New Remains of *Camelus grattardi* (Mammalia, Camelidae) from the Plio-Pleistocene of Ethiopia and the Phylogeny of the Genus

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1 New remains of *Camelus grattardi* (Mammalia, Camelidae) from the Plio-Pleistocene of Ethiopia
2 and the phylogeny of the genus

3
4 By Denis Geraads^{1,2*}, W. Andrew Barr³, Denne Reed⁴, Michel Laurin¹, and Zeresenay Alemseged⁵

5
6 ¹CR2P-UMR 7207, CNRS, MNHN, UPMC, Sorbonne Universités, CP 38, 8 rue Buffon, 75231 Paris
7 Cedex 05, France; denis.geraads@mnhn.fr; michel.laurin@mnhn.fr;

8 ²Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher
9 Platz 6, 04103 Leipzig, Germany;

10 ³Center for the Advanced Study of Human Paleobiology, Department of Anthropology, The George
11 Washington University, Washington DC 20052, USA; wabarr@gmail.com;

12 ⁴Department of Anthropology, University of Texas at Austin. Austin, TX 78712; USA;
13 reedd@austin.utexas.edu

14 ⁵Organismal Biology and Anatomy, University of Chicago, Chicago 60637, USA;
15 alemseged@uchicago.edu;

16
17 * Corresponding author. ORCID id. 0000-0003-2475-8011

18
19 **Running head:** Plio-Pleistocene *Camelus* from Ethiopia

20
21 **Abstract**

22 The Old World fossil record of the family Camelidae is patchy, but a new partial cranium and
23 some other remains of *Camelus grattardi* from the Mille-Logya Project area in the Afar, Ethiopia,
24 greatly increase the fossil record of the genus in Africa. These new data – together with analysis of
25 unpublished and recently published material from other sites, and reappraisal of poorly known taxa –
26 allow for a comprehensive phylogenetic analysis showing that *C. grattardi* is the earliest (2.2–2.9

27 Ma) and most basal species of the genus. We also show that the lineages leading to the extant taxa
28 *C. dromedarius* and *C. bactrianus* diverged much higher in the tree, suggesting a recent age for this
29 divergence. A late divergence date between the extant species is consistent with the absence of any
30 fossil forms that could be ancestral, or closely related, to any of the extant forms before the late
31 Pleistocene, but stands in contrast to molecular estimates which place the divergence between the
32 dromedary and the Bactrian camel between 8 and 4 million years ago.

33

34 **Keywords:** Mammalia, Camelidae, phylogeny, Pleistocene, Eastern Africa

35

36 **Introduction**

37 Most of the early evolution of Old World Camelidae, since their immigration from North
38 America in the late Miocene (Honey et al. 1998; Harris et al. 2010; Rybczynski et al. 2013), seems to
39 have occurred in Eurasia. Late Miocene and early Pliocene forms in Eurasia are usually referred to
40 *Paracamelus* Schlosser, 1903, a genus that is currently diagnosed primarily by the retention of a
41 lower third premolar, which is lost in the extant genus *Camelus* Linnaeus, 1758. *Paracamelus* has a
42 wide distribution from Western Europe (Colombero et al. 2017) to China (Zdansky 1926; Teilhard
43 de Chardin and Trassaert 1937) and through Eastern Europe (Ștefănescu 1895; Khaveson 1954;
44 Kozhamkulova 1986; Logvynenko 2001), but remains very incompletely described. In Africa, it is
45 documented by scrappy remains from the Pliocene of Chad, Tunisia, and Egypt (Harris et al. 2010).
46 Fossil *Camelus* are also poorly known. The fragmentary remains from the Plio-Pleistocene of Omo-
47 Turkana Basin of Kenya and Ethiopia (Howell et al. 1969; Grattard et al. 1976; Harris et al. 2010)
48 have been assigned to *C. grattardi* Geraads, 2014 (Geraads 2014; Rowan et al. 2018), whose type-
49 specimen is from Member G of the Omo Shungura Formation, dated to 2.2 Ma. Until now, the only
50 fossil camel cranium known in Africa was from the late early Pleistocene of Tighennif, Algeria,
51 which is the type locality of *C. thomasi* Pomel, 1893 (Martini and Geraads 2018).

52 In 2014, the Mille-Logya Project (MLP) discovered a relatively complete cranium in the
53 upper Pliocene sediments of the Mille-Logya area, Lower Awash Valley, Ethiopia. Its characters
54 match those of the type-specimen of *C. grattardi*, and we assign it to this species. In addition to
55 considerably expanding the hypodigm of *C. grattardi*, the newly discovered cranium, together with a
56 few additional isolated teeth and postcranial remains from the same stratigraphic unit, allow us to
57 assess the phylogeny of the genus.

58 All data for this article are included in the following text and in the Supplementary
59 Information. Anatomical terminology is translated from Latin, following the World Association of
60 Veterinary Anatomists (1973).

61

62

63 **Geological setting**

64 The Mille-Logya Project (MLP), led by one of us (ZA), has conducted research in the Lower
65 Awash Valley of Ethiopia since 2012. Sediments in this area date to c.a. 3 – 2.4 Ma and largely post-
66 date the Hadar Formation exposed at several nearby sites (Alemseged et al. 2016). The fossil fauna
67 from the new research area, currently under study, is diverse. The abundance of presumably grazing
68 equids and alcelaphin bovids at MLP suggests a relatively open environment with extensive grass
69 cover, as in the nearby Ledi-Geraru sequence (Rowan et al. 2016; Bibi et al. 2017; Robinson et al.
70 2017), but is not consistent with the sub-desertic environments favored by extant camels. The camel
71 cranium described here (NME-MLP-1346), as well as the additional isolated teeth and postcranial
72 remains, are all from the Seraitu unit dated to c. 2.5 – 2.9 Ma. All MLP fossils described here are
73 housed in the National Museum of Ethiopia, Addis Ababa (NME).

74

75 **Old World Camelidae**

76 We compared the MLP fossils to a large sample of extant camels, especially skulls:
77 *C. bactrianus* Linnaeus, 1758 (17 skulls; we include here the so-called *C. ferus* Przewalski, 1878, as
78 there is no evidence that the two species can be distinguished morphologically); *C. dromedarius*
79 Linnaeus, 1758 (34 skulls); hybrids or unidentified (4 skulls), housed in Muséum National d'Histoire
80 Naturelle, Paris (MNHN), Centre de Conservation et d'Etude des Collections, Lyon (CCEC), and
81 Zoological Institute, Saint Petersburg (ZIN). The distinction between extant species has recently
82 been fully analyzed (Martini et al. 2017). In addition, we have examined the following fossil forms:

- 83 1. *Camelus sivalensis* Falconer and Cautley, 1836, from the upper Siwaliks (Falconer and
84 Cautley 1846; Colbert 1935; Nanda 1978; Gaur et al. 1984), housed in the Natural History
85 Museum, London (NHMUK) and American Museum of Natural History, New York
86 (AMNH); R. Patnaik was kind enough to provide us with photos of the relatively complete
87 cranium A/646 (Sahni and Khan 1988). It was the first fossil camel species to be described,

and is also the best represented in collections. Its appearance in the upper Siwaliks is dated at 2.6 Ma, or perhaps slightly older (Patnaik 2013). It differs from extant forms in its supraorbital foramina that open wider apart, more complete P3 lingual crescent, broader molars with stronger ribs and styles, more oblique ramus of the mandible, and the shorter ligament scars on the proximal phalanges.

2. The type-cranium of the Middle Pleistocene *C. knoblochi* Nehring, 1901 (ZIN-8678/8679), a few specimens of the same species from Sjava-Osso-Gol (Boule et al. 1928), stored in MNHN, complemented with photos of other specimens, kindly provided by V. Titov (cranium from Razdorskaya and incomplete skull VSEGEI 7/2932 from Sengiley [Titov 2008]). The species has been reported from a number of middle and upper Pleistocene sites, mostly in Russia, but remains incompletely described. It differs from extant forms mainly in its larger size and a broad infraorbital shelf.

3. *C. thomasi* Pomel, 1893, from the late early Pleistocene of Tighennif (=Ternifine), housed in MNHN, complemented by photos of the specimens (including the type) kept in the Algiers Museum, kindly provided by Y. Chaïd-Saoudi. The species was first erected for some dental and postcranial remains, but C. Arambourg collected more material from the type locality in 1954-1956, including a complete cranium. This material has been fully described (Martini and Geraads 2018). A few other specimens of *C. thomasi* are from the 'Grotte des Rhinocéros' in Casablanca (Geraads and Bernoussi 2016), but most reports from later sites in North Africa and the Middle East are incorrect (Martini and Geraads 2018). The species is characterized by its large size, pachyostosis (especially marked in the mandible), marked sexual dimorphism, V-shaped choanae, anteriorly located palatine foramina, low placement of orbits, jugular process positioned far from the condyles, an anteriorly positioned P1, P3 with a complete lingual crescent, broad molars with strong styles, an absent or anteriorly located p1, long p4, with a long metaconid, and long limb bones.

113 4. Early African Camelidae from the early Pliocene of Kossom Bougoudi in Chad (a mandible
114 and two metatarsals housed in Centre National de la Recherche pour le Développement,
115 N'Djamena, Chad (CNRD), described as *Paracamelus gigas* Schlosser, 1903 [Likius et al.
116 2003] characterized by large size and the presence of a p3); Pliocene of Ichkeul in Tunisia (a
117 calcaneum housed in MNHN [Arambourg 1979; Harris et al. 2010]), Pliocene of Wadi
118 Natrun in Egypt (a cuboid housed in Senckenberg Museum, Frankfurt [Stromer 1902]), Plio-
119 Pleistocene of Turkana Basin of Kenya and Ethiopia (various fragmentary specimens housed
120 in Nairobi National Museum [KNM] and NME [Harris et al. 2010; Howell et al. 1969; Harris
121 1991; Geraads 2014]), late Pleistocene of Algeria (some isolated teeth housed in Université
122 Claude Bernard, Lyon [UCBL; Flamand 1902]).

123 5. North American camels housed in the AMNH: *Megacamelus merriami* (Frick, 1921) from
124 Keams Canyon, Arizona, and Edson Quarry, Kansas; *Megatylopus gigas* (Matthew and Cook,
125 1909) from the Snake Creek Formation of Nebraska; *Megatylopus* sp. from the Guymon area
126 of Oklahoma, and *Aepycamelus major* (Leidy, 1886) from the Mixson beds of Florida.
127 However, because more than one taxon may be present in each of these sites (Harrison 1985),
128 these identifications are not always certain.

