



Detecting the T1 cattle haplogroup in the Iberian Peninsula from Neolithic to medieval times: new clues to continuous cattle migration through time



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ABSTRACT

The spread of domestic animals through time is one of the topics studied by archaeologists to assess human trade and migration. Here we present mitochondrial analysis of 42 archaeological cattle (*Bos taurus*) bone samples, from 16 different sites in the Iberian Peninsula and covering a broad timeframe (from the early Neolithic to the Middle Ages), to provide evidence about the origin and dispersion of the T1 cattle haplogroup in relation to human contacts and movements. The presence of the T1 haplotype in one sample from an early Neolithic site close to the Mediterranean coast of Iberia, and its continuing presence in the Peninsula during Roman and Medieval times, clearly demonstrates that T1 was not solely a Muslim or later introduction. Rather, our molecular data show evidence for a pioneer coastal colonisation of the Iberian Peninsula from the Mediterranean basin, followed by possible further colonisation, leading to a continuity of diversity through time.

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1. Introduction

The origin and diversification of domestic taurine cattle (*Bos taurus*) has been extensively investigated using mitochondrial (mt) DNA analyses of both modern and ancient samples. The majority of modern taurine mtDNA sequences in Europe fall into one of four phylogenetically distinct, yet closely related, star-like haplogroups,

termed T, T1, T2 and T3. High diversity has been documented in Anatolia and the Middle East for both modern (Troy et al., 2001) and Neolithic and Bronze Age (Bollongino et al., 2006, 2012) specimens. The diversity in Europe and in Africa are both subsets of that seen in the Near East, with the most frequently observed haplogroups being T3 and T1 respectively. These results have been interpreted as a scenario of a single Neolithic origin of all T haplogroups in the Near and Middle East and a subsequent spread towards Europe and Africa (Troy et al., 2001; Bollongino et al., 2006; Lenstra et al., 2014). However, it appears that the process of cattle domestication and diffusion was more complex than

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originally thought, with a fifth haplogroup, T5, and two novel haplotypes (Q and R), recently reported from a small number of extant Italian cattle (Achilli et al., 2008, 2009). In addition, evidence of T3 being predominant in Italian aurochs (Beja-Pereira et al., 2006; Mona et al., 2010; Lari et al., 2011) is suggestive that at least some Mediterranean T3 maternal lineages may have a European, rather than a Southwest Asian, origin.

Similarly to T3 in Europe, T1 is fixed in the majority of extant African cattle (Lenstra et al., 2014), but it also found at low numbers in some contemporary Iberian, Italian and Greek breeds (Bradley et al., 1996; Cymbron et al., 1999; Beja-Pereira et al., 2006; Dadi et al., 2009; Bonfiglio et al., 2012). Research supports a spread of domestic T1 cattle from the Near East towards southern Europe and the Mediterranean basin during the Neolithic (Troy et al., 2001; Bollongino et al., 2006; Achilli et al., 2008; Lenstra et al., 2014), with the possibility that hybridisation occurred between migrating domestic populations from the Near East and resident wild African populations (Achilli et al., 2008; Decker et al., 2014).

Specifically for the Iberian Peninsula, different explanations for the presence of T1 mitotypes in Iberian cattle breeds have been hypothesised. There is evidence for a wholly or partially North African origin for domestic cattle in Iberia (Cymbron et al., 1999; Miretti et al., 2002; Anderung et al., 2005; Beja-Pereira et al., 2006; Ginja et al., 2010), and a number of time periods for these origins and subsequent migrations have been identified. Possible introgressions of North African cattle into Iberia have been attested to have occurred: (1) during the Muslim invasion and occupation in the 8th century AD (Cymbron et al., 1999, 2005; Beja-Pereira et al., 2006); (2) as a consequence of the colonial activities in the 18th century AD (Cymbron et al., 1999); or (3) due to recent gene flow from Africa derived in the 1960s and 1970s (Beja-Pereira et al., 2002, 2003). However, the T1 haplogroup has been observed in a single Bronze Age animal from the north of Iberia (Anderung et al., 2005), highlighting that T1 was not only a recent introduction into the area. Taking these considerations into account, the aim of the research reported in this paper was to understand the phylogeny of

Table 1

Data of archaeological Spanish cattle used in this study. Table of archaeological cattle samples studied, with associated information.

