Part 1

THE STATE OF
LIVESTOCK DIVERSITY

Introduction

Part 1 of the report begins by describing advances in research on the origin of the diversity of today's animal genetic resources for food and agriculture (AnGR) – the domestication and history of livestock species. This is followed by a description of the current status and trends of AnGR diversity and the extent to which this diversity is threatened by genetic erosion. The next section describes patterns of international exchange of AnGR. The roles and values of AnGR, including their direct and indirect contributions to livelihoods and economic output, are then described. This is followed by a discussion of the various adaptive characteristics, including genetic resistance and tolerance to specific diseases and parasites, that enable livestock breeds to survive and produce in a range of different production environments. The next section addresses threats to the diversity of the world's AnGR. In the final section of Part 1, livestock diversity is discussed in relation to human nutrition. All sections highlight, in particular, changes that have occurred since the first report on *The State of the World's Animal Genetic Resources for Food and Agriculture* (first SoW-AnGR) (FAO, 2007)[1] was prepared.

AnGR are here taken to include those animal species that are used, or may be used, for food production and agriculture,[2] and the populations within each. Distinct populations within species are usually referred to as breeds. FAO (1999)[3] defines a breed as:

"either a subspecific group of domestic livestock with definable and identifiable external characteristics that enable it to be separated by visual appraisal from other similarly defined groups within the same species or a group for which geographical and/or cultural separation from phenotypically similar groups has led to acceptance of its separate identity."

The broad definition of the term "breed" is a reflection of the difficulties involved in establishing a strict definition of the term. Further information on the development of the breed concept is provided in the first SoW-AnGR.[4]

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[1] FAO. 2007. *The State of the World's Animal Genetic Resources for Food and Agriculture*, edited by B. Rischkowsky & D. Pilling. Rome (available at http://www.fao.org/docrep/010/a1250e/a1250e00.htm).

[2] Fish are excluded as management requirements and breeding techniques are very different.

[3] FAO. 1999. *The Global Strategy for the Management of Farm Animal Genetic Resources*. Executive brief. Rome (available at http://dad.fao.org/cgi-bin/getblob.cgi?sid=-1,50006152).

[4] FAO, 2007, pages 339–340.

Origin and history of livestock diversity

1 Introduction

Genetic diversity provides the raw material for breed improvement and for the adaptation of livestock populations to changing environments and changing demands. Information on the origin and history of animal genetic resources (AnGR) is essential to the design of strategies for their sustainable management (Ajmone-Marsan *et al.*, 2010; Felius *et al.*, 2014). The first report on *The State of the World's Animal Genetic Resources for Food and Agriculture* (first SoW-AnGR) (FAO, 2007) provided a review of the state of knowledge of the domestication of livestock species and their subsequent dispersal around the world.[1] Since the time the first SoW-AnGR was prepared, a considerable amount of research work has been undertaken in this field. In particular, further development of genomic tools (see Box 1A1) has allowed the use of genome-wide information in the investigation of various aspects of the history of livestock species. This section provides an updated overview of the state of knowledge in this field, focusing particularly on recent advances. It describes, in turn, the initial domestication process, subsequent introgression[2] of wild species into domesticated species, adaptations that occurred after domestication and, finally, relatively recent breed formation.

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[1] FAO, 2007, Part 1 Section A (pages 5–22).

[2] Reproductive contacts that have left traces of DNA from one population in another population.

2 The domestication process

Theories about the process of livestock domestication have continued to develop since the time the first SoW-AnGR was prepared (Larson and Burger, 2013; Larson and Fuller, 2014). Animals can be considered domesticated if they are bred in captivity and (after several generations) have become adapted to being kept by humans. Once animals have been domesticated, their reproduction is controlled by their human keepers, who provide them with shelter and feed and protect them against predators (Diamond, 2002; Mignon-Grasteau *et al.*, 2005). Only 15 out of 148 non-carnivore terrestrial mammalian species weighing more than 45 kg have been domesticated (Table 1A1). From the 10 000 avian species, only very few (chicken, turkey, pheasant, guinea fowl, duck, Muscovy duck, goose, pigeon, quail and ostrich) have been domesticated as a source of food. According to Diamond (2002), successful domestication depends on the presence of several traits in the target species:

- behavioural traits that facilitate management by humans (e.g. a lack of aggression towards humans, a tendency not to panic when disturbed and strong social instincts);
- reproductive traits, such as the ability to breed in captivity, short intervals between births and (preferably) large litter sizes; and
- physiological traits, such as rapid growth and a non-carnivorous diet.

