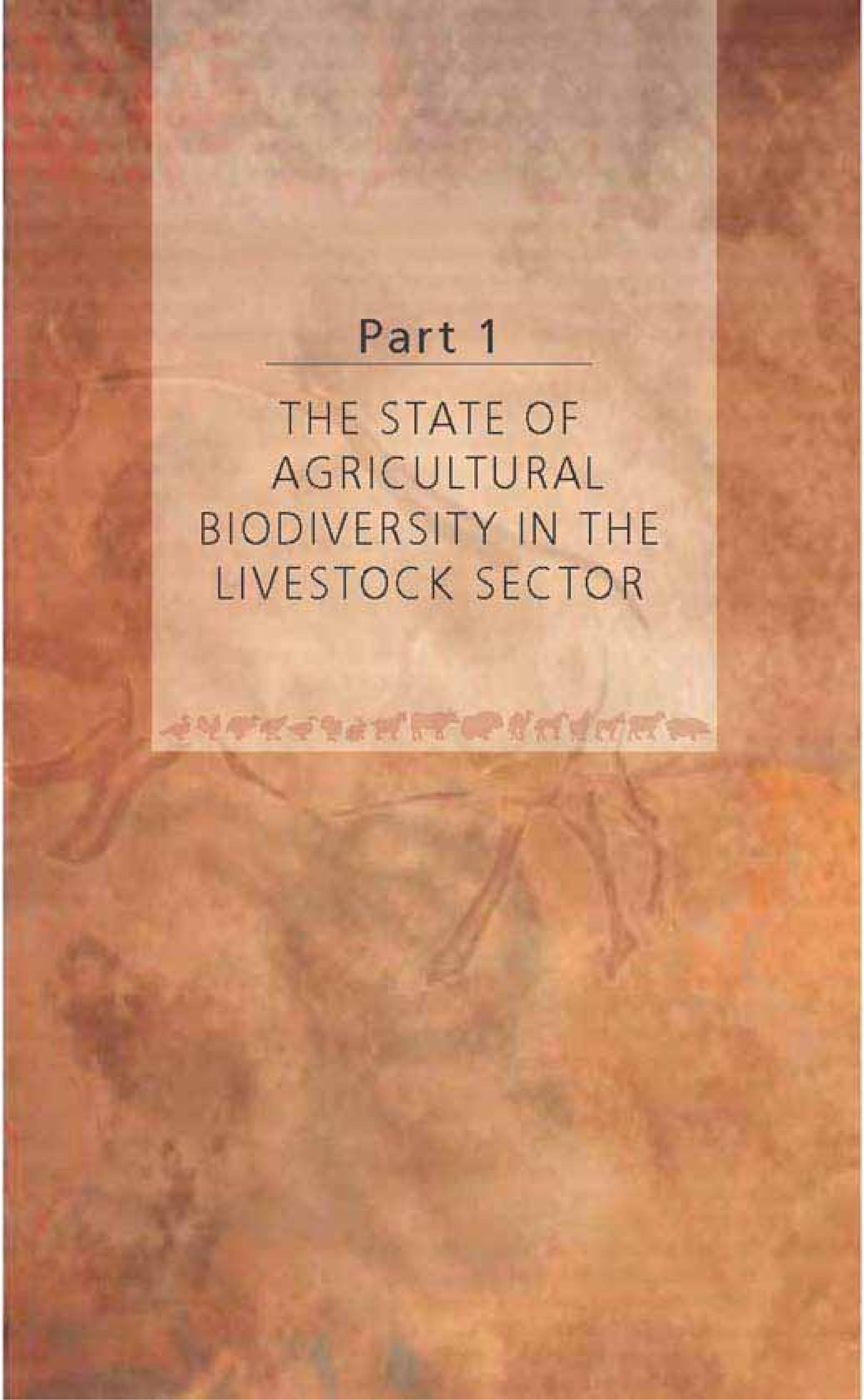

Part 1

THE STATE OF AGRICULTURAL BIODIVERSITY IN THE LIVESTOCK SECTOR

Introduction

The importance of the world's biodiversity – the variety of its plants, animals and micro-organisms, and of the ecosystems of which they form a part, is increasingly recognized. Agricultural biodiversity encompasses the diversity of the cultivated plants and domestic animals utilized by humankind for the production of food and other goods and services. More broadly, it includes the diversity of the agro-ecosystems on which this production depends. The capacity of agro-ecosystems to maintain and increase their productivity, and to adapt to changing circumstances, is vital to the food security of the world's population.

The 40-plus livestock species contributing to today's agriculture and food production are shaped by a long history of domestication and development. Selection pressures resulting from environmental stress factors, and the controlled breeding and husbandry imposed by humans, have combined to produce a great variety of genetically distinct breeds[1]. This diversity, developed over thousands of years, is a valuable resource for today's livestock keepers. Genetically diverse livestock populations provide a greater range of options for meeting future challenges, whether associated with environmental change, emerging disease threats, new knowledge of human nutritional requirements, fluctuating market conditions or changing societal needs.

Part 1 of the Report begins by describing 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 of AnGR diversity on a global scale, 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, and their direct and indirect contributions to livelihoods and economic output in the various regions of the world are then outlined. The importance of genetic resistance to disease as a resource in the field of animal health is also introduced. In the final section of Part 1, threats to the world's AnGR diversity are discussed.

