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# Electronic Journal of Biotechnology



## Review

# Uniparental genetic systems: a male and a female perspective in the domestic cattle origin and evolution



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## ARTICLE INFO

### Article history:

Received 2 March 2016

Accepted 29 June 2016

Available online 4 August 2016

### Keywords:

Animal breeding

Bovine domestication

Cattle genetic diversity

Genetic resources

Genome-assisted selection

Inherited marker systems

## ABSTRACT

Over the last 20 years, the two uniparentally inherited marker systems, namely mitochondrial DNA and Y chromosome have been widely employed to solve questions about origin and prehistorical range expansions, demographic processes, both in humans and domestic animals. The mtDNA and the Y chromosome, with their unique patterns of inheritance, continue to be extremely important source of information. These markers played significant roles in farm animals in the evaluation of the genetic variation within- and among-breed strains and lines and have widely applied in the fields of linkage mapping, paternity tests, prediction of breeding values in genome-assisted selection, analysis of genetic diversity within breeds detection of population admixture, assessment of inbreeding and relationships between breeds, and assignment of individuals to their breed of origin. This approach offers a unique opportunity to save genetic resources and achieving improved productivity. In the past years, significant progress was achieved in reconstructing detailed cattle phylogenies; many studies indicated multiple parental sources and several levels of phylogeographic structuring. More detailed researches are still in progress in order to provide a more comprehensive picture of such extant variability. This paper is focused on reviewing the use of the two uniparental markers as valuable tool for the characterization of cattle genetic diversity. Furthermore, their implications in animal breeding, management and genetic resources conservation are also reported.

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Peer review under responsibility of Pontificia Universidad Católica de Valparaíso.

<http://dx.doi.org/10.1016/j.ejbt.2016.07.001>

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## 1. Uniparental molecular markers

Ove the last 20 years, the two uniparentally inherited marker systems, namely mitochondrial DNA (mtDNA) and the Y chromosome have been widely employed to solve questions about origin and prehistorical range expansions, demographic processes, both in humans [1] and domestic animals [2,3,4,5,6]. Even if whole genomic approaches are now opening up new clues on the livestock complexity and admixture, mtDNA and the Y chromosome, continue to be an extremely important source of information because of their unique pattern of inheritance [7,8,9,10]. As they are uniparentally inherited, they evolve exclusively through the sequential accumulation of mutations along the maternal and paternal lineages, respectively; these markers played significant roles in farm animals, namely in the evaluation of the genetic variation within- and among-breed lineages, moreover have been widely applied in the fields of linkage mapping, paternity tests, prediction of breeding values, genome-assisted selection, analysis of genetic diversity within breeds, detection of population admixture, assessment of inbreeding, relationships between breeds, and assignment of individuals to their breed of origin [11]. This approach often provides not only new insights into the timing and location of domestication events that produced the extant farm animals [12,13], but also even offers a unique opportunity to conserve genetic resources, promote and defend local products [14,15]. In this last case the genetic traceability of livestock products is an essential tool to safeguard public and animal health, and to valorize typical foods [16]. The past few years have seen significant progress in reconstructing detailed livestock phylogenies especially in cattle (here reviewed), dog [17,18], pig [19,20], horse [21,22,23], sheep [24, 25], goat [26,27,28,29] and chicken [30,31] deepening genealogical branching of the tree topologies for both mtDNA and Y chromosome. These studies indicated multiple parental sources and several levels of phylogeographic structuring.

This paper is focused on reviewing the use of the two uniparental markers as valuable tool for the characterization of cattle genetic diversity. Implications in animal breeding, management and conservation of genetic resources are also reported.

## 2. Mitochondrial DNA

Mitochondrial DNA is the best studied among all available genetic markers systems. There are several reasons for this peculiarity:

- 1) its exclusively maternal inheritance makes possible to retrace the genetic history of the female lines.
- 2) its elevated variability in natural populations due to the high mutation rate, estimated to be at least five times higher than that observed in nuclear DNA, can generate signals about population history over short time frames.
- 3) mtDNA may be analyzed in both male and female donors, this facilitates the collection of representative samples.
- 4) the small size of the molecule allows easy amplification and sequencing because of the multiple copies in the cells, moreover the mitochondrial genes are strongly conserved across animals, very few are the duplications, no introns, and very short are the intergenic regions.

Rapidly, the analysis of mtDNA has revealed to be the most convenient and cheapest molecular tool to explore the genetic variability of a species, and became the backbone of molecular genetic investigations in livestock: genetic structure and segregation pattern are still now used to tracing back the origins of breeds as well as to identifying individuals.

The mtDNA has been extensively used as a tool for inferring the evolutionary and demographic past of livestock populations defining their ancestral species and contributing to evidence for the localization of domestication sites [13,22,32,33,34,35,36,37]. Moreover

it has been proven to be highly informative to determine the level of their genetic variability, which is essential in defining conservation priorities for regional breed's specific programs [25,38].

