

Review

On the History of Cattle Genetic Resources

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Abstract: Cattle are our most important livestock species because of their production and role in human culture. Many breeds that differ in appearance, performance and environmental adaptation are kept on all inhabited continents, but the historic origin of the diverse phenotypes is not always clear. We give an account of the history of cattle by integrating archaeological record and pictorial or written sources, scarce until 300 years ago, with the recent contributions of DNA analysis. We describe the domestication of their wild ancestor, migrations to eventually all inhabited continents, the developments during prehistory, the antiquity and the Middle Ages, the relatively recent breed formation, the industrial cattle husbandry in the Old and New World and the current efforts to preserve the cattle genetic resources. Surveying the available information, we propose three main and overlapping phases during the development of the present genetic diversity: (i) domestication and subsequent wild introgression; (ii) natural adaptation to a diverse agricultural habitat; and (iii) breed development.

Keywords: cattle; history; domestication; diversity; genetic resources; conservation

1. Introduction

The introduction of domesticated crops and livestock initiated the cultural development of mankind. Cattle were among the 14 large wild terrestrial species meeting the conditions for successful domestication [1]: an herbivorous diet, fast growth, ability of captive breeding, genetic temperance of aggressive or panicky behavior in captivity, and a social behavior that facilitates handling. Domestic cattle followed the domestication of the smaller and easier to manage sheep and goat [2]. As cattle husbandry required a distribution of tasks and thus imposed a stratification on the pastoral society, its impact was considerable [2–5]. Cattle were also one of the earliest forms of capital [6].

Accompanying mankind since the dawn of civilization, cattle became in various environments an integral part of human society. By supplying milk, meat and hides and by plowing the fields [3], they have become the most important domestic animal species. Their role in social networks, ceremonies, rituals and games also gives cattle a central place in human culture, this in spite of a less affectionate human-animal relationship than has been established, for instance, with horses or dogs.

Over time a large diversity of cattle has emerged, which now may be threatened by the prevailing industrial approach to cattle husbandry and a focus on high productivity. Previously, we have described the bovine breeds and their nomenclature, classification and relevance for conservation [7–9]. To contribute to a rational evaluation of conservation values of existing breeds and populations, we here consider the diversity of cattle in a historical context. On the basis of a history from the initial domestication of cattle in the Neolithic to the creation of modern breeds, we try to answer the question when and how the current diversity of the cattle genetic resources has emerged, which is relevant information for decisions on breed conservation.

After Sections 2–4 on domestication and the dispersal of taurine and zebu cattle, Sections 5 to 12, 13, 14 and 15 describe the histories of cattle in Europe, Asia, Africa and the New World, respectively. Sections 16 and 17 describe recent global developments since WWII. Section 18 summarizes the developments influencing the cattle genetic resources from domestication until the present time.

2. Wild ancestors and Sites of Domestication

Several bovine species have been domesticated [10,11], but taurine cattle (*Bos taurus*, Figure 1a) and zebu (*Bos indicus*, Figure 1b) account for almost all cattle. Both descend from the wild aurochs (*Bos primigenius*), which at the end of the last glacial period (12,000 BP) was endemic over most of Asia, Europe, North Africa and the once green Sahara (Figure 2). This huge and reputedly fierce species has been extinct since 1627, when the last animal died in Poland. Only few contemporary pictures of aurochs exist (Figure 3), but skeletal remains allow reconstructing its morphology (Figure 4). The subspecies *B.p. primigenius* in Southwest Asia and *B.p. namadicus* in India were the ancestors of taurine and zebu cattle, respectively.

The most recent molecular estimates of the divergence time of these aurochs subspecies and thus of taurine and zebu cattle are 147,000 BP [12] or 335,000 BP [13] and 350,000 BP [14]. These estimates have large confidence intervals, but indicate that taurine and zebu cattle have been domesticated separately. In contrast to the wide distribution of the aurochs (Figure 2) these domestications took place in certain areas, reflecting the difficulty of sustained managing and breeding of these large wild animals [15].

Figure 1. Major domestic cattle species: (a) Spanish Tudanca taurine and (b) Pullikulam zebu bull (photographs by Marleen Felius and Anno Fokkinga, 2008, 2005).



Figure 2. Distribution of *Bos primigenius* ca. 12.000 BP [16,17] (Map by Marleen Felius).

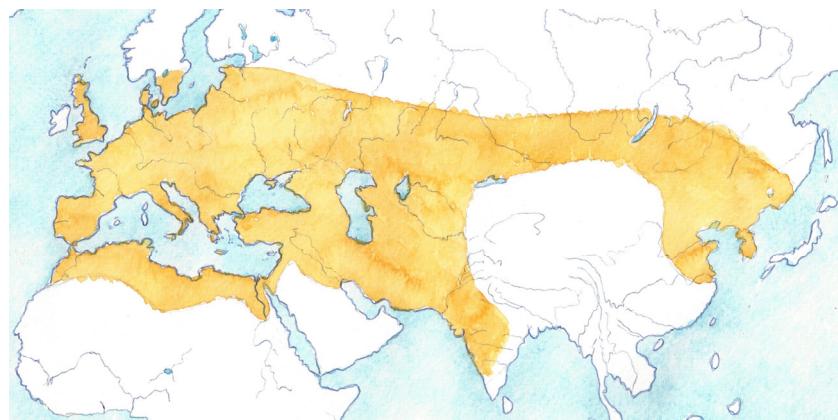
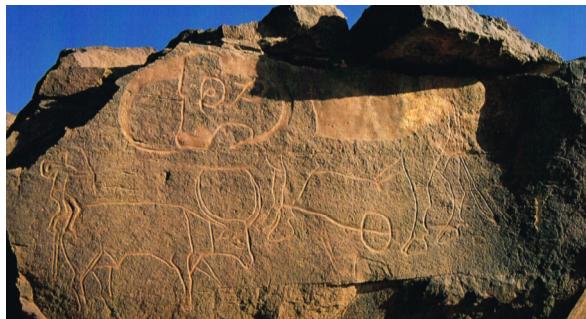


Figure 3. Contemporary pictures of the aurochs: (a) Painting in the Lascaux caves; (b) the Augsburg aurochs, woodcut 1826 after a lost 16th century painting [11]; (c) Rock engraving of African cattle showing a captured aurochs bull (Messak, Lybia, 6000 BP) [10]; and (d) 16th century picture by Philip Galle (Museum Boymans Van Beuningen, Rotterdam, courtesy Rolf Zeegers). Two Latin hexameters in the caption (not shown) suggest how the aurochs became extinct, in translation: *Thus everywhere, with spears, light arrows and swords, in pitfalls they drove the aurochs, strong with horns.*



Figure 3. Cont.

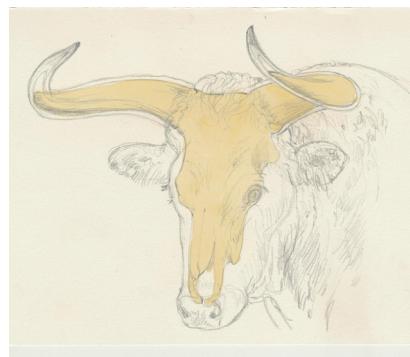
(c)



(d)

Figure 4. (a) Skull of an aurochs bull (The British Museum) and **(b)** reconstruction (drawing by Marleen Felius).

(a)



(b)

Figure 5. Archaeological sites that witness the domestication of taurine cattle (Middle Euphrates [18,25]) and zebu (Mehrgarh, [26]), their early dispersal (Catal Hüyük [27]) and the arrival of taurine cattle in Greece (Argissa-Magula, Nea Nikomedea [2]) and Egypt (Fayum [28–31]). Domestication in Nabta Playa and Bir Kiseiba in South Egypt is not generally accepted [30,32,33]. In addition to the skeletal remains excavated at these sites, cave and wall paintings as well as sculptural objects found at several other sites have evidenced the presence of long-horned, short-horned or zebu cattle [7,28].

Archaeological data indicate that taurine cattle have been domesticated between 10,300–10,800 years ago in the Fertile Crescent, most probably on the western Turkish-Syrian border (Figure 5) [18,19]. The size, shape or gender ratios allow a differentiation of fossil remains from wild and domestic cattle [20,21]. In addition, isotope analysis of organic material revealed traces of milk in excavated pottery, indicating the storage of dairy products already 9000 BP [22].

Bayesian analysis of 15 mtDNA sequences from Neolithic to Iron Age Iranian cattle yielded an estimate of around 80 female aurochs being the maternal ancestors of almost all present day taurine cattle [17]. Modern cattle populations in Southwest Asia still have high haplotype diversity with appreciable frequencies of haplogroups T, T1, T2 and T3 [5,23,24].

Around 2000 years after the taurine domestication, zebu was domesticated in the Indus Valley at the edge of the Indian Desert [5,34]. Fossil remains attributed to zebu have been found in Mehrgarh, a proto-Indus culture site in Baluchistan in southwest Pakistan and were dated at 8000 BP [26].

Taurine cattle arrived in China about 5000 years ago. However, a bovine jaw dated 10,500 BP recently found in Northeast China shows clear signs of stereotypical bar biting often displayed by captive animals and contains taurine mtDNA from a hitherto unknown mtDNA haplogroup, suggesting an independent and early domestication [35]. This domestication would have been abortive, since there is no evidence of domestic cattle in the period between 10,500 and 5000 BP.

Paleontological remains found in the western Egyptian Desert dating from 9000 BP suggested an independent African center of domestication, but the domestic origin of the bones is disputed [30,32,33,36]. Initially an African domestication seemed in line with the predominance of the T1 haplogroup in Africa [37]. However, complete mtDNA sequences have shown that this haplogroup is closely related to the common Southwest-Asian haplotypes [38].

Thus, most of the diversity of domestic cattle has been derived from two cross-fertile species, *Bos taurus* and *Bos indicus*. However, separate domestications of related bovine species did occur in Asia [12,13]. In Tibet and surrounding regions the adaptation of the yak (*Bos grunniens*) to high altitudes [39] has been exploited since *ca.* 4500 BP. The habitats of the gayal or mithun (*Bos frontalis*) in Assam and Myanmar and of the domestic banteng or Bali cattle (*Bos javanicus*, domestic since *ca.* 5000 BP) overlap with the range of zebu [40]. Because all three species hybridize with taurine and zebu cattle, several Asian cattle populations are of mixed species origin and are unique contributions to the cattle resources.

Expansion of the first agricultural societies introduced cattle eventually to most parts of Asia, Africa and Europe [5] and replaced hunter-gatherer societies by sedentary pastoralism. However, if during the winters the available pasture could not feed the herd, this led to the adoption of seasonal transhumance [40]. Seasonal migrations are still common in Alpine Europe, and several parts of Africa and Asia. It may have preceded the nomadic pastoralism, which until recently was common in central Africa and focused on cattle husbandry [40].

3. Early Taurine Dispersal

As is typical for successful innovations, agriculture and livestock husbandry spread to other populations, most likely by expansion of the first agricultural societies [41]. The demographic events that have led to the present distribution of taurine cattle in Asia, Europe and Africa can be reconstructed

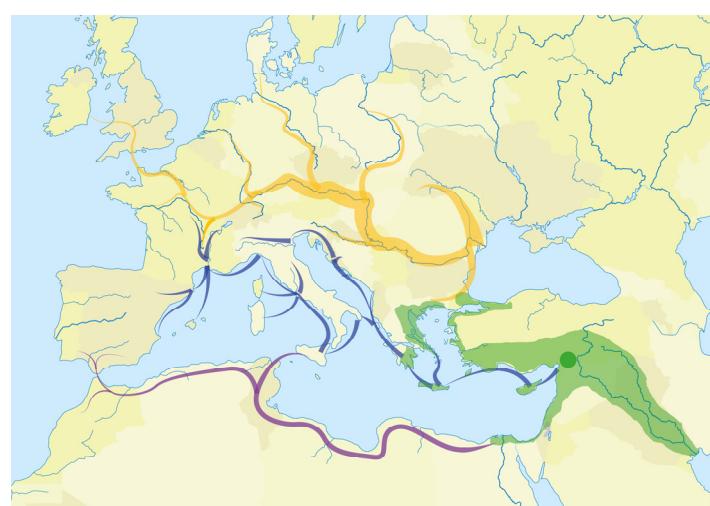
on the basis of archeological evidence combined with comparison of mtDNA, autosomal DNA [5] and Y-chromosomal DNA [42,43]. A westward expansion of agricultural societies brought domestic taurine cattle, together with other livestock and crops, to central Anatolia around 10,000 BP and from 8500 BP into Europe [2,19,27,29,44].

