Bovine satellite DNAs – a history of the evolution of complexity and its impact in the Bovidae family

A. ESCUDEIRO 1,2, D. FERREIRA 1,2, A. MENDES-DA-SILVA 1,2, J. S. HESLOP-HARRISON 3, F. ADEGA 1,2, & R. CHAVES 1,2

1Department of Genetics and Biotechnology (DGB), CAG – Laboratory of Cytogenomics and Animal Genomics (CAG), University of Trás-os-Montes e Alto Douro (UTAD), Vila Real, Portugal, 2Biosystems & Integrative Sciences Institute (BioISI), Faculty of Sciences, University of Lisboa, Lisboa, Portugal, and 3Department of Genetics and Genome Biology, University of Leicester, Leicester, UK

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Abstract

Despite the many questions regarding satellite DNA sequences and their cellular roles, the evolutionary history of eukaryotic genomes seems to have been largely influenced by this dynamic and multifaceted genomic component. The bovine genome is highly rich in diverse satDNA sequences that differ in monomer sequence and length, complexity, chromosomal location and abundance, as well as in their sequences’ evolutionary mechanisms. In the evolution of the Bovidae family, the genomes’ repetitive fraction played a central role in karyotype reorganisation, and in the last few decades several studies have demonstrated and reinforced an association between centromeric satDNAs and the process of chromosome evolution in remodelling genomes of Bovidae species. Here, we review different aspects of the molecular nature and genome behaviour of all the satDNA families identified in the bovine genome, including their organisation, abundance, chromosome localisation, variation in sequence, and evolutionary history in the Bovidae family and in particular in the Bovinae subfamily, taking an integrative perspective.

Keywords: Satellite DNA, Bovidae family, evolution, genome remodelling, karyotype reorganisation

Introduction

The first studies on mammalian satellite DNA (satDNA – tandemly repeated DNA sequences) date back to the 1960s and 1970s and were carried out in the mouse, guinea pig and bovine genomes (Pardue & Gall 1970; Hsu & Benirschke 1973; Macaya et al. 1978). SatDNA families have now been reported in numerous species, giving evidence of the sequences’ evolutionary mechanisms, disclosing phylogenetic relationships between related species, showing details of autosomal and sex chromosome evolution or rearrangement, and helping scientists to understand functions of these ubiquitous DNA sequences (Chaves et al. 2004; Adega et al. 2009; Giannuzzi et al. 2012; Kopecna et al. 2012, 2014; Rojo et al. 2015). Satellite DNA has potential structural and functional roles relating to centromeric function, chromosome stability, and meiotic pairing or segregation (Schmidt & Heslop-Harrison 1998; Plohl et al. 2008; Adega et al. 2009; Giannuzzi et al. 2012; Ferreira et al. 2015).

The hypothesis that the rapid evolution of satDNAs can act as drivers for population and species divergence has been extensively raised (Udarkovic & Plohl 2002; Adega et al. 2009; López-Flores & Garrido-Ramos 2012; Paço et al. 2013; Feliciello et al. 2015; Vieira-da-Silva et al. 2015).
Several satDNA families of different origin are usually found in the genome of a species or a group of species, and these usually differ in the nucleotide sequence, monomer length, complexity, chromosomal location and/or abundance, as well as in their evolutionary history (Ugarkovic & Plohl 2002; Slamovits & Rossi 2002; Kuhn et al. 2008, 2011; López-Flores & Garrido-Ramos 2012; Rojo et al. 2015). SatDNA sequences are known for presenting a rapid generation and elimination in related species (Plohl et al. 2008; Vourc’h & Biamonti 2011); however, some of these sequences seem to have been preserved, at least in a few copies, over long evolutionary periods in some genomes (Mravinac et al. 2002, 2005; Petraccioli et al. 2015; Chaves et al. 2017).

In the evolution of the Bovidae family, the genomes’ repetitive fraction played a central role in karyotype reorganisation, and in the last few decades several studies have demonstrated and reinforced an association between centromeric satellite DNAs and the process of chromosome evolution in Bovidae species’ genome’s remodelling (Chaves et al. 2000a, 2003, 2005; Adega et al. 2006, 2009; Di Meo et al. 2006; Kopecna et al. 2012, 2014; Nieddu et al. 2015). In domestic cattle, the different known satDNA sequences are highly complex in their structure and organisation, variable in copy number and chromosomal distribution, and collectively comprise about 25% of the bovine genome (Macaya et al. 1978; Taparowsky & Gerbi 1982a,b; Modi et al. 1996), thus constituting a good model to study the evolution of satellite DNA.

In this work, we give a comprehensive review of the history and early approaches to the study of bovine satellite DNA, including the different aspects on the molecular nature and genome behaviour of all the satDNA families identified in the genome. We then present an integrative perspective, including their organisation, abundance, chromosome localisation, variation in sequence, and evolutionary history in the Bovidae family and in particular in the Bovinae subfamily. The subject “evolution and satDNA” can and should be addressed from two distinct yet complementary directions: satellite DNA sequences evolution per se and genome evolution promoted by satDNA dynamism, highlighting the phylogenetic information provided by the presence, absence or alteration of a given satDNA family. We will discuss the high dynamism found in bovine satDNA sequences and their influence on the evolutionary history of some Bovidae genomes.

### Evolution of satDNA families in the cattle genome (Bovidae family)

Bovids belong to the Bovidae family, including economically and socially important ruminant species such as cattle, sheep and goat (MacEachern et al. 2009; Groves & Grubb 2011). Moreover, Bovidae is the most diverse family of ungulates, with more than 149 recognised species distributed among 49 genera and seven subfamilies: Bovinae, Caprinae, Hippotraginae, Reduncinae, Alcelaphine, Antilopinae and Cephalophinae (Matthee & Davis 2001; Groves & Grubb 2011). These subfamilies are further divided into several tribes (Gentry 1992; Gallagher et al. 1999; Rubes et al. 2008; Robinson & Ropiquet 2011). Many studies have examined the evolutionary history of the Bovidae through the analysis of mitochondrial DNA (Vaccia et al. 2010), gene sequences (Carcangi et al. 2011), endogenous retroviruses (Chessa et al. 2009) and microsatellites (Vaccia et al. 2011). However, the systematic and phylogenetic relationships among the various species of this family are still under discussion (Rubes et al. 2008; MacEachern et al. 2009; Nieddu et al. 2015). Nevertheless, the comparative study of the nucleotide sequences and locations of repetitive DNA families in related species is providing information about their own evolutionary mechanisms and the species’ evolutionary history, since some repetitive sequences are extremely well conserved between species (Petraccioli et al. 2015; Chaves et al. 2017), while others are so variable that they can resolve taxonomic issues, defining differences between closely related species (Chaves et al. 2000a, 2005; Adega et al. 2006).

