

PART I

OLD WORLD CAMELS

(Tribe Camelini)

Genetic Traces of Domestication in Old World Camelids

When and where did modern camels evolve? These questions about the evolutionary history and domestication of dromedary (*Camelus dromedarius*) and Bactrian camels (*Camelus bactrianus*) have only recently reached the field of molecular genetics. Traditionally, fossil records are used for tracing ancient demography. For Old World camels the split between dromedaries and Bactrian camels was dated at 5 million years (myr) ago, significantly later than estimated by phylogenetic¹ studies (8 myr). Although fossils provide invaluable information they are limited and difficult to assess, particularly if there was continuity between ancient and modern camels. Based on archeological data the domestication of dromedaries took place in the south-eastern part of the Arabian Peninsula around 3,000 to 4,000 years ago. The originally assumed and eponymous center of origin for two-humped camels in Bactria (today's Afghanistan and Turkmenistan) has been replaced by possible domestication center(s) in western Asia between 5,000 and 6,000 years ago.

Genetic data collected from today's camel populations give us insight into ancient demographic events, since they have left imprints in the genetic profiles. Basically two main hypotheses are followed: The multiregional hypothesis suggests that for each camel species the modern domestic form evolved directly from several ancient wild forms in different locations in the Old World. Conversely, the single-origin model argues that only one specific population gave rise to the domestic form for each species, which subsequently expanded demographically. To test these hypotheses we use mitochondrial DNA (mtDNA) inherited solely from the mother and nuclear DNA transferred to the offspring by both parents.

By using modern DNA analysis it is possible to trace the ancestry and migration of different camel populations and thus draw conclusions about potential domestication scenarios. One hypothesis states that the high genetic diversity found in a specific modern camel population might reflect ancient diversity (before domestication) and thus could hint at a possible domestication center. This is based on the assumption that the gene pool is narrowed during domestication, since only a few animals are used for breeding. A possible domestication scenario could also be explained by the "hourglass" metaphor, which refers to the existence of a large genetic pool before domestication, which is reduced by a bottleneck during the domestication phase and is followed by a demographic expansion and breed formation after the initial domestication. An alternative hypothesis assumes that a wide genetic variation in modern camels might also reflect recently accumulated diversity due to demographic expansion after domestication. One possible way of differentiating between the two scenarios is the comparison between domesticated camels and non- and pre-domesticated animals, namely extant wild relatives and samples from extinct ancient specimens. This analysis can tell whether a modern extant population is the closest relative to the domesticated camels or if the direct ancestors are extinct today, as seen in horses (Cieslak et al. 2010).

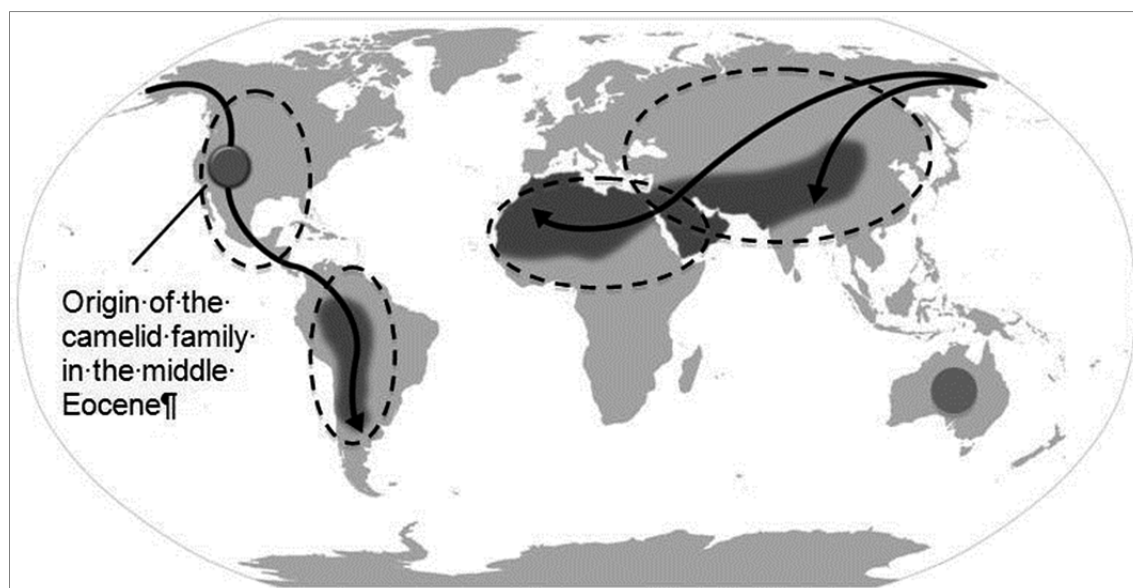
The big challenge in the study of Old World camels' domestication is that the wild dromedary is extinct and the wild two-humped camels are genetically very distant from their domestic counterparts (Silbermayr et al. 2010a, Ji et al. 2009). This is in contrast to other domestic animals, where the wild ancestors still exist (e.g. wild boar, wild goat, wild ass) and are closely

