Part 1

THE STATE OF LIVESTOCK DIVERSITY
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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\(^2\) Fish are excluded as management requirements and breeding techniques are very different.


Section A

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. 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 of wild species into domesticated species, adaptations that occurred after domestication and, finally, relatively recent breed formation.

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

3 Even-toed hoofed animals (cattle, sheep, goats, pigs, camels, etc.).
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 introgression (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).
### TABLE 1A1
Domestication, dispersal and sources of introgression

<table>
<thead>
<tr>
<th>Domestic species</th>
<th>Wild ancestor¹</th>
<th>Date</th>
<th>Domestication site</th>
<th>Domestic range</th>
<th>Sources of introgression</th>
<th>References</th>
</tr>
</thead>
</table>
| Taurine cattle  | *Bos taurus*   | 10250 BP | Southwest Asia¹ | Global | - African aurochs bulls
- European aurochs bulls³
- Zebu in African Sanga | Stock and Gifford-Gonzalez, 2013; Decker et al., 2014; Freeman et al., 2006; Decker et al., 2014 |
| *Bos primigenius* | aurochs       |      |                     |                |                          |            |
| Zebu cattle     | *Bos indicus*  | 8000 BP | Indus Valley²      | 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 |
| *Bos primigenius* | aurochs   |      |                     |                |                          |            |
| Bali cattle     | *Bos javanicus* | 5500 BP | Indonesia          | Indonesia, Malaysia, feral in Australia | Zebu in Malaysia | Mason, 1984; Nijman et al., 2003 |
| *Bos javanicus* | banteng      |      |                     |                |                          |            |
| Mithun          | *Bos frontalis* | 5000 BP | Qinghai–Tibetan Plateau | Qinghai–Tibetan Plateau, adjacent Asian highlands | Zebu cows in Dulong cattle (Yunnan, China) | Mason, 1984; Lenstra et al., 2014 |
| *Bos mutus*¹ | Wild yak | 4500 BP | India               | Italy, Balkans, Southwest Asia, Egypt, India, Brazil, Australia | Wiener et al., 2003 |
| *Bubalus bubalis* | Wild water buffalo | 4500 BP | South China          | South China, Indochina, Philippines, Brazil, Australia | Riser buffalo in China and Bangladesh | Zhang et al., 2012 |
| *Bubalus carabensis* | Wild water buffalo | 5000 BP |                      |                |                          |            |
| Sheep            | *Ovis aries*   | 9750 BP | Southwest Asia      | Global         | Argali and urial ewes | Demirici et al., 2013 |
| *Ovis orientalis* | Asiatic mouflon |      |                     |                |                          |            |
| Goat             | *Capra hircus* | 9750 BP | Southwest Asia      | Global         | Possibly other goat species | Naderi et al., 2008 |
| *Capra aegagrus* | Bezoar         |      |                     |                |                          |            |
| Reindeer        | *Rangifer tarandus* | 2500 BP | North Siberia       | Northern Eurasia |                          | Mason, 1984 |
| Dromedary       | *Camelus dromedarius* | 6000 BP | Arabia?             | North and East Africa, Southwest Asia, Australia | Bactrian males | Spassov et al., 2004; Pott, 2004 |
| Bactrian camel  | *Camelus bactrianus* | 5500 BP | Turkmenistan, Iran  | From Black Sea to Manchuria |                          | Larson et al., 2014 |
| Llama           | *Lama glama*   | 6000 BP | Central–southern Andes | Central–southern Andes | Alpaca | Kadwell et al., 2001 |
| *Lama guanicoe* | Guanaco        |      |                     |                |                          |            |
| Alpaca          | *Vicugna pacos* | 5000 BP | Central–southern Andes | Central–southern Andes | Llama | Kadwell et al., 2001 |
| *Vicugna vicugna* | Vicuna         |      |                     |                |                          |            |

(Cont.)
### Origin and history of livestock diversity

The state of the world’s animal genetic resources for food and agriculture

<table>
<thead>
<tr>
<th>Domestic species</th>
<th>Wild ancestor</th>
<th>Year</th>
<th>Domestication site</th>
<th>Domestic range</th>
<th>Sources of introgression</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pig</td>
<td>Sus scrofa</td>
<td>Wild boar</td>
<td>10000 BP</td>
<td>Southwest Asia</td>
<td>Global</td>
<td>Males and females from several wild boar populations; Chinese pigs in Europe in nineteenth century</td>
</tr>
<tr>
<td>Horse</td>
<td>Equus caballus</td>
<td>Wild horse</td>
<td>5500 BP</td>
<td>Kazakhstan</td>
<td>Global</td>
<td>Wild mares during dispersal, Iberian horses</td>
</tr>
<tr>
<td>Donkey</td>
<td>Equus asinus</td>
<td>African wild ass</td>
<td>5500 BP</td>
<td>Sudan</td>
<td>Global (relatively rare in Europe and North America)</td>
<td>Rosenborn et al., 2015</td>
</tr>
<tr>
<td>Rabbit</td>
<td>Oryctolagus cuniculus</td>
<td>Wild rabbit</td>
<td>1400 BP</td>
<td>Southern France</td>
<td>Global</td>
<td></td>
</tr>
<tr>
<td>Chicken</td>
<td>Gallus domesticus</td>
<td>Red jungle fowl</td>
<td>4500 BP</td>
<td>India</td>
<td>Global</td>
<td>Grey jungle fowl (Gallus sonneratii) in India</td>
</tr>
<tr>
<td>Turkey</td>
<td>Meleagris gallopavo</td>
<td>Mexican turkey</td>
<td>2000 BP</td>
<td>Mexico</td>
<td>Global</td>
<td></td>
</tr>
<tr>
<td>Guinea fowl</td>
<td>Numida meleagris</td>
<td>Helmeted guinea fowl</td>
<td>2000 BP</td>
<td>Africa</td>
<td>Global</td>
<td></td>
</tr>
<tr>
<td>Domestic duck</td>
<td>Anas platyrhynchos</td>
<td>Mallard</td>
<td>1000 BP</td>
<td>Southern China</td>
<td>Global</td>
<td>Wild population, permanently</td>
</tr>
<tr>
<td>Muscovy duck</td>
<td>Cairina moschata</td>
<td>Muscovy duck</td>
<td>4000 BP</td>
<td>South America</td>
<td>Global</td>
<td>Wild population, permanently</td>
</tr>
<tr>
<td>Goose</td>
<td>Anser anser</td>
<td>Greylag goose</td>
<td></td>
<td>Global</td>
<td>Wild populations, permanently</td>
<td>Shi et al., 2006; Wang et al., 2010</td>
</tr>
</tbody>
</table>