The domestic cattle (Bos taurus) genome harbours several distinct centromeric satDNA families (Macaya et al. 1978) with interrelated evolutionary histories (Nijman & Lenstra 2001). The centromeric sequences, that include both tandem satellite arrays and dispersed repeats, reveal a diversified and complex structure and organisation (Pöschl & Streeck 1980; Gaillard et al. 1981; Streek 1981; Pagés & Roizés 1984; Plucienniczak et al. 1985), as well as a widespread chromosomal distribution (Modi et al. 1996, 2004; Chaves et al. 2000a). In 1999, Vaiman et al. reported that bovine satDNA sequences constitute around 25% of the total nuclear DNA content, a value in agreement with more recent analysis of high-volume genome sequencing data. The analysis and comparative study of these bovine satDNA families demonstrated that sequence alterations in association with DNA amplification/contraction events from a common ancestor could be implicated in the origin of the present
satDNA families (Taparowsky & Gerbi 1982b). The
determination of the nucleotide sequence and satDNA
structure reveals that long satellites are often composed
of short tandemly variant repeats organised in complex
patterns that reflect the evolutionary pathways leading
to their generation (Skowronski et al. 1984).

The eight known satDNA families present in the
Bos taurus genome were isolated first in 1978 by
Macaya et al., using density gradient centrifugation
from calf thymus DNA. The different satDNA families
isolated were designated according to their buoyant density in Cs2SO4 and in CsCl (g/cm^3):
SAT1.715, SAT1.706, SAT1.723, SAT1.709, SAT1.711a, SAT1.711b, SAT1.720a and SAT1.720b
(Macaya et al. 1978). In this work, Macaya and col-
leagues identified two satDNA families with the same
buoyant density in CsCl, but with different beha-
vours in Cs2SO4/Ag^+ 1.711 g/cm^3 and 1.720 g/cm^3
satDNAs. A restriction enzyme analysis confirmed
that 1.711a and 1.711b as well as 1.720a and 1.720b were, in fact, different components.

Since then, the bovine satDNA families have been
characterised molecularly (Table I) by several
authors (Pech et al. 1979; Roizes et al. 1980;
Gaillard et al. 1981; Streeck 1981; Pagès & Roizés 1982, 1984; Plucienniczak et al. 1982;
Taparowsky & Gerbi 1982a; Plucienniczak et al.
1985), and the evolutionary relationship between
them began to be unveiled (Kopecka et al. 1978;
Taparowsky & Gerbi 1982b; Jobse et al. 1995;
Chaves et al. 2000a; Adega et al. 2006).

The nucleotide sequence of the 1.715 bovine
satDNA monomeric unit, also named bovine SATI,
analysed in several studies (Roizes et al. 1980;
Gaillard et al. 1981; Plucienniczak et al. 1982; Sano & Sager 1982; Taparowsky & Gerbi 1982b),
constitutes a 1.4-kb tandem repeat comprising 5–9% of the
total cattle genomic DNA (Kurnit et al. 1973; Vaiman
et al. 1999). Plucienniczak et al. (1982) performed an
analysis of the nucleotide sequence of this satellite DNA
family and reported the existence of a 31-bp periodicity
(mers) across the entire length of the 1402-bp higher
order unit of SATI, with 31-bp mers showing consider-
able monomer divergence (similarity between the 31-
bp subunits around 60%) (Taparowsky & Gerbi 1982a). Restriction endonuclease digests have shown that this satDNA sequence possesses a greater complexity than initially expected, being classified as a long-range-periodicity satDNA with a presumed non-
random distribution of methyl groups that could be
essential for its putative role in chromatin organisation
and in the centromeric function (Roizes 1976; Roizes et al. 1980; Pagès & Roizès 1984). In this repeat mono-
mer, 12 highly conserved CpG sites were found (Kang
et al. 2001; Yamanaka et al. 2011), and these seem to
be highly methylated in most tissues (Schnedl et al.
1976; Sturm & Taylor 1981; Pagès & Roizés 1982;
Adams et al. 1983). Additionally, it has been suggested
that these satDNAs (like some others: Biscotti et al.
2015; Chaves et al. 2017) could be transcriptionally
active (Su et al. 1982), being transcribed by RNA
polymerase III.

The structure of 1.706 satellite DNA (or SATIII)
determined by gDNA cleavage with several
restriction nucleases. This satDNA showed some
similarity to the sequence from SATI but a higher
complexity (Streeck & Zachau 1978; Pech et al.
1979). SATIII is organised in an unusual structure of
superimposed long- and short-range repeats, an
unprecedented structure amongst satellite DNAs
(Pech et al. 1979). The nucleotide sequence of
SATIII consists of a long-repeat unit of 2350 bp
composed of complex repetitions of two motifs, the
Sau and Pvu segments, which consist in variants of a
basic 23-bp sequence derived by point mutations
in different positions (Pech et al. 1979). The SATIII
comprises more than 4% of the bovine genome, and
the Sau segments form the major part of this
satDNA family (Pech et al. 1979). The evolution
of this satDNA cannot be explained by mechanisms
of amplification and random divergence; rather, it
seems to have evolved by non-random events, such
as selection, favouring the Sau segment amplifica-
tion, according to Streeck and Zachau (1978).
These authors considered that functional constraints
for heterochromatin organisation have been impor-
tant factors in this satellite DNA expansion.

In 1981, Streeck determined the nucleotide
sequence of the 1.711a bovine satDNA, a 1413-bp
repeat unit that contains SATIII Sau segments. This
repeat unit is composed by two segments represent-
ing variants of a basic 23-bp sequence (23-mer),
which exhibits a high homology to the Sau monomer
of SATIII; and by a third segment of 611 bp,
unrelated to the SATIII sequence and not interna-
tially repeated that is, however, flanked by inverted
repeats from the 23-mers (Streeck 1981). This
structure suggests that the bovine SAT1.711a origi-
nated from an insertion into a Sau repeat unit of
SATIII (Streeck 1981), an event postulated to have
occurred 10 MY ago (Taparowsky & Gerbi 1982a).
Interestingly, several remarkable sequences were
identified inside the 611-bp segment of the
SAT1.711a, such as a TATA box and a stretch of
seven cytosines followed by seven adenines, whose
presence suggests that this segment may be tran-
scribed (Streeck 1981). Unfortunately, the analysis
was not followed up subsequently.
Table I. Summary of the characteristics of the cattle satellite DNA families.

