Chapter 1
The Origins of Cattle

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Archeology and Domestication

The transformation of early human economies from nomadic hunter–gatherers to farmers is a pivotal moment in human evolution. Starting approximately 12,000 years ago, this process is entitled the Neolithic Revolution and encompassed the domestication of a variety of plants and animals (Bar-Yosef 1998). The archeological study of domestication requires a combination of classical and molecular approaches, which include the analysis of settlement patterns, food residues, and human, animal, and plant remains.

Settlement patterns provide an excellent source of evidence for the beginnings of domestication. Firstly, they provide direct evidence of a sedentary lifestyle, which is likely a prerequisite to Neolithisation. Secondly, the production of long-term housing requires specialist builders; these skills could likely only be supported if an agricultural economy was being practiced to offset the loss of labor from hunting. The evolution of particular building technologies within Neolithic core regions can also be informative, for example, the presence of grain stores and larger houses emerge as the Neolithic lifestyle develops (Cauvin 2000). Study of the surrounding areas can provide evidence for early attempts at domestication, for example, the manipulation of the landscape to control animal migration (Vigne 2011).

The analysis of organic residues found on cooking and storage artifacts is a relatively new technique in molecular archeology, which is providing exciting results especially in the field of domestication (Dudd et al. 1999; Copley et al. 2003; Copley et al. 2005; Outram et al. 2009). For example, lipid residues found on pottery can be used to deduce milk use and have allowed for the earliest date of specialized milking to be proposed as the seventh millennium BC (Evershed et al. 2008). Molecular archeology also allows the diet of early farmers to be inferred from the stable isotopes contained within their bones, analyses that have been fruitful in distinguishing the transition into farming (Richards et al. 2003; Liden et al. 2004; Eriksson et al. 2008).

The study of animal remains, however, is still the principal analysis for identifying domestication (Vigne 2011), with the differences in morphology of domesticates compared to their wild progenitor providing clues to this process. Cattle follow the general trend of domestic breeds being smaller than their wild relatives. However, the
usefulness of this factor alone to identify early signatures of domestication has recently been called into question (Zeder 2008, and references therein). More robust evidence for the beginnings of domestication may be found in the kill-off patterns of animals (age at which animals are killed) (Vigne and Helmer 2007). (Most hunters tend to target adult males to maximize the kill. In contrast, herders are thought to slaughter males young, apart from the few needed for herd propagation) (Zeder 2008). This leads to archeological remains dominated by young males and elderly females who are killed once they have passed their prime reproductive age (Vigne and Helmer 2007; Zeder 2008). The number of domesticate finds also increases through time at the proposed Neolithic sites, which allows for the time of domestication to be proposed (Bar-Yosef 1998; Vigne 2011).

Bovine Mitochondrial DNA Diversity and Cattle Origins

The genetic description of a primary division within the genomes of domestic cattle, reflecting the difference between *Bos indicus* and *Bos taurus*, is almost 20 years old. However, the observation of morphological, behavioral, and physiological differences between the two taxa is an older one. In fact, Darwin (an ardent student of domestication), in *The Origin*, speculated that zebu had different domestic wild progenitors from observations on “the habits, voice and constitution etc of the humped Indian cattle,” communicated to him by his correspondent from the subcontinent, Mr. Blyth.

Earlier studies of the bovine mitochondrial genome used both restriction fragment length polymorphism and limited control region sequencing and described two divergent clusters of sequences with limited diversity within each (Loftus et al. 1994). Any calibration of the difference between these clusters corresponded to hundreds of thousands of years and was clearly concordant with separate domestic origins for *B. indicus* and *B. taurus*. Phylogenies of these sequences had a simple structure, two groups separated by a single, long internal branch that suggested an interesting question, “Where was the missing phylogenetic history; were there other undescribed internal branches of bovine mitochondrial diversity?”

Two developments have filled out this internal region of the phylogeny. The first is the recovery of sequences from wild ox fossils. Bones discovered in Central, Northern, and Western Europe dating to periods before and sometimes during the Neolithic, yield a sequence type labeled P (for *Bos primigenius*) that is clearly divergent from the domestic family of sequences labeled T (for *B. taurus*) (Troy et al. 2001). A minority distinct European aurochs sequence, labeled E, has been described once from a German aurochs fossil (Edwards et al. 2007).

