Genetic Aspects of Domestication

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Introduction

The cultural, economic and sometimes religious importance that cattle assume in modern pastoral societies is undoubtedly reflective of that in the earliest herding communities. Although predated by dogs, sheep, pigs and goats, cattle were the largest and subsequently most important of the domesticated animal species. The domestication of an animal of the dimensions of the now-extinct aurochs, or wild ox *(Bos primigenius)*, must have been a formidable task and was one of the definitive points of human development. In addition to products such as milk, meat, hides and dung, it is likely that the traction power represented by the domestic ox would have been instrumental in opening up the heavy soils of Europe for the expansion of agriculture from the Near East.

Cattle species today include: humpless cattle (*Bos taurus*), which predominate in Europe, northern Asia, West Africa and the Americas; humped cattle (*Bos indicus*), which thrive in more arid climes; Bali cattle of South-East Asia *(Bos javanicus)*; gayal or mithan *(Bos gaurus)* of north-west India; and the

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domestic yak *(Bos grunniens)*. From morphology and limits to interfertility, it is clear that the wild progenitors of the latter three were distinct species and, as such, must have involved separate domestications in Asia. However, a distinction between humped (zebu) and humpless (taurine) cattle has been less obvious, and several authors (Payne, 1970; Epstein and Mason, 1984) have favoured a single domestic origin for *B. indicus* and *B. taurus*, centred on the taurine cattle of the early neolithic centres of the Near East. This view holds that zebu morphology developed as a derivative type on the eastern margin of the region. However, the aurochs had a wide range, stretching over much of Eurasia and parts of North Africa, and some geographical variation is detectable in osteological remains. Some archaeologists (Zeuner, 1965; Grigson 1980; Meadow, 1993) have held that the domestication of two or more geographically distinct strains of wild oxen is a more likely explanation of modern and ancient patterns of variation.

In this review, we shall assess the effects of the domestication process on the genetics of the aurochs. Additionally, we shall describe what the study of modern genetic variation implies about the nature of the different *B. primigenius* strains involved.

Present Variations in Cattle Populations

With a global total of almost 1300 million head, cattle are the most numerous of domesticated mammals. This dominant position can be attributed to two factors. As efficient and relatively unselective herbivores, they occupy a complementary position to humans in exploiting plant foods, subsisting largely on inedible forages. Secondly, they have multiple utility in evolving farming systems, providing dung for fuel, hides, work, currency and saving and security functions, as well as milk and meat. Their role is particularly important in pastoral areas, which comprise two-thirds of all agriculturally managed land and which are not suitable, for climatic or other reasons, for crop production.

As agriculture has evolved from subsistence through to commercial systems, the role of cattle has changed considerably. In developed farming systems, cattle now have clearly defined and specialized roles as either milk or meat producers. With the growing demand for livestock products in the diet, as disposable incomes have increased, and the steadily lower cost of grains, as a result of technical advances, the dietary base for cattle production has shifted to a considerable degree from forage to grains, particularly in milk production systems.

These developments have led to sharpening differences between the developed and developing world in the numbers, nature and function of cattle. In the developed world, with low population growth, high consumption levels of cattle products and steady increases in productivity per animal, total animal numbers are decreasing. This is particularly the case in dairy cattle. In developing countries, on the other hand, demand, driven by rising population numbers and income levels, is growing. While productivity per animal is increasing in many countries, cattle numbers are also tending to increase. At present, over 70% of the world's cattle are in developing countries, with a ratio of one bovine to every 4.7 people, while in the developed world, with under 30% of the global population of cattle, the ratio is one bovine to 3.3 people.

The broad variation in today's global cattle populations is most conveniently classified on a geographical and breed basis. To a large degree, these criteria run parallel. The breeds prevalent today in Europe, Asia and Africa are mainly ones native to those continents, while cattle in Australasia and the Americas are derivatives from Old World populations.

Europe

The most comprehensive survey of cattle breeds in Europe is given by Simon and Buchenauer (1993). They list 277 separate breeds within national boundaries, although in many cases these represent national populations of a widely used breed, such as the Holstein Friesian. Using estimates of effective population size and generation interval, they classified breeds according to their degree of endangerment. A breed was regarded as normal if the expected increase in inbreeding over a 50-year period was under 5%. With this criterion, 128 breeds were classified as normal. The remainder, representing more than half of the total, were in some degree endangered, with 57 being rated as critical.

