DNA MARKERS REVEAL THE COMPLEXITY OF LIVESTOCK DOMESTICATION

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A series of recent genetic studies has revealed the remarkably complex picture of domestication in both New World and Old World livestock. By comparing mitochondrial and nuclear DNA sequences of modern breeds with their potential wild and domestic ancestors, we have gained new insights into the timing and location of domestication events that produced the farm animals of today. The real surprise has been the high number of domestication events and the diverse locations in which they took place — factors which could radically change our approach to conserving livestock biodiversity resources in the future.

DOMESTICATION
The process of genetically adapting an animal or plant to better suit the needs of human beings (for example, breeding cattle for milk production).

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Detailing the evolutionary and demographic history of humans, and of the animals and plants that we have DOMESTICATED, has traditionally been the realm of evolutionary ANTHROPOLOGISTS and ARCHAEOBIOLOGISTS. Recently, however, the use of molecular genetics has begun to have a major impact on our understanding of how these events took place. Specifically, recent studies have allowed the identification of the wild ancestors of modern livestock and the nature of livestock expansion in past millennia[1,2]. Information of this type is interesting as it tells us a great deal about ourselves, especially our history and the way in which we have shaped such extraordinary biological diversity in a relatively short period of time. Furthermore, combining evolutionary studies of humans[3], domestic animals[4,5] and crops[1] can give us a unique perspective on human societies throughout the world.

These data potentially have more immediate importance for the management and conservation of today's animal and plant genetic resources. The loss of agricultural diversity in the face of increasing pressures from modern farming is a cause for global concern. First, much of the diversity that is being lost is unknown, including large numbers of whole livestock breeds, and second, diversity that is undocumented at present (for example, that which can be found in locally adapted populations) might contain genetic material of value for

future production. The seriousness of the situation has prompted the Food and Agriculture Organization of the United Nations to initiate an exercise to globally document the state of the World's ANIMAL GENETIC RESOURCES (AnGR) — a process that will complement the same exercise for plants, which was completed 10 years ago[6]. Such an exercise needs to draw on as much relevant data as possible, including the molecular diversity of the World's AnGR, which has been identified as important. Data from molecular studies of livestock domestication can therefore be used to assist in the conservation of the bewildering diversity of livestock AnGR.

In this review, we show how genetic studies can enhance our understanding of domestication, by allowing the identification of wild ancestors and the location and timing of domestication events. In addition, we discuss how the genetic diversity of modern livestock can be assessed on different geographic scales, and how patterns of diversity vary among species. We focus on the large meat- and milk-producing and pack mammals: cattle, horses, sheep, pigs, goats, buffalo and CAMELIDS. Groundbreaking work has also been carried out on domestic carnivores[4], fowl[5] and fish[7], and has shed light on different modes of animal domestication that are beyond the scope of this review. However, it is interesting to note that domestic dog[4], chicken and common carp[7] studies implicate an east Asian centre of domestication,

which is a pattern that is repeated in several of the livestock studies described here.

Domestication and genetic structure

Hypotheses about where and when livestock domestication took place have been generated from numerous ARCHAEOZOOLOGICAL studies (see below). Most livestock domestication events are thought to have occurred at around the same time in southwest Asia, east Asia and the Americas, 8,000–10,000 years before present (YBP), and it is possible that this conjunction was not by chance.

At that time, the climate, which from 18,000 YBP had started to become warmer and more seasonal, favoured plants with large roots and tubers and large seeded annual plants. Such species are easy to harvest, cultivate and store and so are well suited to farming. These species probably became increasingly important food resources during seasons in which food was unavailable. With the climatic reversal of the Younger Dryas cold period (12,200–11,100 YBP), the demand for cultivated and storable food increased and led to the domestication of species such as rice, wheat and legumes[1,8]. As the climate warmed, some human populations started expanding rapidly and population centres became established in regionally important sites. Settlements tended to be located in naturally fertile areas that were suitable for agriculture, or in locations that linked different landmasses, and so were natural stopping-off points for migrating peoples[1]. The indigenous population, together with migratory populations, needed to be supplied with food[9], and this would have provided another stimulus for farming and the domestication of agricultural species. Whether the same pressures led to the establishment of agriculture in different foci is still a matter of debate[10–12].

The three principal areas of livestock domestication are generally accepted as southwest Asia (the FERTILE CRESCENT and its eastern margin, towards the Indus valley

region[1]) and east Asia (China and countries south of China) and the Andean chain of South America (FIG. 1). Cattle, sheep, goats, pigs and buffalo were domesticated in two Asian regions, whereas llamas and alpacas were domesticated in South America. The horse is a notable exception. It is thought to have been domesticated on numerous independent occasions in more northerly latitudes[13,14]. In addition, the horse is apparently the most recently domesticated major livestock species (~6,000 YBP)[14].

The transition of humans from hunting, to the taming of wild animals by animal husbandry, to eventual domestication is an extremely active area of research for archaeozoologists. There is considerable debate concerning the ability of present archaeozoological studies to detect the occurrence and timing of these transitions, as well as to identify changes in the age and sex structure of domesticated populations[15–18]. This leaves open the question of which populations, subspecies or even species of wild ancestors were domesticated and to what degree they have contributed to the gene pool of modern-day domestic livestock. Molecular studies allow these questions to be answered. DNA-based markers, which can be applied to phylogenetics, population diversity and the genetic identification of individuals, have been developing since the 1970s[19,20] but have only been actively applied to studies of animal domestication and diversity since the early 1990s[21,22].