In livestock mtDNA has been used to describe variation in putative wild ancestor populations and modern domestic populations. By now, complete mitogenome sequences are routinely used to produce phylogenetic trees, more and more informative. Although human detailed phylogeny is still too far to be reached, livestock mtDNA surveys led to unravel new genetic flow patterns and phylogeographic structures such as in cattle [39,40,41,42,43], dogs [35], horses [22], pigs [44] and chicken [45].

## 3. Y chromosome

As a consequence of its uniparental transmission and lack of recombination, the DNA sequence of every Y chromosome preserves a unique record of mutational events that occurred in the genome of previous (male) generations. Studies of polymorphisms in the non-recombining portion of the Y chromosome represent an easy and rapid way to detect and quantify male-mediated admixture, and have been proposed for detecting male-mediated migration events, reconstructing paternal history and trace individual founder lines or families [46,47,48,49]. The absence of interchromosomal recombination out of the pseudoautosomal region (PAR) preserves original arrangements of mutational events, and thus male lineages can be traced both within and among populations. Effective population size is often reduced further by the relatively high variability of male reproductive success. As a result, the Y chromosome is a sensitive indicator of recent demographic events, such as population bottlenecks, founder effects and population expansions [50]. In several species, males are more mobile than females and compete for reproduction or, in livestock case, are selected on the basis of breeding objectives. Therefore, while mtDNA variants stay mostly within the herd, Y-chromosomal variants may reflect the origin of sires as influenced by introgression and upgrading. It has been shown that domestic cattle can display marked sex-biased admixture and migration patterns, for example, the zebu genome spread across Africa through male-mediated gene flow [51,52,53,54,55]. This produced different distributions of the maternal mtDNA and paternal Y chromosome, with the autosomal genome representing an independent picture from two uniparental extremes.

Interestingly, while recent developments in cytogenetic technologies should facilitate the isolation of Y-chromosomal specific markers [56], for most livestock species there are still few Y polymorphic sites. This is probably a consequence of the demographic history of domestication and breed formation. In polygynous species, like most livestock, we expect indeed that a small number of male lineages would have contributed to the genetic pool of the species. Beside dog and cats, polymorphic Y microsatellite markers are currently available only for cattle [53,57,58,59,60], yak [61,62], buffalo [63,64,65] and partially for horse [66]. At the present time these markers have not been yet isolated in some major livestock species, e.g. small ruminants, camelids or the domestic pig.

In the study of human male lineages, the use of Y-specific microsatellites has allowed for refined analyses of the genetic diversity of paternal lineages that can be found within major haplogroups [67, 68,69,70,71]. Similarly, in cattle, microsatellite analysis has identified several Y-haplotypes in Portuguese [72], northern and eastern European [73], western-continental, British and Sub-Saharan African [74] breeds, as well as in American Creole [75] breeds. Even though different set of markers were used in these studies, and each only partially covered the diversity pattern of the paternal lineages, they confirmed that Y-markers exhibit a strong phylogeographic structure in cattle. Although Y-chromosome diversity is lower than autosomal, it has been shown that the studies of male lineages added much to what can be inferred only from mtDNA and autosomal variation [6,72,76,77,

78,79,80,81]. Moreover, compared with mtDNA, the small number of males used for breeding and male-mediated crossbreeding has accelerated the loss of Y-chromosomal variation in domestic cattle. For example, several cattle (such as Russian, Ukrainian and Scandinavian) have been influenced by gene flow from commercial cattle breeds leading to the genetic dilution of many worldwide local breeds [73].

#### 4. Genetic resources in domestic cattle

Cattle breeds are recognized as an important part of biodiversity and genetic heritage. According to FAO [82], out of the 1350 cattle breeds worldwide, 14.8% are extinct [83]. Therefore, it is very important to preserve the genetic diversity of the remaining breeds, mostly captured in non-selected autochthonous breeds [84]. This decrease in the number of cattle breeds has several reasons, such as modernization and reorientation of the agricultural production, socio-economic changes and cultural developments. Between the 1950's and 1980's, the willingness to increase productivity, intensification and specialization of animal production has dramatically affected the local cattle breeds and resulted in loss of sequence variation in DNA and breeds diversity [85,86]. However, in the last two decades the interest for preserving the locally adapted breeds has considerably increased and several conservation strategies were implemented in Europe and worldwide.

The development of the cattle genetic resources has been always more a multifaceted and continuously dynamic process, both on the global and local level, strictly tied to human history. It has resulted in a worldwide population of cattle with a considerable phenotypic and molecular diversity. Felius et al. [87] surveyed the complex history of cattle genetic resources throughout the time on different continents, and argued that the current genetic diversity of cattle emerged during three main and overlapping phases: i) domestication and subsequent wild introgression; ii) natural adaptation to a diverse agricultural habitat; and iii) breed development.