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 Mediterranean 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).
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 crossbred 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 (Cymbrom 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 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 post-domestication 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...
### TABLE 1A2
Examples of genes or loci involved in selected traits

<table>
<thead>
<tr>
<th>Trait</th>
<th>Locus, gene</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Most mammalian livestock</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coat colour</td>
<td>Several genes</td>
<td>Ludwig et al., 2009; Linderholm and Larson, 2013; Switonski et al., 2013</td>
</tr>
<tr>
<td>Cattle</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Production traits</td>
<td>Multiple loci</td>
<td>Bovine HapMap Consortium, 2009; Druet et al., 2013; Qanbari et al., 2014; Randhawa et al., 2014; Xu et al., 2015</td>
</tr>
<tr>
<td>Prenatal growth</td>
<td>NCAPG</td>
<td>Eberlein et al., 2009</td>
</tr>
<tr>
<td>Polledness</td>
<td>Intergenic deletions, BTA1</td>
<td>Allais-Bonnet et al., 2013; Rothhammer et al., 2014; Wiedemar et al., 2014</td>
</tr>
<tr>
<td>Slick-hair coat for thermoregulation</td>
<td>SUOX locus</td>
<td>Huson et al., 2014</td>
</tr>
<tr>
<td>Trypanotolerance in African cattle</td>
<td>Multiple loci</td>
<td>Dayo et al., 2012</td>
</tr>
<tr>
<td>Fat content of milk</td>
<td>DGAT1, multiple loci</td>
<td>Kaupe et al., 2004; Stella et al., 2010</td>
</tr>
<tr>
<td>Sheep</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Production traits</td>
<td>Multiple loci</td>
<td>Kijas et al., 2012; Fariello et al., 2014; Randhawa et al., 2014</td>
</tr>
<tr>
<td>Horn size</td>
<td>RLXN1</td>
<td>Johnston et al., 2013</td>
</tr>
<tr>
<td>Milk traits</td>
<td>Multiple loci</td>
<td>Gutierrez-Gil et al., 2014</td>
</tr>
<tr>
<td>Pig</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Domestication, production traits</td>
<td>Multiple loci</td>
<td>Rubin et al., 2012; Ramos-Onsin et al., 2014; Herrera-Medrano et al., 2014; Yang et al., 2014</td>
</tr>
<tr>
<td>Adaptation</td>
<td>Multiple loci</td>
<td>Ai et al., 2015</td>
</tr>
<tr>
<td>Back elongation</td>
<td>NR6A1, PLAG1, LCORL</td>
<td>Rubin et al., 2012</td>
</tr>
<tr>
<td>Meat quality</td>
<td>PRKAG3</td>
<td>Galve et al., 2013</td>
</tr>
<tr>
<td>Fecundity</td>
<td>AHR, ESR1, PRM1, PRM2, TNP2, GPR149, JMD1C</td>
<td>Bosse et al., 2014; Wang et al., 2015</td>
</tr>
<tr>
<td>Horse</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Domestication</td>
<td>Multiple loci</td>
<td>Schubert et al., 2014</td>
</tr>
<tr>
<td>Performance</td>
<td>Multiple loci</td>
<td>Petersen et al., 2013b; Metzger et al., 2014</td>
</tr>
<tr>
<td>Adult size</td>
<td>NCPAG, LCORL, HMGA2, ZFAT, LASP1</td>
<td>Mavandi-Nejad et al., 2012</td>
</tr>
<tr>
<td>Gait</td>
<td>DMRT3</td>
<td>Andersson et al., 2012; Petersen et al., 2013b; Promerova et al., 2014</td>
</tr>
<tr>
<td>Rabbit</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Domestication, behaviour</td>
<td>Multiple loci</td>
<td>Carneiro et al., 2014</td>
</tr>
<tr>
<td>Chicken</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Comb form</td>
<td>HAO1, BMP2</td>
<td>Johnsson et al., 2012</td>
</tr>
<tr>
<td>Domestication</td>
<td>Multiple loci</td>
<td>Rubin et al., 2010</td>
</tr>
<tr>
<td>Yellow skin colour</td>
<td>BCD02</td>
<td>Eriksson et al., 2008</td>
</tr>
<tr>
<td>Fecundity</td>
<td>TS5H</td>
<td>Rubin et al., 2010</td>
</tr>
</tbody>
</table>

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 harbouried 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 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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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.

References


Ramos-Onsins, S.E., Burgos-Paz, W., Manunza, A. & Amills, M. 2014. Mining the pig genome to investigate the domestication process. Heredity, 113: 471–484.