Domestication may have been triggered by climatic changes at the end of the Pleistocene (12000 to 14000 BP) that led to localized expansion of human populations and the emergence of crop farming (Larson and Burger, 2013). Domestication

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Box 1A1
How the history of livestock is reconstructed: archaeology and DNA

Archaeologists use various means to distinguish the skeletal remains of domestic animals from those of wild animals, including studying morphological changes to the teeth, cranium and skeleton to estimate body size and shape and determine growth patterns (Zeder *et al.*, 2006a). The age of organic material can be determined by radiocarbon dating. Isotope analysis of organic residues on pottery may identify milk fatty acids (Evershed *et al.*, 2008). Nitrogen isotope ratios in the teeth of calves may reveal early weaning and thus the use of cattle for dairying (Balasse and Tresset, 2002).

Different categories of polymorphic DNA markers reveal different aspects of the history of livestock (see Part 4 Section B for further information on different types of markers).

- Mitochondrial DNA (mtDNA) is transmitted maternally and has been instrumental in identifying ancestor species, estimating the number of female founders (Bollongino *et al.*, 2012), identifying the geographic regions of domestication (Naderi *et al.*, 2008) and reconstructing migration routes (Groeneveld *et al.*, 2010; Lenstra *et al.*, 2012). Most mtDNA studies target the hypervariable control region of the mitochondrial genome, but complete mtDNA genomes are needed to establish relations between major mtDNA types (the haplogroups[1]) (Achilli *et al.*, 2009). It is no longer believed that the presence of a given number of different haplogroups always indicates the equivalent number of separate domestication events; a single ancestral wild population may harbour more than one haplogroup (Naderi *et al.*, 2008; Cieslak *et al.*, 2010; Bollongino *et al.*, 2012). Because regional haplogroup distributions tend to be stable, mitochondrial DNA often tells us about the earliest migrations (Cieslak *et al.*, 2010; Miao *et al.*, 2013; Lenstra *et al.*, 2014). In the case of cattle, these migrations have been shown to have involved severe population bottlenecks (Lenstra *et al.*, 2014).

- Mammalian Y-chromosomal variation is transmitted via the paternal line and is a powerful tool for tracing gene flow by male introgression, whether in the distant past or more recently (Edwards *et al.*, 2011).

- Autosomal variation is transmitted via both parents. Microsatellite markers have been widely used for analysing autosomal variation and are still useful (FAO, 2011). However, they are being replaced by high-density SNP (single nucleotide polymorphism) analysis (Kijas *et al.*, 2012; Goedbloed *et al.*, 2013; Petersen *et al.*, 2013a; Decker *et al.*, 2014) or whole-genome sequencing (Groenen *et al.*, 2012). Autosomal loci are commonly used for population diversity estimations, detection of the subdivision and differentiation of populations, calculation of genetic distances and quantification of genetic admixture.

An important recent development is the use of Bayesian computations for the analysis of large datasets, which allows detailed reconstruction of prehistoric genetic events (Bollongino *et al.*, 2012; Larson and Burger, 2013; Gerbault *et al.*, 2014).

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[1] A haplogroup is a group of similar haplotypes that share one or more mutations indicative of descent from a common ancestor. Haplogroups most commonly pertain to mitochondrial and Y-chromosome DNA. Haplotype is the combination of alleles from two or more polymorphic sites in a mitochondrial, Y-chromosomal or autosomal DNA segment.

scenarios remain uncertain. However, it is clear that they varied from species to species. Three plausible pathways –"commensal", "prey" and "directed"– have recently been proposed (Larson and Burger, 2013) (see Figure 1A1). The first of these pathways involved animals being attracted to human settlements and then becoming captive as a source of food. The second involved the capture of artiodactyl[3]

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[3] Even-toed hoofed animals (cattle, sheep, goats, pigs, camels, etc.).

FIGURE 1A1
Three pathways of domestication
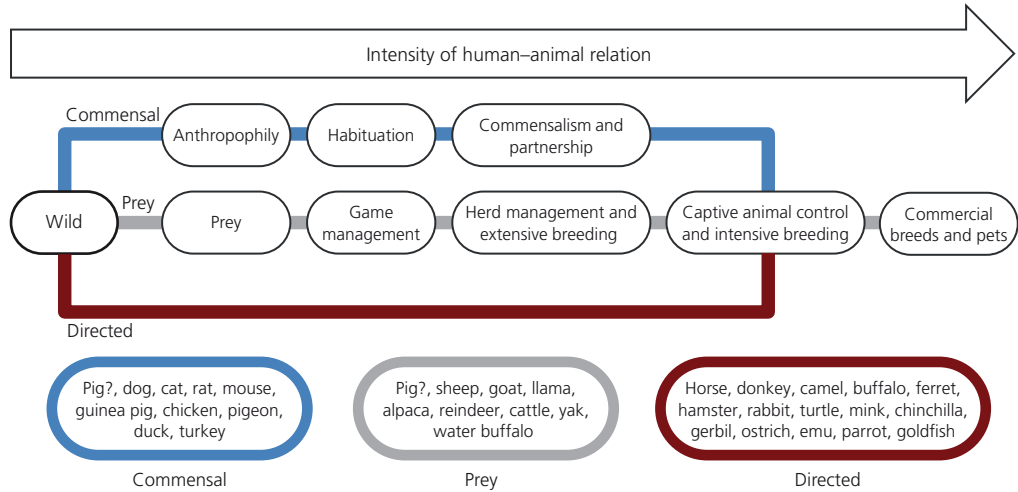
Note: The figure includes some species not included in the scope of the SoW-AnGR.
Source: Larson and Burger, 2013, with permission from Elsevier.