Choosing molecular markers

To help understand the origins of domestication of a livestock species, an ideal molecular marker should have several characteristics. First, it should be sufficiently evolutionarily conserved to allow the identification of the wild taxon or population from which the species descends. Second, the marker should be variable and structured enough across the geographical range of the species so that the approximate locality of domestication can be identified. Third, the marker should evolve at a rapid but constant rate — this feature allows the origin of a particular polymorphism to be dated. This combination of characteristics is difficult to find, but fortunately, in animal evolutionary studies, there is such a marker: mitochondrial (mt) DNA. At present, mtDNA is by far the most widely used molecular tool in domestication studies.

mtDNA is a small plasmid — less than 20 kb in most mammals — that is located only in the mitochondrial organelle. It is highly variable within species, such that in humans for just one highly variable section of mtDNA — the control region — over 500 distinct HAPLOTYPES have been identified[23]. A recent study of the control-region diversity in domestic goats (*Capra hircus*) identified 331 haplotypes from 406 individuals[24]. mtDNA and particularly the control-region sequence (BOX 1) evolves extremely rapidly compared with nuclear DNA, and is consequently a powerful tool for establishing the levels of genetic diversity and phylogenetic structure within a species. mtDNA can also tell us about the recent demographic processes affecting a population, for example whether a population has undergone a
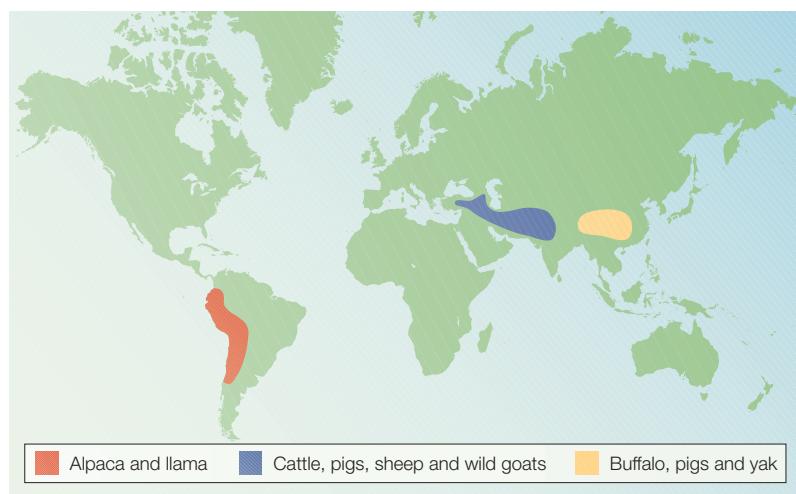
Figure 1 | **The principal centres of animal domestication.** The putative global sites where ancestral populations of modern livestock were domesticated — the northern Andean chain, southwest Asia (including the Indus valley) and east Asia, respectively. It should be noted that the map does not include horses, which were apparently domesticated many times in more northerly latitudes.

Legend:
- Alpaca and llama
- Cattle, pigs, sheep and wild goats
- Buffalo, pigs and yak

recent demographic expansion, or has a more complex history (BOX 1). Mammalian mtDNA is also almost exclusively maternally inherited, is effectively haploid and does not undergo recombination. These characteristics mean that each individual has a single haplotype and that phylogenetic analyses are relatively straightforward to interpret. Indeed, because of these features mtDNA has been the predominant molecule used to determine vertebrate phylogeny for the past 20 years[25].

Although mtDNA analysis can be extremely informative in domestication studies (both within and among species), its uses are limited. It can be a poor predictor of overall genomic diversity, because it behaves like a single locus and is an extra-nuclear genetic marker with specific evolutionary dynamics. Crucially, as it is maternally inherited, mtDNA does not detect male-mediated gene flow, which has had a powerful influence on the evolution of livestock species in modern times[26]. It is useful to consider how mtDNA diversity is 'captured' during domestication, as the segregation of an mtDNA lineage within a livestock population can only have occurred through the domestication of a wild female or through the incorporation of a female into an existing domestic stock[2].

Alternative genetic markers include variable sequences on the Y chromosome. However, this chromosome is much less variable within species than most other genomic sequences, which makes difficult its routine use for phylogenetic analyses. Analysis of the Y chromosome also lacks the power of multiple-band profile

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Box 1 | Mitochondrial DNA in livestock studies

Mitochondrial (mt) DNA is routinely used to produce phylogenetic trees at several taxonomic levels, from within species to among orders of mammals. In livestock it has been used to describe variation in putative wild ancestor populations and modern domestic populations.

Both the cytochrome *b* gene and the control region — a highly variable section of mtDNA — are used because these fast evolving loci are best suited to examining variation at the species level or below.


Cytochrome *b*
This gene has proven to be especially important in livestock studies[24,31] because its tempo and mode of evolution is well understood and is thought to be relatively constant and similar among large-bodied terrestrial mammals[64]. For example, in sheep (*Ovis aries*) and goats (*Capra hircus*), cytochrome *b* evolves at a rate between 3.8 and 5.4% per million years, depending on the interpretation of the fossil record[24]. Consequently, cytochrome *b*, rather than the control region, is often used in conjunction with the fossil record to 'calibrate' a MOLECULAR CLOCK among mitochondrial DNA lineages in livestock.

Control region
The control region shows extraordinary levels of variation within species, which means that it can be used to track geographic patterns of diversity and evolution ('phylogeography'[65]), dispersal, gene flow, demographic expansion, genetic drift and hybridization. The use of standard phylogenetic trees to describe the most likely evolutionary relationship among haplotypes has drawbacks within species and especially in livestock – primarily owing to parallel mutations and reticulation (lineage exchange between divergent populations). So, phylogenetic trees have been augmented by 'networks'. In a network, the haplotype sequence is represented as a node and the genetic distance among nearest-neighbour haplotypes scales the length of the branch connecting them[66,67]. One advantage of this approach is the ability to graphically illustrate alternative, equally probable connections among haplotypes on the same network (for example, see FIG. 2b).

Most importantly it is the high rate of evolutionary change and the ability to detect differentiation between domestic lineages that makes the control region the method of choice for livestock studies. The recent use of 'mismatch distributions' can test different models of demographic expansion that are expected to accompany domestication by man. This is done by examining the distribution of pairwise differences between haplotypes within a population[68]. A recent analysis of mismatch distributions in domestic goats provides a good example (see figure). The pattern best fitting a recent marked demographic expansion is the one seen in the figure, in which most haplotypes are separated by only a few substitutions because there has not been enough evolutionary time for a large number to accumulate compared with the rate of population increase. In addition, a temporal element can be added to the analysis and *C. hircus* haplogroup A is predicted to have started expanding first (it has the most pairwise mismatches), followed by haplogroup C and then haplogroup B[24]. The figure is reproduced with permission from REF. 24 © National Academy of Sciences, USA (2001).
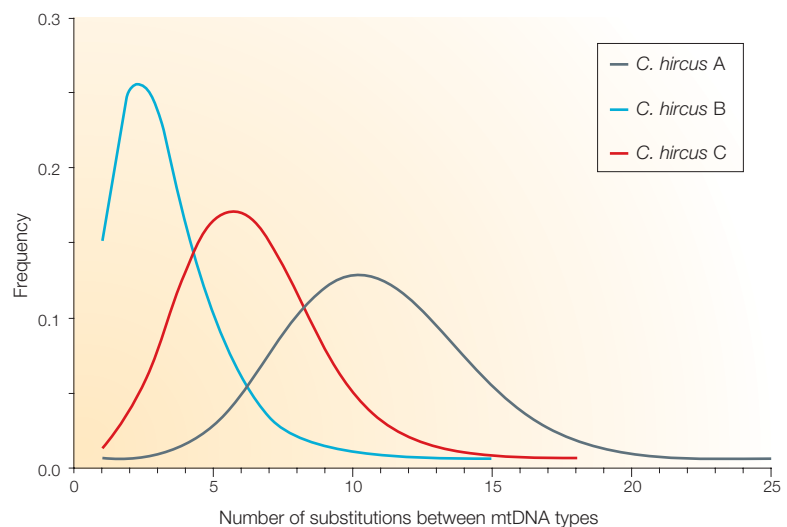
HAPLOTYPES
Genetic loci which co-segregate or are in linkage disequilibrium (LD). As mitochondrial DNA is a small extranuclear molecule, which does not undergo recombination, all markers on this genome are effectively linked as a single haplotype. At present, LD mapping is being used effectively in several species, including humans and livestock, to identify regions of the nuclear genome that have undergone intense episodes of selection.

