2 Genetic Aspects of Domestication

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Introduction

The appearance, characteristics and genetic makeup of cattle have been heavily influenced by domestication and by their dynamic history right up to the present day. Paleontology and molecular-genetic analysis have revealed the approximate place and date of domestication (Zeder *et al.*, 2006). However, documentation of the subsequent history of cattle, although closely connected with human history, is scarce until 250 years ago. In this chapter we summarize the available data on the domestication and history of cattle, including the appearance of phenotypes that today are the subject of genetic research.

The First Domestic Cattle

Domestic cattle appeared in northern and western parts of the Fertile Crescent in Southwest Asia not long after domestic sheep and goats and at about the same time as domestic pigs (Hongo *et al.*, 2009). Together with the introduction of crops, livestock fundamentally changed human demography and eventually led to our present complex society. It is plausible that cattle husbandry, requiring more labour and organization than the keeping of smaller sized sheep, goats and pigs, contributed to the earliest stratification of society (Ajmone-Marsan *et al.*, 2010).

The oldest evidence of taurine domestic cattle was found on both sides of the Turkish–Syrian border northeast of Aleppo and dates from 10,300–10,800 BP (Ho and Shapiro, 2011; Vigne, 2011; Bollongino *et al.*, 2012). Modelling of cattle autosomal DNA sequence variation suggested a predomestic population bottleneck, which was possibly induced by a glaciation period (Murray *et al.*, 2010; Teasdale and Bradley, 2012). Coalescence analysis of mtDNA sequences from Iranian Neolithic and Iron Age cattle led to an estimate of *c.*80 female aurochs (*Bos primigenius*) being the maternal ancestors of almost all present day taurine cattle (Bollongino *et al.*, 2012). The present taurine (T) mtDNA is clearly less variable than the mtDNA of yak or bison and diverged less than 15,000 BP, indicating taurine population expansion after domestication (Ho and Shapiro, 2011).

Zebu (*B. indicus*) (Plate 4) emerged in the Indus valley by a separate domestication of a different aurochs subspecies (*B.p. namadicus*, Chen *et al.*, 2010). Archeological evidence dates the domestication of zebu 2000 years after the taurine domestication (Bradley, 2006; Fuller, 2006; Jarrige, 2006). This is in line with Bayesian estimates of mtDNA variants (Ho and Shapiro, 2011) and with the diversity pattern and broad geographic distribution of the mtDNA haplogroup I1 (Chen *et al.*, 2010; Teasdale and Bradley, 2012). However, the absence in East Asia of the second haplogroup I2, modelling of autosomal gene variation and a more complex I2 diversity cline suggests that there may have been an additional zebu domestication, possibly including introgression of wild females into domestic herds (Murray *et al.*, 2010; Teasdale and Bradley, 2012).

Remarkably, the characteristic hump, which is caused by an overdevelopment of the thoracic part of the rhomboid major muscle relative to the cervical part, does not appear on rock paintings of *B.p. namadicus*. Fossil remains from Mehrgarh in Baluchistan have been attributed to zebu and were dated at 8000 BP (Jarrige, 2006), but the earliest convincing clay figurines of humped cattle are dated at 5000 to 6000 BP, suggesting that the hump emerged after domestication. The earliest clear depictions of humped cattle are from a seal from 4450–4200 BP found in Harappa in the Indus valley and in pictures from south Indian Neolithic sites (Allchin and Allchin, 1974).

Since there are no reproductive barriers between zebu and taurine cattle, they should zoologically be considered as subspecies with designations *Bos primigenius indicus* and *B.p. taurus*, respectively. However, *B. indicus* and *B. taurus* are the more common designations.

As in other domestic species, adaptation to the habitat of early human settlements was accompanied by profound genetic changes in morphology, physiology and behaviour (Hall, 2004). This included decrease in size, reduction of the outspoken sexual dimorphism of the aurochs and increase in intramuscular fat content. Taming implies an attenuation of behaviour, but feral populations such as the Chillingham and Heck cattle regain the typical behaviour of wild herd species with male dominance. The selection signatures are likely to be different in indicine and taurine cattle because of their separate domestications, but selection may have targeted some of the same genes.