An eastward migration reached northern China or Mongolia between 5000 and 4000 BP [40]. This is supported by mtDNA analysis of cattle remains from five archaeological sites in Northern China, aged 4500 to 2300 BP, showing mtDNA haplotypes from the T2, T3 and T4 haplogroups just as is observed in modern East-Asian taurine cattle, including the Northern Siberian Yakut [45]. The T4 haplogroup is a subtype of the common haplogroup T3 exclusive to eastern Asia [38] and most likely emerged by a founder effect during the eastward expansion [24]. The presence of cattle in eastern Asia clearly predates the Silk Route, after 200 AD the major link of Europe and China and proposed as the migration route of cattle to East Asia [46].

Paleontological findings as well as pictorial and sculptural representations revealed the presence of early domestic cattle in Africa [7,28,30,31,40,47,48]. Cattle remains dated 7000–3500 BP have been found in Egypt, Libya and the Sahara. Around 7000 BP dairying pastoralists reached the then green Sahara [49,50] and left rock engravings showing long-horned cattle, which probably were the ancestors of the present West-African cattle. Around 4000 BP a climate change leading to desertification of the Sahara forced pastoralists to leave. Remains of short-and long-horned cattle at several sites in Northeast Africa were dated 5600 to 3000 BP [40,48] before the immigration of zebus (see below). From 2500 BP cattle herding spread to the south [40]. It is likely that taurine cattle also spread from Egypt westward along the North-African Mediterranean coast and then along the West-African Atlantic coast.

A strong maternal founder effect during the colonization of Africa is indicated by the predominance of the T1 haplotype (see above). A frequency of T1 of *ca.* 15% in Spain and Portugal [37] and *ca.* 11% in Sicily [51] indicates immigration of African cattle in Europe across the sea straits (Figure 6), which is confirmed by SNP profiles [46]. This may have occurred as early as the Bronze Age or later during the Muslim occupation [52].

Figure 6. Neolithic migration of domestic cattle in Europe.



- Domestication center;
- Early range;
- Danube route;
- Mediterranean route;
- African route.

The Mesopotamian provenance of the maternal lineages does not exclude an African origin of Y-chromosomal Y2 haplotypes by male introgression of the African aurochs [33,42,43,53]. This would explain the divergent 50K SNP genotypes of African haplotypes [46] and imply that the African aurochs is an additional source of the diversity of cattle.

The earliest signs of domesticated cattle in Europe are the bones found in Pre-Pottery Neolithic at Argissa-Magula, in Thessaly, Greece, dated 8500 BP [2,54]. The remains of the earliest European farms suggest two routes of migration: via the Mediterranean coasts and along the Danube river, respectively (Figure 6). Via the first route farming was introduced in Corsica, the Languedoc, southwest France and the eastern Spanish coast *ca.* 7900 to 7700 BP [55–58]. Approximately 7500 BP domestic cattle reached Central Europe via the Danubian route and Northern Europe 1000 years later [57,59,60]. The migration from Southwest Asia to Northwest Europe led to a clear decline in the autosomal diversity [57].

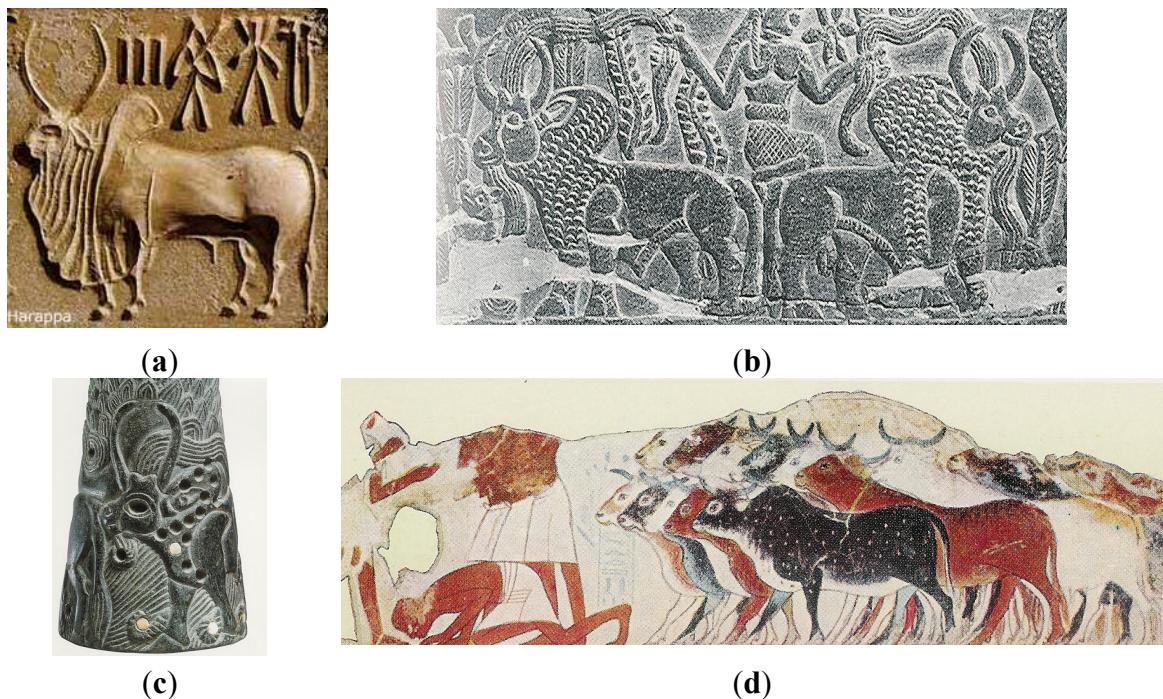
Isotope analyses of traces of bovine dairy fat products in ceramic remains indicate the milking of cattle by European farmers in 7500 BP in southeast [22] and northern [61] Europe and in 6000 BP in Great Britain [62]. This is confirmed by $^{15}\text{N}/^{14}\text{N}$ ratios in calf teeth from ancient French calves as evidence of early weaning [63]. However, milking of cattle may have been restricted to central and northern Europe. This has been suggested because of a low frequency of the human lactose tolerance allele in Mediterranean populations [64,65] and a lack of cattle dairying tradition in the Italian peninsula during the Roman empire [20].

Rare recruitment of cows from European aurochs populations is suggested by the occurrence of low frequencies of the P, Q and R mtDNA haplotypes in European domestic cattle [23,66]. In European cattle west and north of the Balkans the T3 haplogroup is dominant, probably indicating a founder effect during the Danubian migration [23,24]. A clear north-south distribution of two predominant Y-chromosomal Y1 and Y2 haplotypes has been linked to founder effects accompanying the development of dairy cattle in the northern part of the continent and in the Alpine region, respectively [43]. Awaiting genomic information of European aurochs, it is not yet clear if wild bulls have contributed to the diversity of cattle by introgression in the domestic population, as has been suggested for the Hungarian Grey (see below).

4. Early Zebu Dispersal

Zebu cattle is with 800 million head about as numerous as the taurine population [67]. However, their distribution has remained restricted to regions with a climate similar to that of the earlier domestication site in the Indus Valley. Dispersal may have started around 4500 BP when Rig Vedic Aryan invaders from Central Asia descended into the Indus valley via the northern passes. The original occupants of the region then moved eastward with their livestock into the Ganges valley. Around 3500 BP cattle were introduced in Bihar and Bengal ([40]. Terracotta figurines and fragmented bones of zebu cattle [26,68,69] were excavated from Neolithic settlements at three sites in Karnataka on the Deccan plateau of Central India. The Harappan seal (Figure 7a) shows a well-developed thoracic hump and a large, folded dewlap, although other contemporary seals show that in the period 5000–3500 BP humped and humpless cattle coexisted.

Figure 7. Pictorial evidence of the origin and dispersal of zebu. (a) Harappa seal (National Museum, India, [70]), 5000–3500 BP; (b) detail of cylindrical chlorite vessel (Mesopotamia (mid-5th millennium BP, The British Museum, London); (c) detail of conic object from Tarut Island near the Eastern coast of the Arabian peninsula (Metropolitan Museum, NY) and (d) detail of a painting: inspection of cattle belonging to Nebamun, Thebes, ca. 3400 BP, The British Museum, London).



Zebu entered China from the south or southwest from 3000 BP onward [40,70]. Mixing with the taurine cattle from the north generated a genetic North-South gradient of zebu-taurine mtDNA [71] and Y-chromosomal DNA [72]. In South China admixture of bibovine cattle (banteng, gaur or gayal) occurred, which may have been the dominant cattle species until 4500 BP [40,46].

In the east, zebras reached Indonesia at least 1000 years ago. DNA analysis showed sporadic, substantial or even complete maternal banteng ancestry of Indonesian zebu breeds, suggesting that zebras were crossed into herds of previously domesticated banteng (*Bos javanicus*) [73].

Early migration of zebu also took place in western direction. Evidence of the presence of zebras in Mesopotamia comes from figurines of humped bulls excavated in northern Iraq and dated 6500 BP and from Sumerian vase fragments dated 4750 BP [40]. At numerous sites on both sides of the Persian Gulf zebu bulls have been depicted with high cervico-thoracic (neck-shoulder) humps with dates between 5000 to 3000 BP (Figure 7b,c). A shift to a more arid climate in Mesopotamia ca. 4000 BP [74] probably stimulated the immigration of zebu. At present the most northwestern true humped zebu is the Caucasian Zebu in Azerbaijan [7]. Appreciable maternal, paternal and autosomal zebu introgression has been observed in the present taurine cattle from Iraq and Anatolia [24,46,75]. Low levels of introgression of zebu in Europe are indicated by the presence of zebu alleles in South-European cattle [46,57,76].

DNA studies suggest that zebras were first introduced into East Africa about 4000 years ago [40,77]. Egyptian pictures from 3400 BP show humped cattle (Figure 7d) [28], and zebu-type dished vertebrae found in Egypt and Somalia date back to ca. 3500 BP and 3500–2500 BP, respectively [78]. Arabian

traders probably stimulated import of Indo-Pakistani zebu via the Persian Gulf and South Arabia into the horn of Africa after 700 AD. Only zebu bulls were introduced, since mtDNA data showed that all African zebu and taurindicine cattle are maternally of taurine descent [37,78]. The later history of African zebu is described in Section 14.

5. Short-Horned and Small Taurine Cattle in the Bronze and Iron Age

Long horns serve wild bovines by warding off predators and competitors, but in the domestic habitat hinder the handling of animals and the stabbing of the herd. Short-horned taurine cattle appeared in Mesopotamia in the early Bronze Age (5100–2580 BP). Several wall paintings in Egypt bear witness to the gradual replacement of long-horned animals from 5000 BP onward [28]. Short-horned cattle also spread to southern and central Europe (5000–4500 BP) and arrived in Britain between 4000–3000 BP [80]. In the late Bronze Age short-horned cattle became dominant over central and northern Europe [54,80], even though many Mediterranean as well Hungarian cattle remained long-horned. This is in line with the notion that during the Bronze Age in northwestern Europe it became common to stable cattle during the winter [81,82]. A subsequent but less universal adaptation to the North-European domestic environment was the breeding of hornless (polled) cattle, the first remains of which date back to 6000 BP [54].

