Pleistocene Camels from Algeria to Syria: is Camelus thomasi represented in Nadaouiyeh?

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Abstract

The paleontology of the genus *Camelus* is poorly known. The fossil species *Camelus thomasi* Pomel 1893 was described in Tighennif, Algeria (late Early Pleistocene), but has since been widely reported in Northern Africa and in the Middle East. However, the type material from this locality has never been studied in detail. Another locality rich in camelid fossils awaiting description is the Nadaouiyeh Aïn Askar, Syria (Middle Pleistocene). Comparing the samples of the two locality, it is clear that *Camelus thomasi* is not present in Nadaouiyeh, nor is there in fact any reliable identification of this species outside of the Maghreb. The camel from Nadaouiyeh belongs therefore to a new species.

Institutional abbreviations

IPNA = Institute of Prehistory and Science in Archaeology, University of Basel, Basel
MNHN = Muséum National d'Histoire Naturelle, Paris

Introduction

Only a handful of fossil species have been described in the genus *Camelus: C. knoblochi* Nehring 1901 is known from the Middle and Late Pleistocene of Russia and Central Asia (Titov, 2008), *C. sivalensis* Falconer & Cautley 1836 is restricted to the Siwaliks of Pakistan and India (Falconer and Murchison, 1868) (but might better be considered part of the archaic genus *Paracamelus*), *C. grattardi* Geraads 2014 has been recently discovered in the Ethiopian Pliocene (Geraads, 2014) and *C. thomasi* Pomel 1893 was described in Tighennif, Algeria (also known as Ternifine or Palikao) (Pomel, 1893). No fossil camel species is yet known with certainty in the Middle East, but a few remains have been assigned to the Algerian species *C. thomasi* (Gautier, 1966, Grigson, 1983, Peters, 1998). However, these identifications lacked any morphological comparisons to the type material (Harris *et al.*, 2010); the latter remained largely undescribed. A sizeable collection of cranial and postcranial camelid remains from the type locality of Tighennif has been preserved at the MNHN in Paris, but until 2016 has been inaccessible to studies.

The basin of El Kowm (Central Syria), with its wealth of Pleistocene faunal remain (Reynaud-Savioz and Morel, 2005, Jagher and Le Tensorer, 2011, Jagher *et al.*, 2016), offers for the first time the possibility to explore the evolutionary history of camels in the Middle East over an unmatched depth of time (Martini *et al.*, 2015). In the context of my doctoral thesis, I will describe the camelid remains from three of the main sites around El Kowm: Hummal, Aïn al Fil and Nadaouiyeh Aïn Askar. Presently, the collection from the latter site (henceforth Nadaouiyeh) has been analyzed in its entirety, attesting the presence of a species well distinct from the extant *Camelus dromedarius* and *C. bactrianus (*Martini, in preparation). A description of the sample from Tighenif housed in Paris is also forthcoming (Martini and Geraads, in preparation). At the moment of this writing, the material from Hummal and Aïn al Fil have not been completely studied.

The collections of Nadaouiyeh and Tighennif are similar in quantity and quality of the remains: both preserve a mostly complete cranium and abundant postcranials which show morphological homogeneity, suggesting that in each site all camelid remains can be confidentially assigned to the same species (with rare exceptions concerning Nadaouiyeh (Martini, in preparation)). Moreover, both localities have yielded faunal as well as archaeological remains; however, they are different in age. Nadaouiyeh has yielded faunal material which is for its largest part constrained between 0.55 and 0.325 Ma (Jagher, 2011, Jagher, 2016). Only few camelid remains are found in layers younger, respectively older of these dates. On the other hand, the site of Tighennif, Algeria (Geraads *et al.*, 1986) is close to 1.0 Ma, in the Jaramillo subchron, according to recent faunal considerations (Geraads, pers. comm. 2016). Here we compare the camelid samples from Nadaouiyeh and from Tighennif, in order to determine if the remains in the former locality can be ascribed to *Camelus thomasi* or not.

