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Evolution and Recombination of Bovine DNA Repeats

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Abstract. The history of the abundant repeat elements in the bovine genome has been studied by comparative hybridization and PCR. The Bov-A and Bov-B SINE elements both emerged just after the divergence of the Camelidae and the true ruminants. A 31-bp subrepeat motif in satellites of the Bovidae species cattle, sheep, and goat is also present in Cervidae (deer) and apparently predates the Bovidae. However, the other components of the bovine satellites were amplified after the divergence of the cattle and the Caprinae (sheep and goat). A 23-bp motif, which as subrepeat of two major satellites occupies 5% of the cattle genome, emerged only after the split of the water buffalo and other cattle species. During the evolution of the Bovidae the satellite repeat units were shaped by recombination events involving subrepeats, other satellite components, and SINE elements. Differences in restriction sites of homologous satellites indicate a continuing rapid horizontal spread of new sequence variants.

Key words: Satellites — SINE elements — Ruminants — Bovidae — Cattle

A considerable fraction of the eukaryotic genome consists of repetitive elements (Charlesworth et al. 1994). In mammals the most abundant classes of repetitive elements are the LINE and SINE interspersed repeats and the satellite tandem repeats. SINEs have a length of 100–600 bp and occupy 5–10% of the intron sequences and intergenic regions. The LINE elements of the L1 family are up to 7 kb long, have been found in several mammalian species, and are probably self-replicating. Satellites are mostly located in the centromeres and account for up to 20% of the genome.

An intriguing feature of the SINEs and the satellites is their diversity. The SINE elements of the various mammalian orders or suborders are clearly nonhomologous (Weiner et al. 1986; Lenstra et al. 1993; Van der Vlugt and Lenstra 1995), while satellite units may even be specific for individual species (Miklos 1985; Wijers et al. 1993). The rapid evolution of the abundant repetitive elements is in contrast to the conservation of individual genes and their relative positions (O'Brien et al. 1993). SINE elements probably multiply via RNA intermediates (Weiner et al. 1986). The evolution of satellites has been explained by unequal crossing-over and/or saltatory amplification (Singer and Berg 1991; Marçais et al. 1993; Charlesworth et al. 1994).

The bovine genome shares three mutually related SINE elements with the other Bovidae (Lenstra et al. 1993; see Fig. 1A). Seven different bovine satellites (Fig. 1B) have been described (Singer and Berg, 1991), some of which share 31-bp subrepeats, 23-bp subrepeats, or other sequence elements. It has been suggested that the 23-mer has been the ancestor of the 31-mer (Taparowsky and Gerbi 1982).

Here we analyze the evolution of the major bovine repeats by hybridization to DNA of other ruminant and

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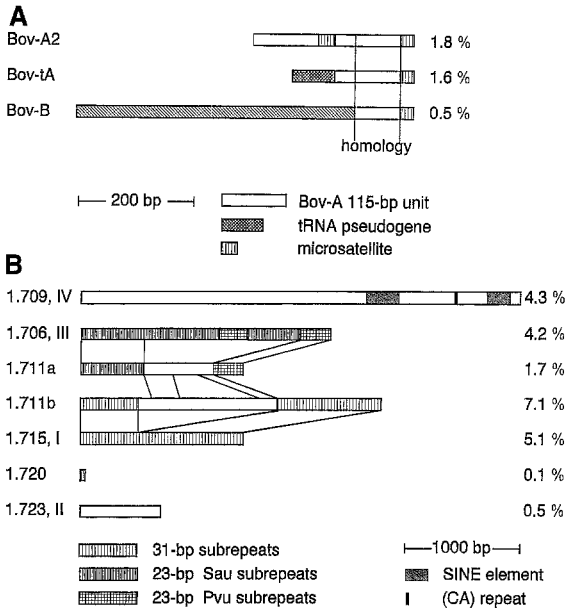

Fig. 1. **A** SINE elements of Bovidae. **B** Repeat units of bovine satellite. The Pvu and Sau 23-mer consensus sequences have been defined by Pech et al. (1979). The percentages indicate the part of the genome occupied by the repeat.

nonruminant species. The extant bovine SINE elements appear to be as old as the ruminants. In contrast, the satellites are subject to a continuing evolution via recombination and the emergence of new sequences. The 23-bp motif appears to be of much more recent origin than the 31-bp motif. The fast evolution of the satellites offers perspectives for studying the phylogeny of closely related Bovidae species.