Lab code	Sample code	Site	Area	Period	Date	Fragment length	Haplogroup	Source
NEOL01	Spain 04	Cova de l'Or	Alicanti	Neolithic	5400 cal. BC	240 bp	T3	this study
NEOL02	Spain 05	Cueva del Mirador	Atapuercra	Neolithic	5400 cal. BC	240 bp	T3	this study
NEOL03	IBE6	La Draga	Girona	Neolithic	5213–5044 cal. BC	240 bp	T1	this study
BRON01	IBE4	Gatas	Almeria	Bronze Age	1900–1700 cal. BC	240 bp	T	this study
BRON02	MAD17	Portalón	Burgos	Bronze Age	1800 cal. BC	240 bp	T3	AY847199
BRON03	MAD2	Portalón	Burgos	Bronze Age	1780 cal. BC	240 bp	T3	AY847188
BRON04	MAD3	Portalón	Burgos	Bronze Age	1780 cal. BC	240 bp	T3	AY847189
BRON05	MAD5	Portalón	Burgos	Bronze Age	1780 cal. BC	240 bp	T3	AY847190
BRON06	MAD8	Portalón	Burgos	Bronze Age	1780 cal. BC	240 bp	T3	AY847192
BRON07	MAD9	Portalón	Burgos	Bronze Age	1780 cal. BC	117 bp	T/T3	AY847193
BRON08	MAD10	Portalón	Burgos	Bronze Age	1780 cal. BC	240 bp	T	AY847194
BRON09	MAD11	Portalón	Burgos	Bronze Age	1780 cal. BC	240 bp	T3	AY847195
BRON10	MAD14	Portalón	Burgos	Bronze Age	1780 cal. BC	240 bp	T3	AY847196
BRON11	MAD18	Portalón	Burgos	Bronze Age	1780 cal. BC	240 bp	T3	AY847200
BRON12	MAD51	Valparaiso de Abajo	Cuenca	Bronze Age	1780 cal. BC	240 bp	T3	AY847211
BRON13	MAD16	Portalón	Burgos	Bronze Age	1740 cal. BC	240 bp	T1	AY847198
BRON14	MAD6	Portalón	Burgos	Bronze Age	1635 cal. BC	240 bp	T3	AY847191
IRON01	MC36	St. Julià Ramis	Girona	Iron Age	5th–3rd c. BC	119 bp	T/T3	JX876556
ROMN01	MC37	Olivet d'en Pujol	Girona	Roman	1st c. BC	119 bp	T/T3	JX876557
ROMN02	MC38	Olivet d'en Pujol	Girona	Roman	1st c. BC	119 bp	T/T3	JX876558
ROMN03	MC1	Vilauba	Girona	Roman	1st c. AD	119 bp	T/T3	JX876553
ROMN04	MC9	Baetulo	Barcelona	Roman	2nd c. AD	119 bp	T/T3	JX876554
ROMN05	MC18	Vila Ametllers	Girona	Roman	1st–3rd c. AD	119 bp	T/T3	JX876555
ROMN06	IBE5	Son Fornés	Mallorca	Roman	2nd BC–1st c. AD	240 bp	T1	this study
ROMN07	EM20	Empúries	Girona	Roman	3rd c. AD	mosaic	?	this study
ROMN08	EM21	Empúries	Girona	Roman	1st c. AD	67 bp	T/T3	this study
ROMN09	EM22	Empúries	Girona	Roman	2nd c. AD	240 bp	T3	this study
ROMN10	EM26	Empúries	Girona	Roman	3rd c. AD	mosaic	?	this study
ROMN11	EM27	Empúries	Girona	Roman	3rd c. AD	316 bp	T3	this study
ROMN12	EM28	Empúries	Girona	Roman	1st c. AD	240 bp	T3	this study
ROMN13	EM50	Empúries	Girona	Roman	1st c. AD	316 bp	T3	this study
ROMN14	EM51	Empúries	Girona	Roman	2nd c. BC	316 bp	T3	this study
ROMN15	EM52	Empúries	Girona	Roman	1st c. AD	175 bp	T/T3	this study
ROMN16	EM55	Empúries	Girona	Roman	1st–3rd c. AD	mosaic	?	this study
ROMN17	EM57	Empúries	Girona	Roman	3rd c. AD	316 bp	T3	this study
ROMN18	EM80	Empúries	Girona	Roman	1st c. BC	316 bp	T1	this study
ROMN19	EM81	Empúries	Girona	Roman	2nd c. AD	203 bp	T1	this study
ROMN20	EM82	Empúries	Girona	Roman	3rd c. AD	175 bp	T/T3	this study
MIDD01	IBE2	Montsoriu	Barcelona	Middle Age	900–1200 AD	240 bp	T1	this study
MIDD02	MAD47	Cueva de Joaquin	Teruel	Middle Age	1120 AD	117 bp + 100 bp	T3	AY847208
MIDD03	MAD19	San Pablo	Burgos	Middle Age	1300–1500 AD	240 bp	T3	AY847201
MIDD04	MAD20	San Pablo	Burgos	Middle Age	1300–1500 AD	240 bp	T3	AY847202
MIDD05	MAD22	San Pablo	Burgos	Middle Age	1300–1500 AD	117 bp + 100 bp	T3	AY847203
MIDD06	MAD23	San Pablo	Burgos	Middle Age	1300–1500 AD	240 bp	T3	AY847204
MIDD07	MAD25	San Pablo	Burgos	Middle Age	1300–1500 AD	240 bp	T3	AY847205

