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ABSTRACT We describe here the whole collection of *Camelus thomasi* from its type-locality, Tighennif (Ternifine) in Algeria. Detailed morphological and metric comparisons with the two species of modern *Camelus*, *C. bactrianus* and *C. dromedarius*, show that it is clearly distinct from both of them. It is mainly characterized by pachyostosis especially marked in the mandible, a size slightly greater than modern forms, broad molars with strong styles, and several unique cranial features. The species seems restricted to the terminal Early Pleistocene and is not definitely known outside Northwestern Africa. A phylogenetic analysis is premature, but *C. thomasi* does not appear to be particularly close to either modern species, and there is no support to regard it as an ancestor of the dromedary.

RÉSUMÉ Nous décrivons ici l'ensemble de la collection de *Camelus thomasi* de la localité-type, Tighennif (Ternifine) en Algérie. Des comparaisons morphologiques et métriques détaillées avec les deux *Camelus* actuels, *C. bactrianus* and *C. dromedarius*, montrent que la forme fossile est clairement distincte de l'une comme de l'autre. Elle est principalement caractérisée par une pachyostose spécialement marquée sur la mandibule, une taille un peu supérieure, des molaires larges avec de forts styles, et plusieurs traits crâniens uniques. L'espèce semble restreinte au Pléistocène inférieur terminal, et n'est pas attestée en dehors du Maghreb. Une analyse phylogénétique serait prématurée, mais *C. thomasi* ne semble pas spécialement proche de l'une ou l'autre des formes modernes, et rien ne permet de la considérer comme l'ancêtre du dromadaire.

INTRODUCTION

In one of his important monographs dealing with fossil mammals from Algeria, Pomel (1893) described a new species of camel as *Camelus thomasii*, based upon a fragment of maxilla, a piece of mandible and an incomplete metatarsal, from the locality then called Palikao, but better known in the literature as Ternifine (now Tighennif; Geraads [2016], and references therein). He noted that the type maxilla differs from that of the modern dromedary in the shape of the maxillo-palatine suture and in the horizontal orbital floor, supposedly giving the animal a less stupid look ['un air moins stupide'] than the dromedary, in which the orbits face more downwards. Further excavations at the site, mostly by C. Arambourg in 1954-56 (Arambourg and Hoffstetter 1963; Geraads et al. 1986), much increased the camel collection,

which is now by far the richest sample of African fossil camels. However, in spite of its importance, this collection remained unstudied, besides short descriptions by Harris et al. (2010). That explains why the species has been erroneously reported from a number of other sites and, most regrettably, its systematic position discussed without reference to the material from the type-locality. Here we describe the whole collection of *C. thomasi* from Tighennif, and discuss its relationships with the extant dromedary *C. dromedarius* and Bactrian camel *C. bactrianus*.

MATERIALS AND METHODS

Most of the material of *C. thomasi* described below is housed in MNHN; in addition, we have seen photos of the specimens (including the type) kept in the Algiers Museum, kindly provided by Y. Chaïd-Saoudi. A few other potential specimens of *C. thomasi* are from the 'Grotte des Rhinocéros' in Casablanca (Geraads & Bernoussi 2016). We have compared them to a good sample of modern camels: *C. bactrianus* (28 skulls), *C. dromedarius* (31 skulls), hybrids or unidentified (3 skulls), housed in MNHN, CCEC, ZIN, ZM, NMBE, NMB, MHNG, MSNM, and EK using the measurements of Martini et al. (2017). We have not attempted to distinguish taxonomically wild, feral and domestic forms of *C. bactrianus*, because such information is almost always missing in osteological collections.

ABBREVIATIONS

CCEC, Centre de Conservation et d'Etudes des Collections, Lyon

EK, Tell Arida research centrum, El Kowm, Syria

INSAP, Institut National des Sciences de l'Archéologie et du Patrimoine, Rabat

IPH, Institut de Paléontologie Humaine, Paris

MGA, Musée de Géologie, Algiers

MHNG, Muséum d'Histoire Naturelle de la Ville de Genève

MNHN, Muséum National d'Histoire Naturelle, Paris

MSNM, Museo Civico di Storia Naturale, Milano

NMB, Naturhistorisches Museum, Basel

NMBE, Naturhistorisches Museum des Burgergemeindes Bern

ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg

ZM, Zoologisches Museum der Universität Zürich

SYSTEMATIC PALAEONTOLOGY

<div align="center">Family CAMELIDAE Gray, 1821</div>

<div align="center">Genus *Camelus* L., 1758</div>

TYPE SPECIES. — *Camelus bactrianus* Linnaeus, 1758.