More recently, the study of bovine mitochondrial DNA (mtDNA) variation has matured into the examination of whole chromosome sequences; Figure 1.1 gives an unrooted phylogeny of a sample of T haplotype chromosomes plus other available complete chromosomes (Achilli et al. 2008, 2009). Interestingly, this has revealed the major *B. taurus* cluster to comprise two somewhat distinct types (T and Q) that were indistinguishable at the lower resolution analysis afforded by control region sequences. Also, two highly divergent lineages emerged in modern samples. After the analysis of several thousand modern sequences, a single P variant emerged...
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Figure 1.1 Neighbor-joining tree of complete bovine mitochondrial DNA chromosomes. Cattle and wild ancestors segregate into discrete clusters, of which two indicine (I1, I2) and two taurine (T, Q) greatly predominate within modern samples.

from a Korean animal of ultimately European ancestry. The other P node is the first whole mtDNA from a bovine fossil—a 6700-year-old aurochs bone from Carenton Pasture Cave, England (Edwards et al. 2010). Second, a new lineage, R, was discovered in European cattle. Three clusters of B. indicus chromosomes are also clear.

This phylogeny invites several conclusions. Firstly, wild ox matrilines were diverse, with a branching complexity akin to patterns observed in wild bovines. The divergence between these implies geological (hundreds of thousands of years) rather than archeological (10,000 years) divergences. Secondly, the capture and subsequent thriving of these lineages in domestic populations was uneven and focused almost exclusively on three indicine, and two taurine lineages. Thirdly, this phylogenetic focus probably reflects a temporal and geographical concentration of domestication processes, and a more detailed examination of these key lineages will inform in more detail on this geography. Lastly, while unusual aurochs lineages do feature in modern samples, their extreme rarity implies limited secondary integration from the wild, rather than a major widening of the spatiotemporal focus of primary domestication.

MtDNA Diversity Within B. taurus

The phylogeography of the major B. taurus lineage, T, has been extensively studied through sampling of short, informative sequences from the control region. T sublineages (labeled T1, T2, etc., and each diagnosed by one or a few substitutions) predominate in indigenous cattle from the Near East, Europe, Northern and Eastern Asia, and Africa. The Near East shows greatest diversity; Southern Europe displays a subset of this, and Northern Europe possesses least, with a single sublineage (T3) dominating. Using Vavilov’s classic principal of diversity indicating domestic centers of origin, this pattern is consistent with the archeological evidence pointing toward domestication of B. taurus in the Near East (Troy et al. 2001). Some recent ancient DNA literature suggests that the wild oxen of Southern Europe may have possessed T haplotypes and that domestication of this lineage may have extended into that region. However, these sequences resemble modern T variation closely and are more difficult to interpret than, for example, a more distinct T type aurochs variant might be
(Beja-Pereira et al. 2006). This should be resolved soon by more complete surveying of Eurasian wild ox variation using next-generation sequencing and retrieval of whole mitochondrial chromosomes.

Two regionally distributed sublineage are worth considering. T4 equals T3 in frequency in far Eastern *B. taurus* populations but is undetected elsewhere, perhaps reflecting an input from wild oxen somewhere to the East of Anatolia or alternatively, a foundation bottleneck effect (Mannen et al. 2004). T1 is the African bovine lineage; here, other variants are secondary migrants from either Europe or the Near East and are restricted to Mediterranean regions. T1 is found only at low frequencies in the Near East and is an introgressor to Southern European populations in Italy and Iberia (Cymbron et al. 1999; Beja-Pereira et al. 2006). This points toward a relationship between the Near East and Africa, which is more distant than that with Europe, although it is currently unclear whether this reflects a more constricted migration of early domestics across the Sinai Peninsula or perhaps less likely, an input from the contemporary African wild ox.

**Archeology and Domestication in the Near East**

The origin of cultivation in the Near East has been extensively studied and gives important insights into the domestication of a number of animal and plant species. The beginnings of the Neolithic lifestyle are thought to have emerged from the end of the Natufian culture, which occupied the Near East from approximately 12,500 to 11,500 cal years BP (Bar-Yosef 1998; Vigne 2011). These people are proposed as the first to have had a sedentary or at least semisedentary lifestyle in the Near East and possibly the world, likely supported by the high carrying capacity of the region at this time (Bar-Yosef 1998). Following this were two further important sedentary cultures: the Pre-Pottery Neolithic A and B (PPNA and PPNB). These are credited with the introduction of farming technologies that led ultimately to the domestication of grain, sheep, goat, cattle, and pig (Cauvin 2000; Vigne 2011).

The first archeological evidence for bovine domestication occurs in the Eastern slopes of the Taurus Mountains during the early PPNB (circa 10,500 BP) (Helmer et al. 2005). These early-domesticated animals are then thought to have spread from this core region through the whole of the Near East.