prey animals as a means of securing a supply of meat. Once domesticated, these species also provided other products, such as milk, wool and leather. Later, some were also used for ploughing. The third pathway, which came into play later in history, involved deliberate efforts to exploit the specific capabilities of the target species (e.g. their potential as pack, riding or draught animals).

There is now consensus about which wild species were the ancestors of the various domesticated livestock species (Table 1A1). Livestock domestication is thought to have occurred in at least 15 areas of the world (Figure 1A2). Inferences regarding the dates of domestication events (Table 1A1) remain approximations. Skeletal remains identified as belonging to domesticated species on the basis of their morphology are never as old as the first domesticates. Close genetic relationships between domestic and wild populations in other parts of the world (i.e. outside the recognized domestication centres) are considered to indicate intro-

gression (Larson and Burger, 2013). Views on the location of domestication centres have evolved since the time the first SoW-AnGR was prepared (Larson *et al.*, 2014). For example, evidence indicating pig domestication in Europe and in Indonesia is now considered to be a result of introgression. Similarly, it is now accepted that Africa was not a centre of cattle domestication and that the river buffalo originated in India rather than in Mesopotamia (although the evidence for the latter conclusion is not abundant). Recent studies have indicated an African origin for the donkey and distinct origins for Chinese and European geese.

Recently, Wilkins *et al.* (2014) proposed, as a general mechanism of domestication, that selection for tameness induced a mild neural crest cell deficit during embryonic development, which attenuated behaviour and also modified several morphological and physiological traits related to domestication (e.g. smaller brain and depigmentation).

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TABLE 1A1
Domestication, disperal and sources of introgresssion

Domestic species	Wild ancestor[1]	Date	Domestication site	Domestic range	Sources of introgression	References
Taurine cattle *Bos taurus*	Aurochs *Bos primigenius[a]*	10250 BP	Southwest Asia[2]	Global	- African aurochs bulls - European aurochs bulls?[3] - Zebu in African Sanga	Stock and Gifford-Gonzalez, 2013; Decker et al., 2014; Freeman et al., 2006; Decker et al., 2014
Zebu cattle *Bos indicus*	Aurochs *Bos primigenius[a]*	8000 BP	Indus Valley[2]	Subtropical and tropical	- 2-way taurindicine hybrids in China - Taurine maternal lineage in nearly all non-Asian zebus and taurindicines - Banteng in southern China - Yak cows in Nepal and Qinghai, China - Banteng cows in Indonesian zebu breeds	Ajmone-Marsan et al., 2010; Decker et al., 2014; Lenstra et al., 2014
Bali cattle *Bos javanicus*	Banteng *Bos javanicus[c]*	5500 BP	Indonesia	Indonesia, Malaysia, feral in Australia	Zebu in Malaysia	Mason, 1984; Nijman et al., 2003
Mithun *Bos frontalis*	Gaur *Bos gaurus[d]*			India–Myanmar border region	Zebu cows in Dulong cattle (Yunnan, China)	Mason, 1984; Lenstra et al., 2014
Yak *Bos grunniens*	Wild yak *Bos mutus[d]*	5000 BP	Quinghai- Tibetan Plateau	Quinghai–Tibetan Plateau, adjacent Asian highlands		Wiener et al., 2003
River buffalo *Bubalus bubalis*	Wild water buffalo *Bubalus arnee[b]*	4500 BP	India	Italy, Balkans, Southwest Asia, Egypt, India, Brazil, Australia		Kumar et al., 2007
Swamp buffalo *B. bubalis carabensis*	Wild water buffalo *Bubalus arnee[b]*	5000 BP	Southern China	South China, Indochina, Philippines, Brazil, Australia	River buffalo in China and Bangladesh	Zhang et al., 2012
Sheep *Ovis aries*	Asiatic mouflon *Ovis orientalis[d]*	9750 BP	Southwest Asia	Global	Argali and urial ewes	Demirci et al., 2013
Goat *Capra hircus*	Bezoar *Capra aegagrus[d]*	9750 BP	Southwest Asia	Global	Possibly other goat species	Naderi et al., 2008
Reindeer *Rangifer tarandus*	Reindeer *Rangifer tarandus[f]*	2500 BP	North Siberia	Northern Eurasia		Mason, 1984
Dromedary *Camelus dromedarius*	Wild dromedary *Camelus dromedarius[a]*	6000 BP?	Arabia?	North and East Africa, Southwest Asia, Australia		Spassov et al., 2004; Pott, 2004
Bactrian camel *Camelus bactrianus*	Wild Bactrian camel *C. bactrianus ferus[b]*	5500 BP	Turkmenistan, Iran	From Black Sea to Manchuria	Bactrian males	Larson et al., 2014
Llama *Lama glama*	Guanaco *Lama guanicoe[f]*	6000 BP	Central–southern Andes	Central–southern Andes	Alpaca	Kadwell et al., 2001
Alpaca *Vicugna pacos*	Vicuna *Vicugna vicugna[f]*	5000 BP	Central–southern Andes	Central–southern Andes	Llama	Kadwell et al., 2001

