

The bovin phylogeny: A review

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Abstract : The evolutionary history of cattle and buffalo has always been a topic of great interest to the evolutionary biologists. The phylogenetic studies of bovin species has been carried out at various levels, varying from the study of domestication and migration of populations to major cladogenesis. Along with the archeological studies there are studies from molecular biology and more recently from genomics. The phylogenetic perspective of the bovins and their evolutionary history, are reviewed in terms of what has been done, what needs to be done and potential challenges in doing it.

Key words : Bovini, Phylogenetics, Domestication, Bos

I. Introduction

The Bovids (Bovidae family) are the most diverse group of living ungulates with 143 recent species (over 55% of modern ungulates). Bovids are primarily old world in their distribution, although a few species are found in North America. The present classification scheme for Bovids has eight subfamilies subdivided into two clades, the Boodontia (with a single subfamily, Bovini) and Aegodontia (composed of all other bovid subfamilies). Some authors do not recognize these two clades, instead reducing the number of subfamilies to two: Bovini (without change) and Antilopinae (with all of the Aegodontid subfamilies as tribes within it). Among the subfamilies, the phylogeny of some groups is well-established while the interrelationships of the subfamilies are still under question. The family Bovids began its evolution in Africa around 19 million years ago and rapidly diversified, with 78 genera known from the Miocene (compared to 50 today). Kingdon (1997)

suggests that a continental divide between Africa and Eurasia may be responsible for the early divergence of the Boodontia (Eurasian in origin) and the Aegodontia (which continued evolving in Africa). The rejoining of the two continental land masses (after these two principal clades had become distinct) at the Arabian Peninsula removed this geographic barrier, allowing both groups to expand into the other's homeland.

Recent years have seen an increase of interest and inquiry into the evolutionary history of Bovini, the clade comprising living oxen (genus *Bos*) and the living buffaloes (genera *Syncerus* and *Bubalus*). A disproportionate interest in the phylogenetics of Bovini, relative to other bovid or ruminant clades, no doubt stems from the importance of bovins as a prime source of human sustenance since at least the Pleistocene. In addition, bovins are widespread (naturally occurring on four continents), ecologically differentiated with wide habitat tolerances, taxonomically diverse, and, given their large size and affinity for wet habitats, possess a high potential for preservation in the fossil record. For these reasons, the evolutionary record of Bovini

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provides an exemplary resource for studies on evolutionary patterns and processes. In the text to follow we had attempted to compile the work done by various researchers on various different levels and with different approaches to address the bovine phylogenetics.

The higher ruminants are believed to have rapidly speciated in the Mid-Eocene, resulting in five distinct extant families: Antilocapridae, Giraffidae, Moschidae, Cervidae, and Bovids. Due to the rapid radiation, the higher ruminant phylogeny has proven difficult to resolve. Systematic work on the Bovids has been difficult, leading to a comment that the Bovids is one of the most troublesome groups of mammals to classify (Simpson, 1945). Previous work employing morphology (Simpson, 1945), immunodiffusion (Lowenstein, 1986), protein sequences (Beintema et al., 1986), and allozymes (Georgiadis et al., 1991) has offered limited insight into the basal subdivisions of the Bovids. All living Bovids may be divided among either Bovini or Antilopinae. Bovini is the clade uniting Bovini (buffaloes and oxen), Tragelaphini (spiral-horned antelopes, including kudu), and Boselaphini (nilgai and chousinga). This classification requires that members of Bovinae be referred to as bovines, while members of Bovini are bovins, though most of the literature still uses the term bovine in reference to the Bovini. Living bovins are further divided among the Bovina (genus *Bos*, including *Bison*) and the Bubalina (*Syncerus* and *Bubalus*). A certain amount of confusion surrounding the taxonomy of domestic derivatives of wild bovine species has also been addressed by a ruling by the International Commission on Zoological Nomenclature. The phylogeny of bovine tribe has been studied by various groups across the globe but it has so far resisted the traditional approaches (Lenstra and Bradley, 1999). The tribe Bovini comprises cattle and buffalo species, several of which have been domesticated. Taurine cattle (ox) and zebu have only survived as domestic animals, while yak and water buffalo still exist in the wild.