| Characteristics | SAT1.715 | SAT1.706 | SAT1.711a | SAT1.711b | SAT1.720 | SAT1.723 | SAT1.709 |
|-----------------|----------|----------|-----------|-----------|----------|----------|----------|
| Monomeric unit  | 1402 bp  | 2350 bp  | 1413 bp   | 2600 bp   | 46 bp    | 680 bp   | 3800 bp  |
| (mers)          | 31 bp    | 23 bp    | 23 bp + 611 bp +23 bp | 31 bp + 1200 bp +31 bp | 23 bp + 23 bp | - | - |
| % of the *Bos taurus* genome | 5–9% | 4% | 1.7% | 7.1% | - | - | 4.3% |
| GenBank reference sequence | V00124.1 | X03116.1 | V00115.1 | AF162499.1 | - | M36668.1 | X00979.1 |
| Tribes where detected | All pecorans, Bovini Tragelaphini Boselaphini | Bovini Boselaphini | Bovini Tragelaphini Boselaphini | - | - | Bovini *Taurotragus oryx, Tragelaphus strepsiceros (Tragelaphini)* |
| Tribes where not detected | - | - | Tragelaphini | - | - | - | Boselaphini, the other Tragelaphini |
| Estimated age | 40–20 MY | 10–15 MY | 6–10 MY | 10–15 MY | - | - | 10 MY |

1Bovinae tribes where the satDNAs have been detected.
2Bovinae tribes where the satDNAs have been looked for but not found.
Later, the structure of the repeat unit of the 1.711b bovine satDNA was determined and analysed by Taparowsky and Gerbi in 1982 (1982b). The SAT1.711b consists of a repeat unit of 2600 bp and contains a 1200-bp-long sequence which exhibits structural similarities to retroviral long terminal repeats inserted into a stretch of tandemly arrayed 31-bp subrepeat (31-mer), which in turn is highly similar to the SATI repeat unit (Taparowsky & Gerbi 1982a; Modi et al. 1996). The total 1402-bp repeat unit of SATI is represented in the 2600-bp repeat unit of SAT1.711b with ~95% sequence similarity. These two satDNAs differ only in a 1200-bp DNA segment that resides in the middle of the 1.711b repeat unit, suggesting that this satDNA originated from an amplification process of a SATI repeat modified by a 1200-bp segment insertion (Taparowsky & Gerbi 1982b). This segment is designated INS-1.711b and shows similarity to an endogenous retrovirus ERV2, designated BTLTR1 (analysis performed using the Censor software tool of Repbase; Kohany et al. 2006).

The SAT1.711b family is more abundant than the SAT1.711a family; they constitute about 7.1% and 1.7% of the bovine genome, respectively, according to Streeck (1981) or Taparowsky and Gerbi (1982b). Both satDNAs are complex structures, as both exhibit a unique sequence integrated into tandemly arrayed short repeats already present in other bovine satDNA families. A comparative study performed by Modi et al. (1996) suggested that the two segments of SAT1.711a (the Sau monomers of SATIII and the 611-bp segment unrelated to the SATIII repeat) originated simultaneously, as opposed to the two components of the SAT1.711b repeat (the segment similar to SATI and the INS-1.711b) which presumably originated at different historical times (around 15 MY apart). This study revealed that SATI apparently originated somewhere between the last common ancestor of the tragulinas and pecorans (40 MY ago) and the time of divergence of modern pecoran families (20–25 MY ago), as revealed by the presence of this satDNA family in all pecorans. In contrast, SAT1.711b seems to have originated only after the divergence of Tragelaphini, Boselaphini and Bovini from the other tribes of the Bovinae subfamily (10–15 MY ago), as suggested by its apparent exclusivity in those genomes. On the other hand, SAT1.711a seems to have originated after the divergence of Bovini and Boselaphini from the Tragelaphini (6–10 MY) (Modi et al. 1996, 2004), as this satDNA family was found only in species from the two first tribes.

The nucleotide sequence of 1.720 bovine satDNA was reported by Poschl and Streeck in 1980 and consists in a tandem array of a 46-bp repeat unit...
The complex evolution of bovine satDNAs in Bovidae

...comprised by two related 23-mers with no detectable higher order periodicity. This satDNA is largely similar to segments of another satellite of the bovine genome, the SATIII, presenting a sequence similarity of 76\% for the Pvu segment and 50\% for the Sau segment (Pöschl & Streeck 1980), which indicates the existence of a common evolutionary pathway for these two bovine satDNA families (Pech et al. 1979; Pöschl & Streeck 1980). The analysis of SATIII and SATI.720 showed for the first time that one basic sequence can originate large stretches of DNA of different complexity (Jobse et al. 1995). Whereas SATIII presents a complex patchwork structure of superimposed short- and long-range repeats with different variants of a basic sequence, SATI.720 seems to have maintained the simple structure of a basic repeat unit tandem array with little sequence divergence (Pöschl & Streeck 1980; Jobse et al. 1995). This aspect seems to be due to the self-complementarity of the two related 23-mers present in the SATI.720 that can be considered an imperfect palindrom (Pöschl & Streeck 1980). Pöschl and Streeck (1980) considered the SATI.720 a molecular fossil because it seems to be the bovine satDNA family that has undergone the least evolutionary alterations.

In sum, the bovine SATI, SATIII, SATI.711a, SATI.711b and SATI.720 exhibit basic internally repeated units with a complex organisation (Streeck & Zachau 1978; Pech et al. 1979; Pöschl & Streeck 1980; Gaillard et al. 1981; Streeck 1981; Plucienniczak et al. 1982; Taparowsky & Gerbi 1982a,b). SATIII, SATI.720 and SATI.711a share a highly homologous 23-bp sequence suggesting a close relationship; SATI presents a 31-bp internal periodicity which is related to the 23-bp sequence found in the bovine SATIII, SATI.711a and SATI.720, since this 31-mer also contains an internal 23-mer which, similarly to the 23-bp repeat unit, is also constituted by two related sub-repeats – a dodecanucleotide and an undecanucleotide (Taparowsky & Gerbi 1982a). In turn, the SATI.711b consists of the SATI repeat unit sequence with an insertion (INS-1.711b). Therefore, all these satDNAs are closely associated with each other (Figure 1), most probably sharing the same ancestral sequence and establishing a group of derivative yet related satDNAs sequences (Plucienniczak et al. 1982; Taparowsky & Gerbi 1982a; Jobse et al. 1995).

