NEW EMBO MEMBER'S REVIEW

Variation in satellite DNA profiles—causes and effects

Đurđica Ugarković¹ and Miroslav Plohl

Department of Molecular Genetics, Ruđer Bošković Institute, Bijenička 54, HR-10002 Zagreb, Croatia

¹Corresponding author
e-mail: ugarkov@rudjer.irb.hr

Heterochromatic regions of the eukaryotic genome harbour DNA sequences that are repeated many times in tandem, collectively known as satellite DNAs. Different satellite sequences co-exist in the genome, thus forming a set called a satellite DNA library. Within a library, satellite DNAs represent independent evolutionary units. Their evolution can be explained as a result of change in two parameters: copy number and nucleotide sequence, both of them ruled by the same mechanisms of concerted evolution. Individual change in either of these two parameters as well as their simultaneous evolution can lead to the genesis of species-specific satellite profiles. In some cases, changes in satellite DNA profiles can be correlated with chromosomal evolution and could possibly influence the evolution of species.

Keywords: concerted evolution/repetitive DNA/satellite DNA library

Biological significance of satellite DNAs

Satellite DNAs are tandemly repeated sequences, organized in long, usually megabase-sized arrays, and located in regions of pericentromeric and/or telomeric heterochromatin (Charlesworth *et al.*, 1994). In some species, they account for the majority of genomic DNA such as in the kangaroo rat *Dipodomys ordii* and in beetles from the coleopteran family Tenebrionidae (Hatch and Mazrimas, 1974; Petitpierre *et al.*, 1995). Earlier studies denied any function for these abundant genomic components, proclaiming them to be junk (Ohno, 1972), or ascribing to them parasitic attributes (Orgel and Crick 1980). In more recent reports, it has been observed that satellite DNAs can be associated with complex organizational features necessary for the function of eukaryotic genomes, such as the formation of heterochromatic genomic compartments important for proper chromosomal behaviour in mitosis and meiosis (Csink and Henikoff, 1998). Satellite DNAs appear to be major constituents of functional centromeres, as has been shown in detail in *Drosophila melanogaster* (Sun *et al.*, 1997) and in humans (Schueler *et al.*, 2001). Centromeric satellites differ in sequence even among closely related organisms, and these differences are followed by changes in corresponding centromeric histones, e.g. in CENP-A in mammals and Cid in *Drosophila* (Henikoff *et al.*, 2001). In isolated popula-

tions, this could result in a loss of compatibility between these elements in hybrids. It has been proposed that rapidly changing centromeric DNA may be driving adaptive evolution of centromeric histones, leading in this way to the speciation process (Henikoff *et al.*, 2001; Malik and Henikoff, 2001).

The potential functional importance of satellite DNAs and the existence of a whole range of satellite sequences either conserved or diverged, even between closely related species, raises the question of dynamics in satellite DNA evolution. In this review, we present a summary of recent contributions concerning the question of how an entire set of satellite sequences in an organism changes in nucleotide sequence and in genomic content, thus generating species-specific differences in satellite DNA composition or satellite DNA profiles.

Concerted evolution of satellite DNAs

It has been postulated that repetitive sequences evolve by means of concerted evolution, resulting ultimately in homogenization of changes among repeats within the genome and their subsequent fixation in members of reproductive populations in a process known as molecular drive (Dover, 1986). Different mechanisms of DNA turnover, such as unequal crossing over and gene conversion, are responsible for the spreading of newly occurring mutations horizontally through the members of the repetitive family. Unequal crossing over is also responsible for a change in satellite DNA copy number affecting in this way the length of satellite arrays (Smith, 1976). Theoretical studies on satellite DNA dynamics explain its loss from the genome by unequal crossing over, demonstrating an inverse correlation between the rate of unequal crossing over and the preservation time of the satellite (Stephan, 1986). Satellite DNAs can also increase in copy number by either replication slippage, rolling circle replication, conversion-like mechanisms or some other unexplained mechanism in a relatively short evolutionary time (reviewed in Charlesworth, 1994). The outcome of all the mechanisms affecting satellite DNA arrays is a high turnover of this part of the eukaryotic genome.