The phylogenetics of ruminant livestock, as with all domestic animals, are profoundly influenced by domestication. The gene pools which these species possess today are all the result of repeated capture and taming of the wild ancestors, which were restricted both spatially and temporally. In the present work we had reviewed the progress that had been made till now in the field of bovine phylogeny.

II. Studies on the Member Species of Bovini

1. Yak

Yak (*Bos grunniens*), an herbivore, belongs to the tribe Bovini, family of Bovids. It is distributed in the mountainous areas of the Central Asia at altitudes ranging from 2500 to 5500 m with severely cold winters, short growing seasons for herbage and no absolutely frost-free periods. The total population of yak is estimated to be 14 million, about 90% of which are found in China. In India, the yak-rearing states are Arunachal Pradesh, Sikkim, Uttar Pradesh, Himachal Pradesh and Jammu and Kashmir. The first three of these, bordering the southern slopes of the Himalayas, have a cold, humid climate, while the two northerly states are cold and arid. The total of about 51,000 yak in 1997 represents a marked decline from the 132,000 yak reported for the year 1977 (Pal, 1993a). Gupta and Gupta (2000) and Nivsarkar et al. (1997) published even lower numbers of around 40,000 for recent years – largely because they suggested a lower number for Jammu and Kashmir. However, changes in numbers of yak over the years seem to differ among states – some having remained static in numbers. Reasons suggested for the decline in size of the yak population include socio-economic causes, one of which is a desire for an easier and more comfortable lifestyle on the part of the younger generations (Pal, 1993a). The closure of the border with Tibet to the former traffic in yak may also be a

Table 1. Origin and domestication of cattle.

Domestic species	Wild Ancestor	Time (B.P.)	Location
Cattle	Aurochs 3 subspecies (extinct)		
<i>B. taurus taurus</i>	<i>B. primigenious primigenious</i>	~8000	Near and Middle East (west Asia)
	<i>B. p. opisthonomous</i>	~9500	northeast Africa
<i>B. taurus indicus</i>	<i>B. p. nomadicus</i>	~7000	northern Indian subcontinent

contributory factor and has affected the availability of new sources of breeding stock. Nivsarkar et al. (1997) suggested that hybridization on a large-scale of yak with local Tibetan cattle was another factor leading to this sharp decline in the pure yak population. Yak has been reared as a multi-purpose livestock, providing a livelihood for the people with milk, meat, wool, fur, and other products. In commercial terms, milk is the most important for the herdsman. In contrast to the milk of dairy cattle, yak milk contains a greater percentage of protein, organic calcium, and rich in conjugated linoleic acid. In the last few years, therefore, there has been an increasing focus on yak milk and milk products.

Yak is the only one of Bovini that can multiply on the high and cold pasturing area. Having originated from China, the yak is an ancient exemplar of cattle. However, it is hard to verify the exact origin and relationship between yak and other species in the Bovini, as these issues are highly debated in the scientific community.

For this reason, the yak's evolutionary relationships have become a study hotspot of the Bovini molecule evolution and phylogeny. There are two different theories: one is that Yak has the nearer relationship to Bos; the other is that yak has the nearer relationship to Bison. Lai et al. (2005) sequenced the yak's D-loop region in mtDNA, then performed sequence variation and phylogeny analysis to the D-loop. As a result, the length of Bovini D-loop sequences varied from 891bp–895bp, 55 polymorphic sites were discovered, the percentage of polymorphic sites was found to be 6.16%, which shows that the polymorphism is very abundant in Bovini mtDNA D-loop region. Based on the sequence alignment and genetic distance results, the authors found that two yak

