

Cattle domestication in the Near East was followed by hybridization with aurochs bulls in Europe

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Domesticated cattle were one of the cornerstones of European Neolithisation and are thought to have been introduced to Europe from areas of aurochs domestication in the Near East. This is consistent with mitochondrial DNA (mtDNA) data, where a clear separation exists between modern European cattle and ancient specimens of British aurochs. However, we show that Y chromosome haplotypes of north European cattle breeds are more similar to haplotypes from ancient specimens of European aurochs, than to contemporary cattle breeds from southern Europe and the Near East. There is a sharp north–south gradient across Europe among modern cattle breeds in the frequencies of two distinct Y chromosome haplotypes; the northern haplotype is found in 20 out of 21 European aurochs or early domestic cattle dated 9500–1000 BC. This indicates that local hybridization with male aurochs has left a paternal imprint on the genetic composition of modern central and north European breeds. Surreptitious mating between aurochs bulls and domestic cows may have been hard to avoid, or may have occurred intentionally to improve the breeding stock. Rather than originating from a few geographical areas only, as indicated by mtDNA, our data suggest that the origin of domestic cattle may be far more complex than previously thought.

Keywords: cattle; wild ox; domestication; Y chromosome; ancient DNA

1. INTRODUCTION

The domestication of wild animals and plants allowed the shift from nomadic and hunter–gatherer behaviour to a settled agrarian way of life (Childe 1957; Diamond 2002). The question of whether animal domestication was limited geographically, or if it was characterized by multiple and independent events and/or local backcrossing with wild ancestors, is of general relevance for understanding the anthropological processes associated with the cultural transition from hunting to farming. The aurochs, or the wild ox (*Bos primigenius*), extinct since 1627, was once widespread throughout Europe, northern Africa, and southern Asia, where Palaeolithic rock and cave paintings indicate that it was important to humans as prey and perhaps also in rituals (Clutton-Brook 1999). Cattle were domesticated from aurochs about 10 000 years ago and, as for most other domestic animal species, domestication was probably limited to a few regions including the Near East (*Bos taurus*) and Asia (*Bos indicus*) (Loftus *et al.* 1994; Bar-Yosef & Belfer-Cohen 1996; MacHugh *et al.* 1997; Clutton-Brook 1999). This is consistent with the observation that in cattle, as well as in the majority of domestic animal species, only a few major mitochondrial DNA (mtDNA) lineages exist (Bruford *et al.* 2003); the only exception to this situation is that found in the horse (Vilá *et al.* 2001, Jansen *et al.* 2003).

The appearance of domestic cattle in Europe coincides with the Neolithisation and the proposed human migration associated with it (Renfrew 1987); cattle became of great economic importance in Central Europe around 5500 BC with the Linearbandkeramik (LBK) culture (Benecke 1994). A predominant view, supported by mtDNA data, is that European cattle descend from aurochs domesticated in the Near East and brought to Europe by the first farmers (Bököny 1974; Bailey *et al.* 1996; Troy *et al.* 2001). More generally, this model reflects domestication as a rare and difficult process that, once it has occurred, generally spreads through trade or migrating human populations rather than by the use of additional wild ancestors in new areas.

Sex differences in, for example, the feasibility of taming wild ancestors, the way early domesticates were exploited and the likelihood for participation in backcrosses are factors that may have left domestic animals with separate genetic legacies for sex-specific markers (MacHugh & Bradley 2001). Analyses based on Y chromosome data may therefore reveal previously unrecognized patterns of animal domestication (Lindgren *et al.* 2004). To this end we set out to analyse the origin of domestic cattle in Europe using Y chromosome markers.

2. MATERIAL AND METHODS

(a) Analysis of modern samples

Male samples from modern cattle breeds were as specified in table 1. Eight introns, in total 3.5 kb, from the Y chromosomal

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Table 1. Distribution of Y chromosome haplotypes among cattle breeds. Breeds are listed by country of current origin. Note that some breeds, e.g. Finnish and Swedish Ayrshire, Finnish Holstein-Friesian, and Swedish Jersey, are likely to represent breeds that have been imported in modern times.