Changes in copy number of satellite repeats

When discussing the evolution of satellite DNAs, two parameters, copy number and nucleotide sequence, can be considered independently. With respect to copy number, satellite DNAs can vary dramatically in their content among related organisms. Within the plant genus *Cucurbita*, two different satellite DNAs are detected in all tested species: a 350 bp satellite differing in copy number among species and a 170 bp satellite present in a similar number of copies (King *et al.*, 1995). Two satellite

Fig. 1. Schematic representation of a satellite DNA library composed of five different satellites shown in different colours. The height of each column denotes the number of copies, while a change in colour marks sequence divergence. (A) In the hypothetical species (population), the satellite profile remains conserved in both sequence and copy number relative to the original satellite set. (B) Variation in satellite profile is obtained by a change in copy number of one or more satellites from the library without sequence change. In this example, the copy number of two satellites is changed. (C) The satellite profile is changed due to a nucleotide sequence divergence of one or more satellites, while copy number remains conserved. In this example, only the sequence of a major satellite DNA is changed, while minor satellites remain conserved in sequence. (D) Variation in satellite profile due to concurrent changes in sequence and in copy number of one or more satellites from the library.

families, initially detected in the rye genome, were also found in all tested species within the tribe Triticeae, but the copy number varies dramatically between species (Vershinin, 1996). Since the tested species belong to genera separated by ~14–18 Myr (million years; Wolfe *et al.*, 1989), it is evident that these two satellites remained in the genomes for a significant evolutionary period. Satellite DNA common to three species from the insect genus *Chironomus* is characterized by a dramatic difference in copy number and chromosomal localization among the species (Ross *et al.*, 1997). Highly abundant satellite DNA from the parasitic wasp *Trichogramma brassicae* has been detected in minor amounts in several congeneric species (Landais *et al.*, 2000). Recurrent amplifications and deletions of satellite DNA are characteristic for species from the rodent genus *Ctenomys* (Slamovits *et al.*, 2001). Within the cattle genome, several distinct satellite DNAs are found (Nijman and Lenstra, 2001). Although the time of divergence among cattle species is relatively short, ranging from 0.2 to ~5 Myr, a considerable fluctuation in the amount of satellites as well as in the amount of their sequence variants is detected among the species. In insect species from the genus *Palorus*, four different satellite DNAs are detected (Meštrović *et al.*, 1998). Species-specific satellite DNA profiles result from amplification of a particular satellite in each of the species into a major, highly abundant satellite DNA, while all the others are present as minor repeats. Major, as well as minor satellites are interspersed in the pericentromeric heterochromatic regions of all chromosomes.

It has become evident that different satellite DNAs co-exist in the genomes of related species and that they are amplified differentially among species (King *et al.*, 1995; Vershinin *et al.*, 1996; Meštrović *et al.*, 1998; Nijman and Lenstra, 2001). This confirms the model proposed by Fry and Salser (1977), according to which related species share

a collection, or a library of satellite sequences (Figure 1). This model explains the occurrence of species-specific satellite profiles as a consequence of fluctuation in the copy number of satellites within the library. The extent of fluctuation can be different in various groups of organisms. In some taxa, due to a high efficiency of turnover mechanisms, satellite profiles change significantly in a relatively short evolutionary time, as in the closely related species from the genus *Palorus* (Meštrović *et al.*, 1998; Figure 1B). In other groups of organisms, the evolution of satellite DNA profiles can proceed much more slowly (Figure 1A). Some species from the insect genus *Pimelia* (Coleoptera), separated by ~5–6 Myr, contain almost the same amount of a preserved PIM357 satellite DNA (Pons *et al.*, 1997).

What would be the biological consequence of the fluctuation of copy number of satellite DNAs? For the rodent species from the genus *Ctenomys*, changes in satellite DNA copy number have been correlated with karyological differences among the species studied (Slamovits *et al.*, 2001). This example revealed an association between copy number change and extensive chromosomal rearrangements, indicating a possible role for satellite DNA in chromosomal evolution. Satellite DNAs in species from the genus *Palorus* are major constituents of pericentromeric heterochromatin, and probably centromeric as well. It has been proposed that extensive amplifications and deletions of satellite DNAs in *Palorus* could act as a driving force in the evolution of this part of the genome (Meštrović *et al.*, 1998). This could reflect further on the fecundity in crosses between individuals differing significantly in amount of satellite DNA, and in this way act as a trigger in the speciation process.

