

Systematics and Phylogeny of Cattle

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Introduction

The mammalian tribe Bovini (subfamily Bovinae, family Bovidae) contains all the most important of the world's larger domestic species. The domestications of these cattle and cattle-like taxa were among the most significant advances of the neolithic transition. With their specialized digestive system, these species can utilize cellulose as an energy source, generating the benefits of dairy, meat and hide production. In addition, cattle provided, for several millennia, the animal draught power that underpinned agriculture in the Old World and have assumed a cultural and even religious importance, which is preserved to the present day in some societies.

In this chapter we describe the wild and domestic cattle species and their systematics, and we review the phylogenetic analyses that have been performed on this closely related and poorly resolved group.

The Phylogenetic Position of the Tribe of the Bovini

The order Artiodactyla and the suborder of the ruminants

Cattle belong to the zoological order of the artiodactyls, or even-toed ungulates, the oldest fossils of which are 50–60 million years old. Artiodactyls were commonly divided into Suiformes (pigs, hippopotamuses and peccaries), Tylopoda (camels and llamas) and Ruminantia (see, for example, Franklin, 1997; Ruvinsky and Rothschild, 1998; <http://www.pathcom.com/~dhuffman/artiodactyla.html>). One of the most striking aspects of recent higher-mammalian phylogeny has emerged from the synthesis of genetics and morphological analyses and indicated that cetaceans (whales, porpoises and dolphins) and artiodactyls possessed a common ancestor not shared by any other group. This close relationship may seem counter-intuitive but has been deduced from very different suites of data: morphological analysis, sequence comparisons and interspersed repeat element (SINE) distributions (Thewissen and Hussain, 1993; Graur and Higgins, 1994; Buntjer *et al.*, 1997).

A recent and more controversial assertion, also based on protein and deoxyribonucleic acid (DNA) sequences (Graur and Higgins, 1994; Gatesy, 1997; Montgelard *et al.*, 1997), has been that cetaceans are deeply nested within the artiodactyl cluster. Surprisingly, not only may cattle be more closely related to whales than to horses, but cattle and whales may even form a clade to the exclusion of other artiodactyls, such as pigs and camels. This provocative finding has been strengthened by an elegant analysis of the species distributions of SINEs (Shimamura *et al.*, 1997). An insertion of one of these elements into a new location in an ancestral genome may be considered to be a unique event, with a negligible probability of independent recurrence. Thus a shared SINE insertion may be a powerful phylogenetic marker for the grouping of taxa (Fig. 1.1). In particular, the finding of a SINE uniquely shared by ruminants, cetaceans and the hippopotamus has suggested a clustering of these animals to the exclusion of pigs and camels (Shimamura *et al.*, 1997) and challenges the existence of a Suiformes clade (see also Montgelard *et al.*, 1997).

The distinguishing feature of the ruminants is their special digestive system, with rumination and consecutive digestions in three or four subdivisions of the stomach, enabling an efficient utilization of grass and leaves as food. The chevrotains of the Tragulidae family, with a three-chambered stomach, are the most primitive ruminants. The other ruminants form the separated infraorder of the Pecora, which comprises the Antilocapridae, Cervidae, Moschidae (with *Moschus* as the only extant species), Giraffidae and Bovidae (Janis and Scott, 1987). The relatively small interfamilial divergence indicates that these families were formed about 25 million years ago within a period of 5 million years (Kraus and Miyamoto, 1991). Phylogenetic studies (Kraus and Miyamoto, 1991; Cronin *et al.*, 1996; Montgelard *et al.*, 1997; see also Chikuni *et al.*, 1995) have suggested an early split-off of the