¹ In phylogenetic studies the evolutionary relationship between different (sub)species or populations is investigated using molecular data.

related (i.e. common shared mitochondrial haplotypes can be found). Moreover, in all genetic studies we observe a panmictic (globally mixed) camel population,² which is likely due to natural and human-induced migration (e.g. caravan transportation). This fact makes it very difficult to define possible domestication centers based on the genetic variation observed in modern camels alone. Intensive research on ancient DNA samples, however, has the potential to shed new light on the riddle of camel domestication.

THE HISTORIC BACKGROUND OF THE OLD WORLD CAMELS (*CAMELINI*)

The early ancestors of the Old World camelids (*Tylopoda*, *Camelidae*, *Camelini*, *Camelus*) originated from North America, where they emigrated via the Bering land bridge to the eastern hemisphere, the “Old World”. The earliest remains of camelids in Asia date to the Middle-Pliocene about 5 myr ago (Prothero/Schoch 2002, Kozhamkulova 1986). The widest distribution of camelid species occurred in the Plio-Pleistocene (2.5 to 1.5 myr ago) when they ranged from East Asia (Kozhamkulova 1986) to eastern Europe and North-East Africa (see graph 1; Howell et al. 1969, Gentry/Gentry 1969). Present-day members of the genus *Camelus*, namely the Bactrian camel (*Camelus bactrianus*), the wild camel (*Camelus ferus*)³ and the dromedary (*Camelus dromedarius*) likely descended from Plio-Pleistocene forms of *Paracamelus*, recorded from localities in northern China, western Mongolia, Tajikistan and Kazakhstan (Kozhamkulova 1986).

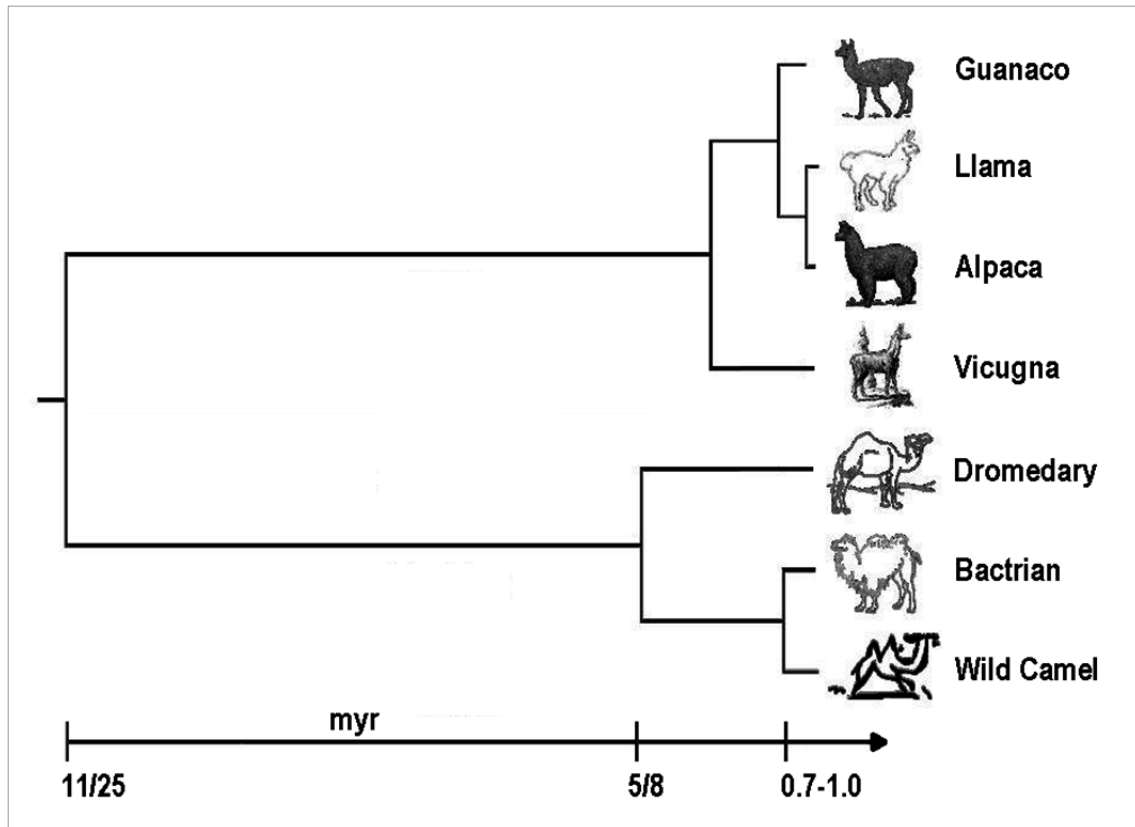


Graph 1: Early plio-pleistocene (dashed lines) and present-day (grey shaded) distribution of the camelid family. Black arrows indicate early migration routes via the Bering land bridge and the Isthmus of Panama. Dromedary camels arrived in Australia only in 1837, where they were shipped mainly from Pakistan. (http://upload.wikimedia.org/wikipedia/commons/1/16/Camelid_locations_and_migration.png; consulted 4 April, 2011; modified according to Prothero/Schoch 2002).