#### 5. The cattle domestication

Domestic cattle are classified into two major species, the taurine or humpless cattle (*Bos taurus*) and the zebu or humped cattle (*Bos indicus*). Both descend from the wild aurochs (*Bos primigenius*). More precisely, the subspecies *B. p. primigenius* in Southwest Asia and *B. p. namadicus* in India were the ancestors of taurine and zebu cattle, respectively.

In his record of the Gallic Wars, Julius Caesar wrote about aurochs: "They are a little below the elephant in size, and of the appearance, color, and shape of a bull. Their strength and speed are extraordinary, they spare neither man nor wild beast which they have espied". At the end of the last glacial period (12,000 years ago) *B. primigenius* was endemic over almost the whole Eurasian continent and Northern Africa. By the 13th century A.D., aurochs were extremely rare and restricted to Eastern Europe, with the last recorded aurochs dying in Poland in 1627 [40]. Only few contemporary pictures of aurochs exist, but skeletal remains allow reconstructing its morphology. The size, shape or gender ratios allow a differentiation of fossil remains from wild and domestic cattle [34].

Cattle domestication represents a major development in the Neolithic transition and was an important step in human history, leading to extensive modifications of the diet, the behavior, and the socioeconomic structure of many populations [88] of the Old World that at different times adopted cattle breeding [89,90]. Archaeological evidences suggest that taurine cattle have been domesticated between 10,300–10,800 years ago in the Fertile Crescent, most probably on the western Turkish-Syrian border [91,92]. In addition, isotope analysis of organic material revealed traces of milk in excavated pottery, indicating the storage of dairy products already 9 kiloyears (ky) ago [93].

A comparison of the mtDNA of taurine and indicine cattle represented one of the first contributions of DNA research to a reconstruction of the

cattle domestication [94]. The divergence of their control regions implied separate domestications, which most likely started 10 ky ago in South-western Asia and the Indus valley respectively [34,95]. The most recent molecular estimates of the divergence time of these aurochs subspecies and thus of taurine and zebu cattle are 147 ky ago [96] or 335 ky ago [40], and 350 ky ago [97]. Although these estimates have large confidence intervals, all indicate that taurine and zebu cattle have been domesticated separately. This was followed by the spread of domesticated herds throughout the Old World accompanying human trade and migration. After domestication, survival and diffusion of *B. taurus* was completely dependent on humans; thus the phylogeographic patterns of cattle genetic diversity should mirror human activities or movements and may provide information complementary to archaeological and anthropological data [98]. When domesticated herds diffused from the Fertile Crescent into Europe, Africa and the rest of Asia, local *B. primigenius* populations were numerous and widespread. Moreover, the coexistence of autochthonous wild aurochs and the newly introduced cattle lasted for thousands of years in many geographical areas, thus providing potential conditions not only for spontaneous interbreeding between wild animals and domestic herds, but also for pastoralists to create secondary centers of domestication involving local aurochs populations. In contrast to the wide distribution of the aurochs domestication events took place in certain areas, reflecting the difficulty of sustained managing and breeding of these large wild animals [99]. The most plausible scenario is a single and regionally restricted domestication process of cattle in the Near East with subsequent migration into Europe during the Neolithic transition without significant maternal interbreeding with the endogenous wild stock [100].

A recent coalescent-based analysis using ancient Iranian taurine samples suggested a severe Near Eastern domestication bottleneck, with an estimated effective size of just 80 female founders [99]. Scheu and colleagues' model suggests that a high proportion (73%) of domesticated cattle in Anatolia and the Near East may have migrated into Europe. This indicates that the expansion into Europe was a far less severe bottleneck than assumed before, and that much of the variation present in the original Anatolian/Near Eastern population survived in initial European cattle populations [100]. While genetic studies support a Near Eastern origin for European *B. taurus* cattle, there is considerable debate regarding the extent of genetic exchange between early domestic cattle and indigenous aurochs during the development of animal herding in Europe. Comprehensive data sets of ancient and modern cattle DNA from other areas reveal a more complex scenario: fossil remains [101], together with the predominance of one taurine mitochondrial haplogroup T1 in Africa [42,102] and a new haplogroup in Eastern Asia, T4, [73,103] suggested at least two other domestication centers.

The identification of sequences of putative aurochs haplogroups Q and R in modern Italian cattle does support the limited local adoption of wild aurochs matriline in Southern Europe [39,40,104].

In contrast to mtDNA studies, analyses of paternally inherited Y chromosome haplotypes remain equivocal as to whether local wild male aurochs contributed to European *B. taurus* populations [79,105,106].