Taurine Cattle Spread over the Old World

Early farms and dairying

The expansions of the first, well-populated agricultural communities from Southwest Asia to the rest of Eurasia and to Africa have so far been reconstructed on the basis of sporadic pictorial representations and by dating of the earliest farms and paleontological remains of livestock. Domestic taurine cattle probably reached central Anatolia between 10,000 (Vigne, 2011) and 8500 BP (Arbuckle and Makarewicz, 2009). This was possibly preceded by intensified management of wild cattle populations, which may have interacted with the smaller imported domesticates.

The subsequent colonization of Europe proceeded via the Mediterranean coast and along the Danube River. Traces of dairy products in remains of pottery and nitrogen isotope ratios as signs of early weaning of calves showed that dairying followed soon after the arrival of domestic cattle (Payne and Hodges, 1997; Price, 2000; Tresset, 2003): in the 9th millennium BP in Southwest Asia; in the 7th millennium in Africa (Dunne *et al.*, 2012); in the 8th millennium in southeastern (Evershed *et al.*, 2008) and northern (Salque *et al.*, 2013) Europe; and in the late 7th millennium in the UK (Copley *et al.*, 2003) and France (Balasse and Tresset, 2002). This was accompanied by a gene flow from the Southwest Asian agricultural societies into the European communities of hunter-gatherers (Pinhasi *et al.*, 2012; Rasteiro and Chikhi, 2013). The emergence of lactase persistence in adult humans in European and African Neolithic populations may be regarded as an example of human–animal coevolution (Beja-Pereira *et al.*, 2003; Gerbault *et al.*, 2011).

Maternal lineages

Archaeological observations do not rule out secondary domestications of taurine cattle outside the Fertile Crescent. Separate domestications have been postulated for African cattle on the basis of fossil remains (Brass, 2012) and East Asian cattle on the basis of the high frequency of the T4 mtDNA haplotype (Fig. 2.1; Mannen *et al.*, 2004). However, the Mesopotamian origin of almost all taurine cattle is supported by a phylogeny of the common taurine mtDNA haplotypes without deep splits and by their geographic distribution (Bradley *et al.*, 1998; Ajmone-Marsan *et al.*, 2010). Southwest Asia has a high haplotype diversity with haplogroups T, T1, T2 and T3 (Fig. 2.1). In contrast T1 is almost fixed in Africa, whereas T3 is dominant in Europe and north-central Asia (Troy *et al.*, 2001; Beja-Pereira *et al.*, 2006; Achilli *et al.*, 2009; Kantanen *et al.*, 2009; Bonfiglio *et al.*, 2010; Jia *et al.*, 2010; Ginja *et al.*, 2010; Stock and Gifford-Gonzalez, 2013).

The shift from ~29% T1 in Southwest Asia to almost 100% in Africa indicates strong maternal founder effects during migrations from Southwest Asia to North Africa and then to West and Central Africa (Fig. 2.1, Bonfiglio

