Maternal and Paternal Lineages in Cross-Breeding Bovine Species. Has Wisent a Hybrid Origin?

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The tribe Bovini comprises cattle and cattle-like species. Reconstructions of their phylogeny have so far been incomplete and have yielded conflicting conclusions about the relationship of American bison and wisent (European bison). We have compared the sequences of three mitochondrial and two Y-chromosomal DNA segments. Mitochondrial DNA indicates that four distinct maternal lineages diverged after an early split-off of the buffalo species, leading to (1) taurine cattle and zebu, (2) wisent, (3) American bison and yak, and (4) banteng, gaur, and gayal, respectively. At a higher level, lineages (1) and (2) and lineages (3) and (4) are probably associated. In contrast, Y-chromosomal sequences indicate a close association of American and European bison, which is in agreement with their morphological similarity, complete fertility of hybrid offspring, and amplified fragment length polymorphism (AFLP) fingerprints of nuclear DNA. One explanation for the anomalous divergence of the mitochondrial DNA from the two bison species is lineage sorting, which implies that two distinct mitochondrial lineages coexisted in the bison-yak branch until the recent divergence of American bison and wisent. Alternatively, the wisent may have emerged by species hybridization initiated by introgression of bison bulls in another ancestral species. This “transpatric” mode of species formation would be consistent with the recent appearance of the wisent in the fossil record without clearly identifiable ancestors.

Introduction

The tribe Bovini comprises the bovine species, several of which have been domesticated as cattle (Lenstra and Bradley 1999). Within this taxon, the earliest divergence 5 to 10 MYA separated water buffalo (Bubalus bubalis), anoa (Bubalus depressicornis), and African buffalo (Syncerus caffer) from the Bos and Bison species (Janecek et al. 1996; Hassanin and Douzery 1999a, 1999b; Bunjert et al. 2002). Speciation of the latter species after a divergence time of about 1 Myr has not been complete, since all female hybrid offspring as well as the male hybrids resulting from ox-zebu and bison-wisent crossings are fertile. Hybridization of bovine species is either spontaneous or by organized crossing. (Lenstra and Bradley 1999; Ward et al. 1999; Nijman et al. 2003; Verkaar et al. 2003).

So far the bovine phylogeny has not been resolved. Morphological features (Bohlken 1961; Groves 1981; Geraads 1992) and nuclear gene sequences (Chikuni et al. 1995) are only partially informative at this level of relatedness. A comparison of mitochondrial cytochrome oxidase II (Janecek et al. 1996) or cytochrome b sequences (Schreiber et al. 1999; Hassanin and Douzery 1999a, 1999b) from complete species panels led to partial phylogenies. Janecek et al. (1996) found an anomalous association of yak with taurine cattle, which was explained by the sampling of an animal descending from a zebu via the maternal lineage (Ward et al. 1999). However, one consistent finding has been an unexpected divergence of the mitochondrial genomes from American and European bison (Janecek et al. 1996; Schreiber et al. 1999; Ward et al. 1999). Comparison of amplified fragment length polymorphism (AFLP) fingerprints of the nuclear genomes (Bunjert et al. 2002) suggested that reticulation has played a role during the evolution of the bovine species. Furthermore, a microsatellite-based tree (Ritz et al. 2000) agreed only partially with the AFLP and mitochondrial trees.

To construct a phylogeny reflecting both the maternal and paternal lineages, we have compared three mitochondrial and two Y-chromosomal gene segments from the extant Bos and Bison species. Our mitochondrial DNA data indicate an early divergence of four maternal lineages in the Bos and Bison species and confirmed the anomalous position of the wisent. However, the Y-chromosomal phylogeny is entirely consistent with the obvious similarity and cross-fertility of the two bison species. This can be explained either by a combination of recent lineage sorting events or by a hybrid origin of wisent after male introgression.

Materials and Methods

Samples

Blood or tissue was collected from the following species: ox (Bos taurus, Limousin breed), zebu (Bos indicus, Sahiwal breed, a gift from D. G. Bradley, Dublin), banteng (Bos javanicus, Blijdorp Zoo, Rotterdam), gayal (Bos gaurus, D. G. Bradley, Dublin; Hellabrunn Zoo, Munich), yak (Bos grunniens, Artis Zoo, Amsterdam), bison (Bison bison, Artis), wisent (Bison bonasus, Artis), African buffalo (Syncerus caffer, Zimbabwe), and water buffalo (Bubalus bubalis, Potenza, Italy). Genomic DNA was extracted from blood using the guanidium/isothiocyanate method as described by Ciulla, Sklar, and Hauser (1988) or from tissues using the proteinase-K/SDS method described by Sambrook, Fritsch, and Maniatis (1989).
Polymerase Chain Reaction (PCR) Amplification and Sequencing