Formal breed definition, with herd-books and rules of registration, began about 200 years ago with Coates' Shorthorn herd-book in Britain. For most breeds, the herd-book is of much more recent origin, with many established in the late 19th century. While herd-books included only a minority of animals, most bulls in use would have been registered, and therefore, over a number of generations, genes from the herd-book section would predominate in the wider population. This process has tended to sharpen the differences between breed types in Europe over the past two centuries. As a result, almost all cattle in Europe can be assigned to clearly defined breed groups.

A contrary trend has been systematic migration of genes from one population to another. With the advent of artificial insemination in the 1950s, this process has become easier, cheaper and more rapid. Much of this gene flow has been between breeds of similar colour. Thus, various Scandinavian Red populations have been systematically exchanging genetic material for some decades, as have the different groups of brown dairy cattle. All populations of black and white cattle now make extensive use of an internationally available pool of bulls.

A third factor affecting breed variability is the rapid process of breed replacement. A century ago, Holstein Friesian-type cattle were essentially limited to their home area of the Netherlands and northern Germany. Today, they constitute almost two-thirds of the dairy cow population of Europe. In the process, many local breeds have disappeared. On a smaller scale, the NRF breed in Norway has replaced seven local populations. This process is driven by ever more effective selection both between and within breeds for economic performance within a specialized production system.

To offset this genetic erosion at breed level, most countries in Europe now have put in place specific programmes to conserve endangered breeds. This is supported by actions at the level of the European Union.

The principal European breed groups are as follows.

Holstein Friesian

Holstein Friesian originated in the Netherlands and northern Germany, where, by the middle of the 19th century, the characteristic black and white colour pattern was predominant. Substantial exports from 1860 onwards led to the establishment of black and white cattle in many European countries and in the USA, where it became the principal dairy breed. With an estimated 70 million head worldwide, Holstein Friesian represents more than one-third of the world's dairy cattle (Cunningham and Syrstad, 1987).

Following trial importations and a major experiment in Poland (Jasiorowski *et al.*, 1988), which demonstrated genetic superiority for milk production in American Holsteins, widespread importations have now largely converted all European black and white populations to American genotypes. There is also considerable gene flow between European populations. European, North American and other Holstein Friesian groups can therefore now be regarded as effectively a single global breed.

Red or red and white

In many European countries, there are significant populations of red or red and white dairy cattle (Montbeliard and Normande in France, MRY in the Netherlands, Red Dane, Finnish Ayrshire, Rotbunte and Angler in Germany). There has been less gene flow between these populations than in the case of Holstein Friesian. However, in most cases, significant genetic change has begun. The Red Dane has largely incorporated American Brown Swiss genes, while many of the other populations have made significant use of American Red Holstein sources.

Brown breeds

These have their origin in native Alpine breeds. They are significant in Germany, Switzerland, Austria, Italy and France. In all cases, the pressures for high-output dairy performance have led to extensive use of American Brown Swiss genes.

Simmental or Fleckvieh

This group of breeds, with origins in southern Germany and Switzerland, has also been extensively used in Hungary, Ukraine and Russia. While used for milk production, it is more heavily muscled than the other dairy breeds. This dual-purpose character has been maintained, and the breed has not been subject to much inward gene flow.

Beef breeds

Specialized beef breeds represent less than 20% of Europe's cattle. Significant purebred groups are important in some countries, notably in France, while crossbred animals are the norm elsewhere. The principal French breeds, Charolais, Limousin and Blonde d'Aquitaine, are all heavily muscled, but differ in some other characteristics. Charolais are white/cream in colour and have a docile temperament and a large adult body size. Limousin are somewhat smaller, brown, less docile and of finer bone and slightly higher meat content. Blonde d'Aquataine are white in colour and large-framed animals that have evolved from a base of several breeds in south-west France.

The principal British beef breeds Angus and Hereford have a worldwide distribution, although their relative position in their home region of Britain and Ireland has declined. They mature at lower adult weights than the French beef breeds and with a higher fat level in the carcass, and are therefore somewhat less suitable for intensive production systems.

Many other local breeds (e.g. Alentejana in Portugal, Retinto in Spain, Maremmana and Marchegianna in Italy, Salers in France) subsist as beef producing breeds in their home regions. Generally they are declining in numbers and involved in conservation programmes.

Asia

Of the approximately 800 identified cattle breeds in the world, one-quarter are found in Asia. However, a large proportion of Asian cattle can be assigned to these breed groups only in the most general sense. Bhat and Taneja (1987) concluded that only 18% of the cattle population of the Indian subcontinent belonged to a well-defined breed.