Material and methods

Camelid fossils from the localities of Tighennif, Algeria (MNHN) and Nadaouiyeh Aïn Askar, Syria (IPNA) are described and compared. The

	Nadaouiyeh	Tighenif	*C. bactrianus*	*C. dromedarius*
Cranium	**NAD F14-671**	**TER-1689**	**N=17**	**N=14**
Maximal length	-	~575	491-539.1-579	462-499.9-534
Length P3-M3	~162	161	135.5-158.5-175	128-144.2-157.5
Palatine foramina to post. palate	79	~107	40-67.4-85.5	88-100.1-120
Width between infraorbital for.	101	101	88-96.5-108	83-88.9-95
Width between orbits (anterior)	187	~225	163-181.2-207	149-164.4-178
Width of postorbital constriction	99	120	80-90.2-102	74-80.4-88
Width of braincase	115	131	112-123.5-136	95-101-110
Width of condyles	84	97	74-81.8-92	78-82.9-91
Superior dentition	**NAD F14-671**	**N=3**	**N=11**	**N=10**
M1, length	~33	24, 26, 29	24-28.267-32.3	23.8-26.4-32
-, width of mesial lobe	~34	~29, 33, ~35	28.5-30.8-34	26-29.9-33
-, width of distal lobe	35	31, 33, 33	26-30.7-35	26-31.1-34
M2, length	39.5	33, 33, 37	32.5-39.1-44.5	26-31.8-42
-, width of mesial lobe	30.5	34, 34.5, 35	28.5-32.1-36	27-31.9-34
-, width of distal lobe	24	26, 28, 30.5	25-29.1-33	23-33.1-39
M3, length	43.5	40, 44	39.5-46.1-51	36-40.3-46
-, width of mesial lobe	~23.5	26, 32	25-29.7-34	22-29.2-32
-, width of distal lobe	~20	22, 29	21-24.7-30	18-24.4-26
Mandibula	**N=3**	**N=7**	**N=11**	**N=11**
Thickness of body (distal to m2)	~42, ~46, 47	39, 41, 42, ~48, ~48, 51, ~51	37.5-40.5-45.5	32.5-36. 5-40
Depth of body (distal to m3)	~70, 93	65, 65, 72, ~74,~78, ~85	65-76. 2-86.5	72.5-80.3-86.5
Greatest height (coronoid proc.)	~205	189, 191, ~230	222-244.5-259	199-209. 5-221

Table 1: *Selected craniodental measurements (in mm) of fossil sample from Nadaouiyeh, fossil sample from Tighennif, C. bactrianus and C. dromedarius. For fossil assemblages all available measurements are given ordered by value; estimations are marked with ~. For extant species the minimal, average and maximal values are given (all data from Martini* et al.*, in revision). Dental measurements are taken at the alveolar level.*

abridged descriptions focus on elements and characters that are most diagnostic and at the same time are adequately represented in both samples: cranium, mandibula, dentition calcaneus, astragalus, metapodia and phalanges. Both samples include additional postcranial remains which are missing or extremely poorly preserved in the other locality, which are therefore excluded from this study. The comparisons with extant species *Camelus bactrianus Linnaeus* 1758 and *C. dromedarius Linnaeus* 1758 are based on my study (Martini *et al.* in press).