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[1] Central to the description of livestock diversity is the notion of the breed (see Part 4 – Section A: 1 for a discussion of the definition of the term "breed")

Section A

Origin and history of livestock diversity

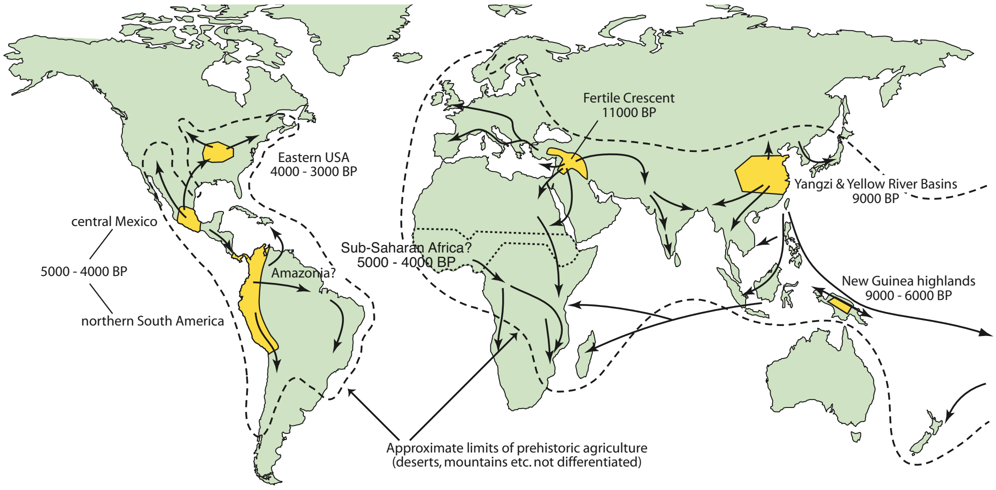
1 Introduction

The history of AnGR started around 12 000 to 14 000 years ago, during the agricultural revolution of the early Neolithic, with the domestication of major crop and livestock species. This control of food production led to major demographic, technological, political and military changes. The domestication of animals and plants is considered to be one of most important developments in history, and one of the prerequisites for the rise of human civilizations (Diamond, 2002). After the initial domestication events, the spread of farming into nearly all terrestrial habitats followed rapidly (Diamond and Bellwood, 2003; Figure 2). Subsequently, thousands of years of natural and human selection, genetic drift, inbreeding and cross-breeding have contributed to AnGR diversity and have allowed livestock keeping to be practised in a variety of environments and production systems.

AnGR diversity is vital to all production systems. It provides the raw material for breed improvement, and for adaptation to changing circumstances. As revealed by recent molecular studies, the diversity found in today's indigenous livestock populations and breeds greatly exceeds that found in their commercial counterparts. Unravelling the origin

FIGURE 2

Archaeological map of agricultural homelands and spread of Neolithic/Formative cultures, with approximate radiocarbon dates



Map drawn by Clive Hilliker and provided by Peter Bellwood.

and distribution of livestock diversity is central to its current utilization, and to its long-term conservation (Hanotte *et al.*, 2006).

2 The livestock domestication process

Very few animal species have been successfully domesticated. Domestication was a complex and gradual process, which altered the behaviour and morphological characteristics of the ancestral animals (Box 1). The circumstances and pressures that triggered the domestication of animals remain uncertain, and may have varied from one geographic area to another and from one species to another.

The roots of animal domestication are probably related to the ubiquitous tendency of hunter gatherers (presumably shared by early humans) to try to tame or manage wild animals (Diamond, 2002). It was, however, at the end of the Pleistocene that the process of domestication actually got underway. At this time, changes in the climate, which became more unpredictable, warmer and/or more seasonal in some areas, led to localized expansion of human populations. These developments triggered the uptake of crop farming, and affected the distribution and density of the wild species hunted for food. In these circumstances, the main driver of animal domestication may have been the desire to secure the availability of "favourite" foods – with the potential of some domesticated species to provide support to crop farming (e.g. ploughing with oxen or buffalo), or as pack and riding animals (e.g. llamas, dromedaries, Bactrian camels, horses, donkeys and even cattle) being realized later.

Among the world's 148 non-carnivorous species weighing more than 45 kg, only 15 have been domesticated. Thirteen of these species are from Europe and Asia, and two originate from South America. Moreover, only six have become widespread on all continents (cattle, sheep, goats, pigs, horses, and donkeys), while the remaining nine (dromedaries, Bactrian camels, llamas, alpacas, reindeer, water buffalo, yaks, Bali cattle, and mithun) are important in more limited areas of the globe (adapted from Diamond, 1999). The proportion is even lower in the case of birds, with only ten species (chickens, domestic ducks, Muscovy ducks, domestic geese, guinea fowl, ostriches, pigeons, quails, and turkeys) currently domesticated out of around 10 000 avian species (the list excludes the many birds domesticated for ornamental or recreational purposes).

With the exception of the wild boar (*Sus scrofa*) the ancestors and wild relatives of major livestock species are either extinct or highly endangered as a result of hunting, changes to their habitats, and in the case of the wild red jungle fowl, intensive cross-breeding with the domestic counterpart. In these species, domestic livestock are the only depositories of the now largely vanished diversity

Box 1
The domestication process

Domesticated animals are here considered to be those species that are bred in captivity, and modified from their wild ancestors to make them more useful to humans, who control their reproduction (breeding), care (shelter, protection against predators) and food supply (Diamond, 2002; Mignon-Grasteau, 2005). Domestication includes the following steps: initial association with free breeding; confinement; confinement with breeding in captivity; and selective breeding and breed improvement (modified from Zeuner, 1963). Archaeologists and animal geneticists use various means to unravel the history of domestication, including study of morphological changes to the teeth, cranium and skeleton; and the construction of demographic age and sex curves which allow the identification of patterns indicative of domestication (Zeder *et al.*, 2006).

TABLE 4
Origin and domestication of livestock species

Domestic species	Wild Ancestor	MtDNA clades	Domestication events*	Time B.P.	Location
Cattle	Aurochs (3 subspecies) (extinct)				
Bos taurus taurus	*B. primigenius primigenius*	4	1	~ 8000	Near & Middle East (west Asia)
	B. p. opisthonomous	2	1	~ 9500	northeast Africa
Bos taurus indicus	*B. p. nomadicus*	2	1	~ 7000	northern Indian subcontinent
Yak	Wild yak				
Poephagus grunniens	*P. mutus*	3	1	~ 4500	Qinghai-Tibetan Plateau
Goat	Bezoar				
Capra ferus	*Capra aegragus* (3 subspecies)	5	2	~ 10000	Near and Middle East, northern Indian subcontinent
Sheep	Asian mouflon				
Ovis aries	*Ovis orientalis*	4	2	~ 8500	Near and Middle East/Turkey (Central Anatolia)
Water buffalo	Asian wild buffalo				
Riverine *B. bubalus bubalus*		ND	1	~ 5000	Islamic Republic of Iran/Iraq, Indian subcontinent
Swamp *B. bubalus carabensis*		ND	1	~ 4000	Southeast Asia, China
Pig	Wild boar				
Sus scrofa domesticus	*Sus scrofa* (16 subspecies)	6	6	~ 9000	Europe, Near and Middle East, China
					Indian subcontinent, Southeast Asia
Horse	Extinct				
Equus caballus		17	multiple	~ 6500	Eurasian steppe
Donkey	African wild donkey				
Equus asinus	*Equus africanus*			~ 6000	northeast Africa
	Nubian wild ass *E. a. africanus*	1	1		
	Somali wild ass *E. a. somali*	1	1		
Llama					
Lama glama	2 subspecies	ND	1	~ 6500	Andes
	L. guanicoe guanicoe				
	L. guanicoe cacsiliensis				