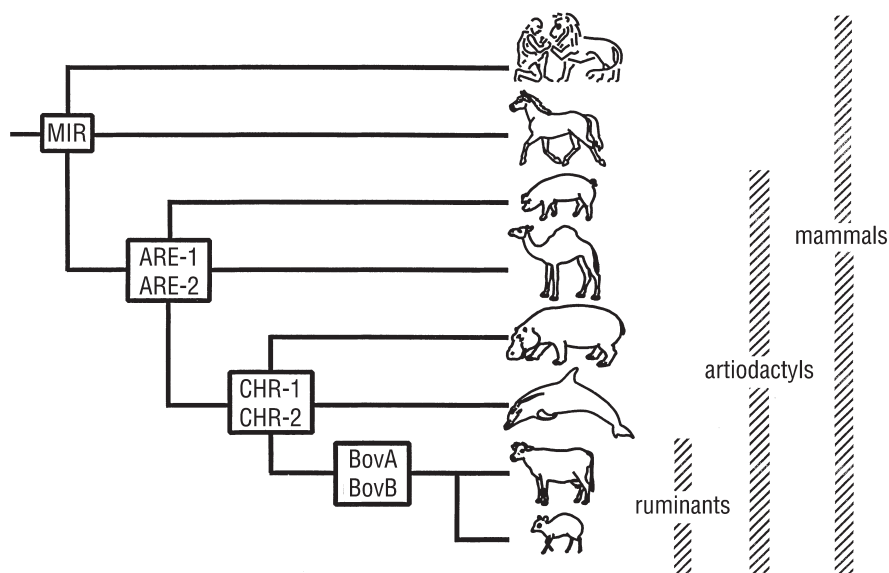


Fig. 1.1. Phylogeny of the order of the artiodactyls, as based on the sharing of interspersed repeat elements: the mammalian-wide interspersed repeat (MIR; Jurka *et al.*, 1995); the artiodactyl ARE-1B and ARE-2B repeats (Alexander *et al.*, 1995; Buntjer *et al.*, 1997); the cetacean/hippopotamus/ruminant CHR-1 and CHR-2 repeats (Shimamura *et al.*, 1997); and the ruminant SINE repeat elements Bov-A and Bov-B (Jobse *et al.*, 1995).

Antilocapridae but do not resolve the branching order of the Cervidae, Giraffidae and Bovidae (Fig. 1.2).

The family Bovidae

Bovidae are distinguished by the presence of permanent hollow horns. After their emergence about 20 million years ago, their fast radiation was probably initiated by the emergence of the African savannah 18 to 23 million years ago (Allard *et al.*, 1992) and has created a great variety of morphologies. Most of the more than 100 species, several of which are represented by large populations, originate from Africa, the rest from Eurasia or North America. Many bovids live in herds, which in open areas reduces their vulnerability to carnivore predators. Usually, the dominance of one or a few sires imposes a strong selection of the male lineage, a phenomenon that has been reinforced by selective breeding practices in domestic species.

Extant bovids are divided into between five and nine subfamilies (Morris, 1965; Gentry, 1978; Franklin, 1997; see Fig. 1.2), with the higher number being supported by molecular studies. Undisputed divisions include the Bovinae (such as cattle, nilgai and eland), Cephalophinae (duikers), Caprinae (sheep, goats and related animals), Hippotraginae (e.g. roan antelope) and Antilopinae (gazelles, dik-diks). Reduncinae (reedbucks) and Ancelaphinae (gnu, hartebeest, etc.) are often classified as tribes within the Hippotraginae (Reduncini