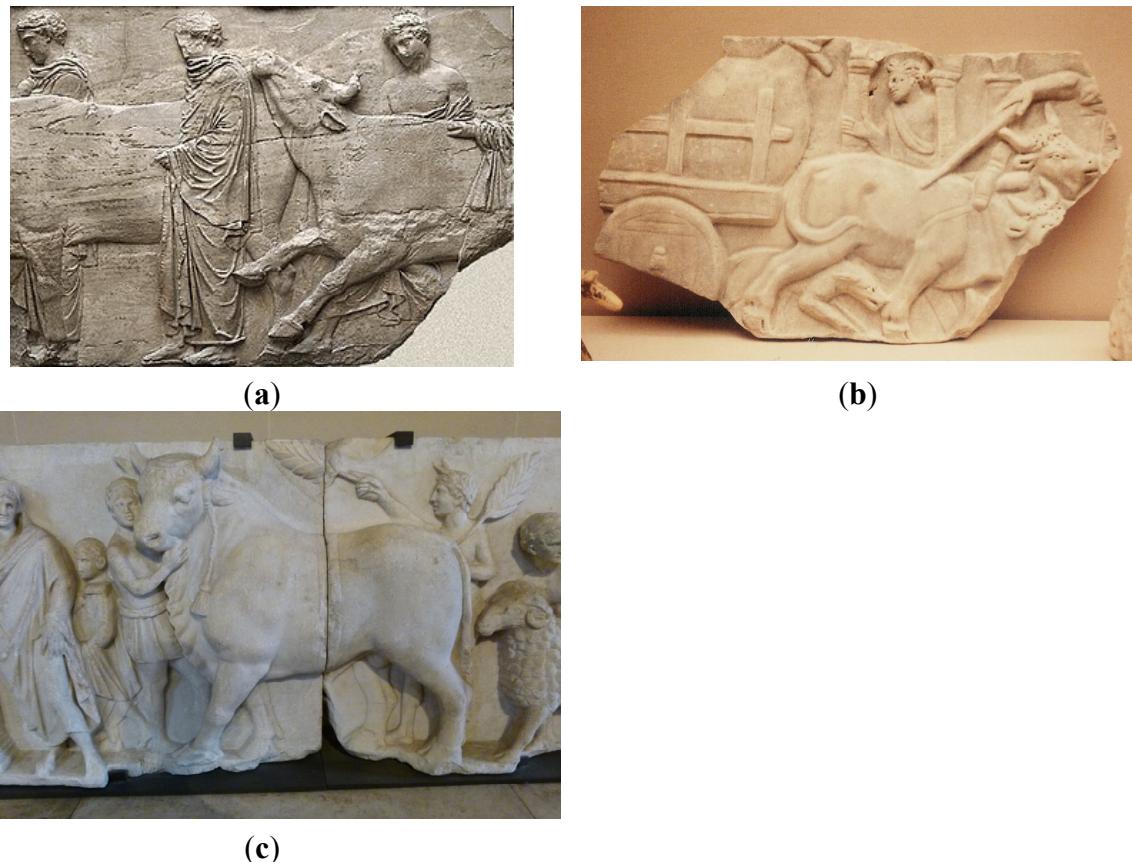
The size of cattle decreased continuously since the Bronze Age, presumably a further adaptation to domestication and to food scarcity during cold winter periods. While aurochs bulls had wither heights of 180 cm and cows of 160 cm, Bronze and Iron Age cattle in France, the Netherlands, Germany, Italy and Central Europe, typically reached 110 cm [20,59,83,84], agreeing with contemporary descriptions of the Friesian and Batavian cattle during the Roman era [85].

6. Large Greek and Roman Cattle

With the advanced literacy during the Greek and Roman civilization came the first detailed contemporary accounts of cattle husbandry. In Greece during the Hellenistic period (*ca.* 330–63 BC), cattle were used for traction, sacrifice, beef production and also milking. According to Aristotle, the rich pasturelands of Epirus were famous for the large size of their livestock with cattle producing 30 L milk per day [86]. Skeletal remains in Kassope in Epirus revealed the development of large cattle in the 7th and 8th century BC with withers heights ranging from 115 to 135 cm [87]. These *Epirote* cattle were exported to several regions in Italy and southern France. In Italy, these cattle were probably the ancestors of the large Roman cattle. In 200 BC three different coat colors (white, black and yellow) and a spotted pattern were described for Sicilian cattle [88].

Cattle also flourished during the Roman Empire [89] as described in detail by Cato, Varro, Columella and Pliny [90]. Cattle provided traction in agriculture and for hauling heavy loads, for which horses, for want of collars (yet to be invented), were not suited. Roman cattle were not milked [64], but Columella and Pliny praised the dairy qualities of the Alpine cows [64,90,91]. Roman writers were the first to describe the diversity of regional cattle with various sizes, colors and performance [90]. Large Roman cattle, ranging from 120 cm to 135–140 cm, with distinctive large horns were found in Etruria [54,84,87]. From the Greek and Roman era also many naturalistic cattle sculptures survived (Figure 8).

Figure 8. Reliefs showing large Greek or Roman cattle. (a) Greek cows, Parthenon frieze, 5th century BC (b) Wine transport, Roman, 3rd century AD (The British Museum) and (c) Roman bull (1st century, Pompeii, Musée du Louvre).



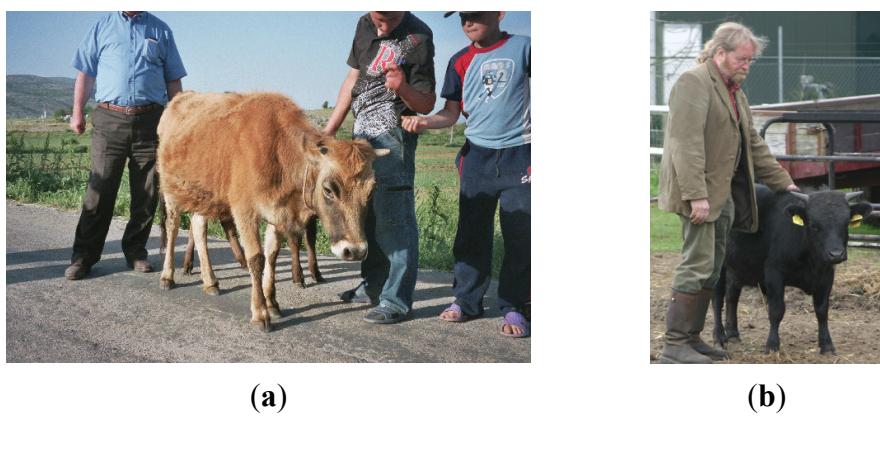
Paleontological evidence indicates that cattle in various parts of the Roman Empire varied widely in size, for example in Britain [92,93] and southern Germany [54,83]. Germanic cattle stood 95–125 cm; those in the Roman provinces 100–150 cm [59]. A survey of 20 sites showed that cows dating from the Empire averaged a withers height of 130 cm and bulls 138–144 cm [87]. The *Pax Romana* and infrastructure of the Roman Empire probably facilitated export of large Italian cattle to the distant provinces, where these cattle lived in the same areas as the small indigenous cattle [54,84]. Strikingly, the large cattle disappeared soon after the fall of the Roman Empire, suggesting that smaller animals fitted better to a husbandry system that had regressed to more primitive practices.

7. Medieval Cattle and Catastrophes

The collapse of the Roman Empire was followed by periods of unrest and large-scale migration of several Germanic and eastern European peoples and their livestock during the fifth and sixth century AD. This initiated a significant cultural regression, a disuse of technology and a decay of the Roman infrastructure. The migrations probably led to a considerable mixing of cattle populations from various European regions. Throughout the rest of the Middle Ages raiding, wars, famines, cattle plagues [94] and inundations decimated local cattle populations. Restocking by importing animals from neighboring regions is likely to have caused intensive gene flow.

During the early Middle Ages small cattle with withers heights of 95–105 cm were dominant in most parts of Europe [54]. Cattle stands in medieval Dutch farming houses were only 75 to 84 cm in width, which is 40 cm smaller than in the Bronze Age [81]. This has been explained by negative consequence of poor nutrition [95] or of the castration of the largest and strongest young males [93], but the small body size was probably also a genetic adaptation to the subsistence farming typical for undeveloped economies. In addition, large animals were most likely to be selected for slaughtering before the winter [93,96] as they were more vulnerable to an uncertain supply of fodder. The role of genetic factors is illustrated by the small size of present-day cattle from four different continents that share an adaptation to marginal rural areas: the Illyrian dwarf cattle in Albania [97], Tibetan cattle in the Himalaya, the West African Shorthorns in the forests and lagoons and several original American Criollo populations (Figure 9).

Figure 9. Present-day small cattle. (a) Albanian Prespa cattle, a dwarf variant of Busha cattle kept in Albanian mountain areas with wither heights of 95–105 cm (photograph by Dr. Kristaq Kume, SGP Small Grants Programme) and (b) African Dahomey bull, wither height 90 cm (photograph by Marleen Felius).



Sparse documentation suggests an appreciable color diversity of medieval cattle [98]. White cattle with colored ears were mentioned in pre-Christian Irish epics [99]. Medieval paintings and illustrations of cattle suggest cattle show mostly uncolored brown or black animals (Figure 10). A stock inventory of the *Marckerhoeft* monastery provides information on the color and pattern of a sample of 115 Dutch cattle in 1344: 71 animals were completely black, red or dun, 20 were white-headed, 12 were white-backed and 12 were pied [100].

Figure 10. Ploughing with oxen, Luttrell Psalter, circa 1335–1340, detail (The British Library).



The introduction of the heavy plough allowed tillage of heavy clay soils and plausibly initiated an agricultural revolution around 1000–1300 [101]. After the introduction of the horse collar around 1000 AD, horses were more and more used for plowing, which depended on the region and the resources of the farmer [102,103]. Although still a source of draught power, cattle as well as other livestock decreased in number by the growing importance of grain cultivation (*cerealization* or *Vergetreidung* [103–105]).

The agricultural revolution allowed the human population to grow. However, in the 14th century European agricultural development suffered two serious setbacks. First, a number of crop failures caused the Great Famine (1315–1317), causing millions of deaths and reducing the North-European population by 10% to 25%. This was followed by the Black Death epidemics (1349–1351), by which a third of the population is believed to have perished. In several regions cultivation was almost abandoned and cattle keeping became extensive [106].

8. Recovery of Cattle

After the catastrophic 14th century the human as well as the livestock populations recovered rapidly. This accompanied the remarkable cultural and technological development of the renaissance society, which was promoted by the earlier invention of the printing press and a growing urbanization [103]. The manorial farming that characterized the Northwest-European feudal society became more and more replaced by tenant farming on rented land [93,103]. Fencing of pastures and cultivation of animal feed became common and storage methods improved, allowing the survival of larger cattle during the winter and a selection of sires to enhance productivity. Since this was done using locally preferred sires, this promoted a differentiation of cattle.

Cattle increased in size, while even long-horned cattle appeared in Southeast England [93,104]. However, local farms could not meet the demand for beef in the growing cities, which came to depend on the transport of cattle on the hoof from regions where they could be reared in large numbers under extensive management: the North-western coastal regions, the Alpine regions and the steppes of Eastern Europe [107]. Since the late Middle Ages so-called “drovers” moved Welsh beef cattle to London [108]. Danish cattle went in huge herds to the Netherlands for fattening [109]. In 1450 the export of Dutch dairy products and fattened cattle was already of considerable importance [110].

In the Swiss Alps triple-purpose cattle were developed, which from the 15th century were exported in large numbers to surrounding countries. In the late 14th century deeds from the Swiss monastery of Einsiedeln refer to export of Braunvieh to Vorarlberg in present-day Austria [91]. Cattle were exported as well from the Swiss Simme and Saane valleys to Italy during the 15th and 16th centuries [111].

Since the 14th century a grey colored long-horned cattle of the so-called Podolian type appeared on the pusztas in the Carpathian basin and replaced the local small cattle during the 14th and 15th centuries [54,106,112]. From the late 14th to the early 18th century Hungarian Grey cattle, the major Podolian breed, were driven for slaughtering to Austria, South Germany and Venice [106,112–114] and then southwards as far as Naples [115]. Import into Italy from Hungary and from Bosnia and Croatia via the Dalmatian port of Zadar continued during the 18th century [115].

Podolian cattle has been named after the region in South Ukraine where the breed was kept in the Middle Ages, but its origin is uncertain. Since no remains of long-horned steppe cattle dating before the 12th century have been found, it is assumed that long-horned cattle resulted from a late-medieval local

selective breeding, but influence of wild aurochs has been excluded [54,106,112]. It is plausible that documented large-scale imports into Italy of oxen as well as fertile animals [106] explain the clear similarities with Italian Podolian breeds (one of which is even named Podolica). MtDNA has shown that Italian and Balkan cattle differ in haplogroup distribution [23,24], indicating that the maternal lineages are still of local descent and that the Podolian gene flow into Italy was male-mediated.

In an alternative or complementary scenario [54,116] the Podolian cattle descend from the large cattle living in the Italian peninsula during the Roman era, which probably descended from Epirote cattle [84]. The giant Chianina, which differs from other Podolian cattle in its small horns, may have retained traits of earlier Italian cattle. With the exception of the crossbreeding in the 20th century of Maremmana sires with Hungarian Grey cattle [112], there is no documented gene flow from Italy eastward.

