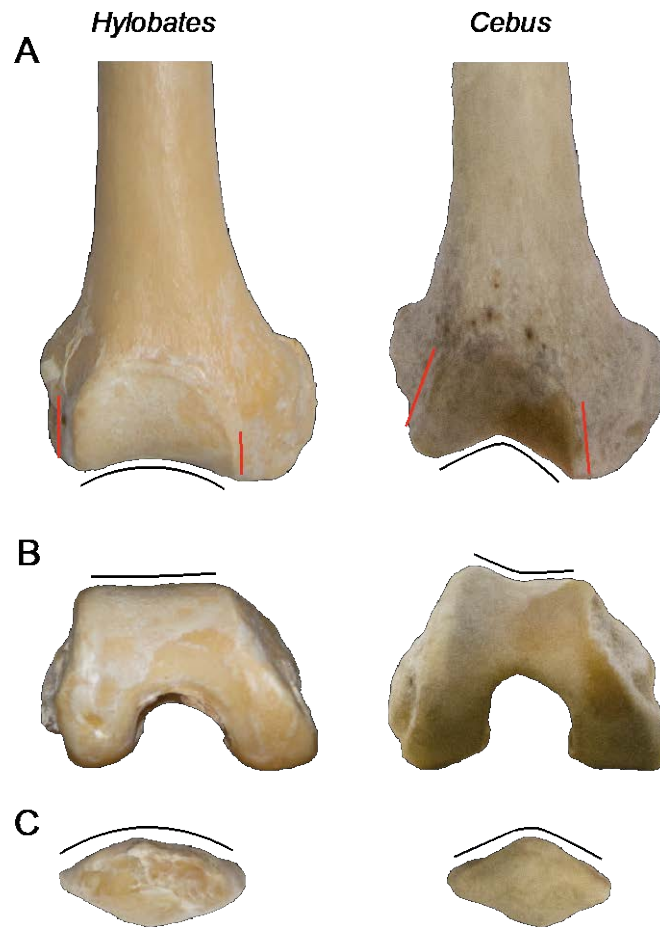
E-mail address: marta.pinamiguel@manchester.ac.uk (M. Pina)



SOM Figure S1. Comparison of the femoral distal diaphysis fragment (posterior views) of *Nacholapithecus kerioi* (KNM-BG 42722; left) with *Equatorius africanus* (cast BNMH M 16332-3; right). KNM-BG 42722 is placed at the shaft location that might correspond with that of BNMH M 16332-3. Scale bar = 20 mm.



SOM Figure S2. Screenshots from 3D models of A) KNM-BG 15333, and B) KNM-BG 13336. Left and right, side views; center, medial view. These two fragments were described by previous authors (Rose et al., 1996), who suggested that both fragments would be femoral heads of the species *Nacholapithecus kerioi*. We amended these attributions in this work, suggesting that (A) is a humeral head of *N. kerioi*; whereas (B) would be a femoral fragment that belongs to a nonprimate mammal (see text for further explanation). Scale bar = 20 mm.



SOM Figure S3. Distal femoral end and patellae of *Hylobates* and *Cebus* in A) anterior, B) distal, and C) proximal views, respectively. Femora are displayed at the same mediolateral width, and patella at the same anteroposterior thickness to facilitate morphological comparisons. Black continuous lines denote the depth of the patellar groove in the femur and its respective morphology at the articular surface of the patella. As shown in the figure, anthropoid monkeys display a deeper patellar groove while it is shallow in apes. Red continuous lines represent the lateral and medial rims of the patellar groove in the femur, highlighting that the rims are parallel in apes and tend to converge in anthropoid monkeys. See also 3D models of femora belonging to *N. kerioi* (KNM-BG 42732), *Hylobates lar*, and *Cebus apella* (SOM 3D Models S1, S2, and S3).

SOM Table S1

Descriptive statistics for APN, SIH, SIN, NL, and TotW in the *Nacholapithecus kerioi* sample. All measurements are taken in mm.

	<i>n</i>	Mean	SD	Min	Max
APN	9	9.89	2.00	7.76	12.90
SIH	9	20.05	3.01	17.00	24.80
SIN	9	14.99	1.76	13.10	18.20
NL	5	20.36	3.97	17.30	25.80
TotW	5	43.68	7.72	37.70	54.20

Abbreviations: APN = anteroposterior neck depth; *n* = sample size; Max = maximum value; Min = minimum value; NL = neck length; SIH = superoinferior height of the femoral head; SIN = superoinferior height of the femoral neck; SD = standard deviation; TotW = total mediolateral width of the proximal femur.

SOM Table S2

Summary of the main femoral traits qualitatively described in this study and compared with previously published reports.