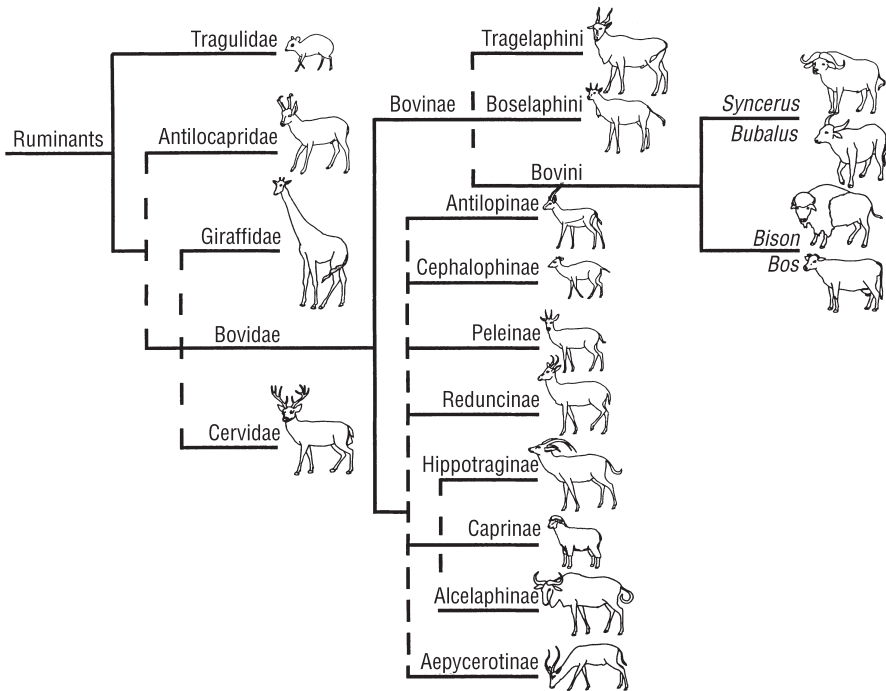


Fig. 1.2. Phylogeny of the order of ruminants, the family of Bovidae and the subfamily of the Bovinae and the main division within the tribe of the Bovini (Buntjer *et al.*, 1997; Gatesy *et al.*, 1997; Montgelard *et al.*, 1997).

and Ancelaphini, respectively), but comparative sequencing of mitochondrial DNA (mtDNA) (Gatesy *et al.*, 1997) supports a subfamily status for both taxa. The mitochondrial phylogeny further supports an assignment of impala to a separate Aepycerotinae subfamily rather than a classification within the Ancelaphinae or Antelopini. Likewise, reebok does not fit readily in one of the other subfamilies and is the sole member of the Peleinae (Gatesy *et al.*, 1997).

The radiation of the Bovidae seems to have been faster than, for example, in the Cervidae (Buntjer, 1997) and has defied attempts to arrive at an unambiguous phylogeny. However, mtDNA sequence analyses (Allard *et al.*, 1992; Gatesy *et al.*, 1997), as well as a study of the genes for nuclear ribonuclease (Beintema *et al.*, 1986), indicate that the first split was of the Bovinae subfamily, comprising the tribes Tragelaphini, Boselaphini and Bovini (Fig. 1.2). Within the other subfamilies, mitochondrial sequences indicate a clustering of the Caprinae, Hippotraginae and Alcelaphinae. The reebok may be considered as sister group of the Reduncinae, but the position of the impala remains unclear (Gatesy *et al.*, 1997). The classification of the Neotragini and Antilopini tribes within the Antilopinae subfamily is confirmed by the similarity of their mtDNA (Allard *et al.*, 1992; Gatesy *et al.*, 1997). However, molecular data disbanded two tribes within the Caprinae tribes, the Saigini (saiga and Tibetan antelopes; Gatesy *et al.*, 1997) and the Ovibovini (musk ox and takin; Groves and Shields, 1996).

The subfamily Bovinae and the tribe Bovini

The subfamily of the Bovinae is divided into the tribes of Tragelaphini or Strepsocerotini (spiral-horned antelopes), Boselaphini (nilgai, four-horned antelope) and large-sized Bovini. This tribe comprises the wild and domesticated buffalo and cattle species and started to diverge more than 4 million years ago. Bovini are sometimes divided in the genera Bubalina (*Bubalus* species, water-buffalo, arni, tamarao and anoa), Syncerina (African buffalo) and Bovina (*Bos* and *Bison* species). However, molecular data (see Phylogeny of Bovini) suggest a dichotomy of buffalo (*Bubalus*, *Syncerus*) vs. non-buffalo (*Bos*, *Bison*, Fig. 1.2). Within the Bovinae, *Bison* (bison, wisent) and *Bos* are considered as subgenera. In other classifications the *Bos* species are split into the subgenera *Poepbagus* (yak), *Bos* (taurine and indicine cattle) and *Bibos* (gaur, banteng, kouprey), but this is not consistent with a suggested clustering of yak with the bison species (Geraads, 1992; Buntjer, 1997).

The *Bos* and *Bison* bovines have karyotypes of $2n = 60$ with acrocentric or telocentric autosomes, except gaur with $2n = 58$ (Gallagher and Womack, 1992). In contrast, African buffalo ($2n = 52$) and water-buffalo ($2n = 50$ for the river type, 48 for the swamp type) have several metacentric autosomes. These differences in chromosome number probably explain why interspecies hybridizations are restricted to the non-buffalo bovines. Within this group, interspecies hybridization occurs spontaneously or as a result of domestic activity. The crosses of *Bos taurus* (common cattle) \times *Bos indicus* (zebu) yield completely fertile offspring. This indicates that the divergence of these species has not yet led to a complete speciation. Other crosses usually yield sterile bulls and fertile cows. The offspring of gayal-zebu crosses and of yak-taurine crosses (see below) may be considered as bovine equivalents of the mule and the hinny, being better suited for specific tasks than their parents.