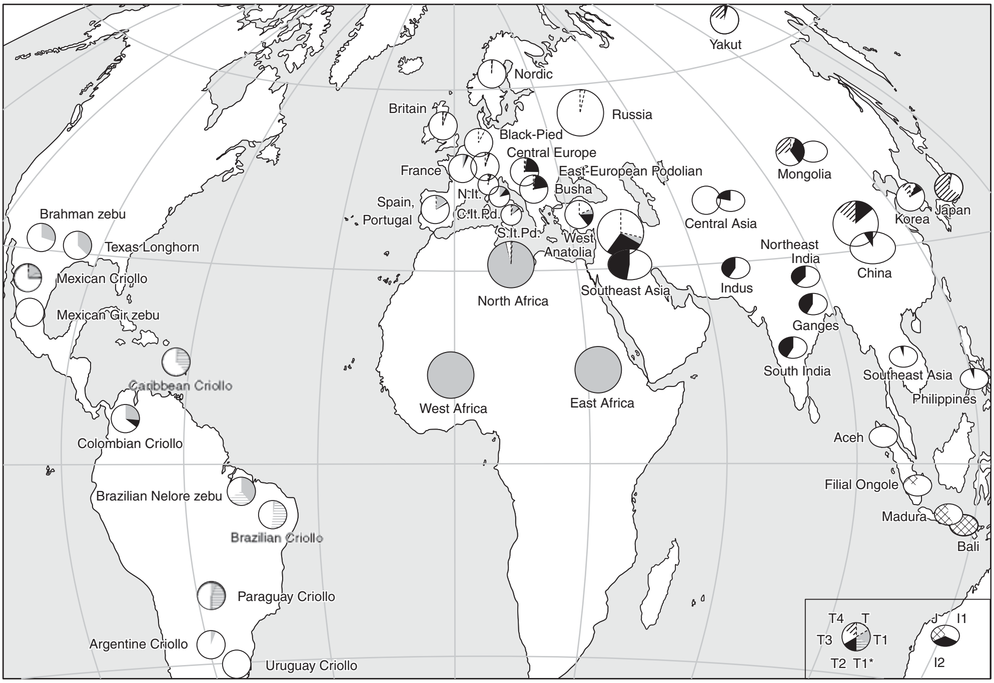

Fig. 2.1. Continental distribution of taurine (circles) and zebu/banteng (ovals) mtDNA haplogroups (Lenstra *et al.*, 2014). Data are from Cymbron *et al.*, 1999; Troy *et al.*, 2001; Magee *et al.*, 2002; Miretti *et al.*, 2002, 2004; Carvajal-Carmona *et al.*, 2003; Kim *et al.*, 2003; Mannen *et al.*, 2004; Komatsu *et al.*, 2004; Lai *et al.*, 2006; Lei *et al.*, 2006; Cortes *et al.*, 2008; Kantanen *et al.*, 2009; Mohamad *et al.*, 2009; Bonfiglio *et al.*, 2010; Chen *et al.*, 2010; Ginja *et al.*, 2010; Armstrong *et al.*, 2013; Horsburgh *et al.*, 2013; and Ludwig *et al.*, 2013. N.It., North Italy; C.It.Pod, central Italian Podolian; S.It.Pod., South Italian Podolian; T to T4, taurine haplogroups; T1*, T1c1a1 subgroup expanded in American cattle; I1, I2, zebu haplogroups; J, banteng mtDNA sequence. Large circles and ovals represent cattle from a continental region. With the exception of haplotypes of Texas Longhorn and Brahman, no mtDNA sequences are available for USA, Canadian, or Australian cattle. Indonesian cattle have not been typed for I1/I2 differentiation.

et al., 2012). Likewise, the T4 is a subvariant of the closely related T3 (Achilli *et al.*, 2009) and probably spread over East Asia by a founder effect during the eastward migration of cattle.

The frequency of the T3 haplogroup increases from ~40% in Southwest Asia to 100% in northwest Europe (Beja-Pereira *et al.*, 2006; Bonfiglio *et al.*, 2010) with a concomitant decrease of T2 (Fig. 2.1). This suggests a large influence of T3 carrying founders, although a predomestic origin of the high T3 frequency in Europe cannot be ruled out (Beja-Pereira *et al.*, 2006; Mona *et al.*, 2010; Lari *et al.*, 2011). Ancient DNA confirmed that most Neolithic European cattle already carried T3 haplotypes (Bollongino *et al.*, 2006). This agrees with Bayesian analysis of the coalescence of taurine mtDNA variants showing population expansion during the last 10,000 years (Finlay *et al.*, 2007).

A few examples show that haplotypes in European cattle other than T3 and T2 may provide additional information on the history of cattle:

- A low frequency (*c.*1/1000) of the P haplotype from European aurochs in European domestic cattle and the sporadic finding of R haplotypes suggests a rare recruitment of cows from the European aurochs population (Stock *et al.*, 2009; Bonfiglio *et al.*, 2010).
- A frequency of 13% T1 in Iberian breeds reflects prehistoric or later gene flow across the Strait of Gibraltar (Cymbron *et al.*, 1999; Beja-Pereira *et al.*, 2006; Ajmone-Marsan *et al.*, 2010; Ginja *et al.*, 2010), which recently has been confirmed by SNP genotyping (Decker *et al.*, 2014).
- The high frequency of T1 in Sicilian and south Italian Podolian breeds may also indicate African influence.
- Podolian breeds in central Italy have appreciable frequencies of both T1 and T2 (Bonfiglio *et al.*, 2010), which for T2 is also observed in east European cattle (Fig. 2.1). Since there are no records of intensive demographic contacts between Africa and central Italy, secondary gene flow from Anatolia (Pellecchia *et al.*, 2007) or Greece (Kron, 2004, see below) well after the introduction of cattle may explain the high mtDNA diversity in central Italy.

Paternal lineages

In contrast to mtDNA, which shows the maternal origin and therefore stays with the herds, Y chromosomal haplotypes are markers of paternal origin and male introgression. So far two major well diverged Y chromosomal haplogroups have been identified in taurine bulls, Y1 and Y2. Y1 is predominant in northern European and in north Spanish breeds, has a low frequency in Southwest Asian bulls and is carried by male offspring of recent European imports (Edwards *et al.*, 2011). Y2 is dominant in central European, Mediterranean, Asian and African taurine bulls.