Materials and Methods

Source and Isolation of DNA. DNA from cattle (*Bos taurus*), sheep (*Ovis aries*), goat (*Capra hircus*), and swine (*Sus scrofa*) was isolated from peripheral lymphocytes by extraction with guanidinium isothiocyanate (Ciulla et al. 1988). DNA samples from water buffalo (*Bubalus bubalis,* river type) lymphocytes were kind gifts of Drs. E.R. Mahfour (Cairo) and A. Rando (Potenza, Italy). DNA from liver tissue of chevrotain (*Tragulus javanicus*), camel (*Camelus bactrianus*), giraffe (*Giraffa camelopardalis*), and roe deer (*Capreolus capreolus*) was isolated by digestion with proteinase K in the presence of SDS (Sambrook et al. 1989).

Amplification of Probes. Probes were amplified in 50 µl PCR reaction mixture containing 50 mM KCl, 10 mM Tris/HCl (pH 9.0), 1.5 mM $MgCl_2$, 0.01% gelatin, 0.1 Triton X-100, 0.2 mM of all four dNTPs, 100 ng genomic DNA, 250 ng of two specific primers (Table 1), and 2.5 U Taq polymerase (Promega) by 35 cycles of 1 min 95°C, 1 min 60°C, and 1 min 72°C. For the amplification of the BovA segment a lower template concentration (1 or 10 ng/50 µl) was essential to prevent the amplification of longer fragments. PCR fragments were purified by agarose gel electrophoresis and binding to glass particles (Geneclean) or by electrophoresis in low-melting-point agarose.

Blot Hybridization. Genomic DNA (2–7 µg) was digested with 20–90 U restriction enzyme and fractionated on a 7% agarose gel (15 V overnight). Care was taken to load approximately the same amounts as judged by ethidium bromide staining. DNA was transferred to Hybond-N (Amersham) nylon membranes and fixed by UV crosslinking. PCR fragments (20–50 ng DNA) were labeled by random priming (Sambrook et al. 1989) with [α-^{32}P]dATP and purified by spun-column gel filtration through Sephadex G50 (Sambrook et al. 1989). Oligonucleotides (150 ng) were labeled by incubation with 10 U T4 polynucleotide kinase and 50 µCi [γ-^{32}P]ATP in 20 µl enzyme buffer for 30 min at 37°C. Blots were hybridized in 6 × SSPE, 5 × Denhardt's solution, 0.1% SDS, 0.1 mg/ml denatured herring sperm DNA, at 60°C overnight, washed in 2 × SSPE (2 × 15 min at 60°C). Autoradiography was done on Fuji X-ray films.

Analysis of PCR Products. For analysis of restriction sites PCR products (100 µl) were purified by gel electrophoresis and binding to glass particles (Geneclean, Bio 101) and digested with the restriction enzyme (10 U) in 25 µl enzyme buffer. The restriction enzyme fragments were analyzed on a 3% NuSieve (FMC)/1% agarose gel in 0.5% TBE (Sambrook et al. 1989).

Results

PCR amplification of the bovine and ovine repeats yielded fragments of the expected length (Table 1). The primers of the bovine satellite IV gave a slightly larger product with template DNA from the water buffalo. The sheep satellite I primers also amplified the homologous goat satellite I. Other heterologous PCR experiments were negative or yielded aspecific fragments.

The homologous amplification products were purified and hybridized to Southern blots with a panel of artiodactyl DNAs. As shown in Fig. 2, both the Bov-A and Bov-B SINE probes hybridized to all true ruminants, i.e., cattle, goat, deer, giraffe, and chevrotain, but not the camel and the pig. Camels belong to the tylopods, which have a digestion system that is different from that of the true ruminants. Strikingly, both *Pst*I sites in the nontruncated BovB elements that delineate an 0.5-kb fragment (Lenstra et al. 1993) are conserved in the ruminants (Fig. 2B).

The repeat unit of the bovine satellite I has a length of 1.4 kb with one *Eco*RI and two *Pst*I sites separated by 0.7 kb. Mutations in these sites give the classical satellite ladder pattern, like shown in Fig. 3A for the *Pst*I digest of cattle DNA. The patterns of satellite I of cattle and water buffalo (not shown) were similar but indicated different frequencies of *Eco*RI and *Pst*I sites.