Results

The cranium NAD F14-671 from Nadaouiyeh has a size comparable to *Camelus bactrianus* (Fig. 1; Table 1). The tip of the rostrum and the zygomatic arches are missing, and the basicranium and all of the teeth are severely damaged; the cranium is dorsoventrally compressed but otherwise not deformed. The low sagittal crest and small erupting P1 suggest that the specimen was a 6-7 years old female (Lesbre, 1903). Its maxilla is laterally bulging, causing the face to appear broad. A maxillar crest is present. The forehead is broad as well, with a shallow, caudally placed postorbital constriction but a relatively narrow braincase. The supraorbital notch is dorsally convex; this character was not observed in any other camel crania, where it is always concave. The orbit has a similar conformation as in *C. dromedarius*, with rostrally constricted superciliar rim (instead of caudally constricted), constricted zygomatic process of the frontal, and wide basal rim; however, it clearly differs from this extant species in having bone which is more than twice as thick. The palate is narrow and has palatine foramina at the level of M1, narrow choana and a caudal nasal spine. M1 is large, M2 has a narrow mesial lobes, M3 is narrow overall. The glenoid fossa has a triangular shape. The occipital condyles have an average size.

The cranium TER-1816 from Tighennif is as large as the biggest crania of extant *C. bactrianus* (Fig. 2; Tab. 1) Its large left canine, large alveoles for I3 and P1, slightly worn M3 and well-developed sagittal crest indicate that the specimen was a middle-age adult male. The maxilla is neither bulging nor concave as in *C. dromedarius*, and a maxillar crest is present. The forehead is broad and the postorbital constriction is shallow. The orbit has a low placement above the dentition (unlike the state mentioned in the original description (Pomel, 1893)). P1 is found in a rostral position, close to the canines. The palatine foramina are advanced to the level of P4. M1 and M2 have broad mesial lobes. The choana is narrow and pointed. The occipital condyles are relatively narrow in their cranial part, but caudally become very broad.

Both samples include several mandibles (Tab.1).

	Nadaouiyeh	Tighenif	*C. bactrianus*	*C. dromedarius*
Calcaneus	**N=5**	**N=4**	**N=12**	**N=11**
Length	(140), 154	162, 170, ~170	134.5-143.9-161.5	127.5-140.1-151
Depth of tuber	(42), 51	46.5, ~52	45.5-47.9-53	38-45.3-49.5
Depth at sustent.	(58), 60, ~64, 65	24, 26, 31, 31	59-66.0-79.5	50-56.1-61
Depth at trochlea	(53), 70, 71, 73	72, 75, 75	65.5-71.1-83	55-62.8-68
Metacarpale	**N=9**	**N=8**	**N=13**	**N=15**
Length	-	~420	295-322.8-353.5	327-348.8-389.5 (N=15)
Proximal width	75, 76	78, 79, 85	67.5-74.2-84.8	62.5-70.9-78 (N=15)
Proximal depth	42, 49	50, 52	42-46.0-55	40-45.6-49 (N=8)
Condyle width*	~40, 42.5, 44, 44.5, 46	42, 42, 42, 44, 44, 44, 52, 55	39.8-44.4-51.3	37.4-42.40-47.3 (N=15)
Condyle depth*	~43, 43.5, 44, 45, ~46, 47	41, 44, 44, ~44, 49, 56	39.3-42.1-47.8	40.3-42.87-46 (N=15)
Metatarsale	**N=9**	**N=9**	**N=13**	**N=15**
Length	-	~415, ~420	304.5-333.0-363.5	338-358.8-381
Proximal width	~64, ~64, 65.5, 66	63, 67, 67, 68, 70, 71, 74, 80	59-63.3-74.5	54.5-59.8-64
Proximal depth	~48, 49, 51.5, 54	51, 52, 54, 55, 56.5, 57.5, 59	45-49.3-53	45.8-49.0-56
Condyle width*	34.5, 35.5, 36, 37	~36, 40, 40	34.8-38.0-43.6	31.6-34.9-38.5
Condyle depth*	37, 38, 38, 39	~38, 40, 41.5	35.5-37.3-42	33.5-36.7-40.1
Ant. prox. phal.	**N=3**	**N=4**	**N=9**	**N=13**
Length	108	120, 122, 126, 126	96-102.1-110.3	92.5-102.7-110.9
Condyle width	38.5	~45, ~46, ~46	36-40.8-47.3	36.5-40.9-46.5
Condyle depth	~27, 27.5	31, 31.5, 31.5	22.8-25.4-29.8	23.5-25.2-28.5
Length axial lip	33	~38, ~40, ~40	28-31.5-35.3	31.25-34.7-38.4
Length abaxial lip	36, 37	~39, ~40, ~42	31.5-34.7-41	32-37.0-41.5
Post. prox. phal.	**N=4**	**N=1**	**N=8**	**N=11**
Length	95, 95	103	85.8-90.9-99	85-91.8-97.5
Condyle width	44, 45, 37	~34.5	32-34.9-39	30-33.9-40
Condyle depth	22, 24, 24,25.5	24	19.8-22.4-26.5	19-22.1-26
Length axial lip	26, 29, 29, 29.5	~32	25.3-27.2-30.5	26-28.9-32
Length abaxial lip	29, 32, 32	~33	27-30.4-34.3	29-32.4-37

