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Chromosome Conservation Among the Advanced Pecorans and Determination of the Primitive Bovid Karyotype

D. S. Gallagher, Jr., J. N. Derr, and J. E. Womack

Extensive monobrachial QFH-band homologies were found among cattle (Bovidae), pronghorn (Antilocapridae), Masai giraffe (Giraffidae), and mule and whitetail deer (Cervidae). The deer species had identical karyotypes (2n = 70, NAA = 70). Interfamily comparisons demonstrated that cattle (2n = 60, NAA = 58) and pronghorn (2n = 58, NAA = 60) were karyotypically the most similar. The giraffe possessed a 2n = 30, NAA = 54, and differed from the other artiodactyls by having a preponderance of biarmed autosomes. The primarily acrocentric deer karyotypes showed several chromosome arm disruptions relative to the other species. Comparative cytogenetic data among the advanced pecorans strongly suggest that the 2n = 60, NAA = 58 karyotype found in several species of the tribe Bovini is probably near the primitive condition for the Bovidae. However, the ancestral conditions of the sex chromosomes within the Bovidae and among the advanced pecorans remain in question.

Living artiodactyls comprise nine families: the (1) Suidae, (2) Tayassuidae, and (3) Hippopotamidae, of the suborder Suina, and the (4) Camelidae, (5) Tragulidae, (6) Cervidae, (7) Giraffidae, (8) Antilocapridae, and (9) Bovidae, of the suborder Ruminantia (Vaughan 1986). Some taxonomists place the genus Moschus in a tenth family, the Moschinae, within the superfamily Cervoidea (Janis and Scott 1988). Families of the suborder Ruminantia are placed in the infraorder Tylopoda (camelids) or Pecora (tragulids, advanced pecorans). The tragulids are viewed as the closest outgroup to the advanced pecorans (cervids, giraffids, antilocaprids, and bovids), with phylogenetic relationships among the advanced pecorans being uncertain. The taxonomic placement of these four families into superfamilies has varied with the morphological characters to assess relatedness (for a review, see Janis and Scott (1988)).

Even though phylogenetic relationships remain unclear, we are aware of no comparative cytogenetic study that has evaluated the potential usefulness of chromosomal homologies as phylogenetic characters through comparisons among all four advanced pecoran families. We find this surprising in light of the fact that chromosomal banding studies have been useful in formulating phylogenies for other mammalian groups (Qumsiyeh and Baker 1988), and that extensive chromosomal homologies have been reported among bovids, cervids, and giraffids (Buckland and Evans 1978; Fontana and Rubini 1990), although the pronghorn has not been considered. A reasonable next step is to document the extent of chromosome conservation among representatives of all four advanced pecoran families.

In this study, we present QFH-band comparisons among indicus cattle (Bovidae), pronghorn (Antilocapridae), Masai giraffe (Giraffidae), and mule and whitetail deer (Cervidae). Direct QFH-band comparisons are made using cattle chromosomes numbered according to the Reading Conference (1980) cattle GTG-band standard. As previously suggested (Gallagher and Womack 1992; Hediger 1988), chromosome homologies established with cattle couple the karyotype of other ruminants to the developing cattle physical gene map. The extensive homologies reported here are then testable through in situ hybridization of probes to genes marking specific cattle chromosomes.

Materials and Methods

We derived chromosomes from fibroblast cells of a male indicus cattle (Brahman, Y2194), male pronghorn (JEW06), male Masai giraffe (KB3332, the San Diego Zoo), female mule deer (JEW01), and male whitetail deer (JEW21). Cell culturing, chromosome harvest, chromosome band-
Results

Cattle
The QFH-band karyotype of indicus cattle (Figure 1) is equivalent to that of domestic cattle (2n = 60, NAA = 58), except for the presence of an acrocentric Y chromosome (Basrur and Gilman 1964). All chromosome pairs are discernible.