Bovine satellite I contains subrepeats consisting of a degenerated 31-bp sequence (Gaillard et al. 1981; Pluciennicczak et al. 1982). Similar subrepeats have also been found in major satellites I from sheep and goat (Buckland 1983; Reisner and Bucholtz 1983; Novak 1984) and from deer species (Yu et al. 1986; Bogenberger et al. 1987a,b). This is reflected in a clear hybridization of the bovine satellite I probe to caprine DNA and in a weak hybridization to DNA from the roe deer (Fig. 3A). No signal was observed with DNA from the giraffe and the chevrotain. Digestion with *Eco*RI (not shown) revealed the characteristic *Eco*RI bands of the goat and sheep

Table 1. PCR primers for Bovidae repetitive elements

Repeat	Accession number	Position[a]	Sequence	Size of PCR product
SINEs				
BovA[b]	X64124/ X64126	83–102/ 10–29	aatggcaacccactccagta	101
		183–164/ 110–91	ctcagtcgtgtccgactctt	
BovB	X64125	134–154	gtcatgtatggatgagagt	247
		380–360	tcagggtcttttccaatgagt	
Satellites				
I, 1.715	V00125	1295–1314	gacttctcctgaggcgctgt	707
		610–581	aacccagggtttcctgcctca	
I, 1.714, (goat/sheep)	Z17215	734–753	tcgcctttcctgtggagagc	815
		733–714	gaggaactccagggtcgtgc	
III, 1.706				
Consensus Pvu segments[c]			aatcawgcagctcagcaggcart[d]	
Consensus Sau segments[c]			gatcacgtgactgatcatgcact[d]	
IV, 1.709	X00979	1–23	aagcttgtgacagatagaacgat	603
	582–603		caagctgtctagaattcaggga	
1.711a/1.711b	V00115	40–59	atgaggaaggaggctcggca	542, 1023
	V00116	156–176		
	V00115	581–561	tgatccagggtattcgaagga	
	V00116	1178–1158		
1.711b	V00116	357–376	ctgggtgtgacagtgtttaac	675
		1031–1010	ccagaaggtaagagaaagaacg	

[a] Primers derived from the complementary strand are indicated by reversed numbering ("183–164")
[b] BovA indicates the monomer from the dimeric Bov-A2 and the Bov-tA SINE elements
[c] See Pech et al. (1979)
[d] Not used as PCR primers but as hybridization probes

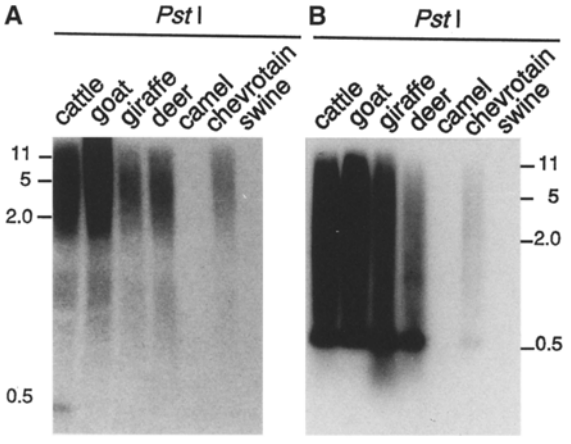

Fig. 2. Hybridization of bovine SINEs to artiodactyl genomes. **A** BovA probe. **B** BovB probe.

satellites (Buckland 1983; Reisner and Bucholtz 1983; Novak 1984). The same cross-hybridization pattern was observed with the sheep satellite I probe (not shown).

All other major satellites were confined to the Bovini species (cattle, water buffalo). Only the 0.6-kb insert of the 1.711a satellite hybridized faintly to caprine DNA (Fig. 3B). In cattle this insert forms together with the 23-mer subrepeats from satellite III a 1.4-kb repeat unit (Streeck 1981). In the water buffalo *Pst*I digest, the major fragments have lengths of 2.5, 5, and 7.5 kb, respectively (Fig. 3B). This indicates the presence of a satellite with a 2.5-kb repeat unit related to the cattle 1.711a insert.

The 1.711b satellite combines the 31-mer subrepeats from satellite I with a 1.2-kb insert, part of which is almost identical to the 1.711a-specific sequence (Streeck 1982). A probe specific for the 1.711b satellite binds to the expected fragments from cattle DNA but relatively weakly to DNA from the water buffalo (Fig. 3C).