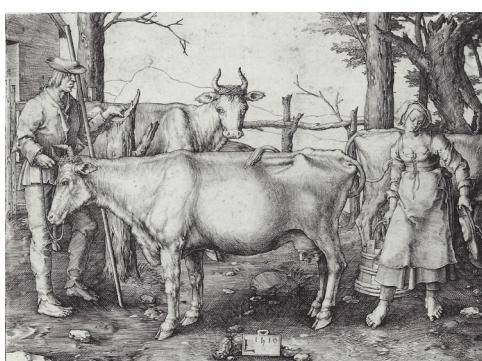
While everywhere in Western Europe cattle were still kept as part of a mixed farming system, mainly for the purpose of traction and dairying, a very different development took place in Spain. The *Reconquista* of Moorish territory in Castilia and Andalusia (900–1492) led to the development of a thriving and highly organized cattle ranching economy where large herds of 1000–15,000 work and beef cattle were kept under extensive management [117,118].

The independent developments of cattle in separate regions stimulated a further geographic differentiation of appearance and performance.

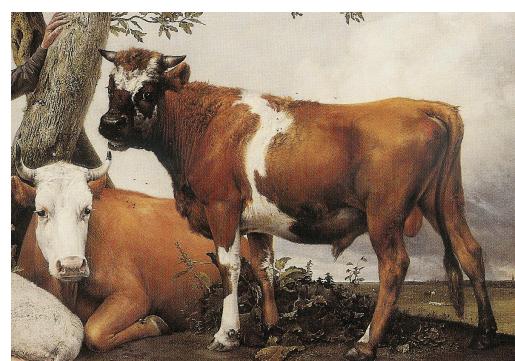
9. Preindustrial Progress

In the mid-16th century prices for dairy products soared. The cows in the Northern Netherlands became famous for their milk production. While in other parts of Europe an annual yield was at most 800 L, Dutch cattle yielding 2000 L were no exception [119]. Dutch cows (Figure 11) were exported to England, France and Germany.

Figure 11. Contemporary depictions of preindustrial Dutch cattle. (a) *The Milkmaid*, engraving by Lucas van Leyden, 1510 (Prentenkabinet, Kunsthistorisch Instituut, Leiden) and (b) *The Bull*, Paulus Potter, ca. 1647, detail (Mauritshuis, Den Haag). When the cattle industry flourished in Holland, scenery with cattle became a popular subject in art. Oxen and dairy cows, symbolizing wealth, were often depicted in Dutch paintings. White-backed and -headed cattle (like the cow on the left) are overrepresented in paintings, since the convenient contrast facilitates the composition. On the other hand, black-pied animals do not blend easily with the color of the landscape and may therefore be underrepresented [120].



(a)



(b)

Written accounts of cattle and husbandry, which after the Roman era had become sporadic, became available again thanks to growing literacy. In the last quarter of the 16th century a number of books on farming were published in France and translated into English, German, Italian and Dutch. These books contained material from Virgil's *Georgica* and described the putative relations between color and performance: a good milking cow is black with tiny white spots or black pied [121] and dark red and black cattle were the best [122]. In 1627 and still in 1782 red was the most desirable color [123,124]. For breeding, a red bull, with or without spots, was recommended. A publication in 1789 described 22 types of cattle in France named after their region of origin [125].

In England in 1614, Black Longhorns were found in Yorkshire, Derbyshire, Lancashire, Staffordshire and the dairy regions of Cheshire [126]. Tall, lean and pied cattle with strong hooves and small crooked horns, suggested to be of Dutch origin, were kept in Lincolnshire. In contrast to Longhorns these were not apt to put on weight. Somerset, Gloucestershire and some parts of Wiltshire were noted for blood-red cattle [126,127].

Throughout Europe the migrations of cattle (see above) continued [107,110,128,129]. Beef cattle reared on Scottish pastures were driven to London and other cities from the early 17th to the early 19th century [130]. The preference of drovers for hornless animals led to the emergence of the polled Galloway [93]. In Central Europe the export of Hungarian Grey cattle to Vienna, Nurnberg, Strasbourg and Venice involved tens of thousands of cattle per year in the 15th and 16th centuries and after 1700 even 100,000 animals [112]. Around the same time Ukrainian cattle moved via Krakow to the west [131]. The Hungarian export decreased when the Viennese court imposed a monopoly in 1622 and was also seriously affected by the wars with Turkey in the 17th century. Export to Venice by Austrian and Ottoman traders continued during the 18th century ([115], see above).

Eventually, West-European cattle husbandry improved and met the demand for beef of the urban populations. The growth of cattle farming also had a downside when the higher density of animals invited outbreaks of cattle plague, which was introduced by Hungarian steppe cattle and in the 18th century harassed continental Europe [115,132–134].

Thus, the cattle types that existed in 18th-century Europe were regionally adapted with clear differences in appearance and performance between regions, but very likely also within herds. Mating was still more or less random, sires from nearby being the most readily available. Until 1760 natural selection and adaptation of landraces to local circumstances prevailed rather than selection for utility or a certain trait [135]. However, the stage was set for an unprecedented and human-controlled acceleration of the evolution and diversification of cattle.

10. The First Breeds

The industrial revolution started in England around 1760. It led to further urbanization and increased demand from the cities for agricultural products. This encouraged the so-called British Agricultural Revolution [136] and a fast acceptance of an important innovation in livestock husbandry: the development of breeds with a deliberate choice of sires and documentation of pedigrees in herd books. The oldest known herd book for cattle was kept between 1775 and 1782 at the Monastery of Einsiedeln in the Swiss canton Schwyz, where the grey-brown mountain cattle (*Braunvieh*) evolved. In 1795 the

cattle from Schwyz were described as the largest and most beautiful of Switzerland thanks to the attention given to keeping and breeding [91].

In 1760, the Englishman Robert Bakewell started improving cattle, sheep and horses [137]. His breeding records have not survived, but it is likely that he started with local long-horned animals that were close to his ideal and that he fixed the desired traits by inbreeding. He selected for beauty of form, quality of flesh and disposition for fattening. He also paid attention to early growth and -by then a novelty- well-being. His cattle were also renowned for their extreme docility. By the turn of the century his improved Longhorn, initially called New Leicester or Dishley (Figure 12), had become the most widely distributed breed in the midland counties [138].

Figure 12. New Leicester bull and cow [139].



Around 1785, Durham cattle, later called the Shorthorn [93,127], was developed by the brothers Charles and Robert Colling. They selected local cattle, mainly Teeswater, which were at least partially of Dutch ancestry (Figure 13a). They applied the same breeding strategy as Bakewell with close inbreeding (*Like engend'ring like* [127]). The Durham soon outnumbered the Longhorn and since 1822 their breeding has been recorded in the Coates Herd Book, the first cattle herd book that lasted to this day. Portraits of extremely fattened animals were published and live animals were widely displayed (Figure 13b). Thus, the Durham stock became the most fashionable breed of the first half of the 19th century, influencing most British and many European breeds (see below).

Following the successes with the Longhorn and Shorthorn, several other British breeds were developed, such as the Hereford (Figure 14a) and Aberdeen-Angus (Figure 14b), both beef cattle, and dairy Ayrshire (Figure 14c) [138]. Breeding was mainly an occupation of the gentry, who emphasized pure bloodlines to the point that purebred cattle with long pedigrees became a symbol of the British ruling class [135,140]. The island breeds Jersey and Guernsey were reputed dairy producers and were kept pure by forbidding the import of other cattle as early as 1789 [7,138].

Together with other invention as the steam engine and the power loom, systematic breeding spread quickly through Europe and North America, although on the European continent the developments were more gradual. Breeding sires were already selected on the basis of strict criteria in several regions in the 18th century. During the 19th century more and more herd books were established for authentic regional types, the so-called landraces, especially in regions with intensive agriculture. Later on in the 19th century, cattle exhibitions catalyzed an exchange of sires between neighboring regions with similar types of cattle, leading to an amalgamation of local populations with more uniform breeding objectives and a common herd book. Table S1 shows that this was a Europe-wide development.

Figure 13. English cows: (a) Cow, 1790 [141]. This animal seems of a solid color. In the 1790 edition the figure caption mentions *Common Cow*, but in the second edition of 1791 *The Holstein or Dutch Breed*, illustrating the recent introduction of the breed concept; (b) Idealized beef type Durham cow from an unknown 19th century artist. This and many similar paintings portray the animals with a square body, with lumps of fat, an unrealistic small head and thin legs.

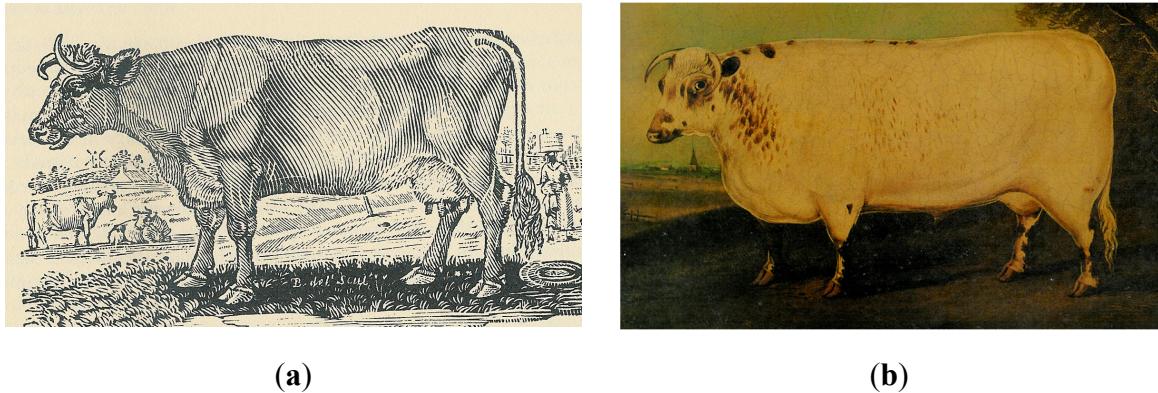
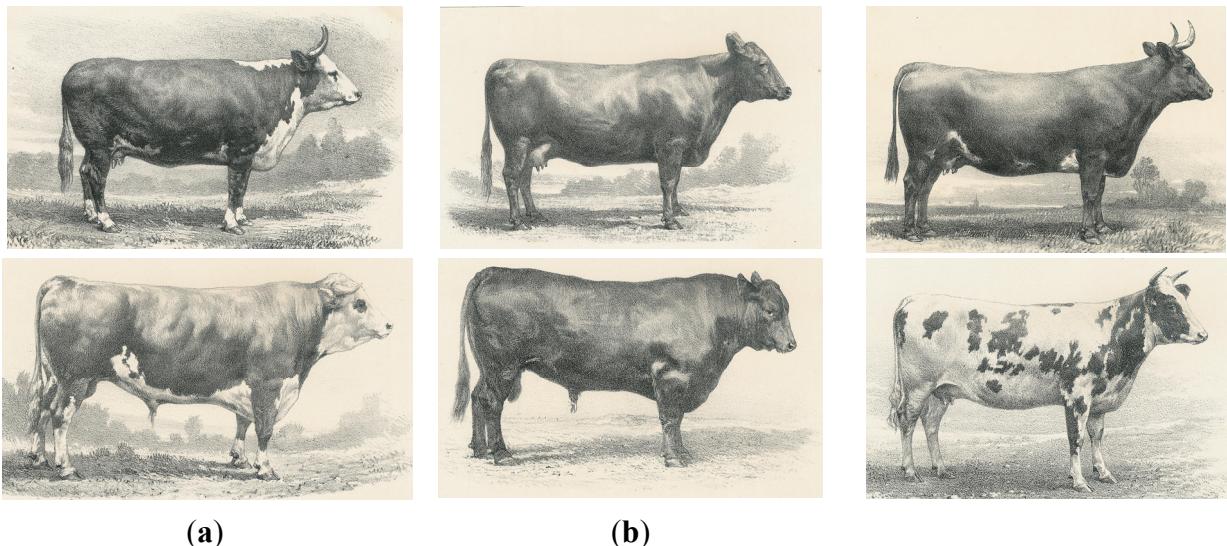


Figure 14. Other British breeds [142] (a) Hereford cow (1855) and Hereford bull (1856); (b) Aberdeen-Angus cow (1855) and bull (1856); (c) Ayrshire cows without (1855) and with (1856) the current spotted pattern.