The interface between early European domestic populations and wild aurochs was significantly more complex than previously thought and important questions remain unanswered, including the phylogenetic status of aurochs, whether gene flow from aurochs into early domestic populations occurred [107].

However, independent domestication in Africa [52,54] and East Asia [103] has also been postulated and ancient DNA data raise the possibility of local introgression from wild aurochs. Zebus were probably imported into Africa after the Arabian invasions in the 7th century [52]. Interestingly, the discovery that African zebus carry taurine mtDNA implies that African zebus were the result of crossing zebu bulls with taurine cows [52]. The first auroch mtDNA sequences, collected in Great Britain, typed far from those of modern cattle

breeds, suggesting little auroch introgression [102]. Later, however, more ancient auroch sequences from Italy and from the Bronze Age of the Iberian Peninsula revealed haplotype distributions similar to those of modern European cattle breeds [78,88]. Only one Iberian sample appeared more closely related to the British auroch sequences [78]. Thus, the introgression of auroch mtDNA into modern cattle breeds has taken place, but it is not clear to what degree or whether this varied depending upon geographical location. Thus, detailed and continent-wide evaluation of the early spatiotemporal demography of *B. taurus* has so far been hindered by the lack of data from the key bridging areas of the Neolithic, namely Anatolia, the Balkans, and the Western Mediterranean.

## 6. Use of uniparental markers in domestic cattle

### 6.1. The female perspective of the mitochondrial DNA

From a genetic point of view, animal domestication can be reconstructed through phylogeographic analyses of both nuclear and mitochondrial genomic data [13]. Early molecular and evolutionary studies on cattle have focused on mtDNA, in particular on short segments of its control region [94,102,103]. However, mtDNA control-region variation is often characterized by high levels of recurrent mutations and reversions, thus blurring the structure of the phylogenetic tree and making the distinction between some important branches within the tree virtually impossible. In fact, following the most detailed approach used for the human phylogeny [108,109,110,111], researches tend to use complete mitogenomes to reconstruct the history of animal domestication such as in cattle [40, 41,42,104], chicken [45], horse [21,22] and sheep [25].

The analysis of mtDNA sequence diversity has provided useful information on the origin and diversification of current cattle populations [102,105,112]. The mitochondrial signals of wild aurochs' domestication can be seen in modern cattle breeds [102,112,113]. In particular cattle domestication in the Near East is thought to have taken place around 10,500 years ago, giving rise to taurine cattle (mainly mitochondrial haplogroup T), whereas domestication in southern Asia has been dated later to about 8500 years ago resulting in modern zebu (indicine) cattle (mitochondrial haplogroup I). Molecular diversity approach revealed that modern taurine mitochondrial genomes cluster within a number of closely related branches, termed T, T1, T2, T3, and T4, geographically well structured: T1 predominantly found in Africa; T2 originates in the Near East and Western Asia; and T3 found in Europe and originates from the expansion of a small cattle population domesticated in the Middle East.

Frequency and geographic distributions of the T lineages were very compatible with the scenario of a single ancestral Near Eastern population source and a later spread out following the domestication event. However alternative models were proposed to explain some peculiar features in the geographic distributions of T1 [114], T3 [88] and T4 [103].

Lenstra and colleagues [8] combined the results of several regional studies of the cattle mtDNA control region resulting in a global meta-analysis suggesting strong founder effects during colonization of Europe, East Asia, Africa and America, but little temporal variation.

The most recent whole mitogenome sequencing approach has revealed the fine phylogenetic structure of what is now termed "macro-haplogroup T" (Table 1). This is dissected in two clades, T1'2'3 and T5 [40,41]. The latter was a previously unknown haplogroup, reported only in Italy [104] and Croatia [83], while T1'2'3 is formed by the previously defined T1, T2 and T3. Haplogroup T4 turned out to be a derived sub-clade within T3 [41,42], probably spread over East Asia by a founder effect during the eastward migration of cattle.

The age estimates of super-haplogroup T (~16 ky), and those of T1, T2, T3 and T5 haplogroups were all compatible with the scenario that their founding haplotypes were present and directly involved in the

domestication event that occurred 10–11 ky ago in the Near East. The exception was T4 whose younger age is suggestive of an origin within domestic cattle, probably while diffusing from the Near East towards Eastern Asia [39,40,42]. Haplogroup T4 was not observed in the west, but has been found in East-Chinese ancient DNA dating to 4500 years ago [115], in modern Korean beef cattle [39] and in more than half of the Japanese cattle [103]. The high T4 frequency (21%) in the Yakutian cattle and control-region haplotypes shared with European samples, suggested that the Yakutian cattle have prehistoric maternal ancestries in domesticated Near Eastern cattle indicating a link between the Yakut and cattle from East-China [73].

Complete mtDNA sequences have allowed not only an accurate phylogeny, but even strengthened a Southwest-Asian origin for all major T haplogroups, including the African T1 and East-Asian T4 [41, 116].