The Bovini

Buffalo species

Although in America often synonymous with bison, the zoological denotation of buffalo refers to the African buffalo (*Syncerus caffer*), the water-buffalo (*Bubalus bubalis*), the Indian wild buffalo or arni (*Bubalus arnee*), the anoa (*Bubalus* or *Anoa depressicornis*) or the tamarao (*Bubalus* or *Anoa mindorensis*).

The African buffalo lives on the African savannah south of the Sahara and is one of the most dangerous game animals. Although it can be tamed, African buffalo has never been domesticated. The anoa is the smallest bovine species and lives in the forests of Sulawesi, Indonesia. The two types of lowland and mountain anoa (the latter sometimes denoted *Bubalus quarlesi*) appear to have quite divergent mtDNA sequences (Tanaka *et al.*, 1996; Kikkawa *et al.*,

1997). The tamarao is also smaller than the water-buffalo and lives on the southern Philippine island, Mindoro.

About 2000 Indian wild buffaloes live in parks in Assam, Nepal and Burma. This Indian wild buffalo is the progenitor of the domestic water-buffalo. Typically, both species seek protection against heat and insects by wallowing in water. Domestication took place 5000 years BC in China (Chen and Li, 1989) and/or 2500 BC in Mesopotamia (Cockrill, 1984; see also Lau *et al.*, 1998) and resulted in tranquil and docile animals. Two types of water-buffalo have been discerned: the swamp type in South-East Asia (sometimes denoted *Bubalus carabanesis*) and the river type on the Indian subcontinent and farther west. The swamp type resembles the arni progenitor most closely. The two types differ in karyotype (see previous section) and at the level of protein and DNA sequences (Beintema *et al.*, 1986; Amano *et al.*, 1994; Barker *et al.*, 1997; Kikkawa *et al.*, 1997; Lau *et al.*, 1998). Estimates on the divergence time of the river and swamp types entirely depend on the calibration of the molecular clock. Extrapolation of recent rates of microsatellite variation and of mitochondrial sequence divergence yielded estimates of 10,000–15,000 years (Barker *et al.*, 1997) and 28,000–87,000 years (Lau *et al.*, 1998), respectively. However, interpolation of mitochondrial sequence variation on the basis of the buffalo–cattle divergence indicated a divergence time of 1.7 million years (Tanaka *et al.*, 1996). The latter used only one sequence per taxon, which may introduce wide errors into the estimates (see also Loewe and Scherer, 1997).

About 148 million water-buffalo (an estimate from 1994; see <http://ww2.netnitco.net/users/djligda/wbfacts/html>) are kept around the world. Most of these (95%) live in Asia, but substantial populations have been established in Egypt, Italy, the Balkans and Brazil. In India and Pakistan, well-defined breeds of the river type are kept (Cockrill, 1984). Swamp buffalo are mainly used as draught animals, while river buffalo are dairy animals. In Italy, buffalo milk, rich in butterfat, is used for the preparation of mozzarella cheese, an essential component of the traditional Neapolitan pizza. Water-buffalo is also an excellent beef animal, yielding tender meat with a low fat content.

Mating with normal cattle occurs, but there are no reliable reports of the birth of hybrids.

Bison species

The American bison (*Bison bison*) are the wild cattle of the North American prairie. A separate subspecies (*Bison bison athabasca*) lives in woodland. The prairie bison underwent a narrow population bottleneck as a result of excessive hunting. In 1894 only 800 animals remained, most of which carried bullets in their bodies. Conservation efforts have resulted in a modern population of about 25,000 animals in national parks. The detection of taurine mtDNA sequences in one modern population (Polziehn *et al.*, 1995) indicates that, in

at least in one case, *B. taurus* cows have been used to restore the bison population.

In addition to these animals, 15,000 bison are reared as a source of meat, which has reputedly a low content of fat and cholesterol (see <http://bigweb.com/mall/buffalo/index.html>). Hybridization with normal cattle has also resulted in the registered beefalo breed, which comprises about 8000 animals (Felius, 1995), although not much is known about its genetic composition. Beefalo meat also has the reputation of being low in fat and cholesterol.