Molecular evolutionary studies estimate the split between Old and New World camels at 11 myr (Kadwell et al. 2001, Stanley et al. 1994) to 25 myr (Ji et al. 2009) and the separation within the *Camelini* at 5 to 8 myr ago.

² This is explained in more detail in the results and visualized in graph 5.

³ The naming of wild and domestic animal species follows the ruling by the International Commission on Zoological Nomenclature (Opinion 2027, March 2003), which fixes the first available specific name based on a wild population (Gentry et al. 2004).



Graph 2: The maximum likelihood tree of the evolutionary relationship among the *Camelidae* is based on the complete mitochondrial genomes⁴ of New World and Old World camels.

The evolutionary relationship between dromedaries and Bactrian camels has been widely discussed. The observations of one-humped dromedaries passing a two-humped stage in their embryonic development (Lombardini 1879) and the fact that crosses between dromedaries and Bactrian camels produce fertile offspring led to the widespread assumption that the one-humped and the two-humped forms descended from a single ancestor, *Camelus ferus* (Peters/von den Driesch 1997 and ref. therein). However, the osteological evidence (Gautier 1966) claiming that the extinct giant camel (*Camelus thomasi*) belonged to the lineage of two-humped Bactrian camels has been refuted: the morphological re-analysis of Paleolithic giant camel bones revealed features characteristic of the one-humped camel *Camelus thomasi* and the species is therefore considered a close relative if not the direct ancestor of the dromedary (Peters 1998, Peters/von den Driesch 1997). Moreover, wild dromedaries must have occurred in considerable numbers on the Arabian Peninsula in Holocene times, as illustrated by the recent discovery of 2nd millennium before common era (BCE) hunting sites along the eastern coast yielding large amounts of bones from this species (von den Driesch/Obermaier 2007, Uerpmann/Uerpmann 2002). Finally, the two-humped embryonic phase of the dromedary observed by Lombardini (1879) has been disproved: the Arabian camel's prenatal development is characterized by the formation of one single hump (Kinne et al. 2010)⁵. In sum, today's evidence clearly suggests a separate ancestry for the two domestic forms.

⁴ The information in graph 2 is based on Genbank accession numbers: gi:219524215 (guanaco) gi:223976134 (llama) gi:38602627 (alpaca) gi:270267350 (vicugna) gi:157394461 (dromedary) gi:157011972 (Bactrian camel) gi:157011955 (wild camel).

⁵ For a more detailed discussion about the embryonic status of the dromedary see the article by Clemens Knospe et al. in this volume.

ARCHEOLOGICAL EVIDENCE OF DOMESTICATION OF OLD WORLD CAMELS

The originally assumed *center of domestication of the Bactrian camel* in eastern Iran or southern Turkmenistan in the 3rd millennium BCE (Uerpmann 1987) is contradicted by the fact that there is no proof that the geographic distribution of its wild two-humped ancestor included this region. Presumably, the area(s) of domestication was (were) located further to the east, such as southern Kazakhstan, north-western Mongolia and northern China, where people were already acquainted with the wild species over a longer period of time (Peters/von den Driesch 1997). However, Carl von Linné (1758) designated the domestic two-humped camel '*Camelus bactrianus*' suggesting Bactria, today's northern Afghanistan and southern Turkmenistan, to be the region of its origin.

The *domestication of the dromedary* likely took place towards the end of the 2nd millennium BCE in the south-eastern part of the Arabian Peninsula (Uerpmann/Uerpmann 2002, Peters 1998, Uerpmann 1987). Domestic camels played an important role in the ancient civilizations of the Old World and even today a number of rural and nomadic societies in north-eastern Africa and in central and eastern Asia depend on these multi-purpose animals in terms of transportation and milk, wool and meat production. Today's range countries of the Bactrian camel include the semi-deserts of central Asia, whereas the dromedary is distributed over northern and eastern Africa, South-West Asia and Australia (Clutton-Brock 1999).