Most Asian cattle breeds are *B. indicus* types. These are characterized by a pronounced thoracic or cervicothoracic hump and are often collectively called zebu cattle. The most recent and thorough description of Asian breeds is given by Payne and Hodges (1997). Their coverage extends to some 80 of the approximately 200 Asian breeds. Cattle are not numerous in the drier west Asian countries. They are generally varied in colour, shorthorn and often known by the Arabic term *Baladi*. Most of these breeds are declining in number or involved in crossbreeding.

From Iran eastward, humped cattle predominate. The hump consists of muscle, connective tissue and variable amounts of fat. The size and shape may vary by breed according to the sex and age of the animal. The function of the hump is not clearly understood, and earlier theories that it was a fat storage depot are not now generally accepted. Zebu cattle tend to have a narrow body, sloping rump and long legs. The hide is loosely attached and the brisket and dewlap are usually well developed, particularly in males. Size varies over a wide range, with breed averages ranging from below 200 to above 400 kg for mature cows.

The body characteristics can be seen as adapted to heat dissipation. In addition to heat tolerance, *B. indicus* cattle have better resistance to ticks than *B. taurus* types, and are better able to withstand periods of low feed intake. Reflecting their different selection history since domestication, particularly in recent centuries, they have a lower milk potential than *B. taurus,* and in particular require the presence of the calf for milk let-down.

The most widespread zebu breed type is the Hariana, predominant in northern India. The bullocks are widely used for draught purposes and cows are milked, giving up to 1000 kg per lactation.

Kankrej (Gujrati) and Gir, both from the western regions of the country, combine good draught ability with acceptable milk yields, and also have a high potential for meat production. The same can be said for Ongole (Nellore), a breed originating from southern India. All three breeds have been exported to Central and South America, are the basis for the zebu breeds that predominate in beef production in Brazil and have also been important in milk production.

Sahiwal and Red Sindhi are zebu breeds originating in Pakistan. Both are reddish in colour, have short horns and have an established reputation as milk-producing cattle. Tharparkar is a third breed from the same region, also with dairy potential; it is usually somewhat larger than Sahiwal or Red Sindhi, and white or light grey in colour.

Zebu cattle are also found in south China, Taiwan and Indonesia, although in all cases some input from Indian breeds may be involved.

Bali cattle, from the island of Bali and neighbouring islands of Indonesia, differ from both *B. taurus* and *B. indicus* types, and are said to originate from a separate domestication. They are classified as *B. javanicus*, and have $2n = 60$ chromosomes, similar to *B. indicus* and *B. taurus*. Their colour is reddish brown, with characteristic reddish-white markings on the rear and underparts. Bali cattle are used primarily for work, but are good meat producers.

In the sub-Himalayan areas of India, Bhutan and China, related taxa are also found in both wild and domesticated circumstances: Gaur (*B. gaurus*), Mithun and Dulong. All three have $2n = 58$ chromosomes and are apparently cross-fertile with cattle, although the offspring, particularly males, may not be fertile.

Africa

Some 120 cattle breeds have been classified for Africa. As in Asia, most cattle can be assigned to breed type only in a general way, and formal herd-books and registration structures are rare. In their discussion of African breeds, Payne and Hodges (1997) offer brief descriptions of 72 breeds.

African cattle fall into three broad groups, though with considerable gene flow between them. In North and much of West Africa, *B. taurus* types predominate. In Egypt, the local *Baladi* cattle can be compared morphologically to similar types in west Asia. A more distinctive group is the Atlas Brown, found in Tunisia, Algeria and Morocco. Their colour is brown to dark, and the animals are described as sturdy. They are used for work, as well as milk and meat production, although productivity is generally low.

B. taurus breeds of West Africa are found primarily in the more humid areas of the countries ranging from Senegal to Nigeria. The best-known breed types are the N'Dama, centred on Guinea but with populations in several other countries, and West African Shorthorn, including Namchi and Kapsiki in Cameroon and Baoulé in the Ivory Coast and Burkina Faso. All are used for meat and milk production, and to some extent for draught purposes. They are of considerable interest because of their demonstrated tolerance of trypanosomiasis, a blood-parasitic disease transmitted by tsetse flies and generally fatal to introduced breeds.

In the drier regions, north of the trypanosomiasis belt, most cattle breeds are of *B. indicus* type. Ranging from west to east, the group includes Maure in Mauritania, Mali, Burkina Faso; Fulani ranging throughout the western Sahel; Baggara in western Sudan; Kenana and Butana in Central Sudan; and Boran in Ethiopia, Somalia and Kenya.

Many of these breeds are kept in nomadic herding systems, and vary considerably in size, colour and other characteristics. Some, including Kenana, Butana and Boran, have a considerable reputation as beef cattle.