MOLECULAR CLOCK
The principle that any gene or protein has a near-constant long-term rate of evolution in all branches of a clade, which means that the amount of sequence divergence between two sequences will be proportional to the amount of time elapsed since their shared ancestor existed.

markers, such as AMPLIFIED FRAGMENT LENGTH POLYMORPHISMS (AFLPs),[27] which assay variation at many loci simultaneously. A disadvantage of AFLP markers is that they show a dominant mode of inheritance, because only one allele is detected per locus. This can reduce the power of population genetic analyses, which generally require more informative codominant markers. Nevertheless, AFLP profiles are highly informative as they produce many polymorphic markers and are therefore being increasingly used in plant and animal domestication studies[1,28].

The other main class of molecular markers that are used in domestication studies are microsatellites[29]. These markers are short repetitive elements in genomic DNA, such as poly-dinucleotide repeats (for example, ACACAC…), that are codominantly inherited. The number of repeats varies between alleles and there are

many thousands of microsatellite loci throughout livestock genomes. Indeed, microsatellites have formed the basis of most of the more recent livestock genetic maps, and they were quickly found to be useful in characterizing diversity within livestock populations and breeds[22].
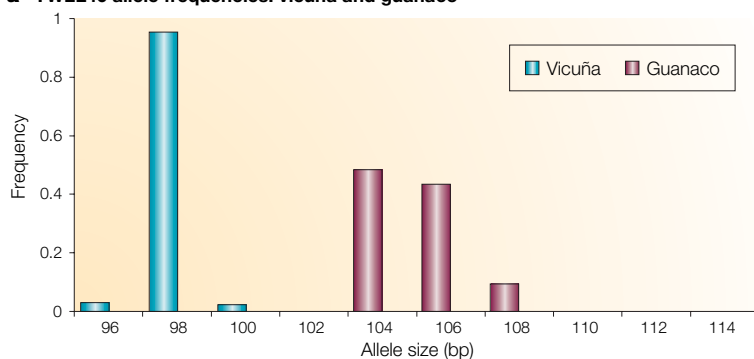
Microsatellites have three primary uses in domestication studies. First, they can be used to quantify genetic variation within and among livestock populations or breeds[30]. Second, they allow the documentation of admixture (genetic mixing) among livestock populations[26,31]. Third, microsatellite data can be used to assign individuals to genetically similar groups at the population, breed or species levels[32–34]. Microsatellites markers are also highly sensitive to genetic BOTTLENECKS and selection[35], both of which are likely to have occurred during domestication events (see section on future directions). An example of how microsatellites can be highly discriminatory when comparing alternative wild species as the genetic ancestors of modern livestock[31] is shown in BOX 2.

Genetic analysis of domestication

The use of genetic markers has revealed an extraordinary amount of variation and complexity in the domestication of livestock, in terms of the numbers and types of progenitors that contributed genetic material during domestication, and the number of occasions that similar stocks were domesticated.

Livestock progenitors. In the American arena of animal domestication, attention has so far focused on the South American camelids[31,36] and whether the modern-day alpaca (*Vicugna pacos*) and llama (*Lama glama*) descended from either the wild guanaco (*Lama guanicoe*) or vicuña (*Vicugna vicugna*). mtDNA analysis has shown that the llama and alpaca have haplotypes that originate from both wild species, but that most of the individuals typed have guanaco-type mtDNA, which indicates that there is a guanaco ancestry for both domestic forms. Subsequent microsatellite analysis showed that this was a misleading picture that was primarily the result of hybridization between male alpaca and female llama[31] (BOX 2). However further mtDNA analysis is required to elucidate the number of domestication events that have contributed to the modern-day llama and alpaca. Both of these livestock species are thought to have originated in the high Andes around 9,000 YBP[37].

Perhaps the first indication that livestock domestication was a more complex process than some authors believed came from mitochondrial studies of cattle[21,38]. There are two principal distinct cattle types found today, zebu and taurine. Zebu cattle have a shoulder hump and are found mainly in eastern Eurasia and eastern Africa. By contrast, the taurine cattle lack a hump and are the predominant cattle of Europe, north and west Africa and the Middle East. Some authors have classified the two types as separate species; *Bos indicus* (zebu), and *Bos taurus* (taurine) cattle. Initially, however, the widely held view was that both types were merely differentiated forms that originated from a single domestication event.