Remains of European aurochs bulls for which their wild origin was validated via their mtDNA all carried Y2 haplotypes (Bollongino *et al.*, 2008). Since these cannot yet be differentiated from European or Southwest Asian Y2 haplotypes, this neither proves nor disproves wild male introgression. Wild–domestic crossbreeding was suggested by intermediate-sized Neolithic bones found in what is now the Czech Republic (Kyselý and Hájek, 2012). The Y1 distribution pattern is interpreted as reflecting later expansions of dairy breeds (Edwards *et al.*, 2011, see below; Bollongino *et al.*, 2008; Svensson and Gotherstrom, 2008).

The finding of African-specific Y2 haplotypes provides evidence for introgression of African aurochs in domestic herds (Perez-Pardal *et al.*, 2010a,b; Stock and Gifford-Gonzalez, 2013). An African origin of taurine cattle, in spite of a Southwest Asian maternal origin, has been confirmed by SNP analysis (Decker *et al.*, 2014).

Adaptation

Fossil remains reveal that skeletal morphology of cattle kept changing after domestication. In Europe the size of taurine cattle continued to decrease in the Stone Age, Bronze Age and Iron Age (Jewell, 1962; Zeuner, 1963; Bökönyi, 1974; Barker, 1985). A selective disadvantage of large cattle may have been imposed by: (i) slaughtering of the largest animals just before the winter; (ii) food shortage during winter in the temperate zones; and (iii) castration of the strongest bulls for use as work animals (Barker, 1985; Clutton-Brock, 1989).

The first domestic cattle were long-horned. This phenotype still persists in several British, French, Mediterranean, Podolian and zebu breeds (see Plates 10, 12, 16, 21, 22, 24 and 26), but did not suit the domestic habitat. About 2000 years after the domestication of long-horned cattle, short-horned cattle appeared in Mesopotamia and reached Africa 6000–5000 BP (Payne and Hodges, 1997), southern and central Europe 4500–5000 BP and Britain 3000–4000 BP. Long-horned cattle persisted in the Bronze Age in eastern Europe when the majority of Swiss and Austrian cattle were already short-horned (Bökönyi, 1974). From 3600 BP short-horns were predominant in Africa and from 3000 BP in Europe (Epstein and Mason, 1984).

Horns became dispensable in captivity because domestic cattle are protected against predation and the bulls do not fight for dominance. Hornless skulls found in Switzerland, Poland and Germany date as early as the 6th millennium BP (Bökönyi, 1974), while English hornless skulls date from 2700 BP (Jewell, 1962). Polled cattle were depicted in the 2nd millennium BC in Egypt, although it is not clear if these animals were also born hornless (Strouhal, 1992; Bard and Shubert, 1999). Herodotus mentioned hornless cattle kept by Scythians (Rawlinson, 1985), while in the north of the Netherlands most hornless skulls date from the Roman era (Lauwerier, 2011).

Molecular analysis localized the horned/polled causative mutation in an intergenic region on BTA1 (Medugorac *et al.*, 2012; Allais-Bonnet *et al.*, 2013; Wiedemar *et al.*, 2014). The congenital absence of horns correlated in a broad panel of breeds from Switzerland, France, the UK and Scandinavia with the presence of one particular indel, whereas a different indel in the same region was associated with polledness in the dairy breeds from northwestern-continental Europe. Remarkably, in spite of the old origin of the trait, its autosomal transmission and an obvious advantage to the farmer, the absence of horns has rarely been fixed within breeds, possibly because of association with unfavourable traits (Allais-Bonnet *et al.*, 2013). However, polledness was favoured in the ancestors of Scottish Angus (Plate 2) and Galloway and of several Nordic breeds, possibly because of the necessity to house cattle during long winter periods (Felius, 1995; Medugorac *et al.*, 2012). Domestication also favoured a diversity in coat colours, ever the most visible trait (see Plates 2–29; Chapter 4).

Zebus around the Equator

Zebu spread after domestication to eastern and southwestern Asia, in the latter region becoming introgressed into pre-existing taurine populations (Fuller, 2006; Edwards *et al.*, 2007a; Ajmone-Marsan *et al.*, 2010; Chen *et al.*, 2010). These migrations again generated a differential distribution of the mtDNA haplogroups I1 and I2, with eastern Asia populated almost exclusively by I1 haplotypes (Fig. 2.1).