One of the most compelling pieces of evidence for this spread and a Near Eastern PPNB domestication of cattle is the early arrival of bovids in Cyprus. It had previously been thought that Cyprus was not colonized till about 8500 BP; however, the last 20 years have seen exciting discoveries that have pushed the earliest dates of human occupation to between 10,500 and 9000 years ago (Zeder 2008). With cattle thought to have been introduced to the island during the ninth millennium BC (Vigne et al. 2003; Peters et al. 2005; Zeder 2008), these early pastoralists would have to have traveled 60 km to the island by boat, taking not only cows but sheep, goats, and pigs with them (Vigne et al. 2003; Peters et al. 2005; Zeder 2008; Vigne et al. 2009). Although the remains of these animals do not display the morphological markers diagnostic of domestication, demographic profiles are consistent with domestication and their presence must have involved deliberate human transportation (Zeder 2008). That humans were willing to take the risks inherent in moving these animals by boat over
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such distances implies both that these animals were of great importance and that they had sufficient husbandry skills to enable their transport.

Archaeological evidence suggests that domestic animals spread to Europe from the Near East during the early part of the seventh millennium BC, with the migrating farmers moving into Greece and the Balkan region (Pinhasi et al. 2005; Tresset and Vigne 2007; Pinhasi and von Cramon-Taubadel 2009). From this region, there are two proposed migratory routes of the Neolithic into the rest of Europe: (1) the Danubian and (2) the Mediterranean routes. The former is a proposed land migration following the Danube Valley; the latter route is suggested to have involved sea-based migration along the Mediterranean Coast into Europe (Price 2000).

Genetic evidence for these migrations is found in the genomes of both modern cattle and humans. Recent genetic data (Bramanti et al. 2009) suggest that the early farmers of Northern Europe were migrants and not descendent from the local hunter–gatherers. One fascinating human genetic variant intimately linked to cattle herding history is the mutation that confers lactase persistence. This trait is almost fixed in parts of Northern Europe, with markedly lower frequencies in Mediterranean regions—pointing toward it being a legacy of dairy-centered economies linked to the Danubian route. This is supported by recent fitting of data to simulated European genetic histories that indicates a Central European origin for the mutation (Ingram et al. 2009; Itan et al. 2009). Interestingly, this milk-related human trait variation mirrors milk protein genetic diversity differences among European cattle breeds, pointing toward culture–genetic coevolution in both species (Beja-Pereira et al. 2003). There are also sharp contrasts between Northern and Southern European cattle genomes in mtDNA, Y chromosomal marker, and autosomal marker diversity that are consistent with origins in separate migrations (Cymbron et al. 2005; Beja-Pereira et al. 2006; Negrini et al. 2007).

The Origins of \( B. \) indicus

Recently, the phylogeography of \( B. \) indicus mtDNA has been comprehensively investigated. The two major lineages (labeled I1 and I2) are somewhat disjunct in distribution; both I1 and I2 are present at high frequency in South Asia. Both are also found in admixed and zebu populations further west but, notably, to the east of the subcontinent, I1 predominates almost absolutely in \( B. \) indicus from Southeast Asia and Southern China (Chen et al. 2010). This distribution gives temptation to conclude that whereas I1 is likely the product of a South Asian domestication center such as the Indus Valley region, I2 may have been initially captured in East Asia. However, an examination of genetic diversity within the lineage denies this latter possibility. Both I1 and I2 show significantly higher levels of diversity within the subcontinent than outside it. A transition from wild to domestic cattle is eminently plausible from archeological evidence from the Baluchistan region (in present day Pakistan), which is a well-documented key Neolithic center (Meadow 1993). I1 diversity is high in this region, which may well have been its site of domestication. The I2 diversity peak is less obvious, and this lineage may represent incorporation from the wild elsewhere in the subcontinent. There is some suggestion from the more limited I2 geographical dispersal of a different origin to I1; perhaps, migrations of animals carrying I1 to the
east occurred from South Asian herds that had not yet incorporated I2 from Asian *B. primigenius*.

Thus, mtDNA clearly suggests a restriction of wild genetic diversity via the domestication process, with many divergent wild lineages being almost completely lost. It seems likely that this is due to a geographical limitation of cattle domestications primarily to the Near East and South Asia. Extremely rare exotic lineages in the modern population serve as exceptions to prove this rule. However, restriction of genetic diversity is not so clearly apparent with examination of autosomal polymorphism. The earliest indication of this came from the assaying of the 50 or so accessible proteins for electrophoretic variation that may be compared for levels of polymorphism across a wide species range. Here, it was clear that cattle showed heterozygosity typical of midsize mammals (Lenstra and Bradley 1999).