Considering the sequence similarity between the 23-mer and the dodecanucleotide sub-repeat, the five satDNA families can be divided in two distantly related groups (Figure 1), with a common evolutionary origin: the first group contains SATIII, SATI.711a and SATI.720 and the other group comprises SATI and SATI.711b (Plucienniczak et al. 1982; Taparowsky & Gerbi 1982b). Taparowsky and Gerbi (1982b) suggested that the 23-bp repeat unit was the ancestor of the 31-bp motif. However in 1995, Jobse et al. contradicted this idea, suggesting that the 23-mer may have a more recent origin than the 31-mer (Jobse et al. 1995). The 31-bp repeat unit found in bovine SATI and SATI.711b is also present in the genomes of species such as sheep and goat, indicating that this sequence motif predates the divergence of the Bovinae and Caprinae subfamilies. The 23-mer, present in other bovine satDNAs such as SATIII, SATI.711a and SATI.720 sequences, seems to have emerged only after the split of the water buffalo and other cattle species in the Bovinae subfamily (Jobse et al. 1995). Jobse et al. (1995) demonstrated that bovine and ovine SATI probes hybridise to each other and also to deer (Cervidae, Cervinae), but not to giraffe (Giraffidae, Giraffinae) and chevrotain (Tragulidae, Moschiola) DNA, suggesting that the 31-bp motif present in this satDNA emerged after the initial radiation of ruminants, later acquiring a species-specific repeat-unit organisation. Furthermore, the absence of the 23-bp motif of water buffalo SATIII suggests that the 23-mer was derived from the 31-bp repeat unit instead of the opposite (Jobse et al. 1995). Considering that the 31-bp and 23-bp repeats (found in all these satDNAs) share a common ancestral dodecanucleotide and considering the different evolutionary times of the bovine satDNAs, the ancestral repeat must have originated variant sequences and integrated DNA segments at different geological times, which clearly evidences the complex evolutionary history of the bovine satellite DNAs.

In contrast to the five bovine satDNA families described so far, the SATI.723 and SATI.709 sequences are not related to each other or to the previously discussed bovine satDNA families (Skowronski et al. 1984).

Plucienniczak et al. (1985) demonstrated that 1.723 bovine satellite DNA is a monomer of 680 bp, where short repetitive sequences do not show any systematic periodic structure (Plucienniczak et al. 1985). The SATI.723 repeat unit seems to have evolved by several duplications of two 100-bp-long sequences (Plucienniczak et al. 1985). Molecular analysis does not show any internal repetition that could associate it with the other bovine satellites (Buckland 1985). There is, however, a region that shows some relation with the dodecanucleotide ancestral sequence of the SATIII...
(Buckland 1985), which raises the possibility of the SAT1.723 family sharing a common origin with SATIII.

The 1.709 bovine satDNA (or SATIV) represents around 4.3% of the bovine genome and presents a markedly different structure and organisation (Skowronski et al. 1984; Jobse et al. 1995). This sequence is considered the evolutionarily youngest satDNA family in Bovidae (Jobse et al. 1995; Modi et al. 1996, 2004; Adega et al. 2006), and has probably undergone independent mutational and amplification events from the other bovine satDNA sequences (Lenstra et al. 1993). The repeat unit of 3800 bp exhibits a long-range periodicity and contains a GC-rich domain, two clusters of di- or trinucleotide repeats (Skowronski et al. 1984), and sequences homologous to other dispersed repeated sequences found in the bovine genome (Lenstra et al. 1993). A more detailed analysis of the 3800-bp monomer using the Censor software tool of Repbase (Kohany et al. 2006) revealed the presence of endogenous retroviral sequences (ERV1-1C-LTR_BT and ERV1-3I_BT), a short interspersed nuclear element (SINE) (BOVA2) and a retrotransposable element (BovB) in the monomeric unit of SATIV.

The structure analysis of almost all the described bovine satDNAs suggests an evolutionary mechanism involving the insertion of segments of DNA into repetitive sequences already present in an ancestral genome, and subsequent mutational and amplification events that originate new repeat units (Streeck 1981; Jobse et al. 1995). Analysing the presence of bovine satDNAs in other ruminants, such as sheep, goat and deer, it was demonstrated that the number and variants of these satDNAs vary considerably (Reisner & Bucholtz 1983; Novak 1984; Buckland 1985; Jobse et al. 1995; Modi et al. 1996). The total copy number and the relative numbers of individual sequence variants of different satellites in several Bovini species were subject to large fluctuations (Nijman & Lenstra 2001). In the initial phase of a satellite life history, interactions of homogeneous repeat units cause rapid expansions and contractions, resulting in variations in the number of copies (Fry & Salser 1977; Nijman & Lenstra 2001). The fluctuations in the relative numbers of satellite sequence variants support the second phase of the model, since mutations originate different sequence variants that amplify and contract independently. Considering that the emergence of a new homogeneous repeat does not require the immediate removal of previous satellite sequences, several satDNA families with different evolutionary origins can coexist in the bovid genome (Modi et al. 1993; Jobse et al. 1995; Nijman & Lenstra 2001). This feedback model proposed by Nijman and Lenstra (2001) has been validated by several studies analysing different satDNA families (Modi et al. 2004; Adega et al. 2006).

![Image of SATI, SATIII, SATIV, SAT1.711a, SAT1.711b, and SAT1.723 on domestic cattle chromosomes.](image_url)
Physical distribution of bovine satDNAs across Bovidae

Physical mapping of the bovine SATI, SATII, SATIV, SATI.711a and SATI.711b was initially done by Modi et al. (1993, 1996) using fluorescent in situ hybridisation (FISH). The analysed bovine satDNA families revealed a (peri)centromeric location on the majority of the cattle autosomes (Modi et al. 1993, 1996, 2004; Chaves et al. 2003). SATI (Figure 2(a)) can be found in all the cattle autosomes, while SATIII (Figure 2(b)) and SATIV (Figure 2(c)) are present only in some of these (Chaves et al. 2003). SATI.711a and SATI.711b appear to be located on the centromeric regions of many chromosomes, SATI.711b (Figure 2(d)) being clearly more abundant than SATI.711a (Figure 2(d); Modi et al. 1993). These satDNAs families further showed a slight to intense interstitial hybridisation in some chromosomes (Modi et al. 1993, 1996). The observation of an interstitial location of the bovine satellites analysed was, at first glance, unexpected since restriction patterns and southern blot analysis showed that these repetitive sequences are tandemly arrayed. These authors proposed that the interstitial hybridisation signals could be produced by specific sequence segments showing similarity to transposable elements. The physical mapping of the SATI.723 showed the presence of this satDNA family in more than half of the chromosomes (Figure 2(f)). None of these satDNA sequences seem to be present on the sex chromosomes of Bos taurus (Modi et al. 1996, 2004). Moreover, the observed variation in intensity of the hybridisation signals on different chromosomes is indicative of an apparent variation in the number of monomer copies of the different satDNA families analysed (Modi et al. 2004).

The three most studied bovine satellites, SATI, SATII and SATIV, seem to be organised on Bos taurus autosomes ordered p-ter-SATIV-SATI-SATIII-q (Chaves et al. 2003). In the chromosomes where SATIII is not detected, the sequences are found in the order p-ter-SATIV-SATI-q; in the chromosomes lacking hybridisation signal of SATIV the order is p-ter-SATI-SATIII-q (Figure 3).