Later migrations took zebu to tropical or subtropical zones of all inhabited continents, populating China, Indochina and Indonesia in the east and Africa and North and South America in the west. Pictures in Egypt at 3800 BP show the earliest African zebu, but large-scale introduction of zebu bulls occurred about 2000 BP (Epstein and Mason, 1984) and again following the Islamic invasions after AD 700 (Ajmone-Marsan *et al.*, 2010; Payne and Hodges, 1997). Importation from India in the 19th century brought zebu to America.

These migrations led to various admixtures with taurine cattle as well as other bovine species (Lenstra and Bradley, 1999). Selembu is the offspring after terminal crossing of zebu with gayal (*Bos frontalis*), which is practised in Myanmar and Malaysia. Indonesian and south Chinese zebu breeds carry 10–30% autosomal alleles from domestic banteng (*Bos javanicus*) with the frequency of banteng mtDNA ranging from 0 to 100% (Fig. 2.1, Mohamad *et al.*, 2009; Decker *et al.*, 2014). Southwest Asian and Chinese cattle from mixed taurindicine descent may carry both taurine and indicine mtDNA or Y chromosomes (Mannen *et al.*, 2004; Lai *et al.*, 2006; Lei *et al.*, 2006; Edwards *et al.*, 2007b; Jia *et al.*, 2010; Li *et al.*, 2013). In contrast, only zebu bulls were exported to Africa and almost only bulls to America; in fact, indicine mtDNA is rare outside Asia (Bradley *et al.*, 1998; Meirelles *et al.*, 1999; Ginja *et al.*, 2010).

African Sanga cattle descend from early taurindicine crosses and around AD 1500 they were the dominant type of cattle in eastern and central Africa (Payne and Hodges, 1997). Various degrees of zebu introgression in taurine and Sanga populations resulted in the present continuous spectrum of taurine, admixed taurine, Zenga (zebu × Sanga) and African zebu breeds. By crossbreeding of Indian bulls to American Criollo breeds, which are of Iberian maternal descent, overall frequency of the zebu-specific Y3 Y chromosomal haplotype is almost 51% (Ginja *et al.*, 2010) and their ancestry became taurindicine (Martinez *et al.*, 2012; McTavish *et al.*, 2013). During the past century, several American and Australian synthetic breeds have been formed by planned crosses of taurine breeds with zebu (Buchanan and Lenstra, Chapter 3, this volume; Felius *et al.*, 2014).

Several traits contribute to the adaptation of zebu to tropical and dry environments: a low metabolic rate, proliferation of large sweat glands, a large skin surface, a predominance of intramuscular instead of subcutaneous fat, a smooth coat, a low susceptibility to insects, ticks and protozoa and good utilization of low-quality fodder (Turton, 1991, see also Chapter 23). The heat tolerance often encouraged zebu introgression in spite of the higher productivity of European taurine cattle. Zebu did not develop the trypanotolerance of West African taurine breeds (see Chapter 9), but has a higher resistance to rinderpest and largely replaced the East African sanga after the epidemic of 1887–1897.

Several distinct indicine and taurindicine breeds have been described. However, selective breeding and genetic isolation of zebu have been less systematic and consequential than for taurine cattle.

Large Taurines during Classical Antiquity

The relatively peaceful Hellenistic and Roman societies and an increase of trading stimulated farming on a larger scale than in earlier pastoral societies. This also coincided with a reversal of the size reduction of taurine cattle in and around the Roman Empire. Already in the 8th century BC large cattle existed in the Greek Messenia region (Kron, 2004). It was probably the first type of cattle that spread over a large region because of its superior qualities: to Epiros, Greece, Anatolia, Sicily, from the 3rd century BC to south Italy and to north Italy and the Mediterranean French coast even before the Roman occupation. If these so-called Epirote cattle are ancestral to the current Italian Podolian breeds, it would explain the maternal genetic link between Anatolia and Italy as evidenced by the high mtDNA in Italy (Pellecchia *et al.*, 2007; Bonfiglio *et al.*, 2010).