TABLE 4 *cont.*

Origin and domestication of livestock species

Domestic species	**Wild Ancestor**	**MtDNA clades**	**Domestication events***	**Time B.P.**	**Location**
Alpaca					
Vicugna pacos	2 subspecies	ND	1	~ 6500	Andes
	V. vicugna vicugna				
	V. vicugna mensalis				
Bactrian Camel	Extinct**				
Camelus bactrianus *C. b. ferus*		ND	1	~ 4500	Central Asia (eastern Islamic Republic of Iran)
Dromedary	Extinct				
Camelus dromedarius		ND	1	~ 5000	southern Arabian Peninsula
Domestic chicken	Red Junglefowl				
Gallus domesticus	*Gallus gallus* (4 subspecies	5	2	~ 5000	Indian subcontinent
	G. g. spadiceus, G. g. jabouillei			~ 7500	China – Southeast Asia
	G. g. murghi, G. g. gallus)				

Source: adapted and updated from Bruford *et al.* (2003); FAO (2005).

*Minimum number of domestication events.**Recent genetic evidence suggests that the endangered wild population are not the ancestral maternal populations of today's domestic Bactrian (Jianlin *et al*., 1999).
ND = not determined.

of the wild ancestors (Table 4). This is a major difference from crop species, in many of which the wild ancestors are commonly found at the centres of origin and represent an important source of variation and adaptive traits for future breeding programmes.

The small number of animal species successfully domesticated is largely explained by the characteristics required (or advantageous) for domestication, which are rarely found together in a single species. All major livestock species were domesticated several thousand years ago. It is improbable that further large mammalian species will be domesticated, at least in the near future, as illustrated by the failure, or at best only partial success, of twentieth century attempts to domesticate new species (e.g. oryx, zebras, African buffaloes and various species of deer). However, the coming years may see further development of the captive breeding of small and "non-conventional" species (sometimes called microlivestock) for human consumption, which may become more important, at least locally or regionally (BOSTID, 1991; Hanotte and Mensah, 2002).

Important or essential characteristics for successful domestication include behavioural traits such as a lack of aggression towards humans; a strong gregarious instinct, including "follow the leader" dominance hierarchies which allow the possibility of a human substitute as leader; a tendency not to panic when disturbed;

the ability to breed in captivity; physiological traits such as a diet that can easily be supplied by humans (domestication of herbivores rather than carnivores); a rapid growth rate; relatively short intervals between births; and large litter size (Diamond, 2002).

The ancestral species of the majority of livestock species have now been identified (Table 4). It is also known that many current domestic animal populations and breeds originate from more than one wild ancestral population, and that in some cases there has been genetic admixture or introgression between species that do not normally hybridize in the wild. These admixture and hybridization events probably occurred after the initial domestication. They were often linked to human migration, trading or simply the result of the requirement of agricultural societies for new livestock phenotypes. Examples include admixture between taurine and Zebu cattle, the presence of cattle genetic background in yaks and Bali cattle, Asian pig hybridization with European breeds, cross-breeding between dromedaries and Bactrian camels, and (as revealed by recent genetic studies) intensive admixture between the two South American domestic camelids (llamas and alpacas) (Kadwell *et al.*, 2001).

Box 2
Molecular characterization – a tool to understand livestock origin and diversity

Recent major developments in molecular genetics have provided powerful new tools, called molecular markers, to assess the origins of livestock species and the geographic distribution of their diversity.

Protein polymorphisms were the first molecular markers used in livestock. A large number of studies, particularly during the 1970s, documented the characterization of blood group and allozyme systems. However, the level of polymorphism observed in proteins is often low, which reduces the general applicability of protein typing in diversity studies.

DNA-based polymorphisms are now the markers of choice for molecular-based surveys of genetic diversity. Importantly, polymorphic DNA markers showing different patterns of Mendelian inheritance can be studied in nearly all major livestock species. Typically, they include D-loop and cytochrome B mitochondrial DNA (mtDNA) sequences (maternal inheritance), Y chromosome-specific single nucleotide polymorphisms (SNPs) and microsatellites (paternal inheritance), and autosomal microsatellites (bi-parental inheritance). Autosomal microsatellites have been isolated in large numbers from most livestock species. FAO/ISAG (International Society of Animal Genetics) recommended lists of autosomal microsatellite markers for genetic diversity studies are publicly available (http://www.fao.org/dad-is).

Different genetic markers provide different levels of genetic diversity information. Autosomal microsatellite loci are commonly used for population diversity estimations, differentiation of populations, calculation of genetic distances, estimation of genetic relationships, and the estimation of population genetic admixture. MtDNA sequences are the markers of choice for domestication studies, as the segregation of an mtDNA lineage within a livestock population will only have occurred through the domestication of a wild female, or through the incorporation of a female into the domestic stock. More particularly, mtDNA sequences are used to identify putative wild progenitors, the number of maternal lineages and their geographic origins. Finally, the study of a diagnostic Y chromosome polymorphism is an easy and rapid way to detect and to quantify male-mediated admixture.

Reproduced and adapted from FAO (2005).