species (*Bos mutus* and *B. grunniens*) have a nearer relationship to *Bison bison*, and a farther relationship to Bos. Based on the Bovini D-loop molecule evolution bell of 10.6% per million year, it is speculated that the divergence time between *B. mutus* and *B. grunniens* is about 0.35 million year ago. The phylogenetic tree based on the Bovini mtDNA D-loop sequence and the first and second varied sequence, showed that *B. mutus* and *B. grunniens* cluster first, then they cluster with *B. bison*, and then cluster with embranchment which contains *B. taurus* and *B. indicus*, which also explains that the yak has higher genetic comparability to *B. bison* than Bos, and has nearer relationship to *B. bison* than Bos. Depending on the molecule evolution bell, it is speculated that *B. grunniens* diverged from *B. taurus* about 0.53 MYA, diverged to *B. indicus* about 0.47MYA, diverge to *B. bison* about 0.32MYA, and diverge to *B. bubalis* about in 0.86MYA. The divergence time between *B. taurus* and *B. indicus* is about in 0.24MYA.

Because the Y chromosome is male-inherited, and most of it is in the non-recombining region, therefore allowing it to be untouched by recombinant and reversion-mutation, it has a very low mutation rate. Sequencing of TSPY and DBY partial sequence in the yak Y chromosome was carried out, and sequence variation and phylogeny analysis was performed to the Bovini. *B. grunniens* and *Bison bison* were found to have the nearest common ancestor. Based on the Bovini TSPY molecule evolution bell, the divergence time between *B. grunniens* and *B. bison* was estimated to be about 1.16MYA. Depending upon the sequence variation and genetic distance results, the genetic comparability and relationship of *B. grunniens* was found to be nearer to

Bison than to *Bos* phylogenetic tree of Bovini based on TSPY and DBY sequences. The yak was found to have nearer relationship to Bison than to *Bos*. Depending upon the TSPY molecule evolution bell, *B. grunniens* was estimated to diverge from *B. taurus* about 2.09 MYA, from *B. indicus* about 1.86MYA, diverge from *Bubalus bubalis* about 16.44MYA, the divergence time between *B. taurus* and *B. indicus* was estimated to be about 1.16MYA. MHC (define what this stands for), a region with the most abundant polymorphism and important function in the genome, and is mainly involved in the immune response of organism, has been used in the research of disease resistance, genetic structure investigation, defining the consanguinity, and evolution process of species. In this research, the authors sequenced DRB Upstream Regulatory Region (URR) of 11yaks, and conducted a Phylogenetic analysis among different species. The result suggested 3 haplotypes (exist?) in the 11 sequenced BoLA-DRB-URR. There also exists highly conserved sequence motifs. The phylogenetic analysis showed that the sequences of Bovini first clustered with the sequences of ovis, and then with swine, which is in accordance to zoology taxonomy result(China-papers).

2. Buffalo

To date, not much is known about the genetics of the water buffalo (*Bubalus bubalis*). The domestic water buffalo holds a great economic potential in the developing countries. It is admired as multipurpose animal for dairy, meat, and drought. The stock of domestic water buffalo is estimated to be around 130 million, which is around 1/9 of the total worldwide cattle population. Nevertheless, there are more people in the world depending on domestic water buffalo than on any other domesticated species (FAO and UNEP, 2000). To develop rational breeding programs knowledge of extent and pattern of genetic variability within a breed or a population is essential. Furthermore, it is a prerequisite

to the conservation of genetic resources.

The phylogeny of water buffaloes (*Bubalus bubalis*) is still a matter of discussion, especially if the two types of domestic water buffalo (swamp and river) were derived from different domestication events or if they are products of human selection. To obtain more insight, Kierstein et al. (2002) analyzed the entire mitochondrial D-loop region of 80 water buffaloes of four different breeds, i.e., 19 swamp buffaloes (Carabao) and 61 river buffaloes (Murrah, Jafarabadi, and Mediterranean), sampled in Brazil and Italy. They detected 36 mitochondrial haplotypes with 128 polymorphic sites. Pooled with published data of South-East Asian and Australian water buffaloes and based on comprehensive median-joining network and population demography analyses, they showed evidence that both river and swamp buffaloes decent from one domestication event, probably in the Indian subcontinent. However, the modern swamp buffaloes have an unraveled mitochondrial history, which can be explained by introgression of wild water buffalo mtDNA into domestic stocks.