The native breeds of Central and Southern Africa generally display a phenotype intermediate between *B. taurus* and *B. indicus*, with, in particular, reduced hump and dewlap. They are collectively called Sanga breeds, and are believed to be the result of crossing between *B. taurus* and *B. indicus* types. Most are involved in pastoral systems with domestic milk production and limited use for draught purposes. Some of the better-known breed types within this group are Ankole in Tanzania, Uganda and neighbouring countries; Barotse in Zambia and Zimbabwe; Tuli and Mashona in Zimbabwe; Nguni and Tswana in the Republic of South Africa, Botswana and Mozambique. Each breed has local subtypes.

Australasia and the Americas

These continents have very large cattle populations, all of postcolonial origin. In Australasia, the initial importations were exclusively of British breeds. In New Zealand, this has largely remained the case, with Angus predominant in beef-producing areas, and Jersey and Holstein Friesian in dairy-farming areas.

In Australia, dairy farming is almost exclusively with Holstein Friesian, but the great bulk of the cattle population is involved in beef production in pastoral areas. In temperate regions, Hereford and Angus types were once dominant. Today, these areas also include numbers of Simmental, Charolais and other types, and crosses between all of these beef breeds. In more tropical parts of the country, *B. indicus* types and crosses have largely replaced European breeds. The *B. indicus* strains involved are largely of North American origin, which in turn derive from Brazilian stock, in their turn based on importations from India in the last century.

The cattle of Latin America were derived from Spanish and Portugese breeds, possibly with some West African influence. Locally adapted descendants of these importations are generally called Criollo. In Brazil, very large numbers of descendants of Indian cattle (Nellore, Guzera, Gir) are used in beef production. In Argentina, the very large beef herd is mainly derived from Hereford and Angus.

North American dairy cattle are today almost exclusively Holstein Friesian. Beef cattle are four times more numerous and include derivatives of all European beef breeds, though with Angus and Hereford still very important. In addition, in southern parts of the country, *B. indicus* types derived from Brazilian imports and their crosses with European breeds, predominate.

The Genetic Effects of the Domestication Process

Phenotype

The main criteria used to decide whether animal remains at an archaeological site are wild or domestic are: the presence of a species outside its normal geographical range; an age and sex structure in the remains which would be atypical in the wild; a sudden increase in the frequency of a species between different time horizons; and evidence for reduction in animal size (Grigson, 1989; Meadow, 1989). The latter is likely to be a consequence, not only of the changed environment in which the animals exist, but of genetic change in the managed herds.

A convincing archaeological record of changing cattle size over the time in which domestication took place is available from two regions: the Near East (Grigson, 1989) and Baluchistan (Meadow, 1993). In each case, when bone dimensions are normalized by comparisons with those of a reference animal, definite and consistent decrease is evident in collections from later levels. For example, the box plot in Fig. 2.1 summarizes the distributions of bone measurements from the western part of the Near East in collections spanning a period of five millennia (based on Grigson, 1989). This type of data from a defined region, coupled with other changes in the patterns of faunal remains, provides strong support for local domestication of the aurochs.

The restriction of cattle foraging and the diseases, which are a consequence of confinement, could have been environmental factors leading to the reduction of animal size that occurs after domestication. However, it is likely that the major source of change would have been genetic. Selection for docility and manageability of animals would have been a strong motivation for early herders. Additionally, the time differences between archaeological levels may be several hundreds of years, representing many animal generations with ample opportunity for selective effects. Size decrease is most pronounced in