The physical distribution of bovine satDNAs in other species has been also analysed. Several studies reported the presence of bovine SATI within several species of the Bovidae family and even in other families of pecoran ruminants (Modi et al. 1996; Chaves et al. 2000a, 2005; Kopecna et al. 2012, 2014) showing some ambiguitities in some tribes. In 1996, Modi et al. did not detect hybridisation signals in Hippotragini, Antilopini and Tragelaphini tribes, in contrast with the results reported by more recent studies (Chaves et al. 2005; Kopecna et al. 2012, 2014). The SATI clone used by Chaves et al. (2005) and the one used by Kopecna et al. (2012) showed 96% similarity; however, some results of the two studies also diverged, concerning the
presence of this sequence in Caprini, Alcelaphini, Aepycerotini and Reduncini tribes. More recently, Nieddu et al. (2015), using a clone from Bos taurus belonging to the SATI family, demonstrated that this probe hybridised only to members of the Bovini tribe and not to members of Caprini, revealing results contradictory to what has been widely reported (Modi et al. 1996; Chaves et al. 2003, 2005; Kopecna et al. 2012, 2014). Moreover, Kopecna et al. (2014) and our own research group (unpublished data) analysed six species from the Tragelaphini tribe, revealing that SATI sequences isolated specifically from this tribe are present in the acrocentric chromosomes of the six species. According to Kopecna et al. (2014) Tragelaphus imberbis, T. angasii and Taurotragus oryx contain SATI in both acrocentric and in the bi-armed chromosomes, whereas in Tragelaphus spekii, T. strepsiceros and T. eurycerus no SATI hybridisation signals were detected in the bi-armed chromosomes, indicating the loss or decrease of this repeat during the fusion events that originated these chromosomes (Kopecna et al. 2014). In 2005, Chaves et al. had already analysed Tragelaphus strepsiceros and Taurotragus oryx, demonstrating the presence of SATI repeats in both acrocentric and bi-armed chromosomes, revealing some inconsistencies with the work of Kopecna et al. (2014). This discrepancy of results may be due to differences in the experimental conditions of the various studies, such as hybridisation stringency and sequence/size of the probes used or alternatively the contradictory presence/absence of SATI in some tribes could be explained by the presence of this satDNA in a lower copy number (below the FISH resolution) or by the existence of different tribe-specific sequence variants. Albeit belonging to the same satDNA family, different DNA sequences were isolated and used in the several studies, suggesting that the SATI family is constituted by different sequence variants not necessarily identical to each other.

Regarding the Bovidae family sex chromosomes, it is well accepted that all acrocentric X chromosomes contain SATI, with the exceptions of the Caprini and Alcelaphini tribes (Chaves et al. 2005). On the other hand, bi-armed X chromosomes do not show a SATI hybridisation signal (Chaves et al. 2005; Kopecna et al. 2012, 2014). In the majority of the Bovidae species, the Y chromosomes do not present SATI, with the exception of certain species from the Antilopini and Tragelaphini tribes (Chaves et al. 2005; Kopecna et al. 2014).

In contrast to the bovine SATI, the SATIV, SATI.711a and SATI.711b are not found in all the Bovidae analysed by FISH (Modi et al. 1996, 2004; Adega et al. 2006). According to Modi et al. (2004), the 1.711b repeat was detected in the genomes of Tragelaphini, Boselaphini and Bovini; SATI.711a was present in Boselaphini and Bovini; and SATIV was apparently found only in the Bovini genomes. However, these last findings were contradicted two years later by Adega et al. (2006), who proved that SATIV is also present in at least two Tragelaphini species, Taurotragus oryx and Tragelaphus strepsiceros, indicating that this sequence predates the divergence of the Bovini and Tragelaphini tribe, 10 MY ago. These contradictory results can be explained by the possible isolation of different variants of this satDNA family and/or different hybridisation stringencies in each FISH analysis. Furthermore, Adega et al. (2006) also suggested the occurrence of amplification events of sex-chromosome specific variants in the Tragelaphini species, considering the presence of highly intense hybridisation signals of SATIV sequences on the Tragelaphus X chromosome. The southern blot and in situ hybridisation analysis performed by these authors indicated that the bovine satDNA sequences on the sex chromosomes and autosomes evolved independently from each other (Adega et al. 2006). The mechanism that led to the fixation of a satDNA sequence variant in specific regions or even on different chromosomes could be constrained for functional reasons such as homologous chromosome pairing during meiosis (Roizes et al. 1980).

The rapid evolution that characterises the bovine satDNA families provides valuable information for studying the phylogeny of Bovidae species. The study of bovine satDNAs and the comparison of homologous sequences between related and unrelated species assisted in the resolution of Bovidae phylogeny. The chromosomal distribution pattern of these sequences is especially informative for analysing alterations that occurred during the divergence of different tribes from a common ancestor (Adega et al. 2006), allowing us to make inferences about phylogeny and simultaneously understand satDNA evolution (Ugarkovic & Plohl 2002; Chaves et al. 2003; Adega et al. 2006, 2009).

Although there are some studies on the bovine satDNA families, there is a need for more comparative studies to assess the true evolutionary path of these sequences in the Bovidae family. With the increasing data from sequencing projects of different species of this family and with more complete cytogenetic studies, we will certainly achieve great advances in our understanding of the evolutionary
mechanisms and the functional significance of these satellite DNA sequences.

SatDNA can provide an engine for Bovidae species evolution through the occurrence of centric fusions (Robertsonian translocations)

Satellite DNAs, among other repetitive sequences, can be considered the ‘engine’ triggering mammalian genome evolution (Adega et al. 2009), the constitutive heterochromatin (CH) regions being ‘hotspots’ for structural chromosome rearrangements (Chaves et al. 2004; Adega et al. 2006, 2009; Vieira-da-Silva et al. 2015) leading to reproductive isolation. In the last few decades a considerable collection of studies have demonstrated that satDNA families promote chromosomal rearrangements due to their dynamic behaviour among non-homologous chromosomes and between different chromosome fields (Wichman et al. 1991; Rossi et al. 1995; Chaves et al. 2000b, 2004, 2005; Slamovits & Rossi 2002; Adega et al. 2006; Paço et al. 2013; Vieira-da-Silva et al. 2015), proposing the involvement of satDNA sequences in karyotype evolution, reproductive isolation and in the speciation process (Adega et al. 2009; Ferree & Barbash 2009; Paço et al. 2013; Rojo et al. 2015; Vieira-da-Silva et al. 2015). In Drosophila, the divergence of centromeric satDNA can inhibit chromosome segregation in hybrids, causing hybrid incompatibilities and postzygotic isolation (Ferree & Barbash 2009). Likewise, in Iberolacerta species the high copy-number polymorphisms and the rapid shifts in centromeric sequence composition could have contributed to and even triggered species radiation (Rojo et al. 2015). Furthermore, Paço et al. (2013) reinforced this role for satDNA, demonstrating that in two hamster species of the genus Phodopus, the high molecular dynamics of repetitive sequences are responsible for chromosomal instability and consequently for chromosome rearrangements, leading to the karyotypes’ divergence since the ancestral Muroidea.