haplogroup T1 in the Iberian Peninsula and the processes that led to its current geographical and breed distribution.

2. Methods

2.1. Samples

Archaeological bones were collected from 20 *Bos taurus* samples retrieved from archaeological sites located in different areas of the Iberian Peninsula (Table 1; Fig. 1). The time periods included were Neolithic, Bronze Age, Roman and Middle Ages.

2.2. Sample extraction and amplification

DNA was successfully amplified from 17 of the 20 samples in three laboratories (Cambridge, Dublin and Grenoble) exclusively dedicated to ancient DNA analyses. Extraction, contamination control and amplification reactions were as described previously (Edwards et al., 2004; Campana, 2007), and followed standard ancient DNA practice. For each sample, at least two independent DNA extractions were performed and extraction and PCR negative controls all produced negative results. 252 base pairs (bp) [16,042–16,158 and 16,179–16,313; see Bollongino et al. (2006) for primer details] of the hypervariable control region of the mitochondrial genome were sequenced. Samples from the Roman site of Empúries were amplified with primers detailed in Campana (2007) [namely BT1F–BT3R, BT2F–BT2R, BosCentreF–BosCentreR and BT1F–BTRUTH], which amplified a longer 316 bp sequence. Five of the 11 samples from Empúries that had endogenous DNA generated this full 316 bp fragment (Table 1).

Inter-lab replication, including sample preparation, extraction and PCR, was undertaken on four samples (NEOL03, BRON01, ROMN06 and MIDD01) and the sequences obtained were consistent across laboratories.

2.3. Data analyses

Sequences from 25 published archaeological cattle were included in the analyses (Anderung et al., 2005; Colominas et al., 2014) to give a total dataset of 42 ancient cattle sequences from Iberia. This is the largest dataset presented from this region. Moreover, a total of 1130 mtDNA sequences from European and African *Bos taurus* (from GenBank) were used to compare archaeological cattle diversity to that of the present day. Details of the number of individuals, breed of origin and geographical areas are shown in Table S1.