Pronghorn
QFH-banding of pronghorn chromosomes (Figure 2) allowed the discrimination of all chromosomal pairs within its karyotype (2n = 58; a biarmed autosomal pair, 26 acrocentric autosomal pairs plus the sex chromosomes). These findings are consistent with previously published karyotypic data for this species (Hsu and Benirschke 1969). Chromosomal comparisons with cattle indicated that QFH-band homologies between cattle and pronghorn are extensive, although a few differences were noted. If we assume that the cattle karyotype is primitive and the pronghorn karyotype derivative, the following chromosomal changes were noted: the telomeric end of chromosome 3 has been translocated to the telomeric end of chromosome 1 or to the centromeric end of chromosome 26; chromosome 28 has been translocated to the telomeric end of chromosome 1 or to the centromeric end of chromosome 26; chromatid has been added to the centromeric end of chromosome 20, and chromosome 20 differs by one or more paracentric inversions; chromosome 27 may differ by a paracentric inversion, although this is equivocal; the sex chromosomes are enlarged. Despite these differences, it is apparent that extensive chromosome band conservation exists between cattle and pronghorn.

Giraffe
QFH-bands of Masai giraffe chromosomes (Figure 3) allowed the discrimination of all chromosomal pairs within its karyotype (2n = 30; an acrocentric autosomal pair, 26 biarmed autosomal pairs plus the sex chromosomes). These findings are consistent with previous karyotypic data for this species (Buckland and Evans 1978). In comparing cattle chromosomes with those of giraffe, we noted a high degree of monobrachial QFH-band homology. If we assume that the cattle chromosomal condition is primitive to that of giraffe, the following chromosomal rearrangements have occurred: numerous centric fusions of autosomes have resulted in a primarily biarmed karyotype; the telomeric end of the homolog to cattle chromosome 1 has been broken and might be represented by the unidentified chromatid of giraffe chromosome 1 or 8; cattle chromosome 23 and 26 are tandemly fused, and form the q arm of giraffe 2. The homolog to cattle chromosome 25 has not been identified with certainty, but is likely represented by chromatin in the centromeric regions of giraffe chromosome 1 or 8. It is apparent that chromosomal conservation between cattle and giraffe is extensive and that the only obvious chromosomal arm disruption involves the giraffe homolog of cattle 1.

Figure 1. A QFH-band karyotype of an indicus bull. The chromosomes have been printed at two contrast levels. White lines mark the centromere position of the sex chromosomes.
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arm number of deer. We were able to associate most but not all mule deer autosomes with putatively homologous chromosomes or chromosomal segments of cattle. Chromosomes or chromosomal segments unaccounted for in this interfamily comparison are the 7 (centric hall), 24, 30, 31, and 32 in deer, and 5 (telomeric hall), 25, 27, 28, and 29 in cattle.

Discussion

Chromosome Homologies and Determination of Primitiveness

The extensive chromosome band homologies that we have documented are summarized in Table 1. As in a previous comparative cytogenetic study of the Bovidae (Gallagher and Womack 1992), we noted numerous monobrachial homologies among the advanced pectorans. The previous study of 12 bovid species representing six subfamilies documented only three QFH-band differences that were indicative of possible syntenic disruption. One of these disruptions involved the homolog of cattle chromosome 3 in Roosevelt's gazelle; the chromosome 3 homolog appeared to be broken near the middle and both resulting segments were translocated to different chromosomes. (In pronghorn, the breakage of the chromosome 3 homolog is nearer the telomeric end, and thus represents a different chromosomal rearrangement than seen in Roosevelt's gazelle.) Also, chromosome band differences have been documented among boids for homologs of cattle chromosome 9 and 14 (Gallagher and Womack 1992). These chromosome band differences were referred to by Buckland and Evans (1978) as the bovine (prominent centromeric G-positive band on the 9 but not the 14; Buckland and Evans’s chromosomes 11 and 12, respectively) and caprine types (prominent centromeric G-positive band on the 14 but not the 9). They speculated that these differences might have resulted from a reciprocal translocation, and are significant because they seem to mark an evolutionary dichotomy within the Bovidae. All Bovidae species studied possess the bovine-type chromosomal conditions, and representatives of other Bovidae subfamilies have the caprine-type (Buckland and Evans 1978; Evans et al. 1973; Gallagher and Womack 1992). Because comparisons with the Cervidae, Giraffidae (Buckland and Evans 1978; our data), and Antilocapridae (our data) have demonstrated the presence of the bovine-type chromosomes in

