

Past Human Migrations in East Asia

Matching archaeology, linguistics and
genetics

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**Alicia Sanchez-Mazas,
Roger Blench,
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20 Understanding yak pastoralism in Central Asian Highlands

Mitochondrial DNA evidence for origin, domestication and dispersal of domestic yak

Xue-bin Qi, Han Jianlin, Roger Blench, J. Edward O. Rege and Olivier Hanotte

Introduction

Today a large human population inhabits the Central Asian Highlands, a vast area characterized by high elevation and cold climate. They are principally pastoralists or agro-pastoralists whose religion and culture are heavily influenced by Tibetan Buddhism (Blench 2001; Joshi 1982; Kreutzmann 2002; Liu *et al.* 1989; Sherchand and Karki 1996; Tshering *et al.* 1996; Wiener *et al.* 2003; Zhang 1989). The earliest prehistoric human occupation on the Qinghai-Tibetan Plateau may date back to *cal.* 25,000 BP to the Upper Pleistocene (Huang 1994; Madsen *et al.* 2006). Aldenderfer and Zhang (2004) review the various published dates, the methods used to establish them and the controversies surrounding them. Reliably dated sites are still very few and most dates are founded on typologies which are themselves controversial.

Recent surveys around the Lake Qinghai basin suggest that the upper elevations were only exploited seasonally by foragers and that it was only with the pastoral Neolithic that all-year-round occupation was possible (Brantingham *et al.* 2003; Madsen *et al.* 2006). However, the first major human occupation phase is thought to have begun *cal.* 20,000 BP (Zhang and Li 2002; Zhang *et al.* 2003), possibly following the peaking of the Last Glacial Maximum at about this period. A second phase began in mid-Holocene times, *cal.* 7,500 BP (Huang 1994), eventually leading to permanent human occupation of the Plateau about 4000–5000 BP (Tong 1990; Aldenderfer and Zhang 2004). Su *et al.* (2000) argue that Y-chromosome analysis of current Sino-Tibetan speaking populations suggests that the Neolithic inhabitants of the upper-middle Yellow River basin about 10,000 BP were likely the ancestors of modern Sino-Tibetan populations in the Himalayas and the Qinghai-Tibetan Plateau. Such a view is now highly controversial, with recent molecular surveys among highland populations suggesting the reverse, namely that the genetic diversity of these isolated populations is very high and that the region might be a source region for the Sino-Tibetans (Kraayenbrink *et al.* 2006).

The yak, *Poephagus grunniens*, a member of Bovini tribe, is endemic to Central Asia and well adapted to the cold and high altitude environment. Yak pastoralism is widespread in the Central Asian Highlands. With a current total population size of 14 million, the domestic yak constitutes one of the most important domestic animal genetic resources in the region and plays an indispensable role in the life of pastoralists and agro-pastoralists (Wiener *et al.* 2003). The geographical distribution of the domestic yak extends from the southern slopes of the Himalayas in the south to the Altai and Hangai Mountains of Mongolia and Russia in the north, and from the Pamir Plateau and Tien-Shan (Tianshan) Mountains in the west to the Qilian Mountains in the east (Figure 20.1). The wild yak, which once roamed throughout the Qinghai-Tibetan Plateau, still survives in remote areas of the Plateau and the Kunlun Mountains, although the total population is less than 20,000 animals and many of those may have suffered partial introgression from domestic yak (Guiquan 1996; Schaller and Wulin 1996). Both domestic and extant wild yak are thought to have originated from a so-called 'ancient or primitive yak'. Fossil evidence unearthed in the Pleistocene layer suggests that such anterior types were extensively distributed over northeastern Eurasia in the late Tertiary period (2.5 million years ago) (Cai 1989; Olsen 1990; Wiener *et al.* 2003).

At present, the mean heights of the Himalayas and Qinghai-Tibetan Plateau are 6100 and 4000 meters, respectively, although before the mid-Pleistocene period they were under 4500 and 2000 meters (Tang and Hare 1995). The persistent uplifting of the Himalayas and the Qinghai-Tibetan Plateau during the Quaternary has dramatically changed the palaeoenvironment in these areas. Forest on the Qinghai-Tibetan Plateau was replaced by alpine meadow, and animals (including the wild yak) became adapted to the higher altitude of the Qinghai-Tibetan Plateau following their migration from Northeastern Eurasia (Wiener *et al.* 2003).

The date and centre of yak domestication as well as the dispersal routes of yak pastoralism remain largely speculative. Textual references point to the beginnings of domestication in the Northern Qinghai-Tibetan Plateau by the ancient 'Qiang' people (a collective name for ancient nomadic people in Western China), with the establishment of yak pastoralism in the late Neolithic, *cal.* 5000 BP (Liu and Peng 1989; Wiener *et al.* 2003; Zhang 1989), i.e. several thousand years *later* than the domestication of cattle. The claim by Zeuner (1963) that yak domestication could have occurred at the same time as the domestication of cattle, in the Neolithic, around 10,000–8000 BP is not supported by any archaeological or genetic data.