The mtDNA sequences were aligned in MEGA (ver. 6; Tamura et al., 2013) to the reference sequence published in Troy et al. (2001), and all were truncated to 240 bp. Median-joining networks were constructed following Bandelt et al. (1995). A three-dimensional statistical parsimony network was constructed using the R script TempNet (found at <http://web.stanford.edu/group/hadlylab/tempnet/>; Prost and Anderson, 2011). In addition, analyses of inter-population genetic distances between extant and ancient populations were performed in ARLEQUIN (ver. 3.5; Excoffier et al., 2007) using published modern regional data from native breeds (Table S1; Cymbron et al., 1999; Troy et al., 2001; Miretti et al., 2002; Beja-Pereira et al., 2006; Pellicchia et al., 2007; Ginja et al., 2010) in ARLEQUIN (ver. 3.5; Excoffier et al., 2007).

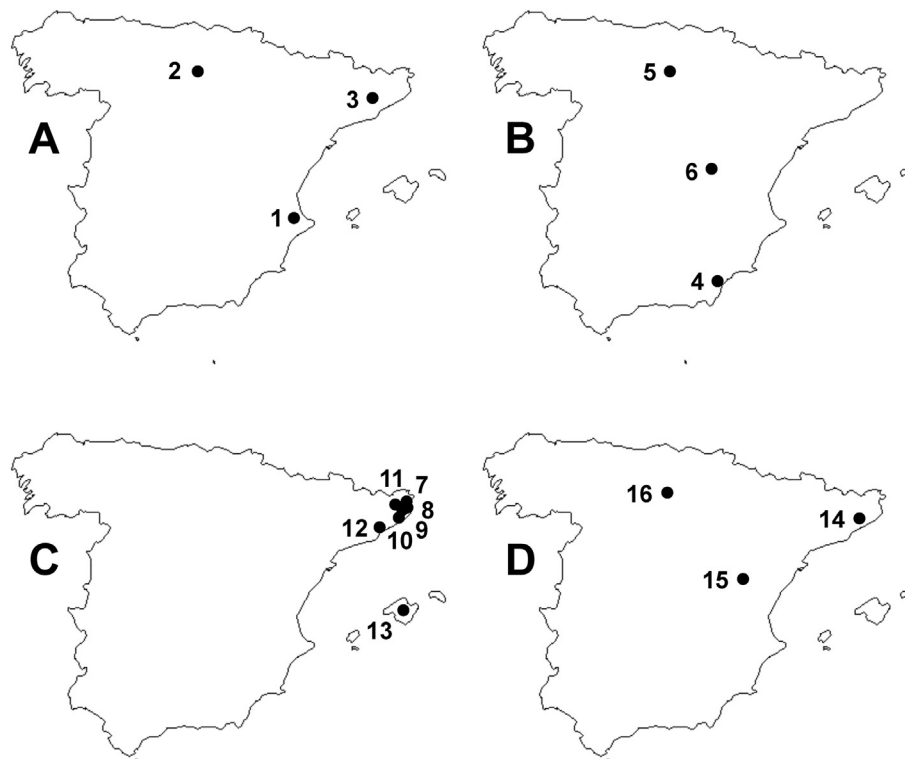


Fig. 1. Location of archaeological Iberian sites by period. (A) Neolithic (5400–5000 cal. BC): 1, Cova de l'Or, Alicante; 2, Cueva del Mirador, Atapuerca; 3, La Draga, Girona. (B) Bronze Age (1900–1600 cal. BC): 4, Gatas, Almería; 5, Portalón, Burgos; 6, Valparaiso de Abajo, Cuenca. (C) Iron Age to Roman (5th c. BC to 3rd c. AD): 7, St. Julià Ramis, Girona; 8, Empúries, Girona; 9, Olivet d'en Pujol, Girona; 10, Vila Ametllers, Girona; 11, Vilauba, Girona; 12, Baetulo, Barcelona; 13, Son Fornés, Mallorca. (D) Middle Age (900–1500 AD): 14, Montsoriu, Barcelona; 15, Cueva de Joaquín, Teruel; 16, San Pablo, Burgos.