<div align="center">*Camelus thomasi* Pomel, 1893</div>

The name *Camelus thomasii* was first published by Pomel in 1886 but remained a *nomen nudum* until 1893.

HOLOTYPE (BY ORIGINAL DESIGNATION). — Right maxilla with M1–M2 and part of the palatine bone, N° 7236001 in the Musée de Géologie, Algiers, Algeria (Fig. 2E); also Pomel, 1893, pl.3, figs. 2−5 (note that Pomel's figures are inverted, and that the association of a M3 with this maxilla is tentative). From the late/terminal Early Pleistocene of Tighennif (formerly spelled Tighenif, also known as Ternifine or Palikao), near Mascara, Algeria.

REFERRED MATERIAL. — The whole collection of *Camelus* from Tighennif is referred to this species; the full list of specimens housed in MNHN and their measurements are given in the Appendix. In addition, we tentatively ascribe to the same species some specimens from the Middle Pleistocene of Oulad Hamida I quarry in Morocco, but they do not contribute to the definition of the species.

DIAGNOSIS. — A *Camelus* slightly larger than the modern species; pachyostosis weakly indicated in cranium (thick nasalia, thickening of the zygomatic arch posteriorly) and strongly so in the mandible; marked sexual dimorphism; V-shaped choanae; palatine foramina located anteriorly, at the level of P3 or P4; facial crest present; low placement of orbits; paroccipital process far from condyles; teeth small relatively to skull size; P1 located anteriorly, P3 with a complete lingual crescent; molars alveolarly broad with strong styles; mandible thick and low, especially anteriorly; coronoid process short, massive, slightly twisted and bent backwards; caudal mental foramen located anteriorly, or absent; p1 absent or located more anteriorly than in modern forms; p4 long, with a long metaconid; limb bones long; tibial tuberosity slender and very prominent; phalanges robust.

AGE OF THE SITE. — Historical data on the excavations and research at Tighennif can be found in Geraads (2016), who provided a faunal list, and concluded that the site is probably older than the Middle Pleistocene, as also assumed by Sahnouni and van der Made ((2007); it can tentatively be dated to c. 1 Ma. It is best known for its hominin remains (Arambourg and Hoffstetter 1963), either referable to *Homo rhodesiensis* Woodward, 1921 (according to Hublin, 2001) or closer to *H. ergaster* (Martinón-Torres et al., 2007).

DESCRIPTION AND COMPARISONS WITH MODERN FORMS. — The best specimen is a relatively complete cranium, TER-1689 (Fig. 1), first figured by Lhote (1987). Its description can be

complemented with that of other cranial elements: the maxilla with imperfectly preserved teeth TER-1816 (Fig. 2A), and the type-specimen MGA-7236001 (on the basis of photos kindly provided by Y. Chaïd-Saoudi, Fig. 2B). Unfortunately, TER-1689 is strongly dorso-ventrally crushed, so that the cranial surface consists of a mosaic of bone fragments among which sutures and details are hard to recognize. This crushing prevents reconstruction of the dorsal cranial profile and of the position of the front teeth relative to the occlusal plane of the cheek teeth. The basicranium is also poorly preserved and the right zygomatic arch is missing. In addition, the premaxillae are somewhat shifted posteriorly, and probably lack a few mm at their tips. By contrast, the moderately worn cheek-teeth are nicely preserved, but all teeth anterior to P3 are missing, except the left canine.

Overall size is close to the maximum seen in extant species. The maximal length (measurement C1) of 575 mm exceeds that of all 31 measured *C. dromedarius*, and was surpassed (by less than 10 mm) in only two individuals out of 28 *C. bactrianus*; given that this measurement is certainly underestimated because of the preservation of the premaxillae, it can reasonably be assumed that this skull was longer than that of all modern *Camelus* in our sample. Beside the larger size, the only proportions that differ significantly from those of the modern forms are the ones that indicate a shorter face and rostrum; considering the imperfect preservation of the premaxilla, these differences can probably be ignored. Dorso-ventral crushing prevents fully reliable estimates of breadth at orbital and post-orbital levels, but on the whole there is no evidence that general cranial proportions differed much from modern forms.