(Cont.)

TABLE 1A1 *(Cont.)*
Domestication, disperal and sources of introgresssion

| Domestic species	Wild ancestor[1]	Year	Domestication site	Domestic range	Sources of introgression	References
Pig *Sus scrofa*	Wild boar *Sus scrofa*[f]	10000 BP 8500 BP	Southwest Asia China	Global	Males and females from several wild boar populations; Chinese pigs in Europe in nineteenth century	Larson *et al.*, 2005; Fang *et al.*, 2006
Horse *Equus caballus*	Wild horse *Equus ferus*[a]	5500 BP	Kazakhstan	Global	Wild mares during dispersal, Iberian horses	Warmuth *et al.*, 2012; Cieslak *et al.*, 2012
Donkey *Equus asinus*	African wild ass *Equus africanus*[b]	5500 BP	Sudan	Global (relatively rare in Europe and North America)		Rosenbom *et al.*, 2015
Rabbit *Oryctolagus cuniculus*	Wild rabbit *Oryctolagus cuniculus*[e]	1400 BP	Southern France	Global		Carneiro *et al.*, 2014
Chicken *Gallus domesticus*	Red jungle fowl *Gallus gallus*[f]	4500 BP 8000 BP	India Indochina	Global	Grey jungle fowl (*Gallus sonneratii*) in India	Tixier-Boichard *et al.*, 2011
Turkey *Meleagris gallopavo*	Mexican turkey *Meleagris gallopavo*[f]	2000 BP	Mexico	Global		Thornton *et al.*, 2012
Guinea fowl *Numida meleagris*	Helmeted guinea fowl *Numida meleagris*[f]	2000 BP	Africa	Global		Larson *et al.*, 2014
Domestic duck *Anas platyrhynchos*	Mallard *Anas platyrhynchos*[f]	1000 BP	Southern China	Global	Wild population, permanently	Larson *et al.*, 2014
Muscovy duck *Cairina moschata*	Muscovy duck *Cairina moschata*[f]	4000 BP	South America	Global	Wild population, permanently	Stahl *et al.*, 2006
Goose *Anser anser* Chinese goose	Greylag goose *Anser anser*[f] Swan goose *Anser cygnoides*[f]			Global	Wild populations, permanently	Shi *et al.*, 2006; Wang *et al.*, 2010

[1] Superscript letters next to the species names indicate their risk status according to the IUCN Red List of Threatened Species (http://www.iucnredlist.org) as of October 2014: a = Extinct; b = Critically endangered; c = Endangered; d = Vulnerable; e = Near threatened; f = Least concern.

[2] Taurine and zebu cattle are commonly considered to have been domesticated separately. Alternatively, zebus may have emerged as a result of wild male and female introgression in taurine cattle introduced from the west (Larson and Burger, 2013).

[3] Female introgression rare (Achilli *et al.*, 2008; Stock *et al.*, 2009); role of male introgression and of the Mediterrean aurochs unclear (Lari *et al.*, 2011). In addition to the references cited in the table, see Mason (1984), Mignon-Grasteau et al. (2005) and Larson et al. (2014).