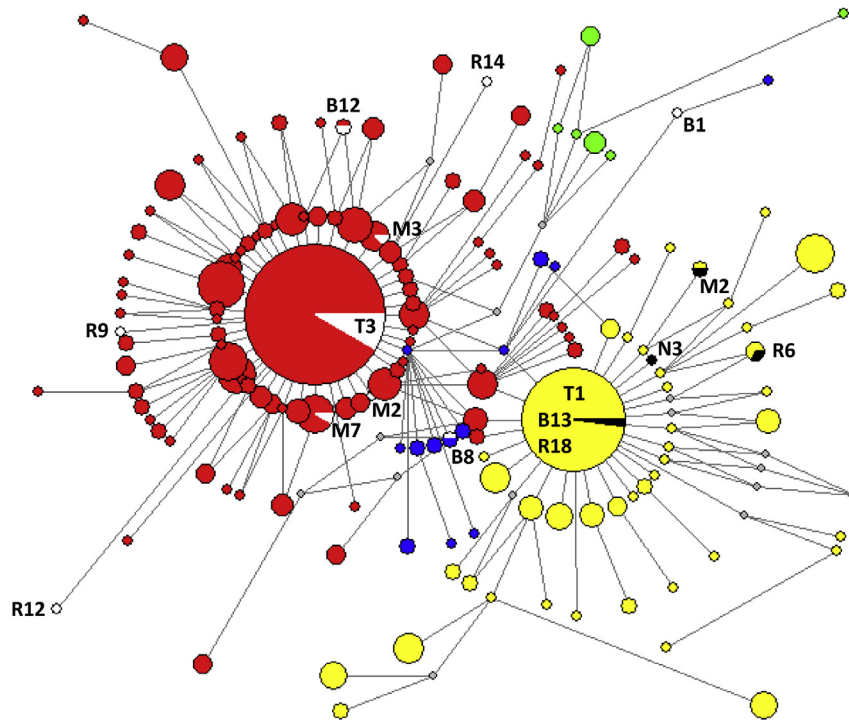


Fig. 2. Median-joining network comparing 13 novel and 16 published archaeological cattle sequences with extant native North African and Iberian breeds. Median-joining network drawn using 240 bp fragment to compare the 29 archaeological samples (13 novel and 16 previously published; Table 1) with 159 individuals from 9 modern North African native breeds and 447 individuals from 24 modern Iberian native breeds (Table S1). Circles are coloured according to which haplogroup the sequences belong to: blue = T; yellow = T1; green = T2; red = T3. Ancient samples are highlighted – T and T3 ancient haplotypes are shown in white, and T1 ancient haplotypes are shown in black. Notable haplotype assignments are indicated (labelled as in Table 2), with N = Neolithic, B = Bronze Age, R = Roman, and M = Middle Age. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

Amplification of a 240 bp section of the control region was successful in 13 of our samples, with a further four samples yielding sequence data of less than 240 bp in length. The sequences were aligned against a highly polymorphic region of the control region as characterised by Troy et al. (2001) (Table 2). All archaeological samples gave sequences similar to those encountered in modern native cattle. The dominant feature among the archaeological samples was the predominance of the T3 haplotype (eight samples). Five individuals had identical sequences to the T3 reference sequence (NEOLO1, NEOLO2, ROMN11, ROMN13 and ROMN17). In addition, a further three individuals grouped within T3 haplotypes, but with one or more nucleotide substitutions (ROMN09, ROMN12 and ROMN14), and one sample (BRON01) had a T haplotype. Three samples, where the full sequence could not be generated (ROMN08, ROMN15 and ROMN20), could only be classified as T/T3, due to the non-amplification of the diagnostic 16,255 position.

Five individuals belonged to haplogroup T1 (Table 2). One individual had an identical sequence to the T1 reference sequence (ROMN18) and four others exhibited a T1 haplotype (NEOLO3, ROMN06, ROMN19 and MIDD01). One individual is from the Neolithic period (La Draga), three are from Roman chronologies (Son Fornés and Empúries) and one is from the medieval period (Montsoriu) (Table 1; Fig. 2).