Table 2: *Selected postcranial measurements (in mm) of fossil sample from Nadaouiyeh, fossil sample from Tighennif, C. bactrianus and C. dromedarius. For fossil assemblages all available measurements are given ordered by value; estimations are marked with ~. For extant species the minimal, average and maximal values are given (all data from Martini* et al.*, in press). Brackets: one small calcaneus is considered to represent an immature individual. *: average of medial and lateral values.*

Three fragmentary specimen from Nadaouiyeh are characterized by low, quite massive body and a coronoid process which is short and thick, subtriangular and gently curving backwards. The seven specimens from Tighenif are even more massive, to the point that they can be considered pachyostotic. The coronoid process is thick; it is narrower at the base than at the tip, it is caudally bent rather than curved, and is twisted laterally. Unlike in extant species, there is no caudal mental foramen. The lower dentition does not show many differences, but it is broader in Tighenif.

Calcanei in Nadaouiyeh (Tab. 2) are dromedary-like in having an overall slender shape, with elongated tuber, thick plantar border and plantar position of the sustentaculum; however, they are larger than in this recent species. The cuboid facet is short and distally prominent. Calcanei are even larger in Tighennif, but in this sample the shape is closer to *C. bactrianus:* the tuber is short and wide, the sustentaculum is placed dorsally, the fibular trochlea is less prominent both laterally and proximally, and the plantar border is of variable thickness.

The astragali (Table 2) found in the Nadaouiyeh sample are not highly distinctive, but they are very similar to each other. The lateral lip of the proximal trochlea has intermediate length between the shorter lip of *C. bactrianus*, and the longer lip of *C. dromedarius.* The calcaneal facet is narrow. The distal trochlea has a relatively large medial facet and a small lateral one. In the Tighennif sample, the overall shape is narrow and the lateral facet of the distal trochlea is small, but otherwise it is not clearly different from either extant species.

Metapodia (Tab. 2) from Nadaouiyeh have a similar size to the same elements in extant species; unfortunately no complete specimen is known. The metacarpale are characterized by narrow condyles, which as a group has less variation than either modern species; in this, they are more similar to *C. dromedarius.* The diaphysis is not represented and the proximal articulation has no remarkable proportions. The metatarsale has an overall broad proximal articulation with a narrow proximal process, a