Deer

Mule and whitetail deer were found to have equivalent karyotypes, which is consistent with previous chromosomal data for these species (Derr et al. 1991; Wurster and Benirschke 1967a,b). QFH-bands of mule (Figure 4) and whitetail deer chromosomes (data not shown) allowed the unequivocal discrimination of most chromosomal pairs within their karyotypes (2n = 70; one biarmed autosomal pair, 33 acrocentric autosomal pairs plus the sex chromosomes). It should be noted that chromosomes 24–26 have similar banding patterns and that we were unable to discriminate chromosomes 30–32 in all cells examined.

Comparison of mule deer chromosomes with those of cattle (Figure 5) demonstrated a high degree of QFH-band similarity. If we assume that the cattle karyotype is primitive to that of the deer, it is apparent that several chromosomal arm disruptions are responsible for the higher autosomal...
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Figure 2. A QFH-band karyotype of a pronghorn. The pronghorn chromosome pairs are positioned directly above each chromosome number, and the equivalent domestic cow chromosome(s) is positioned to the right of each chromosome pair. A white line marks the centromere of domestic cow chromosome 1 and the approximate position on cattle chromosome 3 where its homolog in pronghorn is broken. Note that the homolog of cattle chromosome 28 does not occur as an acrocentric autosome in the pronghorn.

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Although we found extensive monobrachial homologies, homologous biarmed chromosomes were rare. With the exception of chromosome 1 of the mule and whitetail deer, we saw no homologous biarmed chromosomes among the species analyzed, due in part to the fact that only the giraffe possessed a primarily biarmed karyotype. However, we have also compared the 14 biarmed autosomal pairs identified in the present study to 62 biarmed pairs identified among an additional 10 bovids (see Table 1 in Gallagher and Womack 1992) and noted only two possible homologies. One involves giraffe autosome 9 and greater kudu 2, and the other, giraffe 10 and Roosevelt’s gazelle 5. Chromosomes 9 and 2 are comprised of homologs to cattle chromosomes 9 and 22, whereas chromosomes 10 and 5 are comprised of homologs to cattle chromosomes 4 and 28. The most parsimonious explanation is that these biarmed chromosomes are independently derived by centric fusion, since the same monobrachial homologs comprising these biarmed chromosomes are involved in multiple independent centric fusions within the Bovidae (Gallagher and Womack 1992).

Our finding of predominantly monobrachial homologous biarmed chromosomes among the advanced pecorans affirms the Wurster and Benirschke (1968) hypothesis of bovid chromosome evolution by centric fusion, and negates the centric fission hypothesis of Todd (1975). Since we have established monobrachial homologies in at least one outgroup taxon for all cattle autosomes, a karyotype equiv-
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ental to that of cattle ($2n = 60$, NAA = 58) with the bovine-type chromosomes 9 and 14 is probably primitive for the Bovidae. Also, comparisons between the okapi (seven biarmed autosomal pairs) and giraffe have revealed only monobrachial homologies, and that centric fusions are primarily responsible for interspecific karyotypic differences within the Giraffidae (Petit and De Meurichy 1992). Thus, karyotypic evolution within the Giraffidae has likely proceeded from an ancestral karyotype comparable to that of bovids. The pronghorn karyotype is also readily derived from such a karyotype.