These data were compared with published archaeological mtDNA sequences from Iberia (Table 1), establishing a data set of 42 ancient cattle sequences from different time periods, the largest dataset presented from Iberia. From this published data, one individual had a T1 haplotype, a sample from the Bronze Age site of Portalón (Anderung et al., 2005). All other individuals, dating from

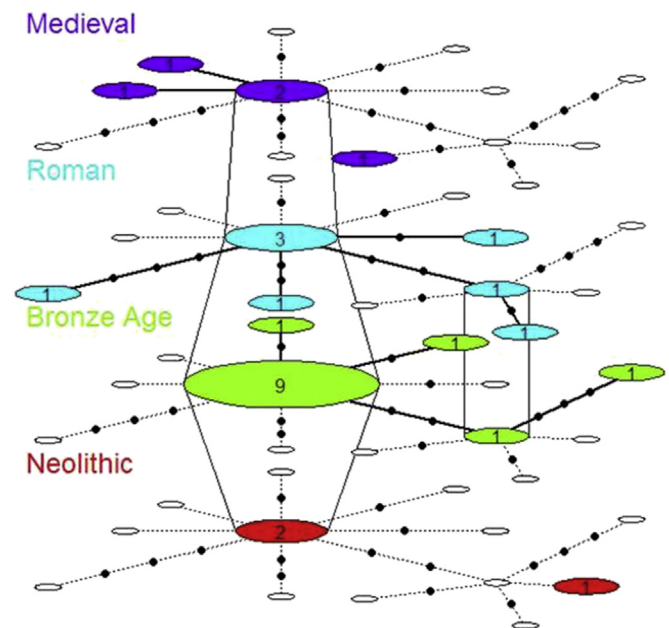


Fig. 3. TempNet showing all ancient Iberian samples. Temporal median-joining network drawn using 240 bp fragment from all ancient Iberian cattle. Circles represent sequence haplotypes, the area being proportional to the haplotype frequency. Points are theoretical intermediate nodes introduced by the median-joining algorithm, and branches between haplotypes represent single nucleotide mutations, unless otherwise indicated. Circles are coloured by the age of the samples: red = Neolithic; bright green = Bronze Age; turquoise = Roman; purple = medieval. Empty nodes at each time frame indicate the absence of that haplotype at that period of time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Genetic diversity values of archaeological cattle. Genetic diversity of the archaeological Spanish cattle populations from Bronze Age Portalon, Roman Empúries and Middle Ages San Pablo, using the 240 bp fragment of the control region.

Country	Site	Period	Number of samples	% Samples per haplogroup				Number of haplotypes	Haplotype diversity
				T	T1	T2	T3		
SPAIN	Portalón	Bronze Age	11	9.1	9.1	81.8	3	0.346 ± 0.172	
3 GROUPS	Empúries	Roman	7		14.3	85.7	5	0.857 ± 0.137	
	San Pablo	Middle Ages	4			100	3	0.833 ± 0.222	

the Neolithic to the medieval period, had a T/T3 haplogroup. The T2 haplogroup was not represented in the data set. The haplotypic diversity values of cattle populations from Roman Empúries and Middle Ages San Pablo sites (Table 3; Fig. 3) revealed large diversity in these two time periods. In all time periods tested (Neolithic, Bronze Age, Roman and Middle Ages), haplotypes were found to belong to both the T1 and T3 haplogroups (Table 1; Fig. 2).

The archaeological samples from the Iberian Peninsula were compared with mtDNA sequences from European and African *Bos taurus* sequences from GenBank (Table S1) to compare past cattle diversity. As can be seen from the median-joining network (Fig. 2), the archaeological data fit within living cattle diversity. The T1 sequences are interesting because the closest matches for these individuals in the modern data set are from a broad geographical range. A complex history of population movements may be reflected in these samples with a number of potential origins for these individuals. NEOL03 matched an extant individual from Guinea, ROMN06 and ROMN19 matched extant individuals from Morocco with 99% homology, and MIDD01 matched an extant individual from Tunisia (Table S2).

