

Meta-Analysis of Mitochondrial DNA Reveals Several Population Bottlenecks during Worldwide Migrations of Cattle

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Abstract: Several studies have investigated the differentiation of mitochondrial DNA in Eurasian, African and American cattle as well as archaeological bovine material. A global survey of these studies shows that haplogroup distributions are more stable in time than in space. All major migrations of cattle have shifted the haplogroup distributions considerably with a reduction of the number of haplogroups and/or an expansion of haplotypes that are rare or absent in the ancestral populations. The most extreme case is the almost exclusive colonization of Africa by the T1 haplogroup, which is rare in Southwest Asian cattle. In contrast, ancient samples invariably show continuity with present-day cattle from the same location. These findings indicate strong maternal founder effects followed by limited maternal gene flow when new territories are colonized. However, effects of adaptation to new environments may also play a role.

Keywords: cattle; breeds; mitochondrial DNA; haplogroups; migrations

1. Introduction

During the past decades, analysis of mitochondrial DNA (mtDNA) has become the backbone of molecular-genetic investigations of animal population diversity and history [1]. Due to its high variability, informative datasets can be collected relatively fast, while its high copy number increases the chance of retrieving DNA from archaeological material. In addition, the interpretation of mtDNA datasets is facilitated by maternal transmission and absence of recombination; the latter generating a straightforward hierarchical clustering [2].

For several livestock species, mtDNA analyses established the ancestral species and contributed to evidence for the localization of domestication sites [3]. The finding of two separate domestication events, one for taurine (*Bos taurus*) and one for zebu (*Bos indicus*) cattle [4,5], corresponded with the archaeological record. The exclusive presence of taurine mtDNA in African zebu [4] indicated that zebu was introduced into Africa by male introgression alone and demonstrated the unique contribution of mtDNA analysis to the reconstruction of agricultural history. Since then, numerous studies have explored the mitochondrial diversity of cattle populations worldwide (Table S1). Five taurine (T) and two indicine (I) haplogroups account for the vast majority of mtDNA haplotypes [6–9]. Complete mtDNA sequences have established an accurate phylogeny and indicated a Southwest-Asian origin for all major T haplogroups, including the African T1 and East-Asian T4 [10,11]. These and other studies also identified the rare haplogroups P, Q and R, with P and R most likely derived from European aurochs [12–14].

Focusing on the major haplogroups, we combined the results of several regional studies of the cattle mtDNA control region (Table S1). This global meta-analysis allows a few generalizations about shifts

in haplogroup distributions, suggesting strong founder effects during colonization of Europe, East Asia, Africa and America, but little temporal variation.

2. Experimental Section

Table S1 shows the sources of cattle mtDNA datasets used in this study with a total of 6695 D-loop sequences. The haplogroups T, T1, T2, T3 and T4 could be differentiated by variation within a 240-bp D-loop segment [6,8,9,12]. In this study haplogroup T denotes the combination of T, T1'2'3 and T5. Haplogroup counts were taken directly from publications or based on haplotype scoring of reported GenBank entries.

3. Results and Discussion

A worldwide geographic plot of haplogroup distributions (Figure 1) visualizes several spatial contrasts. Troy *et al.* [6] already noted the high haplogroup diversity in Southwest Asia with four major haplogroups T, T1, T2 and T3, the dominance of haplogroup T3 in Europe and the almost exclusive occurrence of T1 in Africa. A recent analysis of Neolithic samples from Iran revealed the same haplogroup diversity as observed in present Southwest Asian cattle [15], while T3 was already predominant in Central and Northwestern Europe during the Neolithic [16–23] (Figure 2). The combination of data from several sources now suggests that the entry of cattle into Europe ca. 8,500 BP largely reduced the frequency of haplogroups T and T1. Haplogroup T2 still has appreciable frequencies in Italian, Balkan and Asian taurine cattle, but is found only sporadically in Central, Western and Northern Europe.