LIVESTOCK DOMESTICATION INFERRED FROM GENETIC AND ARCHEOZOOLOGICAL STUDIES

Domestication is not an instantaneous event in which a wild animal is suddenly transformed into a domesticated one. Rather it is thought to be a cumulative process marked by changes on both sides of a mutualistic relationship. Thus human development has been shaped by domestication over hundreds of years. To trace this complex and multi-faceted process it is necessary for geneticists and archeologists to combine collaborative efforts, as improved phylogenetic analysis complements archeozoological documentation (Vigne et al. 2005).

As summarized in table 1, most livestock domestication events occurred at the transition from the Pleistocene to the Holocene and during the Early Holocene in five principal areas: in the South American Andean region (lamas, alpacas), the north-east African region (donkey, taurine cattle), the Near East (taurine cattle, sheep, goat, pig, dromedary), South-East Asia (zebu cattle, pig, chicken) and Central Asia (yak, reindeer, horse, Bactrian camel) (rev. in Bruford et al. 2003).

Origin and Domestication of livestock species

Domestic species	Wild ancestor	MtDNA lineages	Domestication events	Years ago	Location
Cattle	Aurochs 3 subspecies (extinct)				
<i>Bos taurus taurus</i>	<i>Bos primigenius primigenios</i>	4	1	~9,500	Near East (Euphrates Basin)
	<i>B. p. opistonomus</i>	2	1	~9,500	Northeast Africa
<i>Bos taurus indicus</i>	<i>B. p. namadicus</i>	2	1	~8,000	North Indian subcontinent
Yak	Wild Yak				
<i>Poephagus grunniens</i>	<i>Poephagus mutus</i>	3 (4)	1	~4,500	Qinghai-Tibetan Plateau
Goat	Bezoar				Near East (Euphrates Basin), Zagros
<i>Capra hircus</i>	<i>Capra aegragus</i> (3 subspecies)	5 (6)	2	~10,500	North Indian subcontinent

Domestic species	Wild ancestor	MtDNA lineages	Domestication events	Years ago	Location
Sheep	Mouflon				
<i>Ovis aries</i>	<i>Ovis orientalis</i>	4	2	~10,500	Near East (Euphrates Basin)
Pig	Wild boar				
<i>Sus domesticus</i>	<i>Sus scrofa</i> (16 subspecies)	6	5 – 6	~10,000	Europe, Near East, China, Indian subcontinent
Chicken	Red junglefowl				
<i>Gallus domesticus</i>	<i>Gallus gallus</i> (5 subspecies)	6	3	~7,500	China, Southeast Asia
Horse	Wild horse, unknown (extinct)				
<i>Equus caballus</i>	<i>Equus ferus</i>	17	multiple	~6,500	Eurasian steppe, Iberian Peninsula
Donkey	African wild ass				
<i>Equus asinus</i>	<i>E. africanus africanus</i> (nearly extinct)	1	1	~6,000	Northeast Africa or Southwest Asia
	<i>E. a. somaliensis</i> (nearly extinct)	1	1		
Llama	Guanaco (2 subspecies)				
<i>Lama glama</i>	<i>Lama guanicoe guanicoe</i>	ND	1?	~6,500	Andes
	<i>L. g. casciliensis</i>				
Alpaca	Vicugna (2 subspecies)				
<i>Vicugna pacos</i>	<i>Vicugna vicugna vicugna</i>	ND	1?	~6,500	Andes
	<i>V. v. mensalis</i>				
Bactrian camel	Wild two-humped camel, unknown (extinct)				
<i>Camelus bactrianus</i>	<i>Camelus ferus</i>	ND	1?	~5,000	Central Asia (Mongolia, China, Kazakhstan?)
Dromedary	Wild one-humped camel (extinct)				
<i>Camelus dromedarius</i>	<i>Camelus sp.</i>	ND	1?	~3,000	Arabian Peninsula

ND (not defined), BP (before present); adapted and updated from Bruford et al. (2003), Hanotte and Jianlin (2005)

Table 1: Overview of the domestic species, their wild ancestors, how often (domestication events), when (time) and where (location) domestication might have taken place.

In the following I will give some examples, mainly concentrating on domestic animals that have been used for transport and human survival in extreme environments.

The history of *horse* (*Equus caballus*) domestication is still a matter of debate, with two species having been regarded as putative progenitors, namely the Tarpan (*E. ferus*) and the Przewalski horse (*E. przewalskii*). Only the latter has survived until today and has been successfully reintroduced in the Mongolian steppe (Kaczensky et al. 2004). Although very closely related to the domestic horse, the Przewalski horse can now be excluded as the direct ancestor of the domestic form (Lau et al. 2009, Olsen et al. 2006, Wallner et al. 2003). Archeozoological and genetic evidence points to a panmictic Late Pleistocene/Early Holocene horse population ranging from Alaska and the Pyrenees to the Eurasian steppe (Cieslak et al. 2010), with possible domestication centers in the Eurasian steppe (Olsen et al. 2006) and the Iberian Peninsula (Uerpmann 1990).

