

Donkey Domestication

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Abstract Donkeys are one of the least studied large domestic animals, even though they are economically important in many regions of the world. They are predominantly used as transport animals. Consequently, they are not kept in large numbers and this limits the number of archaeological specimens available for study. The donkey's closest relative is the African wild ass, and genetic studies and zooarchaeological analyses of early donkeys indicate domestication of two genetically separate groups of wild asses in Africa. Maternal relationships revealed by mitochondrial DNA show that one group of donkeys was derived from the Nubian wild ass and that one was derived from an unknown ancestor distinct from the Somali wild ass.

Résumé Les ânes sont l'un des animaux domestiques grands moins étudiés bien qu'ils soient très importants économiquement dans plusieurs régions du monde. Les ânes sont usés principalement comme des animaux du transport. Par conséquent ils ne sont pas maintenus en grand nombre et donc il y a une limitation des nombres des

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specimens qu'on peut étudier de manière archéologique. Le parent le plus proche est l'âne sauvage d'Afrique. Des études génétiques et zooarchéologiques indiquent la domestication des deux groupes génétiquement distincts des ânes sauvages d'Afrique. Les relations maternelles indiqués par l'ADN mitochondrial démontrent qu'un groupe dérivent des ânes de Nubie et que l'autre groupe dérivent des ânes inconnus qui sont différents de l'âne sauvage de Somalie.

Keywords Donkey domestication · Ancient DNA · Somali wild ass · Nubian wild ass

Introduction

Animal domestication resulted in widespread economic and social change during the Holocene. Animals provided people with means for transport of goods and households, reliable access to meat and renewable resources such as milk and blood, and labor for heavy tasks including plowing, turning grindstones, and pumping water from wells. Donkeys were the hardiest ancient transport animals of Africa and the Near East. They are particularly suited for transport in mountainous and arid regions and are an important resource in many regions of the world today. The Asian onager (*Equus hemionus*) was once considered a possible ancestor of the domestic donkey (Epstein and Mason 1971), but it is now accepted that the African wild ass (*Equus africanus*) is the ancestor of the donkey (Beja-Pereira *et al.* 2004) and that wild onagers were later bred with domestic donkeys in some regions of Western Asia (Champlot *et al.* 2010). Genetic studies suggest that donkeys were most likely domesticated in northeastern Africa (Beja-Pereira *et al.* 2004).

Archaeological, historic, and ethnographic sources demonstrate that at least three distinct groups of wild asses existed in Africa 2,000 years ago, only two of which survived into modern times (Groves 1986; Marshall 2000) (Fig. 1). The Somali wild ass is distinguished by its large size and striped legs. It is critically endangered (Moehlman *et al.* 2011) but can still be found in Somalia, Ethiopia, and Eritrea. The Nubian wild ass has a prominent shoulder cross and was found in northern Sudan and Eritrea in the nineteenth century. Few animals have been seen in recent years (but



Fig. 1 Representations of wild asses. **a** Atlas wild ass (drawn from El Richa image in Muzzolini (2000)). **b** Nubian wild ass (photo with permission from Powell-Cotton Museum). **c** Somali wild ass (St. Louis Zoo, photo by F. Marshall)

see Kimura *et al.* 2011) and these populations have been feared extinct (Moehlman *et al.* 2002). The Atlas wild ass, known from rock engravings and mosaics to have both a shoulder cross and striped legs, became extinct in Roman times (Lhote 1984; Muzzolini 2000). Based on palaeontological and archaeological finds, it is clear that the ancient distribution of the African wild ass spanned the northeastern part of Africa from at least ~20,000 years ago (Groves 1986; Marshall 2007; Kimura *et al.* 2011). This distribution may also have extended into Yemen and the Levant (Uerpmann 1991). Due to the lack of evidence of African wild ass in the Upper Paleolithic of the Levant and the possibility of conflation of early domestic donkey and wild ass skeletons, there is now some doubt as to whether *E. africanus* ranged into Western Asia (Marshall *et al.* 2010; Marshall and Weissbrod 2011) (Fig. 2).