country/type	breed	haplotype	
		Y1	Y2
Sweden	Swedish Ayrshire	2	
	Swedish Jersey		1
	Swedish Lowland	2	
	Swedish Mountain Cattle	2	
	Swedish Red	2	
	Swedish Red Polled	2	
Finland	Eastern Finncattle	1	4
	Finnish Ayrshire	3	
	Finnish Holstein-Friesian	3	
	Northern Finncattle	3	
Britain	Western Finncattle	3	
	Aberdeen Angus	10	
Holland	Ayrshire	4	
	Friesian	4	
	Charolais		6
	Galloway		2
	Guernsey		4
	Hereford	10	
	Highland cattle		3
	Jersey		8
Germany	Fries	5	
	Groningen Whitehead	5	
	Lakenvelder	2	3
	Meuse-Rhine-Yssel	4	
Switzerland	Angler	4	
	Deutsch Angus	3	1
	Fleckvieh		3
	Gelbvieh		4
	Pinzgaur		4
	Rotbunte	4	
	Schwarzbunte-HF	4	
France	Braunvieh		3
	Ehringer		2
	Red Holstein		3
	Simmentaler	1	4
Portugal	Blonde Daquittin		2
	Limousin		2
Spain	Alentejana		2
	Mertolenga		2
Italy	De Lida		2
	Menorquina	4	
	Chianina		2
Turkey (Anatolia)	Piemontese		4
	Rendena		4
	Romagnola		4
	Anatolian breed		5
total	East Anatolian		4
	South Anatolian		5
		87	93

genes *DBY*, *UBE1Y*, *UTY* and *ZFY* were amplified and sequenced using conserved exonic primers (Hellborg & Ellegren 2003); DNA from female cattle served as control in order to ensure Y-specific amplification. One male each of *Bos indicus*, bison *Bison bison*, and gaur *Bos frontalis* were also sequenced. Polymorphic sites were identified from sequence

alignments using AUTOASSEMBLER and SEQUENCE NAVIGATOR (Applied Biosystems). Subsequent genotyping of segregating sites in modern samples was based on re-sequencing or, for an indel polymorphism, on fragment size analysis. Median joining network was constructed using NETWORK v. 4.1.0.6.

(b) Ancient samples

Nearly all known finds of Holocene aurochs and early domesticated cattle in central Europe come from archaeological excavations and are often found as isolated broken elements. A large series of find complexes from several excavations with reasonable to good bone preservation was reviewed and units originating from culturally well-dated and archaeologically closed contexts were selected for further analysis (table 2). Most samples originated from Saxony, a restricted region between the cities of Dresden and Leipzig in Germany (stored at Landesamt für Ärschäologie mit Landesmuseum für Vorgeschichte in Dresden). This area belongs to the heartland of the Linearbandkeramik (LBK) culture, the first Early Neolithic farmers (Benecke 1994), and can be regarded as having been a topographically and culturally coherent region during this period. Moreover, six samples of Pleistocene and early Holocene aurochs were available from southern Scandinavia, five from northern Italy (Natural History Museum in Stockholm; Ekström 1993), and one from Austria (Wien Naturhistorisches Museum, Archäologisch—Zoologische sammlung), respectively. The material was measured according to the standard used in archaeozoology (von den Driesch 1976). The distinction between aurochs and domestic cattle is based on the size and robustness of the bones only, although during the Neolithic there was a large overlap in the size-distribution of the two. In this study, only those bones that fall clearly outside the accepted size-range of prehistoric domesticates in the region (Dohle 1994, Elburg 1999) are classified as *B. primigenius*. Note that Scandinavian and Italian samples are from Pleistocene or early Holocene sediments and are thus pre-domestic.

(c) Genetic analysis of ancient samples

Because amplification of nuclear DNA in ancient remains is a challenging task, we sought to increase amplification success by selecting samples only from bones of excellent gross morphological preservation, using a DNA preparation method based on selective enrichment and concentration of the target sequence, and by the design of very short amplicons (42–55 bp). Moreover, we used pyrosequencing as a means for single nucleotide polymorphism (SNP) detection with which method it is possible directly to monitor traces of contamination. A detailed description of the DNA extraction protocol from prehistoric samples is provided as electronic supplementary material.

Authentication of the results is a key aspect in analyses of ancient DNA. To this end we followed widely accepted guidelines and recommendations for stringent ancient DNA research (Cooper & Poinar 2000). Thus, all samples were independently replicated in the Uppsala laboratory as well as in a laboratory in Madrid (Centro Mixto UCM-ISCIII de Evolución and Comportamiento Humanos). Common measures to prevent contamination were used, such as a separated area for working with pre-PCR and ancient DNA, the wearing of protective clothing, UV-sterilization of all reagents, and cleaning of all working surfaces and tools with HCl and sodium hypochlorite. Primers were designed in a

Table 2. Description of ancient specimen and results from single nucleotide polymorphism (SNP) typing.