Where this domestication took place remains unclear. The hypothesis of the Northern Qinghai-Tibetan Plateau area was largely based on archaeological findings as well as the fact that the majority of wild yak are found today within this region (Liu and Peng 1989; Wiener *et al.* 2003; Zhang 1989). This area is presently largely inhospitable to human habitation, although geomorphological and vegetation change makes it possible that it was formerly more attractive. An alternative centre of domestication in the Eastern Qinghai-Tibetan Plateau has also been proposed (Qi 2004).

The dispersal routes from the putative centre of domestication to the occupation of current yak territories also remain speculative. One view is that the current northern yak territories, in what is now Mongolia and Russia, were established following a westward migratory route that first occupied an area known as the 'Pamir Knot' covering the Pamir, the Hindu-Kush Mountains, the Trans-Karakoram Mountains, the Kunlun Mountains, and the Tien-Shan Mountains. During the 13th century it expanded further northwards to Southern Siberia (Felius 1995; Zhong 1996). However, it is also possible that yak pastoralism spread directly northwards across the present Gobi Desert before the region became hyper-arid, driving away its resident populations (Figure 20.1).

The rapid development of molecular biology in the past decade has made many molecular markers available for unraveling the major evolutionary issues on the origin, domestication, and dispersal of domesticated animals and plants. Analyses of mitochondrial DNA (mtDNA), with its characteristics such as maternal mode

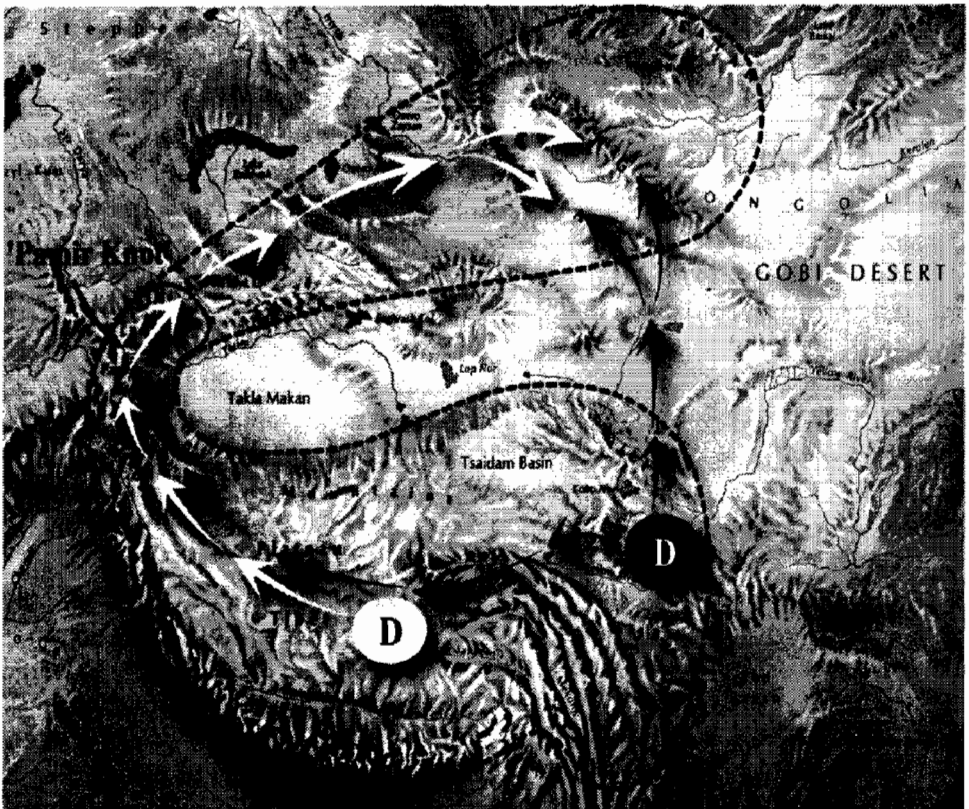


Figure 20.1 The current distribution of yak pastoralism in Central Asian Highlands (highlighted area). The letter D represents putative centres of domestication of yak and the arrows represents dispersal routes by which the domestic yak occupied the current 'Pamir Knot' and Mongolian and Russian territories. The white dispersal represents the 'traditional' view for the domestication and dispersal of domestic yak (Cai 1989; Wiener *et al.* 2003; Zhang 1989; Zhong 1996) while the 'dark' route is the one presented in this chapter using molecular information.

of inheritance, high substitution rate, and lack of recombination, have become a powerful tool in evolutionary genetics. By elucidating the contemporary geographical distribution of major mtDNA lineages across the geographical distribution of a domestic species, we can expect to gain deeper insight into a wide range of issues such as the origin, domestication, and demographic history of the species (see Bruford *et al.* 2003 for review). For example, analyses of mtDNA control region (D-loop) variations in European, African, and Indian cattle have provided convincing evidence for independent domestications of taurines (*Bos taurus*) and zebu (*B. indicus*) in two separate locations (Loftus *et al.* 1994). In addition, analyses of mtDNA D-loop variations also support the origin of European cattle in the Near-East (Troy *et al.* 2001) and a possible African source of taurines supporting independent origin of pastoralism in the two regions (Bradley *et al.* 1996).