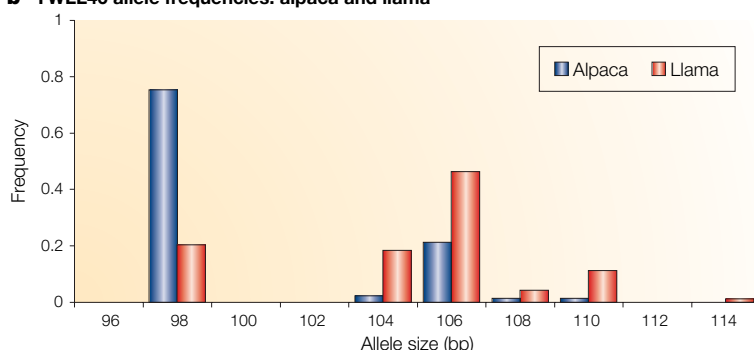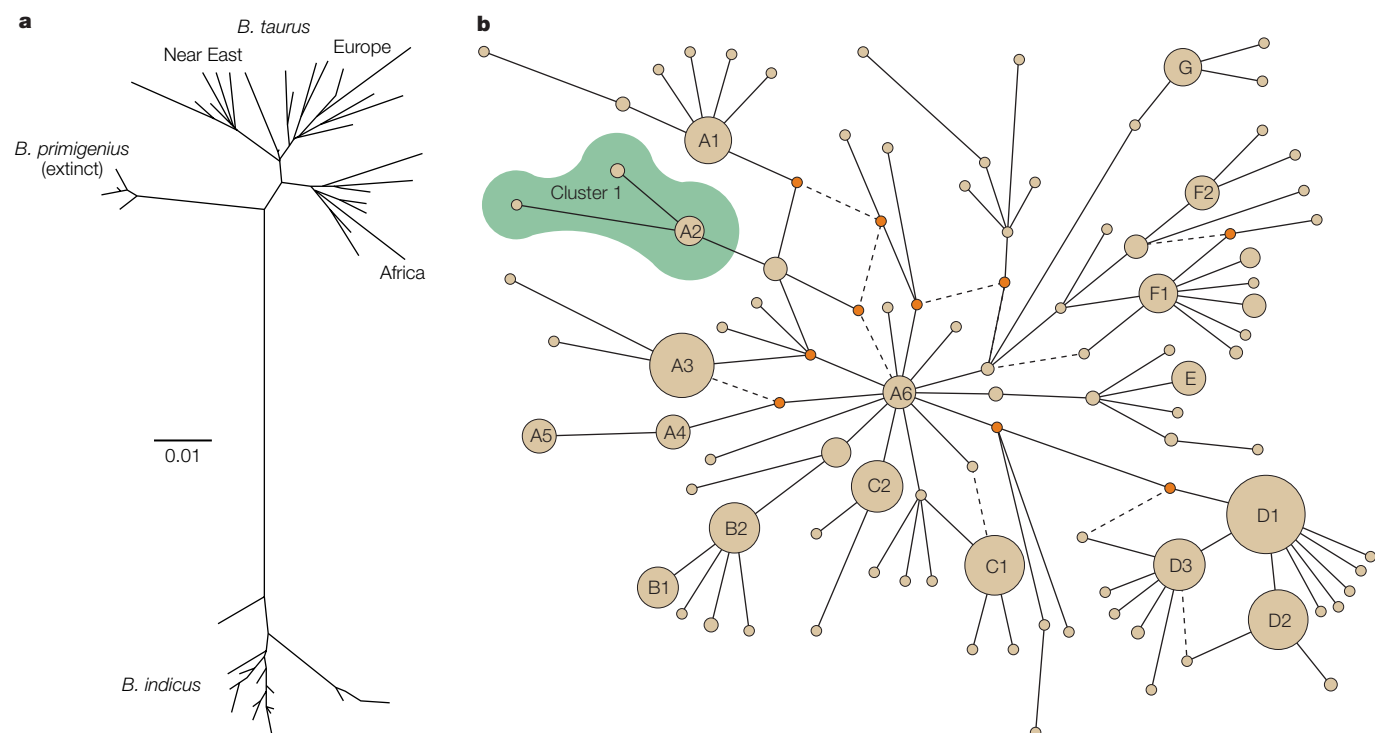### Box 2 | Microsatellites as nuclear markers of domestic origins

The frequency distributions of different sized alleles for the microsatellite locus YWLL46 are shown in the two putative wild ancestors of the modern-day llama (*Lama glama*) and alpaca (*Vicugna pacos*), the vicuña (*Vicugna vicugna*) and guanaco (*Lama guanicoe*). Allele sizes do not overlap between the two wild species (see figure, part **a**). However, although the allele size distributions in alpaca match closely to that of the vicuña and those in the llama similarly match that of the guanaco, the most common guanaco allele is found in alpaca and the most common vicuña allele is found in llama (see figure, part **b**), which indicates that there has been bidirectional hybridization.

These results are in total contrast to the mitochondrial data, for which the majority of both llama and alpaca have a mitochondrial haplogroup that indicates a guanaco ancestry. Deliberate hybridization of alpaca males with llama females to increase body size and fleece weight, followed by subsequent backcrossing with alpaca males to produce a finer fibre is one possible explanation for this pattern. This figure is reproduced with permission from REF. 31 © The Royal Society (2001).

a YWLL46 allele frequencies: vicuña and guanaco

(legend: Vicuña, Guanaco)
Y-axis: Frequency (0 to 1)
X-axis: Allele size (bp) (96, 98, 100, 102, 104, 106, 108, 110, 112, 114)

b YWLL46 allele frequencies: alpaca and llama

(legend: Alpaca, Llama)
Y-axis: Frequency (0 to 1)
X-axis: Allele size (bp) (96, 98, 100, 102, 104, 106, 108, 110, 112, 114)

Figure 2 | **Phylogenetic complexity in modern-day cattle and horses.** The branch lengths are proportional to the amount of evolutionary change that has occurred along them. **a** | A representation of the mitochondrial (mt) DNA tree produced for modern-day humped (*Bos indicus*) and western (*Bos taurus*) cattle and the ancient British aurochs (also known as wild cattle; *Bos primigenius*) that is based on 201 base pairs (bp) of control-region sequence[42]. Note the phylogenetic distinctiveness of the aurochs compared with modern-day European cattle, including breeds from the same island. The scale bar represents 0.01 substitutions per bp. Part **a** is modified with permission from REF. 42 © Macmillan Magazines Ltd (2001). **b** | A reduced median network of the most PARSIMONIOUS connections among 652 mitochondrial haplotypes from the horse (*Equus caballus*) that is based on 247 bp of control-region sequence[13]. The size of the yellow circles represents the number of individuals for which a haplotype sequence was obtained. The orange circles represent putative intermediate haplotypes that have not yet been found. The codes used to label the most common haplotypes correspond to those used in REF. 53. The dashed lines between haplotypes represent unresolved equally parsimonious connections between sequences. Cluster 1 (green shaded area) is found only in Przewalski's horse (*Equus caballus przewalski*), which is a possible ancestral species for domestic horses. Some of the more common haplotypes show limited geographical structure. For example, C1 and E are found predominantly within northern European ponies and D1 is most common in north African and Iberian samples. Overall, the network shows the complex pattern of phylogenetic relationships among mitochondrial haplotypes from the horse. Part **b** is modified with permission from REF. 13 © National Academy of Sciences, USA (2002).