Since the mid-19th century international agricultural exhibitions and fairs were organized in the major European cities. This promoted the export of successful sires from western and central Europe to Eastern Europe for incrossing into local breeds. Except for the Pechora and Yakut, North Russian polled and Great Russian land cattle were eventually completely outcrossed.

Systematic breed development with explicit breeding objectives and the keeping of herd books is largely restricted to the Western countries. However, on the Indian subcontinent several Mysore zebu breeds have a history dating back to the late 16th century [143] and most Indo-Pakistani zebu breeds were described in the 19th century. In addition, for many local non-registered breeds in Africa, sires are

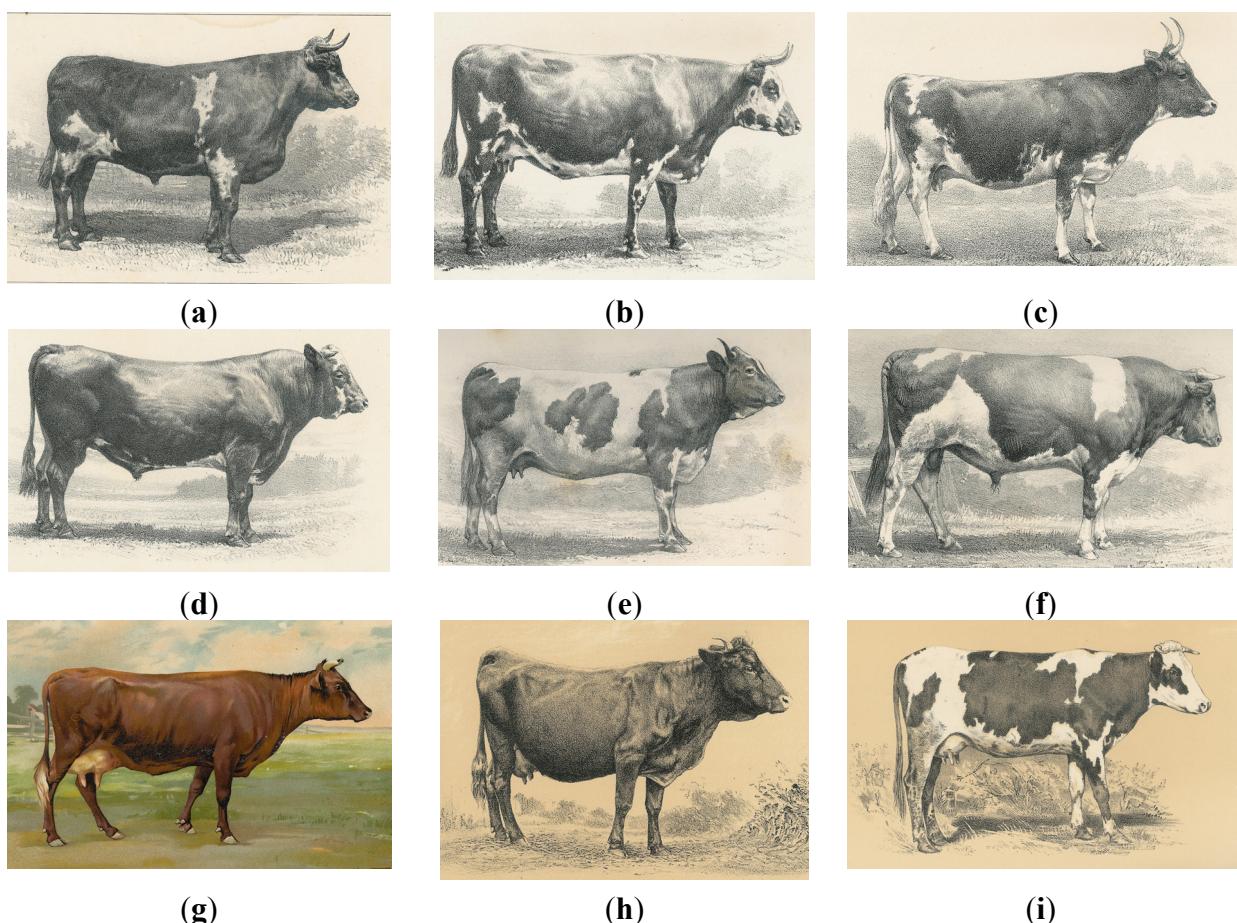
selected according to breeding objectives with partial or complete genetic isolation from other cattle with oral history effectively replacing formal herd books.

An encyclopedia [7], a dictionary [144], a list of breed names [9] and the DAD-IS database [145] mention more than 1000 breeds worldwide.

11. European Breeds of the 19th Century: Tour of the Continent

In the northwestern European lowland and Scandinavia, where traction was done with horses, cattle were bred for dairy production (Figure 15). During the period of *Anglomania* from 1825 to 1860, the successful English Shorthorns were crossed with Northwest-European continental cattle, especially in Belgium and North France [146]. Most Belgian breeds have been influenced by the Shorthorn, such as the dairy red *Flamande* (recognized in 1857, also kept in northern France) and the dual-purpose White-Blue, after 1890 also influenced by the French Charolais. Further development of this breed during the 20th century made the double-muscled beef type an international breed [7].

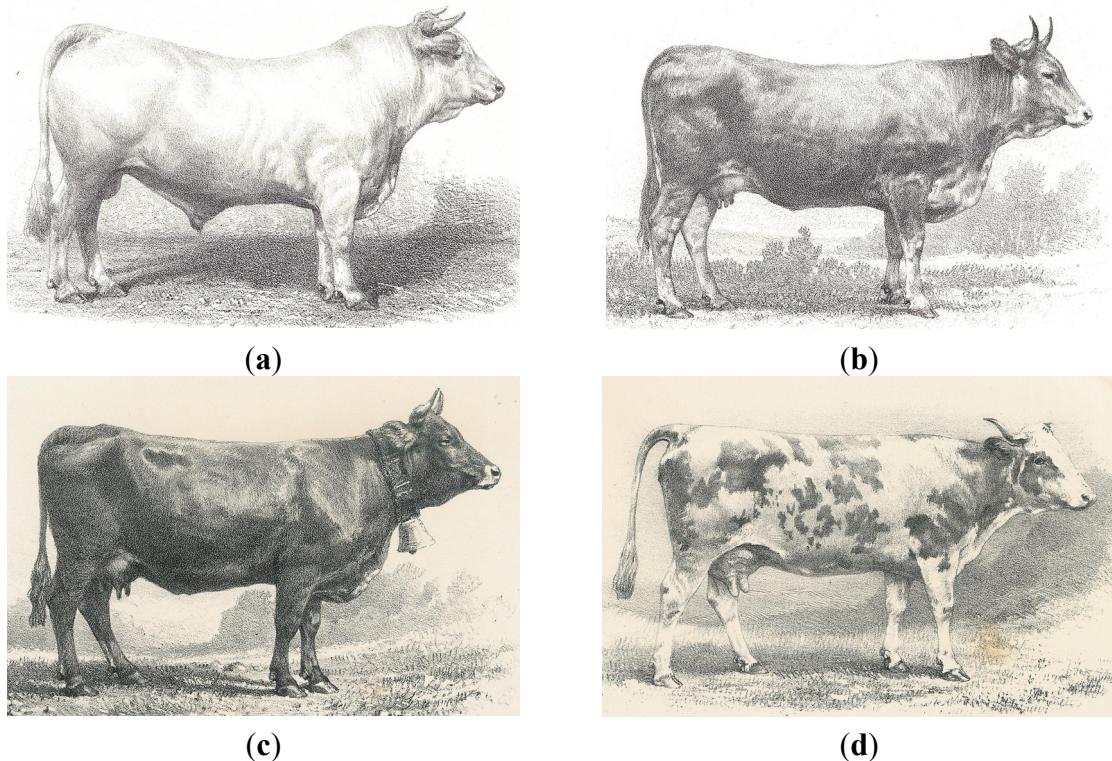
Figure 15. European continental dairy and dual-purpose breeds in the 19th century.
 (a) *Durham-Mancelle* ox, 1856; (b) *Normande* cow, 1856; (c) *Bretonne* cow, 1856;
 (d) *Flamande* bull, 1856; (e) *Comtoise* cow, 1855; (f) North Holland (Dutch) bull, 1855;
 (g) *Angeln* cow, 1890; (h) *Harz* cow, 1855 and (i) *Kholmogory* cow, 1888. Sources:
 (a–f) [142]; (g) [147]; (h,i) [148].



In Normandy, Brittany and northwestern France regional varieties amalgamated (Table S1) and were selected mostly for dairy production. The incrossing of British Shorthorns resulted in the dual-purpose *Durham-Mancelle* (Figure 15a), later developed as the *Maine-Anjou* beef breed and still closely related to the Shorthorns, and in three mainly dairy breeds, the *Normande* (Figure 15b), the *Bretonne Pie Noir* (Figure 15c) and the red *Flamande* (Figure 15d) with herd books established in the 1880s [7].

In eastern France spotted dairy cattle (see below) are represented by the *Montbéliarde*, originating from Switzerland and the related alpine *Abondance*. The blond and pied *Comtoise* landraces (Figure 15e), became absorbed into the *Montbéliarde* and French Simmental. More to the south, several French beef breeds were developed. In 1842 a registry was established for the Charolais beef breed (Figure 16a), which also underwent Shorthorn influence before a separate herd book for “pure” animals was established in 1890. The Limousin (Figure 16b), in 1854 officially recognized as a draught breed, was after 1886 selected towards a beef type and recorded in a herd book. Another well-known French beef breed, *Blonde d’Aquitaine*, emerged in the 20th century by amalgamation of several local breeds.

Figure 16. Central-European breeds in the 19th century [142]. (a) Charolais bull; (b) Limousin cow; (c) Schwyz (Swiss Brown) cow, 1856; (d) Simmental-Saanen cow, 1855.



In the Netherlands the cattle population suffered considerably from the rinderpest epidemics in 1768 and 1786. Afterwards, the cattle population was replenished with cattle from Denmark and within a few generations regained its dairy productivity [133] (Figure 15f). In 1874, the first Dutch herd book was established and in 1879 the second in the province of Friesland. This documented the provenance and was useful for exported cattle as was required by foreign buyers. Dutch exports to European countries and America began to flourish after 1880, which led to the emergence of the highly productive Holstein-Friesian. The black-pied color, at that time most common in the north of the Netherlands,

became an international trademark of the Dutch dairy cattle. In 1920 half the Dutch national cattle population consisted of Black Pied Dutch-Friesians and their numbers kept increasing. Within this population the red color gene variant was suppressed but, being recessive, did not disappear. Red-pied breeds such as the Dutch Meuse-Rhine-Yssel (MRY) were more developed as dual-purpose cattle, but were in the late 20th century influenced by red-pied Holstein sires.

In Germany the dairy cattle in the north is often indicated as *Niederungsvieh*, (lowland cattle) this as opposed to the central and southern *Höhenvieh* (highland cattle), a contrast that correlates with the Y-chromosomal haplotype (see below, [43]). The German black- and red-pied lowland dairy cattle are closely related to Dutch cattle and also to the red lowland dairy cattle. After 1830, the North-German Angeln (*Angler*) cattle (Figure 15g) and the closely related Danish Red reformed many local red highland breeds of central and eastern Europe (Figure 15h) as well as in the Baltic countries and Ukraine. The desired dairy type was described in 1841 and its first herd book published in 1885.

In Scandinavia and Finland cattle were kept since the Middle Ages mainly for dairy production [149]. In the 19th century several breeds were developed on the basis of crosses of local populations to imported sires. Ayrshires were imported on a large scale because of their proven hardiness. In addition, in Russia local cattle have been crossed with various imports, such as Dutch Black-pied, Groningen Whiteheaded, Danish Red, Shorthorns and Herefords. The most important of the early-improved breeds is the black-pied Kholmogory (Figure 15i), which spread across the provinces of Archangelsk and Vologda and to the surroundings of St Petersburg, where dairy products were in great demand. Kholmogory sires were widely used for improving Northern Russian polled land cattle, which all became extinct, except the Pechora cattle [7].