classification	specimen	location	period	date	collagen fraction	marker		
						UTY19	ZFY4	DBY7
Aurochesen, predomestic	Lzz3287	Sweden	pleistocene/holocene	7972±290 BC ^a	0.11	C	C	C
	Lzz3348	Sweden	pleistocene/holocene	9500-6000 BC ^b	0.18	A		C
	Lzz3343	Sweden	holocene	7753±206 BC ^a	0.21	C		
	2M3886	Italy	pleistocene	>9500 BC ^c		C	C	C
	3M3884	Italy	pleistocene	>9500 BC ^c		C	C	C
Aurochesen, morphological classification	4	Italy	pleistocene	>9500 BC ^c		C		
	DD10	Germany	early neolithic, LBK	5500-4900 BC ^c	0.062	C		C
	DD23	Germany	middle neolithic, stroked ware	4900-4400 BC ^c	0.079	C	C	C
	DD56	Germany	early neolithic, LBK	5500-4900 BC ^c	0.048	C		C
intermediate morphology	Aut10:2	Austria	middle neolithic	4600 BC ^c	0.065	C	C	C
	DD73	Germany	middle neolithic, stroked ware	4900-4400 BC ^c		C	C	C
	DD35	Germany	middle neolithic, stroked ware	4900-4400 BC ^c		C	C	C
	DD24	Germany	middle neolithic, stroked ware	4900-4400 BC ^c	0.063	C	C	C
	DD25	Germany	middle neolithic, stroked ware	4900-4400 BC ^c	0.058	C	C	C
	DD27	Germany	middle neolithic, stroked ware	4900-4400 BC ^c	0.09	C	C	C
	DD21	Germany	late neolithic, TRB	3500-2800 BC ^c	0.073	C	C	C
domesticates, morphological classification	DD29	Germany	final neolithic globular amphora	3100-2500 BC ^c		C	C	C
	DD39	Germany	early neolithic, LBK	5054±203 BC ^a		C		
	DD61	Germany	late neolithic, TRB	3500-2800 BC ^c		C		C
unknown	DD64	Germany	bronze age	2000-1000 BC ^c	0.18	C	C	
	DD22	Germany	neolithic/bronze age	5500-1000 BC ^c		C		

^a Radiocarbon dating.

^b This is the time period aurochesen existed in Sweden.

way so that they would not anneal to human DNA, and this was verified by amplification.

3. RESULTS AND DISCUSSION

(a) Y chromosome haplotypes in modern cattle breeds

We screened 3.5 kb of non-coding Y chromosome sequence in 20 male cattle from 12 European breeds, selected to represent a suite of breeds indigenous to different parts of Europe. Two co-segregating sites were found: an A/C SNP in *UTY* intron 19 and a 2 bp insertion-deletion polymorphism in *ZFY* intron 5 (table 3). These two markers, together forming two haplotypes (Y1 and Y2), were subsequently genotyped in a total of 180 domestic cattle from 45 European and three Anatolian breeds (table 1), revealing overall haplotype frequencies of 0.48 and 0.52, respectively (no intermediate was observed). However, it was obvious that haplotypes were

non-randomly distributed among breeds. For 38 out of the 48 breeds only one haplotype was identified, indicating a narrow paternal genetic basis of most breeds. Importantly, there was a clear geographic structure in the distribution of the two haplotypes with Y2 at very high frequency (Iberia, France, and Switzerland) or fixed (Italy) in south European breeds, as well as in Anatolian breeds (figure 1). In contrast, Y1 dominated in north European breeds while central European breeds showed intermediate haplotype frequencies.

In theory, several explanations of the north-south gradient across Europe in the occurrence of the Y1 and Y2 haplotypes are possible. Adaptive genetic differences along latitudinal gradients (or between certain geographical areas; Beja-Pereira *et al.* 2004) as a response to selection can lead to clines in allele frequencies, in this case potentially manifested in Y chromosome haplotype frequencies. However, most genes on the mammalian Y chromosome are involved in male reproduction and it is

Table 3. Description of Y chromosome haplotypes.