Molecular markers were used to investigate the intriguing origins of these cattle. Taurine cattle from Europe and Africa and zebu cattle from India and Africa were compared at the molecular level. Surprisingly, Indian zebu cattle were found to have profoundly different whole mtDNA RESTRICTION FRAGMENT LENGTH POLYMORPHISM (RFLP) profiles[39] and control-region sequences[38] when compared with both European and African taurine cattle and African zebu cattle — which all shared similar sequences. The level of sequence divergence between the two mtDNA lineages was consistent with a most recent common ancestor dating to hundreds of thousands of years BP. However, cattle domestication was known to have occurred much later than this, within the last 10,000 years[40]. So, the most probable explanation for this high level of molecular divergence was that genetically differentiated subspecies of the ancestral wild cattle *Bos primigenius* (also known as aurochs) had been domesticated in different regions of Eurasia[21].

Events since these initial domestications have been harder to disentangle using mtDNA. For example, the data showed that African zebu might only have taurine mtDNA[21], which seemed curious as it was thought that these zebu cattle originally came to Africa from Asia and the Middle East, transported by nomadic pastoralists. However, later studies using microsatellites and Y-chromosome DNA showed that the nuclear DNA of African zebu cattle was most similar to that found in other zebu cattle populations. The reason for this difference was that mtDNA studies were not able to detect zebu genes (passed into the local taurine population by zebu bulls), because male mitochondrial DNA alleles are not transmitted to descendent generations[26]. In livestock breeding selected males often have many offspring, whereas females are limited to only a few. So it is easy to imagine that the genomes of African zebu cattle largely derive from male zebus originating from Asia and the Middle East despite their mtDNA apparently being derived from a few female taurine founders.

Most recently, the origins of European taurine cattle have been illuminated by a large-scale study of the variation in control-region mtDNA variation in 400 cattle from Europe, Africa and the Near East. The study also used ancient-DNA methods, which have been increasingly used to identify phylogenetic affiliations from the remains of organisms ranging from humans to bacteria[41]. Skeletal remains found in the United Kingdom from four wild aurochs were radiocarbon dated to 3,720–7,320 YBP and their phylogenetic relationships were determined. Surprisingly, they were found to be unrelated to modern-day UK domestic cattle, which were instead more similar to modern cattle in the Near East (FIGS 2,3). These data indicate that at least the maternal origins of European cattle are consistent with the spread of cattle by cattle farmers from the Fertile Crescent, and not local, independent domestication[42].

The use of ancient DNA has also proved crucial in unravelling dog domestication, where it seems that the Old World, particularly east Asia, was an important area[4,43]. In addition, analysis of modern samples and DNA from historical remains has shown that domestication of the horse (*Equus caballus*) was also a complex process[13,14,44]. The most recent of these equine studies[13] found that control-region sequences group into ~17 phylogenetic lineages (FIGS 2,3). Some of the groups cluster with modern horse breeds or geographic locations, but many do not. The authors estimated that at least 77 mares must have been domesticated to give rise to the modern levels of control-region diversity. This study used conservative estimates of the mutation rate (1 per 100,000 years) and assumed that domestication first occurred 9,400 YBP. The clear conclusion from these studies is that horses must have been domesticated

numerous times. Further sequence investigation might lead to a more robust estimate of the number of times and places that were involved in horse domestication.

mtDNA analysis has also revealed a complex pattern of domestication in goats[24], with at least three divergent lineages captured during at least two hypothesized domestication events in the Near East and in Asia. Two control-region lineages have also been described in sheep (*Ovis aries*)[45,46], which correlate well, but not completely, with modern fat- and thin-tailed phenotypic varieties (FIGS 2,3), and indicate that at least two domestication events occurred in this species. However, a lack of relevant modern wild sheep samples has hampered the more accurate pinpointing of where and when these events took place. Two divergent mtDNA lineages representing swamp and water buffalo (*Bubalus bubalis*) have also been described, which indicates that there were independent domestication events[47,48]. Finally, this intriguing emerging pattern of East–West duality in domestication is completed in pigs (*Sus scrofa domesticus*), for which mtDNA evidence has consistently supported at least two domestication events, one from a Near Eastern or European wild boar species and one from an Asian species[49–51].

In summary, it seems clear from the divergent mtDNA lineages in all large domesticated meat- and milk-producing livestock, apart from the horse, that highly divergent populations or different species were involved in these domestication events. TABLE 1 summarizes these data and what is known at the molecular level about the ancestors of modern livestock.

