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Embryonic Hump Development and Ancestry in Old World Camels

Since the 1960s it has been postulated that the Arabian and the Bactrian camel originated from a single wild ancestor, *Camelus ferus*. One key argument in this respect was provided by the anatomical study by the Italian researcher Lombardini, who in the annals of the University of Tuscany in 1879 described a second hump-like structure in fetal and juvenile dromedaries. Although frequently cited in literature, Lombardini's results have never been verified. This article is intended to contribute to the discussion of Old World camels' ancestry. It is based on a study in which 33 fetuses of Arabian camels, one of a Bactrian camel and two of *Camelus dromedarius x Camelus bactrianus* hybrids were analyzed. No hump-like structure as such was detected in any of the dromedary fetuses with a crown-rump length below 22 cm, whereas in older fetuses only a single hump structure was observed, extending at its base from the 10th thoracic (T10) to the 5th lumbar (L5) vertebra (Kinne et al. 2010). In the Bactrian camel fetus, a two-humped stage was clearly discernable (T2–T6; T11–L5), whereas the fetuses from dromedary X Bactrian camel hybrids exhibited the largest humps (T8–L6). Based on this study and the results of recently published archeozoological and genetic analyses, the issue of a single wild ancestor for the two domestic Old World camels can finally be put *ad acta*.

ONE ANCESTOR FOR TWO DOMESTIC FORMS?

Old World camels have two domestic forms, the two-humped Bactrian camel (*Camelus bactrianus* Linnaeus, 1758) and the one-humped dromedary or Arabian camel (*Camelus dromedarius* Linnaeus, 1758). However, only a single wild camel survives to-date, namely the two-humped wild camel *Camelus ferus* (Przewalski, 1883). Once widespread throughout Central Asia, wild camels are now confined to restricted areas in south-western Mongolia and north-western China (e.g., Clutton-Brock 1987:126). The possibility that these 20th-century populations are descended from domestic Bactrian camels that have returned to the wild has repeatedly been discussed in literature (e.g., Zeuner 1967:289, Clutton-Brock 1987:126, Herre/Röhrs 1990:53). However, this now seems rather unlikely considering the genetic distance between the wild camel population actually living in the Great Gobi Strictly Protected Area A and the extant Central Asian two-humped breeds (Silbermayr et al. 2010).

Since there were no historic records of a wild population of one-humped camels living in South-West Asia, zoologists postulated a common ancestry for the Arabian and the Bactrian camels (Herre/Röhrs 1973:35, Ahne et al. 2000). Based on this assumption, Köhler (1981:128) hypothesized that the two domestic forms originated from different subspecies of *Camelus ferus*. However, apart from the absence of a wild one-humped ancestor, some other lines of evidence lend support to the assumption of a single wild ancestor for the two domestic forms.

Firstly, cross-breeding dromedaries and Bactrian camels produced fertile hybrids (e.g., Kolpakow 1935), implying – in a biological sense – that one-humped and two-humped camels constitute a reproductive community and hence a single species. This offspring, called the *Tulu*, is characterized by a single large, slightly indented hump and exhibits hybrid vigor; it is a bigger and stronger animal than either of the parental stock and is said to withstand cold conditions better than the dromedary. It was noted, however, that continued breeding rapidly resulted in loss of fertility (Kolpakow 1935). Interestingly, already in Parthian times there is evidence that these hybrid camels were highly esteemed as pack animals (Bulliet 1975:143, 168), and their breeding seems to have been practiced on a large scale, supplying animals for the long-distance caravan trade, e.g., for the Silk Road. Tulus were still in demand in Iran and Asia Minor in modern times,[1] which is why Bactrian sires were introduced in western Asia as late as the 19th century (Leese 1927:133). Secondly, the osteological distinction between the Arabian and the Bactrian camel was considered problematic (e.g., Duerst 1908, Zeuner 1967:208), underscoring the close genetic relationship between the two forms. Thirdly, and the likely most persuasive argument in favor of the hypothesis of a single wild ancestor for the two domestic Old World camels, was the late 19th century anatomical study by Lombardini (1879), who described a reduced second hump-like structure in fetal and adult dromedaries. According to him, this structure would best be visible in animals with short hair and in poor condition. From his observations he concluded that one-humped animals also went through a two-humped embryonic stage, whereas later in life only the caudal hump would develop fully. He therefore considered the dromedary to be a modified breed of Bactrian camel.

Opponents of the common ancestry hypothesis, such as Lesbre (1903:135–137) and Cauvet (1925:25), based their argumentation on the differences in outer appearance, ecophysiological adaptations, zoogeographic range and gross anatomy of the two domestic forms. Comparative osteological studies by Wapnish (1984), Olson (1988) and especially Steiger (1991) lend support to their view, whereas Peters (1997, 1998) noted that *Camelus thomasi* (Pomel, 1893), an extinct camelid inhabiting northern Africa and the Levant during the Late Pleistocene, showed a close osteomorphological resemblance to modern dromedaries. Thus, although a wild relative of the domestic Arabian camel had been identified for the first time, evidence for the species' survival in post-Pleistocene times was missing, although this could be a matter of the poor archeozoological record.