Autosomal microsatellite DNA fragments are another class of molecular marker extensively used in evolutionary and population genetic studies of livestock species. They are characterized by a core sequence of tandemly repeated units with a length of 2–6 base pairs (bp). Microsatellites exhibit a high level of allelic variation, and are found in large numbers, relatively evenly spaced throughout the genomes of all eukaryotic organisms. They have been increasingly used in the past decade to address population genetic issues such as genetic relationship and differentiation of livestock breeds/populations (see Baumung *et al.* 2004 for review), but also more recently to unravel the origin and/or dispersal of pastoralism (Cymbron *et al.* 2005; Hanotte *et al.* 2002). For example, Hanotte *et al.* (2002) analyzed the geographic patterns of allelic variations at 15 microsatellite loci in 50 indigenous cattle populations throughout the entire African continent. They were able to show that the earliest cattle in Africa probably originated from a single geographic area within the African continent, but that genetic influences from the taurines in the Near East and Europe as well as the zebu from Indian subcontinent can also be identified in modern African cattle. The early dispersal of cattle to the southern part of the African continent most likely followed an eastern route rather than a western one, in agreement with the earliest archaeological dates for pastoralism in Eastern, Central, and Southern Africa.

Until now, however, molecular genetic studies have been rare in yak, with only a few populations characterized using autosomal microsatellite DNA markers (Dorji *et al.* 2002; Minqiang *et al.* 2003; Xuebin *et al.* 2002, 2005), a couple of molecular genetic studies assessing the level of cattle introgression into yak populations (Jianlin *et al.* 2002; Xuebin *et al.* in preparation) and a single study on mitochondrial DNA variation in four yak populations (Bailey *et al.* 2002).

We recently examined in detail genetic variation at the complete mtDNA D-loop (897 bp) and cytochrome *b* gene (1140 bp) sequences of 29 representative domestic yak populations spanning the entire geographic region of the species (Figure 20.2). Our purpose was to address the origin, domestication, and dispersal of the domestic yak, as well as the genetic relationships among these populations (Qi 2004; Xuebin *et al.* in preparation). By examining the contemporary geographical pattern of mtDNA diversity across the entire region, we expected to discover whether modern-day domestic yak originated from a single or multiple