The repeat unit from satellite IV consists of a 3.9-kb *Hin*dIII fragment, which contains a Bov-A2 as well as a Bov-B SINE element (Lenstra et al. 1993) and a $(CA)_n$ microsatellite, but no other tandem subrepeats (Skowronski et al. 1984). The satellite IV–specific probe hybridizes to the 3.9-kb *Hin*dIII DNA fragment from both cattle and water buffalo (Fig. 3D). In *Pst*I digests, one bovine fragment (2.5 kb) and three water buffalo fragments (1, 2, and 3 kb) were detected.

The repeat unit of 1.706 satellite III consists entirely of 23-bp subrepeats, which closely conform to two related consensus sequences (Pech et al. 1979). Part of the 1.706 repeat unit is also a component of the repeat unit of the 1.711a satellite (Streeck 1981). Two oligonucleotides corresponding to the two 23-bp consensus sequences were used as probes for the satellite III. After washing at low-to-moderate stringency (2 × SSPE, 60°C), both probes hybridized exclusively to bovine DNA (Fig. 3E). It was checked that the oligonucleotides did not cross-hybridize under these conditions.

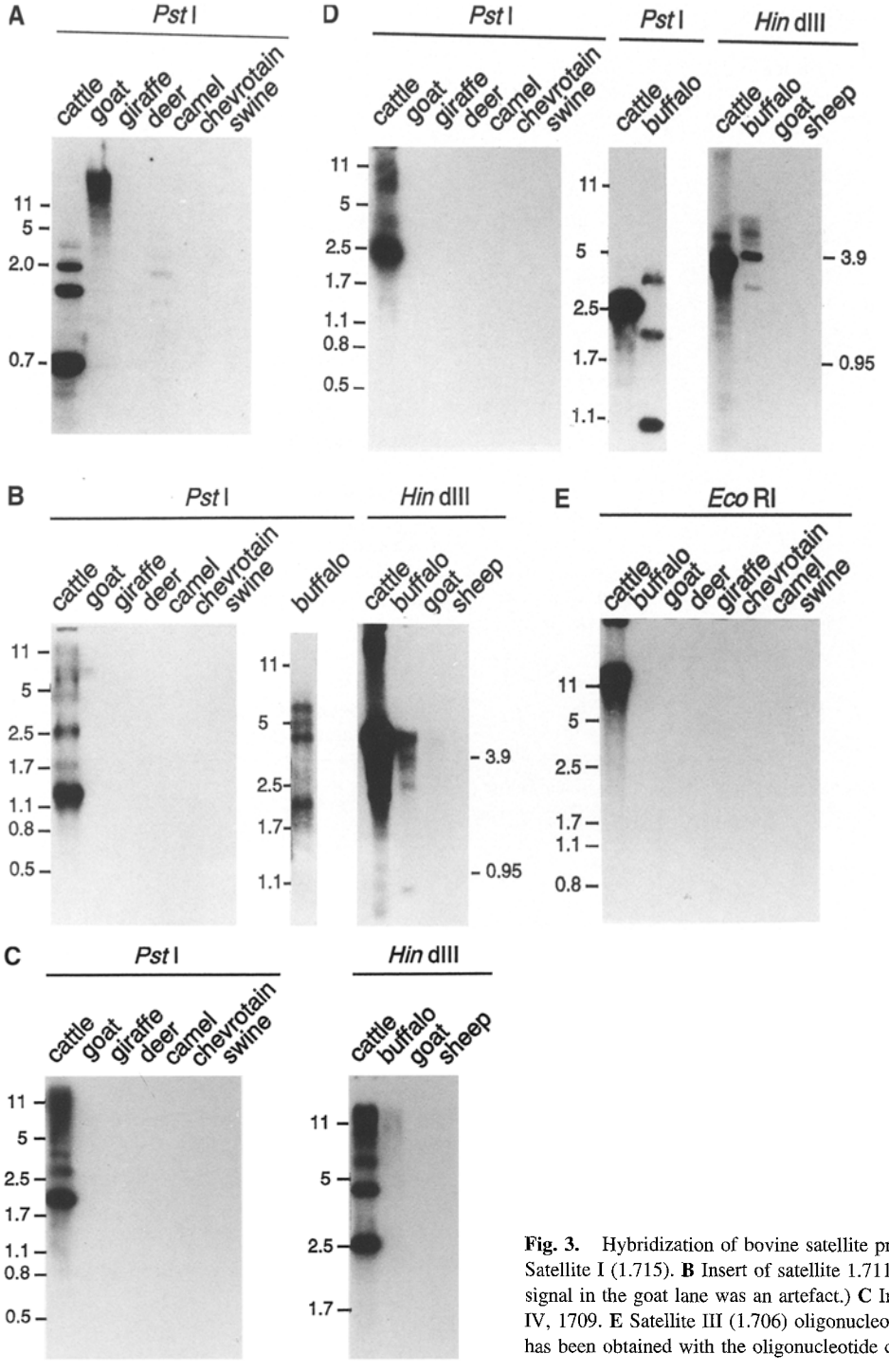

Fig. 3. Hybridization of bovine satellite probes to artiodactyl genomes. **A** Satellite I (1.715). **B** Insert of satellite 1.711a. (It was checked that the spurious signal in the goat lane was an artefact.) **C** Insert of satellite 1.711b. **D** Satellite IV, 1709. **E** Satellite III (1.706) oligonucleotide (Pvu consensus; the same result has been obtained with the oligonucleotide corresponding to the Sau consensus).