The premaxillae taper anteriorly, so that the rostrum appears pointed but it is certainly partly eroded; in both modern forms, its shape is variable, from similar to that of TER-1689 to distinctly broadened. The nasal opening looks small, but this is probably an impression given by the medial folding of the maxilla and misplacement of the premaxilla. Because of this crushing, the topographic relationships of the premaxillae cannot be definitely ascertained. Their most remarkable feature is their thickness throughout their length, which contrasts with their slenderness in the modern forms.

The infra-orbital foramen is located above the limit between P4 and M1; it occupies the same position in the maxilla TER-1816, and usually also in extant forms.

The front border of the orbit is located above the posterior half of M2, thus much like in modern forms, in which it is almost always located above that tooth as well. The orbit itself is too crushed for its real shape and measurements to be estimated, but it was located rather close to the tooth-row (Fig.3). A long facial crest runs more or less parallel to its ventral

border, about 25 mm below it; it fades out anteriorly and posteriorly, without connecting the ventrolateral edge of the zygomatic arch; the maxilla TER-1816 is imperfectly preserved below the orbit, but the facial crest was probably absent. It is almost always wholly absent in *C. dromedarius* (CCEC 5000-2069 being the single exception), but it is at least incipient in *C. bactrianus*, although it usually talks the shape of a tubercle below the anterior orbital border. Another crest underlines the ventral orbital border, about 10 mm below it, and proceeds posteriorly into the ventro-lateral edge of the zygomatic arch, as in modern *Camelus*. The front end of the squamosal is located about 25 mm behind the orbit. As mentioned above, the shape of the nasals cannot be determined. The ethmoid fissure was at most very small, and probably absent; in *C. bactrianus* its size ranges from large to extremely small, in *C. dromedarius* from medium-sized to absent. Around their position, on either side of the posterior part of the nasals, the dorsal part of the skull bears two symmetrical depressions due to post-mortem crushing but whose formation was certainly facilitated by the thinness of bones in this area, and underlying sinuses. The supra-orbital foramina are located not far apart (46 mm), as in modern forms, where they are often multiple.

The sagittal crest suffered no major distortion; it starts behind the post-orbital constriction but remains low and, even in its caudal portion, never becomes blade-like as often occurs in male *C. dromedarius*. As it now stands, the nuchal crest is thin and convex in occipital view, but it is probably incompletely preserved. In the sagittal plane, the occipital crest is stronger than in most recent *Camelus*. There was certainly no large nuchal tubercle above the foramen magnum, as sometimes occurs in *C. bactrianus*.

The ventral view confirms the tapering rostrum and short, pointed premaxillae. The large canine identifies the skull as that of a male. The P1 is missing, and its alveolus cannot be identified, but the individual was probably too young for having shed this tooth, as happens in senile individuals of the modern form. However, if present, this tooth was certainly closer to the canine than to P3, a position closer to the state of *C. dromedarius*, whereas in *C. bactrianus* this tooth is more posterior.

The palate is slightly crushed transversally, so that the outline of the choanae is imperfectly preserved; however, it was certainly much closer to the V shape that is most common in *C. bactrianus*, but is never found in *C. dromedarius*. TER-1816 almost certainly also had narrow V-shaped choanae. The choanae reach the level of the front of M3, which is not rare in *C. bactrianus*, but which we observed in a single, very old specimen of *C. dromedarius*. The course of the maxillo-palatine suture cannot be followed, as is normal in adult camels.

In TER-1689, the palatine foramina open at the level of P4, which is the most common position in *C. dromedarius*, whereas those of *C. bactrianus* almost always open at the level of M1 or M2. They are even more anterior in TER-1816, at the level of the posterior part of P3.

The pterygoid wings are missing, but the pterygoid processes of the basisphenoid consist of thick blades that emerge at the level of the middle of the glenoid fossae; in modern *Camelus*, they remain instead fully anterior to these fossae. The processes lateral to the foramen orbitorotundum are robust.