**Modeling Cattle Demographic History from Autosomal Sequence Variation**

Vila et al. (2005) have argued from the magnitude of MHC diversities across domestic species that these are not consistent with a simple domestication model involving a single capture bottleneck. The most comprehensive analysis of bovine genetic variation to date, by the Bovine HapMap Consortium, finds higher levels of sequence diversity in all breeds surveyed; greater, for example, than those encountered in human and dog populations (Gibbs et al. 2009). However, examination of past population sizes on the basis of linkage disequilibrium decay with distance measured at medium density SNP (single nucleotide polymorphism) coverage estimates a 50-fold declaimed associated with domestication and further decline with the formation of modern breeds (MacEachern et al. 2009).

Recently, we modeled bovine population history based on site-frequency spectra of polymorphisms emerging from a survey of 37 kbp (17 genes), which have been sequenced in panels of African, European, and Indian cattle (Murray et al. 2010). Comparison of these spectra with those emerging from simulations using diffusion–approximation method (Gutenkunst et al. 2009) allowed the building of two best-fit models of past bovine demography (Figure 1.2).

These models (the analysis was limited to consideration in each of the three populations) involved (A) simply African, European, and Indian populations and (B) a better fit was achieved using a single combined African and European *B. taurus* population, a domestic *B. indicus* population, and a parallel South Asian wild ox population with secondary input into *B. indicus*. In each model, migration between populations and past population bottlenecks was allowed.

In model (A), a best fit involved an ancestral *B. taurus* population bottleneck but, notably, one with an onset that significantly predated the separation of African and European *taurus* ancestors by a factor of 2.75. The latter divergence within *B. taurus* is calibrated at 17 kyr ago, but with inherent uncertainty could plausibly overlap the domestic timeframe. The predomestic *B. taurus* bottleneck is also a feature of best-fit model (B) where it maps to between 46 and 36 kyr ago (SD = 11 kyr). This simple model may be forcing a complex population history (that may include a domestication
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Figure 1.2 Alternate best-fit models of bovine population history, each assuming three populations: (A) African and European *Bos taurus*, plus Indian *Bos indicus*; (B) combined *B. taurus*, *B. indicus*, plus a parallel contributing *B. indicus* wild ox population. Note that the domestic time horizon (denoted by shading) is highly approximate and the calibration of modeled events includes substantial uncertainty. However, some features include a separation of African and European that may be pre- or postdomestic (16.8 kyr), a *B. taurus* bottleneck that seems to predate this by a factor of 2.75 in onset (46.9–18.4 kyr), and an early *indicus* vs. *taurus* divergence (184.9 kyr).

population constriction) into a single episode but does seem to point toward an early bottleneck event that could reflect glaciation restriction of the West Asian aurochs. In contrast, the first model does not allow the fit of a bottleneck within *B. indicus* history. Model (B) does fit a *B. indicus* domestication bottleneck, but this is only with a remarkable 80% input from a parallel contemporaneous wild population. The separation of *B. indicus* and *B. taurus* ancestors concords with estimates from mtDNA and is of the order of hundreds of thousands of years.

Any modeling exercise, such as the aforementioned, should not be overinterpreted but it does point toward a complexity within South Asian domestication that is probably facilitated by substantial wild diversity that persists because of a relatively benign glacial period ecology. A contrast in history between the two taxa is mirrored by genetic diversity—nucleotide diversity is higher in *indicus* in a majority of the loci sampled and was observed to be twice as high in a single, extensively resequenced *B. indicus* breed compared to two *B. taurus* breeds by the Bovine HapMap Consortium (Gibbs et al. 2009).

Thus, our models, autosomal sequence diversity, and mtDNA phylogeography all seem to defy a unitary domestication narrative within South Asia. The first archeological evidence for domestic cattle occurs in Mehrgarh, in Baluchistan some 8000–7000 years BP, undoubtedly influenced by communication with the Fertile Crescent cultures and agricultural innovations. Bone morphology and artistic representations have
allowed argument that these were *B. indicus* and transition in the nature of *Bos* bone collections suggests this is a center of zebu domestication (Meadow 1993).

Further cattle domestication centers have been suggested within the subcontinent but no archeology gives as secure a location as Baluchistan (Fuller 2006). However, large bovine bone finds in the eastern and southern parts of South Asia do suggest survival of the wild ox into the domestic period, and additional or continual wild incorporation is surely plausible. Also, wild bovines have certainly been domesticated at least four times to the east of Baluchistan, giving rise to yak, water buffalo, mithun, and domestic banteng. Caesar, in his early description of the aurochs painted a picture of a formidable animal, “Little below the elephant in size . . . Their strength and speed are extraordinary: they spare neither man nor wild beast they have espied.” It might have been assumed that their capture and taming constituted singular and unlikely events in human history. Latest interpretations of genomic data point toward domestication processes that are more complex and repetitive in nature.

References


Bovine Genomics


