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Comparison of GTG-banded karyotypes and microsatellite sequences in some species of the *Bovidae* and *Cervidae* families*

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ABSTRACT

Comparison of GTG-banded cattle, sheep, goat, and fallow deer chromosomes showed conformity of G-banding patterns for chromosomes of fallow deer. In *Bovidae* species, autosomes were shown that were involved in centric fusion, giving a metacentric pair in fallow deer.

Twenty-two microsatellite markers were amplified with the use of bovine specific primers in the investigated species. The results of cross-species amplification showed that microsatellites *BM143*, *CSSM016* and *TGLA53* seem to be conservative across all investigated ruminant species. Sequencing confirmed short tandem repeat motives of the *TGLA53* marker among selected *Bovidae* and *Cervidae* species. About 60% of microsatellite loci were successfully amplified with the use of bovine primers in sheep and red deer species, 50% in goat, 55% in western roe deer, and 36% in fallow deer. This suggests that, on the DNA level, the genomes of red deer and sheep are more closely related to the bovine genome than genomes of the other studied ruminants.

KEY WORDS: comparative cytogenetics, *Bovidae*, *Cervidae*, G-banding, microsatellite markers

INTRODUCTION

Comparative studies of the genomes of different animal species are based mainly on the phenomenon of genetic conservation. This concerns chromosome

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banding patterns (Iannuzzi and Di Meo, 1991, 1995; Ansari et al., 1999), nucleotide sequences (e.g., microsatellite sequences) (de Gortari et al., 1997) and groups of linked or syntenic genes that often have the same relationships even in taxonomically distant species (Slate et al., 2002).

Comparison of karyotypes after differential staining of chromosomes using GTG, RBA, RBG and QFQ techniques reveals conservation of chromosome banding patterns (Ansari et al., 1999; Słota et al., 2001). Identification of homologous chromosomes or their fragments from different animal species is most often conducted within systematic units, providing further evidence that evolutionary relatedness is paralleled by karyotype similarity (Iannuzzi and Di Meo, 1995; Słota et al., 2001).

A large number of papers also reported conservation on the DNA level between different mammalian species, based on anonymous DNA markers such as microsatellite loci (Moor et al., 1991; de Gortari et al., 1997; Slate et al., 1998). Microsatellite markers have been efficiently used in genome mapping projects, pedigree determination, and population genetics in humans and animals. Cross-species utilization of microsatellite loci enables the construction of comparative maps between related species (O'Brien et al., 1993). These tandemly repeated, highly polymorphic, single locus DNA sequences are well distributed over genomes (Tauz, 1989) and are readily adaptable to the polymerase chain reaction method in terms of simultaneously amplifying a number of markers in one reaction (Ziegle et al., 1992). The aim of the presented study was to compare metaphase chromosome G-banded patterns and DNA microsatellite markers of some species from the *Bovidae* and *Cervidae* families.

MATERIAL AND METHODS

Animals

The following animal species were chosen for comparative analyses: cattle (*Bos taurus*), 30 animals; sheep (*Ovis aries*), 10 animals; goat (*Capra hircus*), 10 animals; fallow deer (*Dama dama*), 3 animals; western roe deer (*Capreolus capreolus*), 4 animals; and red deer *(Cervus elaphus),* 2 animals. Cattle, sheep and goats belong to the family *Bovidae,* and fallow deer, western roe deer, and red deer to the family *Cervidae.* The animals originated from the Experimental Stations of the NRIAP *(Bovidae)* or private farms *(Cervidae)*.

Laboratory techniques

Metaphase chromosome preparations obtained after routine *in vitro* lymphocyte culture were analysed. The GTG differential staining technique was used for precise identification of chromosome pairs (Wang and Fedoroff, 1972).

The cattle, sheep, and goat karyotypes were arranged based on the G-banding standards developed by Ansari et al. (1999) and Di Berardino et al. (2001). Because there is no international standard for the G-banding pattern of *Dama dama,* the karyogram for this species was arranged based on chromosome morphology, chromosome size and G-band homology following the guidelines given by Rubini et al. (1990). A comparative karyogram was then made by comparing the G-band patterns on the chromosomes of the cattle, sheep, goats and fallow deer and homology was identified between them.