A recent comprehensive phylogenetic analysis of 64 T1 mitochondrial complete genomes identified eight haplotypes as founders of the African T1 population [41].

Estimates of coalescence times for the T1 sub-haplogroups (6200 to 12,900 years ago) 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. Sporadic in the Old World it reaches 31% of frequencies of in the Caribbean Lesser Antilles islands and even 50% in Brazilian Criollo cattle. Data also suggest that one sub-haplogroup, T1d, might represent a mitochondrial line that has developed in the African continent shortly after the domestication event in the Near East, while T1c1a1, found for the first time in an African breed, it probably originated in North Africa, reached the Iberian Peninsula and sailed to America, with the first European settlers [41]. Ancient gene flow across the Gibraltar Strait has been recently confirmed also by SNP genotyping [117]. Recent data from ancient Neolithic/Chalcolithic Iberian cattle population have pointed out that T1 haplogroup already exists simultaneously in South-Western Europe [118]. Up to date there are no data for the presence of T1 haplogroup in ancient South-Eastern Europe.

The frequency of the T3 haplogroup increases from ~40% in South-West Asia to almost 100% in North-West Europe, with a concomitant decrease of T2. The latter has appreciable frequencies in Italian, Balkan and Asian taurine cattle, but is found only sporadically in the remaining European regions, Northern Africa and in bones from France dating to 5000 years ago [113] and in Switzerland derived from the Roman period [119].

Data available from ancient DNA confirmed that most Neolithic European cattle already carried T3 haplotypes [120,121]. This is in accordance with Bayesian analysis of taurine mtDNA variants coalescence, showing population expansion during the last 10 ky [122]. Even if T3 haplogroup is dominant in Europe and North-Central Asia [40,41,73,75,88,102,123,124], two interesting exceptions in Europe are remarkable:

- i) four ancient breeds from Tuscany have almost the same mtDNA diversity as found in Southwestern Asia, suggesting an ancient maternal origin and a direct link between Tuscan and Western-Asian cattle [125]. For the Chianina breed this was confirmed by microsatellite data [126]. Microsatellites also indicated that the Maremmana and the Cabannina, the two other Tuscan breeds, have been subject to Podolian and Brown Mountain breed introgression respectively.
- ii) the appreciable frequencies of T1 haplogroup in several Spanish and Portuguese breeds, indicated migration from Africa to the north. This may have occurred either during the Neolithic spread of cattle or later, for instance during the Islamic occupation. Importation of Iberian cattle into the newly discovered American continent explains the relatively high frequency of the T1 haplogroup in Caribbean and South American cattle [75,127,128,129,130,131].