Therefore, it seems that sheep, goats, cattle, buffalo and pigs underwent at least two independent domestication events in east Asia, Europe or the Near East.
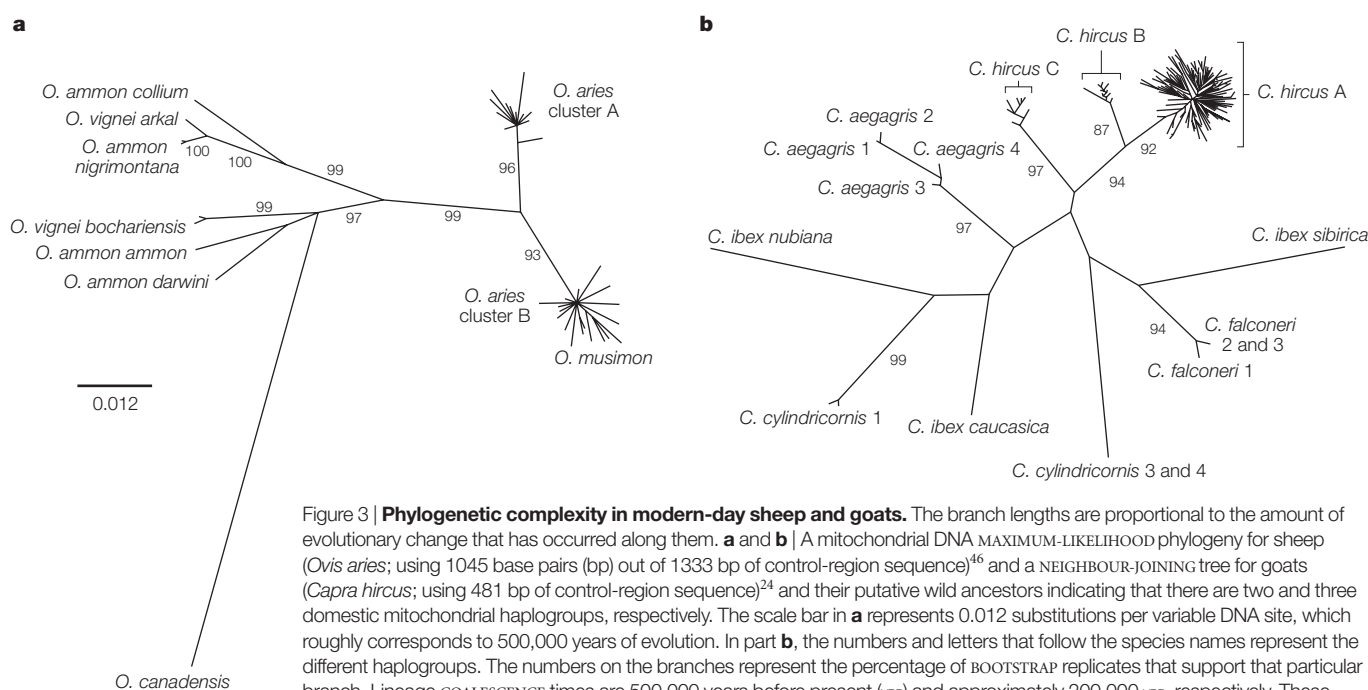
Figure 3 | **Phylogenetic complexity in modern-day sheep and goats.** The branch lengths are proportional to the amount of evolutionary change that has occurred along them. **a** and **b** | A mitochondrial DNA MAXIMUM-LIKELIHOOD phylogeny for sheep (*Ovis aries*; using 1045 base pairs (bp) out of 1333 bp of control-region sequence)[46] and a NEIGHBOUR-JOINING tree for goats (*Capra hircus*; using 481 bp of control-region sequence)[24] and their putative wild ancestors indicating that there are two and three domestic mitochondrial haplogroups, respectively. The scale bar in **a** represents 0.012 substitutions per variable DNA site, which roughly corresponds to 500,000 years of evolution. In part **b**, the numbers and letters that follow the species names represent the different haplogroups. The numbers on the branches represent the percentage of BOOTSTRAP replicates that support that particular branch. Lineage COALESCENCE times are 500,000 years before present (YBP) and approximately 200,000 YBP, respectively. These coalescence times predate domestication by more than an order of magnitude. Part **a** is modified with permission from REF. 46 © The Royal Society (2002). Part **b** is modified with permission from REF. 24 © National Academy of Sciences, USA (2001).

Table 1 | **Genetic diversity in livestock and their potential ancestors**

Domestic species	No. of possible differentiated wild ancestors	No. of extant ancestral species (subspecies)	No. of domestication events*	mt cyt *b* (average) sequence divergence among domestic lineages‡	mt CR (average) sequence divergence among domestic lineages‡
Cattle: taurine (*Bos taurus*) and zebu (*Bos indicus*)	2 subspecies: *B. primigenius primigenius* (taurus) and *B. primigenius namadicus* (zebu)	0	2 for *B. p. primigenius* (Eurasia and Africa) 1 for *B. p. namadicus* (Asia)	0.015 (REF. 38; between *B. taurus* and *B. indicus*)	0.057 (REF. 70; between *B. taurus* and *B. indicus*)
Sheep (*Ovis aries*)	3 species§: *O. musimon/O. orientalis*, *O. ammon* and *O. vignei*	3§	≥2 for *O. musimon/O. orientalis* (the mouflon)	0.007 (REF. 52)	0.059 (REF. 45)
Goat (*Capra hircus*)	2 species: *C. aegagrus* and *C. falconeri*	2 (3 within *C. aegagrus*)	3 (potentially all from the *C. aegagrus* subspecies)	ND	0.35 (REF. 24)
Horse (*Equus caballus*)	Multiple wild populations of a single species (*E. caballus*)	0‖	ND	ND	0.026¶ (REF. 14)
Pig (*Sus scrofa domesticus*)	2 species: *S. scrofa* and *S. indicus*	2	≥1 for *S. scrofa* and 1 for *S. indicus*	0.015 (REF. 49)	0.018 (REF. 71)
Water buffalo (*Bubalus bubalis*)	2 subspecies: *B. b. bubalis* and *B. b. carabanesis*	2	2 for *B. b. bubalis* and *B. b. carabanesis*	0.027 (REFS 47,48)	0.074#
Llama (*Llama glama*)	2 species, 4 subspecies: *Lama guanicoe guanicoe*, *L. guanicoe cacsiliensis* and *Vicugna vicugna vicugna*, *V. vicugna mensalis*	2 (4)	ND	0.012 (subspecies), 0.088 (species) (REF. 31)	ND
Alpaca (*Vicugna pacos*)	2 species, 4 subspecies: *Lama guanicoe guanicoe*, *L. guanicoe. cacsiliensis* and *Vicugna vicugna vicugna*, *V. vicugna mensalis*	2 (4)	ND	0.012 (subspecies), 0.088 (species) (REF. 31)	ND

*This assumes that each highly divergent mitochondrial (mt) DNA lineage originates from a separate domestication event and not simply from introgression or hybridization with wild populations[21]. ‡The sequence divergence rate for cytochrome *b* (cyt *b*) is often only about 0.02–0.05 (2–5%) per million years[72]. The divergence among many mammal species cyt *b* sequences is about 0.02. In humans, the most different mtDNA genomes are approximately 0.005 divergent overall, this value is slightly higher at more variable loci such as cyt *b* and is far higher for the control region (CR)[73]. §*O. vignei* is the urial (according to some nomenclatures[74]); *O. musimon* and *O. orientalis* could be the same species (the mouflon), and *O. orientalis* is also called *O. gmelinii* in the literature; the number of subspecies is also highly controversial. ‖The last free-ranging wild horses (Preswalski's horse; *Equus caballus preswalski*), which were seen in Mongolia in 1969. ¶0.026 is the average divergence, some haplotypes are actually shared between subspecies. #Kierstein, G. *et al.*, unpublished data; Genbank submission AF197196, AF197197, AF197199, AF197200, AF197202–AF197204, AF197206–AF197208, AF197210, AF197215, AF197217, AF197219–AF197223. ND, not determined.

