

# African matrilineages in American Creole cattle: evidence of two independent continental sources

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## Summary

In order to clarify the historical origin and phylogeographic affinities of Creole cattle matrilineages throughout the American continent, we analysed published D-loop mtDNA sequences ( $n = 454$ ) from Creole, Iberian and African cattle breeds. The Western European T3 haplogroup was the most common in American Creole cattle (63.6%), followed by the African T1 (32.4%) and the Near Eastern T2 haplogroups (4%). None of the sequences were found in *Bos indicus* types. Within the African T1 haplogroup there were two subclades, T1a and T1\*, whose geographic distribution in America was clearly disjointed. T1a is a highly divergent clade originally reported for Creole cattle from Brazil and the Lesser Antilles, but whose geographic distribution in Africa remains unknown. In contrast, lineages attributable to T1\* are restricted in America to the region colonized by the Spaniards. We propose a new hypothesis for the origins of Creole cattle that summarizes all previously published historical and genetic data. While the African T1\* fraction in Creole cattle may have arrived in America through the Iberian breeds, the divergent T1a lineages may have been introduced by Portuguese and other European crowns from some unknown, not-yet-sampled African location. Additional molecular studies will be required for pinpointing the specific African regional source.

**Keywords** *Bos taurus*, Creole cattle, migration routes, mitochondrial DNA phylogeny.

Nowadays, there are Creole cattle breeds in almost all American countries (<http://www.ansi.okstate.edu/breeds/cattle/>). Cattle were first introduced to the American continent by the Spanish conquerors, who transported the first animals to the Caribbean Islands after the second trip of Columbus in 1493. However, some of the Caribbean Islands, in particular the Lesser Antilles, were colonized by other European countries such as the UK, France and the Netherlands. By the first half of the 16th century, Spanish conquerors moved cattle from the Caribbean Islands to their continental settlements (De Alba 1978; Wilkins 1984; Primo 1992; Felius 1995). Direct shipments of Portuguese cattle to Brazil have also been reported (De Alba 1978; Primo 1992).

During the last few years, four studies were published describing mtDNA control region polymorphisms in

American Creole cattle breeds (Magee *et al.* 2002; Miretti *et al.* 2002, 2004; Carvajal-Carmona *et al.* 2003; Mirol *et al.* 2003), supporting the existence of African and European mtDNA haplotypes. However, each of these studies had only a partial geographical subset of data. Based on all published data together, we propose a new hypothesis for the origin of Creole cattle and provide an alternative explanation for the existence of a disjointed geographic distribution of African subgroups in the Americas.

A total of 454 bovine mitochondrial DNA control region sequences from South America, Caribbean, Iberia and Africa were included in the analysis (Table 1). A 240-bp D-loop fragment spanning positions 16023–16262 in the complete mitochondrial genome sequence (V00654; Anderson *et al.* 1982) was aligned with ClustalW, and median joining (MJ) networks were constructed using the median algorithm of Bandelt *et al.* (1995) according to NETWORK 4.1 (<http://www.fluxus-engineering.com/sharenet.htm>).

Haplogroup T3, the most prevalent in Western Europe, was also the most commonly found in American breeds, with an overall frequency of 0.64. The common sub-Saharan haplogroup T1 was found 81 times (32%), while haplogroup T2, which is frequently observed in the Near

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**Table 1** Percentage of mtDNA haplogroup sequences with substitutions for each geographic region. These regions include breeds described in Fig. 1.

Breed	n	Haplogroups			
		T1*	T1a	T2	T3
Colombia <sup>1</sup>	110	26	–	9	65
Argentina and Bolivia <sup>2,3</sup>	23	30	–	–	70
Brazil <sup>4</sup>	30	–	53	–	47
Caribe <sup>5,6</sup>	87	2	31	–	67
Portugal <sup>7</sup>	49	22	–	–	78
Spain <sup>8,9</sup>	40	12	15	–	73
West Africa <sup>7,8,9</sup>	103	98	–	–	2

<sup>1</sup>Carvajal-Carmona *et al.* 2003.

<sup>2</sup>Miretti *et al.* 2004.

<sup>3</sup>Mirol *et al.* 2003.

<sup>4</sup>Magee *et al.* 2002.

<sup>5</sup>Miretti *et al.* 2002.

<sup>6</sup>Cymbron *et al.* 1999.

<sup>7</sup>Troy *et al.* 2001.

<sup>8</sup>Loftus *et al.* 1994a,b.

<sup>9</sup>Bradley *et al.* 1996.