In Central Europe most breeds were triple purpose. In remote Alpine valleys productivity was improved only late in the 19th century by better feeding and management. In 1875 *Schwyz* cattle and two other *Braunvieh* varieties from different Alpine altitudes were recognized, which were combined as the Swiss Brown with a common herd book in 1879 (Figure 16c). These cattle became the ancestors of several Alpine, Italian and Spanish brown cattle and later of the American Brown Swiss. In the same year a herd book was established for Bernese *Fleckvieh*, now better known as Simmental (Figure 16d). This type of cattle influenced several spotted cattle breeds in Central Europe and was also outcrossed to local breeds in Eastern Europe, including Russia [7,150].

In Central Germany crosses of imported sires, mainly Bernese and *Schwyz* to red land cattle (*Rotes Höhenvieh*, Figure 15h) resulted in several local yellow breeds, which eventually were combined in the German Yellow (*Gelbvieh*). Incrossing in the amalgamated Austrian blond breeds resulted in the Austrian Yellow.

In regions where ox traction was the main purpose, such as the larger part of the Iberian Peninsula and southern Italy, herd books were established only after 1920 or 1930. Spanish and Portuguese cattle breeds developed in many different types with relatively little influence from outside (Figure 17). Dairying was only important in the northwestern *Asturiana* cattle. For breeding of fighting bulls several genetically isolated *castas* (strains) of fighting cattle evolved from a mixture of Iberian races, including the central and southern black or red cattle of central and southern Spain and the northwestern Chestnut breeds.

Figure 17. Iberian cattle. (a) Pyrenean ox team from Puigcerda, N.W. Spain, 1920s postcard; (b) *Serrana Negra* or *Negra Iberica* bull; Spain (c) *Minhota* cow, Portugal 1960s; and (d) *Barrosã* bull, 2006 (c,d: photographs by Marleen Felius).



(a)



(c)



(d)

During the 1950s, Iberian *breeds* were upgraded with exotic sires having matching coat colors, such as English South Devon, Austrian Yellow and Swiss Brown for the Northwest-Spanish Galician Blond (*Rubia Gallega*) and German Yellow for the Portuguese *Minhota*. About 20 years later French *Salers* was crossed into the central Spanish *Retinta* and the South-Portuguese *Alentejana*. Upgrading was not extensive, however, so the Iberian breeds retained genetically their regional identity [8] with the exception of the *Minhota*, which became largely identical to the German Yellow (Figure 17c).

Spotted, brown and grey Alpine cattle have influenced several North-Italian breeds. The *Piemontese* was developed into a large beef breed by combining grey local strains and incrossing of several Swiss and French cattle; a herd book was established in 1887. Central and South Italy harbor several Podolian draught and beef breeds, such as the large white *Chianina* (Figure 18) and the semi-feral *Maremmana* in Tuscany, the grey *Romagnola* around Bologna, the *Marchigiana* in the Marche, the *Podolica* in the south and the work-dairy red *Modicana* in south Sicily.

The breed formation changed the partitioning of the diversity in three ways. First, groups of herds constituting a breed became uniform and differences between breeds were emphasized. Second, successful breeds spread beyond their region of origin and were even, as detailed below, exported to other countries or continents. In contrast, locally adapted but less productive breeds declined in number or disappeared. Third, genetic isolation of breeds decreased the diversity at the molecular level, which can be monitored via an increase in homozygosity.

Figure 18. Chianina draught cattle. (a) *The Autumn*, Jacob Philipp Hackert, painted ca. 1784 in Italy, detail (Wallraf-Richartz-Museum, Cologne) and (b) San Gimignano, 1967 (photograph by Veronica Hekking).



At the same time, breed also became a social concept. Through breeding societies and cattle exhibitions breeds grew into club icons with inherent, if unrealistic, perceptions of their history and conservation value [9]. However, cattle breeds were from the outset never static, but new phenotypes were developed that improved productivity [7]: several landraces were upgraded by crossbreeding with breeds from the same country or with foreign imports and other breeds were split or amalgamated (Table S1). Changes in the 20th century were even more consequential (see below), leading to a perception that breeds imported during the 19th-century belong to our past and are as authentic as the landraces of older local origin.

12. Breed Groups and Clusters

On the basis of a genetic survey of the present European and Turkish breeds analyzed with microsatellites and in agreement with SNP analysis [151], five major groups of breeds and several clusters of related breeds can be distinguished [8]:

- (1) North-European cattle, comprising the following breed clusters:
 - (a) Four clusters corresponding to the expansion of popular dairy breeds (black-pied, red-pied, Baltic red and Nordic Ayrshire);
 - (b) Three regional clusters of related but diverse breeds (British, Nordic and Russian-Siberian); and
 - (c) A loose cluster of Shorthorn with several Belgian and North-French, dairy-beef and beef breeds influenced by the Shorthorn, including the *Maine-Anjou* and Charolais.
- (2) Central European cattle, with many dual purpose (beef-work or dairy-work) and triple-purpose breeds, comprising three major and two minor breed clusters:
 - (a) Two breed clusters corresponding to the expansion of the Simmental and Swiss Brown breeds, respectively. The Simmental cluster also contains related Swiss, French and Italian cattle from the western Alps, the German and Austrian yellow and blond breeds and the German *Hinterwälder* and *Vorderwälder*;
 - (b) The unicolored beef and beef-work breeds from South France;
 - (c) Two minor clusters of Alpine Grey cattle and of the spotted dairy cattle from the eastern Alps (*Pinzgauer*, *Pustertaler* and *Cika*). The *Piemontese* beef breed also belongs to the Central-European cattle, but does not belong to a breed cluster.

- (3) Iberian cattle, with a large variety of coat colors and horn morphology and mainly used as beef, work and fighting cattle.
- (4) The mostly long-horned and grey Podolian cattle, primarily developed as beef and work animals.
- (5) The genetically diverse breeds of the Balkans and Anatolian breeds, still representing the undeveloped taurine cattle.

Cattle from the first group predominantly carry Y-chromosomes from the Y1 haplogroup. All other breeds have an Y2 Y-chromosome with the exception of a few Spanish breeds. The molecular-genetic classification is largely in agreement with the integrated geographic-morphological classification [7,8]. The development of dairy cattle in northern (group 1) and central Europe (group 2) may have narrowed the diversity of the paternal lineages. This would explain the geographic contrast of two dominant Y-chromosomal haplotypes from the Y1 and Y2 in group 1 and 2, respectively [43].

A correlation of genetic clustering with geographic origin indicates that *isolation by distance* governs the molecular divergence of the breed clusters. Most alleles of neutral markers are shared by a majority of the breeds, do not correspond to the breed-specific traits and are via linkage disequilibrium only informative for a small part of the genome.

13. Asian Cattle

The history of cattle in Asia is not as dynamic as we have described for Europe. Anatolian cattle that live close to the domestication site of taurine cattle have retained a high genetic diversity [152], but now require protection [153].

Other indigenous Southwest Asian cattle consist of small, triple purpose local landraces (Baladi) and larger, elegant dairy type Damascus breeds. Due to outcrossing and replacement by temperate-type dairy and beef breeds these are declining very rapidly [40]. The Israeli Holstein has been developed since 1922 and comprises strains that are adapted to temperatures of 40–45 °C [154]. Near the cities of other Southwest-Asian countries and especially in Saudi Arabia Holstein-Friesian cows are kept on large farms in climate-controlled stables.

Siberian, Mongolian and Central Asian taurine cattle have since the 1920s been outcrossed by imported West European dairy, beef and dual-purpose breeds such as dairy Black Pieds, Simmental, Swiss Brown, Shorthorn and Hereford. Recently the Kazakh Aulyakol has been developed by continuous crossbreeding with Charolais without taking measures to protect the extremely hardy local breeds [155]. Since 2001 a conservation program in the Sakha Republic protects the Yakut as the only surviving authentic Siberian landrace [156].

In China, the Central and South Chinese Yellow cattle were developed as work cattle [7]. Dairy cattle have been developed since the early 19th century by crossbreeding with European or American cattle and recently with purebred Holsteins.

In 1867, the ban on meat consumption in Japan was lifted. At the same time, the consumption of dairy products was stimulated. In order to convert the Japanese working cattle into beef types in 1872 West-European breeds were introduced [157]. The Japanese Black was developed by incrossing with Devon and Shorthorn [158]. In 1994 it accounted for 90% of the national beef cattle population and is

the source of the Kobe beef, the most expensive beef of the world [159]. In America, Australia and Europe the exported Japanese beef cattle populations are collectively known as Wagyu, the name for the original Japanese cattle. Japanese beef cattle have a high frequency of the mtDNA T4 haplogroup (see above). Since 1889, milk has been produced by imported Holsteins [7].

In India and Pakistan the vast majority of cattle are *desi*, local non-descript animals [160], also including the *nadudana* dwarf zebus (Figure 19). However, these countries also count 35 recognized zebu breeds. A large variety of Indo-Pakistani zebu breeds and landraces were described in the 19th century [161]. For several breeds herd books were established in the early 20th century. Since the 19th century a few breeds were exported to Southeast Asia and the Americas [162]. Most zebu breeds are developed as draught cattle [160], but Sahiwal, Red Sindhi and Gir are specialized dairy cattle and the Kankrej and Ongole are dairy-work cattle. The southern Indian Mysore breeds were already bred in the 17th century for fast road transport [161].

Figure 19. Tamil Nadu dwarf zebu, Madras (postcard, probably from the 1930s).



Several factors contributed to the recent decrease of the Indo-Pakistani zebu populations: increase of mechanized agriculture, dwindling grazing areas in densely populated regions, exclusion of herds from forest grazing, crossbreeding programs and increase of the number of dairy river buffaloes. Dwarf zebus adapted to extreme conditions almost vanished by crossbreeding with taurine imports, but the small northwestern Pakistan Achai was described in 2012 [163] and the miniature Vechur breed was reestablished [164]. Further, new pure zebu breeds are being developed or have been recognized [165–168].

In Indochina and on the Philippines the swamp buffaloes outnumber cattle [169]. As in China, Indochinese cattle were used for work and eventually slaughtered but not milked. After 1950 European, American and Australian production cattle were being imported. At the end of the 19th century Ongole zebus were imported in Indonesia for traction on paved roads, for which the soft hooves of the water buffaloes were not suitable. Domestic banteng is still kept pure as Bali cattle on the island of the same name and has been exported to other Indonesian isles [73].

The gayal or mithun, the domestic form of the gaur, is kept as semi-feral cattle in the forests at 1000–3000 m in eastern India, Bhutan, the western part of Myanmar and in the southeastern Chinese Yunnan province (Dulong cattle). Although crossing with gaur occurs, gaur and gayal bulls have remained clearly different in size, behavior and morphology, most notably of the horns of the bulls. Mainly reared for meat the animal plays an important role in the socio-economic and cultural life of the local tribal populations [170]. Dulong gayals carry zebu mtDNA [171], indicating a hybrid origin.

The Malaysian Selembu is the first-generation offspring of gayal and zebu. The sterile males are strong work cattle and the females excellent dairy producers [7].

14. African Cattle

As described in Sections 3 and 4, both taurine and zebu cattle immigrated into Africa. As in Europe, long-horned preceded short-horned taurine cattle [40]. Cross-breeding in East Africa led to the development of taurindicine cervico-thoracically humped sanga cattle, which expanded southward and reached South Africa 250–500 AD [40]. Most sangas have retained a taurine Y-chromosome, indicating that male zebu introgression in these cattle was only partial. By around 1500 AD sanga cattle were the dominant form of cattle in East and Central Africa [40].

Zebus gradually migrated to the west after 700 AD [28,172] or even earlier [40]. The presence of zebu in West Africa in the early 19th century is testified by the export of Senegal zebu in 1828 to the Lesser Antilles [173].

At the end of the 19th century a devastating cattle plague spread throughout the African continent [174]. The rinderpest epidemic started in Eritrea in 1887 and reached the Atlantic Ocean in 1893 and South Africa in 1898, according to some accounts killing 90% of all African cattle [175,176] (Figure 20). The partial resistance of zebu to rinderpest with a mortality of only 10%–30% led to a drastic replacement of many taurindicine sanga populations by thoracically humped zebu with substantially more indicine ancestry in West, Central and East Africa. Zebu is now the dominant species in West and East Africa, but is not kept in the coastal regions infested with tsetse flies. In those areas the trypanotolerant African taurine cattle have remained the most pure, especially the Lagune [46,79]. The miniature West African short-horned taurines lost ground, mainly by the increasing Fulani zebu influence. On the other hand, the larger and long-horned taurine N'Dama expanded from Guinea over most of West Africa.