4. Discussion

Our analyses show that haplogroup T3, which dominates among modern domestic European cattle, was the most frequently occurring haplogroup in Iberia since the Neolithic. However, our data also show a presence of T1 haplotypes in Iberia from the Neolithic period through the Bronze Age into the Roman period and the Middle Ages. The presence of T1 haplotypes in Neolithic Iberia, and their chronological and spatial recurrence, clearly demonstrates that T1 was not solely a Muslim or later introduction, as some have argued (Cymbron et al., 1999, 2005; Beja-Pereira et al., 2002, 2003, 2006; Pérez-Pardal et al., 2010), though additional and/or new T1 haplotypes may have been introduced during these periods.

The Neolithic T1 cattle in our data most likely represent populations that expanded out of the Near East in the company of early farmers moving along the Mediterranean coastal route. T1 haplotypes could have reached the coast of eastern Iberia from the Near East as early as ~5400 cal. BC (Price, 2000; Zilhão, 2001), when human migrations and contacts through the Mediterranean basin are archaeologically attested (Winiger, 1998; Gkiasta et al., 2003; Berrocal, 2012). Domestic cattle are well documented along the western Mediterranean (Tresset and Vigne, 2007) and coast of Spain (Saña, 2013) at this time, with La Draga being one of the earliest Neolithic Iberian sites where domestic cattle are found (Saña, 2000). The site of La Draga has close connections with the Mediterranean route of diffusion of the Neolithic, both culturally (Saña, 2013) and due to its location on the eastern coast of the Peninsula (Fig. 1). As the earliest cattle in the coastal areas of north-west Africa are dated significantly later than the earliest Neolithic farming sites found there (Jousse, 2004; Mulazzani, 2013; Manen, 2014), it is unlikely that cattle could have arrived at La Draga via an African route. The presence of the T1 haplotype at La Draga

implies, therefore, that this haplotype travelled with the earliest wave of domestic cattle from the Near East to the north-western Mediterranean.

The contacts between the Iberian Peninsula and the rest of the Mediterranean continued during the Bronze and Iron Ages (Ruiz-Gálvez, 1993; Stampolidis, 2003; Celestino et al., 2008), and during Roman and medieval times, with the development of a large and regular sea trade along all the Mediterranean Sea (Rauh, 2003; Arnaud, 2005; Tchernia, 2012; Broodbank, 2013). The large diversity seen in the Roman mtDNA sequences are suggestive of more intensive contacts during this period (Fig. S1). Empúries was a trading post since the 6th century BC (Aquilué et al., 1999), and the genetic distinctness of the haplotypes found there may either represent a local maintenance of cattle introduced during the Neolithic from the Near East, or new introductions, from other regions of Europe or directly from Africa. Although T1 is seen at low frequencies in extant Iberian and Italian breeds, our results suggest that the haplogroup was lost from the majority of European populations sometime after the Middle Ages.

5. Conclusions

Domestic animals have been one of the key pillars of social and economic change during the last ten millennia. Our results show the presence of the two most common haplogroups in domestic cattle in Europe (T3) and Africa (T1) in three early Neolithic sites in Iberia. These haplogroups are also documented in Iberia during the Bronze and Iron Ages, as well as in the Roman and Medieval periods. The absence of the T2 haplogroup, which has an appreciable frequency in several Eastern European and Italian cattle breeds (Bradley et al., 1996; Beja-Pereira et al., 2006; Pellicchia et al., 2007; Achilli et al., 2009), is striking and requires special attention in future studies.

Our results provide important data about the phylogeny of cattle haplogroup T1 in the Iberian Peninsula, and open new issues about cattle movements through time. Further studies of the geographical distribution of the T1 haplogroup in Europe prior to ~5400 cal. BC, when the Neolithic arrived into the Iberian Peninsula, would shed more light on this topic. In addition, we would suggest further studies concentrate on analysis of Y-chromosomal diversity, thus obtaining paternal information about cattle movements in the past, and a systematic DNA analysis of Mesolithic aurochs in Europe, especially in the south of the continent.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jas.2015.04.014>.

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