In contrast, the domestication of the *donkey* (*Equus asinus*) seems to have followed a simpler process. Mitochondrial studies point to the Somalian wild ass (*E. a. somalensis*; close to extinction) and the Nubian wild ass (*E. a. africanus*; close to extinction or extinct; IUCN 2006) as the subspecies of origins and ruled out the Asiatic wild ass as a possible progenitor for the domestic species (Beja-Pereira et al. 2004). Although *E. asinus* fossil records from north-eastern Africa and south-western Asia suggest that domestication took place approximately 6,000 years ago (Clutton-Brock 1999) recent morphological findings from Egypt emphasize a long-term evolutionary change in the process of domestication (Rossel et al. 2008).

For the domestic yak (*Poephagus grunniens*), endemic to Central Asia, three maternal lineages have been described, suggesting a single domestication event in the Tibetan Plateau (Lai et al. 2007) Its ancestor, the wild yak (*P. mutus*), still ranges on the Qinghai – Tibetan Plateau. Similar to the yak the domestication of the reindeer (*Rangifer tarandus*) has allowed human pastoral communities to occupy habitats which otherwise would have been largely unsuitable for human existence. Genetically very little is known about reindeer domestication, but the oldest definitive archeological evidence comes from the Altai (Siberia) and dates about 2,500 years ago (Skjenneberg 1984).

The wild origin of the South American *camelidae* was unraveled with the guanaco (*Lama guanicoe*) and the vicuna (*Vicugna vicugna*) as the ancestral species of the domestic llama (*L. glama*) and alpaca (*V. pacos*) respectively (Kadwell et al. 2001). Archeozoological work points out the Andes around Lake Titicaca as the region of llama domestication some 6,000–7,000 years ago, while the alpaca appears to have been independently domesticated in the Peruvian Andes at the same time. Today large-scale introgression between the two domestic species has been revealed (Wheeler et al. 2006).

The earliest evidence for the presence of the Bactrian camel (*Camelus bactrianus*) has been found in eastern Iran approximately 5,000 years ago, but most likely the domesticated form was introduced in this region (Peters/von den Driesch, 1997). The Arabian Peninsula is proposed as the region of origin of the dromedary camel (*Camelus dromedarius*) with 3,000–4,000 years ago as the period of domestication (Uerpmann/Uerpmann 2002, Peters 1998).

The wild camel (*Camelus ferus*), which has been considered as the ancestor of both domesticated camel forms, can now be excluded as direct predecessor of the domestic Bactrian camel (see graph 3 in the result section).⁶

HABITAT AND CONSERVATION OF THE WILD TWO-HUMPED CAMEL (*CAMELUS FERUS*)

Once extensively distributed throughout Central Asia the range of the wild camel has become severely reduced to only four locations worldwide: three in China (Gashun Gobi and Arjin Mountains in the Lop Nur desert and Taklamakan desert) and one in Mongolia (Great Gobi desert).⁷ The Great Gobi Strictly Protected Area “A” (GGSPAA) is located in the south-western part of Mongolia bordering with the People’s Republic of China. The extremely harsh environment has given rise to a unique ecosystem with particularly well-adapted species, some of which are found nowhere else in the world, namely the Gobi bear (*Ursus arctos gobiensis*), the snow leopard (*Uncia uncia*) the argali (*Ovis ammon*) and the Asiatic wild ass (*Equus hemionus*). The wild camel population is listed as endangered by the IUCN as the estimates for the remaining animals are 400 to 600 in China (Luzhang et al. 2005, Hare 1997) and 500 to 600 in the GGSPAA (Walzer et al. 2006, Reading et al. 2001). The general belief is that the population is

⁶ For a detailed discussion on ancient Bactrian camel DNA analysis see the article by Alexandra Trinks in this volume.

⁷ For a detailed discussion on the habitat and distribution of wild camels in Mongolia and China see the articles by Adiya Yadamsuren et al. and Yuan Lei et al. in this volume.

stagnating or declining due to low recruitment of calves caused by wolf predation, habitat deterioration, illegal hunting and illegal mining (Hare 1997).⁸

The genetic status of *Camelus ferus* was heavily debated, since morphological similarities with its domestic counterpart (*Camelus bactrianus*) led to the assumption that wild camels were merely descendents of domestic animals that had returned to the wild (Peters/von den Driesch 1997 and ref. therein). However, genetic (Silbermayr et al. 2010a, Ji et al. 2009, Jianlin et al. 1999) and morphologic differences between wild and domestic camels in body size, hair color and skull structure strongly suggested that the two-humped camel discovered by Przewalski should be considered as an original wild form (see picture 2).