Export probably accounted for the large size of several cattle during the Roman period in the European part of the Roman Empire (Kron, 2004; Bökönyi, 1974; Schlumbaum *et al.*, 2003). In the peripheral regions of the empire large cattle coexisted with small local short-horns (Jewell, 1962; Bökönyi, 1974; Riedel, 1985). One of these cattle found in the Alpine region appeared to carry the T2 mtDNA haplotype, which is rare in current Swiss cattle (Schlumbaum *et al.*, 2006).

Written documentation from Greek and Roman sources provides the first contemporary reports of different types of cattle. White cattle were already reported in the Mycenean period on Pylos (Bökönyi, 1974; McInerney, 2010). Archimedes (287–212 BC) mentioned four coat colours or colour patterns on Sicily: creamy white, ebony black, yellow and spotted (Archimedes, 1999). Several Roman authors described a large variety of Italian cattle of different sizes and coat colours, which were used mainly for draught and played a role in religious rituals (Barker, 1985; MacKinnon, 2010). Beef was consumed, but fetched in AD 305 a lower price than pork (Diocletian Price Edict, Leake, 1826). Roman cattle were not milked in contrast to Alpine and Germanic cattle (Caesar, 50–40 BC; Strabo, 1969; MacKinnon, 2010).

Small Cattle in Medieval Europe

After the fall of the Roman Empire, cattle accompanied the migrations of various Germanic tribes. Fossil remains, which have outlasted any written evidence, show a swift disappearance of the large Roman cattle with the possible exception of Italian cattle (Zeuner, 1963; Barker, 1985; Kron, 2002). Thus most cattle found in the graves from the empire of the Azars in Balkan from the 6th and 9th century were small and short-horned (Bökönyi, 1974). Presumably, these small cattle were adequate for local demands and represent an adaptation to medieval farming practices and to the vicissitudes of the unruly societies (Jewell, 1962). This phenotype has been preserved in the Balkan Busha cattle and in American Criollo, which descend from 15th-century Iberian cattle.

Presumably, frequent depletion of local livestock populations during famines or by plundering maintained gene flow between neighbouring regions. For instance, the clear phylogenetic relationship of southern French and Swiss breeds (Buchanan and Lenstra, Chapter 3, this volume) may indicate import into France from the Alpine regions, which were less affected by the devastating Roman conquest, medieval wars and 14th-century famines. Nevertheless, it is plausible that already during the Middle Ages local developments generated geographic differentiation. At least the characteristic phenotypes found at the European periphery have medieval or even older origins: the small Nordic polled cattle, several long-horned or short-horned British types of cattle, the long-horned Podolic cattle in Italy and the Balkan steppe, and the large variety in coat colour and horns in Iberian cattle (Bishko, 1953; Felius, 1995). Present cattle from these regions also have high Y chromosomal diversity (Ginja *et al.*, 2010; Edwards *et al.*, 2011).

Iberian cattle expanded to the south during the Reconquista from AD 900–1492. Incorporation of south Iberian cattle introduced the T1 mtDNA haplogroup (Cymbron *et al.*, 1999). On regained territories a beef cattle ranching economy with extensive management developed, which after 1492 was also introduced in the New World (Bishko, 1953). The high frequency of the mtDNA T1 haplogroup in Latin American Criollo cattle (Fig. 2.1, 29%) as well as SNP genotyping (Decker *et al.*, 2014) indicate an Iberian ancestry. The increased frequency of the T1 subvariant T1c1a1 (originally named AA, Miretti *et al.*, 2004; Ginja *et al.*, 2010; Bonfiglio *et al.*, 2012) reflects a founder effect, which very well may have taken place on one of the Caribbean islands before transport of cattle to the American continent.

The origin of the Podolian-type of cattle in Italy and the Balkans is unclear: a landrace with roots in the antiquity (Ciani and Matassino, 2001), which may have originated from the Epirote cattle (see above) and may in the 5th and 6th centuries have been influenced by cattle brought in by various German tribes; as suggested by their name, importation from Podolia in the Ukraine; or, as proposed on the basis of fossil evidence, an emergence in Hungary since the 14th century by selective breeding (Bökönyi, 1974) stimulated by their large-scale export as beef animals (see below). Podolian cattle in Italy continued the Roman tradition of using cattle as draught animals, although Aragonian rule in south Italy encouraged sheep ranching at the expense of cattle (Kron, 2004). Remarkably Italian and east European Podolian mtDNA haplogroup distributions are clearly different (Fig. 2.1), emphasizing that gene flow was mostly male-mediated.