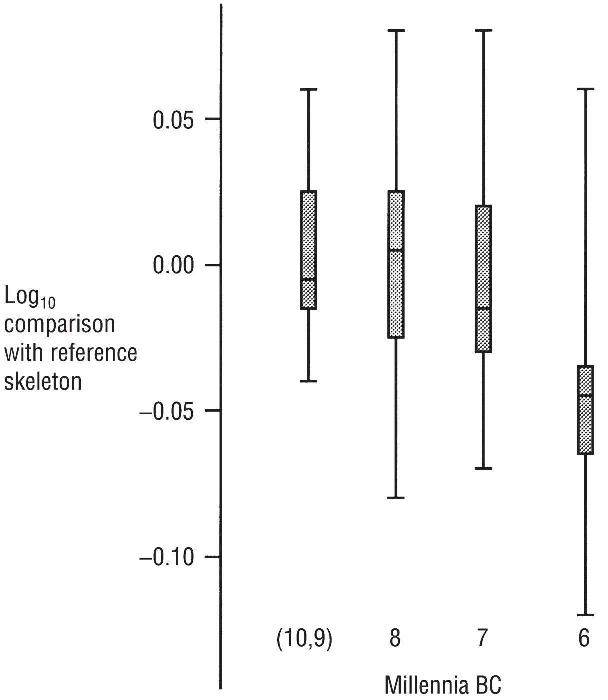

Fig. 2.1. The size of *Bos* remains in the western part of the Near East from the tenth to the sixth millennium BC. Adapted from Near Eastern bovine data presented and analysed by Grigson (1989). The data shown consist of logarithmic comparisons of bone measurements with those taken from the elements of a standard skeleton, in this case that of a female auroch found in Denmark. A clear dimunition in size in sixth-millennium cattle is apparent and is taken to be a result of, and also evidence for, the domestication process.

male cattle and the marked sexual dimorphism of the aurochs, typical of *Bovini*, is almost absent in domestic cattle.

Genetic change seems to have been a continuing process in cattle domestic history. The earliest cattle of Europe were relatively large long-horned beasts and have mostly been replaced by the smaller short-horned varieties, which predominate today. Overall, we can see today an enormous range of local breeds, strains or types. In the course of human history, these have been moved with the migration of peoples, crossed with other local strains, and selected continuously both by human intervention and by the forces of natural selection operating in the particular farming system of which they are a part.

Change in the farming system involves changed breeding objectives for livestock. In traditional systems, number of livestock rather than output per head is often the main consideration. In these circumstances, traits related to survival in the face of nutritional, health and climatic stress predominate. As farming systems become more market-orientated, volume and value of saleable product take over. In these circumstances, selection goals often change from multipurpose use to much narrower targets. They shift to such traits as prolificacy, early maturity, individual growth rate and milk yield, and aspects of milk composition and carcass quality.

Selection for such traits has transformed the genetic constitution of many developed breeds. For example, in many non-market traditional cattle systems, cows first calve at 4–5 years and thereafter at 2-year intervals, producing perhaps 500 l of milk year^{-1}. In modern, highly developed, dairy production systems, cows first calve at 2 years, and thereafter at yearly intervals, and produce up to 10,000 l of milk year^{-1}. The genetic change in the animal has made possible the intensification of the system, while the evolution of the system of feed supply, management and health care has made possible the support for high-producing genotypes. The net result is a dramatic improvement in efficiency of resource use.

In addition to the direct effect of selection on the genetic constitution of livestock populations, changes in breeding objectives can also promote inter-population gene flow. Thus, in West Africa, demand for beef animals of higher body weight has led to substantial crossbreeding of larger *B. indicus* on the smaller *B. taurus* populations. Such patterns of crossbreeding can, over a few generations, effectively lead to total replacement of the domestic pool of genetic diversity. In some cases – where artificial insemination is widely used or where domestic strains are simply bypassed by the importation of totally new genotypes – this can happen very rapidly.

Genotype

The principal product of a domestic animal is its progeny. Domestication of cattle may have involved the capture of a relatively small number of aurochs, from which the 1300 million head alive today are descended. One question is whether such an initial restricted sampling of the genetic variation from the wild progenitor, together with subsequent population bottlenecks experienced in early herds, has reduced genetic variability in the species.

One of the most valuable indicators of genetic variation in a species is the examination of protein polymorphisms through electrophoretic assay. A similar array of enzymatic and non-enzymatic proteins is accessible for study in a range of mammalian species, and the amount of heterozygosity observed at these loci is a useful comparative indicator of total variability. Estimates for average heterozygosity in *B. taurus* populations have varied between 4 and 8% (Baccus *et al.*, 1983), and compare well with the mammalian mean of 4.14 ± 0.25%. Figure 2.2 illustrates the distribution of average heterozygosity estimates obtained from studies of 183 mammalian taxa (after Bancroft *et al.*, 1995; see also Nevo *et al.*, 1984). The relatively high level of estimates from cattle are indicated. Figures from *B. taurus* are comparable to, or greater than, those from other ungulates. Notably, those species that are known to have undergone historical population bottlenecks, such as *Bison* sp., have yielded lower heterozygosity values (Hartl and Pucek, 1994).