A major threat to the wild camel is the *hybridization* with the domestic camel (Enkhbileg et al. 2006, Walzer et al. 2006, Luzhang et al. 2005). The wild camel population of about 1000 individuals in China and Mongolia is directly confronted at the human-livestock-wildlife interface with their domesticated relatives. The extent of hybridization within the Mongolian wild camel population is currently being investigated using nuclear microsatellite markers developed for this purpose (Silbermayr et al. 2010b).⁹

METHODS: MOLECULAR MARKERS IN DOMESTICATION STUDIES

Molecular markers are specific gene sequences that are used to identify different regions in the DNA. Choosing the right molecular marker to understand the origins of domestication is critical. The analysis of information based on a multitude of highly polymorphic molecular markers is essential to draw reliable conclusions about closely related individuals or populations (rev. in Schlötterer 2004). The most commonly used polymorphic markers in domestication studies so far are single nucleotide polymorphisms (SNPs) in the *mitochondrial DNA* (mtDNA) reflecting the maternal inheritance, in *autosomes* (parental), and in *Y-chromosomes* corresponding to the paternal lineages (rev. in Zeder et al. 2006). MtDNA sequence analysis of *ancient DNA* (aDNA) has proved to be crucial in resolving domestication processes (e.g. Cieslak et al. 2010, Fernandez et al. 2006). Another class of molecular markers used in domestication studies are microsatellites, short repetitive motives (e.g. ACACAC) in the *nuclear DNA* following the co-dominant inheritance. Autosomal microsatellite loci are important tools to measure population diversity (Silbermayr et al. 2010b), genetic variation and genetic admixture among livestock breeds or between wild and domestic animal species (rev. in Bruford et al. 2003). New SNP markers for domestication studies are being developed as complete genome data from next-generation sequencing is becoming available (e.g. Al-Swailem et al. 2010).

GENOTYPING AND POPULATION GENETIC ANALYSIS

As nuclear sequence and/or SNP data have not been available for Old World camels until recently (Al-Swailem et al. 2010), in this project we used 804 bp (Bactrian camel) and 867 bp (dromedary) of mtDNA covering parts of cytochrome b and the control region and 20 autosomal microsatellites (KS1-11, VOLP08, VOLP10, VOLP32, VOLP59, YWLL29, YWLL36, YWLL38, LCA65, CVRL07, Silbermayr et al. 2010b, Mariasegaram et al. 2002). The genotyping and data analysis was performed as described before (Silbermayr et al. 2010a, Silbermayr 2009). In brief, median-joining haplotype networks were constructed with Network 4.5 software (Bandelt et al. 1999) and individuals were assigned to distinct clusters using a Bayesian approach in the Bayesian Analysis of Population Structure software BAPS 5.2 (Corander/Tang 2007, Corander/Marttinen 2006). Phylip 3.69 software was used to generate a neighbor-joining

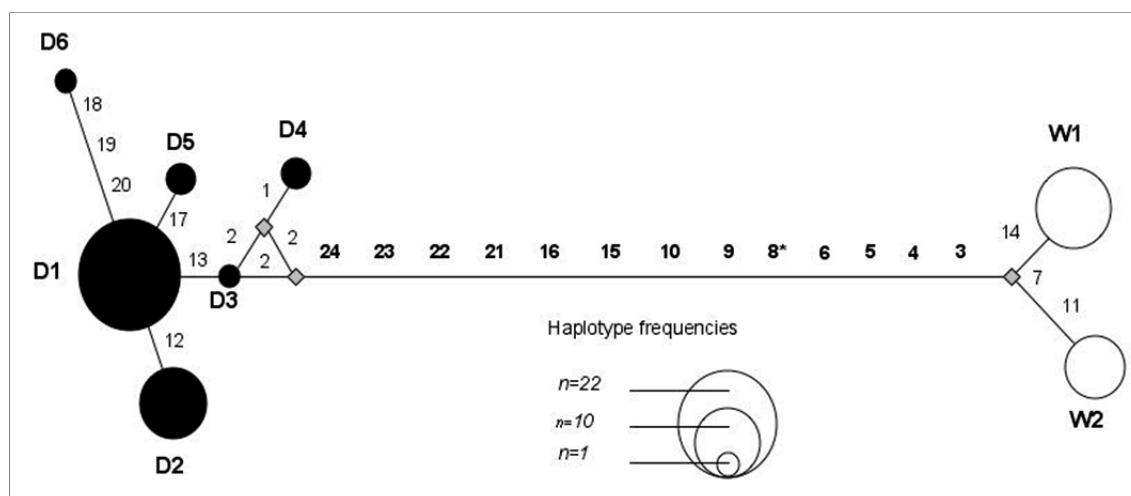
⁸ For a more detailed discussion on the census size of wild camels in Mongolia and China see the articles by Adiya Yadamsuren et al. and Yuan Lei et al.