129 Other species are known to us through the literature. The name *Camelus alutensis* was
130 erected (Ștefănescu 1895) for a small mandible from Romania with a p3, a long symphysis, and a
131 shallow corpus, of which we have seen a cast. The species was later transferred to *Paracamelus*
132 (Khaveson 1954). The name *Camelus kujalnensis* Khomenko, 1912, is probably a synonym (Titov
133 2003), and *Paracamelus minor* Logvynenko, 2001, could be identical as well. This species has also
134 been tentatively reported from the lowermost Pleistocene of Sarikol Tepe in Turkey (Kostopoulos
135 and Sen 1999), but remains poorly known and poorly defined (Ștefănescu 1910; Topachevskiy 1956;
136 Baigusheva 1971; Rădulescu and Burlacu 1993; Logvynenko 2000; Titov 2003). Taxonomy of these
137 small forms is debatable, but the upper molars from Turkey are unlike those of other Camelidae in
138 their U-shaped valleys, and this small-bodied lineage is probably distinct from other forms.

139 The genus *Paracamelus* was erected for *P. gigas* from the late Neogene of China (Schlosser
140 1903); it is based upon two upper molars, of which one was selected (Van der Made and Morales
141 1999) as lectotype; unfortunately, this tooth is no longer part of Schlosser's collection in München
142 (G. Rössner pers. comm.). From the figure (Schlosser 1903: pl. 9, figs. 14 and 26), this molar differs
143 from those of *Camelus* in that both the mesostyle and the buccal pillar of the paracone are distinctly
144 broader, especially near the base, the central anterior valley is wider, and the labial crescents have a
145 less regular thickness. Taken together, these features give the tooth a distinct overall pattern, even
146 suggesting that it might not be camelid at all, but much less scrappy camelid material from Loc. 102
147 in Henan, China, was assigned to *P. gigas* by Zdansky (1926) so that his material became the
148 reference for this taxon, although species identification was merely based upon size; for the sake of
149 nomenclatural stability, we shall continue using Schlosser's name. Additional material comes from
150 Shansi (Teilhard de Chardin and Trassaert 1937). The species was identified (Teilhard de Chardin
151 and Piveteau 1930) from the early Pleistocene of Nihowan on the basis of absence of a mediopltantar
152 astragalar facet on the calcaneus, but this facet may also be lacking in *C. bactrianus* and *C. thomasi*
153 so this identification is unsupported.

154 The name *Paracamelus alexejevi* Khaveson, 1950, was erected for the abundant material of
155 the Odessa catacombs; later its author (Khaveson 1954) revised Old World camels and provided the
156 first diagnosis of *Paracamelus*, as then understood. It included: 1) presence of p3 and dp2; 2) strong
157 ribs and styles on molars; 3) long P3; 4) paraconid distinct from parastylid on p4; 5) cranium longer
158 and narrower than in *Camelus*, and 6) some differences in mandibular proportions, especially a
159 longer lower jaw. In fact, the morphology that he described and illustrated for the p4 of *P. alexejevi*
160 may be present in *C. dromedarius* as well, although he correctly observed that this species differs
161 from *C. bactrianus* in that the central valley is never closed lingually. The long P3 and presence of
162 p3 are clear, and the long mandible is probably also a valid difference, but other differences in
163 cranial and mandibular proportions remain to be fully documented because the most complete
164 illustrated skull (Khaveson 1954: pls 2 and 10) is largely reconstructed in plaster; in a more reliable

165 cranium (Khaveson 1954: fig. 1), the position of the orbit is similar to that of *Camelus*. The species
166 *P. alexejevi* was defined (Khaveson 1954) by its slender limbs and by the small difference in the
167 mean lengths of the metacarpal and metatarsal (3 mm), but this value is well within the range of
168 extant forms (Martini et al. 2017, and our observations). We have not seen the Ukrainian and Russian
169 material of *Paracamelus*, but some data and photos were provided by T. Krakhmalnaya and
170 N. Podoplelova, and a cast of the type specimen of *P. alutensis* was examined in UCBL.

171 In addition, several species of poorly constrained age were erected on scrappy material. These
172 are *Procamelus khersonensis* Pavlow, 1904, based upon a juvenile cranium, *Camelus bessarabiensis*
173 Khomenko, 1912 (Simionescu 1930, 1932), and *Camelus praebactrianus* Orlov, 1927 (Orlov 1929),
174 based upon some postcranial bones.

175 In the purported *Gigantocamelus* sp. from Ukraine (Svistun 1971), the length of the lower
176 molar series looks overestimated, and the distal metapodial is really large only if it is a metatarsal, as
177 assumed by him, but even smaller than in *C. knoblochi* if it is in fact a metacarpal. In
178 ‘*Gigantocamelus longipes*’ from Kazakhstan (Aubekerova 1974) the measurements of a metacarpal
179 match those of a metatarsal of *P. gigas* (Teilhard de Chardin and Trassaert 1937), and should
180 probably be attributed to this species.

181 *Paracamelus aguirrei* Morales in Van der Made and Morales, 1999 (this species was first
182 described in an unpublished thesis [Morales 1984]; it seems that the name was validated only in
183 1999) from Venta del Moro (Morales et al. 1980; Morales 1984; Pickford et al. 1995; Van der Made
184 and Morales 1999) and Librilla (Alberdi et al. 1981) is the earliest camel of Europe, of latest
185 Miocene age. It is poorly known but the upper molars are distinctly brachydont, broad, and have
186 strong styles. A juvenile lower dentition from the upper Miocene of Çoban Pinar, Turkey, was
187 assigned to *Paracamelus* cf. *P. aguirrei* (Van de Made et al. 2002); its provenance remains uncertain
188 (Sen 2010; Van der Made and Morales 2013) but the long, high-crowned m1 matches extant forms.
189 The few postcranials from the middle (?) Pliocene of Garaet Ichkeul in Tunisia (Arambourg 1979)
190 were also assigned to *P. aguirrei* (Van der Made and Morales 1999), with poor support. The same

191 species was reported (Titov and Logvynenko 2006) from the northern shore of the Black Sea in sites
192 assumed to be earlier in age than Venta del Moro and Çoban Pinar.

193 Probably the most interesting sites for the history of Old World camels are those recently
194 excavated in Syria by the University of Basel. No details have been published yet, but various sites
195 ranging from the early to the late Pleistocene have provided as many as three different species, two
196 of them being giant forms (Martini et al. 2015). It is likely that the very incomplete remains from
197 Latamne (Hooijer 1961) and Ubeidiyeh (Haas 1966; Geraads 1986) will have to be referred to one or
198 more of them.

199

200 **Description and comparisons**

201 **Mille-Logya material:**

202 The specimen NME-MLP-1346 consists of several parts, including some teeth and fragments
203 recovered by screening, but due to their close physical proximity and identical preservation there is
204 no doubt that they all belong to the same individual (Figs. 1-2; Supplementary Information 1). The
205 largest piece is the posterior part of a cranium with parts of the orbits; in addition, there are the left
206 and right maxillae with most of the teeth, parts of the left and right zygomatic bones, and a piece of
207 the snout consisting of partial palate, vertical part of the maxilla, and partial premaxilla. The cranium
208 is dorsoventrally crushed but distortion affected mostly the braincase itself, while the occiput looks
209 virtually undistorted; in addition, the left squamosal is rotated counterclockwise by about 70°, so that
210 the zygomatic arch is now directed almost ventrally. Dental dimensions suggest that this specimen
211 was a young adult female; the great width of the molars compared to their length, the narrow fourth
212 upper premolar, and the strong labial styles match the type specimen of *C. grattardi*.

213 The only measurement that can be taken accurately, width across occipital condyles, is within
214 the range of extant *Camelus*, although close to its upper limit. Postorbital width is above the extant
215 range, but may have slightly increased because of deformation. Thus, on the whole it is comparable
216 in size to *C. bactrianus*, *C. thomasi*, and *C. sivalensis*, but smaller than *C. knoblochi*.

217 The snout fragment comprises parts of the palate, the ascending part of the maxilla, and the
218 premaxilla. The last is distinctly narrower than in *C. thomasi* (Martini and Geraads 2018); it certainly
219 did not widen posteriorly, in contrast to that of *C. sivalensis* (AMNH-FM19832) and of most extant
220 specimens, and it is very unlikely that it reached the nasals. The erupting permanent canine is
221 preserved within the bone; its tip just reaches the palatal level; the relatively small size of this tooth,
222 reflected in the lack of lateral inflation of the maxilla, suggests that the cranium is from a female
223 individual. In front of the canine, the alveolus of the missing (shed ?) deciduous canine is visible.
224 Not far behind, about one half of a large P1 alveolus is preserved; it is usually located more
225 posteriorly in *C. bactrianus* (Martini et al. 2017). This (missing) tooth was not much smaller than the
226 canine, confirming the sex of the animal. The P1 may be absent in extant forms and in *C. knoblochi*;
227 it is absent in the one known specimen of *P. gigas*, but given the documented variation in *Camelus*,
228 this is insufficient to bar this species from the ancestry of *Camelus* (contra Zdansky 1926). At the
229 level of the canine, the maxilla reaches the sagittal plane whereas in extant forms the posterior
230 processes of the premaxillae intervene; this suggests that the incisive fissures were located more
231 rostrally in the fossil form. In front of the cheek-teeth, there is no evidence of a crest bordering the
232 palate, nor of a sharp narrowing of the latter anterior to P3. The missing palatine bone reached the
233 limit M1/M2, a position that is within the range of variation of the extant forms. There is a single
234 pair of palatine foramina at the level of the first lobe of M1, a position more common in
235 *C. bactrianus* than in *C. dromedarius*; they are even more posterior in *C. knoblochi*, but in
236 *C. sivalensis* and *C. thomasi*, the main pair of foramina opens at the level of P4, as in most
237 *C. dromedarius*. The choanae are not preserved, but the lateral palatine notches do not reach beyond
238 the posterior border of M3.

239 The zygomatic bone is almost intact on the left but only a piece of the right bone is preserved;
240 they can be satisfactorily oriented. Posteriorly, the deep groove for the squamosal reaches farther
241 anteriorly, by at least 1 cm, than the level of the posterior border of the orbit. In contrast, in all extant
242 specimens, in *C. knoblochi*, *C. thomasi*, and *P. gigas*, the most rostral point of the squamosal remains

243 distinctly more caudal. The only species showing a squamosal reaching the orbital level is
244 *P. alexejevi* (Khaveson 1954: fig. 1), and the same condition is also observed in *Megacamelus*
245 *merriami*. Under the orbit, the zygomatic bone forms a flat shelf, about 2 cm deep, facing laterally
246 more than ventrally. It is limited by a clear ventral edge and proceeds posteriorly into the lateral face
247 of the zygomatic arch, whose ventral edge is concave at this level. The maxilla shows that this shelf
248 extends forwards as far as the anterior orbital border and forms a flange over a well-marked
249 longitudinal groove. This shelf is weak in the dromedary, but moderate or variable in other *Camelus*,
250 except in the three specimens of *C. knoblochi*, where it is broad. The small infraorbital foramen is
251 located above P4, as in other Old World camels.