From the blot hybridizations it was apparent that satellites I and IV have different restriction patterns in cattle and water buffalo. For satellite IV this could be confirmed by digestion of satellite PCR products (Fig. 4), indicating different frequencies of *Hae*III and *Hin*fI sites. The amplification products of satellites I of goat and sheep, respectively, have different frequencies of *Eco*RI and *Alu*I sites. This confirms the results of Buckland (1983) based on Southern blotting of genomic DNA.

Discussion

Evolution of SINE Elements

Our results indicate that both the Bov-A and the Bov-B SINE sequences that have been described for the Bovidae species (Lenstra et al. 1993) are in fact specific for the Ruminantia or true ruminants. In the Bovidae, two Bov-A elements form a dimer (Bov-A2), while one

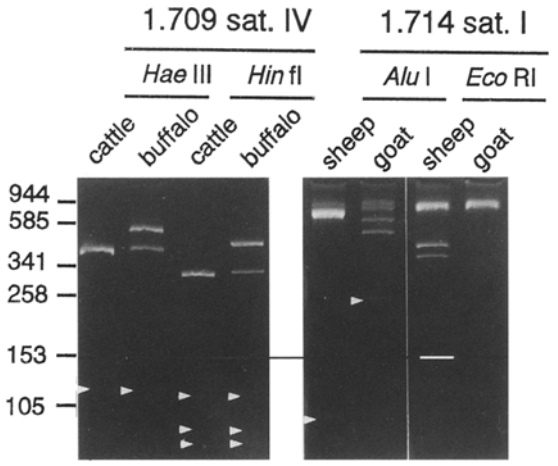

Fig. 4. Cleavage patterns of PCR fragments of homologous satellite units. *White arrowheads* indicate vague bands.

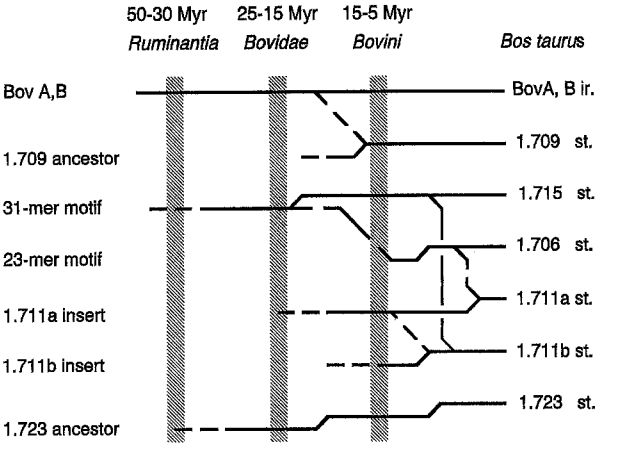

Fig. 5. Recombination of bovine DNA repeats. *ir,* interspersed repeats; *st,* satellites. The *vertical bars* indicate the approximate dating (Buckland 1985; Allard et al. 1992; Amano et al. 1994) of the common ancestors of the Bovini (domestic cow, the water buffalo, and other cattlelike species), the Bovidae (cattle, water buffalo, sheep, and goat), and the Ruminantia (Bovidae, deer, giraffe, and chevrotain, but not the camels).

Bov-A preceded by a tRNA-like sequence forms the SINE Bov-tA. Our results do not permit any conclusion about the occurrence of Bov-A2 and Bov-tA in other ruminants. However, the length of the Bov-B elements has been conserved, as witnessed by the conservation of the 0.5-kb *Pst* fragment.