Within the family of Bovids, the tribe of Bovini consists of the genera *Bos*, *Bison*, *Pseudoryx*, *Bubalus*, and *Syncerus* (Hassanin and Douzery, 1999a). The latter two genera belong to the group of buffaloes, the Asian and African buffaloes. These are different lineages, separated from the other bovines during the Pliocene, demonstrated by archaeological findings of *Syncerus* remains in South Africa (Savage and Russell, 1983) or even in the end of the late Miocene demonstrated by molecular evolution of the bovid cytochrome b gene (Hassanin and Douzery, 1999b). During the Pleistocene, *Bubalus* was distributed from southern Asia to Europe. With increasing dry climate the area of distribution decreased to India, Indonesia, and parts of Southeast Asia (Cockrill and Mahadevan, 1974; Nachtsheim and Stengel, 1977). The genus *Bubalus* is divided into the subgenera *Bubalus* and *Anoa* with four living wild species (Tanaka et al., 1996). The group of *Anoa* encompasses

the Lowland anoa (*B. depressicornis*) and the Mountain anoa (*B. quarlesi*) on Sulawesi, Indonesia, and the Tamaraw (*B. mindorensis*) on Mindoro, Philippines. The wild water buffalo (*B. bubalis*), inhabiting India, is thought to be the founder of the modern domestic buffaloes. The wild water buffalo is subdivided using karyotyping (Fischer and Ulbrich, 1968; Iannuzzi, 1994; Ulbrich and Fischer, 1967), along with morphological and ethological criteria (Cockrill, 1981; Cockrill and Mahadevan, 1974), into the swamp ($2n \frac{1}{4} 48$) and river ($2n \frac{1}{4} 50$) buffaloes. The domestication of buffaloes most likely took place in the civilization of the Indus, the Yangtze, and the Euphrates and Tigris in the third millennium BC (Cockrill, 1981; Nachtsheim and Stengel, 1977) and/or in China during the fifth millennium BC (Chen and Li, 1989). Buffaloes were introduced to Italy from central Europe in the sixth century or by the Bay of Tunis in the seventh century at the time of the Arab conquest (Salerno, 1974).

Import of water buffaloes to Africa, Australia, and South America took place only recently. The common understanding about water buffaloes is that they are divided into two types. Within this division, the river buffalo are subdivided into at least 18 well-defined classes, whereas the swamp buffalo solitary exists with one breed (Cockrill, 1981), sometimes referred to as Carabao. Cockrill and Mahadevan (1974) describes the origin of the word Carabao in his introduction the Malay used in the Philippines to distinguish the local swamp buffalo from the introduced Indian river buffalo. He recommended not applying the word Carabao for just any type of water buffalo. However, as some of the Brazilian swamp buffalo population was imported from the Philippines, the term Carabao is used in Brazil. Nevertheless, especially in the southeastern provinces of China, a huge variety of genetic resources of swamp buffaloes have been described in terms of attitudes, adaptation to environment, and distribution (Chunxi and Zhongquan, 2001). The authors referred to 18 different breeds of swamp buffaloes, evolved separately in each

area, but no genetic study has been conducted so far. Despite a variety of investigations on water buffaloes' molecular phylogeny, the exact phylogenetic relationship between the two types of water buffaloes is still debated. The estimations of divergence of river and swamp buffaloes range from 10,000 to 1.7 million years (Amano et al., 1994; Barker et al., 1997a; Lau et al., 1998; Ritz et al., 2000; Tanaka et al., 1996). These extreme differences depend on the variety of methods (Restriction fragment length polymorphism, sequencing of mitochondrial coding and non-coding regions, microsatellite analysis) and on the sample size used for the analysis. The determination of the divergence of buffaloes is of interest, because the current estimations of the more recent divergence (Lau et al., 1998) coincide with the presumed domestication time of buffaloes. Hence, buffaloes either diverged into the river and swamp buffaloes after domestication, thus by human selection, or the two types were domesticated independently.