252 The braincase is rounded and clearly limited anteriorly at the level of the postorbital
253 constriction, but also posteriorly where it is distinctly pinched before the nuchal crest; it may be that
254 deformation increased its greatest width which is located at mid-height. The strong, prominent
255 sagittal crest extends from the nuchal crest to the middle of the braincase, where it gently diverges
256 into the temporal lines. There is a single supraorbital foramen on either side, and they are located far
257 apart (66 mm between their centers). In extant *Camelus*, and in *C. knoblochi*, there are usually
258 multiple foramina, and they are always closer to the midline (Supplementary Information 2–3). The
259 condition in *C. sivalensis* is observable in NHMUK-PV-OR36664: it is similar to that of NME-MLP-
260 1346, with a distance of 64 mm between the centers; the cranium A/646 (Sahni and Khan 1988) has
261 multiple foramina but they are also located rather far apart (photos provided by R. Patnaik).

262 The mandibular fossa is virtually flat. It is bordered posterolaterally by a postglenoid process,
263 but there is no lateral tubercle on the ventral border of the zygomatic arch. This paraglenoid tubercle
264 is always present in all other species of *Camelus*.

265 There is no evidence of transverse deformation of the auditory region, cranial base, and
266 occipital, at least on the right side and, save for the left squamosal that is rotated, this area is
267 symmetrical, and distortion is probably minimal. The braincase is somewhat crushed dorsoventrally
268 and it may be that some transverse compressing occurred behind it. The imperfectly preserved right

auditory region displays a relatively large tympanic bulla, with inflation anteromedially of the tympanohyal vagina. The basioccipital is strongly pinched in front of the occipital condyles, forming large, deep depressions between the midline and the bullae, as in *C. sivalensis* (NHMUK-PV-OR39597, AMNH-FM19785). Although this is hard to quantify, the basicranium looks short; in contrast, the *C. sivalensis* cranium AMNH-FM19785 looks long, but its central part is incorrectly reconstructed in plaster. The plane of the incomplete jugular process is inclined at more than 45° to the sagittal plane, thus slightly more transversally than in extant forms, *C. knoblochi*, and *C. sivalensis* (NHMUK-PV-OR39597, A/646), and distinctly more so than in *C. thomasi*, in which it is located far away from the occipital condyle. The hypoglossar foramen is not visible.

The central part of the occipital surface, above the foramen magnum, forms a broad pillar that is much more prominent caudally than the lateral parts of the occipital, above the condyles. However, the dorsal part of this raised area is depressed on either side of a weak occipital crest, below the central part of the nuchal crest. Laterally, the nuchal crest is perhaps slightly damaged, but the outline of the occipital was clearly bell-shaped, even accounting for slight transverse crushing. In extant forms, the shape of the occipital mainly depends on the development and degree of flaring of the nuchal crest, but it never looks so narrow; *C. sivalensis* (NHMUK-PV-OR39597; AMNH-FM19785; A/646) and *C. thomasi* (Martini and Geraads 2018) also have broad occipitals.

All cheek-teeth are preserved, either on the right or left sides (Fig. 1; Table 1; Supplementary Information 1). The P3 consists mostly of a buccal crescent, with parastyle, metastyle, and a rounded pillar located slightly mesially, about as prominent as the styles. A crest descends from the distal part of the buccal wall towards the lingual side, and curves mesially to meet a low ridge best indicated mesiolingually and distally, at the base of the main buccal wall. Although this ridge is clearly homologous with a lingual crescent, it clearly remains below occlusal level until late wear. There is much variation in size and morphology of the P3 of Old World camels. In extant forms the lingual crescent is rarely almost complete; it is usually mostly restricted to its distal part, and may be as weak as in NME-MLP-1346. *Camelus knoblochi* also has an incomplete lingual crescent, like

295 *P. gigas* (Zdansky 1926). In *C. sivalensis*, instead, all three P3s (NHMUK-PV-M100160, NHMUK-
296 PV-XX40570, AMNH-FM19832) have a fully-formed lingual crescent, and this also seems to be
297 true of other specimens (Gaur et al. 1984; cranium A/646). The single known P3 of *C. thomasi*
298 (Martini and Geraads 2018) also has a complete lingual crescent.

299 The P4 is still unworn, while M3 is slightly affected by wear. The reverse occurs usually, but
300 not always, in extant forms; the sequence of tooth eruption further differs from that of the extant
301 forms in that all molars are touched by wear before the full eruption of the canine. The buccal
302 crescent of P4 is very similar to that of P3 but, in addition, there is a fully formed lingual crescent
303 that sends a strong distal spur into the central valley; such a spur is smaller or absent in extant
304 *Camelus*, *C. thomasi*, and *C. sivalensis*. Still, this tooth remains long and narrow.

305 The molars have a faint metacone rib and a more distinct paracone rib. The parastyle and
306 mesostyle are strong, and distinctly overlap the preceding lobe (paracone, or metacone of the
307 preceding tooth); in these strong styles, NME-MLP-1346 resembles more *C. thomasi* and
308 *C. sivalensis* than the average condition of the extant species. Although measurements must be used
309 with caution because length of the molars decreases dramatically with wear, the upper molars are
310 broad relative to their length. This is also true of fossil *Camelus* in general (Supplementary
311 Information 2).

312 All teeth are rather brachydont, although they possess some cementum cover. Although
313 height cannot be precisely measured on the molars, the height of M3 was certainly less than its
314 length. The unworn P3 is only slightly taller than long, and P4 is only moderately hypsodont. This
315 contrasts with extant *Camelus*, and with the fossil *C. sivalensis* and *C. thomasi* (Table 2). In labial
316 view (Fig. 1F), cusp shape is high and sharp on the little-worn M3s, but more rounded on the M1s
317 (and on isolated, more worn teeth), suggesting a basically browsing behavior.

318 NME-MLP-2680 best matches the morphology of a lower canine, and is probably from a
319 female individual, and probably of the same individual as NME-MLP-2665 and NME-MLP-2684,

320 two upper molars; the metacone wall is flat, but the mesostyle and paracone rib are better indicated
321 than in extant forms (Fig. 3A–B), and these teeth are broad relative to their length.

322 Most measurements of the distal tibia NME-MLP-2584 (Fig. 3C) are above the maximum
323 recorded ones for extant *Camelus* (Martini et al. 2017), but the proportions are similar. As in
324 *C. sivalensis*, the medial malleolus is weaker than in extant forms, *C. thomasi*, and *C. knoblochi*, but
325 this feature is variable in North American forms. As for the cranial remains, the large size of the tibia
326 suggests an animal somewhat taller than the living forms, but probably not heavier than well-fed
327 domestic animals, which can reach about 1000 kg.

328 NME-MLP-1189 is a complete astragalus (Fig. 3D), and NME-MLP-1144 a distal half; the
329 extant forms display a great intraspecific variation but some differences can be observed (Steiger
330 1990; Martini et al. 2017). NME-MLP-1189 is not broader than other *Camelus*, but taller
331 (Supplementary Information 2–3). The part of distal trochlea that corresponds to the cuboid is
332 narrower than in all *C. dromedarius*, and more like *C. bactrianus*, *C. sivalensis*, and *C. thomasi*, but
333 this cuboid facet is broader in NME-MLP-1144, as in *C. dromedarius*. In lateral view, the tibial facet
334 is strongly convex and its proximal end extends far towards the plantar side (see also Steiger 1990:
335 fig. 52) as being a characteristic of *C. dromedarius* compared to *C. bactrianus*, but also found in
336 *C. sivalensis*, whereas *C. thomasi* resembles more *C. bactrianus*. The lateral calcaneal facet is not
337 contiguous with the plantar one, in contrast to the usual condition in extant forms. Obviously, fossil
338 forms display a mixture of the characters of both extant species, and it would be misleading to search
339 for the extant types of astragali among them, but NME-MLP-1189 is unlike all other species in its
340 slenderness.

341 **Additional material of *Camelus grattardi* from Omo:**

342 The type specimen of *C. grattardi* is from Member G of the Shungura Formation at Omo,
343 Ethiopia (Geraads 2014); these deposits are somewhat younger than all localities in the MLP area. It
344 clearly differs from both extant species in its narrow P4 and broad molars; these characters match
345 those observed in the MLP camel and, given the geographic and chronological proximity, we

346 confidently assign the MLP camel to *C. grattardi*. Thus, features observable on the material from the
347 MLP area can be complemented by those of other specimens of *C. grattardi*. Only some of those
348 from the Omo Shungura Formation have been published (Howell et al. 1969; Grattard et al. 1976;
349 Geraads 2014; Rowan et al. 2018), but we have now been able to examine all specimens from the
350 early expeditions; they are briefly described below.

351 NME-L480-7 from lower Member G is a piece of mandible with heavily cracked, incomplete
352 m1–m3 (Fig. 4A). At ca. 2.2 Ma, it is the earliest specimen demonstrating the absence of p3. All
353 three molars display an incipient goat fold; although they are worn and damaged, they are relatively
354 high-crowned. The unnumbered lower molar collected by Arambourg in 1933 (Fig. 4C), probably
355 from a similar level, also bears a weak goat fold. This is also true of the m3 in the mandible fragment
356 NME-Omo28-67-494 (upper Member B; Fig. 4D), which has a narrow corpus (thickness at m1–m2
357 = 33 mm) that is even less thick than that of *C. bactrianus*, but this specimen is older than those
358 formally identifiable as *C. grattardi*.

359 The color and weathering of the proximal humerus NME-L1-68-36 from Omo Shungura
360 Upper Member B differ from those of the *Camelus* distal humerus NME-L1-68-76, so that there is
361 no evidence that they are from the same individual, in contrast to what was hypothesized (Geraads
362 2014). Its identification is not straightforward; it was compared with modern *Camelus* (Grattard et al.
363 1976) but the tuberculum minus is much lower, the tuberculum majus higher, and the medial part of
364 the intertubercular sulcus (bicipital groove) narrower and deeper; it differs in the same features from
365 North American giant camels, and we conclude that NME-L1-68-36 probably belongs to *Giraffa*
366 Brisson, 1772, instead, although not a perfect match with this genus. The distal humerus NME-L1-
367 68-76 is definitely camelid but, at ca. 3 Ma, it is older than other specimens of *C. grattardi*, and it
368 now seems safer not to include it in the hypodigm of the species.

369 The proximal phalanges NME-Omo 28-67-577 (Upper Member B; Fig. 4E) and NME-Omo
370 119-68-14 (Member D; Fig. 4B) were, probably correctly, assigned to the anterior and posterior
371 limbs, respectively (Grattard et al. 1976). Both phalanges have relatively shorter distal condyles, and

372 shorter ligament insertions on the palmar/plantar face than in extant *Camelus*. However, whereas in
373 extant forms the posterior proximal phalanx is basically a smaller version of the anterior one, these
374 two Omo phalanges differ little in length, but strongly so in their morphology, NME-Omo 119-68-14
375 being almost as long as NME-Omo 28-67-577 but distinctly more slender. The former can probably
376 be identified as *C. grattardi*; it differs from extant *Camelus* in its very deep (antero-posteriorly)
377 proximal articulation. The latter can hardly be assigned to the same species and, like other specimens
378 from Shungura Upper Member B, we prefer to leave it as ?*Camelus* sp.