Because of the extensive variation of the sex chromosomes among the pectorals, the bovid ancestral conditions for the X and Y chromosomes remain uncertain. Bovid sex chromosomes have been shown to vary in banding, centromere placement and size, and even autosomal to sex chromosome translocations have been documented (Efron et al. 1976). In fact, it was once speculated that the ancestral bovid karyotype was comparable to that of some species of the Antilopinae, which have 28 biarmed autosomes in females plus an autosome to X chromosome translocation (Todd 1975), but, as discussed previously, the available comparative cytogenetic data define the ancestral bovid karyotype as 58 acrocentric autosomes plus the sex chromosomes. Autosome to sex chromosome translocations within the Bovidae [e.g., Tragelaphini t(Y; 13) and t(X; 5) Antilopinae] must be considered derivative, because no outgroup taxa to the Bovidae have been shown to possess autosome to sex chromosome translocations. Also, because cytogenetic comparisons have documented that homologs of the same autosomes shown to be fused to sex chromosomes are involved in multiple translocation events within the Bovidae (Gallagher and Womack 1992), the most parsimonious explanation is that autosome to sex chromosome translocations are derived character states.

Although sex chromosomes are variable, QFH-band comparisons within the Bovidae have shown that the chromosomal region corresponding to cattle Xq is relatively conserved while Xp is more variable (e.g., centromere placement, banding, and amount of chromatin) (Gallagher and Womack 1992). Because our QFH-band comparisons have shown conservation of cattle Xq among all the advanced pecoran species analyzed, this putative X chromosomal homology was likely present before the adaptive radiation of the advanced pecorans. Otherwise, sex chromosome variation within the Bovidae and among the advanced pecorans is so great that no conclusions can be drawn regarding primitiveness.

As with cattle Xq, monobrachial homologies occurring in all four families (Table 1) are presumed to have been present in the ancestral lineage leading to the advanced pecorans. In those instances where chromosomal rearrangements have been documented (e.g., cattle 6, and deer 8 and 34), we cannot be sure of the direction of chromosomal change, because we have been unable to establish the primitive condition for the advanced pecorans through comparisons with outgroup taxa. Cytogenetic comparisons made with the Tragulidae (Javan chevrotain), Camelidae (llama), and Suidae (domestic pig) did not allow polarization of character transformations because chromosomal band homologies were rare (data not shown). Comparisons with other outgroup species might prove more fruitful, but our initial comparisons suggest that this is unlikely. However, it might prove possible to establish primitive conditions for some or all of the character transformations by cytogenetically analyzing additional advanced pecoran species, especially within the Cer.
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The autosomal arm numbers are shown. The syntenic group designation in parenthesis follows those cattle chromosomes to which genetic markers have been assigned (Barendse et al. 1994, Womack et al. 1993). Cattle chromosome numbers in bold type are of autosomes shown to be conserved in representative species of all other pecoran families. Homologs to the remaining cattle autosomes determined to be conserved in one or two of the other families are in bold type.

1. The placement of the centromere differs from that in cattle chromosome 1.
2. The placement of the centromere differs from that in cattle, and a telomeric portion representing cattle chromosome 1 bands 42–46 may be present at the pericentromeric region of giraffe 1 or 8.
3. A telomeric portion homologous to cattle chromosome 3 bands 34–37 is represented by 1p or 26p.
4. Deer chromosome 14 is homologous to the centromeric half of cattle 5 bands 11–24, whereas the chromosomal material homologous to the telomeric half of cattle 5 bands 25–35 has not been identified in the deer karyotype.
5. Chromatin in the pericentromeric region of giraffe chromosome 1 may be homologous to cattle chromosome 5 or 25 or cattle 1 bands 42–46.
6. Pronghorn chromosome 20 differs from that of cattle by having additional pericentromeric chromatin and one or more paracentric inversions.
7. Chromatin in the pericentromeric region of giraffe 8 may be homologous to cattle chromosome 5 or cattle 1 bands 42–46, and the Q-positive band of giraffe 8q, which is believed to be homologous with cattle 20 band 21, is not as bright in giraffe.
8. The centromeric half of giraffe 2q is homologous to cattle chromosome 23.
9. The homolog to cattle chromosome 25 has not been identified in giraffe, but may be represented in the pericentromeric region of giraffe 1 or 8.
10. The homolog to cattle chromosome 25 has not been identified in deer.
11. The telomeric half of pronghorn 26 is homologous to cattle 26, whereas the centromeric half is homologous to cattle chromosome 28 or 3 bands 34–37.
12. The telomeric half of giraffe 2q is homologous to cattle chromosome 26.
13. The telomeric half of deer chromosome 7 is homologous to cattle 26.
14. Chromosome 27 of pronghorn may differ from that of cattle by a paracentric inversion.
15. The identity of the homolog of cattle chromosome 28 in pronghorn is uncertain, but it is likely represented by 1p or the centromeric half of chromosome 26.