Polymerase chain reaction was performed with 50 ng of genomic DNA, 50 ng primers specific for the mitochondrial and Y-chromosomal gene segments (see table 2 in the Supplementary Material online) in 25 μl standard PCR reaction buffer (1.5 mM MgCl₂, 0.2 mM dNTPs), and 1 U Taq polymerase. After 3 min at 95°C, 35 cycles were performed for 15 s at 95°C, 30 s at 58°C, and 45 s at 72°C, followed by a final extension step of 5 min at 72°C. Fragments were purified by agarose gel electrophoresis and QIAquick isolation (Qiagen). Sequencing from both ends was performed with 200-ng PCR product, the same primers used for amplification or internal sequencing primers (see table 2 in the Supplementary Material online), a Cy5 Big Dye terminator kit (Applied Biosystems), and an ABI Prism 310 Sequencer. GenBank accession codes are listed in table 3 of the Supplementary Material online.

Tree Reconstructions

Sequences were aligned with the program BioEdit (Hall 2002, www.mbio.ncsu.edu/BioEdit/bioedit.html) and the alignments were corrected manually (see fig. 3 in the Supplementary Material online). As indicated in the Supplementary figure 3, large indels and variable regions where the alignment was ambiguous were not used for phylogeny reconstructions. Substitution saturation in the aligned sequences was measured with the program DAMBE (Xia et al. 2003). The optimal model of likelihood was determined by using the program Modeltest (Posada and Crandall 1998) The best fit the data were obtained HKY + G for the hierarchical Likelihood Ratio tests and GTR + I + G (Nst = 6, Gamma distribution shape = 0.7088) if the Akaake Information Criterion (AIC; Akaake 1974) was taken into account. Partition homogeneity tests and maximum likelihood tree reconstructions with the models GTR + G + I and HKY85 + G, respectively, were performed as implemented in the PAUP packages (V 4; Swofford 2000). Bayesian tree reconstructions were performed by using the program MrBayes (Huelsenbeck and Ronquist 2001). All trees were plotted with African buffalo and water buffalo as outgroups. Split decompositions in the mtDNA data (Bandelt and Dress 1992) were calculated and plotted using the SplitsTree software (Huson 1998, http://bibiserv.techfak.uni-bielefeld.de/splits). A median network plot of the Y-chromosomal sequences (Bandelt et al. 1995) was constructed using the Network 3.1.0.1. program (Fluxus Technology Ltd, www.fluxus-engineering.com).

Results

Mitochondrial DNA

Segments of the cytochrome b gene (874 bp), the control region (522 bp without insertions) and cytochrome oxidase II gene (517 bp) from the bovine species were amplified and sequenced. To verify the origin of our samples, we compared our data with partial or overlapping sequences from several sources (see table 3 of the Supplementary Material online). The intraspecies variation depended on both the species and the gene segment, but it was lower than the interspecies variation except for three previously published sequences. Moreover, in trees constructed on the basis of all available data sequences from the same species were clustered (not shown). The three exceptions were a cytochrome oxidase II sequence from one yak, which now can be identified as descending from a zebu cow (Ward et al. 1999), a cytochrome oxidase II sequence from a Brahman zebu, which is of taurine origin (Janecek et al. 1996; Ward et al. 1999), and a cytochrome b sequence from a dwarf zebu (Schreiber et al. 1999), which deviates from the sequences of all other Bos or BISON species.

We conclude that our mitochondrial sequences represent the authentic maternal lineages of the respective bovine species. Plots of the sequence divergence against the percentage transversions in the third codon positions of the cytochrome b and cytochrome oxidase II genes (fig. 4 of the Supplementary Material online) showed that at more than 10% to 15% sequence divergence the control region and, to a lesser degree the cytochrome b gene, started to become saturated with mutations. This has been observed before (Rosel, Haygood, and Perrin 1995; Brant and Orti 2002) and was most notable in the comparisons of the Bos and BISON species with the African buffalo and water buffalo, respectively. However, saturation analysis (Xia et al. 2003) indicated that the sequences of cytochrome b, cytochrome oxidase II, as well as the control region were phylogenetically informative. A partition homogeneity test (Farris et al. 1994) further indicated that the tree topologies generated by the cytochrome b, cytochrome oxidase II, and control region, respectively, were not significantly different (P = 0.25), although this value appeared to be sensitive to small modifications in the alignment of the control region.