⁹ For a more detailed discussion about the hybridization between wild and domestic Bactrian camels see the article by Katja Silbermayr in this volume.

tree based on the proportion of shared alleles (Felsenstein 1989) and genetic diversity parameters were calculated with Arlequin 3.11 (Excoffier et al. 2005).

GENETIC RELATIONSHIP OF WILD AND DOMESTIC BACTRIAN CAMELS

In 2003 the International Commission of Nomenclature (ICZN) fixed the first available specific name based on a wild population “*Camelus ferus*” for the wild two-humped camel (Gentry et al. 2004). Genetic analysis of the mitochondrial DNA clearly separated the wild camel from the domestic Bactrian camel, with high levels of sequence divergence ranging from 1.9% (Silbermayr et al. 2010a) to 2.4% (Ji et al. 2009). This is comparable to the divergence seen in other extant wild and domestic camelids (e.g., 1.7%; *L. guanicoe*, gi:38602627; *L. glama*, gi:219524215). The separation between the wild and domestic Bactrian camel was estimated at 0.7 myr in the Pleistocene (Ji et al. 2009), long before domestication took place (4,000–5,000 yr). Consequently, we can exclude that the extant wild camel population in Mongolia is the direct ancestor of current domestic Bactrian camels.



Graph 3: The mitochondrial haplotype¹⁰ network shows the genetic differentiation between domestic Bactrian (left) and wild camels (right). The nucleotides differentiating the two species are highlighted in bold. The circle sizes of the haplotype nodes are proportional to the number of individuals belonging to the specific haplotypes. The nucleotide difference that is discriminated in the PCR-RFLP assay as described in Katja Silbermayr’s article is marked with an asterisk.

In addition to the mitochondrial marker, which gives information about the maternal lineage, we also investigated 20 autosomal microsatellite loci (Silbermayr 2009, Silbermayr et al. 2010b). We found slightly higher amounts of average expected heterozygosity in the domestic ($H_E = 0.467$) than in the wild camel ($H_E = 0.343$) population. A significant degree of differentiation ($F_{ST} = 0.336$; $p = 0.0001$) between the wild and domestic camel populations was detected over all loci. In a neighbor-joining tree analysis based on the proportion of shared alleles between individuals (D_{PS}) all wild camels clustered in a distinct clade (71% bootstrap support; 100 iterations) and separate from their domestic relatives (Silbermayr 2009; see graph 14 in the article of Katja Silbermayr in this volume). This furthermore confirms the genetic status of the wild camel as an evolutionary significant unit, *Camelus ferus*.

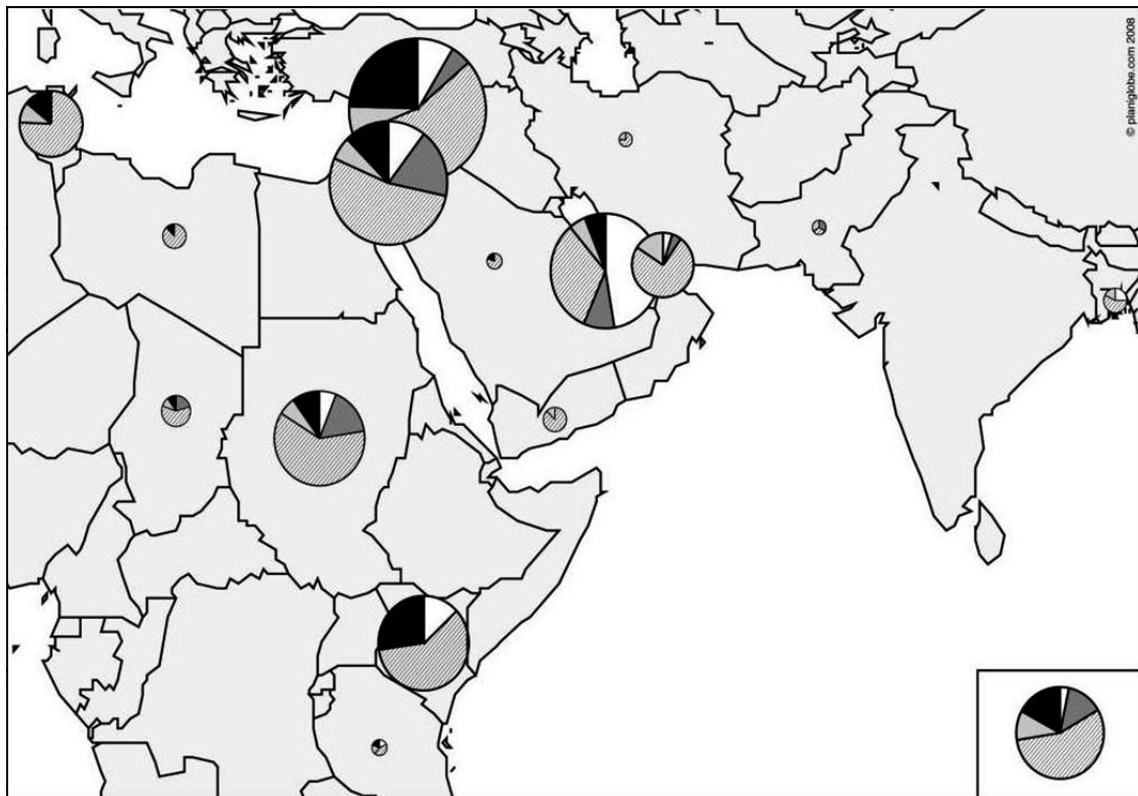
Although we can clearly differentiate between the wild and domestic Bactrian camel, the place of the domestication of the Bactrian camel remains elusive. The phylogeographic analysis of domestic Bactrian camels from Mongolia, Russia, Kazakhstan and China revealed that mitochondrial haplotypes are shared between animals originating from different countries (see graph