The wisent (*Bison bonasus*) is the European relative of the bison and suffered an even more severe population bottleneck. All 3332 animals (1990 count), which are now kept in zoos and parks, descend from only 23 bulls and 23 cows, which, in 1923, were available for breeding. Interestingly, in a phylogenetic analysis of mitochondrial COII gene sequences from banteng, gaur, cattle, yak, bison and wisent, the latter two did not cluster. Rather, the bison sample was substantially divergent from all other non-buffalo sequences, including the sequence of American bison (Janecek *et al.*, 1996). This anomalous phylogenetic situation may be the result of lineage sorting in an ancestral species and is a caution against overinterpreting data from a single locus in comparisons of closely related species. American bison mtDNA variants have been detected in two wisents and are possibly a consequence of crossbreeding in the species' recent regeneration (R.T. Loftus, personal communication).

Yak

The most typical characteristic of the yak is their long and woolly hair, necessary for their natural habitat at altitudes of 3000–5000 m. Their distinctive grunt gave the animal the systematic name of *Bos grunniens*. Since wild yaks only grunt during the mating season, these animals were baptized *Bos mutus*. In 1983 only a few hundred wild animals still lived in Tibet. Like most wild bovine species (including the extinct aurochs), cows have only one-third of the weight of the bulls, a sexual dimorphism that is always reduced by domestication (Bonnemaire, 1984; Felius, 1995).

Domestication was early and perhaps took place when agriculture first appeared (Zeuner, 1963). At present, about 12 million animals are kept at regions above 2000 m in China (mainly in Tibet), Pamir, Tien Shan, Mongolia and neighbouring regions in Siberia. Domestic animals are smaller and have a greater variety of coat colour than in the wild. The yak is a sturdy animal and may negotiate and graze in terrain inaccessible to normal cattle. They provide many products, such as unusually rich milk (up to 7% fat) for the production of butter, meat, dung as fuel, leather and hair for ropes, tents and felt (Bonnemaire, 1984; Lensch, 1996).

Yak–taurine hybrids, or yakows, are mostly derived from taurine bulls and yak cows at altitudes of 1500–2000 m (Bonnemaire, 1984; Felius, 1995). Male

hybrids are invariably sterile. By hybrid vigour, the F₁ hybrid offspring is larger than the parents and the cows yield more milk. In Mongolia, the F₁ hybrid, or khainag, is traditionally used as a pack and draught animal. Female khainags are used to produce B₁ and B₂ backcrosses with both species (Tumennasan *et al.*, 1997).

South-East Asian cattle

Small populations of wild banteng (*Bos* or *Bibos javanicus*) number together a few thousand animals in hilly woodlands below 2000 m in South-East Asia, Java and Kalimantan. Bantengs are shy animals, with, again, a large size difference between bulls and cows.

Banteng is the wild progenitor of Bali cattle, and was domesticated before 3500 BC in Indonesia or Indochina. About 1.5–2 million animals are kept on the island of Bali and other islands in Indonesia (Rollinson, 1984) and are used for tillage and slaughter. Bali cattle tolerate heat, but tend to be nervous and shy. Their meat is reputed to be lean and exceptionally tender.

The Madura zebu breed on the island of Madura ('the racing bull') is supposed to be a hybrid of zebu and banteng, and there are some molecular data that suggest an admixture in cattle of that region (Namikawa, 1981; Kikkawa *et al.*, 1995). However, experimental crossing of taurine or indicine breeds with banteng has met with little success.

From the gaur, or Indian bison (*Bos* or *Bibos gaurus*), only a few thousand animals still exist in tropical forests and woodlands in India, Indochina and the Malay peninsula. The gaur has a stubborn disposition, with a typical sexual size dimorphism, which is reduced in their domestic relatives, the gayal or mithan (*Bos* or *Bibos frontalis*). Domestication probably dates back to 500 BC (Felius, 1995) and may have exploited the animal's fondness for salt (Simoons, 1984). About 150,000 gayals are kept near the eastern border of India. Gayals are friendly animals, used primarily for traditional sacrifice and increasing the social status of their owners. Animals are often permitted to range around the village, and matings with gaur bulls probably take place frequently.