Figure 20. Rinderpest epidemic in South Africa, 1897 (Onderstepoort Collection).



Y-chromosomes of West-and East-African zebus have haplotypes of indicine origin due to the exclusive use of zebu bulls [78,177]. Autosomal DNA shows for most tropical African cattle a mixed ancestry with variable taurine-indicine ratios. Zebu alleles still have the highest frequency in East Africa [77,178]. Evidently, the separate domestications of taurine and indicine cattle, two interfertile

species with different environmental requirements, created the opportunity to breed, in addition to the pure species, many intermediate taurindicine breeds, expanding the adaptive repertoire of domestic cattle. Adding further to the diversity of African cattle, Friesian cattle were introduced in 1850 into South Africa and in 1908 into Kenya, in South Africa followed by other productive European and North American cattle. Crossbreeding European and African breeds in South Africa resulted in several successful new breeds, such as the Bonsmara and Drakensberger. In Kenya the Sahiwal zebu, first imported in 1939, spread as purebred or crossbred dairy cattle. Conversely, African N'Dama, Boran, Tuli, Afrikander and Bonsmara are exported to the tropical and subtropical regions in America and Australia and crossed with cows of British origin.

15. Cattle in the New World

The arrival of the Spanish explorers in the Americas in 1492 opened up a new world for Europeans and their cattle. On his second voyage in 1493 Columbus took cattle to the Caribbean island of Hispaniola [40,118]. For the next fifty years, every Spanish ship sailing for America carried five or six young cattle, only two or three of which were expected to survive. It is estimated that at most 300 Spanish cattle entered the Americas via this route. Many of these came from the Canary Islands on the northwest coast of Africa, in Spanish possession since 1479 and the last port of call before the long voyage west. By 1525, already more than 1000 cattle populated the Caribbean colonies, from where they spread to the Spanish colonies in America (Figure 21). The mtDNA haplotype distribution in the present-day Caribbean cattle with T3 and T1 haplotypes is compatible with a Spanish and possibly also African origin [179,180].

Figure 21. Brazilian cattle *Sugar Mill*, Frans Post, detail, 1640 (Royal Museum of Fine Arts, Brussels).

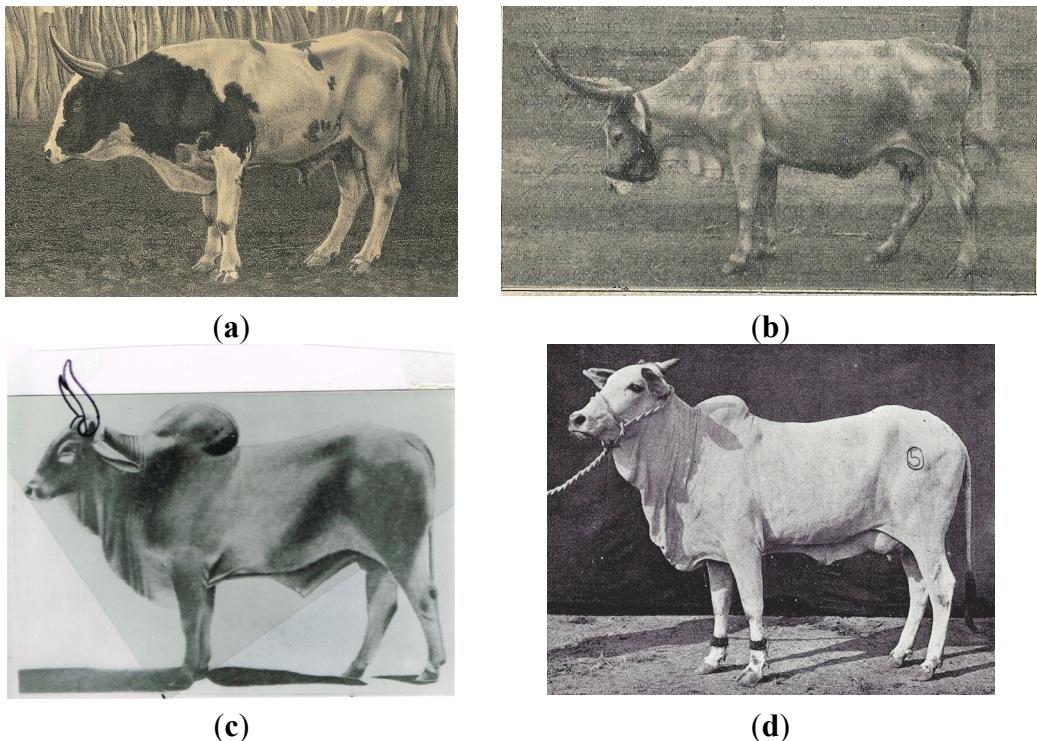


Cattle entered Mexico in 1521. In 1540 the first herd of 500 Spanish cattle crossed the Rio Grande as 'meat on the hoof' for the "conquistadors" of present-day Texas [119] and became the ancestor of the Texas Longhorn. In 1524 Spanish cattle entered Santa Marta in the present-day Colombia and more imports to the coast of Central and South-America were to follow.

In North America, the present-day *Canadienne* cattle descend from animals imported from Normandy and Brittany between 1608 and 1660 [181]. English colonists appeared in 1607. The first traceable import of English cattle to Virginia dates back to 1609. In 1610 a few animals were imported to Jamestown from the West Indies. Dairy cattle arrived in North America with colonists from the Netherlands (1620s), Denmark (1633) and Sweden (1638) and mixed with the other cattle [181]. Importation of cattle stopped after the financial crisis of 1640 and was only resumed at the end of the 18th century. The influence of the original imports in America, commonly called *Native Cattle* [118], persisted until the 20th century [182].

Thus, at the end of the 18th century the cattle population in North America consisted of animals of North-European or Iberian descent variants (Figure 22a,b) and mixtures of these two [46,118]. The Texas Longhorn was at that time the only North American beef breed. The demand for food of the growing populations was met by import of specialized British dairy and beef breeds, starting with the arrival in 1783 of a few Shorthorns. In the 19th century herd books for cattle started to become established, initially only for dairy cattle. The first black-pied Dutch Friesian cattle were imported in 1852. It turned out to be the most productive dairy cattle and soon became popular under the name Holstein.

Figure 22. Criollo and zebu breeds. (a) Mexican Criollo bull [149]; (b) Brazilian *Franquero* cow, 1913 [183]; (c) the zebu bull Lontra, probably of the *Kankrej* breed, imported in 1889 and one of the most important founders of the Brazilian zebu breeding (picture reconstructed); (d) Ongole heifer sent to Brazil [143].



Since 1830, beef cattle from the southern states were transported to the northern cities. After the American Civil War (1861–1865), the prairies in Texas harbored an expanding population of about five million crossbreds of British beef cattle and Texas Longhorn, living under semi-feral or feral conditions. Starting in 1866, large herds were rounded up and driven north as meat-on-the-hoof. The now romanticized

era of the cowboys ended after the disastrous winter of 1886–1887, when 90% of the prairie cattle perished. British Hereford and Angus cattle then became the predominant beef cattle. These were kept under more intensive management with breeding recorded in herd books as already common for dairy breeds [181,184].

A subsequent development in both North and South America was the import of Indian zebus. The first of these came to Brazil in 1813 from Malabar, India's southwest coast. In 1835 or 1849 the first zebus were imported into North America [185,186]. After a few more sporadic imports into Bahia, larger numbers of various Indian breeds were imported in the 1870s (Figure 22c,d; Table S2). Most imported animals were from the Kankrej (*Guzerá* in Brazil), Ongole (*Nelore* in Brazil) and later also the Gir breeds. These were bred pure, crossed with other zebus in order to develop the synthetic *Indubrasil* zebu breed or used to upgrade Criollo taurine cattle. Thus, most Criollo became admixed with zebu as shown by microsatellite [187] and Y-chromosomal genotyping [180].

In the 1880s several Texan breeders imported zebus from Brazil and Mexico. Between 1882 and 1906 zebus were imported directly from India to Texas (Table S2). In the Gulf coast states, from a mixture of these zebus the Brahman and several taurindicine beef breeds were developed, which in the 20th century became popular in tropical countries around the world. In tropical and sub-tropical America zebus and the new taurindicine breeds have largely replaced Criollo cattle.

From the beginning New World breeders have created synthetic taurine, taurindicine and zebu breeds (Table S3). In addition, gaining in popularity is crossbreeding, which exploits the first-generation heterosis [188,189]. The most popular crossbreds result from a Holstein × Jersey cross (*Kiwi* in New Zealand) or from Hereford × Angus crosses (*black baldy* in North America, Figure 23). A minor development is the breeding of several types of miniature cattle for small-scale farming. Thus, the phenotypic repertoire was expanded by recombining the cattle genetic resources and new breeding objectives.

Figure 23. Hereford cow with black baldy calf on the plains, Nebraska, 2007 (photograph Marleen Felius).



In Canada and the USA, the Angus has surpassed the Hereford as the preferred beef breed. The Beef Shorthorn lost much terrain in the USA but is still important in Argentina and Australia. Since 1967 the North-American beef cattle industry was transformed by the so called *exotic cattle boom*, starting in Canada: large scale imports of continental-European beef breeds, especially of Limousin, Gelbvieh, Charolais and Simmental. In comparison with the British beef breeds these cattle offer leaner meat and a faster growth rate [181,190]. However, Angus and Hereford still have the highest registration numbers.

Branding campaigns like Certified Angus Beef emphasized Angus breeding and black-hided cattle again became popular, even for the imported European breeds. Hence, over the last 25 years it is common to find in the USA black Limousin, Simmental, Gelbvieh, Salers or Chianina cattle.

In Australia, similar developments took place [191]. In the 19th century mainly British breeds were imported; zebus arrived from India at the end of the 18th century and after 1843 in larger numbers; and Dutch Friesian were introduced from 1885, followed after 1890 by the Holstein. Many Shorthorns, Herefords, Angus and taurindicine cattle are kept under extensive management or live in feral populations. In 1896 the cattle tick became endemic and subsequently tick-borne diseases seriously threatened the productivity of beef cattle in Queensland, still of British descent. The gradual incrossing of Indian and American zebus, which are resistant against tick-borne diseases, continued until after WWII and restored cattle husbandry in the tropical parts of Australia. New Zealand imported only taurine cattle, mainly dairy breeds of English and Dutch origin [192]. In this country, 36% of the dairy cattle are now crossbreds of Jersey and Holstein.

16. Cattle without Borders

Since the 19th century the breeds that were developed in Europe, Asia and Africa were not only exported to the New World, but also to many other countries [7,9,193]. Table S2 shows that a fair part of the diversity of European cattle dispersed to other continents, although Iberian and Nordic breeds are underrepresented.

During World War I the development of breeds temporarily stopped in most European countries and a few breeds in the combat zone did not survive at all. After the war, agriculture in Europe, Australia and America became more and more focused on production. Accustomed to continuous technical progress, government programs stimulated the development of the most productive breeds, established national herd books, regulated the keeping of breeding bulls and stimulated animal health care. Local breeds, if considered non-productive, were either marginalized or upgraded with neighboring or even exotic stock.

Genetic development of cattle breeds became thoroughly influenced by technological progress. The tractor became popular since the First World War and gradually replaced cattle and horses as source of draught power in agriculture. Consequently, during the 1950s the triple-purpose cattle of central Europe were converted to dairy-beef types and the Mediterranean work-beef breeds changed into single-purpose beef types. The introduction of milking machines in the 1960s intensified the development of specialized single-purpose dairy breeds, which were also selected for an udder and teat morphology fitting the machinery.

Application of modern breeding techniques [194] began in the 1930s with artificial insemination (AI), which soon became widespread. Since the 1970s AI is complemented by multiple ovulation and embryo transfer (MOET). Both AI and MOET allow desirable genetic material to be moved over the globe. In that way several breeds of European origin, such as the Dutch Friesian, Swiss Brown, Hereford and Aberdeen-Angus were bred in America into production types that differ from the original stock (allopatric development [8]). When subsequently American sires were repatriated, mostly in the form of semen, the European ancestor populations became Americanized (Table S2).

Since the 1960s, the breeding of cattle has been supported by intensive research. A comprehensive study compares the performance of nearly 40 American, British, European, zebu and Criollo beef breeds [195,196]. Worldwide progress in quantitative and molecular genetics intensifies the selective breeding with genomic selection, which becomes more and more realistic for several traits [197,198].