Neighbor-Joining, maximum parsimony, maximum likelihood, as well as Bayesian analysis consistently grouped the mitochondrial sequences of the Bos and BISON species into four lineages: (1) ox and zebu; (2) wisent; (3) bison and yak; and (4) banteng, gayal, and gaur (fig. 1). The clustering of these lineages depended on both the algorithm and the mitochondrial gene segment (table 1). However, the two maximum likelihood models (HKY + G and GTR + I + G with AIC), as suggested by Modeltest (Posada and Crandall 1998), generated identical topologies, which were consistent with the Bayesian analysis. The cytochrome oxidase II data favor an early split-off of the wisent, but this is not compatible with data of the control regions (table 1), which indicate an association of wisent with lineage (1). The same cluster is also generated by maximum-likelihood, Bayesian, and SplitsTree analysis of the cytochrome b sequences and by the combined data. Most trees further indicated a clustering of lineages (3) and (4).

Y-Chromosomal Sequences

Previously sequenced SRY fragments from other banteng, yak, and wisent bulls (see table 2 of the Supplementary Material online) agreed with our data, indicating the authenticity of the paternal lineages of these animals. We identified 32 mutations in 1,510 bp from SRY and 437 bp from ZFY, which are both on the male-specific part of the Y chromosome. From gaur and water buffalo,
only partial SRY sequences were available. The gaur sequences were similar to the corresponding sequences from gayal (results not shown).

The partition homogeneity test showed that the Y-chromosomal and mitochondrial topologies are significantly different \( (P = 2 \times 10^{-3}) \). A median network (fig. 1) shows which mutations are shared between species (Bandelt et al. 1995). At one position a G residue was shared by yak, American bison, wisent, and water buffalo, suggesting a G → A change in the Bos species. These species do not share other mutations, so taurine cattle, zebu, banteng, and gayal all occupy separate branches in the network. However, an association of American bison and wisent is supported by four mutations.

Discussion

After diverging for 1 Myr or less, the speciation within the Bovini is not yet complete and female hybrid offspring from Bos and Bison species are fertile. The AFLP fingerprints of nuclear DNA indicated a sharing of biallelic polymorphisms and reticulation (Buntjer et al. 2002).

By comparison of our data with published sequences, the authentic maternal and paternal descent of our samples has been verified. Except for gaur (Bos gaurus) and gayal (Bos frontalis), we found a clear segregation of species-specific mitochondrial sequences. This was confirmed by PCR-RFLP tests on mitochondrial DNA of several bovine individuals (Verkaar et al. 2001). Trees constructed on the basis of the separate mitochondrial DNA segments were generally in agreement with the topology shown in figure 1, but alternative clusterings were supported by bootstrapping values of up to 65% (table 1). Although the mitochondrial gene segments generated different topologies, the partition homogeneity test suggested that these are stochastic effects of partitioning.

Phylogenetic tree reconstructions indicate four distinct mitochondrial lineages, one of these represented by the wisent. The association of ox (Bos taurus) and zebu (Bos indicus) reflects the fertility of female as well male hybrid offspring and their divergence time of 100,000 to 200,000 years (Bradley et al. 1996). The clustering of the South-East Asian Bos species banteng and gaur is in agreement with previous data (Janecek et al. 1996; Schreiber et al. 1999) and is also consistent with the former designation of these species as Bibos javanicus and Bibos gaurus, respectively. Our data also indicate a close relation of the wild gaur and the domestic gayal or mithan (Bos or Bibos frontalis) and do not support alternative hypotheses on the origin of the gayal (Simoons 1984).

We further provide molecular evidence for a relation of bison (Bison bison) and yak (Bos grunniens), which confirms morphological evidence (Groves 1981; Geraads 1992), their association in trees of incomplete sets of Bovini species (Hassanin and Douzery 1999a; Schreiber et al. 1999; Ward et al. 1999), and AFLP fingerprinting (Buntjer et al. 2002). An early association of the banteng-gaur-gayal and the bison-yak lineages (fig. 1) has the highest bootstrapping values and appears on the basis of the present data the most likely topology. This would imply that Bos is not a monophyletic taxon.

The most striking feature of the bovine phylogeny is the divergence of the mitochondrial lineages of bison (Bison bison) and wisent (Bison bonasus), species that can produce completely fertile hybrid offspring and have similar AFLP patterns (Buntjer et al. 2002) as well as Y-chromosomal sequences (this study). Because this has been observed consistently with mitochondrial DNA fragments generated by several different PCR primers (Janecek et al. 1996; Schreiber et al. 1999; Ward et al. 1999), this work), an artifact caused by the amplification of nuclear copies of mitochondrial DNA (Zhang and Hewitt 1996) does not seem likely. The present data on three mitochondrial DNA segments from a complete panel of bovine species indicate either an association of wisent with the ox-zebu lineage or, with about equal bootstrapping support, an earlier divergence of wisent. However, because the latter possibility is not supported at all by the control region data and is also not indicated by maximum likelihood, Bayesian analysis, and SplitsTree analysis, we propose the wisent-zebu-indicus clustering as the most plausible topology.