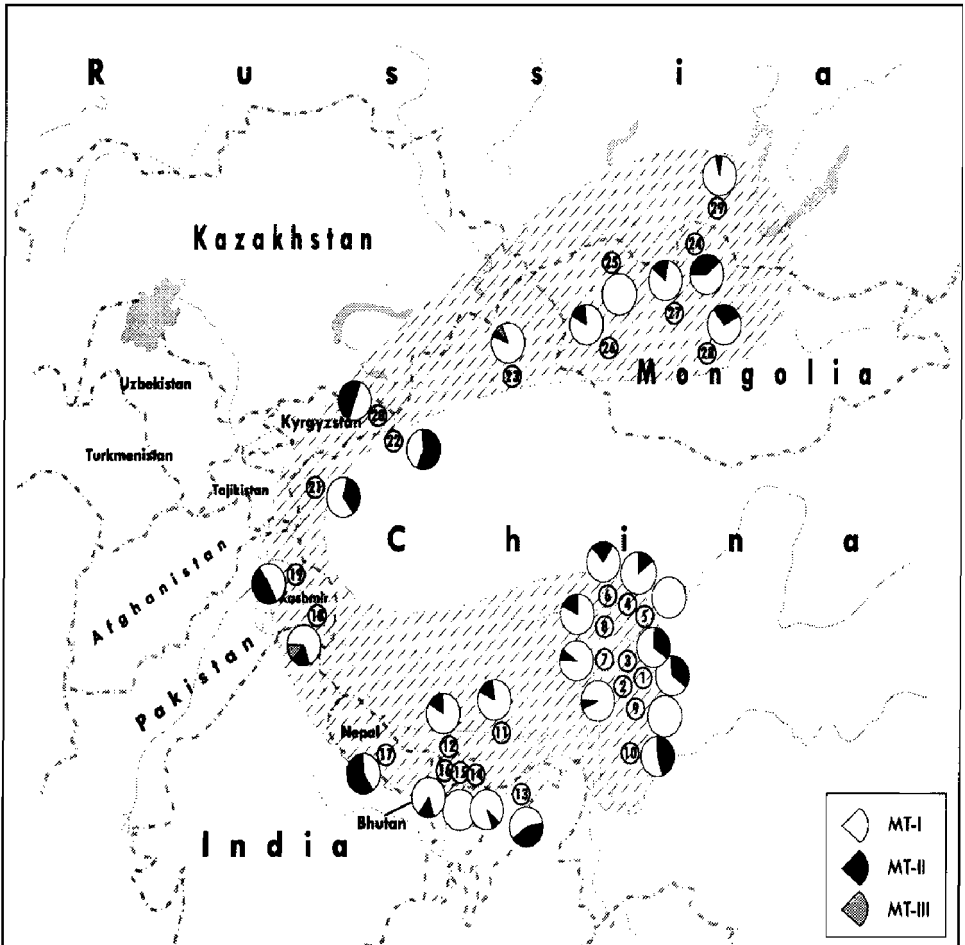


Figure 20.2 The sampling sites for this study. The pie graph represents the distribution of three yak mtDNA lineages in domestic yak populations. Population names: 1 Luqu; 2 Maqu; 3 Xiahe; 4 Tianzhu Black; 5 Tianzhu White; 6 Sunan; 7 Jianzha; 8 Datong; 9 Maiwa; 10 Jiulong; 11 Jiali; 12 Pali; 13 Northeast Indian; 14 East Bhutanese; 15 Central Bhutanese; 16 West Bhutanese; 17 Nepalese; 18 Northwest Indian; 19 Pakistani; 20 Kyrgyzstan; 21 Kashi; 22 Aksu; 23 Bazhou; 24 Hovsgol; 25 Ubs; 26 Gobi Altai; 27 North Hangai; 28 South Gobi; 29 Buryatia.

domestication event(s), where and when such event(s) took place and how yak pastoralism spread through the entire Central Asian Highland region.

Domestication of yak

The complete D-loop of mtDNA was sequenced for a total of 428 yak samples from 29 populations collected in China, Bhutan, Nepal, India, Pakistan, Kyrgyzstan, Mongolia, and Russia (Figure 20.2 for sampling locations). One hundred and thirteen haplotypes with polymorphisms at 87 sites including six insertion/deletions (indels) were identified. As illustrated in Figure 20.3,

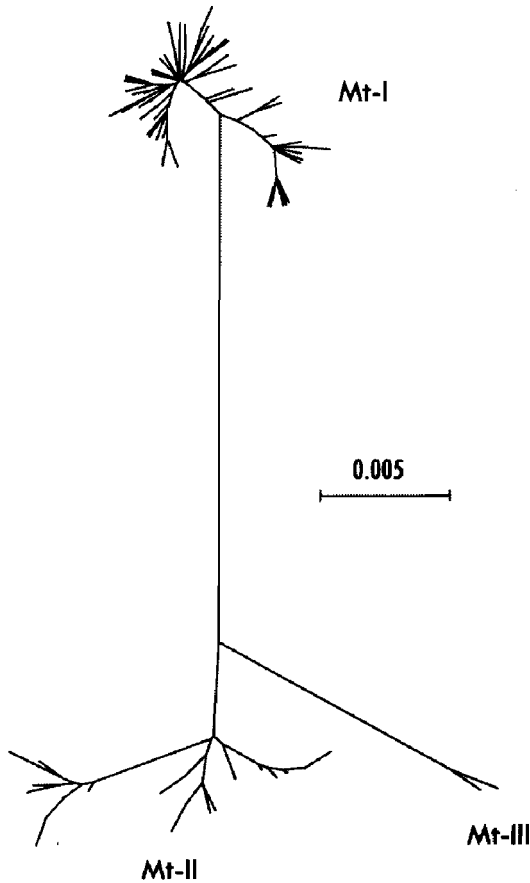


Figure 20.3 Unrooted neighbour-joining phylogeny of domestic yak constructed with 113 mtDNA complete D-loop haplotypes identified in 428 yak samples collected from 29 representative domestic yak populations across entire yak distribution.

phylogenetic analysis clusters these domestic yak D-loop haplotypes into three divergent mtDNA lineages: Mt-I, Mt-II, and Mt-III, with Mt-II and Mt-III being more closely related to each other than to Mt-I.

The mean sequence diversity within yak mtDNA lineages is 0.0051 (Mt-I), 0.0064 (Mt-II), and 0.0035 (Mt-III) (Table 20.1). The values of Mt-I and Mt-II are similar to those observed within taurines (0.0062) and zebu (0.0057). The mean sequence divergences between yak mtDNA lineages range between 0.0218 and 0.0471 nucleotide substitutions per site (Table 20.1). When a substitution rate of 3.1×10^{-4} nucleotide substitutions per site per year or 1 bp substitution per 3243 years, as estimated for the cattle/bison complete D-loop sequences, was applied (Qi 2004; Xuebin *et al.* in preparation), a divergence time of 63,000–136,100 BP was obtained between the yak mtDNA lineages. However, because D-loop sequence might evolve at different rates across lineages (Ingman *et al.* 2000), we also sequenced the complete cytochrome *b* gene for 19 complete

Table 20.1 Mean mtDNA D-loop sequence divergences within and between yak mtDNA lineages and their approximate divergence time

	<i>Mt-I</i>	<i>Mt-II</i>	<i>Mt-III</i>	<i>Bison bison</i>
Mt-I	0.0051	119,600	136,100	308,000
Mt-II	0.0414	0.0064	63,000	264,000
Mt-III	0.0471	0.0218	0.0035	276,000
Bison bison	0.1066	0.0913	0.0955	0.0064

Shown are the sequence divergences within yak mtDNA lineages (on the diagonal), the sequence divergences between yak mtDNA lineages (below the diagonal), and the divergence time between yak mtDNA lineages (above the diagonal).