In the evolution of the Bovidae family, the genomes’ repetitive fraction seems to have played a central role in genome remodelling (Chaves et al. 2004, 2005; Adega et al. 2009). The Bovidae family is characterised by a relatively high autosomal conservatism, since the number of autosomal arms has remained constant (NF = 56–58) for most species (Gallagher & Womack 1992; Gallagher et al. 1994). The range in the diploid number reported (30–60) is explained by the occurrence of centric fusions or Robertsonian translocations (robs) during the species’ karyotype evolution (Buckland & Evans 1978; Gallagher & Womack 1992; Gallagher et al. 1994). That the ancestral karyotype of bovids had an all-acrocentric chromosomal complement with a diploid number of 60 has long been accepted. In the divergence of the various species, several fusion events between the acrocentric chromosomes occurred, leading to the presence of metacentric and submetacentric chromosomes (Di Berardino & Iannuzzi 1981; Gallagher & Womack 1992; Gallagher et al. 1999) but maintaining 60 autosomal chromosome arms. Nevertheless, two karyotypes (cattle and goat) have been used as references to study the evolution of the entire Bovidae family, since these are thought to resemble the ancestral bovid karyotype (Gallagher & Womack 1992).

Considering the great variety, complexity and dynamics of the collection of bovine satDNAs families described in the first section of this review, and the high diversity in karyotypes of the Bovidae species, it is reasonable to assume that the two features are related. Here we postulate that the rapid evolution that occurred in this family was due in part to the contribution of satDNA sequences facilitating the Bovidae karyotype reorganisation. The illegitimate recombination between homologous sequences, such as satDNA on non-homologous chromosomes, has been suggested as a possible path to the arrangement of rob chromosomes in mice and humans (Therman et al. 1989; Page et al. 1996). In fact, the high frequency of rob chromosomes related to genome remodelling can be caused not only by the homology of the satDNA sequences shared by the acrocentric chromosomes involved in each rob, but also by the nicking activity of the CENP-B protein originating the double strand breaks preceding the fusion events (Garagna et al. 2001). CENP-B protein binds the CENP-B box motif present within centromeric satDNA repeats (Masumoto et al. 1989) and could play an important role in recombination events leading to rob translocations (Kipling & Cooke 1990). Furthermore, the diploid chromosome number reduction by the occurrence of robs in the karyotypes of Bovidae family is inevitably followed by a loss of constitutive heterochromatin from the centromeres (Iannuzzi et al. 1987; Modi et al. 1996; Chaves et al. 2000b; Di Meo et al. 2006; Rubes et al. 2008) and a loss of centromeric satDNA (Modi et al. 1996; Chaves et al. 2000a,b, 2003, 2005; Kopecná et al. 2012, 2014). Robertsonian translocations are complex rearrangements that require, in addition to the double strand breaks, mechanisms that repair those breaks in the chromosomes, the silencing of the possible additional centromere and the adjustment of the amount of CH over time, in order to maintain chromosome...
viability (Chaves et al. 2003; Iannuzzi et al. 2009). Considering that acrocentric chromosomes are indeed primitive, it is possible to suggest that (peri)centromeric heterochromatin is reduced after the translocation event to stabilise the derived chromosomes. This assigns a primordial task to satDNA in the control, success and viability of the rob events (Adega et al. 2009; Iannuzzi et al. 2009).

The evolution of genomes inside the Bovidae family includes alterations in both nucleotide sequence and copy number of centromeric satDNA sequences (Chaves et al. 2000a, 2003, 2005; Adega et al. 2006; Kopecna et al. 2012, 2014). The satDNA changes might be expected as the breakpoints preceding rob rearrangements take place at the region harbouring most of these repetitive sequences. SATI is largely present at the centromeres of all the acrocentric chromosomes and much reduced (not detected by in situ hybridisation) from the bi-armed chromosomes in several Bovinae species from Bovini, Tragelaphini and Boselaphini tribes (Modi et al. 1996; Chaves et al. 2000a, 2005; Kopecna et al. 2012, 2014), being considered primitive (Chaves et al. 2000a, 2003). These results suggest the partial or total loss of these sequences during or after the fusion events that originated these chromosomes (Chaves et al. 2000a, 2003; Kopecna et al. 2012, 2014). Similarly, the amount of SATIV observed by Adega et al. (2006) seems to be lower in the submetacentric chromosomes of the Tragelaphini species analysed. Taken together, it seems probable that both satDNA families are involved in the Robertsonian translocations originating the present bi-armed Bovinae chromosomes. Moreover, the Bovinae rob chromosomes show considerable variations in the amount of these satDNA sequences. If we consider that the loss of centromeric repetitive sequences after a centric fusion or during the process of homogenisation is gradual, progressive and constant (Chaves et al. 2000a, 2003), these data indicate different timings for the submetacentric chromosomes’ formation (Adega et al. 2009). The amount of satDNA sequences in the centromeric regions of the bi-armed chromosomes can be used as a “clock” for estimating the age of a particular Robertsonian translocation.

The rob(1;29) chromosome – a case of complex satDNA reshuffling

Robertsonian translocations are the main chromosome rearrangements triggering karyotype evolution in Bovidae, with some species exhibiting half the number of chromosomes of others, despite a constant fundamental number observed across the lineages. Robs are, however, frequently found in the domestic cattle (completely acrocentric autosomal complement) and referred to as a chromosomal abnormality (Ducos et al. 2008; Iannuzzi et al. 2009). Amongst these, rob(1;29) assumes a special importance, as it has been found as the most widespread chromosome rearrangement occurring in domestic cattle and has been studied since the 1960s (Gustavsson 1969; Dyrendahl & Gustavsson 1979; Rangel-Figueiredo & Iannuzzi 1991, 1993). This chromosome alteration was also found in other species from the Bos lineage (Mastromonaco et al. 2004). Although a chromosomal abnormality in Bos species, rob(1;29) is commonly found as a constitutional chromosome in several wild bovid species, such as most of the Tragelaphini (Rubes et al. 2008). The fact that chromosome rob(1;29) is established in the Tragelaphini karyotype and is a reoccurring rearrangement in the Bos lineage represents a unique opportunity to study the mechanism of a translocation event that occurred millions of years ago. The analyses of the sequences at the breakpoint regions preceding a translocation are crucial in understanding the translocation mechanism. In rob, these sequences correspond to centromeric satDNA; thus, detailed physical and organisational analysis of the different satDNA families in rob(1;29) greatly contributes to the understanding of the mechanisms behind one of the most important rearrangements not only in Bovidae, but of the mammalian genome evolution (Chaves et al. 2003; Di Meo et al. 2006).