The presence of T1 in the Iberian peninsula suggests prehistoric and/or later African influence [19,24,25]. This is also the most likely explanation for a similar frequency of T1 in the Podolian breeds from Sicily and South Italy. The maternal lineages in Central-Italian large white and Podolian cattle (Chianina, Maremmana, Romagnola, Marchigiana), with frequencies for both T1 and T2 of around 10%, are intermediate between those of the South-Italian and Balkan Podolian cattle. Thus, a proposed Anatolian origin of maternal lineages from Tuscany by immigration of cattle well after the Neolithic colonization of Italy [26] can be extended to neighboring Podolian breeds. A genetic link between mtDNA from Anatolian and Italian cattle, implying transport of cows, may have been mediated by the Tuscans [26] and/or correspond to the documented import since the 8th century BC of large cattle from Epirus (present South Albania-Northwest Greece) to Italy [27]. In Africa, haplotypes from haplogroups other than T1 have been found only in Egypt (combined frequency 38.5%) and Northwest Africa (less than 2%) and are completely absent in the rest of the continent. A recent comprehensive study of whole mtDNA of the T1 haplogroup identified eight haplotypes as founders of the African T1 population [11]. Estimates of coalescence times for the T1 sub-haplogroups (6,200 to 12,900 BP) and their current geographic distributions are compatible with a Southwest-Asian origin for most T1 sub-haplogroups, which for sub-haplogroup T1c1 has been confirmed by its discovery in Iraq [14]. It is not clear yet how to explain the overrepresentation in Africa of different sub-haplogroups exclusively from the T1 haplogroup. Possible explanations include positive selection of T1 mtDNA (see below), inherent uncertainties in time estimates and overestimations of the divergence times for recent taxa [28,29]. Shorter divergence times would allow an alternative scenario of a small herd with a high frequency of T1 reaching Africa, expanding and only then splitting into the different T1 sub-haplogroups.

Figure 1. Distributions of major taurine and indicine haplogroups. T1* indicates T1c1a1 [11], previously denoted as AA [8].