Advantages of Domestic Donkeys

Cattle were the first domesticated large mammal in Africa (Lhote 1959; Wendorf *et al.* 1984; Marshall and Hildebrand 2002), and they spread throughout the Sahara with pastoralists 8,000–7,000 years ago. It is thought that cattle were domesticated for meat, but the additional use of cattle for transport and milking is evidenced by rock paintings found in the interior Sahara (Lhote 1959; Muzzolini 2000). However, as desert conditions began to develop and the climate became drier, pastoralists needed to move more frequently to sustain themselves. Cattle are not an ideal form of transport under arid conditions, as they require substantial watering at least every other day (Dahl and Hjort 1976). Wild asses, on the other hand, are adapted to hot and harsh environments and require less because they do not ruminant. Asses are also able to digest coarse grasses, have labile metabolic rates, and numerous water-sparing mechanisms (Maloiy 1970; Maloiy and Boarer 1971; Marshall 2007). African wild ass, therefore, possessed distinct advantages over cattle as domesticates for transport use during times of increasingly unpredictable rainfall and desertification. The



Fig. 2 Map showing the historic distribution of African wild asses, their hypothesized ancient range (in pale shadowing) and sites mentioned in the text. A Atlas wild ass, B Nubian wild ass, C Somali wild ass

distribution of the remains of ancient donkeys in pastoral regions of Africa at locations distant from the Nile suggests that at least some of these animals were domesticated by African herders (Marshall 2007).

Archaeological, Ethnographic, and Linguistic Evidence for Donkey Domestication

Donkeys are normally kept in low numbers and are rarely eaten, so few archaeological remains exist with which to study the process of their domestication. As a result, changing age profiles are not useful for indicators of early donkey management or domestication processes. Size decrease has been shown to be a late indicator of domestication, but has been used to argue for the presence of domestic donkeys at the Egyptian predynastic sites of El Omari, dated to ca. 4,800–4,500 BC, and Maadi, dated to ca. 4,000–3,500 BC (Bökönyi 1985; Boesneck *et al.* 1989, Boesneck and von den Driesch 1990; Marshall 2007). Genetic data do not clarify further identification of early domestic donkeys because domestication processes act on a subset of animals selected from the wild; as a result, the same mitochondrial DNA (mtDNA) haplogroups may exist both among domestic herds and in the wild. The presence of two maternal haplogroups in modern donkeys does suggest, however, that people domesticated donkeys twice or, alternatively, that donkey herders later recruited female donkeys to their herds from different wild populations. Based on the predynastic dates for the presence of small donkeys on the Nile, domestication of the earliest donkeys occurred by ~7,000–6,000 years ago (Beja-Pereira *et al.* 2004; Marshall 2007; Kimura *et al.* 2011). Domestic donkeys were present in the Levant by ~3,000 BC, but it is less likely that the domestication occurred in that region, as there are no clearly identified African wild asses in the Levant. However, African wild asses or early domestic donkeys have been identified from the site of Ash Shumah in Yemen, dating to as early as ~6,500 BC (Cattani and Bökönyi 2002; Marshall 2007). Cattani and Bökönyi (2002) argued on the basis of morphological variability that these animals were in the process of domestication. However, the early stages of donkey domestication may not have produced significant morphological change. Remains from Abydos in Egypt (ca. 3,000 BC) showed evidence of strain-induced spondylitis of the anterior spine caused by bearing heavy burdens, clearly identifying these as domestic donkeys, but they retained a morphological signature of African wild ass (Rossel *et al.* 2008). This finding raises the possibility that the Ash Shumah animals and others in Yemen and the Levant identified as wild asses may be early domestic donkeys from Africa (Marshall 2007). Due to the difficulty in identifying early domestic donkeys and the lack of equids identified as African wild ass dating to 10,000–20,000 (*i.e.*, definitely predating domestication), in our opinion, there are at present no securely identified African wild asses in the Levant or Arabia (Marshall *et al.* 2010). In order to resolve this issue, further research is needed on both the morphology and genetics of Upper Paleolithic equids in Southwestern Asia.