(*DBY1* SNP, position 425 in GenBank AY928816; *DBY1* microsatellite, position 363 in AY928816; *DBY7*, position 165 in AY928817; *UTY19*, position 423 in AY936543; *ZFY4*, position 120 in AY928828; *ZFY5* SNP, position 609 in AY928827; *ZFY5* indel, position 651 in AY936548.)

haplotype	taxon	marker						
		<i>DBY1</i>	<i>DBY1</i>	<i>DBY7</i>	<i>UTY19</i>	<i>ZFY4</i>	<i>ZFY5</i>	<i>ZFY5</i> ind
Y1	<i>B. taurus</i>	C	(AT) ₁₀	C	C	C	C	–
Y2	<i>B. taurus</i>	C	(AT) ₁₀	C	A	C	C	TG
Y3	<i>B. indicus</i>	T	(AT) ₈	T	A	T	T	TG

not obvious how artificial selection during domestication would imply different selection regimes related to such traits across a geographical gradient in Europe. Another possibility is that Y1 and Y2 distributions are the result of two different migrations of stock from the Near East, along the northern Danubian route and an alternative Mediterranean southern route. The alternating prevalence of Y1 and Y2 in these routes could result from sampling and bottleneck effects, but would not explain why Y1 is absent in modern breeds from Anatolia.

A remaining interpretation is that the first domestic cattle brought to Europe from the Near East during Neolithisation carried Y2. When these cattle subsequently spread northwards through Europe, local hybridization with aurochs bulls may have introgressed Y1 in the breeding population. Geographical structure in the distribution of Y chromosomal haplotypes among ancient aurochs, as has been found for mtDNA haplotypes (Troy *et al.* 2001), would add support to this interpretation. Specifically, we should expect to see Y1 at high frequency among European aurochs.

(b) Ancient DNA analysis

To test this idea we attempted amplification of Y chromosome polymorphisms in DNA prepared from 39 ancient bone samples of European *Bos* (from Germany, Sweden, Italy and Austria) dated from Late Pleistocene, i.e. pre-domestication, to Bronze Age (>9500–1000 BC). Twenty-one of the 39 samples successfully amplified for the *UTY* SNP distinguishing Y1 and Y2 (table 2). Out of these, 11 were aurochs (>9500–4400 BC) based on pre-domestic dates or morphology, five were morphological intermediates between aurochs and domesticates (4900–4400 BC) and six were early domesticates or of unknown status (5500–1000 BC). Twenty showed the *UTY* 'C allele' of Y1 while only one showed the 'A allele' of Y2 (table 2). This indicates that Y1 was at high frequency among European aurochs prior to the arrival of domestic cattle and that it was also frequent among aurochs contemporary with the first domestic cattle.

A phylogenetic analysis including *Bos indicus* (full-bred Sahiwal), bison and gaur reveals Y1 to be the derived form (see figure 3 in the electronic supplementary material). However, the observation of Y1 in Pleistocene and Neolithic European aurochs excludes the possibility that Y1 has an origin in post-domestic mutation from Y2 haplotype, occurring and becoming fixed in northward migrating domestic populations. Moreover, the finding of Y1 in early domesticates from Germany (table 2) shows that the occurrence of Y1 in central European domestic cattle is not a recent consequence of breed structure or

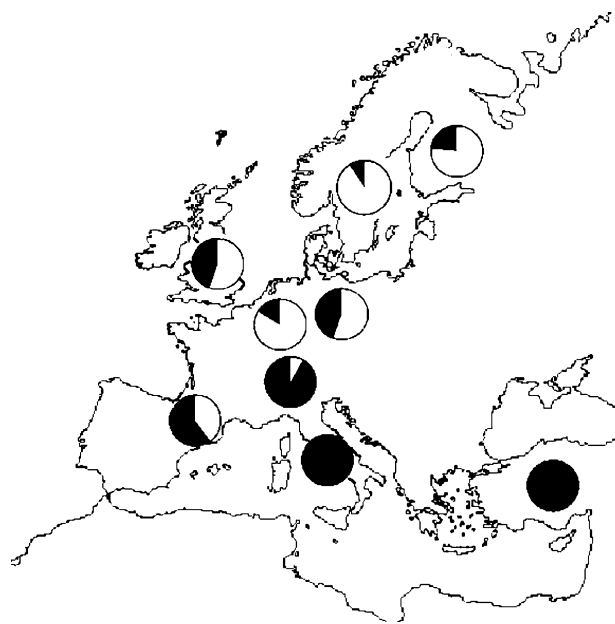


Figure 1. Map showing the distribution of the Y1 (open) and Y2 (filled) Y chromosome haplotypes among modern cattle breeds in Europe, defined by country of origin. Size of the sectors is defined by the number of animals identified within each region with either haplotype. Due to small sample size, data from France, Spain, and Portugal are combined into a single chart.

artificial selection. Overall, these data thus support the idea of European aurochs' introgression of haplotype Y1 into domestic cattle through local hybridization.