DNA of the studied animals, derived from blood or hair roots, was amplified using bovine specific primers for 22 microsatellite markers (Table 1) in two PCR reactions of the multiplex type. Eleven markers (*BM1824, BM2113, ETH10, ETH225, ETH3, INRA23, SPS115, TGLA122, TGLA126, TGLA227* and *TGLA53*) were amplified with the use of Stock Marks for Cattle PCR-typing Kit (PE Applied Biosystems, Foster City, CA) with PCR conditions as described in the kit protocol. For the markers forming the additional panel for cattle parentage verification used by the authors, PCR multiplex was earlier elaborated to amplify bovine genomic DNA. PCR products were subjected to vertical electrophoresis in 4% denaturing polyacrylamide gel on a Genetic Analyser (ABI PRISM 377). The allele sizes in base pairs (bp) were determined after processing of raw data using the software packages GENESCAN 2.0 and GENOTYPER 2.1 (Applied Biosystems). A single-band PCR product was considered to be a conserved microsatellite only if the observed band showed a distinctive 'stutter' pattern and was close to the size range of the observed cattle product. As an example of conservation of a DNA sequence, some of the STR alleles were sequenced to determine the structure and conservative region of tandem repeats among four species (cattle, fallow deer, sheep and goat). Namely, a new set of *TGLA53* primers was designed to obtain longer PCR products for the sequencing reaction (around 400 bp). Direct sequencing of *TGLA53* PCR products was performed from both strands using Big Dye Terminator Chemistry (Applied Biosystems). Only repeat regions were considered in the comparison of sequencing reads between species.

RESULTS

Karyotype analyses were performed in cattle, sheep, goats, and fallow deer and the compared karyograms are presented in Figure 1.

Comparison of GTG-banded cattle (2n=60, NF=58), sheep (2n=54, NF=58), goat (2n=60, NF=58), and fallow deer (2n=68) chromosomes showed conformity of G-banding patterns for 28 pairs of fallow deer autosomes (one pair of metacentrics and 27 pairs of acrocentrics) and heterosomes. We did not find homologous or homeologic chromosomes in cattle, sheep, and goat karyotypes for fallow deer