In marked contrast, horses (and possibly dogs) have a more complex history that is characterized by numerous domestication events worldwide; it will be interesting to see how these apparently simple and more complex stories develop with more data, especially data that involves ancient DNA. However, ancient-DNA studies might prove increasingly difficult because at present identifying the precise localization of domestic events is hampered by difficulties in amplifying DNA from archaeological sites in warmer regions. It is also a challenge to comprehensively sample extant wild populations. Once these technical and logistical problems are overcome future studies should be able to resolve these issues. The domestication histories of several Eurasian domestic species — notably the yak (*Bos grunniens*), donkey (*Equus asinus*) and camel (*Camelus bactrianus* and *Camelus dromedaries*) — are as yet poorly characterized by molecular markers. However, these species are now being studied, and it will be extremely interesting to see whether the patterns that emerge follow the simple (for example, single, local origin) or complex patterns that have been found in the livestock species already studied.

Genetic diversity today

So, what do these complex patterns of past domestication imply for modern patterns of genetic diversity across individuals, breeds, domestic 'species' and geographical zones?

Species such as cattle and sheep were domesticated in the Near East and are now under intense husbandry in Europe and other parts of the world where livestock rearing is a major industry. In the absence of large-scale recurrent gene flow, we might expect that most of the genetic diversity for these species would be present in the Near East where they were first domesticated. This diversity is expected to decline as the distance from the domestication centres increases because the Neolithic cattle farmers responsible for originally transporting these livestock westwards only took small samples of the diverse eastern stock. This pattern is indeed seen in cattle and sheep[42,52], but it is not so evident in goats[24].

Analysis of molecular variance (AMOVA) finds that in goats only 10% of mtDNA variation is partitioned among continents (FIG. 4), as opposed to >50% in cattle[38] and 35% in sheep[52]. Interestingly, this indicates that goats might have been more easily or more widely
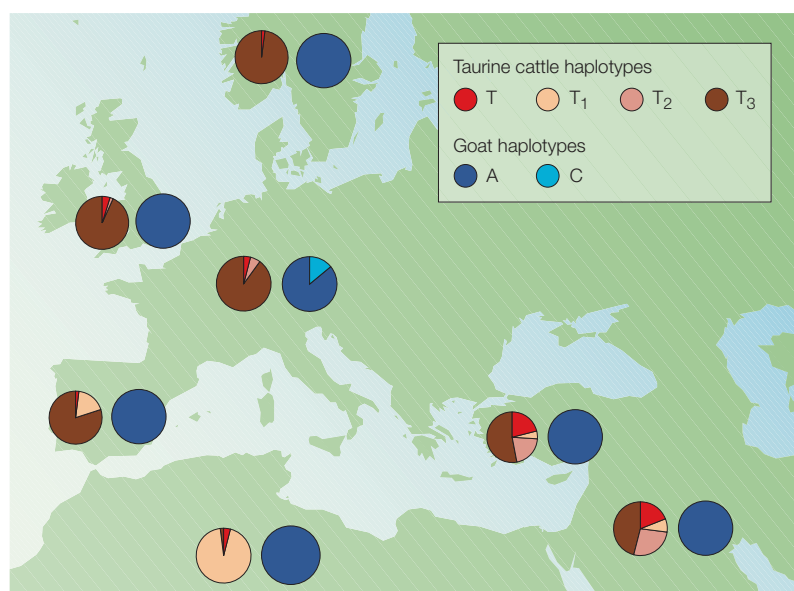
Figure 4 | **Cattle and goat mitochondrial diversity in Eurasia.** Each pie diagram represents the total sampled control-region haplotypes in a particular area for either cattle (*Bos taurus* and *Bos indicus*; on the left) or goats (*Capra hircus*; on the right). Each specific haplotype is represented by a different colour (see key). Goats and cattle show contrasting patterns of mitochondrial (mt) DNA control-region lineage diversity over their geographic range in western Eurasia. Cattle show a broad decline in diversity from east to west, as predicted from a gradual loss of diversity compared with their ancestral population during the Neolithic expansion from southwest Asia to northern Europe[42,69]. Interestingly, the principal African haplotype (T1) occurs rarely in the Near East, indicating that there is a more sharp divergence possibly owing to separate wild origins (that is, T1 might originate from north east Africa). By contrast, goats show much less structure, which could be attributed to their relative 'portability'[2,24] and the fact that they have been much more extensively transported across the globe. Modified with permission from REF. 24 © National Academy of Sciences, USA (2001).

The overlaid patterns of both European and Asian cattle introgression are also clearly shown in patterns of microsatellite allele frequency variation[56] — illustrating the power of these markers to unpack numerous ancestral influences, sometimes when mtDNA alone gives an incomplete picture.

In sheep, the two mitochondrial lineages were first discovered in New Zealand[57], which indicates that mtDNA from both domestication events have found their way into the New Zealand flock. Subsequent mtDNA studies in European sheep have shown that more recent introgression has probably occurred from east to west, as the eastern sheep mitochondrial lineage is now found in a few western European breeds, in marked contrast to the general pattern of subdivision of diversity across continents[45].

In other species, comprehensive studies of geographical patterns of genetic diversity have either yet to be published or the results seem to be very different. In horses, for example, there is some association between mitochondrial lineages and geography. For example, northern European ponies share a distinct mitochondrial lineage, as do Iberian and northwest African breeds[13]. However, it is hard to discern other obvious geographic patterns in horse genetic diversity. As with goats, this is likely to be the result of the extensive movement of horses. In fact, horses have extremely low intercontinental population differentiation (as assessed by AMOVA) compared to other livestock species, which is consistent with their use mainly for transportation (A. Beja-Pereira and G.L., unpublished data). In European pig breeds, such as the Large White and Landrace, haplotypes of the Asian wild boar are found as a result of recent introgression, probably during breeding programmes[50].

So, in summary, the combined effects of portability/mobility on the one hand (goats and horses) and introgression on the other (cattle, sheep and pigs) has shaped the distribution of genetic diversity that we see in livestock on a global scale today. The question therefore arises, what kind of diversity do we wish to conserve in these species, and what demographic and genetic processes do we hope to facilitate in the future?

Implications for conservation
The implications of the many recent molecular genetic studies for different domestic species are clearly different in each case. However, the relevance of this information and how it might be incorporated in management plans for endangered livestock has some general implications.