East with a minor presence in European breeds, was detected in only 10 individuals (4%). We grouped the reported sequences into four regions on the South American continent based upon colonial America geo-political criteria: former Spanish viceroyships of Nueva Granada (Colombia), Rio de la Plata (Argentina and Bolivia), former Portuguese colony (Brazil) and non-Spanish/non-Lusitan Lesser Antilles. The distribution of the haplogroups was heterogeneous, varying significantly both among and within the four regions (Table 1, Fig. 1).

The African T1 mtDNA lineages described for American Creole breeds can be sorted into two clusters. We define here the monophyletic sub-haplogroup T1a as the one that contains those sequences that share four transitions at positions 16053, 16122, 16139 and 16196 with respect to the nodal T1 haplotype, itself defined by the co-existence of three transitions with respect to the nodal T3 haplotype (Troy *et al.* 2001). For the sake of simplicity, the remaining T1 sequences were grouped in the paraphyletic cluster T1\*, composed by the nodal T1 haplotype and those departing by 1–5 mutations from it.

Lineages attributable to T1\* were described by Bradley *et al.* (1996) and Troy *et al.* (2001) in breeds from North, East and West Africa, as well as in Iberian breeds from Portugal (Cymbron *et al.* 1999), Spain (Miretti *et al.* 2004) and American Creole (Miretti *et al.* 2002; Carvajal-Carmona *et al.* 2003; Mirol *et al.* 2003). Sequences of the sub-haplogroup T1a were initially reported for the Creole cattle from the Caribbean Islands of Antigua, Guadeloupe and St Lucia, as well as for the 'zebu' Nelore Brazilian breed (Magee *et al.* 2002), the Brazilian Creole (Miretti *et al.* 2002) and the Retinta breed from Spain (Miretti *et al.*

2004). Interestingly, these sub-haplogroups showed a reciprocal disjointed geographical distribution; while T1\* was found in Argentina, Bolivia and Colombia (former Spanish colonies), T1a was restricted to Brazil and the non-Spanish Caribbean Islands (Fig. 1).

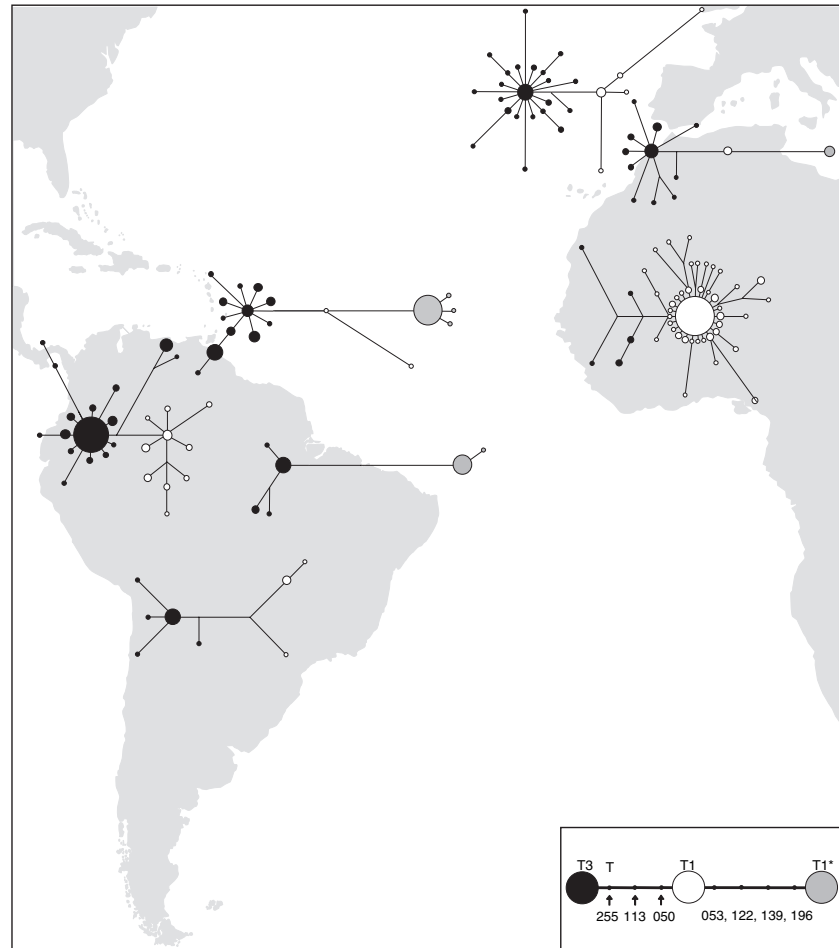
Different explanations have been proposed for the geographical origin of 'African' lineages. Surprisingly, Miretti *et al.* (2004) postulated that haplogroup T1a (AA1 in their nomenclature), which is restricted to the non-Spanish ex-colonies, would have originated in Spain, while T1\* would have arrived in America from West Africa. Carvajal-Carmona *et al.* (2003) explained the presence of haplogroup T1\* in Colombia as originating from North Africa, probably as the result of the Arab occupation of Iberia prior to European migration to the New World. Finally, Magee *et al.* (2002) suggested that the African influence in Creole is, at least in part, attributable to the direct historical importation of West African cattle to the Caribbean.