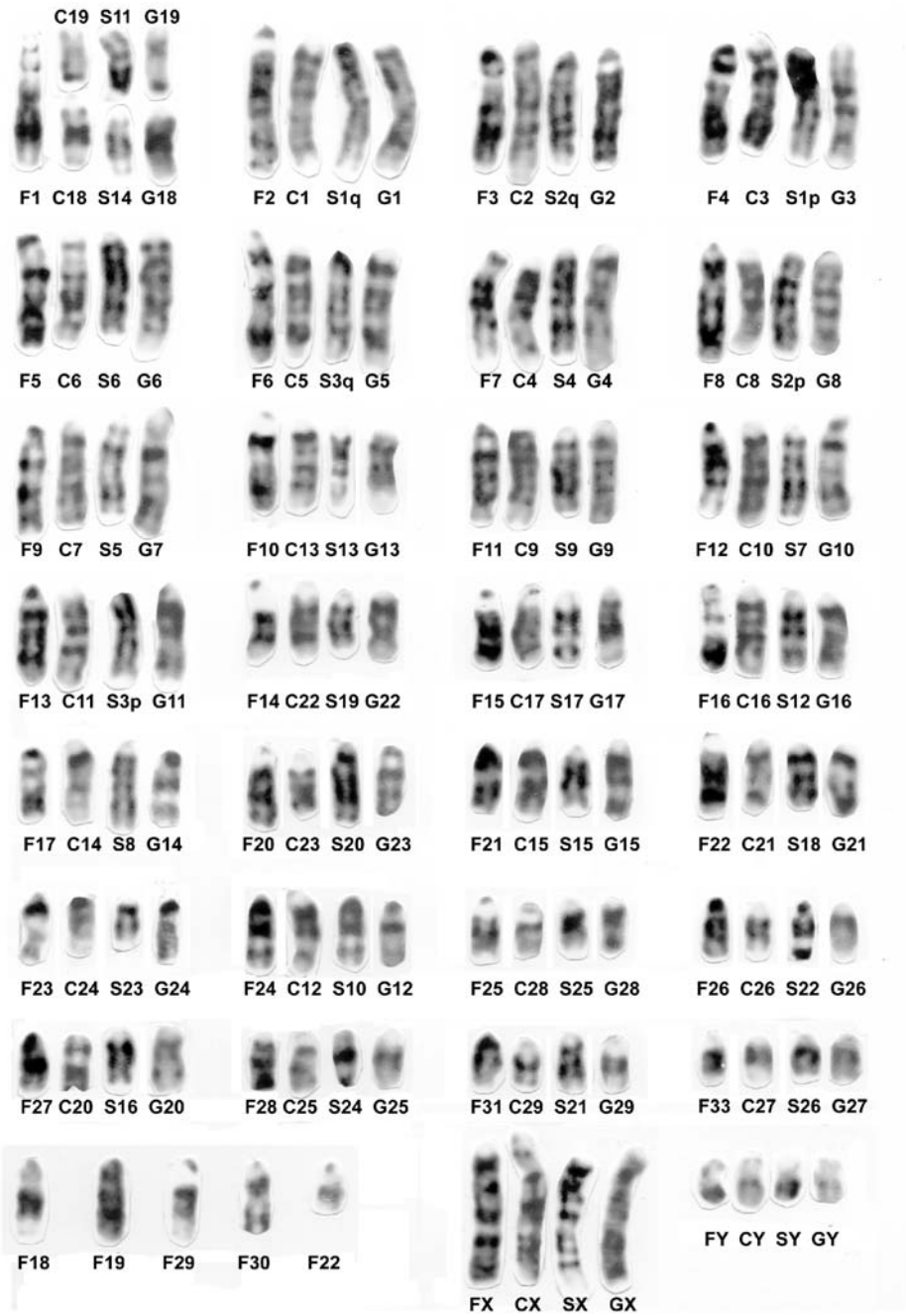

Figure 1. Comparison between the G-banded karyotype of the fallow deer (F), cattle (C), sheep (S) and goats (G)

Table 1. PCR results for 22 microsatellite markers among *Bovidae* and *Cervidae* species

Species	*AGLA 293*	*BM 143*	*BM 1818*	*BM 1824*	*BM 2113*	*BM 2830*	*CSSM 014*	*CSSM 016*	*CSSM 042*	*ETH 10*	*ETH 225*	*ETH 3*	*INRA 23*	*MB 026*	*SPS 115*	*TGLA 122*	*TGLA 126*	*TGLA 227*	*TGLA 263*	*TGLA 53*	*TGLA 57*	*TGLA 73*
Cattle (*Bos taurus*)	223*	100	261	178	125	153	138	167	175	217	140	117	206	208	248	141	115	79	107	162	94	116
	231	102	263	180	127	157	146	171	179	219	146	121	208	210	252	147	117	81	111	164	96	118
	233	104	265	182	131	159	150	173	183	223	148	125	210	212	254	149	119	83	119	168	98	120
	243	106			135	161	152	175	185		150		214	214	256	151	121	91	125	172	100	122
		110			137	167	154	177	201				216	220	260	153	123	93	127	183	104	124
		112			139	169		179	211					222		163	125	97			106	126
									219					224		175		101				130
									223							183		103				
Sheep (*Ovis aries*)	-**	114	-	168	-	207	122	147	183	207	146	97	-	-	236	149	117	-	119	152	-	-
		122		172							148	105			242		127			162		
Goat (*Capra hircus*)	-	102	-	-	137	207	-	141	-	209	150	-	-	214	250	-	133	-	-	148	88	-
								143		213				226								
Red deer (*Cervus elaphus*)	-	104	-	178	125	-	134	163	-	219	142	119	202	-	246	139	109	97	-	154	-	-
		108		188	131						146		206			141	117	99		164		
					135						154					163				176		
											158									184		
Fallow deer (*Dama dama*)	-	108	-	-	123	-	-	147	197		138	-	-	212	-	161	-	-	-	164	-	-
Western roe deer (*Capreolus capreolus*)	223	120	-	166	-	-	-	159	-	225	-	117	-	232	-	153	-	83	109	158	94	-
								161						242		155				166		
																				168		
																				180		

* base pairs
** lack of PCR product

autosome pairs: 18, 19, 29, 30 or 32. In these three species of *Bovidae,* autosomes were shown that were involved in centric fusion giving a metacentric pair in fallow deer (Figure 1).