Intensive dairy farming was practised in at least two regions, in the Alps with the vertical transhumance between summer and winter pastures and on the rich pastures of the North Sea and Baltic coastal regions. This probably continued a tradition predating the Roman era. In both regions a single Y chromosome is now predominant, a northern Y1 haplotype and a central European Y2 haplotype (Edwards *et al.*, 2011). These haplotypes are separated by a sharp genetic boundary that divides both France and Germany in northern and southern parts. This now reflects the contrast of specialized dairy cattle from the northwestern continental green lowland with the beef or dual-purpose cattle from the more hilly and mountainous regions (Comberg, 1984). However, it also coincides with historic cultural differences between northern and southern Europe, in France corresponding to the *langue d'oïl* and *langue d'oc* and Germany to the *Niederdeutsch* and *Hochdeutsch*, respectively.

Modernization of Cattle Husbandry

In post-medieval society higher literacy rates led to a more extensive documentation of agricultural history, so we can identify the several processes that led to the development of modern cattle, which shows a few clear parallels with Hellenistic and Roman agriculture.

- An increased demand for beef and dairy products stimulated international trade and large-scale movements of cattle. If the urban centres could not be directly supplied with locally produced beef, cattle were produced in extensive cow-calf operations on more distant breeding grounds and driven to the cities. Already in the Middle Ages Welsh cattle were moved along the so-called droves to London. From early 17th- to early 19th-century London and other English cities were supplied by cattle raised on Scottish grazing fields. Hungarian Grey cattle reared on the puzsta were driven westwards to Munich, Vienna and Venice in the 16th and 17th century (Bartosiewicz, 1997). During the same period The Netherlands and Germany were supplied by Danish cattle (Petersen, 1970). Both Danish and Hungarian cattle suffered competition from Ukrainian cattle driven via Krakow to the west (Carter, 1994). The cattle drives declined following improved husbandry practices that increased productivity of cattle bred near the urban centres. Most cattle were moved as meat-on-the-hoof, but in Italy Podolian cattle may have been recruited as breeding material (see above). In the 16th century Dutch, Holstein and Danish dairy cattle were imported in Sweden (Falk, 2012) and in the 17–18th century Dutch cattle contributed to the Shorthorn, Ayrshire, Hereford and other British breeds (Hall and Clutton-Brock, 1989; Felius, 1995).

- Improvements in agricultural practices allowed larger cattle to be kept, especially the increased availability of fodder during the winters. It is likely that selection contributed to the gradual size increase since the Middle Ages.
- A higher density of cattle probably played a role in the frequent occurrence of rinderpest epidemics (Broad, 1983; Spinage, 2003). In The Netherlands this necessitated the import of cattle from Jutland and Holstein, which were the ancestors of the Dutch black and red pied dairy cattle (Felius, 1995).
- From the 18th century, breed formation had a most profound influence on the appearance, productivity and genetic constitution of cattle. This was achieved by systematic selection of breeding bulls according to explicit breeding objectives within genetically isolated regions. Pedigrees and performance were documented in herd books and organized by breeding societies. Eventually this led to the development of hundreds of specialized breeds, which over time became integral parts of local tradition (Felius, 1995; Buchanan and Lenstra, Chapter 3, this volume). Inbreeding by genetic isolation was for many breeds counteracted by introgression and crossbreeding. In the UK, the Nordic countries, south France and the Iberian Peninsula, local breeds with minimal crossbreeding to cattle from other regions have retained their common ancestry and constitute regional clusters of genetically related breeds (Felius *et al.*, 2011). Distance analysis indicates also a cluster of Russian and Siberian breeds in spite of crossbreeding with west European breeds (Li and Kantanen, 2010; Felius *et al.*, 2011).
- Other more international clusters of related breeds were created in the 19th century by systematic crossbreeding of local breeds with sires of successful breeds (Felius, 1995). In the first half of the 19th century, English Dairy Shorthorn bulls (Plate 19) were crossed into several Belgium and north French breeds (Béranger and Vissac, 1994). Hardy dairy Ayrshire cattle from Scotland were imported to Finland and Scandinavia and crossed into several local breeds, generating a Nordic Ayrshire breed cluster. Dairy Black-Pied cattle (Plate 11) and dual-purpose Red-Pied breeds were kept in most north European countries. Baltic Red dairy cattle (Plate 7) spread along the Baltic coasts and were also crossed into German Highland Red Cattle. Spotted dual-purpose cattle descending from the Swiss Simmental (Plate 20) became popular in Central Europe and the Balkans (Epstein and Mason, 1984; Averdunk and Krogmeier, 2011). Another dairy breed, the Swiss Brown, was crossed into mountain breeds in France, Germany, Italy and Spain. Finally, Podolian breeds (Plates 6 and 12) are now kept in the Balkan countries and Italy.
- Massive exports of European and Asian cattle to America, Australia and New Zealand replicated in the 19th and 20th centuries a large portion of the cattle genetic resources in the New World (Ajmone-Marsan *et al.*, 2010). Holstein Friesians (Plate 11) originating from The Netherlands and the British Jersey (Plate 13) became the major dairy breeds. British Hereford and Angus (Plates 2 and 9) are still the dominating beef cattle, but since 1960 several European continental breeds have been imported as well. Zebus were imported in large numbers into Brazil, the USA