The glenoid fossae are incompletely preserved; they are deeply concave and bordered laterally by a thick, but low tubercle that is less lateral than in modern forms, because some thickening of the posterior root of the zygomatic arch occurred, laterally to this tubercle.

The auditory region is too poorly preserved for description, but a sharp difference with both modern species is that the paroccipital processes are located much farther from the occipital condyles, from which they are separated by a long, deep fossa, which is much shorter in modern camels; consequently, the tips of the paroccipital processes are farther apart than in modern forms. The condyles are broad (Fig. 4) and markedly extend onto the basioccipital, as in most *C. bactrianus*, whereas they may be shorter antero-posteriorly in *C. dromedarius*, but the morphology of *C. thomasi* is within the variation of both modern species.

In contrast to skull length, length M1−M3 of the complete skull (C34 = 114 mm), is close to the mean value for *C. bactrianus*, but it is even distinctly lower (102 mm) in TER-1816, close to the mean of *C. dromedarius*. The cheek-teeth are little worn and very well preserved. Although no tooth is quite fresh, the slight wear of the premolars, and of the M3 tentatively associated with the type-maxilla, show that the degree of hypsodonty was very similar to that of modern *Camelus*. No cement cover is preserved on any tooth, in contrast to modern forms in which it is present; it was probably destroyed during fossilization, or removed during preparation, because it is present in some lower teeth, and because Pomel (1893, pl. 4, fig. 1) figured cement on an upper molar from Tighennif. The P3 has a complete lingual wall; the central valley is fully closed lingually, and opens mesially 13 mm above the cervix. The lingual crescent is never complete in *C. dromedarius*, and very rarely complete in *C. bactrianus*; in these forms, P3 is usually a reduced tooth, quite different from P4, whereas they are similar in *C. thomasi*. Thus, although this tooth is present only in TER-1689, the difference with modern forms is clear. P4 differs from P3 only in being larger and more symmetrical; on both teeth the buccal central rib is quite weak, and the mesial and distal styles are buccally prominent. M1 has a small basal cingulum along the lingual side; this tooth is

distinctly smaller than M2, which is about as large as M3. On all molars, the buccal paracone rib is better indicated than the vestigial metacone rib, the parastyle is thicker than the mesostyle but both are quite prominent bucally, in contrast to the metastyle, which is distinct on M3 only. All these dental features are similar on the other specimens TER-1816 and MGA-7236001. In modern forms, the styles are less prominent buccally, especially the parastyle, which is not stronger than the mesostyle; there is variation in this regard, but the fact that both the type and TER-1816 also have prominent styles suggest that this is a valid difference.

In addition, the molars differ from those of modern forms in being broader, in particular the mesial lobe of M1 and M2 (Figs. 5-6); although these can be accurately measured only in TER-1689, this was clearly also true in the smaller maxilla TER-1816 (Fig. 1H).

Pomel (1893, pl. 4, fig. 3–4) tentatively ascribed to *C. thomasi* a mandible not found *in situ*, and now preserved in MGA; it fails to show the typical characters of the species, described below, and is probably of a historical *C. dromedarius* instead. The MNHN collection of *C. thomasi* from Tighennif includes seven partial mandibles, of which five are illustrated here: TER-1683 (Fig. 2F; almost certainly of the same individual as TER-1684); TER-1685 (Fig. 2G); 1900-27, collected by Pallary (Fig. 2C); TER-1686 (Fig.2E); TER-1688 (Fig. 2D); two additional mandibles are stored in IPH and MGA.

Their most obvious character is the strong pachyostosis, the corpus being low but extremely thick below the cheek-teeth, and even thicker than deep below p4-m1 (Fig. 7); this thickening extends to the ascending ramus. The coronoid process is rather cylindrical with a flattened anterior surface, not blade-like. It is slanted backwards, with a weak curvature; its apex is transversally compressed, antero-posteriorly deeper than the base and has a slight lateral twist. This morphology contrasts with both species of modern *Camelus*, which are also different from each other. The condyle is preserved on TER-1685; it is rectangular, and antero-posteriorly short. This contributes, in addition to the shape of the coronoid process and reduction of the sigmoid notch, to the antero-posterior narrowness of the ramus at this level, in the three specimens in which this part is preserved.