3 Ancestors and geographic origins of our livestock

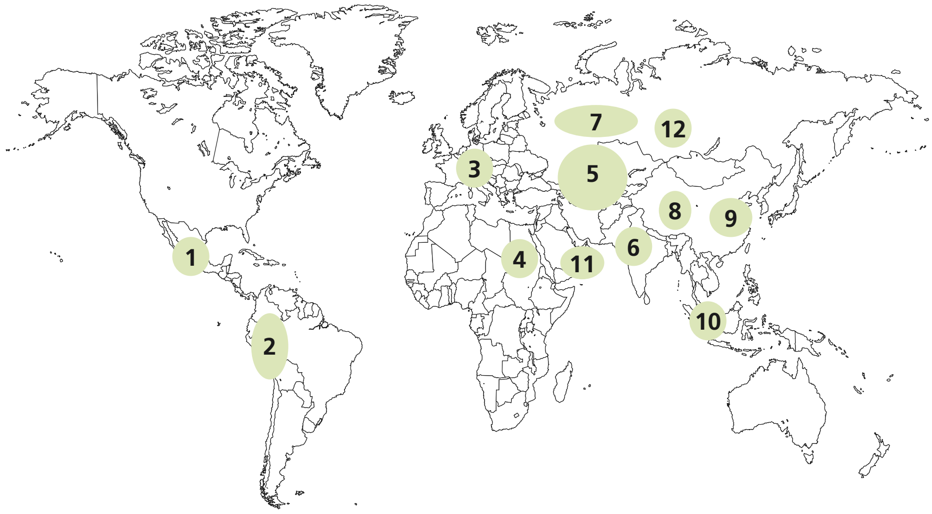
One of the most exciting areas of intersection between archaeology and genetics has been in documenting the locations of livestock domestication (Zeder *et al.*, 2006), with archaeology guiding genetic research, and genetics providing support to some controversial archaeological theories or revealing possible new geographic origins for livestock species and their diversity. More particularly, it is now known that nearly all major livestock species are the result of multiple domestication events in distinct geographic areas (Table 4 and Figure 3); and that subsequent to the initial domestication events, genetic introgression between wild relatives and their domestic counterparts often occurred.

It should be noted that apparently independent livestock domestication events were not necessarily culturally independent. Some independent domestication events may have represented the movement of a few domesticated individuals into a new area, with the genetic signatures of the introduced founders subsequently submerged by the recruitment of local wild animals (Zeder *et al.,* 2006). Alternatively, ancient signatures of local domestication events may now be hidden by more recent arrivals of livestock from other centres of origin. Osteometric information from archaeological sites, and ancient livestock DNA studies are important tools to address these questions.

Livestock domestication is now thought to have occurred in at least 12 areas of the world (Figure 3). Interestingly, not all centres of domestication are closely associated with the homelands of our crop species (see Figure 2). While in some cases (e.g. the Fertile Crescent), domestication centres of both crops and livestock are intermingled, in others (e.g. the African continent) crop and livestock domestication seem largely to have occurred independently. While uncertainties still surround the existence of some domestication centres for some species, the following geographic areas are important primary centres of origin, and therefore diversity, of livestock species: the Andean chain of South America (llamas, alpacas, guinea pigs); central America

FIGURE 3

Major centres of livestock domestication – based on archaeological and molecular genetic information



(1) turkey (2) guinea pig, llama, alpaca, (3) pig, rabbit (4) cattle, donkey, (5) cattle, pig, goat, sheep, Bactrian camel (6) cattle, goat , chicken, river buffalo, (7) horse, (8) yak, (9) pig, swamp buffalo, chicken, (10) chicken, pig, Bali cattle (11) dromedary, (12) reindeer.

(turkeys, Muscovy ducks); northeast Africa (cattle, donkeys); southwest Asia including the Fertile Crescent (cattle, sheep, goats, pigs); the Indus valley region (cattle, goats, chickens, riverine buffaloes); Southeast Asia (chickens, Bali cattle); east China (pigs, chicken, swamp buffaloes); the Himalayan plateau (yaks); and north Asia (reindeer). Additionally, the southern part of the Arabian Peninsula is thought to be the region of origin of the dromedary, the Bactrian camel may originate from the area that is now the Islamic Republic of Iran, and the horse from the Eurasian steppes.

While domestication occurred in several places, it also happened at different times. Exact dating of domestication events has, however, proved particularly challenging. Animals undergoing the initial process of domestication would not have been significantly different in morphology from their wild ancestors, and dates relying on morphological markers will undoubtedly underestimate the age of domestication events (Dobney and Larson, 2006). The process of molecular dating, while independent of morphological changes, is typically characterized by large error rates, and often relies on uncertain calibration points. Approaches including demographic profiling techniques for identifying initial attempts at livestock management by humans, and calibration of molecular clocks using ancient DNA information, are providing new avenues for pinpointing the dates of domestication (Zeder *et al.,* 2006).

New archaeological and genetic information is constantly improving our understanding of the origin of livestock species. The first animal to be domesticated was the dog. This probably occurred at least 14 000 years ago – the animals being used for hunting and as watchdogs. It is unclear where the initial domestication took place, but many maternal lineages have been found in modern dogs – indicating multiple introgressions from their wild ancestor the grey wolf (*Canis lupus*) in the Old World. Domestic dogs were, apparently, not independently domesticated in the New World; the mitochondrial lineages identified so far in the Americas are of European origin (Wayne *et al.,* 2006).

Goats were domesticated as early as 10 000 years ago in the Zagros Mountains of the Fertile Crescent (Zeder and Hesse, 2000). The bezoar (*Capra aegragus*) was probably one of the ancestors of the domestic goat, but it is possible that other species such as *C. falconeri*, contributed to the genetic pool of the domestic species. Today, five distinct maternal mitochondrial major lineages have been identified in domestic goats (Luikart *et al.,* 2001; Sultana *et al.*, 2003; Joshi *et al.*, 2004). One of these lineages predominates numerically, and is present worldwide, while a second seems to be of contemporary origin. They probably reflect the primary caprine domestication process in the Fertile Crescent, where archaeological information suggests two to three areas of domestication (Zagros Mountains, Taurus Mountains, Jordan Valley). The other lineages are more restricted in their geographic distribution, and may correspond to additional domestications or introgressions in other areas including the Indus Valley (Fernández *et al.,* 2006).