The present-day Iberian pattern of African introgression does not easily reconcile with the American Creole pattern (Fig. 1, Table 1). In fact, only T1\* haplotypes have been found in Portuguese cattle breeds (Cymbron *et al.* 1999), in contrast with the situation in the former Portuguese colony of Brazil, where only T1a lineages have been reported (Miretti *et al.* 2002).

The pattern of African mtDNA occurrences in present-day Retinta cattle is also puzzling. Given its geographical distribution as the most common breed in southern Spain, Retinta shares a recent common ancestor with the American Creole cattle but possesses African T1a lineages at high frequency (0.375; Miretti *et al.* 2004), in sharp contrast with the Creole breeds present in the former Spanish colonies, where only T1\* has been detected. This apparent disagreement is reconcilable when we consider that southern Iberian breeds were often crossed with Nelore females in the 1960s to 1970s (Sanchez-Belda 1984; Beja-Pereira *et al.* 2003). The finding of T1a in present-day Retinta animals may be a consequence of recent gene flow from Brazilian Creole cattle through Nelore dams rather than its ancient presence in the Iberian Peninsula. This scenario is further supported by the finding of greater haplotype diversity in American vs. Iberian T1a lineages: while four haplotypes have been reported in the Americas, only one is found in Europe.

We propose a hypothesis that may explain the discordance between Iberian and American patterns of mtDNA diversity, which is an alternative to the introduction of the African haplotypes from Iberia. This hypothesis suggests the possibility of introgression of at least part of the African mtDNA haplotypes from somewhere in mainland Africa, perhaps following the slave trade routes (Rouse 1973; Maillard *et al.* 1993; Felius 1995). The restricted presence of T1a in American Creole cattle from the Lesser Antilles and Brazil supports this hypothesis. This clade has not yet been found in African or European breeds, with the exception of

**Figure 1** Median-joining (MJ) networks were constructed using the median algorithm of Bandelt *et al.* (1995). For comparative purposes, 240 bp of the bovine mitochondrial DNA control region from 454 sequences were grouped in seven geographical regions. Median-joining networks are shown for: Spain, Portugal, Africa, Caribbean Islands, Brazil, Colombia and Argentina plus Bolivia. The relationship between European (T3, black circles) and African (T1a, white circles) central haplotypes is defined by transitions at nucleotide positions 16255, 16113 and 16050, while the African T1\* haplogroup (gray circles) diverges from T1a in four transitions at position 16053, 16122, 16139 and 16196. Haplogroup T2 – defined by transitions at 16185 and 16255 plus a transversion at 16 057 – is included with the European T3. Circle areas are proportional to the frequency of each haplotype. Lines connecting circles denote nucleotide substitutions.



Retinta (as discussed above). The apparent absence of T1a in Africa is a probable consequence of limited geographical sampling, because only one North- and several East- and West-African breeds have been examined (Bradley *et al.* 1996; Troy *et al.* 2001). Furthermore, T1a is a highly divergent star-shaped clade composed of only five haplotypes, four of which are present in single individuals and are one-step derivatives from the nodal haplotype (Fig. 1). This reduced variability points to a restricted geographical origin for T1a lineages present in America and to a rapid and recent diversification of the haplogroup.

In conclusion, the presence of both African and European mtDNA lineages in Creole cattle is indisputable, but our analysis suggests the existence of two independent continental sources for the African component in the American cattle. While the African T1\* fraction in Creole cattle may have arrived in America through the Iberian breeds, we propose that the divergent T1a lineages stem from some unknown, not-yet-sampled African location, and may have reached the continent in parallel with the slave trade. In addition, the disjointed distribution of the different African matrilineages in America correlates with the former colonial political entities, with T1\* present in the previous Spanish continental colonies and T1a in

Brazil and the Lesser Antilles, both under the rule of the Portuguese and other European crowns. Additional molecular studies are required for pinpointing the specific African regional source.

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