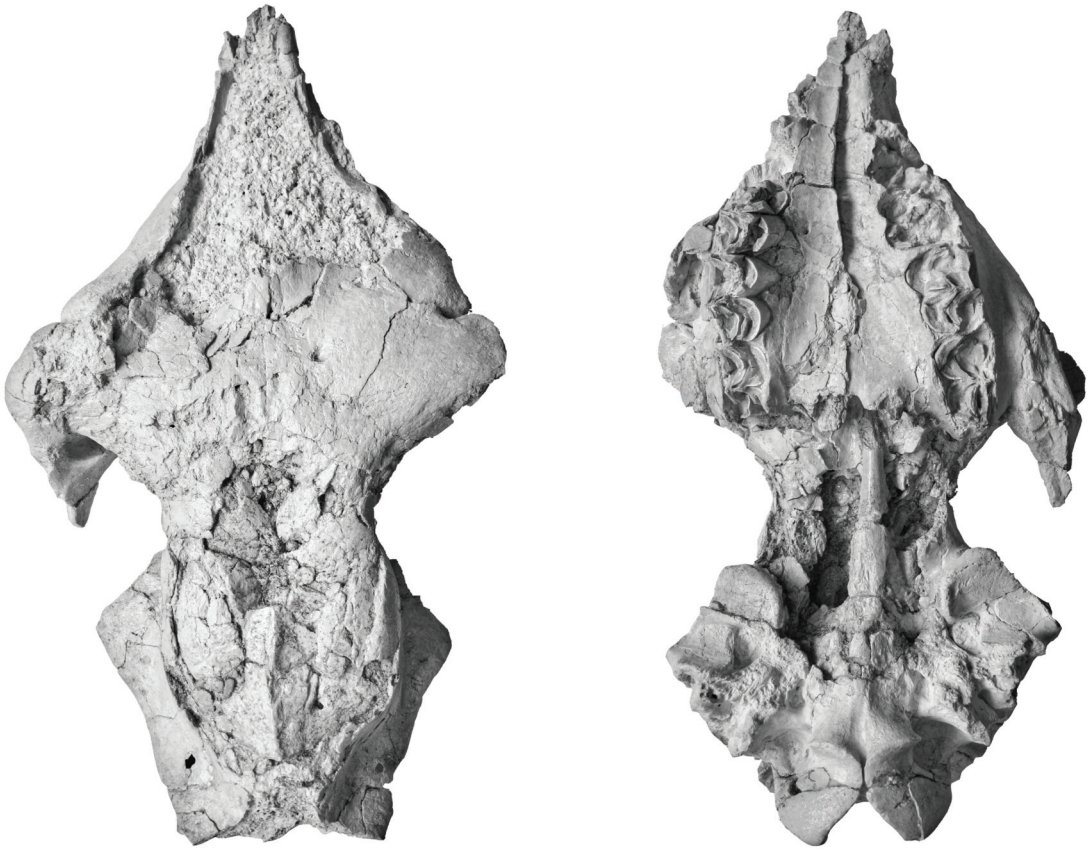

Figure 1: *Cranium NAD F14-671 from Nadaouiyeh (c.7). Left, frontal view; right, basal view. Total length of the specimen (in dorsal view) is 407 mm.*

narrov III facet (dorsolateral) and a wide IV facet (plantolateral). The condyles are again deep and narrow. On the other hand, metapodia are abundant at Tighennif but many specimens are damaged and cannot be described in great detail. Both metacarpale and metatarsale are much larger than in either extant species. The metacarpale has a massive diaphysis, a proximal articulation without peculiar traits, and relatively small and narrow condyles. The metatarsale has a relatively small proximal articulation, with a short and broad proximal process and a wide but short IV facet. The proportions of the diaphysis and of the condyles cannot be judged.

The proximal phalanges (Tab. 2) are similar in the anterior and posterior limbs, but they can be differentiated based on the smaller size and more asymmetric proximal facet of the posterior phalanx. In Tighennif there are several anterior phalanges and only one posterior; the opposite is true for the other assemblage. In Nadaouiyeh, the proximal phalanges are larger than the average of extant species; the condyles are narrow and deep, with lips shorter than in *C. dromedarius* but longer than in *C. bactrianus.* The proximal phalanges in Tighennif are well above the size variation in modern species and show a massive diaphysis. The condyles (all of them damaged) are deep and narrow, although not as much as in Nadaouiyeh; their lips are more symmetric, with an abaxial lip barely longer than the axial lip. Other forms always have a distinct difference in length that can be used to determine the side of a phalanx.