FIGURE 1A2

Major centres of livestock domestication as inferred from archaeological and molecular genetic evidence
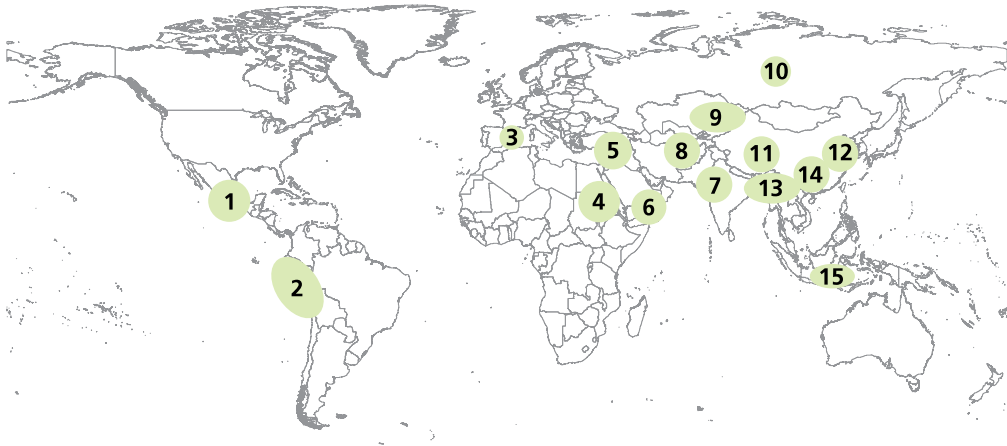
Note: (1) turkey; (2) guinea pig, llama, alpaca, Muscovy duck; (3) rabbit; (4) donkey; (5) taurine cattle, pig, goat, sheep; (6) dromedary, (7) zebu cattle, river buffalo; (8) Bactrian camel; (9) horse; (10) reindeer; (11) yak; (12) pig; (13) chicken; (14) swamp buffalo; (15) Bali cattle.
Sources: Mignon-Grasteau *et al.*, 2005; Larson *et al.*, 2014; references in Table 1A1.

3 Dispersal of domesticated animals

Knowledge of the dispersal of livestock species from their centres of domestication during the prehistoric period is based on a synergic combination of archaeology and molecular genetics. For later periods, written and pictorial documentation is also available. More information is available on cattle (followed by sheep) than on other livestock species, and migrations within Europe are better documented than those in other regions. Zebu cattle and water buffalo only migrated within tropical and subtropical climate zones, while the distributions of dromedaries, Bactrian camels, llamas, alpacas, reindeer, yaks, Bali cattle and mithun are even more restricted. Since the first SoW-AnGR was prepared, molecular studies have filled several gaps in our knowledge of the dispersal of livestock species.

In Europe, the introduction of crops and livestock from Southwest Asia occurred around

8500 BP. Domesticated livestock followed two major routes into Europe, the first along the Mediterranean coast and the second along the Danube, arriving in the British Isles around 6500 BP (Gkiasta *et al.*, 2003). A detailed archaeological study in Anatolia that reconstructed the westward movements of sheep, goats, cattle and pigs (Arbuckle and Makarewicz, 2009) suggested that these species migrated independently of each other. The occurrence of the T1 mitochondrial haplotype from African cattle in Spain indicates that gene flow also occurred across the Strait of Gibraltar (Bonfiglio *et al.*, 2012). Short-horn cattle emerged around 5000 BP in southwest Asia and gradually replaced the original long-horn cattle in most parts of Europe (Mason, 1984). The introduction of the horse was associated with the spread of the Indo-European language around 4500 BP and was probably accompanied by migrations of people and other livestock (Balter and Gibbons, 2015).

During the Roman Era, cattle and sheep were exported from Italy to other parts of the Empire. From the fourth to the eighth century, the Germanic migrations also led to large-scale movements of livestock. Presumably, these migrations preceded the paternal founder effects that are believed to have led to the north–south contrast detected in the Y-chromosomal variation of cattle in Europe (Edwards *et al.*, 2011). A Y-chromosomal haplotype in sheep of British or Nordic origin (Niemi *et al.*, 2013) and the fixation of a goat Y-chromosomal haplogroup in central and northern Europe (Lenstra, 2005) indicate similar paternal founder effects.

In Asia, sheep, goats and taurine cattle migrated to China before 4500 BP (Jing *et al.*, 2008). Cattle arrived in Japan around 2500 BP (Minezawa, 2003). Further to the south, zebu cattle were introduced around 3000 BP (Payne and Hodges, 1997). The introduction of the domestic swamp buffalo, which is more suitable than cattle for ploughing rice paddies, followed the spread of wet rice cultivation in China, Indochina, the Philippines and Indonesia. The river buffalo, domesticated in India, arrived around 900 to 1000 AD in Egypt, the Balkans and southern Italy.

Taurine cattle and other livestock species arrived in Africa around 7000 BP from southwest Asia (Brass, 2012). As in Europe, the original long-horn cattle were replaced by short-horns, although long-horns still exist in some parts of Africa. There are pictures of zebus in Egypt dating from around 4000 BP, but substantial zebu populations were not established at that time (Payne and Hodges, 1997). Import of zebu bulls into Africa was probably stimulated by the Arabian invasions after 700 AD. Cross-breeding to taurine cattle generated taurindicine populations, such as the sanga, which remained mainly taurine and 500 years ago was the dominant type of cattle in central and eastern Africa. Gene flow into western African taurine populations was stimulated by nomadic Fulani pastoralists. The Bantu expansion southwards from the Great Lakes region led to the introduction of sheep into southern Africa around 2000 BP and sanga cattle around 1500 BP (Payne and Hodges, 1997). At the end of the nineteenth century, a rinderpest epidemic led to the spread of zebu cattle with little taurine ancestry in East and West Africa.