D-loop haplotypes representing the two major yak mtDNA lineages (Mt-I and Mt-II). The mean cytochrome *b* gene sequence divergence between Mt-I and Mt-II is 0.007 substitutions per site. These sequence divergences correspond to a divergence time of 95,000 bp when a substitution rate of 8.4×10^{-5} nucleotide substitutions per site per year or 1 bp substitution per 11,902 years (estimated for cattle/bison complete cytochrome *b* gene sequences) was applied (Qi 2004; Xuebin *et al.* in preparation).

Overall, a typical signature of population expansion is observed at Mt-I lineage (Tajima's $D = -1.631$, $P = 0.018$; Fu's $F_s = -25.308$, $P = 0.000$), while the Mt-II lineage seems to have not been experiencing a similar overall population expansion since domestication (Tajima's $D = -0.117$, $P = 0.524$; Fu's $F_s = -6.829$, $P = 0.029$) (Xuebin *et al.* in preparation). Multiple star-like phylogenies within lineage Mt-I are observed (Xuebin *et al.* in preparation), suggesting that multiple founder haplotypes have contributed to this lineage. The age of the founder haplotypes in Mt-I lineage was estimated to be 5158 ± 1355 bp, assuming the mutation rate of bovine D-loop as of 1 bp in 3243 years (Qi 2004; Xuebin *et al.* in preparation). This suggests that the domestic yak population started to expand around 5000 bp. This molecular dating of the domestic yak population expansion is in accordance with archaeological evidence that yak domestication may have taken place around 5000 bp (Liu and Peng 1989; Wiener *et al.* 2003; Zhang 1989).

The Qinghai-Tibetan Plateau was not entirely covered by an ice sheet during the latest glaciation in the second half of the Pleistocene (Zhang and Li 2002). Wild yak populations could have survived in distinct refugia, leading to differing mitochondrial DNA lineages. Following the end of the glaciation period, these wild yak populations could have intermixed before domestication, leading to several mitochondrial DNA lineages in today's domestic yak populations following a single domestication event. Alternatively, multiple domestication events may have happened in separated geographic areas from genetically distinct wild yak populations, each at the origin of at least one of the three mitochondrial DNA lineages observed in this study.

To assess the presence of single or multiple domestication event(s) in yak, we examined the geographic distribution and diversity of the three mitochondrial DNA lineages. We grouped the 29 yak populations in four geographic areas: the

Chinese Qinghai-Tibetan Plateau (12 populations, $n = 164$), Mongolia and Russia (6 populations, $n = 91$), the Eastern Himalaya (6 populations, $n = 77$) and the Western Himalaya (5 populations, $n = 96$). See Figure 20.4 for the grouping of the yak populations in four regions. Geographically, the Chinese Pali yak borders with Bhutanese yak but is isolated from other Chinese yak populations, therefore we grouped Chinese Pali yak into the Eastern Himalayan group. Lineage Mt-I is present in 326 samples and in all 29 yak populations, with the highest haplotype diversity found in the Chinese Qinghai-Tibetan Plateau area and the lowest in the Western Himalayan area, while the Eastern Himalayan area and Mongolian and Russian yak populations exhibited an intermediate haplotype diversity (Figure 20.4 and Table 20.2). Mt-II lineage is less common and present in only 25 yak populations ($n = 97$). Mt-III lineage is very rare and only found in four Northwest Indian yak samples and one Chinese Bazhou yak sample (Figure 20.2), and it is therefore excluded from the following analysis and discussion.