Discussion

The cranium from Tighennif and the cranium from Nadaouiyeh Aïn Askar share some similarities (broad forehead, shallow postorbital constriction, presence of maxillar crest), but the differences between them are more important: in the Nadaouiyeh specimen, the palatine foramina are more posterior, the palate is narrower, there is a caudal nasal spine and the occipital condyles are not as broad.

Further differences are found in the dentition. In Tighnenif the M1 has a broad mesial lobe but is not overall enlarged as in Nadaouiyeh; the M3 is similar to modern species, while in Nadaouiyeh it is narrow. M2 has a larger mesial lobe in both fossil specimens, although in Nadaouiyeh this is mostly due to the distal lobe being narrower than the average.

The mandibles are similar in having a body which is more massive than in extant species; this trait is exagerated in Tighennif. On the other hand,

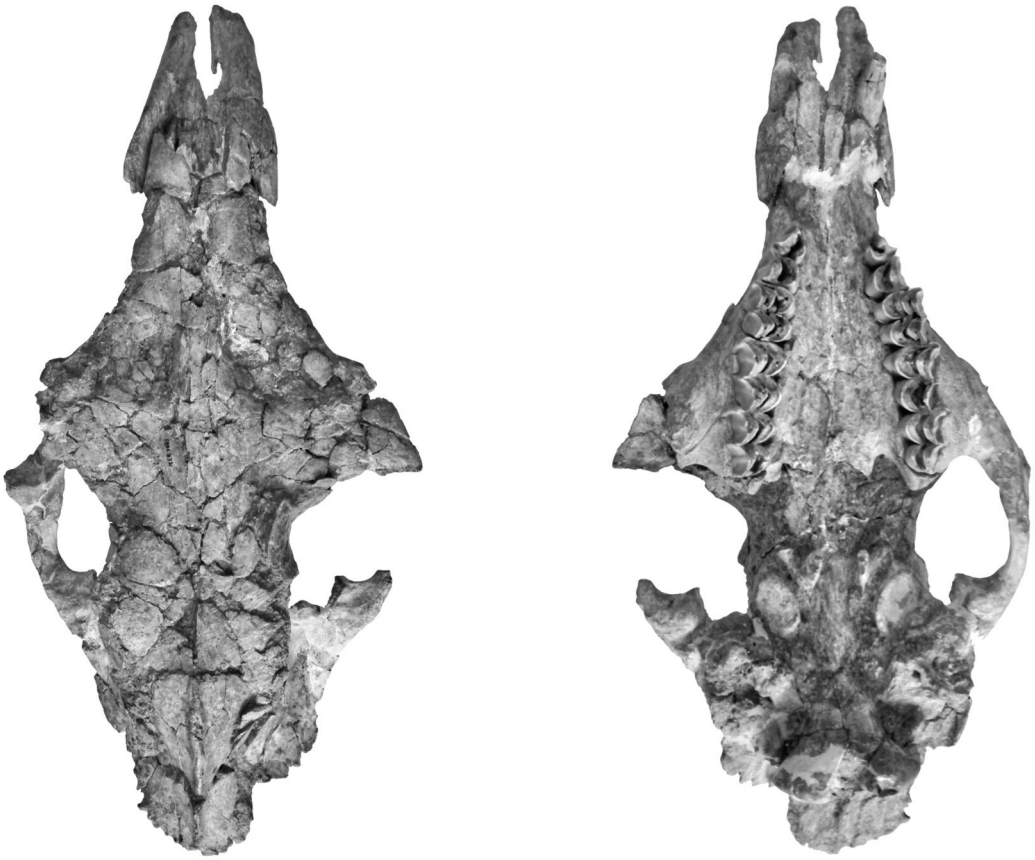

Figure 2: *Cranium TER-1816 from Tighennif. Left, frontal view; right, basal view. Total length of the specimen (in dorsal view) is 575 mm.*

the shape of the coronoid processes is very different not only between the fossils Tighenif and Nadaouiyeh, but also among them and both extant species. It is thick, bent backwards, twisted laterally and with a wider apex than basis in Tighenif; thick, short, triangular and slightly curved backwards in Nadaouiyeh; thin, short, straight and with a square apex in *C. dromedarius*; long, thin and clearly curved backwards in *C. bactrianus*. This character allows a clear separation of these four forms.