Initially, rob(1;29) was considered of monocentric nature, involving the complete loss of the centromere of BTA29 and the retention of the centromere of BTA1 (Iannuzzi et al. 1987). However, in 2000, Chaves and colleagues suggested that this chromosomal abnormality might not be a simple single event. Later, in 2003, using centromeric satDNA sequences, they showed that the rob(1;29) chromosome exhibits centromeric elements from both chromosomes 1 and 29, evidencing for the first time the two-step mechanism of this rearrangement (Chaves et al. 2003). In the rob(1;29) chromosome, SATI DNA sequences from both BTA1 and BTA29 were eliminated during the rearrangement event, while SATIV from BTA29 and SATIII from BTA1 were retained and reorganised in the translocated chromosome. In this model, the first event is a reciprocal translocation whose breakpoints were on the SATIII centromeric block from BTA1 and the SATIV block from BTA29 (Chaves et al. 2003). SATI from BTA1 and some SATIII and SATIV repeats from BTA29 are
lost as a chromosomal fragment. A second event involves the elimination of SATI and some sequences of SATIV from the rob(1;29) chromosome (corresponding to BTA29). These authors mention the possibility of an additional step prior to the fusion event, involving a pericentric inversion in BTA29. Thus, SATI repeats from BTA29 would recombine with SATI from in BTA1, leading to this satDNA loss during the fusion step (Chaves et al. 2003). After this work, where the rearrangement complexity of rob(1;29) was evidenced for the first time, Di Meo et al. (2006) using both satDNA and BAC probes, validated the pericentric inversion proposed by Chaves et al. (2003). This pericentric inversion would be probably necessary for the satDNA reorganisation at the centromeric level, highlighting the active role of satDNA sequences in the translocation mechanism and reinforcing the functional meaning of these repetitive sequences in chromosome reorganisation (Chaves et al. 2003; Adegaa et al. 2009). A more recent analysis of rob(1;29) genomic structure (De Lorenzi et al. 2012) confirmed the model reported by Chaves et al. (2003) and further specified that during the fusion process around 5.4 Mb of the pericentromeric region of BTA29 moved to the q-arm, close to the centromere of rob(1;29), and in this process this fragment further underwent an inversion. Although no gene-coding sequences seem to have been disrupted during these events, we cannot exclude that some of the sequences involved can take part in the regulation of coding genes (De Lorenzi et al. 2012), giving additional impact to the event.

The frequency of a particular genetic alteration is usually maintained or increased in a population only if the carrier animals present some adaptive advantage (Joly 2011). However, in the case of cattle rob(1;29), this has not yet been demonstrated and the consequences of this “abnormality” for carrier animals are still a controversial subject (Rodero-Serrano et al. 2013). In fact, most of the data available are in agreement with a negative effect of this translocation on the fertility of the carriers (Dyrendahl & Gutavsson 1979; Rangel-Figueiredo & Iannuzzi 1993; Bonnet-Garnier et al. 2008; Iannuzzi et al. 2009). Currently, despite the collection of studies involving the cattle rob(1;29), it is still unclear whether it is a “common” chromosomal abnormality or an ongoing evolutionary step leading eventually to a reduction in the diploid number of cattle from 60 to 58, which could provide the genome (or species) with an advantage derived from a new genetic linkage between chromosomes 1 and 29 (Buckland & Evans 1978; Rangel-Figueiredo & Iannuzzi 1993).

Involvement of satDNA in Bovidae sex chromosome evolution

Sex chromosomes are exposed to different evolutionary forces compared to autosomes (Adega et al. 2009), and Bovidae does not seem to be an exception. In the evolution of these chromosomes, several lines of evidence suggest the involvement of satDNA sequences (Chaves et al. 2005; Adega et al. 2009; Cabelova et al. 2012; Kopecna et al. 2014). In contrast to the autosomal conservatism, the Bovidae X chromosome presents a considerable variation between subfamilies and tribes (Buckland & Evans 1978; Gallagher & Womack 1992), mostly as a consequence of the CH amount and position variation and centromere transpositions (Gallagher et al. 1999; Iannuzzi et al. 2000), as well as in its molecular composition variation (Chaves et al. 2004, 2005; Di Meo et al. 2005). Several authors suggested that the primitive condition for the Bovidae X chromosome was most probably acrocentric with several regions of CH, facilitating intrachromosomal rearrangements during the X chromosome evolution (Gallagher et al. 1999; Iannuzzi et al. 2000). The cattle X chromosome is submetacentric, while in the Tragelaphini species X is found in both acrocentric and submetacentric form. In goat and sheep the X chromosome is also acrocentric, with the p-arm particularly small (Iannuzzi et al. 2009). In Tragelaphus imberbis and T. spekei the X chromosome is fused with an autosome (homologous to BTA 13), and in T. eurycerus two forms of X chromosomes were identified: an acrocentric X in males, and a submetacentric X in females. The different morphology of these two X chromosomes is due to heterochromatin additions and deletions, since the p-arm of the submetacentric X is C-band-positive (Rubes et al. 2008). In 2005, Chaves et al. established that part of the CH variation observed in the Bovidae X chromosome was due to SATI losses or gains during this chromosome’s evolution, accompanying its morphological metamorphosis. Analysing the X chromosomes, these authors indicated that the acrocentric chromosome was the primitive form, harbouring SATI sequences at the centromere. The X chromosome from Tragelaphini tribe is considered the most primitive, since it exhibits SATI easily observed by FISH, in contrast to the Bovini X chromosome, that apparently lacks this satDNA family (Chaves et al. 2005; Kopecna et al. 2014).

Similarly to the X chromosome, the Bovidae Y also evolved by complex chromosome rearrangements such as inversions and centromere transpositions (Iannuzzi et al. 2009). This chromosomes also varies greatly in size, proportionally to the amount of heterochromatin present (Cabelova et al. 2012), and
in morphology (Rubes et al. 2008; Iannuzzi et al. 2009). The domestic cattle (Bovini) Y chromosome is submetacentric in the sub-species Bos taurus but has a subterminal centromere in B. taurus indicus. The Bubalus and Syncerus (Bovini) Y is acrocentric, and the Y from some Caprini such as goat and sheep is metacentric. Except for Tragelaphus imberbis and T. angasi, which present an acrocentric Y chromosome, the Tragelaphini species have a submetacentric Y. In all Tragelaphini species this sex chromosome originated from a fusion between the Y chromosome and the homologous BTA13 autosome, t(Y;13) (Cabelova et al. 2012). Benirschke et al. (1982) postulated that T. imberbis and T. angasi separated first and retained the original acrocentric Y chromosome, and then, after the separation of these two species, a pericentric inversion resulted in a submetacentric Y shared by the remaining species. In T. imberbis, unlike other Tragelaphini, the Y is fused not only with an autosome but also with the X chromosome, suggesting that this species separated earlier from other taxa in the Bovininae subfamily (Benirschke et al. 1982).