To sum up, the strongest argument in support of a common ancestry of the two domestic forms at the end of the 20th century remained the study of the embryonic hump development by Lombardini, whose results had never been verified in the 130 years since their publication. In order to test his results and the conclusions based on them, a series of unborn and newborn camels was collected for anatomical study at the Central Veterinary Research Laboratory in Dubai.

MATERIAL AND METHODS

In total, 33 fetuses of Arabian camels, one of a Bactrian camel and two of *C. dromedarius* x *C. bactrianus* hybrids (*tulus*), were analyzed (see table 5). We also investigated old hump morphology and anatomy in a two-month calf. Since 1999 research has been performed on materials obtained as freshly as possible from the slaughterhouse or in the frame of necropsy work at the Central Veterinary Research Laboratory in Dubai. From these individuals, we documented either the crown-rump length (CRL) or the weight, enabling us to estimate individual ages, following Hussein et al. (1991). Also the length, height and the exact position of the hump to the spine were measured and documented in longitudinal sections, enabling us to compare the position of the cranial and caudal hump in the Bactrian and the single large hump in *Tulus* with the position and development of the hump in dromedaries.

In addition, histology of the rump was performed in some of the smaller fetuses using standardized procedures.[2]

[1] For a more detailed discussion of dromedary x Bactrian camel hybrids see the article by Bernard Faye and Gaukhar Konuspayeva in this volume.

[2] These embryos were fixed in Klotz' solution (900 ml water, 50 g sodium chloride, 90 g sodium hydrogen carbonate, 110 g sodium sulfate, 100 g chloral hydrate, 100 ml formalin), dehydrated in ethanol and embedded in paraplast®. Serial section of 4–5 µm were made with the Microm HM360 microtom and stained HE or GRA (a trichrome method according to Knospe/Mitterer 2010, with gallocyanin (G) for dark blue nuclei, chromotrop 2R

Collection Number	Crown-rump Length	Weight Sex	Age (days) notes	Hump Length	Hump Height	Hump Position
Camelus dromedarius						
Wani1s	3.5 cm	-	-	-	-	-
Wani1	4.2 cm	-	52	-	-	-
Wani2	6.0 cm	-	62	-	-	-
Wani3	6.3 cm	-	62	-	-	-
Wani2s	6.4 cm	-	-	-	-	-
Wani3s	6.7 cm	-	-	-	-	-
Fet7cm	7 cm	-	-	-	-	-
Fet7cmB	7 cm	-	-	-	-	-
Wani4s	7.5 cm	-	-	-	-	-
Wani5s	7.9 cm	-	-	-	-	-
Fet8cm	8 cm	-	-	-	-	-
Fet8cmB	8 cm	-	-	-	-	-
Fet9cm	9 cm	20 g/M	-	-	-	-
Fet9cmB	9 cm	-	-	-	-	-
Wani4	9.7cm	-	72	-	-	-
05-168B	11.5 cm	36 g	-	-	-	-
Fet12cm	12 cm	40 g/M	-	-	-	-
DUBCA	13 cm	-/M	-	-	-	-
05-168A	13 cm	44 g	-	-	-	-
Fet15cm	15 cm	90 g/F	-	-	-	-
Fet17cm	17 cm	120 g/M	-	-	-	-
Fet18cm	18 cm	120 g/F	-	-	-	-
Fet19cm	19 cm	130 g/M	-	-	-	-
05-847	20 cm	150 g	-	-	-	-
Fet22cm	22 cm	250 g/M	-	28 mm	5 mm	T11–L2
05-825	25 cm	300 g	-	35 mm	7 mm	T11–L2
05-s228	33 cm	-	-	50 mm	10 mm	T10–L5
07-2391f	58 cm	6,400 g	-	120 mm	30 mm	-
07-2360	70 cm	10,500 g/M	-	190 mm	60 mm	-
07-2391m	70 cm	9,300 g	-	180 mm	30 mm	-

(R) for red cytoplasm and aniline blue (A) for blue connective tissue). The sections were stained in gallocyanin solution (1.5 gallocyanin with 50g potassiumsulfate in 1000 ml distilled water) for 24–48 h, rinsed in distilled water, dehydrated in ethanol and stained for 30 minutes in chromotrop 2R (0,2 g chromotrop 2R in 200 ml ethanol (96%) with 2 drops acetic acid), rinsed in 1% acetic acid, differentiated for 20 seconds in 5% tungstic acid, rinsed in 1% acetic acid and stained for 2 minutes in diluted (1:4) aniline blue solution (0.5 g aniline blue and 8 ml acetic acid in 100 ml distilled water), rinsed in 1% acetic acid, dehydrated in ethanol, xylol and embedded. The slides were analyzed and scanned with the Olympus BX51 Dot slide system with the OlyVia-Program.