3. Cattle (*Bos taurus* and *Bos indicus*)

More than 800 cattle breeds are known to exist in the present day world. Two primary areas of domestication in the Middle East/Europe and the Indian subcontinent resulted in taurine and Indicine or zebuine types of cattle, respectively (Table1). Origin and domestication of different cattle breeds is still unsettled. Using genomic tools, McTavish et al. (2013) investigated the ancestry of cattle from across the world and suggested multiple independent domestication events. To resolve the issue of breed origins, Decker et al. (2009) constructed phylogenetic networks. Within *B. taurus*, African taurine cattle were inferred to be more divergent from European cattle than are the Asian *B. taurus* breeds. There were long branches between *taurine* and *indicine*, indicating divergence long before domestication. The networks are also consistent with the biogeography of breeds, with European, East Asian,

Dollin et al., 1991a, b). However, the observed configurations and the levels of XY-autosomal associations and autosomal asynapsis were deemed unlikely to cause fertility problems (Switonski et al., 1990; Dollin et al., 1991b; Switonski and Stranzinger, 1998). This assumption is supported by reproductive parameters such as sperm motility, sperm concentration, and non-return rates of *B. taurus*, *B. indicus* hybrid males, which appear to be characterized by hybrid vigor effects (Thrift and Aaron, 1987). The molecular data had shown taurine-zebuine dichotomy for cattle breeds in Europe and Asia, respectively, but suggested that African zebu cattle originated from earlier *B. taurus* strains by ancestral crossbreeding and male-mediated introgressions of *B. indicus* genetics (Bradley et al., 1996; MacHugh et al., 1997; Nijman et al., 1999). The mtDNA haplotypes recovered from archaeological specimens of European and Near Eastern aurochs and early domestic cattle have been interpreted as evidence for a Near Eastern origin of European *B. taurus* cattle that was followed by male-mediated European aurochs introgression (Troy et al., 2001; Götherström et al., 2005; Edwards et al., 2007). The deep divergence between *B. taurus* and *B. indicus* mtDNA sequences points to two independent primary domestication events from genetically discrete aurochs strains, each possibly with a subspecies status (Loftus et al., 1994; Bradley et al., 1996). The latter studies assumed a minimum divergence time for the *Bos/Bison* split of 1 million years ago (MYA) based on fossil records but without giving specific details. From this, and evolutionary parameters taken from studies of the human mtDNA control region (CR), the evolutionary rate of an approximately 400 nucleotide segment of the bovine CR was calculated for estimating cattle divergence times, including the *B. taurus* and *B. indicus* split at 0.2-1 Mya. Several studies on cattle domestication and diversity have based their divergence time estimates on this approach (MacHugh et al., 1997; Troy et al., 2001; Verkaar et al., 2004; Lai et

al., 2006). Hiendleder et al. (1998) have used complete mitochondrial genome sequences to estimate the *B. taurus* and *B. indicus* divergence time, and analyzed mtDNA CR sequences to reconstruct and clarify the phylogeny of extant *B. taurus* and *B. indicus* in a *B. primigenius* context. In the past two decades, with the advent of high throughput technologies, a consistent support for the cattle phylogeny has been observed.

III. Conclusion

An important achievement of the past two decades of molecular phylogenetic analyses has been recurrent and consistent support for a systematic classification of Bovins. With the arrival of high throughput techniques like Genome wide SNP chips, great progress has been made by workers in different fields towards stable systematic classifications in recent years. Continued progress requires an effort to better integrate the different results of the geneticists, ecologists, archaeologists, and paleontologists working on the origins of bovins. Improved communication among workers in different fields and high throughput data will greatly enhance the output, precision, and accuracy of results in studies to come.

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