The identification of domestic donkeys is also complicated by practices geared to improve donkey stocks. Ethnographic studies suggest that domestic donkeys may have been breeding with wild asses (Marshall 2007). Maasai women noted that jennies sometimes ran off to mate (Marshall and Weissbrod 2009), and donkeys kept

by people in Awassa, Ethiopia were not supervised (Mohammed 1991). At times and in areas where wild asses were present, such management practices would have allowed mating of donkeys with wild asses (Marshall and Weissbrod 2011). Ethnographic records also document historic pastoralists of the Sudan and Eritrea actively encouraging jennies to breed with wild asses (Baker 1867; Murray 1935). Tuareg capture of wild asses took place as recently as the first half of the twentieth century (Nicolaisen 1963). Given their similar patterns of behavior, it is likely that wild asses were also recruited to supplement ancient domestic holdings. In some cases, historic Beja pastoralists of the Sudan separated wild foals from their mothers and captured young wild animals that had become stuck in mud (Baker 1867; Murray 1935). Such practices provided a supply of wild traits and genetic material to domestic donkeys and may obscure or delay morphological change in the domestic population until they were removed from areas with wild animals. The load-carrying donkeys at Abydos are an example of this, as they were still similar in size to wild ass at 3,000 BC, even though small donkeys were present earlier at nearby Hierakonpolis (Rossel *et al.* 2008).

Linguistic evidence also points to more than one domestication event in Africa. There are three different Afroasiatic terms for donkey, *i.e.*, *kuur*, *harre*, and *ayul* (Blench 2000). The term *kuur* has spread to other areas of Africa, whereas *harre* is used in Ethiopian languages and *ayul* in Berber. Blench (2000) believes that the existence of several word roots within a single language family suggests that the donkey was domesticated several times in different areas of northeastern Africa.

Genetic Studies

Genetic studies of relationships among species, subspecies, and individuals analyze autosomal nuclear DNA, most typically nuclear microsatellites, Y-chromosomal DNA, or mtDNA. There are advantages and disadvantages to each. Nuclear DNA is inherited as one copy from each parent and is subject to recombination, so its analysis is more complicated. Microsatellites are repeated sequences of nucleotides that vary in the number of repeats. They are commonly used in forensic cases, as they are very polymorphic and can distinguish between individuals. The Y chromosome is only found in males and thus shows the paternal history of domesticated animals and people. Mitochondria are organelles in our cells. The circular mitochondrial genome contains genes for proteins involved in energy production and a noncoding region that includes the control region. Cells that use much energy have many mitochondria and thus many copies of mtDNA. Consequently, it is easier to extract mtDNA than nuclear DNA, and in archaeological samples, it may only be possible to obtain mtDNA because the single-copy nuclear DNA will degrade more quickly than the multicopy mtDNA. mtDNA also accumulates mutations faster than nuclear DNA, which provides more genetic variation with which to study more recent evolutionary processes. One drawback is that mtDNA is only inherited maternally and, therefore, does not show paternal contributions to the gene pool. Changing interpretations of the history of cattle in Africa provides an example of the strengths and weaknesses of these different genetic samples. African indicine and taurine cattle breeds cannot be distinguished based on mtDNA (Loftus *et al.* 1994), which led to the hypothesis that

zebu bulls were bred with African taurine cows. This hypothesis was subsequently corroborated by microsatellite studies of nuclear DNA that showed a difference in nuclear DNA of zebu and taurine African cattle (MacHugh *et al.* 1997; Hanotte *et al.* 2002; Freeman *et al.* 2006).

Genetic Variation Between and Within Equid Species

The family Equidae includes horses, asses, and zebras. The genetic variation among equids shows that horses likely separated from the other species about two to three million years ago, while asses and zebras diverged later (Oakenfull *et al.* 2000). Phylogenetic analysis of the mitochondrial 12S RNA gene and control region (Oakenfull *et al.* 2000), the mitochondrial control region alone (Vilà *et al.* 2006), and the cytochrome *b* gene (Orlando *et al.* 2009) give virtually identical results, showing a clear separation among horses, zebras, Asian wild asses, and donkeys. The donkey is most closely related to African wild ass and is well-separated from other equid species. Indeed, as few as 171 base pairs of the control region are sufficient to give good phylogenetic separation of African wild ass from the other equid species (Kimura, unpublished data). As hybrids between donkeys and horses, zebras, or Asian wild asses are infertile (Epstein and Mason 1971), it is not surprising to see a clear genetic separation between these species.