Sheep were also probably first domesticated in the Fertile Crescent, approximately 8 000 to 9 000 years ago. Archaeological information suggests two independent areas of sheep domestication in Turkey – the upper Euphrates valley in eastern Turkey, and central Anatolia (Peters *et al.*, 1999). Three species of wild sheep (the urial, *Ovis vignei*; the argali, *O. ammon*; and the Eurasian mouflon, *O. musinom/orientalis*) have been proposed as ancestors of domestic sheep (Ryder, 1984) or at least to have introgressed some local breeds. However, recent genetic work has indicated no contribution from the urial or argali (Hiendleder *et al.,* 1998). This supports the view that the Asian mouflon (*O. orientalis*), which is found in a wide region stretching from Turkey at least as far as the Islamic Republic of Iran, is the only progenitor of domestic sheep. The European mouflon (*O. musinom)* is now considered to be a descendant of feral sheep. Four major maternal mitochondrial DNA lineages have been recorded in domestic sheep (Hiendleder *et al.,* 1998; Pedrosa *et* *al.,* 2005; Tapio *et al.,* 2006), one or two of which could correspond to distinct domestication events, and the others to subsequent wild introgression. To date, no clear associations have been described between these mitochondrial DNA lineages and phenotypic sheep varieties (e.g. fat-tailed, thin-tailed or fat-rumped sheep).

The ancestor of the domestic pig is the wild boar (*Sus scrofa*). Extensive zooarchaeological findings indicate that pigs were domesticated around 9 000 years ago in the Near East. Material from several sites in eastern Anatolia indicates gradual changes in pig morphology and demographic profiles over several thousand years, providing evidence of the domestication process and its morphological consequences. Both archaeological and genetic evidence indicate a second major independent domestication centre in East Asia (China) (Guiffra *et al.,* 2000). At least 16 distinct subspecies of wild boar have been described in Eurasia and North Africa and, perhaps not surprisingly, a recent survey of mitochondrial DNA diversity among Eurasian domestic pigs and wild boar revealed a complex picture of pig domestication, with at least five or six distinct centres across the geographic range of the wild species (Larson *et al.,* 2005).

Domestication of cattle has been particularly well documented, with clear evidence of three distinct initial domestication events for three distinct aurochs (*Bos primigenius*) subspecies. *B. primigenius primigenius,* domesticated in the Fertile Crescent around 8 000 years ago, and *B. p. opisthonomous,* possibly domesticated as early as 9 000 years ago in the northeastern part of the African continent (Wendorf and Schild, 1994), are the ancestors of the humpless *B. taurus* cattle of the Near East and Africa respectively. Humped Zebu cattle (*Bos indicus*), are now believed to have been domesticated at a later date, around 7 000 to 8 000 years ago, in the Indus Valley region of modern-day Pakistan (Loftus *et al.,* 1994; Bradley *et al.,* 1996; Bradley and Magee, 2006). Recently, a fourth domestication centre has been suggested in East Asia (Mannen *et al.,* 2004), but it is unclear whether it occurred independently or represents local aurochs introgression in cattle of Near Eastern origin.

The ancestor of the domestic water buffalo (*Bubalus bubalus*) is undoubtedly the wild buffalo of Asia. Two main types are recognized, based on their phenotypes, karyotypes and recent mitochondrial DNA work (Tanaka *et al.,* 1996): the riverine buffalo, found in the Indian subcontinent, the Near and Middle East, and eastern Europe; and the swamp buffalo, found in China and Southeast Asian countries. The two types hybridize in the northeastern part of the Indian subcontinent. They were probably domesticated separately, with possible centres of domestication of the riverine buffalo in the Indus Valley and/or the Euphrates and Tigris valleys some 5 000 years ago; and of the swamp buffalo in China, where it was domesticated at least 4 000 years ago in association with the emergence of rice cultivation.

There is an ongoing debate as to when and where the horse (*Equus caballus*) was domesticated. The ancestor of the domestic horse is extinct. Two species have been regarded as putative wild ancestors – the tarpan (*E. ferus*) and the Przewalski horse (*E. przewalskii*). The Przewalski horse, although very closely related to the wild ancestor, is probably not the direct progenitor of the domestic species (Olsen *et al.,* 2006; Vilà *et al.,* 2006). It is difficult to assess whether archaeological horse remains are wild or domestic. Substantial evidence from north Kazakhstan (Botai culture) supports the view that horses were domesticated in this area during the Copper Age around 3700 to 3100 BC (Olsen, 2006). Recent molecular studies indicate that the diversity of the horse on the maternal side probably originates from several populations in different geographic areas. However, the data are not yet conclusive as to whether there was a single domestication event and subsequent introgression, or multiple independent domestication events (Vilà *et al.,* 2001; Jansen *et al.*, 2002).

In contrast, the domestication of the donkey *Equus asinus* seems to have followed a much simpler process. Mitochondrial DNA studies have confirmed an African origin for the domestic donkey, and have ruled out the Asiatic wild ass as a possible progenitor (Beja-Pereira *et al.,* 2004). Two mitochondrial lineages suggest two domestication events. One lineage is closely linked to the Nubian wild ass (*E. asinus africanus*), which is still found today living wild in northeastern Sudan close to the Red Sea. The other lineage shows some affinities to the Somali wild ass (*E. asinus somaliensis*). It could, therefore, also have an African origin, although domestication in a neighbouring area (Arabian Peninsula or Fertile Crescent) cannot be excluded. Archaeological evidence from Egypt supports an African centre of domestication for the donkey, and suggests a domestication date of around 6 000 to 6 500 years ago (Clutton-Brock, 1999).

The domestic yak (*Poephagus grunniens*) is endemic to Central Asia and well adapted to a cold and high-altitude environment. Yak pastoralism is widespread in the Central Asian Highlands, and the introduction of yak pastoralism was crucial to the development of year-round sustainable occupation of the higher altitude zones of the Himalaya Plateau. It may have been connected with the establishment of Tibetan–Burman populations in this region. Today, some wild yaks (*P. mutus*) are still found on the Qinghai-Tibetan Plateau, but they may have been heavily introgressed with feral domestic yak. Three mitochondrial DNA lineages have been identified. However, similar geographic distributions of mitochondrial DNA diversity suggest a single domestication event in the eastern part of the Qinghai-Tibetan Plateau rather than multiple domestication events (Qi, 2004; Guo *et al.,* 2006). Molecular findings also indicate that the dispersal of domestic yaks followed two separate migratory routes from their centre of domestication: the yak reached the “Pamir Knot” by following a westward route through the Himalaya and Kunlun Mountains; and reached Mongolia, and what is now the Russian Federation, by following a northward route through the Mongolian South Gobi and Gobi Altai Mountains (Qi *et al.,* in press).