Four substitutions (in *DBY* and *ZFY*), plus a microsatellite length polymorphism (*DBY*), were found to distinguish the *indicus* (haplotype Y3) from all European *taurus* (table 3). This lends support to the independent origin, from separate domestication events, of taurine and indicine cattle, a pattern for which data from maternal (Loftus *et al.* 1994; MacHugh *et al.* 1997) and paternal (Hanotte *et al.* 1997) markers are thus concordant.

Neighbour-joining trees based on interpopulation divergence among European aurochs, north and south European domesticates, and *Bos indicus* summarize the contrasting patterns of domestication revealed by Y chromosome and mtDNA data (figure 2). These trees show two aspects of the data. First, both mtDNA and Y haplotype data exhibit three divergent lineages. Second, the distribution of these lineages differ for maternal and paternal ancestry. In each case, the most divergent lineage is represented by *Bos indicus*. However, while domestic cattle from northern and southern Europe share the same

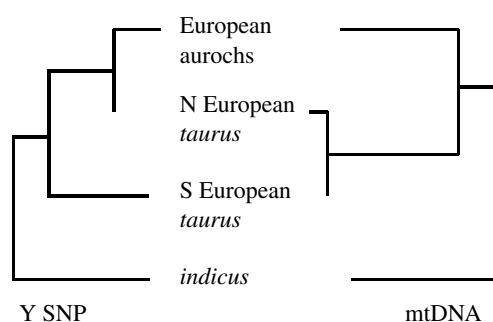


Figure 2. Neighbour-joining trees based on interpopulation pairwise F_{st} divergence among European aurochs, north and south European domestic cattle, and *Bos indicus*. The left-hand tree used Y SNP data and the right-hand mtDNA control region sequence. The Y SNP haplotypes used were: the aurochs sample described herein including those from animals of intermediate morphology; a north Europe domestic cattle sample of haplotypes from Sweden, Finland, Britain, Holland, and Germany; a south European domestic cattle sample from Switzerland, France, Portugal, Spain, Italy and Anatolia; and three pure African zebu populations were used as a *Bos indicus* outgroup. The mtDNA data were taken from and Cymbron *et al.* (1999) and Troy *et al.* (2001).

mtDNA lineage, domestic cattle from northern Europe show closer affinity with aurochs Y chromosome haplotypes sampled locally than with domestic southern European or Anatolian populations. Thus, while hundreds of assayed European domesticates show no maternal contribution from European aurochs (e.g. Troy *et al.* 2001), north European cattle Y chromosomes seem predominantly to be a local legacy of wild ox. It would be valuable to analyse aurochs from Near East to formally test that Y1 was absent or rare in this region. Unfortunately, aurochs remains from Near East tend to be poorly preserved and amplification of mtDNA has proven difficult (D. G. Bradley, unpublished data).

(c) Cattle domestication

Early domestic cattle were probably kept with little control compared to modern standards (Clutton-Brook 1999). There is little archaeological evidence of fencing and cattle barns, and strategies for the keeping of cattle are likely to have involved free-roaming herds without confined paddocks. To provide the animals with access to adequate sources of fodder, herds are likely to have been driven between suitable pastures created by clearing and burning woodland. During times without close cattle control, the possibility of unintentional mating between aurochs and domestic cattle may have been difficult to avoid. If such hybridization took place, a genetic imprint on domestic cattle is most likely to have been left by crosses of aurochs bulls with domestic cows; calves from opposite crosses would not have been integrated with the domestic stock. Moreover, crosses may have been deliberately arranged to improve or increase the breeding stock.

Domestication has been regarded as a difficult process limited to a few regions from which domesticates subsequently spread (Clutton-Brook 1999; Diamond 2002). For most domestic animals, this model is supported by data from mtDNA where most haplotypes cluster in a few lineages only (Bruford *et al.* 2003). Our observations from European cattle suggest a more complex scenario in which local backcrosses and

hybridization with wild ancestors, in areas other than that of the origin of domestication, have diversified the domestic gene pool. There is evidence that many domestic mammals, including cattle, show extensive levels of nucleotide diversity in autosomal DNA sequences (Vilá *et al.* 2005), seemingly at odds with a narrow genetic basis as indicated by mtDNA. Hybridization and backcrossing with wild ancestors may thus have been a common phenomenon during domestication, with the prevailing direction of such events being crosses of wild males with domestic females, meaning that it is not detected by analyses of mtDNA. Indeed, this is known in contemporary bovids such as the mithan (domesticated gaur), females of which are deliberately mated with wild gaur bulls.

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The electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2005.3243> or via <http://www.journals.royalsoc.ac.uk>.

NOTICE OF CORRECTION

Table 3 is now presented in its correct form.

A detailed erratum will appear at the end of the volume

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