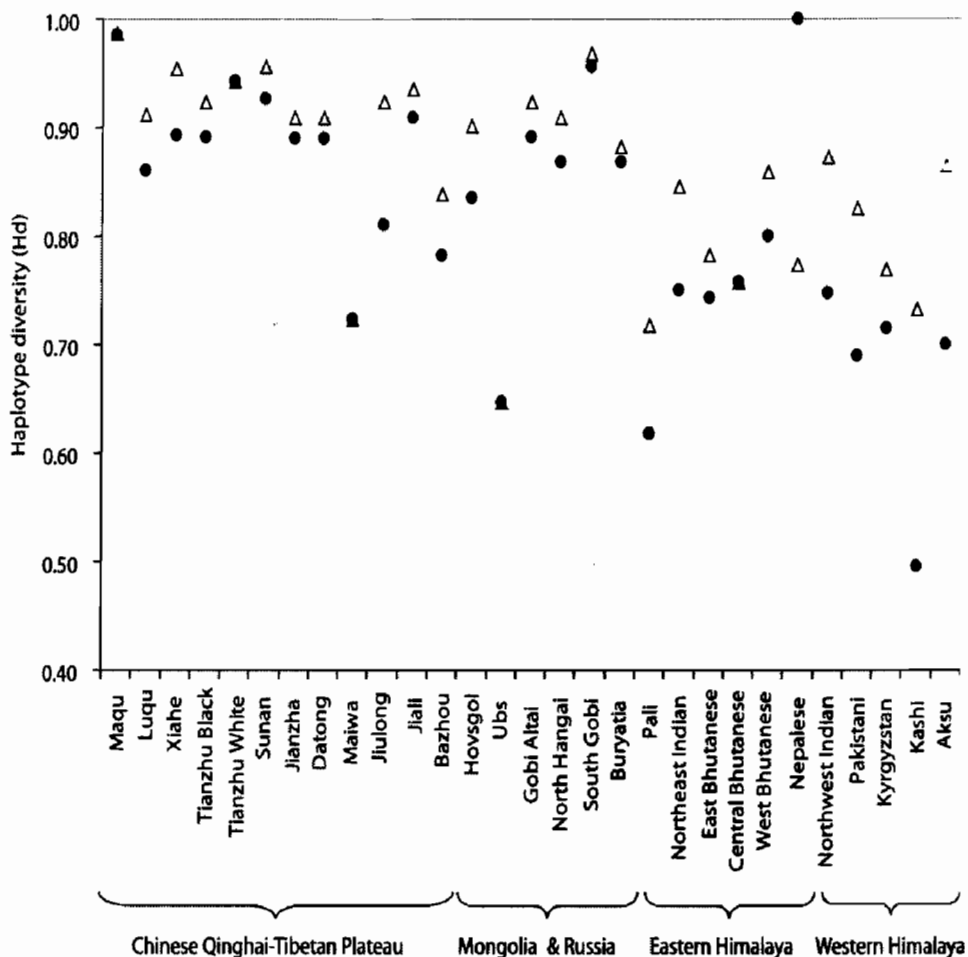


Figure 20.4 The mtDNA D-loop haplotype diversity (Hd) observed in 29 domestic yak populations. The signs 'Δ' and '●' represent the Hd calculated based on all mtDNA lineages and Mt-I lineage alone, respectively.

Table 20.2 The mtDNA diversity in four geographic areas of domestic yak

Population	N	H	Hd	SD (Hd)	π	SD (π)	Tajima's D	Fu's Fs
<i>Mt-I lineage</i>								
Qinghai-Tibetan Plateau	136	45	0.906	0.019	0.0036	0.0002	-1.554*	-25.618**
Eastern Himalaya	59	24	0.848	0.043	0.0029	0.0003	-1.4727	-15.5888**
Western Himalaya	56	10	0.690	0.062	0.0019	0.0003	-1.044	-5.016*
Mongolia & Russia	75	16	0.876	0.018	0.0046	0.0004	-0.1202	-2.143
Overall	326	71	0.882	0.015	0.0035	0.0002	-1.631*	-25.308**
<i>Mt-II lineage</i>								
Qinghai-Tibetan Plateau	27	13	0.897	0.038	0.0048	0.0003	-0.113	-4.581*
Eastern Himalaya	18	6	0.719	0.093	0.0028	0.0007	-0.815	0.136
Western Himalaya	36	7	0.679	0.062	0.0042	0.0005	0.915	0.956
Mongolia & Russia	16	5	0.800	0.057	0.0039	0.0007	0.561	0.923
Overall	97	22	0.880	0.018	0.0050	0.0002	-0.117	-6.829*

N = number of samples; H = number of haplotypes; Hd = haplotype diversity; π = nucleotide diversity; SD = standard deviation. Tajima's D (Tajima 1989) and Fu's Fs (Fu 1997) statistics are used to test population expansion; * $P < 0.05$; ** $P < 0.01$.

The total number of haplotypes is not statistically different among yak populations within or between geographic areas ($P = 0.79$). However, we observe a higher frequency of Mt-II lineage in the Western Himalayan area (37.5 per cent) compared to the Chinese Qinghai-Tibetan Plateau area (16.5 per cent), the Eastern Himalayan area (23.4 per cent), and the Mongolian and Russian yak populations (17.6 per cent), while Mt-I lineage is most commonly observed in all areas. This difference of frequency between the two lineages is a first indication of the possible presence of two distinct geographic centres of origins for the mitochondrial DNA lineages observed today in domestic yak. To further assess this possibility, we analysed the diversity of the observed haplotypes in different geographic areas. Table 20.2 summarizes the mtDNA D-loop haplotype diversity and Tajima's D (Tajima 1989) and Fu's Fs (Fu 1997) statistics for population expansion among four geographic areas. The Western Himalayan area showed the lowest Mt-II haplotype diversity among four geographic areas with the highest Mt-II haplotype diversity being observed in the Chinese Qinghai-Tibetan Plateau area. Among four geographic areas, only the Chinese Qinghai-Tibetan Plateau area showed a significant population expansion. The higher frequency of Mt-II lineage with the least haplotype diversity and without a population expansion observed in the Western Himalayan area may suggest the occurrence of recent bottleneck(s) or founder event(s) in those yak populations. Such demographic phenomena could account for the lack of a clear geographic pattern of genetic diversity and may have played an important role in reshaping the genetic landscape of domestic yak.