The selembu is a gayal–zebu hybrid in Bhutan and India, which is valued as a dairy animal, while the sterile males are used for draught. Accidental hybrids of a gaur bull with taurine or indicine cattle display considerable heterosis and may also have potential for meat production (Bongso *et al.*, 1988).

The kouprey or Cambodian wild ox (*Bos* or *Bibos sauveli*) is a severely threatened species, of which only a few hundred animals may persist in Cambodia and Vietnam (see <http://www.wcmc.org.uk/infoserv/country/vietnam/app4.html>). It lives in open parts of the jungle, occasionally in mixed herds with banteng (Felius, 1995).

Zebu and taurine cattle

Common cattle (*B. taurus*) and zebu (*B. indicus*) both descend from the aurochs (*Bos primigenius*). This was a large animal that once lived in North Africa and Eurasia, ranging from the Atlantic to the Pacific coast. However, it has been extinct in Europe since 1627 and from earlier times in other continents. Domestication took place as early as 7000 BC and more than 1200 million cattle are kept today, chiefly as sources of milk, meat and hides.

Analyses of microsatellite variation and mtDNA sequences (Loftus *et al.*, 1994; MacHugh *et al.*, 1997) have revealed that the ancestors of zebu and taurine cattle diverged some hundreds of thousands of years ago and must therefore be the result of at least two biologically independent domestication events. Evidence that separate strains of aurochs have been incorporated into African and European *B. taurus* has emerged from a more extensive mtDNA analysis (Bradley *et al.*, 1996). Successful extraction and polymerase chain reaction (PCR) amplification of mitochondrial DNA from 12,000-year-old British auroch bones have been achieved and have revealed sequences of divergent, but unmistakably *B. taurus* type (Bailey *et al.*, 1996).

About 800 different cattle breeds are recognized (Felius, 1995; <http://dad.fao.org>; <http://www.ansi.okstate.edu/breeds/>), many of which are genetic isolates (see Chapter 24). Selection has been directed primarily towards production of milk and/or meat, but often also towards their appearance (coat colour, horns). There has been inherent selection for local disease resistance and docility, except in breeds used for bullfighting. Most developed taurine breeds have superior production, but zebu breeds are better able to survive in dry and warm climates. Dairy taurine breeds have been commonly crossed to local zebu breeds in the tropics, but the favourable effects of heterosis are mainly in the first generation (McDowell *et al.*, 1996).

The classification of breeds may be based on geography, history and morphology (Epstein and Mason, 1984; Felius, 1995). The primary distinction is between humped (*B. indicus*) and humpless (*B. taurus*) cattle, although many breeds are of intermediate morphology and genetically admixed origin, particularly those in the greater part of Africa (Felius, 1995; Frisch *et al.*, 1997; MacHugh *et al.*, 1997). Further taxonomic division into long-horned and short-horned types is sometimes employed, but it is perhaps unlikely that this subdivision is clearly reflected at the genomic level.

Phylogeny of Bovini

The phylogeny of the Bovini has been studied by morphological analysis (Groves, 1981; Geraads, 1992), nuclear ribosomal DNA (rDNA) restriction fragment length polymorphism (RFLP) analysis (Wall *et al.*, 1992), sequencing of the mitochondrial cytochrome oxidase gene (Janecek *et al.*, 1996) and PCR-generated fingerprinting (Buntjer, 1997). This latter study is based on the variation of many nuclear loci distributed over the genome; 69 markers