Domestic donkeys vary in appearance and several breeds are typically recognized (Epstein and Mason 1971; Kugler *et al.* 2008). However, microsatellite studies of donkey breeds in Spain and Croatia showed little genetic distinction among breeds, with almost all of the genetic variation found among individuals of the same breed (Aranguren-Méndez *et al.* 2001, 2002; Ivankovic *et al.* 2002). This is an advantage when looking for relationships between individuals, such as paternity, but less helpful for analysis of groups of animals. mtDNA studies also failed to show a clear separation among breeds (Ivankovic *et al.* 2002; Chen *et al.* 2006; Zhang *et al.* 2010). It is possible that breeds may show different proportions of specific haplotypes once more individuals have been analyzed, which could aid in studies of their origin and spread.

However, mitochondrial genetic variation does consistently divide donkeys into two groups, named clade 1 and clade 2 (Beja-Pereira *et al.* 2004; Chen *et al.* 2006; Zhang *et al.* 2010). Our analysis of 440 bases of the mitochondrial control region showed that clades 1 and 2 are separated by 10 mutations and they diverged at least 100,000 years ago, *i.e.*, well before domestication (Kimura *et al.* 2011). Both clades are found worldwide in approximately equal proportions. Although Beja-Pereira *et al.* (2004) showed a higher proportion of clade 1 in West Africa compared to other regions of Africa, the number of animals sampled was too small to draw conclusions. In a study of Italian donkey breeds, one out of five contained only clade 2 mtDNA (Pellecchia *et al.* 2007). However, phylogenetic analysis of domesticated donkeys in Europe is complicated due to the decline of donkey populations of up to 80 % in the twentieth century (Aranguren-Méndez *et al.* 2001). This result may be due, therefore, to loss of clade 1 animals. Larger studies of Chinese donkeys revealed no partitioning of the clades by donkey breed, size, or geographic origin (Chen *et al.* 2010; Zhang *et al.* 2010). Thus, to date, the distribution of the clades shows no clear geographical pattern.

Beja-Pereira *et al.* (2004) compared mitochondrial control region sequences from donkeys around the world and found higher genetic diversity in northeastern Africa, suggesting that the donkey was first domesticated in that area. The nucleotide diversity for clade 1 was 0.0177 in Northeast Africa and 0.0101 in Africa as a whole, with the highest diversity outside Africa being 0.0076 in the Near East. Clade 2 showed even greater levels of nucleotide diversity in Northeast Africa, *i.e.*, 0.0976, as well as 0.0118 in Africa as a whole and 0.0140 in the Near East (Vilà *et al.* 2006).

Possible Ancestors of Domestic Donkeys

It is difficult to determine which subspecies of African wild ass were the ancestors of the two donkey clades. The original study of Beja-Pereira *et al.* (2004) compared mitochondrial control region sequences of contemporary donkeys from different parts of the world, with samples from three Somali wild asses and two putative Nubian wild asses. They concluded that clade 1 was closely related to the Nubian wild ass and that clade 2 may have been derived from the Somali wild ass. The first domestication-oriented study to focus on wild ass rather than domestic donkeys analyzed DNA samples from over 30 extant Somali wild asses and ancient DNA (aDNA) from 9 historic Nubian wild ass specimens from museum collections (Fig. 3) (Kimura *et al.* 2011). The results of Kimura *et al.* corroborated the conclusion of Beja-Pereira *et al.* (2004, 2006) that the Nubian wild ass was the ancestor of clade 1, but showed that the Somali wild ass could not be the ancestor of clade 2 because 12 mutations separate Somali wild ass and clade 2 (Kimura *et al.* 2011). Consequently, the African wild ass subspecies that gave rise to clade 2 is unknown. Possible ancestors for clade 2 include the Atlas wild ass, wild ass in Yemen, or another now-extinct African wild ass.