Three explanations have been proposed for the mitochondrial divergence of the bison species (Janecek et al. 1996): phenotypic convergence, lineage sorting, and an ancient hybridization event. The first explanation can be ruled out on the basis of the complete interfertility of bison and wisent and the similarity of their AFLP patterns and Y-chromosomal sequences.

Lineage sorting is an obvious possibility and would imply an early divergence of the (American) bison/yak and zebu/taurine/wisent mitochondrial sequences, followed by a split of the zebu/taurine and wisent lineages before the first split on the species level (fig. 2). In the branch leading to both bison species, two lineages would have persisted. By four sorting events, a single lineage was fixed in the branches leading to zebu/ox, yak, American bison, and European bison, respectively, possibly during a recent or former population bottleneck.

An ancient hybridization would have been facilitated by the social structure of herd species, in which most males are excluded from reproduction by the dominating bulls and
live solitary or form separate herds. Interestingly, an introgression of bison bulls in wisent herds (fig. 2) would be compatible with paleontological records (Skinner and Kaisen 1947; Kurten 1968; Flerov 1979; McDonald 1980; Pucek 1986, 1991). These data indicate that during the Late Pliocene–Early Pleistocene the ancestral bison originated in Southern Asia from the ancestral Leptobos and spread over the temperate zone. In the Early Pleistocene, immigrants in North America were the ancestors of the Bison antiquus, from which the extant Bison bison descended (McDonald 1980). European variants were the Bison priscus (steppe wisent) and Bison schoetensacki (Pleistocene woodland wisent). Bison priscus was depicted in cave paintings of Altamira and Lascaux 17,000 to 19,000 years ago, but died out about 10,000 BC (Kurten 1968; Harington 1996). Like the extant wisent (Bison bonasus), it had relatively long hind legs, but it was larger in size and is not considered to be its ancestor. A recent mitochondrial DNA analysis of Bison priscus bones (Nielsen-Marsh et al. 2002) revealed a control region sequence that was more related to Bison bison (4.5% difference; fig. 5 in the Supplementary Material online) than to Bison bonasus (7.2%). Although the much rarer Bison schoetensacki was of the same size as Bison bonasus, it is also considered to have died out without extant descendants (Kurten 1968). Bison bonasus appeared not before the Late Pleistocene or Holocene (Flerov 1979; Pucek 1986) and is supposed to have descended from American bisons (Kurten 1968; McDonald 1980).

Combining these paleontological data with male introgression as explanation of the molecular data, we propose a tentative scenario in which the phenotype as well as the nuclear DNA of an ancient Eurasian cattle-like population was changed by systematic introgression of Bison bison, Bison priscus, or possibly Bison schoetensacki bulls. Repeated introgression eventually created a new species with a bison-like appearance, autosomal genes and Y chromosome, but with the original mitochondrial DNA from the maternal ancestor. This scenario would explain the sudden paleontological appearance of the extant wisent without clearly identifiable ancestors and may be amenable to experimental testing by molecular analysis of fossil remains (Nielsen-Marsh et al. 2002; Willerslev et al. 2003).

### Table 1

Clusters in Mitochondrial Trees: Bootstrapping Values and SplitsTree Topologies

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*NOTE.*—(1), (2), (3), and (4) indicate the numbering of the mitochondrial lineages used in the text. For maximum likelihood, values for the models HKY + G and GTR + G + I, respectively are separated by a slash. Values for the Bayesian analysis correspond to the fractions the respective clades occur among the trees sampled. In the maximum-parsimony tree of the control region bison was clustered with lineages (1) and (2) and yak with lineage (4). The clusters generated by the SplitsTree algorithm have the following designations: 1, common ancestor connected by one line to the rest of dendrogram (i.e., complete bifurcation); 2, connected by two lines; 3, connected by three lines.
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There are three canonical categories of speciation, allopatry by differentiation after genetic isolation; parapary by differentiation of neighboring populations, often separated by a hybrid transition zone (Hewitt 2001); and sympathy by differentiation within the same region. Peripatry (Barraclough and Vogler 2000) after isolation of a small founder population is special case of allopatry. However, these modes of speciation do not include a relatively fast conversion of an existing population by male introgression. Here, we propose the term transpatry, which would not be common but rather a phenomenon unique for species with a herd organization, female philopatry, and few dominating males. For the wisent, transpatry is still hypothetical, but it probably has played a role in the evolution of deer (Cathey, Bickham, and Patton 1998), macaques (Tosi, Morales, and Melnick 2000), the domestic alpaca (Kadwell et al. 2001), and goat species (N. Pidancier, G. Luikart, P. J. Weinberg, and P. Taberlet, unpublished results). The breeding of African zebus by crossing imported Indian bulls into taureine breeds (Bradley et al. 1996) may be considered an artificial form of transpatry, which has expanded the domestic habitat range of the endogenous cattle.

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