TER-1683 (Fig. 2F) preserves a large part of the corpus anterior to p4, up to about 1 cm in front of the anterior mental foramen, and there is no evidence of a p1, so that this tooth was either absent, or more anterior. In modern *Camelus*, p1 is almost always present, and can be shed only in individuals distinctly older than TER-1683; it is never as anterior as it must have been if present in TER-1683.

The posterior mental foramen is located below the anterior part of m1 in TER-1685, but is certainly absent in TER-1683/1684, probably a consequence of pachyostosis. It is not visible in the other specimens, which preserve only the posterior part of the mandible, but if present it was always anterior to the middle of m1, a position more similar to that observed in *C. bactrianus*, whereas it is more posterior in *C. dromedarius*.

The only preserved p4 is that of TER-1685. It is longer than that of modern form; the metaconid is antero-posteriorly expanded to form a complete lingual wall; this sometimes occurs in *C. bactrianus*, but never in *C. dromedarius*.

In all camel species, the upper part of the lingual wall of the lower molars is concave between the stylids, but as wear proceeds, the styles fade away, and the lingual walls become more or less flat; they may even become slightly convex, perhaps especially so in *C. thomasi*. There is some variation in the shape of the third lobe of m3, but its lingual wall is less oblique than the average condition of modern forms.

There are a number of post-cranial bones in the Tighennif sample but preservation of most of them is imperfect, and precise measurements can seldom be taken. Still, it is clear that they are larger than those of living *Camelus*; in particular, all long bones whose length can be measured or reasonably estimated are longer than the modern maxima.

The scapula, humerus, radio-ulna, and carpals are not represented. There are some, mostly incomplete metacarpals (Fig. 8A); those of the Bactrian camel differ from those of the dromedary in being shorter and stouter; those of *C. thomasi* are significantly longer than all of them, but the diaphyses are relatively as robust as in *C. bactrianus*. In contrast, the distal articulation is narrow. TER-1652 is aberrant in its wide distal condyle, but the morphology of this part suggests plastic distortion. Other individuals show condyles which are deeper than wide, closer in this respect to dromedaries.

There is no femur, but there is an almost complete tibia TER-1682 (Fig. 8B) and two incomplete distal epiphyses. This bone is also longer than all modern ones, and distinctly more gracile than those of the Bactrian camel (Fig. 9). The proximal epiphysis differs clearly from both modern species in the narrow, transversely compressed but antero-posteriorly expanded anterior tuberosity (Fig. 8B2); it is much thicker and much less prominent in modern forms.

The single fibula is large and it is in particular wide. Although the distal tibiae are poorly preserved, the lateral facet of the distal cochlea appears to agree with the proportions of the fibula.

The calcanei (Fig. 8D) are large and overall similar to *C. bactrianus*, particularly in their shorter and less constricted tuber and the anterior placement of the sustentaculum; but the fibular trochlea is smaller and less prominent, and the plantar border is broad (except in TER-1665 that may not be fully adult), more like in the dromedary.

There are four astragali, of which only one is well-preserved (Fig. 8C). The proximo-lateral lip ranges from short as in *C. bactrianus*, to long as in *C. dromedarius* (Steiger 1990). Distally, the facet for the navicular (the lateral part of the trochlea) is relatively small (Fig. 10), more similar to *C. bactrianus* than to *C. dromedarius* (in which this facet is more similar in width to the facet for the cuboid).

A single cuboid (Fig. 8E), collected in 1982 (Geraads et al. 1986) is large and high; the astragalar facet is narrow, as in *C. bactrianus*. On the lateral side, the groove for the tendon of the m. peroneus longus is shallower than in modern forms.

The navicular (Fig.8F) is represented by two specimens that are low and wide, with proportions rather similar to *C. bactrianus*. Other known small bones include the trapezoideum and the intermedio-lateral cuneiform, which are similar to extant species.

The two metatarsals whose length can be estimated are, like the metacarpals, much longer than in modern *Camelus* (Fig. 11). The proximal epiphysis is relatively small. The facet for the cuboid is transversally wide, while the facet for the medial cuneiform is shortened. The distal articulation of the metatarsal is narrower than in *C. bactrianus*.