Two possible geographic areas of domestication have been proposed on the Qinghai-Tibetan Plateau: the Northern Qinghai-Tibetan Plateau (Liu and Peng 1989; Wiener *et al.* 2003; Zhang 1989) and the Eastern Qinghai-Tibetan Plateau (Qi 2004). Few domestic yak are currently found in the Northern Qinghai-Tibetan Plateau, a today largely inhospitable area to human settlements. Figure 20.4 shows that the highest mtDNA haplotype diversity is present in Eastern Qinghai-Tibetan Plateau populations (e.g. Maqu, Luqu, Xiahe) with lower diversity found in the Jiali and Pali, the two yak populations closest to the Northern Qinghai-Tibetan Plateau putative centre of domestication. Our molecular findings therefore do not support the Northern Qinghai-Tibetan Plateau as a centre of domestication of yak, but rather point to the Eastern Qinghai-Tibetan Plateau, a purely pastoral area. However, it should be pointed out that only two yak populations close to the Northern Qinghai-Tibetan Plateau putative centre of domestication were examined.

The results obtained here support the idea that the divergent maternal lineages Mt-I and Mt-II found in modern yak populations follow from a single domestication event, around 5000 BP, possibly in the Chinese Eastern Qinghai-Tibetan Plateau, and at least three divergent mtDNA lineages which survived at different refugia may have been recruited and reproduced successfully. However, the location of the centre of domestication would be more secure if data for more populations along the Northern Qinghai-Tibetan Plateau were available. Similarly, the date of domestication could be more accurate if there were a better calibration of bovine mtDNA mutation rates using complete mtDNA sequence and archaeozoological material.

Movements and migration of domestic yak

It is assumed that neutral genetic diversity in livestock populations would decline during the course of dispersal from the centre of their origin, with the least loss of genetic diversity in populations closest to the centre of domestication. Autosomal microsatellite and mitochondrial DNA markers provide a powerful tool to address these questions (e.g. Troy *et al.* 2001; Hanotte *et al.* 2002). The traditional view is that yak dispersed from their centre of domestication in the Qinghai-Tibetan Plateau, reaching Mongolian and Russian territories by migrating through the Pamir Knot (Figure 20.1). A migration northwards through today's Gobi Desert from the centre of domestication in Qinghai-Tibetan Plateau is also theoretically possible. We therefore tested for the route(s) by which domesticated yak might have dispersed out from the putative center of origin on the Qinghai-Tibetan Plateau. If this was via the Pamir Knot, today's Mongolian and Russian yak populations would have exhibited the lowest haplotype diversity, and the Pakistan, Kyrgyzstan, Kashi and Aksu populations (Western Himalaya) an intermediate level. Alternatively, a direct northern migration may be characterized by a lower diversity in the Western Himalaya region compared to Mongolia and Russia.

We fail to see a decline of mtDNA haplotype diversity in domestic yak populations versus geographic distance from either the Northern or the Eastern

Qinghai-Tibetan Plateau along a single migratory route (Figure 20.5, A; and Figure 20.1, white route).

Instead, as illustrated in Figure 20.5, a significant decline of mtDNA haplotype diversity was visible along two separate routes: a westward migratory route via the 'Pamir Knot' (represented by Northeastern Indian, Pakistani, Kyrgyzstan, Kashi, and Aksu populations), passing through the Himalayan and Kunlun Mountains; and a northward migratory route for Mongolian and Russian yak populations passing through South Gobi and Gobi Altai Mountains in Mongolia (Figure 20.1, dark route). These findings provide strong genetic evidence that the dispersal of domesticated yak followed two separate migratory routes from the Eastern Qinghai-Tibetan Plateau (Figure 20.1, dark route). That is, the domestic yak dispersed to the 'Pamir Knot' by following a westward route passing through the Himalayan and Kunlun Mountains and to Mongolia and Russia by following a northward route passing through Mongolian South Gobi and Gobi Altai Mountains.

Pastoralism and the dispersal of Tibetan-Burman populations

Although the Himalayas were probably exploited by low density foragers since the Early Pleistocene, the introduction of yak pastoralism must have been crucial to developing year-round sustainable occupation in the higher-altitude zones. The Himalayas today are also the centre of linguistic and genetic diversity for the Sino-Tibetan language phylum (van Driem 2001) and it is likely that this diversity reflects both ancient low-density forager populations and the impact of incoming yak pastoralists. Van Driem (1998) has argued that the culture responsible for the Majiayao Neolithic (dated to 3900–1800 BC) in Gansu moved westward through Sichuan into Tibet and the Himalayas around 5000 BP and that this can be identified with the Western Tibetan-Burmans (Bodish, Lepcha, etc.). If such people were yak pastoralists, this would correlate well with the loss of genetic diversity westwards of Qinghai. The median levels of genetic diversity amongst Mongolian (Bynie 2004) and Russian (Dmitriev and Ernst 1989) populations suggest that transfer of yak pastoralism northwards must have been at an early period rather than in medieval times. Since there are no Sino-Tibetan populations in this region, there would probably have been an early transfer to Altaic speakers. The climate of the Mongolian Plateau has deteriorated severely in the last 5000 years, and it may well be that the adoption of the yak helped *in situ* populations to adapt to climate change in the mountains north and west of Mongolia and the adjacent Altai.