Domestic chickens appeared around 8000 BP in Southeast Asia and were introduced around 4500 BP into India and Oceania, around 3000 BP into Europe and around 2300 BP into Africa. It is thought that Polynesians had already brought chickens to South America via the Pacific before 1492 (Storey *et al.*, 2012).

The European colonization of America after 1492 introduced cattle, sheep, goats, pigs, horses, donkeys and chickens. South and Central America and the southern part of North America initially received Iberian livestock, including horses, which transformed the sedentary indigenous societies of the prairies. Further to the north, English-speaking settlers imported northwest-European livestock. In the nineteenth century, cattle of Iberian descent were largely replaced by, or cross-bred with, zebus from South Asia.

As well as accompanying human migrations into new areas, the dispersal of livestock populations was also stimulated by the need to import animals from neighbouring regions following major losses caused by epidemics, famines or plundering. Gene flow was further stimulated by trading, the use of horses and dromedaries for transport, the nomadic lifestyles of cattle-herding peoples and the seasonal transhumant movements of cattle and sheep in several parts of the Old World.

The wide dispersal of the major livestock species had the following effects:

- genetic "isolation by distance", which led to the development of many regional types, many of which already existed in the eighteenth century, when livestock diversity started to be documented;
- a decrease in molecular genetic diversity correlating with distance from centres of origin, caused by founder effects; this effect has been observed in European goats (Canon *et al.*, 2006), African and European cattle (Cymbron *et al.*, 2005; Freeman *et al.*, 2006), the mtDNA

of cattle worldwide (Lenstra *et al.*, 2014) and Arabian horses (Khansour *et al.*, 2013); however, founder effects were often counteracted by cross-breeding with wild or other domestic populations (see Subsections 4 and 6 below); among sheep, the spread of the Merino breed from the the sixteenth century onwards anticipated the spread of other successful livestock breeds in the nineteenth and twentieth centuries;

- so-called "diversity enhancing gene flow" (FAO, 2007), the development of additional diversity as a result of adaptations to diverse environments (see Subsection 5 below).

4 Introgression from related species

The genetics of several livestock populations were enriched after the initial split from the wild ancestral species (Table 1A1). Plausible scenarios include capture of wild animals to replenish domestic populations and introgression from wild males.

Taurine and zebu cattle descend from different aurochs populations. A major contribution from African aurochs bulls is plausible (Decker *et al.*, 2014). However, it is not clear whether there was substantial input from European wild bulls (Beja-Pereira *et al.*, 2006; Lari *et al.*, 2011). Local populations in Asia have received maternal input from other *Bos* species (Lenstra *et al.*, 2014). In several tropical and subtropical regions, taurine and zebu cattle introduced during different periods along different routes formed taurindicine populations when brought into contact. Chinese yellow cattle populations harbour both taurine and zebu Y-chromosomes and mtDNA and the African sanga combines both Y-chromosomal types with taurine mtDNA (Hanotte *et al.*, 2000; Li *et al.*, 2013). Other taurindicine cattle carry a zebu Y-chromosome and taurine mtDNA (Ajmone-Marsan *et al.*, 2010).

The origins of domestic sheep and goats are relatively uncomplicated because of the narrow geographical ranges of their wild ancestors. However, possible introgression from other sheep and goat species has not been investigated. The European mouflon is a feral descendant of the first domestic immigrants and has been shown to breed with domestic sheep in Sardinia (Ciani *et al.*, 2014).

In Europe, the first domestic pigs were immigrants from southwest Asia. As a result of continuous introgression, these populations came to be closely related to the European wild boar (Larson and Burger, 2013). In the case of horses, it has been also proposed that the first domesticates were crossed with wild animals, but the relative homogeneity of the horse Y-chromosome suggests that only wild females were added to the domestic population (Warmuth *et al.*, 2012). A similar scenario has been suggested for chickens, in which mtDNA patterns suggest postdomestication introgression from various Asian red jungle fowl populations (Miao *et al.*, 2013). Introgression from the grey jungle fowl of India introduced a *BCDO2* gene variant, which confers yellow skin colour and has reached a high frequency in domestic chicken (Eriksson *et al.*, 2008).

5 Adaptation of livestock following domestication

After domestication, livestock species adapted to being kept by humans via changes to their behaviour, morphology, appearance, physiology and performance (Mignon-Grasteau *et al.*, 2005). Species that spread beyond their centres of domestication also had to adapt to new physical environments (new climates, feeds, diseases, etc.).