Regarding the presence of SATI sequences in the Y chromosome, Kopecna et al. (2014) reported the absence of in situ hybridisation signals in the majority of the Bovidae species, except for some species within the Tragelaphini tribe (Tragelaphus imberbis and T. eurycerus) and Antilopini tribe (Gazella leptoceros and Antilope cervicapra). During the evolutionary process of the Y chromosome one or more repeats were often amplified, leading to species-specific satDNA repeats within the same tribe (Cabelova et al. 2012). Some centromeric repeats isolated from T. eurycerus were shown to be specific only to the members of the Tragelaphini that present a submetacentric t(Y;13), suggesting that the fusion event of chromosomes Y and 13 determined its centromeric repeat contents, since these repeats were not detected in species exhibiting an acrocentric t(Y;13) (Cabelova et al. 2012). The specific study of Y chromosome repetitive DNA sequences together with karyotype analysis proved to be a useful tool in disclosing Bovidae phylogenetic relationships (Cabelova et al. 2012). The existence of Y-specific repeats suggests different phylogenetic results in comparison with other published work, evidencing the importance of including the repetitive fraction of the Y chromosome in studies of karyotype evolution within this family. All the studies mentioned here extensively suggest that the evolution of chromosomes – both autosomes and sex chromosomes – is mediated by satDNA sequences and other repetitive sequences. However, the exact mechanisms underlying the alliance between satDNA and chromosome evolution is still matter of debate.

**Contribution of satDNA transcription in chromosomal rearrangements**

The analysis of bovine satDNAs has revealed the complex nucleotide structure for these sequences and suggested a dynamism that raises the hypothesis of these sequences being transcriptionally active (Streeck 1997; Su et al. 1982). In 1982, Su et al. suggested, for the first time, that transcription of SATI may in fact occur in the cattle genome and although it was not proved yet, these sequences were already successfully demethylated (Hornsby et al. 1992; Kang et al. 2001; Yamanaka et al. 2011). In recent years, numerous non-coding RNAs that originated from centromeric and pericentromeric satDNAs have been discovered (Bouzinba-Segard et al. 2006; Pezer & Ugarković 2008; Carone et al. 2009; O’Neill & Carone 2009; Rošić et al. 2014) and these seem to be very important for centromeric function, as alterations in their transcriptional status were related to chromosome segregation errors in several eukaryotic species. Recent experimental evidence supports that a precise chromosome segregation is assured by the inhibition, degradation or overexpression of satellite DNAs (Eymery et al. 2009; Gent & Dawe 2012; Ferreira et al. 2015; Cáceres-Gutiérrez & Herrera 2017). Centromeric transcripts have been demonstrated to be essential for the deposition of CENP-A in human cells, as depletion of these transcripts leads to mitotic defects (Gent & Dawe 2012; Quénet & Dalal 2014). Studies in this field have clearly established that the satDNA centromeric transcriptional profile is tightly regulated and that both its overexpression and repression are crucial for proper centromere function.

Interestingly, the expression of the centromeric and pericentromeric regions is altered in cellular conditions associated with chromosomal instability (Eymery et al. 2009; Ting et al. 2011; Zhu et al. 2011; Ferreira et al. 2015). It has been hypothesised that demethylation in certain DNA regions, including the pericentromeric satDNAs, assists the pericentromeric chromosomal rearrangements in lymphoblastoid cells incubated in vitro with DNA demethylating agents (Ji et al. 1997). Additionally, several studies evidence that DNA demethylation of repetitive DNA might predispose cells to chromosomal rearrangements such as translocations, deletions and isochromosome formation (Narayan et al. 1998; Ehrlich 2009; Tilman et al. 2012; Ferreira et al. 2015; Cáceres-Gutiérrez & Herrera 2017). It is thus possible that satDNA transcriptional regulation may constitute the missing piece...
to increase our understanding on the establishment of chromosomal instability, contributing to the occurrence of chromosomal rearrangements in the genome remodelling leading to Bovidae speciation.

Conclusions

Here, we aimed to demonstrate the impact of satellite DNA sequences on Bovidae genome evolution, highlighting the high dynamism and diversity of these repetitive sequences that led to their rapid and complex evolution. Additionally, we discussed the contribution of these sequences to karyotype reorganisation and subsequently to the speciation process. The genomic model of Bovidae presents valuable characteristics in relation to satDNAs families and karyotype and chromosome evolution.

This review supports the idea that rapidly evolving satDNAs may be a useful tool in resolving controversy over the systematics of Bovidae. As they are able to differentiate taxa at the subfamily or tribal level, different satDNA families provide information that helps in clarifying phylogeny. It has been shown that satDNA sequences used as molecular cytogenomic markers have been extremely informative to understand the evolution of the Bovidae tribes, allowing us to increase the resolution of the evolutionary tree of cetartiodactyls (Jobse et al. 1995; Modi et al. 1996, 2004; Chaves et al. 2000a, 2005; Adega et al. 2006; Robinson et al. 2008; Giannuzzi et al. 2012; Kopecna et al. 2012, 2014).

Besides the phylogenetic value of satDNA, these sequences also provide important tools for population genetics, and production or traceability studies (Verkaar et al. 2002; Adega et al. 2006, 2009). Male-specific repeat units of the Y chromosome may be applied as molecular/cytogenetic tools for gender identification in diverse Bovidae species (Cabelova et al. 2012). Some fields of medicine, such as clinical and cancer cytogenetics, can also benefit from a better knowledge of the mechanisms involved in the reorganisation of karyotypes and the occurrence of robs mediated by satDNAs (Chaves et al. 2005; Adega et al. 2009), and probably their transcripts. The use of satellite DNA sequences as routine diagnostic tools for chromosomal rearrangements that involve the (peri)centromeric regions of chromosomes should be seriously considered.

Finally, the recent boom in centromeric satellite non-coding RNA studies has enriched our understanding about the role of satDNA in genomes, specifically in kinetochore and centromere establishment and maintenance (Gent & Dawe 2012; Quènet & Dalal 2014). The transcription of centromeric and pericentromeric satDNA sequences was revealed to be a conserved feature of numerous eukaryotes (Bouzinba-Segard et al. 2006; Pezer & Ugarković 2008; Carone et al. 2009; O’Neill & Carone 2009; Rošić et al. 2014). In the future, it is expected that more studies addressing the possible impact of the transcriptional profiles of these ncRNAs in chromosomal rearrangements may provide important insights about the process of genome remodelling, particularly in the Bovidae family.

In the last few decades, several studies have demonstrated the active role of satellite DNA in karyotype reorganisation and genome remodelling in Bovidae species evolution. Robertsonian translocations were undoubtedly the mechanisms that shaped the evolution of the Bovidae, and centromeric satDNA were surely the engine behind it.

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ORCID

A. Escudeiro http://orcid.org/0000-0002-6139-7131
D. Ferreira http://orcid.org/0000-0002-7094-4969
A. Mendes-da-Silva http://orcid.org/0000-0002-4523-034X
J. S. Heslop-Harrison http://orcid.org/0000-0002-3105-2167
F. Adega http://orcid.org/0000-0001-5646-5534
R. Chaves http://orcid.org/0000-0002-5970-7428

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