There are four anterior and one posterior phalanges. They are longer than in modern forms, and more massive, being less constricted at mid-length. The condyles appear narrow and seem to have less asymmetric lips than in extant species, where the abaxial lip is longer.

DISCUSSION

The first issue regarding the Tighennif camel sample is that of its species homogeneity. Although size variation of the post-cranial remains can be accommodated within a single species, there are important size differences between, e.g., skull TER-1689 and maxilla TER-1816, or between the mandibles TER-1683/1684 and all other mandibles. However, all mandibles share the same remarkable pachyostosis and related features, and both TER-1689 and TER-1816 share strong styles, broad molars, and anteriorly located palatine foramina. We therefore conclude that the whole collection belongs to a single species, whose important size variation can be explained by sexual dimorphism.

The most remarkable feature of *C. thomasi* is its pachyostosis, which strongly affects the mandible, moderately the skull, but not the postcranials. This tissue distribution is similar

to what is found in several megacerine Cervidae (see references in Morales et al. 1993), in which the mandible is also the most affected part, but not to what occurs in the lower Miocene *Lorancameryx* from Spain (Morales et al. 1993), in which it is the anterior limb that underwent the most spectacular pachyostosis. Besides some aquatic forms, in which it is obviously related to the need for increasing density, pachyostosis (defined as deposition of extra bone, by comparison with closely related forms) is rare in mammals and restricted, as far as we know, to a few Cetartiodactyla and *Homo* of the *erectus* group, so that general explanations are unlikely to be valid. The occurrence of pachyostosis in Cervidae, in which large amounts of bone are deposited every year, might be explained as a side-effect of antler formation, but its origin in *C. thomasi* remains obscure. Clearly, the heavy mandible of all camels, compared with similar-sized selenodont Cetartiodactyla, provided a basis for this hyper-ossification. This pachyostosis might be dependent of environmental conditions and therefore it might be limited to the Tighennif population, but since this is the type locality we include this character in the diagnosis of this species

Some of the other morphological and metric features described above are closer to those of *C. dromedarius*, more of them are closer to *C. bactrianus*, but there are also some major features which unambiguously demonstrate that *C. thomasi* is distinct from both modern species, as listed in the diagnosis. Pending full study of recently collected material from Syria and Ethiopia, critical to the history of Old World Camelidae, a phylogenetic analysis would be premature, but now that *C. thomasi* is satisfactorily characterized, some conclusions regarding the distribution of the species can be drawn.

From the 'Grotte des Rhinocéros' near Casablanca, dated to c. 0.5 Ma, Geraads and Bernoussi (2017) reported some remains that they assigned to this species. Two upper molars OH1-GDR F14-87 do not have strong styles but are broader than in modern forms, as at Tighennif; a m3 E12-26 is broad as well. A virtually complete metacarpal GDR-5271 is about as long as the largest Tighennif bones, and remarkably robust, as several of its measurements even exceed the Tighennif ones. We can assume that these remains represent an advanced form of *C. thomasi*, which further increased the size and robustness of its bones, but positive identification cannot be reached without cranial or mandibular material.

Gautier (1966) reported *C. thomasi* from Northern Sudan, in a site dated to c. 22,000 BP. He estimated, on the basis of field photographs, that the length of some limb-bones was about 1.2-1.4 longer than in modern forms (compared to one individual of each species). In fact, some of the bones (distal tibia, calcaneum) indicate that this animal was significantly larger than *C. thomasi*. This large size is partly confirmed by a mandible (not figured) whose

measurements are slightly above those of modern *Camelus*. Moreover, Gautier's identification was not supported by any morphological feature, and in particular there is no mention of mandibular pachyostosis. Unfortunately, this paper led the way to numerous mentions of *C. thomasi* in the African and Arabian Late Pleistocene to Holocene, giving the deceitful impression that this species was widespread and persisted until historic times. For instance, Grigson (1983) suggested that a very large camel from the late Pleistocene of Israel might represent *C. thomasi*; again, the measurements that she provided are much larger than those of this species (e.g., breadth of distal metapodial condyle = c. 58 mm, vs. 36−52 mm at Tighennif; breadth of proximal metacarpal = c. 90 mm vs. 63−80 mm), and this identification must be rejected. Peters (1998) restudied the material seen by Gautier, accepting his identification as *C. thomasi*, and concluded that this species was morphologically identical to the domestic dromedary and might be considered its wild ancestor. Later authors accepted and reinforced his proposal (Von den Driesch & Obermaier 2007). However, no morphological or metric comparison with the material from the type-locality of *C. thomasi* had ever been conducted, thus any discussion of the affinities of this species were lacking a sound basis. Our detailed study shows instead that *C. thomasi* differs clearly from both extant forms, rejecting other opinions found in the literature.