379

380 **Systematic paleontology**

381 CAMELIDAE Gray, 1821

382 *CAMELUS* Linnaeus, 1758

383 Type species—*Camelus bactrianus* Linnaeus, 1758.

384 *CAMELUS GRATTARDI* Geraads, 2014

385 *Holotype*—NME-Omo75S-70-956, maxilla fragment with P4–M3; from lower Member G (G4 to
386 G13), Shungura Formation, lower Omo valley, Ethiopia; ca. 2.2 Ma.; housed in NME.

387 *Referred material from Mille-Logya*—NME-MLP-1346, incomplete cranium including the braincase,
388 parts of the orbits, palate, maxilla, and most of the tooth-rows, found in 2014 by Moges Mekonnen
389 (geographic coordinates 11.56437° N, 40.83878° E); NME-MLP-2680, lower canine; NME-MLP-
390 2665, upper molar; NME-MLP-2684, incomplete upper molar, probably M3; NME-MLP-1189,
391 astragalus; NME-MLP-1144, incomplete astragalus; NME-MLP-2584, distal tibia. All this material
392 is from the Seraitu unit, ca. 2.9 – 2.5 Ma.

393 *Diagnosis*—A large member of *Camelus*, with supraorbital foramina located wide apart, squamosal
394 reaching the orbital level, narrow occiput, mesial border of the mandibular ramus strongly inclined
395 backwards, upper molars only slightly longer than broad, with prominent styles, P4 much narrower
396 than M1, proximal phalanges with short posterior scars, posterior proximal phalanx with a deep
397 proximal articulation. Differs from species of *Paracamelus* in the deeper infraorbital shelf, loss of

398 p3, smaller P3, weaker molar ribs, and shorter scars on the proximal phalanges. Differs from all other
399 species of *Camelus* in: tall occiput, squamosal reaching the orbital level, absence of paraglenoid
400 tubercle, deeper mandibular corpus, narrow P4, less hypsodont teeth, and tall astragalus. Differs
401 additionally: from extant *C. bactrianus* and *C. dromedarius* in its late canine eruption, deep
402 infraorbital shelf, supraorbital foraminae wide apart, more oblique anterior border of mandibular
403 ramus, broader molars, stronger, thicker styles in the upper teeth, more cylindrical and more
404 transverse distal humeral articulation, and proximal phalanges with shorter ligament scars; from the
405 Pleistocene North-African *C. thomasi* in its deep infraorbital shelf, supraorbital foraminae wide
406 apart, much less complete P3 lingual crescent, lack of pachyostosis, longer lateral lip and broader
407 cuboid trochlea on the astragalus, and shorter scars on the proximal phalanges; from *C. sivalensis*
408 from the Siwaliks in the deeper infraorbital shelf, less complete P3 lingual crescent, and weaker
409 molar ribs.

410

411 **Parsimony analysis**

412 Old World fossil camels have to date been mostly represented by incomplete remains. Most
413 previous studies assumed, a priori, that they were more closely related to one or the other of the
414 extant forms than to other stem camelids. The new finds from the MLP area, in conjunction with the
415 recent reappraisal of the distinguishing features between the extant taxa (Martini et al. 2017), the
416 study of the only other significant African sample (Martini and Geraads 2018), and the revision of
417 incompletely described samples allow for a comprehensive analysis of their relationships
418 (Supplementary Information 2 and 4). A total of 22 characters, all ordered (Supplementary
419 Information 2–4), were used in a parsimony analysis, using TNT (Goloboff et al. 2003; Goloboff and
420 Catalano 2016) and PAUP*4 (Swofford 2003). To the *Camelus* species mentioned above, we added
421 *P. gigas*, *P. alexejevi*, and *P. alutensis*. Because Old World camels immigrated from North America,
422 the outgroup taxon must be sought there. We chose *Megacamelus merriami*, which is the best-
423 documented close relative of Old World camels.

424 Our parsimony analysis yields three equally parsimonious trees that differ only in the
425 branching pattern within *Paracamelus* (the resolution of this trichotomy with the highest bootstrap
426 frequency is shown in Fig. 5). The trees indicate that *Camelus grattardi* is the most basal branch of
427 the *Camelus* clade. It is followed by the southern Asian *C. sivalensis*, and the North Africa
428 *C. thomasi*; this succession is consistent with the ages of these species, *C. sivalensis* being of early
429 Pleistocene age, *C. thomasi* of late early to early middle Pleistocene age. The newly recovered MLP
430 material provides the oldest evidence (at 2.9 – 2.5 Ma) of one of the most diagnostic characters for
431 the species, a small P3. By contrast, on the mandible KNM-ER 2608 from the Koobi Fora Formation
432 dated to ca. 3.5 Ma (Harris 1991), the absence of p3, functionally correlated with a small P3, cannot
433 be definitely ascertained, and the predental portion is extremely long, suggesting that KNM-ER 2608
434 potentially documents instead one the latest occurrences of *Paracamelus* in Africa. *Camelus*
435 *grattardi* thus suggests that the genus *Camelus* arose in eastern Africa ca. 3 Ma, when *Paracamelus*
436 went extinct.

437 The precise dating of *C. grattardi* has important consequences on the chronology of the
438 origin and diversification of the genus *Camelus*. The results of the parsimony analysis are consistent
439 with the chronology of the fossil record. Our results are only moderately robust, but the most robust
440 clade is precisely that which includes only crown camelids, with a bootstrap of 70% and a decay
441 index (Bremer 1988) of 2. Our estimate of the minimal age for the crown group, for the divergence
442 between *C. dromedarius* and *C. bactrianus*, is about 0.6 to 0.8 Ma and matches the age of the oldest
443 known remains of *C. knoblochi* (Titov 2008). No fossil form that could be part of this crown clade is
444 known before the middle Pleistocene, so there is no fossil evidence that this crown clade predates the
445 middle Pleistocene. In fact, even this age could be too old, as it rests upon the poorly known
446 *C. knoblochi* (Titov 2008); should detailed study of this species show that it is in fact no more
447 closely related to *C. dromedarius* than to *C. bactrianus*, a possibility raised by the low Bremer index
448 (1) and low bootstrap frequency (50%) of the node uniting *C. knoblochi* to *C. dromedarius*, the
449 divergence between the extant taxa could even be younger. The position of *C. knoblochi* in the crown

450 of *Camelus* dispels doubts that the topology of crown *Camelus* is influenced by domestication
451 because if the latter had caused considerable phenotypic convergence between *C. dromedarius* and
452 *C. bactrianus*, the long extinct (hence, undomesticated) *C. knoblochi* should logically be excluded
453 from the crown.

454

455 **Conclusion**

456 Our estimate of the minimal divergence date between the lineages leading to the extant
457 species, certainly not earlier than the middle Pleistocene and perhaps late in this age, is much more
458 recent than the estimates provided by molecular analyses: ca. 4.4 Ma using the whole genome (Wu et
459 al. 2014), and ca. 4.1 Ma by comparison with the genome of the late middle Pleistocene American
460 *Camelops* Leidy, 1854 (Heintzmann et al. 2015). On the basis of the mtDNA sequence, it was even
461 suggested (Cui et al. 2007) that this divergence occurred before the Camelidae immigrated into the
462 Old World, ca. 8 Ma.

463 Our analysis based on morphological and stratigraphic data suggests *Camelus* dates from the
464 late Pliocene, and the divergence of the extant lineages is much younger than estimated by molecular
465 analyses. Of course, part of the discrepancy may reflect the fact that paleontological data directly
466 provide only minimal divergence age estimates, whereas molecular ages attempt to provide unbiased
467 estimates of divergence dates, but this factor alone is unlikely to account for the five-fold difference
468 or more between our paleontological estimate and molecular estimates. A number of increasingly
469 sophisticated and realistic methods have been developed to get unbiased estimates and confidence
470 intervals from paleontological data (e.g., Strauss and Sadler 1989; Marshall 2008), but this requires
471 extensive dataset compilation and the use of methods that are beyond the scope of our study.
472 Nevertheless, our estimate is also supported by the fertility of *C. dromedarius* $\times$ *C. bactrianus*,
473 whose hybrids are fertile up to the F4 when backcrossed with either species (Faye and Konuspayeva
474 2012). Among other artiodactyls, fertile hybrids are unknown between species whose divergence is
475 earlier than the Pleistocene (Gray 1972).

476 Extant *Camelus* developed a number of physiologic adaptations to life in subdesertic
477 conditions (Wu et al. 2014). By contrast, stem *Camelus* seem to be associated with a variety of fossil
478 assemblages, and might have been able to thrive in diverse environments, but none of them is
479 suggestive of subdesertic conditions. Pending detailed analysis of the ecology of fossil Old World
480 camels, the adaptation to desert conditions may be another, recently acquired synapomorphy of
481 extant *Camelus*.

482

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495

496 **Supplementary Information:**

497 **Supplementary Information 1.** 3D reconstruction of NME-MLP-1346 (made with Agisoft
498 Photoscan). [File Geraads&al_Camelus_SupInfo1.pdf]

499 **Supplementary Information 2.** Description of the characters used in the parsimony analysis;
500 matrix and character list, in TNT format. [File Geraads&al_Camelus_SupInfo2.docx]

501 **Supplementary Information 3.** Raw measurements used in Supplementary Information 1 [File
502 Geraads&al_Camelus_SupInfo3.xlsx]

503 **Supplementary Information 4.** Matrix used in the parsimony analysis, in Nexus format. [File
504 Geraads&al_Camelus_SupInfo4.nex]

505

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712

713 Figure captions

714 Figure 1. Main elements of NME-MLP-1346. A: braincase in occipital view; B: braincase in left
715 lateral view; C: braincase in dorsal view; D: left zygomatic arch; E: left upper tooth row with P3–
716 M3, occlusal view; F: same specimen, buccal view. Scale bar, 20 cm for Figs A–C, 10 cm for Figs
717 D–F. See also Supplementary Information 4.

718

719 Figure 2. Schematic reconstruction of NME-MLP-1346. Distortion of the temporal and orbital areas
720 prevents accurate reconstruction.

721

722 Figure 3. *Camelus grattardi* from Mille-Logya. A: upper left molar NME-MLP-2665. B: incomplete
723 upper right molar NME-MLP-2684. C: distal right tibia NME-MLP-2584. D: left astragalus NME-
724 MLP-1189. Scale bar, 5 cm for Figs A–B, 10 cm for Figs C–D.