A further increase of productivity was accomplished by an increase in scale of both dairy and beef production. Modern dairy farming requires intensive management with an automated feeding system, veterinary care, close monitoring, year-round stabling and even climate control. Holstein-Friesians are by far the most popular dairy breed. Beef cattle are kept either under semi-intensive management, as the American calf-cow operations combined with grain feeding in large-scale feedlots, or under extensive management with herds grazing freely on natural pastures.

These developments have an obvious disadvantage. The focus on the most productive breeds is at the expense of the less productive local landraces. Many of these were either replaced or crossbred to the point that they have effectively disappeared (Table S4). However, local breeds have often developed adaptation to local, sometimes extreme conditions and are able to thrive under extensive management (Figure 24). Although the diversity of the current cosmopolitan cattle is still large enough to belie the claim that cattle become an endangered species [199], loss of local breeds does erode genetic resources that are difficult to replace [200].

Figure 24. (a) Sukuma cow, Tanzania, 2005; (b) Sahiwal cow, Pakistan, 1990 (photographs by Marleen Felius). In 2014, a Sahiwal cow in Pakistan was reported to give 39 L per day [201].



Although in America and Australia crossing of indicine and European taurine cattle has led to successful breeds (Table S3), this is generally much less successful in developing countries where cattle are kept under traditional extensive management. Incrossing of cosmopolitan productive cattle, vigorously promoted by the Western breeding industry and supported by national governments, is as often as not counterproductive as the exotic breeds and their crossbreds do not thrive in the harsh environment (Figure 25). Crossbreds are generally considered a failure in India as well as Africa [202].

Figure 25. Exotic crossbreds and Friesian cow in India, 2005 (photographs by Anno Fokkinga).



17. New Life for Local Breeds

Following a general skepticism since the 1960s regarding the side effects of technological progress, scientists, breeders and government agencies in Europe became aware of the disappearance of old local breeds and the ensuing loss of genetic variety. Local rustic breeds are now valued as more frugal, healthy and hardy than the industrial cattle. Their adaptation and suitability for extensive management, natural grazing and vegetation management may even be economically advantageous by allowing production in conditions where modern breeds would perish (Figure 25). Furthermore, these breeds belong to our cultural heritage and are of local cultural importance, even if most breeds are only one or two centuries old [9]. This is a major stimulant for conservation, even if breeders and owners of animals are not always realistic in their perception of the uniqueness of a breed and of its history.

The growing realization that genetic diversity may get lost led to several initiatives. The first association that raised public awareness to the conservation of farm animal genetic resources was the Rare Breeds Survival Trust, established in 1973 in the United Kingdom, the cradle of selective breeding. Similar associations were established elsewhere in Western Europe and in the USA, such as the American Livestock Breeds Conservancy (ALBC). These collaborate in international organizations as Rare Breeds International (RBI) and Safeguard for Agricultural Varieties in Europe (SAVE). Since the 1980s the European Association for Animal Production (EAAP) and the Food and Agriculture Organization (FAO) of the United Nations have compiled together the “Global Data Bank of Domestic Livestock” [203]. An international management policy has been formulated in the Global Plan of Action for Animal Genetic resources [204].

Although many developing countries still put their trust in technological progress, African and Indian scholars now advocate avoiding or at least being careful with the introduction of high productive breeds into their local, well-adapted breeds: *“What we should do in Africa is to ignore the use of exotic breed for crossbreeding because the resulting hybrids cannot be as adapted to the local environment as the zebu and will therefore need a lot of costly input for survival”* [202].

The following examples illustrate that local breeds are now acknowledged in breed surveys:

- Whereas the French breed catalogue of 1963 [205] listed only 27 French breeds and four imported ones the 2010 version [206] mentions 48 French breeds, 10 imported, as well as five extinct breeds.
- In the breed catalogues compiled by the Spanish Ministry of Agriculture the number of indigenous cattle breeds described has increased from 25 in 1981 [207] to 40 in 2009 [208].

- In the 1960s the Greek Shorthorn was described as one landrace population [209], but by 2010 eight distinct local varieties were recognized [210]. In addition to the 33 recognized indigenous breeds of Ethiopia, several more have been identified and reported in recent years [211–216].
- For Fipa cattle, a zenga type of southwest Tanzania, two varieties were described in 2011 [217].
- Recently the formal national recognition of several Indian *desi* (local') breeds has increased the number of zebu breeds in India to more than 30.
- For the all but vanished Florida Cracker and Pineywoods cattle of the southern United States, 5 and 15 distinct local lines and herds, respectively, are now recognized [218].
- In Ecuador four local types of Sierra Criollos, kept at different altitude, have been differentiated [219].

On the other hand, recognition of various varieties with different names does not imply as many independent contributions to the genetic resources [9]. Several strategies for conservation of endangered breeds or varieties are followed:

- Rescue and maintenance of the remaining populations (*on the hoof*). An extreme example is the rescue of the feral cattle on Enderby Island [220]. Using oocytes and clones from the single surviving cow and semen collected from one of the bulls shot in 1991, resulted in six calves being born in 2006.
- Sustainable conservation, for instance by advertising (*branding*) presumed unique qualities of a local breed (e.g., grass finished beef or slow food): “*If you want to save a breed, they have to have a job.*” [221].
- Cryoconservation of semen samples in the USA and several other countries [222,223].
- Selection of animals from related breeds that resemble the animals from the endangered breed. Examples:
 - In 1986 the Austrian *Tux-Zillertaler* was reconstituted by crossings the approximately 30 remaining females with Swiss *Hérens* sires.
 - Rebreding of the *Ansbach-Triesdorfer*, which had vanished in 1940, began in 1987 by selection of German *Fleckvieh* cows from the Ansbach region with the characteristic speckled color patterns on head and feet.
 - The French *Bordelaise* was considered extinct in 1960, but has been reconstituted since 1987 by using crossbred animals descending from the original breed.

Breed conservation is supported by molecular-genetic investigation of farm animal genetic resources, both at the national and the global level. Molecular diversity studies, which often allow reconstruction of the history of livestock [224], have now been recognized in the animal genetic science as new field of research, complementing the analysis of genotype-phenotype relations.

DNA analysis with panels of genetic markers invariably finds that most breeds contain a large portion of the total diversity of the species, typically 80% or more. Most alleles have broad breed distributions and breeds differ mainly in allele frequencies. Paradoxically, breeds that clearly contribute to the phenotypic diversity by a unique phenotype tend to be inbred and thus carry little diversity in their DNA. Breed-specific molecular traits are rare and several breeds also share functional mutations [225]. Genomic studies now offer new approaches to characterize into more detail the differences between breeds as well as the diversity within breeds [226]. This information may very well be useful for an

effective protection of genetic resources, anticipating future market demands, new diseases and climate changes.

18. On the History and Future of Diversity

Surveying the complex history of cattle throughout the time on different continents, we propose that the genetic diversity of cattle emerged during three overlapping phases:

- (I) Domestication and subsequent interaction with wild populations;
- (II) Migrations followed by natural adaptation to agricultural habitats in diverse environments and during the subsequent periods of human history; and
- (III) A relatively recent systematic breed-oriented selection.

This may be generalized to other livestock species, but the events and processes during the three phases acting on the diversity depend strongly on the species.

(I) Domestication of cattle and subsequent interaction with wild populations. As revealed by archaeological investigations complemented by DNA analysis, especially the sequencing of mtDNA, this involved the following:

- A sampling of a part of the diversity of the ancestor species, but is usually followed by introgression of wild animals during the dispersal of the domesticates [226]. The taurine domestication was estimated to involve only 80 females [17], but later introgression of aurochs males on different continents probably introduced additional diversity. For African taurine cattle this is now accepted [33].
- Zebu and taurine cattle are the domestic forms of two well-diverged but cross-fertile aurochs subspecies from Southwest Asia [79] and the Indus Valley [34]. These were adapted to different environments, which with the many intermediate crossbreds ensured a potential adaptation of the domestic animals to climates ranging from temperate to tropical.
- In addition to taurine and zebu cattle Asia harbors also domestic cattle descending from other bovine species with many combinations of mixed-species origin.

(II) Migrations followed by ecological adaptation to agricultural habitats in diverse environments and during subsequent periods of human history. This governed the distribution of the taurine and zebu genotypes and brought about several changes in phenotype [5]. Especially taurine cattle adapted to a wide range of climates, even including Siberian conditions. The acquisition of adaptive traits can now be investigated by studying the breed distribution of causative mutations [227–229]. A survey of the events preceding the development of specialized breeds:

- Europe remained completely taurine with mere traces of putative zebu introgression, while Asia, Africa, America and Australia harbor both taurine, zebu and taurindicine breeds in different climactic zones.
- In Africa, the diversity pattern has been determined by consecutive immigrations of short-horned taurine, long-horned taurines and zebras, by introgression of African aurochs, by disease resistance (trypanotolerance, resistance to rinderpest), by the wide range of management systems (sedentary, transhumance, nomadic pastoralism).

- The modulation of horn development illustrates an early and flexible adaptation to local requirements or preferences, short-horned or hornless animals being convenient for stabling.
- Coat color and color patterns are post-domestic features [230] that make animals visibly distinct, easily invoke perceptions of the animal value and are obvious targets of selection. Several of these already existed during antiquity [88].
- The decrease in size is a domestic adaptation, but may also reflect the capacity of feeding cattle during the winter period. During antiquity the large Epirote cattle and its Roman descendants created a difference with the more common small cattle, but this may not have survived during the Middle Ages [54]. European cattle started to regain their size since the 15th century.
- In the Roman era, production purposes were multiple as evidenced by the preponderance of draught cattle in Italy and of dairy cattle in central and northern Europe [90].
- Because the migration of the Germanic tribes were the last major movements of European people, it is plausible that from the Middle Ages differentiation of European cattle was mainly due to *isolation by distance*. This process was only partially undercut by trading of cattle causing gene flow between neighboring regions and is still reflected by the genetic clustering of the present breeds [8].
- In the tropical zones, diversity patterns were decided largely by the tropical adaptation and resistance to rinderpest. This has led to widespread incrossing of zebu in African and American taurine populations.
- Cattle were introduced in America only after 1492 with the import of Iberian and Northwest-European cattle, followed in the 19th century by English, Dutch and zebu breeds and in the 20th century by European continental beef breeds.

(III) Systematic breed-oriented selection. Although this started only 250 years ago, it has been most consequential and may be considered as the most dynamic period in the evolution of cattle.

- After the Middle Ages, cultural and technical progress and the growing demand for food rationalized the European cattle husbandry. Starting in the 18th century this led to an organized management of regional breeds: genetically isolated groups of phenotypically homogeneous animals. This took place all over Europe, where cattle exhibitions soon catalyzed the merging of early breeds from neighboring regions. This improved the productivity of European breeds, changed appreciably their appearance and emphasized the differences between breeds.
- Since the 19th century several highly productive breeds spread to other countries and continents (Table S2), where separate herd books were kept. Thus, several groups of closely related breeds were formed differing mainly in nationality.
- A less productive and often abortive development was the introduction of highly productive European breeds in tropical countries where the intensive management required for these cattle cannot be ensured.
- In the New World, a creative attitude to breeding led to a number of taurine or taurindicine synthetic breeds, the result of crossing cattle from different origins. Several of these are highly successful (Table S3).

- A focus on productive breeds diminished the population sizes of local breeds, several of which disappeared by crossing with sires from productive breeds. This is being counteracted by successful conservation efforts.

We conclude that the development of the cattle genetic resources has been a multifaceted and continuously dynamic process, which ever kept pace with human history on the global and local level. It has resulted in a worldwide population of cattle with a considerable phenotypic and molecular diversity. Concerns about genetic erosion tend to focus on the loss of diversity generated by the breed development during the third phase [9], but should not ignore diversity generated during the earlier phases. The most consequential threat is the loss of cattle adapted to local conditions and extensive management. Future management of the diversity will benefit from a further genome-wide characterization of DNA variation causative for valuable phenotypes.

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Author Contributions

Marleen Felius and Johannes A. Lenstra collected literature and wrote the first draft. Marie-Louise Beerling, David S. Buchanan, Peter A. Koolmees, and Bert Theunissen contributed additional material and commented on the text.

Supplementary Materials

Supplementary materials can be accessed at: <http://www.mdpi.com/1424-2818/6/4/705/s1>.

Conflicts of Interest

The authors declare no conflict of interest.

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