In the swine, a representative of the Suidae branch of the artiodactyls, a different SINE element has been identified (Singer et al. 1987; Frengen et al. 1991). Other mammalian SINE sequences are specific for the orders of the primates, rodents (Weiner et al. 1986), carnivores (Coltman and Wright 1994; Van der Vlugt and Lenstra 1995), or Equidae (Sakagami et al. 1994). The evolution of SINE elements may be explained by amplification of pseudogenes of a tRNA (Sakamoto and Okada 1985; Okada and Ohshima 1993) or other small RNAs, during which sequence variants with the highest frequency of retroposition accumulate and established copies acquire random mutations. Apparently, the time scale of these changes in relation to the mammalian speciation is such that SINE elements are specific for zoological orders or suborders.

Several others (Quentin 1988, 1989, 1994; Batzer and Deininger 1991; Leeflang et al. 1993) described the emergence of human or mouse species-specific SINE subfamilies. Species-specific subfamilies may explain the relatively weak hybridization of the bovine SINE probes to the genomes of distantly related ruminants (Fig. 2).

Satellites

Several sequence elements are present in the repeat units of two of the satellites (Fig. 1B). The hybridization of bovine satellite probes to DNA from other ruminants allows an estimation of the relative age of these satellite components and a reconstruction of their complex history (Fig. 5).

A 31-mer motif is the subrepeat of bovine satellites I (Pluciennicczak et al. 1982) and 1.711b (Streeck 1982), ovine/caprine satellites I (Buckland 1983; Reisner and Bucholtz 1983; Novak 1984), deer satellites IA (Bogenberger et al. 1987b), and a pronghorn satellite (Denome et al. 1994). The bovine and ovine satellite I probes hybridize to each other and to the deer satellite, but not to DNA of giraffe and chevrotain. This suggests an amplification of the 31-mer motif just after the initial radiation of the ruminants, after which tandem arrays of motifs are organized as species-specific satellite repeat units.

Other bovine satellite components emerged after the radiation of the Bovidae as indicated by their virtual absence in goat and sheep DNA. The new satellites may either have amplified in the branch leading to cattle or result from a rapid concerted evolution of repeats already present in the common ancestor of the Bovidae. The second mechanism is probably responsible for the divergence of the minor satellite II from cattle, sheep, and goat (Buckland 1985).

The 1.709 satellite IV amplified independently from the other satellites, but includes a Bov-A2 SINE, a Bov-tA SINE, and a microsatellite (Skowronski et al. 1984; Lenstra et al. 1993). Other repeat units have been formed by recombination of existing satellite components. The sequence of the 1.711a insert has been coupled to a fragment from the recently emerged satellite III containing the 23-mer subrepeat. However, in water buffalo it is part of a 2.5-kb *PstI* satellite (Fig. 3B), apparently without the 23-mer subrepeats. The 1.711b-specific sequence appears younger that the 1.711a insert, since it hybridizes only weakly to the DNA of the water buffalo. By insertion of this sequence within the 1.711a insert and coupling to a fragment of satellite I, the complete repeat unit of the 1.711b satellite has been formed.

The 23-mer subrepeat of satellite III appears to be related to the 31-mer of satellite I (Taparowsky and Gerbi 1982). However, its absence in the water buffalo implies that the 23-mer has been derived from the 31-mer instead of vice versa. This is confirmed by the homogeneity of the 23-mer (Pech et al. 1979; Streeck 1981) as opposed to the degeneration of the 31-mer (Gaillard et al. 1981; Plucienniczak et al. 1982). After the recent formation of the repeat unit of satellite III, which contains two basic variants of the 23-mer (Pech et al. 1979), part of this unit became a component of the 1.711a satellite.

The differences in restriction sites of homologous satellites of related species (Figs. 3 and 4) show that established satellites remain subject to homogenization processes during which new sequence variants continuously replace older variants. Apparently, the satellite evolution includes a rapid mechanism to spread the new satellite and sequence variants over all chromosomes (Modi et al. 1994).

The dynamic evolution of the satellites may offer perspectives for studying phylogeny. Sharing of satellites or satellite sequence variants would indicate common descent, while the rapid horizontal evolution should allow a discrimination of closely related species or subspecies. With satellites from pupfish it has even been demonstrated that the sequence depends on the population (Elder and Turner 1994). Although this approach yields inherently qualitative data, it would complement the analysis of mutations in mitochondrial DNA, which could not resolve completely the phylogeny of the Bovidae (Allard et al. 1992; Gatesy et al. 1992; Amano et al. 1994).

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