**Table 1**  
Sources and haplogroup affiliation for the *Bos taurus* complete mtDNA sequences.

Macroarea and breeds	T1'2'3	T1	T2	T3*	T3a	T3b	T3c	T3d	T4	T5	I	P	Q	R	Total	References and GenBank accessions	
<b>America</b>		<b>5</b>													<b>5</b>		
Creole		5													5	[41]	
<b>Eastern Asia</b>			<b>2</b>	<b>13</b>	<b>2</b>	<b>4</b>			<b>6</b>		<b>3</b>				<b>30</b>		
Hanwoo			1	1											2	[147]; HQ025805	
Japanese Black						4				3					7	AB074962-AB074968	
Korean			1	12	2				3						18	AY526085; DQ124371-DQ124386; NC006853	
Mongolian														1	1	[40]	
Nandan														1	1	KT033901	
Unknown														1	1	KP143771	
<b>Iran and Iraq</b>		<b>1</b>	<b>5</b>	<b>5</b>						<b>2</b>	<b>3</b>				<b>16</b>		
Iranian			4	2											7	[39]	
Iraqi		1	1	3										2	2	9	[39]
<b>Greece</b>			<b>2</b>												<b>2</b>		
Greek			2												2	[39]	
<b>Northern Europe</b>		<b>2</b>	<b>1</b>	<b>24</b>	<b>2</b>	<b>20</b>	<b>2</b>	<b>2</b>	<b>1</b>		<b>1</b>				<b>55</b>		
Angus		1		7		7		1							16	[148]; AY676857; AY676859; AY676862-AY676873	
Charolaise				1		1									2	AY676858; AY676861	
Fleckvieh				1											1	[149]	
Galbvieh				1											1	AY676860	
Heck cattle						1									1	HM045018	
Holstein-Friesian				7	2	5			1		1				16	DQ124403-DQ124418	
Hungarian Grey						1									1	GQ129207	
Limousine		1	1												2	[41]; AY676856	
Longhorn				1											1	[148]	
Red Mountain				2		3		1							6	[150]	
Simmental				1											1	AY676855	
Ukrainian grey						1									1	GQ129208	
White Park				3		1	2								6	[151]	
<b>Iberian Peninsula</b>		<b>2</b>		<b>2</b>											<b>4</b>		
Alentejana		2													2	[41]	
Betizuak				2											2	[39]	
<b>Italy</b>	<b>1</b>	<b>35</b>	<b>6</b>	<b>12</b>	<b>1</b>	<b>6</b>				<b>2</b>			<b>16</b>	<b>10</b>	<b>89</b>		
Agerolese		3												1	4	[40,41]	
Bruna		1													1	[41]	
Cabannina	1		2										3		6	[39,104]	
Calvana		1													1	[41]	
Chianina		8	3	3		4							5		23	[39,40,104,41]	
Cinisara		5		1										2	8	[39,40,41]	
Frisona italiana		1		3											4	[39]	
Grigia Alpina													2		2	[104]	
Marchigiana		7												1	8	[104,41]	
Maremmiana		3		2											5	[39,41]	
Modicana				1											1	[39]	
Pettiazza				1											1	[39]	
Pezzata rossa italiana				1									1		2	[40]; JQ967333	
Piemontese						1				1					2	[39]	
Podolica		3			1										4	[39,41]	
Rendena			1												1	[39]	
Romagnola		3											5	6	14	[40,104,41]	
Valdostana						1				1					2	[39]	
<b>Malta</b>							<b>1</b>	<b>1</b>							<b>2</b>		
Maltese							1	1							2	[43]	
<b>Northern Africa</b>		<b>18</b>	<b>6</b>	<b>5</b>									<b>2</b>		<b>31</b>		
Domiati		8	3	1									2		14	[41,42]	
Menofi		10	3	4											17	[41,42]	
<b>Africa</b>		<b>36</b>													<b>36</b>		
Nguni		34													34	[152]	
Sheko		2													2	[41]	
<b>Unknown</b>	<b>1</b>	<b>2</b>	<b>20</b>		<b>2</b>				<b>3</b>		<b>1</b>				<b>29</b>		
Hybrid bison/cattle				12											12	[148]	
Unknown		1	2	8		2			3					1	17	[153]; DQ124387-DQ124402	
<b>Total</b>	<b>1</b>	<b>100</b>	<b>24</b>	<b>81</b>	<b>5</b>	<b>32</b>	<b>3</b>	<b>3</b>	<b>10</b>	<b>4</b>	<b>7</b>	<b>1</b>	<b>18</b>	<b>10</b>	<b>299</b>		

In bold: total number of mtDNAs in the specific macroarea. T3\*: all T3 mtDNAs that did not cluster within any of the defined subclades.

The most recent finding based on both prehistoric aurochs and cattle populations defined a new Balkan-specific T6 haplogroup and argued the possibility for an independent event of Neolithic cattle domestication on the South-eastern Balkans followed by a second wave of parallel dissemination of cattle herds via the Mediterranean route [132].

Although the vast majority of modern cattle harbor mitogenomes belonging to haplogroups T and I, other haplogroups have been

identified (named Q, P and R), all radiating prior to the T node, thus phylogenetically closer to T than to I (Table 1). Haplogroup P was the most common haplogroup in European aurochs and has so far been identified in only two modern cattle [39,133]. Its occurrence in the modern cattle gene pool is generally explained by rare introgression events between female European aurochs and domesticated cattle introduced from the Near East [40]. Haplogroup Q is relatively close to

haplogroup T sequences and has been suggested to have entered the cattle mtDNA gene pool during the initial domestication process in the Near East. In contrast, haplogroup R is phylogenetically very distinct from P, Q and T and has so far only been found in modern Italian cattle [104]. As haplogroup P, it most probably represents a remnant of introgression from wild aurochs into the early domestic cattle gene pool.

While there is very little doubt that the uncommon haplogroups P and R are derived from European wild aurochs cows either because of sporadic interbreeding events (naturally occurring and/or human-mediated) or possibly, in the case of haplogroup R, as consequence of a minor event of *B. primigenius* domestication in Italy [104], the origin of haplogroup Q is less clear.

With an estimated age of about 48 ky for the QT node, haplogroup Q is the closest to super-haplogroup T; it was first discovered in a local Italian breed (Cabannina, two mtDNAs with the same haplotype), following other fourteen additional Q mitogenomes, but all derived from Italian breeds (Cabannina, Chianina, Grey Alpine, Italian Red Pied, and Romagnola) [39,40,104]. Haplogroup Q is found both in ancient Neolithic and modern cattle [80,104].