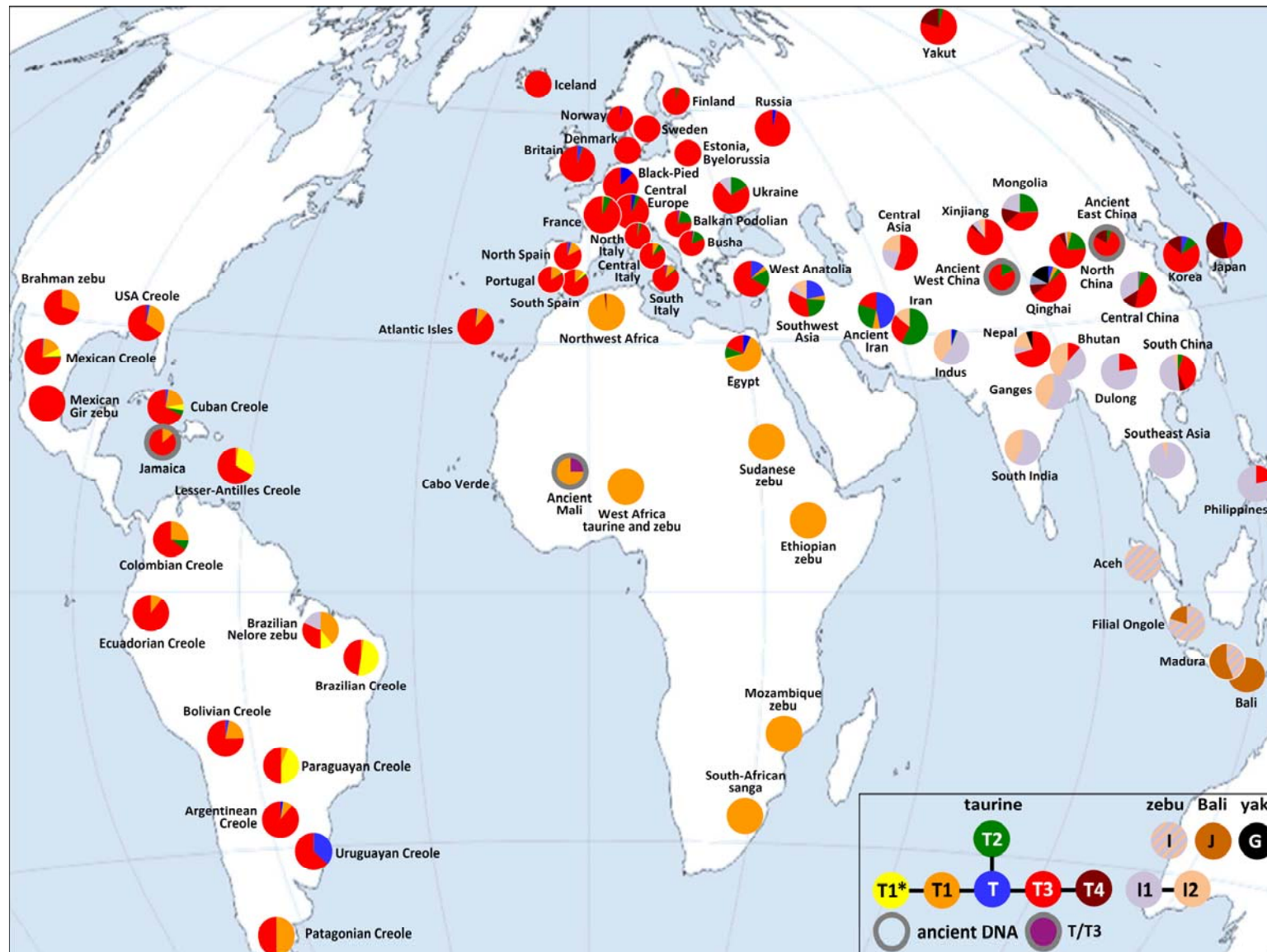
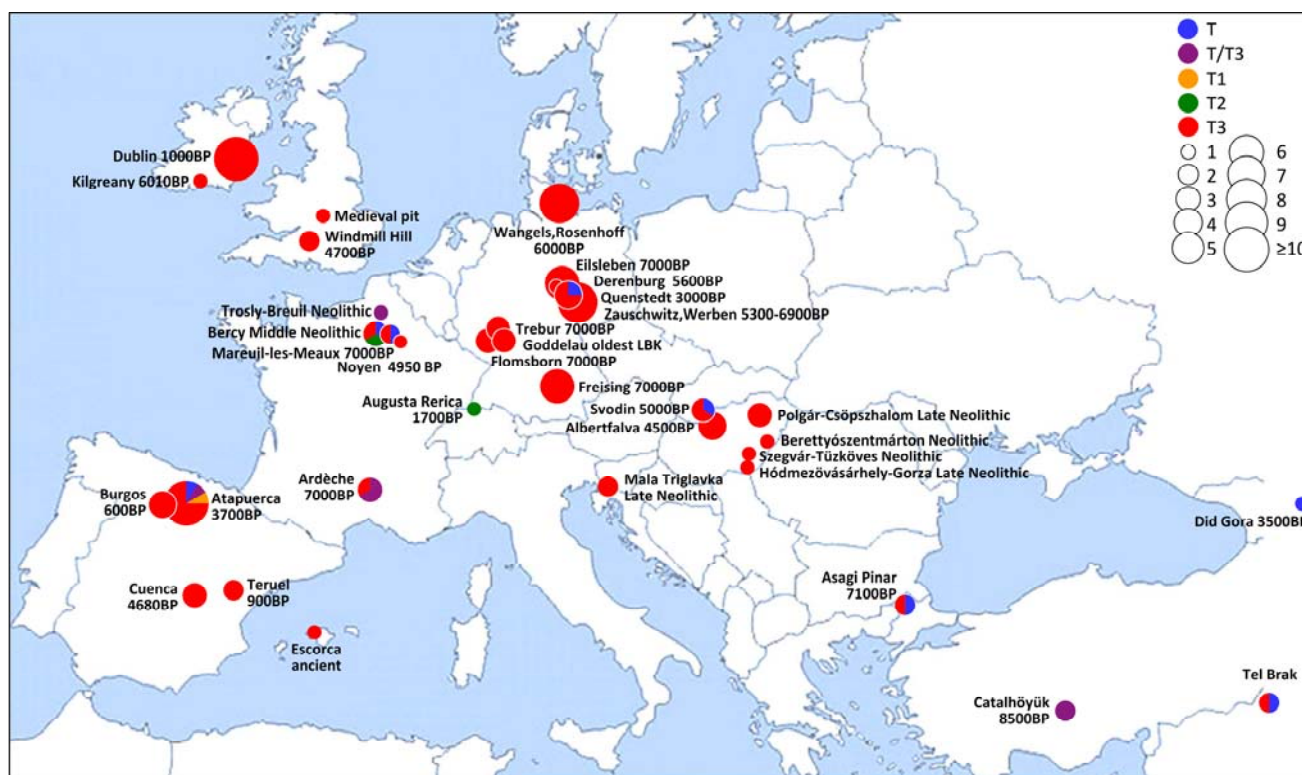


Figure 2. Mitochondrial DNA (MtDNA) haplogroup distributions in European and Southwest-Asian ancient DNA samples from domestic cattle. Data are from [16–23].



Migration from Central to East Asia led to the expansion of haplogroup T4. This is a subvariant of T3, which is not observed in the west, but has been found in East-Chinese ancient DNA dating to 4500 BP [30], in modern Korean beef cattle [10] and in more than half of the Japanese cattle [31]. It is also at a frequency of 21% in the North-Siberian Yakut [32], indicating a link between the Yakut and cattle from East-China.