As in the case of the yak, the domestication of the reindeer (*Rangifer tarandus*) has allowed pastoral communities to occupy habitats that would otherwise be largely unsuitable for livestock keeping. Very little is known about reindeer domestication. The wild reindeer was possibly the latest large mammalian species to be domesticated. The oldest definitive archaeological evidence of reindeer domestication was discovered in the Altai Mountains of Siberia, and has been dated to about 2 500 years ago; it indicates that reindeer riding was practised at the time (Skjenneberg, 1984). There is no reliable information as to how reindeer domestication reached Europe; it could have developed independently in Scandinavia, or may have been adopted by the Saami people through contact with other north Eurasian pastoral communities. Reindeer husbandry is believed to have developed among the Saami sometime after 1600 AD. The wild reindeer is known as the caribou in North America; it is believed never to have been domesticated on this continent (Clutton-Brock, 1999).

The domestication of the Bactrian camel (*Camelus bactrianus*) may have occurred in the area that is now the Islamic Republic of Iran/Turkmenistan, or further east, in southern Kazakhstan, northwestern Mongolia or northern China (Bulliet, 1975; Peters and von den Driesch, 1997). The earliest evidence of domestic Bactrian camels is from the site of Sahr-i Sokta in the central part of the Islamic Republic of Iran, from where camel bones, dung, and woven fibres dating from approximately 2600 BC have been recovered (Compagnoni and Tosi, 1978).

Recent genetic work indicates that the wild camel (*C. ferus*) populations of the Gobi Desert, which successfully hybridize with the domestic species, are probably not the direct maternal ancestors of domestic or feral camels (Jianlin, *et al*., 1999). The wild ancestor of the one-humped dromedary (*C. dromedarius*) is now extinct. Domestication of the species is believed to have started around 5 000 years ago in the southeastern part of the Arabian Peninsula.

The origin of the South American camelidae has now been unravelled, with the guanaco (*Lama guanicoe*) and the vicuña (*Vicugna vicugna*) being the ancestral species of the domestic llama (*Lama glama*) and alpaca (*Vicugna pacos*), respectively (Kadwell *et al.,* 2001). Archaeozoological evidence points to the central Peruvian Andes as the centre of origin of the alpaca, 6 000 to 7 000 years before present. The llama was probably domesticated at the same period in the Andes around Lake Titicaca. Large-scale introgressions between the two domestic species have been revealed (Wheeler *et al.,* 2006) – an ongoing hybridization process which probably began with the Spanish conquest, which destroyed the traditional breeding structures and management of the two species.

The ancestor of Bali cattle is the banteng (*Bos javanicus*), of which three endangered subspecies have been recognized. The domestication of the species did not, in fact, occur on the Island of Bali, where there is no evidence for the presence of the wild ancestor. The species could have been domesticated in Java and/or on the Indo–Chinese Peninsula. *B. taurus* and *B. indicus* introgression has been found in Bali cattle, and Bali cattle genetic background has also been inferred in several Southeast Asian cattle breeds, suggesting that the domestic species once had a wider distribution than it has today (Felius, 1995).

The ancestor of the mithun (*B. frontalis*) is the gaur (*B. gaurus*). As in the case of Bali cattle, the centre of domestication of the species in unknown. Archaeological excavation in northeastern Thailand (Non Nok Tha) suggests that both species might have been domesticated as early as 7 000 years ago (Higham (1975) in Felius, 1995).

The domestic chicken (*Gallus domesticus*) is descended from the wild red jungle fowl (*Gallus gallus*), with five possible progenitor subspecies. While previous molecular studies suggested a single domestic origin in Southeast Asia (Thailand) (Fumihito *et al.,* 1994; 1996), at least six distinct maternal genetic lineages have now been identified (Liu *et al.,* 2006), suggesting more than one domestication centre. Archaeological information indicates a centre of chicken domestication around the Indus Valley 5 000 years ago, and another in eastern China maybe as early as 7 500 to 8 000 years ago (West and Zhou, 1988).

4 Dispersal of domesticated animals

If the domestication process was the major initiating event in the development of today's livestock diversity, the subsequent dispersion and migration of domesticated species across all five continents was equally important. This process played a major role in the emergence of the current geographic distribution of livestock diversity. The main factors at the root of the early dispersion of livestock species were the expansion of agriculture, trade and military conquests.

The exact mechanisms through which agricultural expansion occurred are still debated. The process probably varied from one region to another (Diamond and Bellwood, 2003). It certainly involved both the movement of human populations, and cultural exchanges between populations – as illustrated by the adoption of farming by many hunter–gatherer societies. Important examples of agricultural expansions include that of the Neolithic, which brought cattle, sheep and goats into Europe, and may have triggered the local domestication of the wild boar. Domesticated livestock followed two distinct major routes into Europe – the Danubian and the Mediterranean (Bogucki, 1996; Cymbron *et al.*, 2005).

The Bantu expansion which started around 2000 BC was a major event in African history, and was probably responsible for the adoption of pastoralism (cattle, sheep and goats) by the Khoisan peoples of the Southern Africa region about 2 000 years ago (Hanotte *et al.*, 2002) (Box 3). The origins of the indigenous pigs and chickens of the African continent remain largely undocumented.

European colonization of the Americas led to the arrival of cattle, sheep, goats, pigs, horses and chickens in the New World. In the case of cattle there is genetic evidence for some African ancestry (Liron *et al.*, 2006), which maybe a legacy of the slave trade between the two continents.

Box 3
The history of African pastoralism

Until recently, the history of African pastoralism was controversial and poorly understood. However, genetic marker analysis of indigenous cattle populations from all over the continent have now unravelled the major events in the history of pastoralism in Africa (Figure 4). The earliest African cattle originated within the continent, possibly as early as around 8000 BC. The exact centre(s) of domestication remain(s) unknown, but archaeological information suggests that it might have taken place in the northeastern part of the continent (Wendorf and Schild, 1994). These first African cattle were humpless *Bos taurus* animals. They initially dispersed north, as well as south to the borders of the tropical rainforests. Today, the only remaining descendants of these indigenous African taurine cattle are the trypanotolerant West African breeds (e.g. N'Dama and Baoulé), the Kuri, and the Sheko breed from Ethiopia. All these populations are now being intensively cross-bred with Zebu cattle (*Bos indicus*), and their unique genetic make-up is disappearing through unbalanced genetic admixture.