Unfortunately, Kimura *et al.* (2011) were unable to recover genetic material from archaeological samples of Atlas wild ass or equids from Yemen. However, 3,000-year-old domestic donkey samples from Uan Muhaggiag and an historic Nubian wild ass specimen from the Tibesti area yielded DNA. Both mitochondrial control region sequences fell within clade 1, as did seven other historic Nubian wild ass samples from Eritrea and Sudan (Kimura *et al.* 2011). The presence of clade 1 animals deep into the Sahara makes it less likely that the Atlas wild ass ranged into northeastern Africa, where the ancestors to clade 2 are likely to have been domesticated. The role of the Atlas wild ass as an ancestor of the domestic donkey is, therefore, unclear but perhaps less likely. The possible wild asses found in Yemen are closer to the putative domestication area, but modern donkeys on the Arabian Peninsula show much lower nucleotide diversity than those in Northeast Africa, 0.0028 *versus* 0.0976 (Vilà *et al.* 2006), suggesting Arabia is a less likely place of domestication. Furthermore, the equids in Yemen could be early domestic donkeys from across the Red Sea in Eritrea or Ethiopia. An extinct relative of Nubian and Somali wild asses is not unlikely as an option for the ancestor of clade 2 donkeys. When the Sahara became hyperarid, pastoralists with their domestic animals moved south into the remaining grasslands of the Sahel and Eastern Africa. Although better adapted for arid conditions than many ungulates of the Sahara and Horn, African wild ass would still have been vulnerable to the effects of habitat loss and fragmentation, as well as competition and