A similar expansion occurred during the colonization of the New World since the end of the 15th century. Haplogroup distributions, with T3 as major and T1 as minor, reflect the Iberian ancestry of American cattle. Although the T1 haplotype T1c1a1 is sporadic in the Old World it reaches frequencies of 31% in the Caribbean Lesser Antilles islands and even 50% in Brazilian Criollo cattle [8,14,33]. Portuguese colonists imported the first cattle to Brazil in 1534 from Cabo Verde near the West-African coast [34], while the English and French colonists settled only in the 17th century in the Lesser Antilles. This suggests a scenario in which cattle carrying the T1c1a1 haplotype originated either from Portugal or Africa, grew in number on Cabo Verde or in Brazil and were later exported to the nearby Caribbean isles.

Indicine maternal lineages from haplogroups I1 and I2 diffused from South Asia to Southwest and Central Asia [9,35]. Haplogroups I1 predominated in the cattle that moved eastwards to Southeast Asia and China. Populations with a mixed taurine and indicine maternal origin are found in Southwest Asia, the Indus Valley, Central Asia, Nepal, Bhutan, China, Mongolian and Brazil. The gayal population from Yunnan in South China combines I1 and T3 mtDNA with paternal lineages from the gayal (*Bos frontalis*) or wild gaur (*Bos gaurus*) [36]. In Indonesia, zebu introgressed into local populations of domestic

banteng (*Bos javanicus*), which have partially retained their original javacine origin in their mtDNA [37]. Maternal yak (*Bos grunniens*) introgression has been observed in Nepal [38] and Qinghai [39].

Geographic differentiation of cattle mtDNA is clearly stronger than observed for sheep, goat and horse, which exhibits a broader distribution of the major mtDNA haplogroups [1]. Sequencing of ancient mtDNA from remains of domestic cattle found in Europe, Iran, China and the Caribbean invariably shows continuity with present-day animals from the same region. This suggests that abrupt shifts in haplotype frequencies were caused by strong founder effects during the earliest migrations of cattle, which apparently involved only a few individuals. It is plausible that it was easier to transport larger groups of the smaller and more manageable goats and sheep, while mobility of horses was promoted by trading and wars. The strong geographic differentiation of mtDNA in the Chinese population of swamp type of water buffalo [40] supports the hypothesis that differentiation of maternal lineages correlates with a low mobility of the herds.

Selection offers an alternative explanation for the strong phylogeography seen in bovine mtDNA. Purifying selection acting on mtDNA has been demonstrated for both bovine and other mammals [41], although it may be weaker for domestic livestock than for wild species [42]. Positive selection may improve the adaptation of cattle to different environments. One of the T4-specific substitutions leads to an L380M mutation in the cytochrome *b* gene and the G1324A substitution in T1c1a1 causes a mutated rRNA. However, no differences have been found in production and reproduction traits between Brazilian Guzerat zebus carrying taurine mtDNA and those carrying indicine mtDNA [43]. Nonetheless, there is no *a priori* reason why mtDNA-encoded gene products cannot be involved in selection and contribute to traits relevant for adaptation or production, thus leading to geographic differentiation of mtDNA.

4. Conclusions

We conclude that the meta-analysis of bovine mtDNA sequences from both present and archaeological samples allows for a global picture of geographic differentiation of the maternal lineages, which have been shaped by population bottlenecks during the worldwide dispersal of cattle. As shown for haplogroup T1 in Africa [11,44], whole-mtDNA sequencing may detect additional sub-haplogroups informative for movements of cattle between or within continents and expansion of populations. Ancient DNA studies contribute essentially to the historic reconstructions by providing geographic and historic anchor points for specific haplotypes.

Supplementary Materials

Supplementary materials can be accessed at: <http://www.mdpi.com/1424-2818/6/1/178/s1>.

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Author Contributions

Johannes A. Lenstra initiated this study and wrote the first draft. Paolo Ajmone-Marsan, Albano Beja-Pereira, Ruth Bollongino, Daniel G. Bradley, Licia Colli, Anna De Gaetano, Ceiridwen J. Edwards, Luca Ferretti, Catarina Ginja, Peter Hristov, Juha Kantanen, Juan Pedro Lirón, David A. Magee, Riccardo Negrini and Georgi A. Radoslavov contributed to data compilation, Paolo Ajmone-Marsan, Luca Ferretti and Marleen Felius to the historic interpretation and Ceiridwen J. Edwards to final editing.

Conflicts of interest

The authors declare no conflict of interest

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