CONCLUSION

The material of *Camelus thomasi* from the type-locality Tighennif is sufficient to satisfactorily define the species, even though several bones remain unknown. Besides perhaps in the Thomas - Oulad Hamida cave complex in Morocco, there is no published convincing evidence of this species elsewhere. The hypothesis that *C. thomasi* was a widespread species from which the modern dromedary derives is not supported by the current morphological evidence.

The history of fossil camels in Afro-Arabia and the Near East remains poorly documented; hopefully, recently collected material from Syria and Ethiopia will shed new light on their evolution.

to Y. Chaïd-Saoudi for photos of the Algiers material. Thanks also to the reviewers, J. Morales and J. van der Made, for their helpful comments.

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Captions to figures

Figure 1. *Camelus thomasi*, Tighennif, cranium MNHN-TER-1689. A: left lateral view, B: ventral view of the cranial basis (stereo), C: ventral view, D: dorsal view. Scale bar = 40 cm.

Figure 2. *Camelus thomasi*, Tighennif. A: maxilla TER-1816, occlusal view. B: maxilla with M1−M2 and tentatively associated M3, holotype n°7236001 (B1: right lateral view, B2: occlusal view). C: partial mandible 1900-27, dorsal view. D: partial mandible TER-1688, dorsal view. E: partial mandible TER-1686, dortsal view. F: mandible TER-1683 (F1: dorsal view, F2: lateral view). G: mandible TER1685 (G1: dorsal view, G2: medial view). Fig. B in Musée de Géologie, Alger, all others in MNHN. Scale bar = 40 cm for Figs. F2 and G2, 20 cm for all others.

Figure 3. Bivariate plot of cranial measurements showing the position of the orbit (C24 vs. C14 of Martini et al. 2017).

Figure 4. Bivariate plot of measurements of occipital condyles (C74 vs. C73 of Martini et al. 2017).

Figure 5. Bivariate plot of M2 mesial width vs. length of molar row (C34 vs. Ds24 of Martini et al. 2017).

Figure 6. Bivariate plot of distal vs. mesial widths of M2 (Ds25 vs. Ds24 of Martini et al. 2017).

Figure 7. Bivariate plot of depth vs. thickness of the mandibular corpus (M20 vs. M15 of Martini et al. 2017).

Figure 8. *Camelus thomasi*, Tighennif. A: metapodials; from left to right metatarsals TER-1664, TER-1690, and metacarpals TER-1648, TER-1681, and TER-1652. B: right tibia TER-1682 (B1: lateral view, B2: proximal view). C: left astragalus TER-1670 (C1: anterior view, C2: plantar view, C3: medial view, C4: distal view). D: left calcaneus TER-1666 (D1: anterior view, D2: plantar view, D3: medial view). E: left cuboid 1982-5-60 (E1: proximal view, E2: distal view, E3: medial view). F: right

navicular TER-1679 (F1: proximal view, F2: distal view, F3: lateral view). Scale bar = 40 cm for Figs. A and B, 20 cm for all others.

Figure 9. Bivariate plot of width of shaft vs. length of the tibia (Ti13 vs. Ti3 of Martini et al. 2017).

Figure 10. Bivariate plot of the widths of the navicular and cuboid facets of the astragalus (Ta14 vs. Ta15 of Martini et al. 2017).

Figure 11. Figure 8. Bivariate plot of width of shaft vs. length of the metatarsus (Mp1 vs. Mp12 of Martini et al. 2017).

Appendix. Catalogue and measurements of all specimens of *C. thomasi* from Tighennif housed in MNHN. All measurements in mm. Measurements of extant *Camelus* species are from Martini et al. (2017). Estimated measurements are in red. * = see remarks in the text.