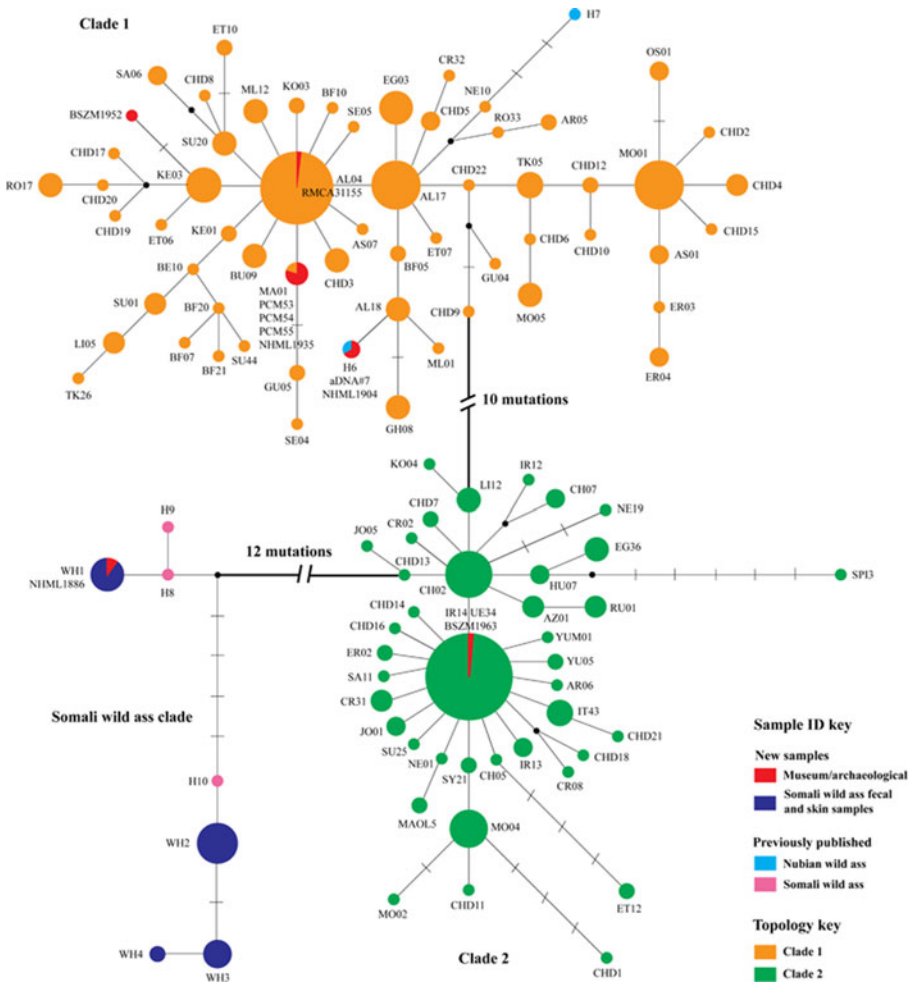


Fig. 3 Reduced median-joining network of mtDNA haplotype sequences from domestic and wild asses. Reprinted with permission from Fig. 2 of Kimura *et al.* (2011: 54). This figure appears in color in the online version of this article

interbreeding with pastoral donkeys. Wild ass population numbers must have been substantially reduced by these continental-scale processes. Local groups could have been driven to extinction.

However, these evolutionary processes were operating on a range of genetic variability of a much earlier origin. The genetic separation between clade 1, clade 2, and the Somali wild ass is approximately equidistant and coalescence analysis indicates that the most recent common ancestor lived more than 100,000 years ago (Kimura *et al.* 2011). These deep branches suggest an early split into three East African wild ass groups, but extinct and/or unsampled wild asses could partially fill in the deep branches, indicating a more recent and more complex history for African wild asses. Even though Nubian and Somali wild ass are well-separated genetically, historically they have been in close geographic proximity. The Red Sea Hills and Ethiopian highlands may have served as barriers separating groups of wild asses that

diverged into Somali wild ass, Nubian wild ass, and the clade 2 ancestor. Subsequently, two of these three groups were domesticated. As explained above, much less is known about the ancestor of clade 2 donkeys than the other two wild ass groups. However, one animal captured in Eritrea in the 1930s and then identified as Nubian wild ass may in fact have belonged to the extinct group that gave rise to the clade 2 donkeys. The mitochondrial control region sequence obtained from this specimen was identical to a common clade 2 haplotype. This animal was kept at the Munich Zoo and was unusually large for a Nubian wild ass (Rossel *et al.* 2008).

Insights into the Process of Domestication

Geneticists commonly visualize the inferred evolutionary relationship between DNA sequences using networks of circles and lines. These are based on similar DNA sequences, called haplotypes and represented by circles, and the number of mutations distinguishing sequences is indicated by the length of the line between the circles. The size of the circle indicates the number of individuals with that haplotype. The structure of the network can give information on the domestication process. In one scenario, a single domestication event followed by breeding of domestic animals would be expected to yield a starburst pattern network, with many individuals belonging to a core haplotype and smaller nodes separated from the core haplotype by single or a few mutations that accumulated over time. Over longer time spans, additional starbursts based on nodes would be expected, as some animals colonize new areas and give rise to more individuals. However, a starburst pattern can also be obtained if the sampling missed the original geographic area of domestication, *i.e.*, analyzed the genetic diversity derived from a few founder animals. In a second scenario, multiple domestications from a genetically diverse wild progenitor population would be expected to show an unstructured network, with more and smaller nodes and greater separations between nodes. Over time, some nodes would develop starburst patterns. However, if additional wild animals were domesticated later in time, the number of haplotypes would increase and more nodes would be incorporated in the network.

The network for clade 1 (Fig. 3) contains a large number of haplotypes and shows Nubian wild asses sharing haplotypes with domestic animals. This pattern follows the second scenario and would be expected if individuals were obtained from groups of wild animals in different geographic regions and/or over a long time span. As we know that wild asses were still being incorporated into domestic stock (Baker 1867; Murray 1935) in the last century, we believe it is likely that prehistoric herders caught, tamed, and ultimately domesticated wild asses encountered during their seasonal migrations in search of grazing land for their cattle. The normal territorial range for Somali wild asses is 12–40 km² (Klingel 1998), and a similar range is likely for the Nubian wild ass. It is tempting to hypothesize that the shared Nubian wild ass and domestic donkey haplotypes indicate places of domestication, in this case the Tibesti region in Chad, the Red Sea Hills, and the Atbara region in Sudan, but it must be noted that the deteriorating climate likely caused migrations of both domestic and wild animals.