**Figure 5.** Chromosome comparisons between the domestic cow and the mule deer. A haploid set of cattle chromosomes is displayed, and each bovine chromosome is positioned above a large number or letter corresponding to the Reading Conference (1980) designation. Male deer chromosomes or chromosome segments are positioned to the left or right of homologous bovine chromosomal regions. The mule deer chromosomes are numbered according to Figure 4, with a small number or letter placed at the centromere of each chromosome. Note that the telomeric half of deer 7 (below the white line) appears homologous with cattle 25.
Figure 5. Chromosome comparisons between the domestic cow and the mule deer. A haploid set of cattle chromosomes is displayed, and each bovine chromosome is positioned above a large number or letter corresponding to the Reading Conference (1980) designation. Mule deer chromosomes or chromosome segments are positioned to the left or right of homologous bovine chromosomal regions. The mule deer chromosomes are numbered according to Figure 4, with a small number or letter placed at the centromere of each chromosome. Note that the telomeric half of deer 7 (below the white line) appears homologous with cattle 26.

vidae. For example, because the deer species that we have studied might have relatively derived karyotypes, examining the karyotypes of other cervids might reveal additional conserved chromosomal homologies between the Cervidae and the other advanced pecoran families (e.g., the homolog of cattle chromosome 6 was shown to be disrupted in the mule and whitetail deer but not in the giraffe or pronghorn; see Table 1). In this example, if we were to identify a homolog to cattle 6 in the karyotype of a cervid, the presence of a cattle 6 homolog would be considered the primitive condition for this character transformation.

Table 1. Autosomal arm homologies among the advanced pecorans

<table>
<thead>
<tr>
<th>Cattle</th>
<th>Pronghorn</th>
<th>Giraffe</th>
<th>Deer</th>
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<tbody>
<tr>
<td>1 (U10)</td>
<td>1q</td>
<td>2p</td>
<td>1p, 1q, 33</td>
</tr>
<tr>
<td>2 (U17)</td>
<td>2</td>
<td>3q</td>
<td>23, 27</td>
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<tr>
<td>3 (U6)</td>
<td>3, 1p or 26p</td>
<td>5q</td>
<td>2</td>
</tr>
<tr>
<td>4 (U13)</td>
<td>4</td>
<td>10q</td>
<td>3</td>
</tr>
<tr>
<td>5 (U3)</td>
<td>5</td>
<td>4q</td>
<td>14*</td>
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<tr>
<td>6 (U15)</td>
<td>6</td>
<td>1q</td>
<td>8, 34</td>
</tr>
<tr>
<td>7 (U22)</td>
<td>7</td>
<td>6p</td>
<td>4</td>
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<td>8</td>
<td>1p</td>
<td>22, 26</td>
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<td>9</td>
<td>9q</td>
<td>18, 29</td>
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<td>10 (U5)</td>
<td>10</td>
<td>7q</td>
<td>6</td>
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<td>11 (U16)</td>
<td>11</td>
<td>4p</td>
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<td>12</td>
<td>12q</td>
<td>9</td>
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<td>13q</td>
<td>10</td>
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<td>5p</td>
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<td>20*</td>
<td>84q</td>
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</tr>
<tr>
<td>21 (U4)</td>
<td>21</td>
<td>12p</td>
<td>28</td>
</tr>
<tr>
<td>22</td>
<td>22</td>
<td>9p</td>
<td>25</td>
</tr>
<tr>
<td>23 (U20)</td>
<td>23</td>
<td>2p*</td>
<td>15</td>
</tr>
<tr>
<td>24 (U28)</td>
<td>24</td>
<td>14</td>
<td>19</td>
</tr>
<tr>
<td>25</td>
<td>25</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>26 (U36)</td>
<td>26*</td>
<td>2q*</td>
<td>?</td>
</tr>
<tr>
<td>27</td>
<td>27*</td>
<td>8p*</td>
<td>?</td>
</tr>
<tr>
<td>28 (U29)</td>
<td>1p or 26p</td>
<td>10p</td>
<td>?</td>
</tr>
<tr>
<td>29</td>
<td>29</td>
<td>13p</td>
<td>?</td>
</tr>
</tbody>
</table>