The calcanei are large in both fossil samples, but while those from Nadaouiyeh can be compared to *C. dromedarius*, those from Tighennif are rather similar to *C. bactrianus*; the differences between the extant species are clear and numerous, and the same is true between the fossil samples. In contrast, astragali are less distinctive among the four forms; only *C. dromedarius* differs from the others in having a large lateral part of the distal trochlea, and a small medial part.

The metapodia are characterized in both species by relatively narrow condyles, unlike in *C. bactrianus.* The proximal articular process of the metacarpale is long and narrow in Nadaouiyeh and *C. dromedarius,* while it is short and broad in Tighennif and *C. bactrianus.* Another difference is the large size of the latter fossil specimens.

In proximal phalanges the shape of the condyle is a distinctive traith of both samples. Condyles in both samples have a generally narrower and deeper shape than extant species, but while in Nadaouiyeh the length of condylar lips are intermediate, in Tighenif they are distinct by being almost symmetric, instead of having a clearly longer abaxial lip as in all other forms. The phalanges from Tighenif are larger than those in Nadaouiyeh and those of modern camels.

Conclusion

In general, the two fossil samples show several relevant differences, indicating that they represent separated *Camelus* species. Cranium, mandible, dentition and calcanei offer numerous diagnostic characters. Other postcranial elements, such as astragalus, metapodia and proximal phalanges differ to a smaller degree, but are consistently larger in the Algerian material. Tighennif represents the type locality of the species *Camelus thomasi;* we can therefore conclude that the material from Nadaouiyeh represents a different species.

No other Middle East remain can be assigned to *C. thomasi.* The first identification of *C. thomasi* outside of its type locality was by Gautier (Gautier,

1966), who only observed photographs of a very large camel and failed to consider morphological characters, not to mention consult the type material of this species. His determination has to be rejected. Unfortunately, following this superficial study, other workers have accepted the presence of *C. thomasi* in the Pleistocene of the Middle East (Payne and Garrard, 1983, Spassov and Stoytchev, 2004, Studer and Schneider, 2008, Grigson, 1983), in some cases going as far as to suggest that this species was the direct ancestor of domestic *C. dromedarius* (Peters, 1998, von den Driesch and Obermaier, 2007). Again, no morphologic data supports any of these identification (Geraads, 2014). The only argument given in one istance is the large size of some remains from the Negev Desert (Far'ah) (Grigson, 1983); but in fact, the measurements given largely exceed those from the Tighennif sample. At present, *C. thomasi* is unknown in El Kowm, in the whole Middle East and more in general outside of the Maghreb (Harris *et al.*, 2010).

It is premature to speculate about evolutionary relationships (Lesbre, 1903, Spassov and Stoytchev, 2004); the fossil samples of Nadaouiyeh and Tighennif and share similarities and differences among them but also with either extant species. Apparently, these and other fossils forms (like *C. knoblochi*) show more similarities overall with *C. bactrianus*. I argue that this impression has little meaning, because *C. dromedarius* probably is a more derived species with advanced characters such as smaller size, compression of the rostrum and greater reduction of the premolar row. Therefore, provided that both observation will be confirmed in the future, numerous traits shared by *C. bactrianus* and the other fossil species should be considered primitive (symplesiomorphies) and thus not indicative of a direct descent to the exclusion of *C. dromedarius*. A formal phylogenetic analysis will be necessary to settle this matter.

Acknowledgements

Reto Jagher provided access and informations on the Nadaouiyeh material; Denis Geraads provided the same for the Tighennif material and Loïc Costeur gave useful advice on the study of the fossils and access to comparative material of extant camels. I am thankful to Marin Mikelin for the help with illustrations.

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