The results of cross-species amplification in 22 microsatellite loci are presented in Table 1. All markers are located on bovine autosomes. From 22 bovine microsatellite markers 14 loci were successfully amplified in sheep (*Ovis aries*), 11 in goat (*Capra hircus*), 14 in red deer (*Cervus elaphus*), 8 in fallow deer (*Dama dama*) and 12 in western roe deer (*Capreolus capreolus*). For marker *BM1818*, *INRA23* and *TGLA73* PCR amplicons were obtained only with the use of bovine DNA. The number of observed microsatellite alleles in species other than cattle ranged from 1 to 4, depending on locus. From a total of 119 bovine alleles observed in this study, 31 were amplified in other species. In sheep these are 7 alleles (*CSSM042*-183 bp, *ETH225*-146 and 148 bp, *TGLA122*-149 bp, *TGLA126*-117 bp, *TGLA263*-119 bp, *TGLA53*-162 bp), in goats, 4 alleles (*BM143*-102 bp, *BM2113*-137 bp, *ETH225*-150 bp, *MB026*-214 bp), in red deer, 12 alleles (*BM143*-104 bp, *BM1824*-178 bp, *BM2113*-125, 131 and 135 bp, *ETH10*-219 bp, *ETH225*-146 bp, *INRA23*-206 bp, *TGLA122*-141 and 163 bp, *TGLA126*-117 bp, *TGLA227*-97 bp), in fallow deer, 2 alleles (*MB026*-212 bp and *TGLA53*-164 bp), and in western roe deer, 6 alleles (*AGLA293*-223 bp, *ETH3*-117 bp, *TGLA122*-153 bp, *TGLA227*-83 bp, *TGLA53*-168 bp and *TGLA57*-94 bp). The structures of the repeat region of allele *TGLA53*-164 bp in cattle and fallow deer, allele *TGLA53*-152 bp in sheep and *TGLA53*-148 in goat are presented in Figure 2. Sequencing of the repeat region of microsatellite *TGLA53* revealed no differences in the repeat structure between cattle and fallow deer species [$(AT)_{12}(AC)_5GC(AC)_5$]. A shorter repeat region of the *TGLA53* allele was revealed in sheep [$(AC)_{17}(AT)_5$] and goat [$(AC)_{14}$].

Description:

CH239917: Genbank Accesion No. of bovine reference sequence

cattle and fallow deer allele: *TGLA53*–164 bp [$(AT)_{12}(AC)_5GC(AC)_5$]

sheep allele: *TGLA53*–152 bp [$(AC)_{17}(AT)_5$]

goat allele: *TGLA53*–148 bp [$(AC)_{14}$]

* consensus sequence

Figure 2. Sequence alignment of TGLA53 alleles among selected *Bovidae* and *Cervidae* species

DISCUSSION

The first comparative study in the *Bovidae* family showed band homology on the chromosomes of cattle, sheep and goats (Evans et al., 1973). These findings were confirmed by Iannuzzi and Di Meo (1995), who identified autosome pairs with a homologous pattern of G- and R-bands in these three species. These authors also performed detailed analyses of the X heterosome in cattle, water buffaloes, sheep and goats, and based on the analogies identified, suggested possible rearrangements of this chromosome in the evolutionary process (Iannuzzi and Di Meo, 1995).

Comparison of GTG-banded, haploid sets of sheep (2n=54) and aoudad (*Ammotragus lervia*) chromosomes (2n=58) revealed complete chromosome homology in the karyotypes of both species and indicated that centric fusions of autosomes led to evolutionary rearrangements (Słota et al., 2001).

It is assumed that in the course of evolution, the number of chromosomes was reduced as a result of Robertsonian translocations of acrocentric chromosomes. These suggestions were confirmed by studies of polymorphic forms of karyotype in wild *Ovis* species, in which different diploid numbers of chromosomes were observed: 2n=58 (*Ovis vignei)*, 2n=56 (*Ovis ammon),* 2n=54 (*Ovis dalli, Ovis musimon, Ovis orientalis*), and 2n=52 (*Ovis nivicola*) (Bunch and Nadler, 1980).