¹⁰ The mitochondrial DNA is solely maternally inherited, thus we also refer to a mitochondrial genotype as a haplotype.

4; Burger et al. unpublished data). This is also reflected in the fact that the paleogenetic analysis of 12 Bactrian camel bones from Late Bronze and Early Iron Age sites in Uzbekistan and Siberia resulted in the same mitochondrial haplotypes as described in modern domestic Bactrian camels. The high level of homogeneity between Bronze/Iron Age samples from Uzbekistan and Siberia and modern domesticated camels from China and Mongolia leads to the assumption of a single domestication centre rather than multiple one (Trinks et al. 2010). The study also showed that the current Mongolian wild camels are neither the descendants of Late Bronze and Early Iron Age nor the ancestors of modern domestic Bactrian camels (Trinks et al. 2010). This means that though they share a common ancestor, the Late Bronze and early Iron Age camels are genetically more closely related to modern domestic camels than they are to modern wild camels.

MITOCHONDRIAL EVIDENCE FOR PANMIXIA IN THE GLOBAL DROMEDARY POPULATION

The dromedary is one of the most important domesticated species in North Africa and South-West Asia and has been utilized for centuries particularly for transportation and for milk, wool and meat production. The intensive trading and movement of camels around North Africa and the Arabian Peninsula is reflected in the mitochondrial (maternal) genetic profile of the global camel population: in our study we found a *panmictic* (globally unstructured) dromedary population ranging from North and East Africa to Pakistan and Australia (Charruau et al. 2010). The 310 camels originating from 16 different countries were assigned to five distinct clusters with a high posterior probability (BAPS; PP=0.999). However, these clusters were evenly distributed over the global range of the dromedaries as presented in Figure 4.



Graph 4: Worldwide distribution of the mitochondrial haplogroups in the global dromedary population. The circle size is proportional to the number of individuals, the pies are colored/structured according to their assignment to distinct haplogroups. We see that the same mitochondrial haplogroups are represented throughout the dromedaries' worldwide distribution (panmixia).

It is interesting to note that the current Australian camels display the same haplotype diversity as seen in the global dromedary population (see graph 4). Australia is not a native habitat of

the dromedary, but today it has the biggest feral camel population, with more than one million individuals. In the 70 years after 1837, when the first animals were imported from Pakistan, Afghanistan (Stevens 1989) and the Canary Islands (Phillipson 1899, cited in Schulz 2010), approximately 20,000 camels were introduced to the continent, and later (after the development of vehicles) randomly released to the wild (McKnight 1969). The high mitochondrial diversity found in the Australian camel population reflects the diversity in camels worldwide and thus leads to the assumption that this level of genetic variation already existed two centuries ago and is probably even more ancient. However, this needs to be investigated using early-domesticated and pre-domesticated dromedary samples.

CONCLUSIONS

One of the missing links in the history of our livestock species is the understanding of Old World camelids' domestication. Contrary to previous assumptions of a single origin of the Old World camelids, there is genetic and archeozoological evidence for the separate origins of dromedaries and Bactrian camels. Due to the absence of phylogeographic structure in the global modern camel populations the localization of domestication in Old World camels remains a challenge. However, combined modern and ancient DNA analyses have led us to the conclusion that there was a single domestication event in Bactrian camels and that the wild camels in Mongolia and China are not the direct ancestors of their domestic counterparts. In dromedaries, modern mitochondrial DNA analysis points to maybe two domestication scenarios. However, due to the lack of ancient DNA analysis of pre- and early-domesticated camel remains, we cannot draw firm conclusions about the possible domestication centers. The effective conservation of the remaining wild camel populations as well as their domestic relatives will help to conserve the future biodiversity of the most important livestock species in (semi-) arid regions worldwide. Our special attention should be given to the world's last wild camels in China and Mongolia.

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