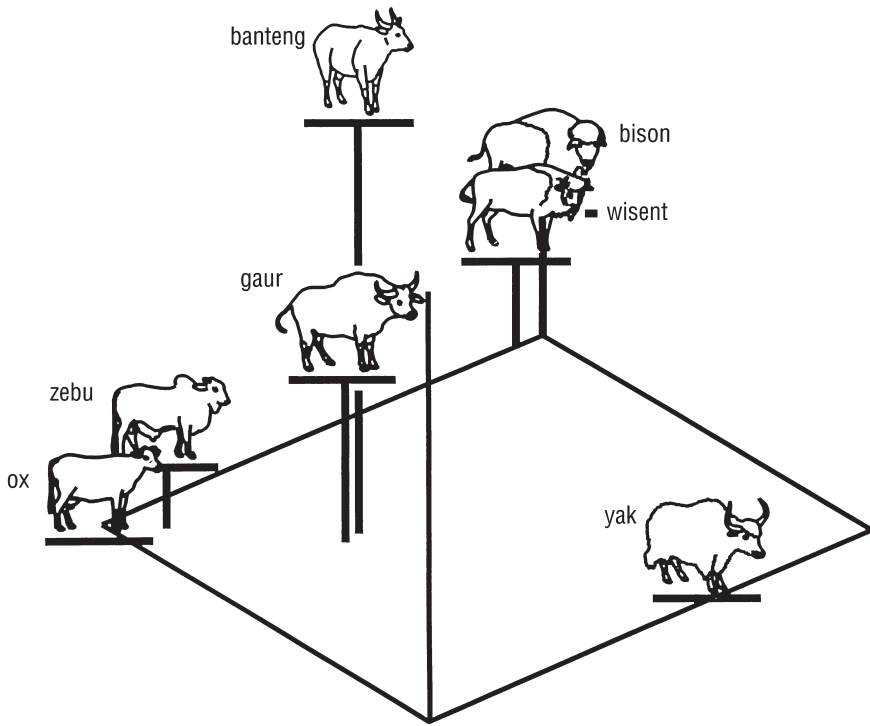


Fig. 1.3. Principal-coordinate analysis representing 72% of the interspecies variation of 85 AFLP markers informative for the non-buffalo Bovini species (Buntjer, 1997).

generated by a PCR specific for the mammalian-wide interspersed repeat (MIR) and 361 amplified fragment length polymorphisms (AFLP).

With the exception of Geraads (1992), all studies consistently cluster together the buffalo taxa (*Bubalus*, *Anoa* and *Syncerus*) relative to the *Bos* and *Bison* species. On a lower taxonomic level, the clustering of *Bubalus* and/or *Anoa* species (arni, water-buffalo, tamarao, anoa) is indicated by morphology (Groves, 1981), rDNA analysis (Wall *et al.*, 1992) and MIR-specific fingerprinting (Buntjer *et al.*, 1997). Tanaka *et al.* (1996) found that the tamarao is more closely related to the water-buffalo and the arni than to the anoa.

Data on the phylogeny of the other Bovini are largely conflicting. Morphological studies (Groves, 1981; Geraads, 1992) do not agree on the separate position of the *Bison* species. Ribosomal DNA restriction sites (Wall *et al.*, 1992) are hardly informative at this level, while the large divergence of the mitochondrial sequences of bison and wisent, together with a miniscule difference between yak and cattle (Janecek *et al.*, 1996), may indicate anomalies in maternal lineages. Also, mtDNA chromosome data, which are based on a single segregating unit, may not be representative of whole genomes, due to stochastic lineage survival and loss in ancestral species. In the study of phylogeny in closely related taxa, surveys of variation at a range of separately

segregating sites are likely to yield more accurate reconstructions. In comparisons of nuclear fingerprints generated by PCR, bison and wisent are clearly similar and different from the *Bos* species (Buntjer, 1997). MIR-specific PCR, and AFLP analysis (Buntjer, 1997) also indicate a clustering of yak with both *Bison* species, in agreement with Geraads (1992).

The gaur and the banteng, often designated as *Bibos* species, are clustered by the rDNA data as well as the mitochondrial sequences. These species have no stable positions in the trees constructed on the basis of the nuclear fingerprints. However, a principal-coordinate plot of the AFLP data (Fig. 1.3) does indicate the phylogenetic proximity of gaur and banteng (Buntjer, 1997).

Buntjer (1997) proposed that the retention of ancestral polymorphisms and recombination events interfere with the reconstruction of phylogenetic trees. This may explain the lack of agreement between the different phylogenetic reconstructions. Additionally, the principal-coordinate plot, which represents 66–72% of the total variation in the nuclear fingerprints, suggests an interesting correspondence between genetic distance and geographical origin of the species. The positions of the taxa stretch from *B. taurus* (Middle East), through *B. indicus* (India) to the South-East Asian species *B. javanicus* and *B. gaurus*. The *Bison* species and the yak, both adapted to colder climates, are clearly different from the other non-buffalo Bovini. It is a compelling hypothesis that, at this taxonomic level, geographical factors may have determined the degree of exchange of genetic material between the ancestral populations and hence the genetic similarity of extant species.

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