Karyotype studies of different species of the *Cervidae* family (elk, roe deer, red deer, sika deer, and fallow deer) living in the wild, conducted by Gustavsson and Sundt (1968), concerned routinely stained metaphase chromosomes, which were classified according to size and morphology. For the *Dama dama* species, the 68,XY or 68,XX karyotype as well as the number of arms of autosomal chromosomes (68) were determined. Among the autosomes, one pair of long metacentric and 32 pairs of acrocentrics were identified. Concerning sex chromosomes, X was identified as the acrocentric chromosome and Y as a small submetacentric.

In the next step of determining the karyotype of fallow deer, the following differential staining techniques were used: GTG, with 350 G-bands obtained on metaphase chromosomes (Rubini et al., 1990) and RBA, with 527 bands obtained on prometaphase chromosomes (Lioi et al., 1994).

In our analyses, the GTG-banding karyotype of fallow deer, used for comparison with G-banding patterns on the metaphase chromosomes of cattle, sheep, and goats, revealed 450 bands and helped to pinpoint homologous chromosomes in the compared species, indicating that a level of 450 bands is sufficient for comparative studies.

A remarkable homology of most autosomes of fallow and roe deer *(Capreolus capreolus)* was revealed by comparison of the G-banded karyotypes (Rubini et al., 1990). According to these authors, the metacentric pair in the fallow deer

retains the same band patterns as the two acrocentric pairs in the roe deer, while the X chromosomes of the roe deer differ as a result of pericentric inversion.

A comparison of R-banded chromosomes of Vietnamese sika deer (*Cervus nippon pseudaxis*, 2n=66) with bovine R-banded chromosomes was described by Bonnet et al. (2001). Next, the probes for twenty-nine Texas nomenclature type I markers for each cattle autosome, sixteen other type I and fourteen microsatellite markers were used in FISH technique on sika deer chromosomes. A complete correspondence between sika deer and cattle chromosomes was established, however, autosome pair 7 of sika deer presented the most complex rearrangement as compared with cattle chromosomes.

According to our findings based on G-banding patterns, metacentric chromosomes in the fallow deer karyotype involve chromosomes having the following homology: p arm – cattle pair 19, sheep 11 and goat 19 and q arm - cattle pair 18, sheep 14 and goat pair 18. Comparison between G-banding patterns on cattle, sheep, goats and fallow deer chromosomes confirmed the chromosome homology in the *Bovidae* family described by Iannuzzi and Di Meo (1995).

To investigate the karyotype relationships between Chinese muntjac *(Muntiacus reevesi)*, forest musk deer *(Moschus berezovskii)* and gayal *(Bos frontalis)*, Chi et al. (2005) assigned a complete set of Chinese muntjac chromosome-specific painting probes to G-banded chromosomes of these three species. In total, the 22 autosomal painting probes of Chinese muntjac delineated 33 and 34 conserved chromosomal segments in the genomes of forest musk deer and gayal, respectively. The combined analysis of comparative chromosome painting and G-band comparison reveals that most interspecific homologous segments show a high degree of conservation in G-banding patterns. Eleven chromosome fissions and five chromosome fusions differentiate the karyotypes of Chinese muntjac and forest musk deer, twelve chromosome fissions and six fusions are required to convert the Chinese muntjac karyotype to that of gayal, one chromosome fission and one fusion separate the forest musk deer and gayal. The musk deer has retained a highly conserved karyotype that closely resembles the proposed ancestral pecoran karyotype but shares none of the rearrangements characteristic of the *Cervidae* and *Bovidae*.

The results obtained after comparison of the *Bovidae* and *Cervidae* families belonging to the suborder *Ruminantia* suggest that genetic conservatism is a phenomenon also frequently observed between larger systematic units than the family.