725

726 Figure 4. Camelidae from the Omo Shungura Formation; A–C: *Camelus grattardi*; D–E: ?*Camelus*
727 sp. A: left mandible with m1, m2, incomplete m3, and roots of p4, NME-L480-7, oblique view. B:
728 proximal (posterior ?) phalanx NME-Omo 119-68-14, plantar view. C: right lower molar (probably
729 m2), collected by C. Arambourg, occlusal view. D: right mandible with m3, NME-Omo 28-67-494,
730 occlusal view. E: proximal (anterior ?) phalanx NME-Omo-28-67-577, palmar view. Scale bar, 10
731 cm.

732

733 Figure 5. One of the most parsimonious trees obtained by TNT and PAUP. L = 48; ci = 60; ri = 64.
734 *C.* = *Camelus*; *M.* = *Megacamelus*; *P.* = *Paracamelus*. Extant taxa are in bold. Support values are
735 given as bootstrap / Bremer (decay) index values. Unambiguous synapomorphies are: Node 6: length
736 c–m1 / length m1–m3 (0→1). Node 5: p3 present (0→1); P3 relative to P4 (0→1). Node 4:
737 paraglenoid tubercle (0→1); WP4 / WM1 (0→1). Node 3: mandibular thickening (0→1); scars on
738 proximal phalanges (0→1). Node 2: ramus ascendens (0→1); WP4 / WM1 (1→2); molar

739 length/breadth (0→1); upper molar styles (0→1). Node 1: choanae (0→1). *Paracamelus alutensis*:
740 size (1→0); mandibular thickening (0→1). *P. gigas*: size (1→2); squamosal reaches orbital level
741 (0→1); metapodials relative to femur (2→1). *C. thomasi*: mandibular thickening (1→2); p4
742 molarization (1→2). *C. bactrianus*: metapodials relative to femur (0→1). *C. dromedarius*:
743 infraorbital shelf (1→0); mandibular thickening (1→0); p4 molarization (1→0); astragalus cuboid
744 facet (0→2). *C. knoblochi*: size (1→2); infraorbital shelf (1→2); p4 molarization (1→2).

745

746 Table captions

747 Table 1. Dental measurements of NME-MLP-1346 (L = length; W = width).

748

749 Table 2. Tooth height in some *Camelus*; height of unworn molars cannot be measured in most
750 specimens, because their base is concealed in bone. Height of unworn teeth is underlined.

SUPPLEMENTARY INFORMATION 2

Character description (their numbers follow those of the data matrix (at the end of this files in TNT format; also in Nexus format as Supplementary Information 4); those that were regarded as too variable, too ambiguous to be used, or autapomorphic, are listed separately and identified by letters. Figures are not to scale; see also figures of the main text for *C. grattardi*.)

0) overall size is rather homogeneous but *Megacamelus*, *P. gigas*, and *C. knoblochi* are larger, whereas *P. alutensis* is smaller.

1) the choanae are V-shaped in most species, but those of *C. dromedarius* are usually more U-shaped (Martini *et al.* 2017); unexpectedly, those of the Razdorskaya skull of *C. knoblochi* (Titov 2008, fig.2) are rather U-shaped.

2) The ventral orbital margin is narrow in *C. dromedarius* and *C. thomasi*, but forms a variably deep shelf in other species.

Character 2, ventral orbital margin. 1) *Megacamelus merriami* (AMNH FM23201), broad; 2) *Camelus dromedarius* (CCEC 5000-2069), narrow; 3) *Camelus knoblochi* (ZIN 8678), broad

3) the squamosal tongue on the zygomatic arch reaches the level of the orbit in *C. grattardi* (Fig. 1 of the main text) and *P. alexjevi* (Khaveson 1954, fig. 1), and comes close to it in *M. merriami*, but is distinctly behind it in other species (not scored in *C. sivalensis* because, although several specimens preserve this area, the sutures are not clearly identifiable).

Character 3, anterior extent of the squamosal tongue 1) *Megacamelus merriami* (AMNH FM23201), almost reaching orbital level 2) modern *Camelus*, behind it.

4) The supra-orbital foramina are close to each other in modern *Camelus* and *M. merriami*, but wider apart in *C. sivalensis* and *C. grattardi*; the condition is unknown in *Paracamelus*.

Character 4, distance between the supra-orbital foramina (raw data in Supplementary Information 3)

5) the paraglenoid tubercle, lateral to the glenoid fossa, is present in most *Camelus* but absent in *C. grattardi*, American forms, and at most weak in *Paracamelus* (Zdansky 1926:5 'Der dieselbe bei rezenten Kamelen aussen begrenzende Vorsprung ist kaum vorhanden.'; Khaveson 1954, fig. 1)

Character 5, paraglenoid tubercle. 1) *Megacamelus merriami* (AMNH FM104395), absent; 2) *Camelus bactrianus* (MNHN ZM.1970-44), present.

6) the length of the muzzle can be estimated by the length between the lower canine and m1 (thus obviating for the rare preservation of the incisors and the irregular presence of p3). This measurement separates *Paracamelus*, in which it is distinctly greater than the length m1–m3, from *Camelus* and N. American forms, in which it is at most slightly longer. The shortness of the muzzle in *C. grattardi* is inferred from the juvenile specimen KNM-WT-39366, from just below the Lokalalei tuff at c. 2.55 Ma, in which it is as short as in modern *Camelus* of similar ontogenic age. The incomplete mandible KNM-ER-2608 probably had a longer pre-dental portion, but could belong to *Paracamelus* instead. No measurement can be taken on *C. thomasi*, but MNHN TER-1685 unambiguously shows that the muzzle was short.

Character 6, relative length of the predental portion of the muzzle, a proxy for the length of the muzzle. The smallest modern *Camelus* is a very old specimen, in which wear has reduced molar length (raw data in Supplementary Information 3).

7) the ascending ramus of the mandible displays significant differences, with limited intra-specific variation (in *Camelus*, the shape of the coronoid process is a good distinguishing feature at species level [Martini *et al.* 2017; Martini & Geraads 2018]). The anterior border of the ramus is usually oblique, but vertical or even slightly inclined forwards in younger forms, but also in *M. merriami*.

Character 7, anterior border of the ascending ramus. 1) *Megacamelus merriami* (AMNH FM23216), vertical; 2) modern *Camelus*, vertical; 3) *Camelus grattardi* (KNM-WT 16454), oblique; 4) *Camelus thomasi*, oblique.

8) all camels have a robust mandibular corpus; although there is much intra-specific variation, this is especially marked in *C. bactrianus*, *C. knoblochi*, and *P. alutensis*, and still more so in *C. thomasi*, whose pachyostosis is highly characteristic.

Character 8, plot of mandibular corpus depth vs. thickness between m1 and m2 (raw data in Supplementary Information 3).

9) The loss of p3 is the best diagnostic character of *Camelus*, unambiguously distinguishing it from *Paracamelus* in the Old World. The earliest precisely dated fossil lacking this tooth is the mandible NME-L480-7 from Omo Shungura G3 at c. 2.2 Ma.

10) a shortening of P3 is probably functionally correlated with the loss of p3.

11, 12) It seems that this loss of p3 is associated with a trend towards a greater molarisation of P3 and p4, through the development of a lingual wall. The lingual crescent of P3 is complete in all

known specimens of *C. sivalensis* (NHMUK-M 15347, AMNH-FM19832, Gaur et al., 1984, fig.2) and *C. thomasi* (Martini & Geraads 2018). The p4 is variable in *C. sivalensis* and *C. bactrianus*, but on the average it is more molarized in the latter species than in *C. dromedarius*. The p4 has a clear lingual wall in the single available specimens of *C. thomasi* and *C. knoblochi*.

Character 12, molarisation of p4: 1) *Megacamelus merriami* (AMNH F23216), not molarized; 2) *Camelus bactrianus* (MNHN.ZM.1971-50), molarized; 3) *Camelus thomasi* (MNHN TER-1685), molarized.

13, 14) in younger species of *Camelus*, the molars are narrower at their base, both relative to the width of P4, and relative to their length, than in early forms.

Character 13, relative widths of P4 and M1 (raw data in Supplementary Information 3).

Character 14, width of M2 relative to length of M1–M3 (raw data in Supplementary Information 3).

15) upper molars ribs (labial central pillars on the paracone and metacone) are weak in most *Camelus*, but they are better marked in *C. sivalensis*, in *P. alexejevi*, in a number of isolated finds possibly attributable to *Paracamelus* (Orlov 1929, pl.42, fig.3; van der Made & Morales 1999, fig. 22.1; Rybczynski *et al.* 2013, fig.3c), and in the N. American *M. merriami* and *Aepycamelus major* (but they are distinctly weaker in *Megatylopus*).

16) upper molar styles are usually more reduced in younger species of *Camelus*, although there is significant variation, especially with wear.

Characters 15-16, upper molar ribs and styles. 1) *Megacamelus merriami* (AMNH F23202), strong; 2) *Camelus bactrianus* (MNHN 1970-44), weak; 3) *Camelus sivalensis* (NHMUK PV OR 3664), strong.

17) Geraads (2014) showed that the distal articulation of the humerus of *C. grattardi*, like that of other early forms, is more nearly perpendicular to the long axis of the bone than that of modern ones.

18) the astragalus provides several distinctive criteria, but most of them display high intra-specific variation. The lateral lip of the proximal trochlea extends farther towards the plantar side in the dromedary than in the Bactrian camel, and only *C. thomasi* is similar to the latter.

Character 18, plantar extent of the lateral tibial lip. 1) *Megacamelus merriami* (AMNH FM104232), long; 2) *Camelus dromedarius*, long 3) *Camelus bactrianus*, short; 4) *Camelus thomasi* (MNHN TER-1656), short.

19) in *C. dromedarius*, the cuboid facet is relatively wider than in *C. bactrianus* (Steiger 1990; Martini *et al.* 2017); there is much variation in other taxa, but *P. gigas* (Zdansky 1926, pl. 4, fig. 11) and *P. alexejevi* (Khaveson 1954, pl. 7, fig. 5) are similar to the dromedary.

Character 19, width of the cuboid facet 1) *Camelus dromedarius*, broad 2) *Camelus bactrianus*, narrow

20) on the palmar/plantar side of the proximal phalanges, the ligament scars of the proximal end extend farther distally in geologically younger species than in earlier forms, including *P. aguirrei* from Venta del Moro (van der Made & Morales 1999, fig. 22.3), and the Plio-Pleistocene Yukon camel (Rybczynski *et al.* 2013); however, according to Zdansky (1926), *P. gigas* has long scars.

Character 20, length of the ligament scars on the proximal phalanges. 1) *Megacamelus merriami* (AMNH FM104251), short; 2) modern *Camelus*, long; 3) *C. sivalensis* (AMNH FM19832), short; 4) *C. thomasi* (MNHN TER-1674), long.