	Rose et al., 1996	Nakatsukasa et al., 1998	Ishida et al., 2004	Nakatsukasa et al., 2012	Kikuchi et al., 2018	This study ^a
Proximal FH				Strong anteversion; weak anterior displacement of the FH center related to FN axis	Inclined weakly anteriorly; rounded	Absence of strong anteversion
Articular surface FH		Moderately wide	Mediolaterally deep	Extensive and mushrooms over the neck	Moderately wide coverage, mushroomed around the neck	Hemispherical
FH-GT projection			FH slightly above GT	FH slightly above GT	FH higher than GT	FH above GT
FH/FN relation				Large	Large (FN constricted superoinferiorly relative to the FH)	Small relative FH
Fovea capitis				Antero-posteriorly oblong, posteroinferiorly situated	Faint, positioned posteroinferiorly	Shallow; positioned in the distal half of the FH
FN length			Relatively short	Apparently short	Relatively short	Moderately long
NSangle		High	High	High		Moderately high
Lateral flare GT	Protuberant	Flare of the m gluteus minimus insertion		Protuberant insertion of m gluteus minimus	Projects laterally (mainly the distal part)	Inconclusive

	LT	More lateral than posterior projection	Large	Posteromedially directed	Superoinferiorly wide and projects medially	High position, long, projecting medially and moderately posteriorly	Posteromedial direction, close to the FN
	Gluteal tuberosity	Discrete and protuberant		Prominent	Proximally placed (close to the insertion of the m gluteus minimus)		Marked, close to the GT
Distal	Patellar surface		Wide	Squared-shaped	Squared-shaped and wide		Squared-shaped and shallow
	Epicondyles			Similar mediolateral breadth	Symmetrical		Symmetrical

Abbreviations: FH = femoral head; FN = femoral neck; GT = greater trochanter; LT = lesser trochanter; m = muscle; NSangle = neck-shaft angle.

^aSee also Pina et al. (2018).

SOM Table S3

Descriptive statistics for $SIH/(\sqrt{SIN*APN})$ (upper row), relative NL (middle row), and NSangle (bottom row) for each species in the sample of extant anthropoids.

Species	<i>n</i>	Mean	SD	Min	Max
<i>Cebus apella</i>	33	1.55	0.07	1.41	1.70
	27	49.70	3.98	40.70	59.04
	27	121.16	5.40	111.99	133.20
<i>Ateles</i> sp.	8	1.67	0.13	1.51	1.94
	8	48.60	5.50	39.88	56.73
	8	127.60	6.24	118.20	134.15
<i>Aloutta</i> sp.	45	1.70	0.11	1.48	1.97
	28	45.09	4.29	31.14	52.62
	30	123.62	6.02	111.03	134.48
<i>Presbytis</i> sp.	34	1.47	0.06	1.37	1.66
	25	42.48	4.00	34.29	53.36
	33	113.23	4.23	103.77	122.19
<i>Colobus</i> sp.	28	1.44	0.09	1.27	1.63
	32	41.59	5.15	30.45	49.49
	27	112.94	6.24	97.86	126.27
<i>Nasalis larvatus</i>	25	1.43	0.09	1.24	1.57
	25	38.14	4.06	29.24	47.52
	25	111.55	4.71	101.33	120.52
<i>Chlorocebus</i> sp.	16	1.45	0.08	1.32	1.60
	10	40.23	4.19	33.25	46.41
	—	—	—	—	—
<i>Cercopithecus</i> sp.	49	1.46	0.09	1.17	1.70
	37	42.27	5.69	32.00	55.61
	14	112.11	4.89	104.15	123.18
<i>Macaca</i> sp.	30	1.44	0.09	1.31	1.64
	27	38.67	5.07	26.36	46.76
	26	110.53	4.67	101.93	120.16
<i>Lophocebus</i> sp.	15	1.49	0.08	1.37	1.65
	7	39.31	4.07	33.71	45.92
	—	—	—	—	—
<i>Mandrillus</i> sp.	13	1.46	0.11	1.31	1.69 ^a
	10	45.40	6.32	37.39	57.11
	10	109.32	6.26	97.84	117.42
<i>Papio</i> sp.	25	1.57	0.10	1.38	1.78
	18	42.91	4.71	35.77	53.70
	20	112.70	5.65	100.18	119.31
<i>Hylobates lar</i>	26	1.89	0.14	1.65	2.12
	25	35.08	3.65	28.33	42.19

	26	123.95	5.16	115.43	134.82
<i>Pongo pygmaeus</i>	12	1.93	0.14	1.70	2.14
	11	48.84	5.83	38.10	54.69
	12	134.93	5.81	127.29	145.07
<i>Pan t. troglodytes</i>	29	1.63	0.08	1.46	1.78
	17	44.47	5.67	36.73	52.97
	—	—	—	—	—
<i>Pan t. schweinfurthii</i>	25	1.68	0.10	1.53	1.94
	21	42.98	5.34	30.50	53.24
	26	123.00	5.11	114.27	132.69
<i>Pan paniscus</i>	20	1.66	0.10	1.53	1.84
	20	38.44	4.65	28.82	44.80
	20	122.77	5.31	114.23	130.86
<i>Gorilla g. gorilla</i>	31	1.65	0.09	1.48	1.81
	20	44.87	5.00	34.08	56.63
	26	121.95	3.98	113.31	127.82
<i>Gorilla b. graueri</i>	21	1.66	0.08	1.49	1.87
	22	42.49	3.75	34.31	50.51
	20	116.89	4.27	107.75	122.61
<i>Gorilla b. beringei</i>	10	1.60	0.07	1.47	1.77
	7	42.00	4.05	33.22	44.79
	9	120.96	4.92	113.94	129.04

Abbreviations: APN = anteroposterior neck depth; n = sample size; Max = maximum value; Min = minimum value; NL = neck length; NSangle = neck-shaft angle; SIH = superoinferior height of the femoral head; SIN = superoinferior height of the femoral neck; SD = standard deviation.

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