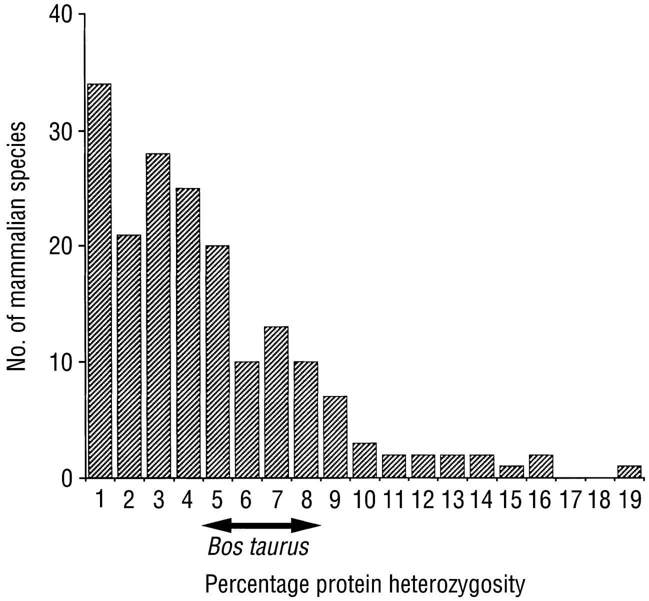

Fig. 2.2. Distribution of average protein heterozygosity for 183 mammalian species or subspecies (adapted from Bancroft *et al.*, 1995). The range of a series of estimates calculated for domestic cattle populations is denoted by an arrow on the horizontal axis.

The persistence of significant genotypic variation in modern cattle is also evidenced by deoxyribonucleic acid (DNA) studies. Extensive typing of microsatellite markers has revealed substantial variability both within and among populations (MacHugh *et al.*, 1997), although such data are difficult to compare across species because of a bias due to the initial selection of microsatellites for high polymorphism in the species of origin.

Many DNA studies of intraspecific variation have centred on highly polymorphic sequences of the major histocompatibility complex. This gene-rich genomic segment contains several genes important in the immune response, and it is well established that deeply divergent alleles or haplotypes are maintained by balancing selective forces, sometimes even across species boundaries (Takahata, 1990). Similarly to sheep and goat, cattle exhibit many alleles, high heterozygosities and substantial divergence between alleles in sequence studies of class II *DRB* loci (Mikko, 1997). This is in contrast to the situation in American bison where the number of alleles seems to have been noticeably reduced by the severe hunting-induced bottleneck of the last century, although genetic divergences between alleles themselves are similar to those within cattle (Mikko *et al.*, 1997).

Thus it seems there is little evidence from autosomal genetic systems for any significant reduction in bovine variability as a result of the domestication process. This is perhaps explainable in several ways. Firstly, the undoubted population bottleneck which would have resulted from the initial capture of a limited number of wild aurochs may have been short-lived. The genetic effects of a bottleneck are dependent on a number of factors, including the number of generations for which it is endured. It may be that wild oxen were initially adopted into systems in which cattle numbers were expanding, and thus little loss of genetic variation was effected. Secondly, the process of incorporating aurochs into the ancestral domestic pool may have been an often-repeated one, resulting in a high proportion of the genetic variation in the wild species being harnessed. That variation may have been considerable, the aurochs itself being a successful, wide ranging species. Lastly, more sensitive molecular tools may be required to detect any diversity loss induced by domestication.

The effects of a population bottleneck, while not detectable using autosomal markers, may in fact be discerned through examination of mitochondrial DNA (mtDNA) haplotypes. These possess an effective population size, which is one-quarter that of nuclear DNA, and are more susceptible to lineage loss in reduced populations. Indeed, extensive study of mtDNA variation in widely sampled populations has revealed the imprint of the domestication process and allowed novel inference about the nature of events some 10,000 years ago (Bradley *et al.*, 1998).

Archaeological Inferences from Patterns of Genetic Variation

DNA variation

An initial survey of mtDNA control region sequence variation, using 26 samples from Western Europe, Africa and India (origins shown in Fig. 2.3), revealed the existence of two substantially divergent clades (Loftus *et al.*, 1994). The sequences of European, *B. taurus* origin showed approximately 5% difference from those of Indian *B. indicus* provenance. Sequences from Africa, sampled from both taurine and zebu breeds, were much more similar to those from Europe but showed some consistent difference (averaging 0.76%). The right-hand side of Fig. 2.4 includes a simplified phylogenetic tree, which summarizes these data.