21) Khaveson (1954) observed that the distal part of the limbs in *P. alexejevi* is relatively longer than in modern forms. *Camelus sivalensis* and *M. merriami* also have long metapodials, while *P. gigas*, instead, is more similar to *C. dromedarius* in this regard, *C. bactrianus* being the most different in its short metapodials.

Character 21. Relative length of some long bones (*Camelus dromedarius* = 100). The metatarsal is short relative to the femur in *C. bactrianus*, moderately long in *C. dromedarius* and *P. gigas*, and long in *M. merriami*, *P. alexejevi*, and *C. sivalensis*.

Characters not used:

A) Cranial proportions are hard to evaluate, because most fossil crania are distorted and/or largely reconstructed. *Camelus* crania are clearly broader over the orbits than the well-preserved cranium of *Megatylopus* AMNH-FM14071, but probably not broader than those of the distorted crania of *Megacamelus*.

B) As observed by Zdansky (1926), it is only in *Megatylopus* (AMNH-FM14071) that the lachrymal bone reaches the lachrymal vacuity, which is much larger than in the other taxa.

C) A possible synapomorphy of modern *Camelus* is the early fusion of facial sutures; by contrast, they are still clearly visible in adults of *Megacamelus merriami*. However, the condition in many fossil species is too uncertain for a reliable use of this feature.

D) The skull of *Camelus sivalensis* AMNH-FM19832 is unique in having a I3 located far from the canine but the variability of this feature and the condition in most fossil species are unknown.

- E) The position of the orbit relative to the tooth-row is very variable in modern forms, and no fossil specimen is outside this variation. Khaveson (1954) stated that it is more posterior in *P. alexjevi*, but this is based upon a largely reconstructed cranium.
- F) the proportions of the occiput display much intra-specific variations, but it does look less broad in *C. grattardi* than in other taxa. If so, the condition in this species is autapomorphic.
- G) Khaveson largely based his new subgenus *Neoparacamelus*, based upon *P. alutensis*, on the absence on goat folds in lower molars, but this is hard to understand, because a goat fold is clearly present on the m3 of the type specimen (cast in UCBL). The goat fold is frequent in Camelidae but is never strongly expressed.
- H) *C. grattardi* is clearly less hypsodont than other *Camelus* (the original material of *C. thomasi* includes an unworn M3, and several specimens of *C. sivalensis* preserve exposed unworn molars), but the degree of hypsodonty is often hard to evaluate with precision, because the base of unworn molars is still embedded in bone. In addition, the slight hypsodonty of the outgroup *M. merriami* is obviously a derived feature, and its use would invert the polarity.
- I) In the astragalus, the size of the lateral spine is a good distinguishing feature between living species, but is too variable to be reliably used in fossils.
- J) the lateral and plantar calcaneal facets are usually contiguous in modern *C. bactrianus* and in *C. thomasi*, but never (5 specimens) in *M. merriami*; they are also separate in NME-MLP-1189, but there is too much intra-specific variation for this character to be used.
- K) the proximolateral calcaneal facet reaches distally the distolateral facet in *M. merriami*, but not in Old World camels. However the proximolateral facet is short in South-American Camelidae, suggesting that the contact in *M. merriami* is merely an effect of its large size.
- L) The unfused part of the metapodials is on the average longer in specimens assigned to *Paracamelus* (*P. gigas*: Zdansky 1926, pl. 2, fig. 10 and pl. 4, fig.15; Teilhard de Chardin & Trassaert 1937, pl. 1, fig. 4; *P. alexjevi*: Baigusheva 1971, pl. 6, fig. 2; Svistun 1971, fig. 1; Titov & Logvynenko, 2006, fig. 5c) than in *Camelus*, but there is much variability in species of both genera (*P. gigas*: Zdansky 1926, pl. 2, fig. 13; *P. alexjevi*: Khaveson 1954, pl. 6; an early Pliocene metatarsal from Chad assigned to *P. gigas* [Likius *et al.* 2003, fig. 3] has a short unfused part).

Matrix and character list, in TNT format:

xread

'Camelidae'

22 10

```
M_merriami 2020100100000000001002
C_grattardi 1?2000000110?0010?110?
C_dromedarius 1101110101100211111211
C_bactrianus 1011110111101211110010
C_sivalensis 101?010001111100001002
C_knoblochi 212111011110221111?0??
C_thomasi 10111100211121010?001?
P_gigas 2011?01000000?000?1211
P_alexjevi 1?10?010000?000000?2?2
P_alutensis 0?????10100?0??0?0????
;
```

ccode +[0.21

;

cnames

```
{ 0 size small medium large ;
{ 1 choanae V-shaped U-shaped ;
{ 2 infra-orbital_shelf narrow moderate broad ;
{ 3 squamosal_reaches_orbital_level yes no ;
{ 4 supra-orbital_foramina wide_apart close ;
{ 5 paraglenoid_tubercle at_most_weak distinct ;
{ 6 length_c-m1/length_m1-m3 short long ;
{ 7 ramus_ascendens oblique vertical ;
{ 8 mandibular_thickening no slight strong ;
{ 9 p3_present absent ;
{ 10 P3_relative_to_P4 large small ;
{ 11 P3_internal_crescent incomplete complete ;
{ 12 p4_molarisation no variable yes ;
{ 13 WP4/WM1 narrow intermediate broad ;
{ 14 molar_breadth/length broad narrow ;
{ 15 upper_molars_ribs moderate weak ;
{ 16 upper_molars_styles strong weak ;
{ 17 distal_humerus transverse oblique ;
{ 18 astragalus_lateral_lip short long ;
{ 19 astragalus_cuboid_facet narrow variable broad ;
{ 20 scars_on_proximal_phalanges short long ;
{ 21 metapodials_relative_to_femur short intermediate long ;
```

number	origin	taxon	W M2	L M1-M3
			modern	modern
1951-102	MNHN	<i>C. bactrianus</i>	33,3	101
1896-2017	MNHN	<i>C. bactrianus</i>	33	113
no # 2	MNHN	<i>C. bactrianus</i>	36,5	124
1974-60	MNHN	<i>C. bactrianus</i>	31,9	105
1991-695	MNHN	<i>C. bactrianus</i>	33	118,5
1962-183	MNHN	<i>C. bactrianus</i>	33,2	116,5
1970-44	MNHN	<i>C. bactrianus</i>	31	123,5
1985-243	MNHN	<i>C. bactrianus</i>	32,8	110,5
1972-35	MNHN	<i>C. bactrianus</i>	31,5	118
1985-1900	MNHN	<i>C. dromedarius</i>	30,5	100,5
2007-1438	MNHN	<i>C. dromedarius</i>	28	108
1991-302	MNHN	<i>C. dromedarius</i>	31	107,4
1931-101	MNHN	<i>C. dromedarius</i>	32,6	104
1929-46	MNHN	<i>C. dromedarius</i>	28,5	106
1912-442	MNHN	<i>C. dromedarius</i>	27,6	108,7
1934-59	MNHN	<i>C. dromedarius</i>	31	96
1912-151	MNHN	<i>C. dromedarius</i>	31	98,3
2007-1432	MNHN	<i>C. dromedarius</i>	31	102
1985-202	MNHN	<i>C. dromedarius</i>	33	113,3
1964-213	MNHN	<i>C. dromedarius</i>	35	124,7
1865-1	MNHN	<i>C. dromedarius</i>	30,8	94,6
1852-564	MNHN	<i>C. dromedarius</i>	31	108,7
1897-337	MNHN	<i>C. dromedarius</i>	29,6	104
5000-2064	MNHN	<i>C. dromedarius</i>	32,2	106,3
5000-2065	MNHN	<i>C. dromedarius</i>	29,58	103,5
5000-2068	MNHN	<i>C. dromedarius</i>	27,2	111,5
5000-2069	MNHN	<i>C. dromedarius</i>	30,5	108
			<i>C. grattardi</i>	<i>C. grattardi</i>
Omo75s-70-956	NME	<i>C. grattardi</i>	40	112,8
MLP-1346	NME	<i>C. grattardi</i>	37	116
			<i>C. thomasi</i>	<i>C. thomasi</i>
TER 1816	MNHN	<i>C. thomasi</i>	35,1	105
TER 1689	MNHN	<i>C. thomasi</i>	35,3	120
			<i>C. knoblochi</i>	<i>C. knoblochi</i>
ZIN 8678	Titov, 2008	<i>C. knoblochi</i>	38	139
ROMK	Titov, 2008	<i>C. knoblochi</i>	37,25	123,5
VSEGEI	Titov, 2008	<i>C. knoblochi</i>	36,3	143,15
			<i>C. sivalensis</i>	<i>C. sivalensis</i>
36664	NHMUK	<i>C. sivalensis</i>	37	123
15347	NHMUK	<i>C. sivalensis</i>	35,4	103,5
16405	NHMUK	<i>C. sivalensis</i>	33,8	116
PUA Rh 23/83		<i>C. sivalensis</i>	29,3	121,7
FM19832	AMNH	<i>C. sivalensis</i>	36,2	105,6
FM19785	AMNH	<i>C. sivalensis</i>	37,2	123

number	origin	taxon	Height of the medial side
			<i>C. grattardi</i>
MLP-1189	NME	<i>C. grattardi</i>	79
			<i>C. sivalensis</i>
NHMuK42564	NHMuK	<i>C. sivalensis</i>	75
NHMuK40593	NHMuK	<i>C. sivalensis</i>	63
NHMuK40597	NHMuK	<i>C. sivalensis</i>	81,7
			<i>C. thomasi</i>
MNHN-TER-1669	MNHN	<i>C. thomasi</i>	79
MNHN-TER-1670	MNHN	<i>C. thomasi</i>	75
			<i>P. gigas</i>
	Zdansky, 1926	<i>P. gigas</i>	88,5
			<i>M. merriami</i>
FM104232	AMNH	<i>M. merriami</i>	82,7
FM104231	AMNH	<i>M. merriami</i>	89,5
FM104236	AMNH	<i>M. merriami</i>	81,8
FM104234	AMNH	<i>M. merriami</i>	83
FM104230	AMNH	<i>M. merriami</i>	88,5
			<i>C. bactrianus</i>
1851-466	MNHN	<i>C. bactrianus</i>	65,7
1898-239	MNHN	<i>C. bactrianus</i>	71,5
1926-151	MNHN	<i>C. bactrianus</i>	70
1971-50	MNHN	<i>C. bactrianus</i>	71,3
1972-35	MNHN	<i>C. bactrianus</i>	67,7
MHNG ARCO 826.20-1501.1	Martini et al., 2017	<i>C. bactrianus</i>	64,75
NMB 2430	Martini et al., 2017	<i>C. bactrianus</i>	68
MHNG MAMO 1168.053	Martini et al., 2017	<i>C. bactrianus</i>	71
NMB 10390	Martini et al., 2017	<i>C. bactrianus</i>	70,75
NMB 5918	Martini et al., 2017	<i>C. bactrianus</i>	66
NMBE 1023261	Martini et al., 2017	<i>C. bactrianus</i>	64
ZM 20382	Martini et al., 2017	<i>C. bactrianus</i>	69
MSNM Ma 6415	Martini et al., 2017	<i>C. bactrianus</i>	67,5
MHNG MAMO 1063.089	Martini et al., 2017	<i>C. bactrianus</i>	76,75
MHNG MAMO 810.035	Martini et al., 2017	<i>C. bactrianus</i>	72
MHNG ARCO 826.20-1501.2	Martini et al., 2017	<i>C. bactrianus</i>	71,5
NBM 10902	Martini et al., 2017	<i>C. bactrianus</i>	68
			<i>C. dromedarius</i>
1892-15	MNHN	<i>C. dromedarius</i>	76
1876-259	MNHN	<i>C. dromedarius</i>	61,8
1884-2210	MNHN	<i>C. dromedarius</i>	70
1895-387	MNHN	<i>C. dromedarius</i>	63
1899-96	MNHN	<i>C. dromedarius</i>	71,2
2007-1435	MNHN	<i>C. dromedarius</i>	69,8
1925-205	MNHN	<i>C. dromedarius</i>	67
Ek2	Martini et al., 2017	<i>C. dromedarius</i>	63,5
Ek3	Martini et al., 2017	<i>C. dromedarius</i>	68
MHNG MAMO 78.028	Martini et al., 2017	<i>C. dromedarius</i>	62,5
ZM 13130	Martini et al., 2017	<i>C. dromedarius</i>	65
Ek5	Martini et al., 2017	<i>C. dromedarius</i>	71
MHNG ARCO 826.20-1502.6	Martini et al., 2017	<i>C. dromedarius</i>	66,5
MHNG ARCO 826.20-1502.4	Martini et al., 2017	<i>C. dromedarius</i>	67,5
NMBE 1023266	Martini et al., 2017	<i>C. dromedarius</i>	65,5