The ability to use PCR across species depends on the conservation of priming sites. Point mutations within the priming sites result in poor or no amplification (Moor et al., 1995). Despite synteny existing between cattle and other ruminants for numerous investigated loci (see Table 2) (information from INRA BovMap and arkdb Deerbase), these loci were not amplified with bovine-specific primers on DNA of ruminant species other than cattle. In our study about 60% of micro-

Table 2. Chromosomal location of 22 microsatellite markers in investigated species (information from INRA BovMap and arkdb Deerbase)

Species	*AGLA 293*	*BM 143*	*BM 1818*	*BM 1824*	*BM 2113*	*BM 2830*	*CSSM 014*	*CSSM 016*	*CSSM 042*	*ETH 10*	*ETH 225*	*ETH 3*	*INRA 23*	*MB 026*	*SPS 115*	*TGLA 122*	*TGLA 126*	*TGLA 227*	*TGLA 263*	*TGLA 53*	*TGLA 57*	*TGLA 73*
Cattle (*Bos taurus*)	5	6	23	1	2	5	4	11	2	5q25	9	19q23	3	23	15	21	20	18	3	16	1	9
Sheep (*Ovis aries*)	5	6	23	1	2	5		11		5	9	19q23	3	-	15	21	20		3			9
Goat (*Capra hircus*)			23	1	2					5	9									16		9
Red deer (*Cervus elaphus*)	5		23			5	4	11	2	5	9		3				20				1	

satellite loci were successfully amplified with the use of bovine primers in sheep and red deer species, being comparable to such a study in sheep performed by de Gortari et al. (1997) and much higher than the results obtained in red deer by Kuhn et al. (1996) (around 50% loci typed). Slate et al. (1998) obtained a substantially higher yield of microsatellite amplification in sheep and two deer species (above 70%) after extensive optimization of PCR conditions with the use of bovine primers for both species. In case of goat, our amplification reached 50% of bovine microsatellite loci and was lower than in the study of Pepin et al. (1995) (60% of loci typed). For other investigated ruminant species we reached a 55% amplification yield of bovine microsatellites in western roe deer and only 36% in fallow deer.

The PCR amplification yield of bovine microsatellite loci among different species of *Ruminantia* determined by conservation of priming sites and the presence of microsatellite alleles with the same size between species illustrate to some extent the level of their divergence in relation to the cattle genome. The presence of PCR products for *BM143, CSSM016* and *TGLA53* in all ruminant species shows that genomic regions containing these loci may be conservative across these species; however, the sequence of these regions needs to be verified to confirm specificity not only of the primers but also of the amplified region (Sun and Kirkpatrick, 1996). Stronger evidence for the conservation of the studied microsatellite markers may be the presence of alleles with the same size common for different species. In our study, the greatest number of loci with alleles equal in size to the cattle microsatellite alleles was detected in red deer. This may suggest that the genomes of these two ruminant species are most closely related than other investigated ruminants. In this regard sheep and western roe deer take the second position in phylogenetic divergence to the cattle genome and fallow deer is most distantly related. However, these findings are slightly inconsistent with syntenic data, where the number of microsatellite loci with known synteny in other ruminants, the same as bovine loci, is greater for sheep (16 loci) than red deer (11 loci). As mentioned above, this bias is caused by mismatches in primer binding sites during cross-species amplification. For example, Slate et al. (1998) pointed to close relationships between cattle, red deer and sheep genomes based on a similar proportion of markers yielding a product of cross-amplification in all three species; however, as pointed out in the work of Sun and Kirkpatrick (1996), such results must be confirmed through sequencing data. In this term sequencing of the repeat region of microsatellite *TGLA53* revealed two conserved blocks of $(AC)_5$ and $(CA)_3$ motive among selected *Bovidae* and *Cervidae* species. No differences in the repeat structure between cattle and fallow deer species are consistent with the same fragment size of the investigated *TGLA53* allele in both species. Smaller allele sizes observed in sheep and goat result from the shorter repeat region of the sheep and goat *TGLA53* allele.

CONCLUSIONS

Cytogenetic comparative analyses make it possible to identify chromosome markers common to species belonging to different families, for example cattle, sheep, goats and fallow deer, based on chromosome homologies for these species. These homologies could be useful in evolutionary research and in diagnostics of chromosome abnormalities found in wild species, because our knowledge about their karyotypes and banding patterns is insufficient.

Different amplification yields for microsatellite loci among the investigated ruminant species and also the presence or absence of microsatellite alleles with the same size common to different species are associated with the different genomic organization in particular species and thus, with different levels of conservatism of particular genomic regions. This affects not only the conservatism level of primer binding sites but also the sequence of the amplified region.

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