Collection Number	Crown-rump Length	Weight Sex	Age (days) notes	Hump Length	Hump Height	Hump Position
07-2222	70 cm	-	-	150 mm	50 mm	-
Main Lab	75 cm	-/F	-	120 mm	17 mm	-
05-1975	85 cm	22,000 g	300	150 mm	20 mm	T10–L5
05-594	120 cm	45,000 g	calf, 2 months	300 mm	35 mm	T10–L6
Camelus bactrianus x Camelus dromedaries						
07-2377	65 cm	9500 g	Tulu	200 mm	70 mm	T8–L6
07-2229	65 cm	6800 g	Tulu	200 mm	80 mm	T8–L6
Camelus bactrianus						
05-1876	70 cm	12,000 g	Caudal Hump Cranial Hump	50 mm 50 mm	15 mm 15 mm	T11–L5 T2–T6

Table 5: Details of the camels analyses in the frame of this study.

RESULTS

A major finding of our work is the fact that no hump-like structure could be detected in any of the dromedary fetuses with a crown-rump length below 22 cm (see picture 9 and 10). In older fetuses (see picture 11), the hump extended at its base from the 10th thoracic to the 5th lumbar vertebra, approximating the position of its homologue in the adult (Peters/von den Driesch 1997). The hump consisted of white fat tissue, which was directly connected to the subcutaneous adipose tissue, but clearly separated from the trunk muscles by the deep fascia of the trunk (see picture 12). At no time did we observe a rudimentary second cranial hump in the dromedary fetuses or calves. This is in clear contrast to the situation in the Bactrian camel, in which a cranial and a caudal hump are expressed from the very beginning in older fetuses (see picture 13). In the Bactrian specimen studied we noted that the cranial hump was situated from the 2nd to the 6th thoracic vertebra and the caudal hump from the 11th thoracic to the 5th lumbar vertebra. The position of the latter is similar to that in the dromedary. Although comparable to its homologue in the dromedary from a histological viewpoint, we noted that in the Tulus the hump was clearly more elongated; it also exhibited a slight indentation in the frontal part of the hump (see picture 14).

DISCUSSION

Our anatomical study does not corroborate the findings by Lombardini, since it clearly shows that in Arabian camels, prenatal development is characterized by the formation of a single hump. Lombardini's findings can possibly be explained as an artifact of fixation due to the poor state of preservation of the adult dromedary at his disposal. As such, Lombardini observed a thin layer of fat tissue in front of the caudal hump, but it is not argued why this tissue should indeed represent the rudimentary cranial hump. Moreover, based on our study material, one of the two fetal dromedaries he analyzed, a specimen measuring 160 mm, must definitely have been too young to show a hump, whereas in his anatomical description of the second specimen, measuring 260 mm, the presence of two humps is not mentioned explicitly. Finally, it is possible that some of the animals studied by Lombardini were hybrids. This is supported by our results (see picture 14) but can no longer be ascertained.

From our work we conclude that the domestic Arabian and Bactrian camel descend from different wild ancestors, as was already postulated in earlier publications (e.g. Peters/von den Driesch 1997 and the additional literature cited there). Recently, large numbers of osseous remains attributable to wild dromedaries have been excavated in archeological contexts in the eastern Arabian Peninsula dating from the 5th to the 1st millennium BCE (e.g. Uerpmann/Uerpmann 2002, von den Driesch/Obermaier 2007, M. Beech, pers.comm. 2010). This implies that the wild ancestor of the one-humped camel (a descendant of *Camelus thomasi*?) was still present in this part of South-West Asia during late Holocene times. A diachronic comparison of bone size in dromedaries indicates that domestication of the wild one-humped camel likely took place at the end of the 2nd millennium or the beginning of the 1st millennium BCE (Uerpmann/Uerpmann 2002). Recent work dealing with the genetics of modern wild and domestic two-humped and domestic one-humped camels has also confirmed that the wild camel should be excluded as the ancestor of the Arabian camel. Applying the molecular clock,[3] the split between the one-humped and the two-humped wild form would represent a much earlier event, estimated to have taken place some five (Stanley et al. 1994) to eight million years ago (Ji et al. 2009).[4] However, estimates based on molecular clocks must be treated with caution, especially when dealing with domestic animals (Ho/Larson 2006).

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3 The molecular clock hypothesis is based on the assumption that genetic differences between species (or taxa) can be used to estimate their time of divergence.

4 For a detailed discussion about the ancestry of Old World camels see the article of Pamela Burger in this volume.

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