and Australia. Since then, many new taurine as well as taurindicine synthetic breeds have expanded considerably the cattle genetic repertoire (Buchanan and Lenstra, Chapter 3, this volume; Felius *et al.*, 2014).

These developments accelerated the evolution of cattle and expanded the phenotypic differentiation with regard to dairy or beef production, correspondingly influencing milk composition and meat quality (see Chapters 16–18). Dairy development in north or central Europe induced the typical wedge shape of dairy conformation (Plates 7, 11 and 17) in stark contrast to the appearance of muscular-hypertrophic beef cattle (Plate 3).

The continental lowland dairy cattle and the central European dairy cattle, carry different Y chromosomal haplotypes (Edwards *et al.*, 2011). Together with the separate development of the dairy island breeds Jersey and Guernsey, both free of crossbreeding since 1789, this indicates multiple origins of specialized dairy cattle. Therefore, different sets of genomic variants may confer the dairy productivity traits in cattle from the north European lowland, from central Europe and from the Channel Islands, respectively.

Autosomal DNA allows a monitoring of inbreeding and crossbreeding. By phylogenetic analysis it reveals local and international breed clusters mentioned above, which underlie a comprehensive classification of European breeds (Edwards *et al.*, 2011; Felius *et al.*, 2011; Buchanan and Lenstra, Chapter 3, this volume). However, the genetic surveys also demonstrate that breeds have considerable genetic overlap and still contain a large part of the total variety of the species (European Cattle Genetic Diversity Consortium, 2006; Decker *et al.*, 2009).

Industrial Cattle, Crossbreds and Local Breeds

Since World War II the development of cattle has been intensified and facilitated by modern reproductive techniques such as artificial insemination (AI) and multiple ovulation embryo transfer (MOET). The introduction of the tractor ended the requirement for draught power (Averdunk and Krogmeier, 2011). A growing role of the American cattle is illustrated by the allopatric development of highly productive breeds on the basis of imported European breeds (Felius, 1995; Felius *et al.*, 2011). Several beef breeds have in recent decades been bred for solid black colour by crossbreeding with Angus cattle.

Genomic approaches now accelerate the identification of genetic signatures of selection and of sequence variants that are causative of phenotypic variation. In addition, genomic selection of favourable quantative trait locus (QTL) variants is expected to offer a viable alternative for traditional selection, which evaluates animals on the basis of the phenotypic characteristics of the individual or its immediate relatives (see Chapters 15 and 19).

To counteract negative consequences associated with selection for high productivity, crossbreeding is gaining popularity, with Holstein Friesian × Jersey becoming a usual combination for dairying (Freyer *et al.*, 2008; Sørensen *et al.*, 2008). In New Zealand 36% of dairy cattle are now crossbred. In Europe the Viking Red is being developed by combining animals from Danish, Norwegian and Swedish Red breeds and Finnish Ayrshire (http://www.genusbreeding.co.uk). Crossbreeding has also created several taurine or taurindicine synthetic beef breeds (Plate 18) both in America and Australia, several of which are suitable for extensive management.

Concerns about the growing focus on productivity have also led to a renewed interest in local breeds that are characterized by low productivity but are better suited for extensive management (FAO, 2007). Such traits would be useful for a new purpose of cattle: rewilding of uninhabited areas by the release of cattle and other megaherbivores (www.megafauna-foundation.org). The crossbred Heck cattle, a much disputed attempt to revive the aurochs (Felius, 1995), is often used for this purpose, but an alternative is being developed (www.taurosproject.com). The new feral cattle populations may very well develop new adaptations to their environment and reverse some of the changes associated with domestication.

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