An obvious, if superficial, difference between most domestic species and their wild ancestors is in the colour of their coats, plumage or skins. Driven by human aesthetic sense rather than the need for camouflage or signal display, several colours and patterns emerged in domestic animals that are not observed in wild species (Ludwig *et al.*, 2009; Linderholm and

Larson, 2013). In several species, domestication was accompanied by a reduction in size, which made the animals easier to handle (Zeder *et al.*, 2006b). In addition, sexual dimorphism in bovine species was greatly reduced, because males no longer had to fight for dominance. In Europe, taurine cattle gradually decreased in size between the Neolithic and the end of the Middle Ages, with a temporary preference for large animals in the Roman Empire (Lenstra *et al.*, 2014; Felius *et al.*, 2011). In the post-Medieval period, a shift from subsistence farming to market production, together with improvements in animal husbandry, led to larger cattle again being preferred. Similar changes occurred in goats, sheep and pigs. Another aspect of the adaptation of cattle, sheep and goats to the domestic environment was a reduction in horn length. A step further, the complete loss of horns, occurred in several breeds of cattle and sheep (Medugorac *et al.*, 2012).

In several livestock species, adaptation led, at an early stage, to the development of different conformational types:

- the humpless taurine and humped indicine cattle ecotypes, resulting from independent domestications (see Subsection 2);
- the thin-tailed, fat-tailed and fat-rumped sheep ecotypes, the latter two adapted to desert environments (Wang *et al.*, 2014); and
- warmblood, coldblood and pony horses.

Molecular genetic studies, especially genome-wide association studies and whole-genome sequencing, allow adaptive traits to be linked to genomic regions, genes or even mutations. Several examples are listed in Table 1A2. Several traits have been subject to selection within breeds (see Table 4B1 in Part 4, Section B), but the corresponding mutation may have predated breed formation. For instance, the breed distribution of the derived *DGAT1* allele in cattle, which was identified as a result of efforts to localize milk quantitative trait loci (QTLs) in the Holstein, reveals an old origin and an early role in the development of dairy cattle (Kaupe *et al.*, 2004).

6 The recent history of livestock diversity

The last 250 years have seen changes on a scale unprecedented in the history of livestock diversity. From the earliest times, livestock keepers had influenced the characteristics of their animals through selective breeding. However, developments in England during the late eighteenth century marked the beginning of a new era and had major consequences for the future of livestock diversity throughout the world. Systematic performance recording, identification of animals and pedigree recording, managed by breeders' associations and documented in herd books, led to the development of more homogenous breeds. Explicit breeding objectives accentuated the existing differences between geographically separated populations. This led not only to the fixation of breed-specific traits, with coat colour being the easiest target (Linderholm and Larson, 2013), but also to an increase in production. Within half a century, the new breeding practices had been widely adopted in Europe and North America. The degree of genetic isolation varied from one breed to another. Island and fancy breeds were often isolated and became inbred, but most breeds continued to interact with others as a result of upgrading, intentional cross-breeding or unintended introgression. Not all newly formed breeds were equally successful. Even before the end of the nineteenth century several had been absorbed by other populations (Felius *et al.*, 2014; 2015).

Other developments also had a major effect on the geographic distribution of livestock diversity. In the nineteenth century, railways increased mobility and facilitated the long-distance transportation of livestock. Steamships enabled the transportation of large numbers of animals across the oceans. These developments initiated what is referred to in the first SoW-AnGR as the "second phase of global gene flow", which lasted from the nineteenth to the mid-twentieth century and saw a large expansion in the geographical distribution of several successful breeds (Valle Zárate

PART **1**

TABLE 1A2

Examples of genes or loci involved in selected traits

Trait	Locus, gene	Reference
Most mammalian livestock		
Coat colour	Several genes	Ludwig *et al.*, 2009; Linderholm and Larson, 2013; Switonski *et al.*, 2013
Cattle		
Production traits	Multiple loci	Bovine HapMap Consortium, 2009; Druet *et al.*, 2013; Qanbari *et al.*, 2014; Randhawa *et al.*, 2014; Xu et al., 2015
Prenatal growth	*NCAPG*	Eberlein *et al.*, 2009
Polledness	Intergenic deletions, *BTA1*	Allais-Bonnet *et al.*, 2013; Rothammer *et al.*, 2014; Wiedemar *et al.*, 2014
Slick-hair coat for thermoregulation	*SLICK* locus	Huson *et al.*, 2014
Trypanotolerance in African cattle	Multiple loci	Dayo *et al.*, 2012
Fat content of milk	*DGAT1*, multiple loci	Kaupe *et al.*, 2004; Stella *et al.*, 2010
Sheep		
Production traits	Multiple loci	Kijas *et al.*, 2012; Fariello *et al.*, 2014; Randhawa *et al.*, 2014
Horn size	*RLXN1*	Johnston *et al.*, 2013
Milk traits	Multiple loci	Gutierrez-Gil *et al.*, 2014
Pig		
Domestication, production traits	Multiple loci	Rubin *et al.*, 2012; Ramos-Onsin *et al.*, 2014; Herrero-Medrano *et al.*, 2014; Yang *et al.*, 2014
Adaptation	Multiple loci	Ai *et al.*, 2015
Back elongation	*NR6A1, PLAG1, LCORL*	Rubin et al., 2012
Meat quality	*PRKAG3*	Galve *et al.*, 2013
Fecundity	*AHR, ESR1, PRM1, PRM2, TNP2, GPR149, JMJD1C*	Bosse *et al.*, 2014; Wang *et al.*, 2015
Horse		
Domestication	Multiple loci	Schubert *et al.*, 2014
Performance	Multiple loci	Petersen *et al.*, 2013b; Metzger *et al.*, 2014
Adult size	*NCAPG/LCORL, HMGA2, ZFAT, LASP1*	Makvandi-Nejad *et al.*, 2012
Gait	*DMRT3*	Andersson *et al.*, 2012; Petersen *et al.*, 2013b; Promerova *et al.*, 2014
Rabbit		
Domestication, behaviour	Multiple loci	Carneiro *et al.*, 2014
Chicken		
Comb form	*HAO1, BMP2*	Johnsson *et al.*, 2012
Domestication	Multiple loci	Rubin *et al.*, 2010
Yellow skin colour	*BCDO2*	Eriksson *et al.*, 2008
Fecundity	*TSRH*	Rubin *et al.*, 2010