Further analysis of a shorter region of the mtDNA chromosome has brought the number of sequences analysed to over 100 and this basic pattern of variation has been confirmed (Bradley *et al.*, 1996). The deep phylogenetic division between Indian mtDNA haplotypes and the rest has been interpreted as reflecting that between the progenitor of *B. indicus* and the ancestor of *B. taurus* cattle. A number of analyses attest that the grouping of these sequences into continental groups is justifiable (Bradley *et al.*, 1996) and this allows an inference to be drawn from comparisons based on quantitative divergence. The time depth of the divergence between the two major clades may be estimated by either applying the mtDNA control-region molecular clock, which has been calibrated in other species, or by using comparison with the equivalent *Bison* sequence and a corresponding palaeontological estimate of at least 1 million years for that interspecific separation. Several calculations

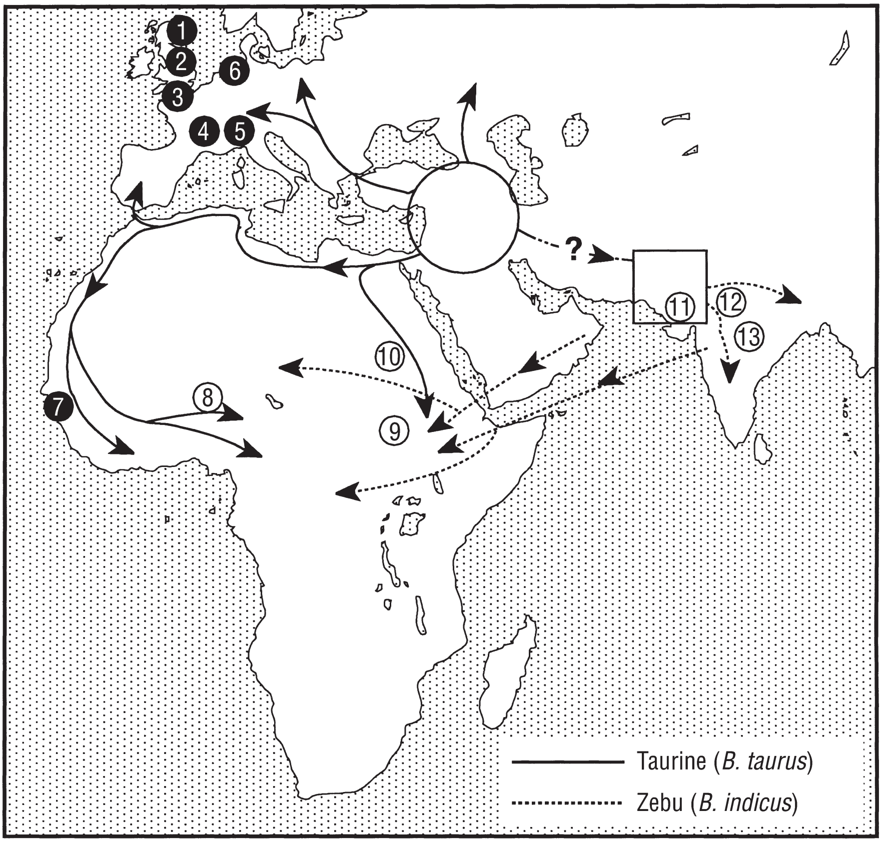

Fig. 2.3. Postulated migratory routes of cattle across western Asia, Africa and Europe (reprinted from Loftus *et al.*, 1994). Geographical origins of breeds sampled for mtDNA analysis are represented by numbered circles (taurine, black; zebu, white).1, Aberdeen Angus; 2, Hereford; 3, Jersey; 4, Charolais; 5, Simmental; 6, Friesian; 7, N'Dama; 8, White Fulani; 9, Kenana; 10, Butana; 11, Tharparkar; 12, Sahiwal; 13, Hariana. The large circle represents the original domestication event and the square represents the formation of Asian zebu. The data discussed here are not consistent with zebu having developed as post-domestic derivatives of Middle Eastern taurines – indicated with a dotted line broken by a question mark.

have yielded figures for the Indian vs. Europe/Africa bifurcation as occurring in the order of hundreds of thousands of years BP (Bradley *et al.*, 1998). This is consistent with other data, such as that from microsatellites and biochemical polymorphisms, which emphasize zebu/taurine divergence (Manwell and Baker, 1980; MacHugh *et al.*, 1997) and leave it difficult to imagine that all modern cattle might have come from a single strain of wild ox domesticated only approximately 10,000 BP (see Fig. 2.3). There is strong support from these data for assertions that *B. indicus* cattle are descended from eastern *B. primigenius* variants, which may have been domesticated in centres such as Mehrgarh, Baluchistan (Meadow, 1993).