A recent phylogenetic analyses conducted on 31 Egyptian mitogenomes from Nile Delta taurine breeds confirmed the prevalence of haplogroup T1 in North African cattle, but also showed rather high frequencies for haplogroups T2 (19.4%), T3 (16.1%) and Q1 (6.5%), with an unexpected extreme haplotype diversity [42]. Researchers argued that the Egyptian Q1 mitogenomes are direct local derivatives from Q1 founder mtDNAs brought to Egypt by the first domestic herds. In other words, similar to T1, T2 and T3, Q1 was among the haplogroups involved in domestication in the Near East, from where it spread along with the others. Recent data on the ancient cattle population (from Neolithic to Bronze ages) have shown predominate presence of Q haplogroup up to 50% in Iran (7000–5000 BC) as well as in South-Eastern Europe (the Balkans, 6200–2200 BC) [100] and in a Northern Finnish Post-Medieval sample [134]. The new Q1 lineage found in the Pirenaica extend the geographical distribution of the Q haplogroup to the south-west of the European continent [135].

Regarding zebu cattle, mtDNA sequences allowed the identification of two major haplogroups: I1 and I2. These indicine maternal lineages diffused from South Asia to Southwest and Central Asia [136,137]. Haplogroups I1 predominated in the cattle that moved eastwards to Southeast Asia and China. I2 haplogroup is a rare and more ancient than I1 haplogroup; it was only detected in Yunnan–Guizhou Plateau, Tibet region and Mongolia [123,138,139].

Chen and colleagues [136] suggested that zebu domestication involved at least two different wild female populations [140] or, more likely, a single domestication event in the Indus Valley with a subsequent introgression process of wild (I2) females into proto-domesticated herds. Populations with a mixed taurine and indicine maternal origin are found in Southwest Asia, Central Asia, China, Mongolian and Brazil [8].

Finally, two haplogroups, termed E and C, have been reported only in ancient specimens and are probably extinct. Haplogroup, E, was identified in a 6 ky old aurochs from Germany [80,133], while haplogroup C was found in a specimen that might represent an early Holocene attempt to manage cattle in northern China [141].

## 6.2. The male perspective of the Y chromosome variation

In contrast to mtDNA, which shows the maternal origin and therefore stays with the herds, Y chromosomal haplotypes are markers of paternal origin and male introgression.

Generally Y chromosome phylogenetic surveys are few and most have been focused on taurine and zebuine crosses [53,80,142,143]. Furthermore, lower levels of genetic diversity have been found in the Y chromosome than in autosomes, probably due to commonly used breeding schemes of a few selected males that produce a large number of offspring [81,144]. The identification of five SNPs has permitted the classification of extant breeds into three Y-chromosome haplogroups, named Y1, Y2 and Y3 [106] (Fig. 1 and Table 2). Y3 haplogroup was identified only in zebu, while Y1 and Y2 are so far the two major and well divergent. Y1 was found to be predominant in