Distal breadth
<i>C. grattardi</i>
51,5
<i>C. sivalensis</i>
53,4
46
59,6
<i>C. thomasi</i>
59,5
54,5
<i>P. gigas</i>
62
<i>M. merriami</i>
67
63
63
60
65
<i>C. bactrianus</i>
48,3
50
53,5
48,6
53,7
47
51
50
50,5
47
49
47,5
46,5
57,5
49,5
51
51
<i>C. dromedarius</i>
55
45,5
52,5
47,5
52,5
51
52,5
44
50
45
50
54
48
48
51,5

number	origin	taxon	L M1-M3	W between sup-orb. Foramina
			<i>C. bactrianus</i>	<i>C. bactrianus</i>
1951-102	MNHN	<i>C. bactrianus</i>	101	50
1896-2017	MNHN	<i>C. bactrianus</i>	113	37
no # 2	MNHN	<i>C. bactrianus</i>	124	55
1971-50	MNHN	<i>C. bactrianus</i>	120	50
1974-60	MNHN	<i>C. bactrianus</i>	105	37
1991-695	MNHN	<i>C. bactrianus</i>	118,5	56
1962-183	MNHN	<i>C. bactrianus</i>	116,5	52,5
1970-44	MNHN	<i>C. bactrianus</i>	123,5	60
1985-243	MNHN	<i>C. bactrianus</i>	110,5	52
1972-35	MNHN	<i>C. bactrianus</i>	118	53
			<i>C. dromedarius</i>	<i>C. dromedarius</i>
1985-1900	MNHN	<i>C. dromedarius</i>	100,5	26
2007-1437	MNHN	<i>C. dromedarius</i>	89	18
1991-302	MNHN	<i>C. dromedarius</i>	107,4	48
1912-150	MNHN	<i>C. dromedarius</i>	106	12
1929-46	MNHN	<i>C. dromedarius</i>	106	21
1912-442	MNHN	<i>C. dromedarius</i>	108,7	37
1934-59	MNHN	<i>C. dromedarius</i>	96	38
1912-151	MNHN	<i>C. dromedarius</i>	98,3	48
2007-1432	MNHN	<i>C. dromedarius</i>	102	42
1985-202	MNHN	<i>C. dromedarius</i>	113,3	40
1964-213	MNHN	<i>C. dromedarius</i>	124,7	48
1865-1	MNHN	<i>C. dromedarius</i>	94,6	37
1897-337	MNHN	<i>C. dromedarius</i>	104	32
5000-2063	CCEC	<i>C. dromedarius</i>	106,5	45
5000-2064	CCEC	<i>C. dromedarius</i>	106,3	38,5
5000-2065	CCEC	<i>C. dromedarius</i>	103,5	33
5000-2066	CCEC	<i>C. dromedarius</i>	108,4	31,5
5000-2067	CCEC	<i>C. dromedarius</i>	111,5	27,3
5000-2068	CCEC	<i>C. dromedarius</i>	111,5	21,5
5000-2069	CCEC	<i>C. dromedarius</i>	108	36,5
1908-101	MNHN	hybrid	120	42
			<i>C. grattardi</i>	<i>C. grattardi</i>
MLP-1346	NME	<i>C. grattardi</i>	116	66
			<i>C. thomasi</i>	<i>C. thomasi</i>
TER 1816	MNHN	<i>C. thomasi</i>	105	46
			<i>C. sivalensis</i>	<i>C. sivalensis</i>
36664	NHMUK	<i>C. sivalensis</i>	123	64
			<i>M. merriami</i>	<i>M. merriami</i>
23202	AMNH	<i>M. merriami</i>	140	58
23202A	AMNH	<i>M. merriami</i>	155	60

number	origin	taxon	L m1-m3	L c-m1
			<i>C. bactrianus</i>	<i>C. bactrianus</i>
1951-102	MNHN	<i>C. bactrianus</i>	111	106
1896-2017	MNHN	<i>C. bactrianus</i>	113	130
1971-50	MNHN	<i>C. bactrianus</i>	130	132,5
1974-60	MNHN	<i>C. bactrianus</i>	116	112
1991-695	MNHN	<i>C. bactrianus</i>	112	137,3
1962-183	MNHN	<i>C. bactrianus</i>	123	132
1970-44	MNHN	<i>C. bactrianus</i>	131	137,5
1985-243	MNHN	<i>C. bactrianus</i>	108	131
1926-151	MNHN	<i>C. bactrianus</i>	130	138
1972-35	MNHN	<i>C. bactrianus</i>	124,6	130
			<i>C. dromedarius</i>	<i>C. dromedarius</i>
2007-1437	MNHN	<i>C. dromedarius</i>	115	118
1991-302	MNHN	<i>C. dromedarius</i>	115	120
1912-150	MNHN	<i>C. dromedarius</i>	115	110
1929-46	MNHN	<i>C. dromedarius</i>	116	115
1912-442	MNHN	<i>C. dromedarius</i>	123	128
1934-59	MNHN	<i>C. dromedarius</i>	101	115
1912-151	MNHN	<i>C. dromedarius</i>	111	112
2007-1432	MNHN	<i>C. dromedarius</i>	110	108
1985-202	MNHN	<i>C. dromedarius</i>	120	125
1964-213	MNHN	<i>C. dromedarius</i>	130	133,5
1865-1	MNHN	<i>C. dromedarius</i>	99	132
1852-564	MNHN	<i>C. dromedarius</i>	114	136,5
1897-337	MNHN	<i>C. dromedarius</i>	111	120
5000-2063	CCEC	<i>C. dromedarius</i>	111	130
5000-2064	CCEC	<i>C. dromedarius</i>	108	130
5000-2065	CCEC	<i>C. dromedarius</i>	106	109
5000-2066	CCEC	<i>C. dromedarius</i>	112,5	128
5000-2067	CCEC	<i>C. dromedarius</i>	115	114
5000-2068	CCEC	<i>C. dromedarius</i>	111,5	122
5000-2069	CCEC	<i>C. dromedarius</i>	113	116
			<i>P. alutensis</i>	<i>P. alutensis</i>
FSL 17886 (cast of holotype)	Université Claude Bernard, Lyon	<i>P. alutensis</i>	96,5	145
			<i>P. alexejevi</i>	<i>P. alexejevi</i>
OGUM 3267	Khaveson, 1954	<i>P. alexejevi</i>	129,5	168
OGUM 3271	Khaveson, 1954	<i>P. alexejevi</i>	133	180
			<i>P. gigas</i>	<i>P. gigas</i>
Loc.11-12987	Teilhard and Trassaert, 1937	<i>P. gigas</i>	135	194
			<i>C. knoblochi</i>	<i>C. knoblochi</i>
VSEGEI 7/2942		<i>C. knoblochi</i>	146	155
			<i>C. sivalensis</i>	<i>C. sivalensis</i>
NHMK 17558	NHMK	<i>C. sivalensis</i>	135	135
			<i>M. merriami</i>	<i>M. merriami</i>
FM 23216	AMNH	<i>M. merriami</i>	151	182