First, although the wild progenitor species are extinct for some species (such as cattle and horses), the identification of ancestral populations for other livestock could be very important for two reasons. It is probable that some are endangered (for example, the vicuña) and such information might give extra impetus for their conservation. Moreover, ancestral populations (and closely related species) might be a source of alleles of economic value that have been lost by chance during domestication[58,59]. In addition, in species for which domestication has occurred in both the East and the West (for example, cattle and pigs), ancestor populations

transported throughout historical times than sheep or cattle, which is consistent with goats being extremely hardy and adaptable[24].

The molecular signature of rapid demographic expansions that are associated with large-scale domestication and diffusion across the globe can be seen in the mtDNA mismatch distributions (BOX 2) of these domestic species[24,52]. Most new sequence variants are the result of recent mutations and are relatively closely related within different domestic mitochondrial lineages.

However, in other parts of the world the patterns of genetic diversity will not necessarily be the same. Isolated and/or recently established livestock populations (for example, those established at the time of European colonization) typically show more complex genetic signatures owing to their unusual histories. The impact of geography, transportation and INTROGRESSION on genetic diversity can clearly be seen in studies of cattle from Asia to South America[53–55]. Most recently, comprehensive surveys of African cattle using mtDNA and microsatellites support the model that they might have originated from the local domestication of African wild oxen. These animals were undoubtedly genetically similar to those that gave rise to European and Near Eastern cattle, but have left a genetic legacy that is sufficiently distinct to support archaeology that indicates a North African domestication[42,56].

INTROGRESSION
The transfer or genetic material from one species to another by hybridization and repeated backcrossing.

might be genetically highly divergent and the use of these resources must take this fact into account. Clearly, care must be taken when using these precious but imperilled populations to ensure that they are conserved.

Second, the characterization of genetic diversity within and between breeds, and the identification of the geographical component of this variation, allows region-specific conservation measures to be put in place. For some domestic species in Eurasia, the eastern-most breeds or those nearest the putative centres of domestication have repeatedly been shown to contain greater genetic diversity than breeds located further away from these points. Management strategies and global priorities for the maintenance of genetic diversity must not ignore these data: these higher diversity breeds should receive a concomitant higher priority for conservation.

In a phylogenetic sense, some important discoveries have been made that apparently rule out certain candidate species as potential progenitors of modern livestock. For example, neither the wild urial or the argali are likely to be the progenitors of sheep[46] and the guanaco almost certainly did not give rise to the alpaca (although it has made some genetic contribution)[31]. Conversely, such studies have successfully identified species that should be a priority for conservation because they represent the most likely progenitors of livestock[51]. In this context, the relative paucity of information on genetic diversity in Asian populations of livestock and their putative ancestors needs to be addressed, given the general pattern of East–West divergence in several species. In other species, for which the wild progenitors have still to be identified or are already extinct, the value of phylogenetics in their conservation is less clear. Furthermore, owing to the extensive effects of introgression in modern livestock and the lack of concordance between different genetic markers in many studies, some of the widely used phylogenetic units of conservation that have been developed for wild species, such as the EVOLUTIONARILY SIGNIFICANT UNIT and the MANAGEMENT UNIT[60], seem inapplicable.

The extensive within-breed diversity and the often contradictory way in which different molecular markers segregate in domestic species poses special challenges for AnGR conservation in livestock. Recently, the application of diversity-based methods for prioritizing livestock breeds for conservation has centred on the use of the 'Weitzman Approach'[61]. Weitzman's concept involves a 'diversity function', which is the diversity encompassed by a set of breeds under economic consideration for conservation. To become a priority for conservation any new breed that is to be added to the list must add new diversity elements. This extra diversity might be summarized by pairwise genetic distances with the existing breeds in the set and be represented in a cluster analysis or as part of a dendrogram. Breeds that add the highest overall genetic distance to the remainder of the set (and which should be located at the tips of the most distinct and longest branches of the dendrogram) would be given the highest priority for conservation.

However, by summarizing breed diversity to a single genetic distance measure this approach fails to account adequately for the diversity and geographical structure that can be found within some breeds. It also fails to take into account the fact that genetic distance estimates will vary greatly according to the marker used and the recent demographic history of the breed (for example, whether it has passed through a population bottleneck). For example, a severely bottlenecked breed will have a large genetic distance owing to genetic drift, but often will contain little genetic diversity relative to other breeds.

Future directions

A great challenge awaits livestock conservationists who wish to use molecular data in the future. The complexity of accounting for the phylogenetic component of diversity in modern breeds and the need to maintain desired levels of variation within those breeds could produce conflicting management strategies. Therefore, the integration of these aims into a general management approach to conserve AnGR might not be possible or even desirable.

However, to effectively document and conserve diversity within and between breeds, it seems imperative that different marker types are used to assay variation. The utility of mtDNA and microsatellites has been discussed in this review, but given the huge influence that male-mediated gene flow can have on diversity at often very large spatial scales[26], Y-chromosome markers will be highly influential in genetic management studies of the future[62]. At present, however, the molecular markers used to characterize diversity in livestock have little to do with the genes under selection for economically important traits. The identification of causative mutations for phenotypic variation will add a new dimension to the characterization of animal domestication, as it will allow researchers to trace selection and the spread of economically important alleles. Such analysis is potentially very powerful, especially when combined with single nucleotide polymorphism (SNP) screening methods, and indicates that there are exciting new avenues of research in this area[63].

With the publication of genome sequences for key domestic species due in the near future and the increasing availability of expressed sequence tag (EST) databases, the prospects look good for an exponential increase in the availability of polymorphic markers of both neutral and selected varieties. It is exciting that in the future we should be able to simultaneously detect male and female demographic history and the signatures of selection, past and present, within the genomes of our domestic livestock. Advances in ancient-DNA approaches and collaborations between geneticists and archaeologists will advance livestock domestication studies and enhance our ability to infer their evolutionary and demographic history[42,43]. Ancient DNA will help us to pinpoint the geographic locations of origin for the different livestock lineages, and to determine the timing and routes of their spread across the Old World. Finally, the use of molecular markers, in combination with a diversity approach that is based on Weitzman's model[61], promises to offer a rational way ahead and to reveal in more detail the genetic diversity in livestock populations that are in increasing need of genetic management.

EVOLUTIONARILY SIGNIFICANT UNIT
Populations that share a common ancestor, but that have been demographically independent for long enough that they no longer share mitochondrial DNA haplotypes.

MANAGEMENT UNIT
Populations that have significant allele or haplotype frequency differences at mitochondrial DNA and nuclear DNA.

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Food and Agriculture Organization of the United Nations:
http://www.fao.org/
2002 IUCN Red List of Threatened Species:
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