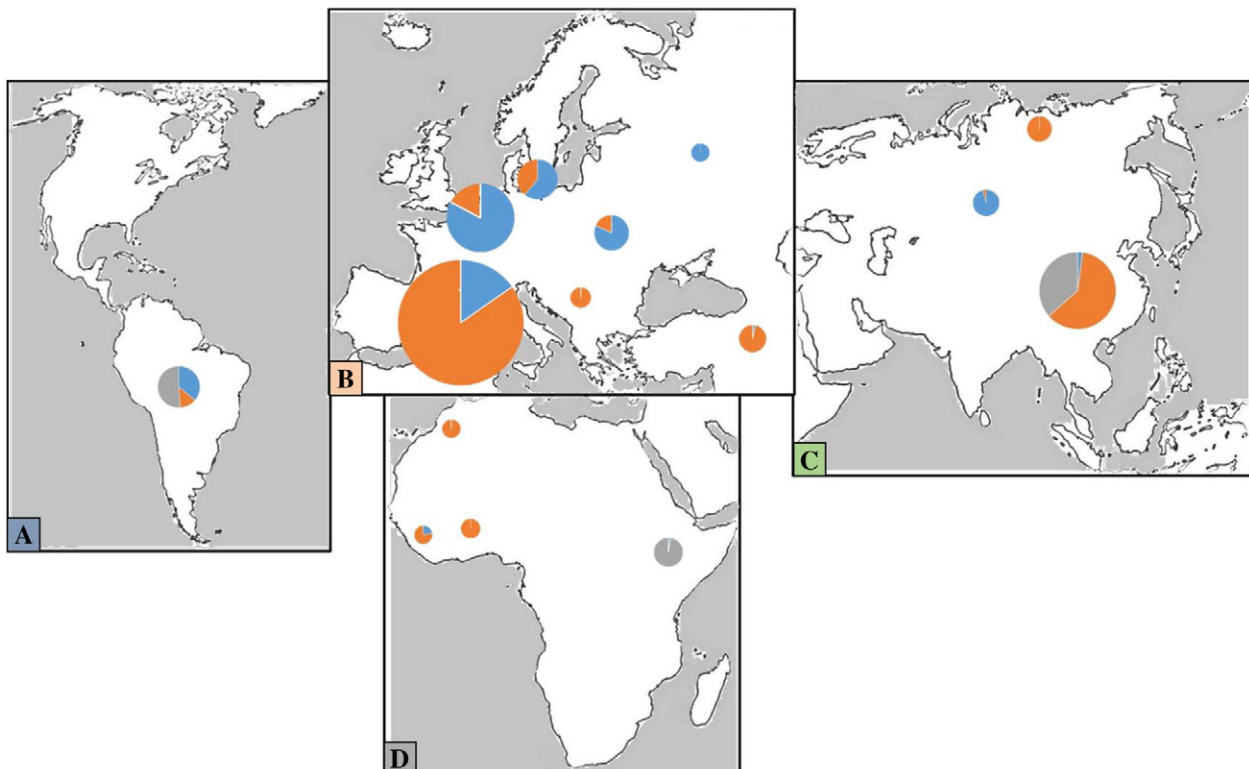


Fig. 1. Geographical distribution of the Y haplogroups among the world's cattle breeds (for further details see Table 2).

Table 2

Sources and Y haplogroup distribution for the *Bos taurus* in the world.

Region	Section map	Number of breeds/populations	Y1	Y2	Y3	Reference
South of America	A	158	57	20	81	[75]
Eastern Europe		65	53	12	-	
Northern Europe		184	112	72	-	
Southern – central Europe	B	1543	236	1307	-	
Southeastern Europe		10	-	10	-	
Western Europe		404	334	70	-	[134] [39]
Anatolia peninsula		32	1	31	-	
Western Russia		9	9	-	-	
Central Russia		25	24	1	-	
Russian Siberia	C	23	-	23	-	
China		584	12	359	213	[153]
Morocco	D	10	-	10	-	
Burkina Faso		8	-	8	-	[74]
Guinea		9	2	7	-	
Ethiopia		40	1	-	39	[81]

The colours identify the four section maps reported in Fig. 1.

northern European and in north Spanish breeds, has a low frequency in Southwest Asian bulls and it is carried by male offspring of recent European imports [50]. Y2 is prevalent in Central and South Europe, with a clear dividing zone in central Europe [43,50], and Anatolian and African taurine bulls. Remains of European aurochs bulls for which their wild origin was validated via their mtDNA all carried Y2 haplotypes [105]. Since these cannot yet be differentiated from European or Southwest Asian Y2 haplotypes, this neither proves nor disproves wild male introgression. Wild-domestic crossbreeding was suggested by intermediate sized Neolithic bones found in what is now the Czech Republic [145]. The Y1 distribution pattern is interpreted as reflecting later expansion of dairy breeds [50,105,106]. Specific Y2 haplotypes provides evidence for introgression of African aurochs in domestic herds [6,124]. An African origin of taurine cattle, in spite of a Southwest Asian maternal origin, has been confirmed by autosomal SNPs analysis [117].

Overall a north–south gradient of genomic diversity in modern European cattle has been reported, resulting in an almost complete fixation of the Y1 type in the contemporary northern cattle breeds most likely due to recent demographic events [106,134].

Some authors assessed the paternal gene pools of cattle breeds and the influence of foreign bulls during crossings by microsatellite markers. A set of five cattle Y-specific microsatellite loci was surveyed in several cattle breeds reared in different geographical areas [6,50,73] or local breeds such as Ethiopian cattle [81], Portuguese cattle [72], the [59] and from Poland [146].

These studies have allowed for refined analyses of the genetic diversity of paternal lineages, identifying several Y-haplotypes within major haplogroups. However, with the exception of INRA189 marker, an overall low diversity of the Y-chromosome markers was observed, possibly due to either a low mutation rate or selection affecting the allelic diversity [50,59,72,146].

It has been also shown that particular microsatellite alleles were either indicus-specific allele, such as INRA189 (88 bp) [76], INRA124 (130 bp) [53,76] and BM861 (156 bp) [60,76], or were found only in a few individuals from indigenous breeds of different geographical origin, specifically INRA189 (90 bp), INRA189 (82 bp) [73] and INRA124 (134 bp) [60].

## 7. Conclusions

The outcome of combined mitogenome analyses and Y chromosomal studies has greatly improved our understanding of the origin of extant cattle, providing the reconstructing of its evolutionary history. However, refined comparative analyses with preserved *B. primigenius* specimens highlighted the complexity of the cattle domestication process and left some question unsolved.

Uniparental genetic systems contributed essentially both to the male and female heritage reconstructions by providing geographic and historic anchor points for specific breeding and conservation programs.

## Conflict of interest statement

The authors have no conflicts of interest to disclose.

## Acknowledgements

The authors want to thank the two anonymous referees for their valuable comments and constructive suggestions.

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