approximate, measured on photograph

approximate, measured on photograph

approximate, measured on photograph

approximate, measured on photograph

number	origin	taxon	thickness at m1-m2	H at m1-m2
			<i>C. bactrianus</i>	<i>C. bactrianus</i>
MNHN-1951-102	MNHN	<i>C. bactrianus</i>	34,4	48,2
MNHN-1896-2017	MNHN	<i>C. bactrianus</i>	34,5	40,8
MNHN-no# 2	MNHN	<i>C. bactrianus</i>	35,7	53,1
MNHN-1971-50	MNHN	<i>C. bactrianus</i>	41,4	55
MNHN-1974-60	MNHN	<i>C. bactrianus</i>	34,2	53,3
MNHN-1898-239	MNHN	<i>C. bactrianus</i>	32,7	50,7
MNHN-1991-695	MNHN	<i>C. bactrianus</i>	35	48,3
MNHN-1962-183	MNHN	<i>C. bactrianus</i>	36,3	48,5
MNHN-1970-44	MNHN	<i>C. bactrianus</i>	34,7	57,7
MNHN-1985-243	MNHN	<i>C. bactrianus</i>	35	53,9
MNHN-1926-151	MNHN	<i>C. bactrianus</i>	39	52,7
MNHN-1972-35	MNHN	<i>C. bactrianus</i>	36,7	47
NMB 5918	Martini et al., 2017	<i>C. bactrianus</i>	33,5	54,5
ZM 20382	Martini et al., 2017	<i>C. bactrianus</i>	36,5	55
NMBE 1023261	Martini et al., 2017	<i>C. bactrianus</i>	32,5	41
NMB 5270	Martini et al., 2017	<i>C. bactrianus</i>	33	58,5
NMB 10390	Martini et al., 2017	<i>C. bactrianus</i>	35,5	42,5
ZM 17970	Martini et al., 2017	<i>C. bactrianus</i>	40,5	60
ZM 17685	Martini et al., 2017	<i>C. bactrianus</i>	36,5	59,5
ZM 17950	Martini et al., 2017	<i>C. bactrianus</i>	37	58
ZM 16783	Martini et al., 2017	<i>C. bactrianus</i>	38	54,5
NMB 2430	Martini et al., 2017	<i>C. bactrianus</i>	37	57,5
ZM 16784	Martini et al., 2017	<i>C. bactrianus</i>	37	51
			<i>C. dromedarius</i>	<i>C. dromedarius</i>
MNHN-1876-259	MNHN	<i>C. dromedarius</i>	28	48,1
MNHN-2007-1437	MNHN	<i>C. dromedarius</i>	29	44,9
MNHN-1991-302	MNHN	<i>C. dromedarius</i>	33	49,8
MNHN-1931-101	MNHN	<i>C. dromedarius</i>	34	48,1
MNHN-1912-150	MNHN	<i>C. dromedarius</i>	27,5	49
MNHN-1929-46	MNHN	<i>C. dromedarius</i>	30,5	52,3
MNHN-1912-442	MNHN	<i>C. dromedarius</i>	28,3	50,5
MNHN-1934-59	MNHN	<i>C. dromedarius</i>	28	52,9
MNHN-1912-151	MNHN	<i>C. dromedarius</i>	29,5	51,2
MNHN-2007-1432	MNHN	<i>C. dromedarius</i>	33	47,9
MNHN-1985-202	MNHN	<i>C. dromedarius</i>	40	50,2
MNHN-1964-213	MNHN	<i>C. dromedarius</i>	36	49,4
MNHN-1865-1	MNHN	<i>C. dromedarius</i>	32	55,4
MNHN-1925-205	MNHN	<i>C. dromedarius</i>	33	54,6
MNHN-1852-564	MNHN	<i>C. dromedarius</i>	30	50,8
MNHN-1897-337	MNHN	<i>C. dromedarius</i>	30,4	48,4
5000-2063	CCEC, Lyon	<i>C. dromedarius</i>	28	52
5000-2064	CCEC, Lyon	<i>C. dromedarius</i>	36	55,5
5000-2065	CCEC, Lyon	<i>C. dromedarius</i>	35	47,3
5000-2067	CCEC, Lyon	<i>C. dromedarius</i>	33,5	49,3
5000-2069	CCEC, Lyon	<i>C. dromedarius</i>	26,8	49
Ek1	Martini et al., 2017	<i>C. dromedarius</i>	30,5	53
NMB 1022	Martini et al., 2017	<i>C. dromedarius</i>	31	54
ZM 13130	Martini et al., 2017	<i>C. dromedarius</i>	30	56
Ek3	Martini et al., 2017	<i>C. dromedarius</i>	29	56,7
NMB 1583	Martini et al., 2017	<i>C. dromedarius</i>	27	56,5
ZM 13620	Martini et al., 2017	<i>C. dromedarius</i>	34	59,5
ZM 14499	Martini et al., 2017	<i>C. dromedarius</i>	31	58,5
ZM 10811	Martini et al., 2017	<i>C. dromedarius</i>	28	55,5
NMB 2128	Martini et al., 2017	<i>C. dromedarius</i>	30,5	52,5
ZM 10812	Martini et al., 2017	<i>C. dromedarius</i>	35	47,5
Ek5	Martini et al., 2017	<i>C. dromedarius</i>	29	58,5
			<i>C. thomasi</i>	<i>C. thomasi</i>
TER 1683	MNHN	<i>C. thomasi</i>	39	37
TER 1684	MNHN	<i>C. thomasi</i>	38	36
TER 1685	MNHN	<i>C. thomasi</i>	41,5	39,5
TER 1687	MNHN	<i>C. thomasi</i>	43,5	39
TER 1688	MNHN	<i>C. thomasi</i>	35,8	43
TER 1900-27	MNHN	<i>C. thomasi</i>	45	43
			<i>M. merriami</i>	<i>M. merriami</i>
FM 23216	AMNH	<i>M. merriami</i>	43	81
			<i>C. grattardi</i>	<i>C. grattardi</i>
Omo L4807	NME	<i>C. grattardi</i>	30	45
			<i>C. sivalensis</i>	<i>C. sivalensis</i>
AMNH19832	AMNH	<i>C. sivalensis</i>	29,5	74
NHMLUK 100163 (4	NHMLUK	<i>C. sivalensis</i>	30	50
NHMLUK 17558	NHMLUK	<i>C. sivalensis</i>	42,5	56
NHMLUK 39599	NHMLUK	<i>C. sivalensis</i>	35	61
NHMLUK16165	NHMLUK	<i>C. sivalensis</i>	32	69
			<i>P. alutensis</i>	<i>P. alutensis</i>
FSL 17886 (cast of holotype)	Université Claude Bernard, Lyon	<i>P. alutensis</i>	27,2	35,7
			<i>P. gigas</i>	<i>P. gigas</i>
18911	Teilhard and Trassaert, 1937	<i>P. gigas</i>	35	57
	Zdansky, 1926	<i>P. gigas</i>	41	89
KB3.97.316, Chad	CAR, N'Djamena	<i>P. gigas</i>	33	58

approximate measurements

approximate, measured on photograph

approximate, measured on photograph

approximate measurements

number	origin	taxon	W P4	W M1
			modern	modern
1896-2017	MNHN	<i>C. bactrianus</i>	26,8	30,5
no # 2	MNHN	<i>C. bactrianus</i>	27,1	34
1971-50	MNHN	<i>C. bactrianus</i>	25,4	33
1974-60	MNHN	<i>C. bactrianus</i>	24,3	30
1991-695	MNHN	<i>C. bactrianus</i>	24,8	28,3
1962-183	MNHN	<i>C. bactrianus</i>	24,6	29,7
1970-44	MNHN	<i>C. bactrianus</i>	27	31
1985-243	MNHN	<i>C. bactrianus</i>	24,8	29,6
1972-35	MNHN	<i>C. bactrianus</i>	25,2	32
1876-259	MNHN	<i>C. dromedarius</i>	22,4	28,5
1985-1900	MNHN	<i>C. dromedarius</i>	24,6	27,7
2007-1438	MNHN	<i>C. dromedarius</i>	23,5	27
1991-302	MNHN	<i>C. dromedarius</i>	25	29,6
1931-101	MNHN	<i>C. dromedarius</i>	22,8	28,8
1912-150	MNHN	<i>C. dromedarius</i>	21,5	26,6
1929-46	MNHN	<i>C. dromedarius</i>	23,5	29
1912-442	MNHN	<i>C. dromedarius</i>	22,7	27
1934-59	MNHN	<i>C. dromedarius</i>	23,2	27,4
1912-151	MNHN	<i>C. dromedarius</i>	24,1	28,6
2007-1432	MNHN	<i>C. dromedarius</i>	24,3	28,7
1985-202	MNHN	<i>C. dromedarius</i>	27,5	30
1964-213	MNHN	<i>C. dromedarius</i>	26,3	32,4
1865-1	MNHN	<i>C. dromedarius</i>	24,2	28,8
1852-564	MNHN	<i>C. dromedarius</i>	21,5	28,3
1897-337	MNHN	<i>C. dromedarius</i>	24,8	27,8
2007-1435	MNHN	<i>C. dromedarius</i>	23,9	28,4
5000-2064	CCEC	<i>C. dromedarius</i>	24,5	31,6
5000-2065	CCEC	<i>C. dromedarius</i>	23,5	29,6
5000-2066	CCEC	<i>C. dromedarius</i>	23,4	28,2
5000-2067	CCEC	<i>C. dromedarius</i>	25,8	29,5
5000-2068	CCEC	<i>C. dromedarius</i>	23,9	29,8
5000-2069	CCEC	<i>C. dromedarius</i>	24	28
5000-2070	CCEC	<i>C. dromedarius</i>	22,5	31
1908-101	MNHN	<i>C. dromedarius</i>	24	28
			<i>C. grattardi</i>	<i>C. grattardi</i>
Omo75s-70-956	NME	<i>C. grattardi</i>	25,6	38,6
MLP-1346	NME	<i>C. grattardi</i>	23,3	35,3
			<i>C. thomasi</i>	<i>C. thomasi</i>
TER 1816	MNHN	<i>C. thomasi</i>	24,7	32
TER 1689	MNHN	<i>C. thomasi</i>	27,8	33
			<i>P. alexejevi</i>	<i>P. alexejevi</i>
mean	Logvynenko, 2000	<i>P. alexejevi</i>	22,59	31,9
			<i>P. gigas</i>	<i>P. gigas</i>
22192	Teilhard and Trassaert, 1937	<i>P. gigas</i>	28	37
	Zdansky, 1926	<i>P. gigas</i>	29,6	38,5
			<i>C. knoblochi</i>	<i>C. knoblochi</i>
ZIN 8678	Titov, 2008	<i>C. knoblochi</i>	29,2	33,5
ROMK	Titov, 2008	<i>C. knoblochi</i>	27,55	33,55
VSEGEI	Titov, 2008	<i>C. knoblochi</i>	29,15	34,2
			<i>C. sivalensis</i>	<i>C. sivalensis</i>
36664	NHMK	<i>C. sivalensis</i>	26,8	33,3
15347	NHMK	<i>C. sivalensis</i>	24,5	32,8
16405	NHMK	<i>C. sivalensis</i>	24,4	30
PUA Rh 23/83	Gaur et al., 1984	<i>C. sivalensis</i>	19,6	28
FM19832	AMNH	<i>C. sivalensis</i>	21,3	34,2

	length of long bones				
	<i>C. sivalensis</i>	<i>P. gigas</i>	<i>P. alexejevi</i>	<i>C. dromedarius</i>	<i>C. bactrianus</i>
reference	AMNH FM 19832	Zdansky, 1926	Logvynenko, 2000; mean	Martini et al., 2017; mean	Martini et al., 2017; mean
humerus	420		426	389	398
metacarpal	408	462	425	349	323
femur	514	635	518	490	505
tibia	493	600	518	450	442
metatarsal	410	475	429	356	331

<i>P. merriami</i>
Harrison, 1985
533
510
609
670
494

Table 1. Dental measurements of NME-MLP-1346 (L = length; W = width).

LP3	WP3	LP4	WP4	LM1	WM1	LM2	WM2	LM3	WM3	M1–M3
21	15	24	23	37	35	44	37	43.2	30+	116

Table 2. Tooth height in some *Camelus*; height of unworn molars cannot be measured in most specimens, because their base is concealed in bone. Height of unworn teeth is underlined.

	<i>C. grattardi</i>		<i>C. dromedarius</i>	<i>C. sivalensis</i>			<i>C. thomasi</i>
	NME-MLP-1346		extant	NHMUK			type
			N=3	40570	40561	15357	
Tooth	P3	P4	P3	P3	M1	M2	M3
Length	21	24	mean 17.4	19.8	50.3	54.4	39
Height	<u>24.2</u>	<u>33</u>	26– <u>30</u>	28++	<u>58</u>	<u>62</u>	50+