Note: For further information see Braunschweig (2010) and Nicholas and Hobbs (2012) in addition to the references cited in the table. Also note that Table 4B1 in Part 4, Section B lists several traits and associated genes/loci that have been identified as being specific to one or more breeds.

et al., 2006; Felius, 2015). Most of these breeds were of European origin, but (as noted above) Indian zebus were exported to the Americas and Chinese pigs were crossed with European pig populations (Bosse, 2014; Felius, 2015).

During the period following the Second World War, artificial insemination became common in cattle and pig breeding. This helped to break down genetic isolation by distance, and catalysed the "third phase of global gene flow",[4] which is still continuing. As a result of these developments, a limited number of transboundary breeds (see Part 1 Sections B and C) have become very widespread and increasingly dominate livestock production throughout the world. This has tended to lead to the decline of locally adapted breeds (see Part 1 Sections B and F). At the same time, crossing of breeds from different parts of the world has added to the breed repertoire, for instance, through the development of synthetic taurine and taurindicine cattle breeds in the United States of America and Australia (Felius, 2015) and the Assaf sheep in Israel.

The genetic diversity harboured in today's breeds is being actively researched (FAO, 2011), to date mainly using neutral markers (i.e. markers that have no known effect on the phenotype) (Groeneveld *et al.*, 2010). As described above (see in particular Box 1A1), diversity studies are instrumental to the reconstruction of genetic events that have shaped the present diversity patterns of livestock species, including ancestry, prehistoric and historical migrations, admixture and genetic isolation. Some general conclusions about the current state of livestock diversity drawn from molecular studies are summarized in Box 1A2. See Part 4 Section B for a detailed discussion of the use of molecular tools in the characterization of livestock diversity.

7 Conclusions

Over recent years, the latest molecular tools have contributed to a better understanding of the genetic basis of domestication and have

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Box 1A2
Livestock diversity as revealed by molecular studies

- Individual breeds carry a substantial part (typically 80 percent) of the total molecular variation of the respective livestock species; only a small part of the total diversity is accounted for by variation among breeds.
- Breeds vary in their molecular genetic diversity, with the lowest diversity generally being found in breeds that are isolated by geography or management and the highest diversity in breeds located near sites of domestication, panmictic populations (those in which there is random mating) and cross-bred populations (Groeneveld *et al.*, 2010; Herrero-Medrano *et al.*, 2014).
- Well-defined breeds with unique and appreciated traits tend to be inbred and have low molecular genetic diversity, while non-descript local populations tend to have high molecular genetic diversity (Groeneveld *et al.*, 2010).
- Breeds from the same region, or from nearby regions, tend to be closely related.

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helped in the identification of a growing list of genes involved in adaptation. Four sources of the genetic diversity present in today's livestock populations can be distinguished:

1. sequestration of part of the genetic repertoire of the wild ancestral species;
2. acquisition of additional diversity as a result of contact with other populations or related species during the dispersal of domesticated species;
3. selection of gene variants conferring adaptation to a variety of environments and capacity to serve a variety of different purposes; and
4. breed formation and systematic breeding, which accentuated differences between populations and increased productivity while decreasing overall molecular genetic diversity.

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[4] FAO, 2007, pages 53–55.

Conservation efforts have tended to focus on the fourth, and most recent, source of diversity, i.e. on diversity generated by breed formation. However, diversity derived from the third source, environmental adaptation, is likely to be old in origin and is highly relevant to the maintenance of future breeding options.

The genetic constitution of livestock species and breeds will probably be as dynamic in the future as it has been in the past. Moreover, our growing knowledge of the molecular characteristics of current livestock populations may very well be used to direct the ongoing domestication of other species, such as various types of deer and ratites.

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