Clade 2 shows a network pattern more similar to the first scenario, indicating fewer domestication events or sampling outside the geographic area of domestication. A few animals differ, but the majority of animals are within two mutations of the central haplotype. The central haplotype also includes the unusually large Nubian wild ass captured in Eritrea and brought to the Munich Zoo. The outliers may represent wild animals later incorporated into the preexisting domestic population. A possible scenario suggested by Marshall (2007) is the domestication of the unknown ancestor by herders in the Horn of Africa, after the Sahara became uninhabitable.

The Somali wild ass clade is separated from clade 2 by 12 mutations, and the pattern shows separation among haplotypes as would be expected from wild animals that have accumulated mutations over time, which supports estimations of an early, pre-domestication divergence. The haplotype diversity of the Somali wild ass was lower than that of domestic donkey clades, 0.7417 *versus* 0.9309 and 0.8212 for clades 1 and 2, respectively (Kimura *et al.* 2011), suggesting loss of some ancestral wild ass populations. This is consistent with the hypothesis of reduction of wild ass populations due to habitat loss with the expansion of the hyperarid Sahara after the mid-Holocene and a concurrent increase in long-term competition with domestic stock.

Future Directions

At this point, our knowledge of donkey domestication is limited. It is clear that modern domestic donkeys separate into two groups based on maternally inherited DNA and that clade 1 is derived from Nubian wild ass. In addition, we have shown that 3,000-year-old domestic donkeys from Uan Muhaggiag belong to clade 1. It is not known what the distributions of clade 1 and clade 2 donkeys were prior to 3,000 years ago, nor between then and modern times. However, donkeys spread throughout the world after domestication and a better understanding of the trajectories and timing of the two different clades will aid in our understanding of the domestication, spread, and use of donkeys. It is interesting that one animal from Pompeii originally suggested to be either horse or mule may have been a clade 2 donkey (Di Bernardo *et al.* 2004; Gurney 2010). Gurney (2010) notes that most modern Italian donkeys belong to clade 2, which could mean that the two donkey clades were unequally distributed in Roman times.

Specific questions that could be addressed with aDNA include the question of whether clade 2 donkeys were spread throughout Europe and North Africa by Romans or whether they arrived prior to or later than the Roman period. Knowledge of which clade first reached various areas outside Africa might also help indicate the place of origin and, hence, area of domestication of donkeys of mitochondrial clades 1 and 2. Archaeological samples from the Arabian Peninsula, the Near East, and Spain would help narrow down the spread of donkeys of these haplogroups. Another key question is the scale of interactions between North Africa and the Iberian Peninsula. Analysis of archaeological samples from these regions could indicate whether Iberian donkey haplotypes were more similar to North African or French donkeys, and shed light on the spread of donkeys in Europe and the route by which the donkeys reached the Iberian Peninsula. These

types of studies need to be performed with archaeological samples as the diminished use of donkeys, especially in Western Europe, may have obscured the original distribution.

It is also important to look at the paternal structure of both modern and ancient donkeys. Y chromosome microsatellites have been used successfully to investigate the paternal history of cattle (Pérez-Pardal *et al.* 2010) and a similar strategy would be valuable for donkeys and wild asses. Pérez-Pardal *et al.* (2010) were able to estimate the time of divergence for three major haplogroups, identifying an African taurine domestication and an ancient indicine introgression into Africa. Y chromosome microsatellites used by Wallner *et al.* (2004) accurately differentiated among equid species, and one of these differed in length in one out of three donkeys, separating the donkeys into two haplotypes. However, Ling *et al.* (2010), using the same microsatellites, found only a single haplotype among 30 Chinese donkeys. Obviously, many more samples from different regions must be studied before the paternal history of donkeys can be reconstructed. In addition to determining the number and diversity of patrilineal lines in domestic donkeys, the Y chromosome microsatellites could also be valuable in conservation efforts for both Somali and Nubian wild ass.

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