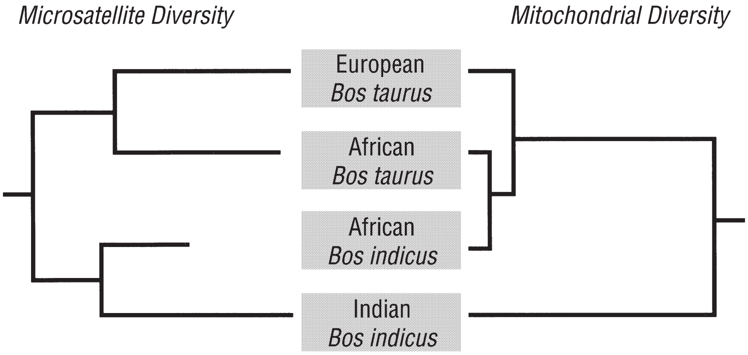

Fig. 2.4. Summary of phylogenetic tree topologies derived from microsatellite diversity (left-hand side) and mitochondrial sequence diversity (right-hand side) (reprinted from Bradley *et al.*, 1998). Both types of data reveal the deepest phylogenetic division within cattle, that between *Bos indicus and Bos taurus.* However, the positioning of the African zebu is ambiguous. These cluster with Indian zebu (with truncated branch lengths) in microsatellite analyses and with the African taurines in mtDNA-derived phylogenies. Thus, African zebu seem to be hybrids, with the majority of their genome derived from introgressing *Bos indicus* but with maternally inherited mtDNA variation that is representative of the original *Bos taurus* domesticates of that continent. Both phylogenetic reconstructions illustrate some divergence between African and European taurines.

Microsatellites and African cattle origins

One surprising feature of mtDNA variation is that the zebu cattle of Africa, which are unmistakably *B. indicus* in morphology and physiology, exhibit sequence types which show no distinction from those of neighbouring *B. taurus* breeds. This is likely to reflect a hybrid origin for African zebu. An investigation of these and some additional cattle populations, using 20 microsatellite markers, has given a phylogenetic reconstruction that ties more closely with breed morphology (MacHugh *et al.*, 1997). The simplified left-hand phylogeny in Fig. 2.4 shows African *B. indicus* clustering with Indian cattle and a grouping of the *B. taurus* populations from Europe and Africa. Branch lengths of African zebu in neighbour-joining trees, which are constructed from allele frequency-derived genetic distances, are truncated and this is a further suggestion that these populations may be hybrid in origin.

Particularly strong inferences concerning hybridization may be drawn from frequencies of microsatellite alleles that are zebu-specific. Certain loci show allele length distributions in pure taurine (such as European and certain West African populations) and pure zebu (such as those of southern Indian provenance) cattle which are separate and distinctive. Consequently, it is possible to identify private alleles in approximately half of the markers tested which are specific to *B. indicus* and their hybrids, and which allow the estimation of the extent of admixture in breed ancestry. The descendants of primeval African cattle persist in parts of humid West Africa and are pure *B. taurus* in nature. Due to their long association with the continent, they display a suite of adaptations to the prevalent disease challenges, including, notably, a tolerance for trypanosomiasis, which is arguably the most important African livestock disease (Murray *et al.*, 1982). Microsatellite-based estimation of zebu genetic influence in a range of breeds has illustrated a cline of admixture which stretches from the exclusively taurine N'Dama cattle of Guinea both northward to Sahelian zebu cattle, such as the Mauritanian Maure breed, and eastward, to the Sudanese Butana and Kenana breeds, which have displayed the highest *B. indicus* influence (MacHugh *et al.*, 1997).

A Y-chromosome polymorphism that distinguishes between the two taxa has also been described (Bradley *et al.*, 1994). In an examination of the frequency of the zebu form in the same series of breeds, stretching north–south from Mauritania to Guinea, it was striking that the paternally inherited Y variant seemed to be the most aggressively introgressing genetic element. These data, together with the apparently total absence of *B. indicus* mtDNA chromosomes on the continent, suggest that most African cattle are the products of a progressive, male-driven, admixture between the indigenous taurine breeds and immigrating zebu cattle, which have made major incursions within the last millennium and a half (Bradley *et al.*, 1998).

The time depth of the ancestral divergence between African and European *B. taurus* cattle has been estimated, using both microsatellite and mtDNA variation (Bradley *et al.*, 1996; MacHugh *et al.*, 1997). These estimates (the lowest of which is 22,000 BP), are suggestive of the input of separate aurochs strains into these two continental gene pools. However, it must be noted that calibrations of the genetic divergence in both these genetic systems are difficult and potentially subject to wide errors. Further evidence from cattle breeds of the Near East and Egypt should do much to clarify the nature of the early domestication process in the Levant and, potentially, the Nile valley.

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