Conclusion

At least three divergent maternal yak lineages survived at different refugia and may have been recruited or were reproductively successful and contributed to the formation of the earliest domesticated yak population with the divergent maternal lineages found in present day domestic yak populations likely the result of a

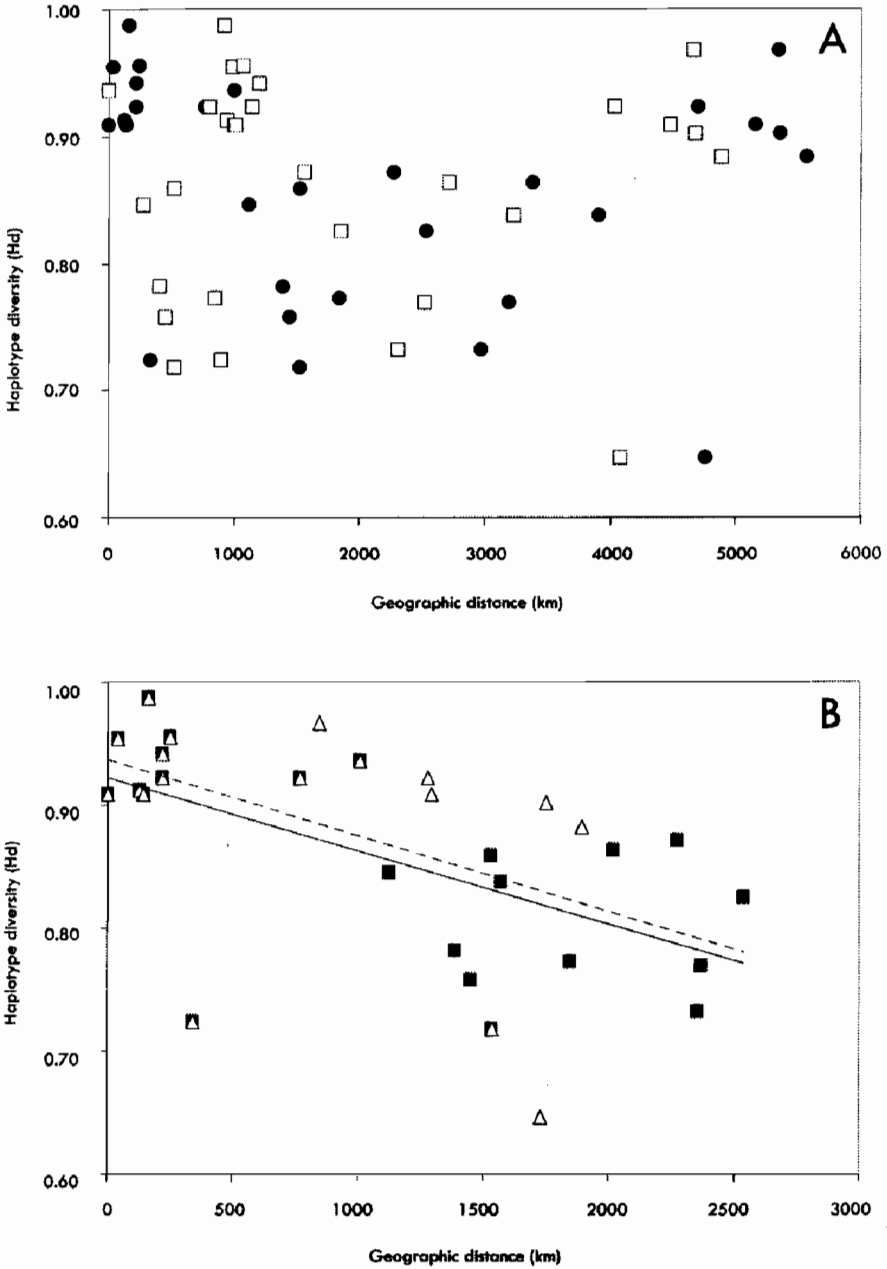


Figure 20.5 Regression of mtDNA D-loop haplotype diversities versus geographic distances in domestic yak populations. (A) The mtDNA haplotype diversities versus geographic distances along a single dispersal route (white route in Figure 20.1): '□', from the Northern Qinghai-Tibetan Plateau (represented by Jiali) $r = 0.027$, $p = 0.888$; and '●', from the Eastern Qinghai-Tibetan Plateau (represented by Maqu) $r = 0.031$, $p = 0.361$; (B) The mtDNA haplotype diversities versus geographic distances along two separate dispersal routes (dark route in Fig. 20.1) from the Eastern Qinghai-Tibetan Plateau (represented by Maqu): '■' and solid line, westward, $r = -0.63$, $p < 0.01$; and 'Δ' and dashed line, northward, $r = -0.44$, $p = 0.06$.

single domestication event. Yak-based pastoralism is also probably responsible for the all-year round occupation of high alpine pastures in the Himalaya and may be connected with the establishment of particular Tibetan-Burman populations in this region.

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