Zebu cattle arrived in Africa much later. The earliest evidence for the presence of humped cattle is provided by Egyptian tomb paintings dating from the Twelfth Dynasty of the second millennium BC. It is probable that these animals were brought to Egypt in limited numbers as war treasure and, therefore are not connected to the later presence of Zebu cattle in Africa. It is, however, thought that the Zebu was present in small numbers in the eastern part of the continent perhaps as early as 2 000 years ago as a result of early Arab contact or long-distance sea trade, and that this initial arrival resulted in the first introgression of Zebu genes into African taurine cattle. The major wave of Zebu arrival probably started with the Arab settlements along the East Coast of Africa from about the seventh century AD. The major inland dispersal of Zebu cattle probably followed the movement of pastoralists (e.g. Fulani throughout the Sahel), and was certainly accelerated by the rinderpest epidemics of the late nineteenth century.

Southern Africa was the last area of the continent to acquire cattle pastoralism. Genetic data are now excluding a movement of cattle from the western part of the continent. It appears that herding spread southward from the Great Lakes region, which 2 000 years ago was the site of an Eastern Bantu core area. These farmers ultimately came into contact with San hunter–gatherers who acquired livestock from them. Influences from the Near East centre of cattle domestication are today found in the northeastern, northwestern and southern parts of the continent. The latter is probably a result of the settlement of European farmers in this part of the continent.

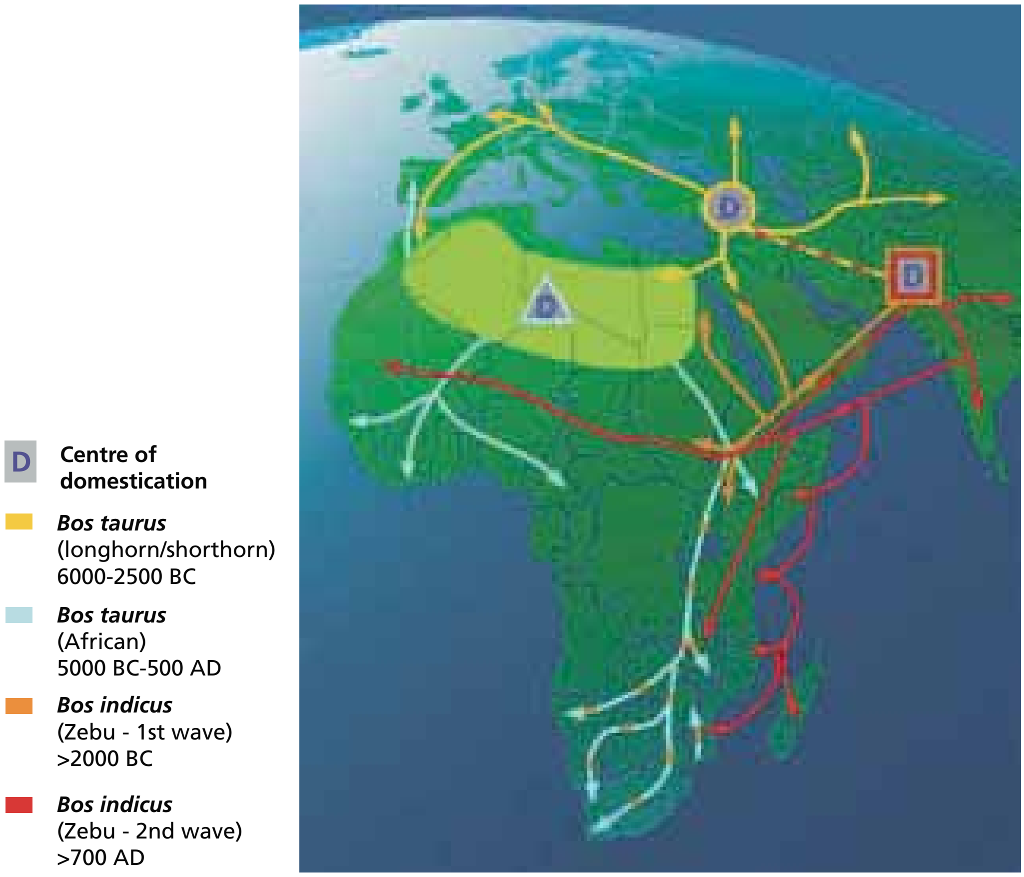
Adapted from Hanotte *et al.* (2002).

In Asia, the arrival of domestic livestock in the Japanese archipelago probably followed the establishment of farmers of Korean origin around 400 BC, but ancient influences from other geographic areas are also likely. In the Pacific, pigs and chickens had spread across western Polynesia by 900 to 700 BC, and the later Polynesian expansion carried these species as far as Rapa Nui (Easter Island) by 900 AD.

Beside human migrations, ancient overland trading networks played an important role in the dispersion of livestock species. The domestication of livestock enabled large-scale overland trading between civilizations, and livestock were themselves often a traded product. The main livestock species used as pack animals in the Old World were the donkey, horse, dromedary and Bactrian camel, and in South America, the llama. It is believed that domestication of the horse led to military expansion of horse-riding nomadic pastoralists in the Eurasian steppe, and subsequent dispersion of the species across the Old World. Bactrian camels were also used in warfare to a limited extent (Clutton-Brock, 1999), and the dromedary played an important role in the expansion of Arab civilization.

FIGURE 4

Origin and migration routes of domestic cattle in Africa



Source: Graphics unit, ILRI (2006).

There is increasing evidence of the importance of ancient sea trading routes in the dispersion of livestock. For example, recent molecular genetic studies in cattle have revealed that Zebu animals were introduced into Africa via an Indian Ocean corridor rather than overland through the Isthmus of Suez or the Sinai Peninsula (Hanotte *et al.*, 2002; Freeman *et al.*, 2006). Similarly, both archaeological and genetic information suggest that the spread of pastoralism in the Mediterranean basin followed not only terrestrial costal routes, but also maritime routes (Zilhão, 2001; Beja-Pereira *et al.*, 2006).