The autosomal arm numbers are shown. The syntenic group designation in parentheses follows those cattle chromosomes to which genetic markers have been assigned (Barendse et al. 1994; Womack et al. 1993). Cattle chromosome numbers in bold type are of autosomes shown to be conserved in representative species of all other pecoran families. Homologs to the remaining cattle autosomes determined to be conserved in one or two of the other families are in bold type.

The placement of the centromere differs from that in cattle chromosome 1.

The placement of the centromere differs from that in cattle, and a telomeric portion representing cattle chromosome 1 bands 42–46 may be present at the pericentromeric region of giraffe 1 or 8.

A telomeric portion homologous to cattle chromosome 3 bands 34–37 is represented by 1p or 26p.

Deer chromosome 14 is homologous to the centromeric half of cattle 5 (bands 9–14), whereas the chromosomal material homologous to the telomeric half of cattle 5 (bands 25–35) has not been identified in the deer karyotype.

Chromatin in the pericentromeric region of giraffe chromosome 1 may be homologous to cattle chromosome 25 or cattle 1 bands 42–46, and the Q-positive band of giraffe 8q, which is believed to be homologous with cattle 20 band 21, is not as bright in giraffe.

The centromeric half of giraffe 2q is homologous to cattle chromosome 23.

The homolog to cattle chromosome 25 has not been identified in giraffe, but may be represented in the pericentromeric region of giraffe 1 or 8.

The homolog to cattle chromosome 25 has not been identified in deer.

The telomeric half of pronghorn 26 is homologous to cattle 26, whereas the centromeric half is homologous to cattle chromosome 28 or 3 bands 34–37.

The telomeric half of giraffe 2q is homologous to cattle chromosome 26.

The telomeric half of deer chromosome 7 is homologous to cattle 26.

Chromosome 27 of pronghorn may differ from that of cattle by a paracentric inversion.

The identity of the homolog of cattle chromosome 28 in pronghorn is uncertain, but it is likely represented by 1p or the centromeric half of chromosome 26.
Chromosomes as Phylectic Characters

Before beginning this study, we had hoped that genome conservation among the advanced pecorans would be extensive enough so that chromosome band homologies could be recognized, and that the chromosomal data might provide insights into phylogenetic relationships. In fact, chromosome conservation was found to be so extensive that many chromosomal characters (e.g., monobrachial homologies; see Table 1) were found to be invariable among the advanced pecorans studied. Chromosomal characters for which the ancestral condition has been shown to be retained in one or more species of each family are useless in evaluating interfamily phylogenetic relationships, but may prove useful in determining intrafamily relationships (e.g., the bovine- versus caprine-type chromosome 9 and 14). On the other hand, those chromosomal characters shown to vary among the advanced pecorans but representing character transformations for which the direction of change is undetermined are potentially useful for evaluating interfamaly relationships. However, the determination of primitiveness within these transformation series is critical since only shared-derived character states are valid indicators of relatedness (Qumsiyeh and Baker 1988).

References