A loss of diversity is to be expected following the dispersion and movement of livestock populations from their centres of origin. However, molecular markers have revealed a more complex picture, with some movements resulting in an increase in diversity following admixture between populations originating from different centres of domestication. Additionally, detailed molecular studies indicate not only that cross-breeding between livestock populations was common, but also that genetic introgression from wild populations occurred after the initial domestication events. When they occurred outside the species' geographic area of origin and after its initial dispersion, these wild introgressions may have resulted in localized livestock genetic populations with unique genetic backgrounds. Examples include local aurochs introgression in European (Götherström *et* *al.*, 2005; Beja-Pereira *et al.*, 2006) and possibly also in Asian cattle (Mannen *et al.*, 2004).

Unravelling the geographic pattern and history of the dispersal of livestock is essential to the identification of geographic areas with high levels of diversity, which are potential priority areas for conservation efforts. This requires extensive mapping of genetic diversity. Up to now, very few studies have been undertaken in this field. However, a recent study of cattle, covering Europe, Africa and West Asia, indicates that the highest degree of diversity is found in areas that are at the crossroads of admixture between populations from different centres of domestication (Freeman *et al.*, 2006). An extensive survey of goat diversity in Europe and the Near and Middle East clearly indicates a geographical partitioning of goat diversity, with a large proportion of the genetic diversity among breeds explained by their geographic origins (Cañón *et al.*, 2006).

Today, local and regional, as well as transcontinental movement of livestock genotypes is accelerating as a result of the development and marketing of high-yielding breeds, new breeding technologies, and the increasing demand for livestock products. This modern dispersion, essentially restricted to a few breeds, and almost exclusively involving transfers from developed to developing countries, represents a major threat to the conservation and utilization of indigenous AnGR (see Section C for a further discussion of current gene flows).

5 Transformations in livestock following domestication

Mutation, selective breeding, and adaptation have shaped the diversity of livestock populations. The domestication process resulted in many changes some of which may still be ongoing. Particularly important have been morphological changes. Domestic animals are generally smaller than their wild ancestral counterparts (the notable exception being the chicken). Smaller animals are easier to manage and to handle, they may reach puberty sooner, and large flocks or herds can be kept more easily (Hall, 2004). The small West African cattle, sheep and dwarf goats are extreme examples of size reduction, possibly the result of genetic bottlenecks following adaptation to the tropical humid environment and its parasitic disease challenges. In some cases, human selection has deliberately resulted in extreme size differences – illustrated by the small size of the Shetland pony and the large size of the Shire horse (Clutton-Brock, 1999).

The body conformation of domestic animals may also be distinct from that of the wild ancestors – adapting, for example, to satisfy demand for meat products (e.g. European beef breeds), or to cope with new environmental pressures (e.g. Sahelian goats). Selection for muscular mass has often resulted in greater muscular development of the hind quarters relative to the shoulders (Hall, 2004). An extreme example of selection for muscular mass is the double-muscling trait observed in some European beef breeds, and in some sheep and pigs breeds. In cattle, the trait results from mutation at a single gene – the myostatin gene (Grobet *et al.*, 1998). In sheep, it involves the callipyge gene (Cockett *et al.*, 2005).

The pattern of fat deposition may also show changes following domestication. For example, reduced predation has encouraged fat deposition in domestic poultry. In domesticated mammals, the hump of the Zebu and the tails of fat-tailed and fat-rumped sheep are striking examples of selection for fat deposition. This exaggerated fat deposition may be quite ancient, with fat-tailed sheep already common in western Asia by 3000 BC, and humped cattle depicted on cylinder seals from the ancient civilizations of Mohenjo-Daro and Harappa in the Indus Valley about 2500 to 1500 BC (Clutton-Brock 1999).

Great variation is found in the wool and hair coats of most domestic species. For example, sheep breeds of alpine regions have particularly thick woolly coats, while breeds from the African Sahel lack wool. It is probable that these changes were the result of mutations followed by artificial selection, perhaps as early as 6000 BC, as illustrated by a statuette of a woolly sheep found in the Islamic Republic of Iran (Clutton-Brock, 1999).

Coat and plumage coloration were also selected by the environment, with light coloured animals being more adapted to hotter environments and dark coloured animals to cooler environments (Hall 2004). Coat colours have also been influenced by cultural selection. Livestock breeders in the developed world often favour uniformity in coat colour, but in the tropics, diversity in coat colour may be preferred for ceremonial reasons, or simply to facilitate the identification of individual animals. An illustration of the latter is the great diversity in coat colours and patterns observed among the Nguni cattle of the Zulu people (Poland *et al.*, 2003).

It is important to realize that local adaptation, human and/or natural selection will not always result in reduced genetic variation or functional diversity in the livestock population. For example, natural selection may favour adaptive diversity within herds kept in changing environments (e.g. as a result of climatic variation). A recent study of the genetic diversity of the six most important milk proteins in cattle revealed higher diversity in a relatively restricted geographic area of northern Europe, with selection pressure imposed by early (milk drinking) pastoralists being the most likely explanation (Beja-Pereira *et al*, 2003).

6 Conclusions

Understanding of the origin and subsequent history and evolution of AnGR diversity is essential to the design of sustainable conservation and utilization strategies. Livestock diversity originates from the wild ancestors, and was subsequently shaped through the processes of mutation, genetic drift, and natural and human selection. Only a subset of the diversity present in the ancestral species survived in the domestic counterparts. However, domestic livestock diversity has been continuously evolving. Reshuffling of genes at each generation, mutation, and cross-breeding or admixture of different gene pools has offered new opportunities for natural and human selection. This has been the basis of the enormous gains in output achieved in commercial breeds, and of the adaptation of indigenous livestock to highly diverse and challenging environments.

However, the world's livestock diversity is currently shrinking – with rapid and uncontrolled loss of unique and often uncharacterized AnGR. If a breed or population becomes extinct, this means the loss of its unique adaptive attributes, which are often under the control of many interacting genes, and are the results of complex interactions between the genotype and the environment.

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