Evolution of satellite DNA sequence

Within a species, satellite DNA exhibits internal sequence variability that depends on a ratio between the mutation and homogenization/fixation rates (Dover, 1986). Different satellite DNAs that co-exist in the same species can vary significantly in their sequence homogeneity (King *et al.*, 1995; Vershinin *et al.*, 1996). This indicates that each satellite DNA can be considered as an independent evolutionary unit, not only concerning the independent change of copy number but also in relation to sequence evolution. In addition, turnover mechanisms can spread mutations unequally between chromosomes, and in this way create chromosome-specific satellite subfamilies (Dover, 1986), or can induce extensive sequence rearrangements that will generate a novel satellite repeat. The genesis of complex monomer units of many satellite DNAs can be explained by amplification, rearrangement and subsequent mutations of simple sequence motifs. In this manner, a 234 bp mouse satellite monomer is based on a 9 bp motif (Horz and Altenburger, 1981), a bovine 1.715 kb satellite is formed from a diverged basic 31 bp subrepeat (Jobse *et al.*, 1995) while satellites belonging to the insect genus *Diadromus* are derived from a basic 20 bp motif (Rojas-Rousse *et al.*, 1993). Rearrangements of an existing satellite repeat together with insertion of a sequence segment have generated new satellite DNA in the insect *Tribolium madens* (Ugarković *et al.*, 1996a).

Dynamics of satellite DNA sequence divergence

Satellite DNA sequence divergence (the difference between sequences of two different species or populations) has been studied in related taxa which share the same satellite DNA (e.g. Arnason *et al.*, 1992; Bachmann and Sperlich, 1993). These studies revealed that satellite DNA sequence divergence proceeds in a gradual manner mostly due to the accumulation of nucleotide substitutions, while deletions and insertions represent rare events. Divergence of satellite DNA sequence can be detected at different taxonomic levels. In some instances, the evolution of satellite sequence precedes the evolution of species, as in the pupfish, where sequence divergence is detected at the population level (Elder and Turner, 1994). Homogenization of satellite DNA sequence at the level of species has been observed in the fish family Sparidae (Garrido-Ramos *et al.*, 1999), in species from the *Drosophila obscura* group (Bachmann and Sperlich, 1993) or among whales of the order Cetacea (Arnason *et al.*, 1992). The latter satellite is at least 40 Myr old, which is the proposed time of separation of two suborders of Cetacea. The substitution rate in the 180 bp satellite of *D. obscura* group was estimated to be 3% per Myr (Bachmann and Sperlich, 1993), while the cetacean satellite of ~1600 bp is evolving at the much lower rate of 0.2% per Myr (Arnason *et al.*, 1992).

Divergence of satellite DNA sequences in some instances cannot be detected at the taxonomic level of species. In the insect genus *Pimelia* (Coleoptera), mutations in the PIM357 satellite sequence are not species specific, but are detected at the level of geographically related species groups (Pons *et al.*, 2002). The evolutionary dynamics of this satellite in species endemic to the Canary Islands is different from that of the continental *Pimelia* species, which has been explained by distinct phylogenetic and demographic patterns related to the colonization of the islands. A satellite DNA abundant in the beetle *Palorus ratzeburgii* could not be distinguished from its low-copy number counterparts in all examined congeneric species which diverged at least 7 Myr ago (Meštrović *et al.*, 1998, 2000). In addition, the unaltered sequence has been detected and localized to the region of pericentromeric heterochromatin in all chromosomes in the distant species *Pimelia elevata*, which, according to phylogeographic data, separated from the genus *Palorus* 50–60 Myr ago (Mravinac *et al.*, 2002). Sequence uniformity has been maintained for at least 20 Myr in the 370 bp satellite, common to eight species from the *Drosophila virilis* species group (Heikkinen *et al.*, 1995). Among vertebrates, a 170 bp *HindIII* satellite DNA is shared by six of the seven analysed fish species from the sturgeon family (de la Herran *et al.*, 2001). This 170 bp *HindIII* satellite does not exhibit sequence divergence despite the fact that according to biogeographic and molecular-phylogenetic data these species have been separated for >80 Myr.

It is not clear why some satellite sequences remained conserved for such long evolutionary periods, while others experience dynamic nucleotide changes. In any case, differences in rates of divergence between satellite sequences present within a library contribute significantly

to the variation in satellite profiles (Figure 1C and D). One possible explanation for the ‘freezing’ of satellite sequences in evolution might be a bias in turnover mechanisms favouring a particular sequence variant over others, although the molecular basis for this is not known (Dover, 1987; Mravinac *et al.*, 2002). The most drastic example of conserved satellite DNA is the simple dodeca satellite, which is preserved in evolutionarily distant organisms such as *D. melanogaster*, *Arabidopsis thaliana* and *Homo sapiens* (Abad *et al.*, 1992).

Constraints on satellite DNAs

Satellite DNAs within a library usually differ significantly in sequence, and in some instances no evolutionary relatedness between them can be discerned. Despite the sequence heterogeneity, satellite DNAs could retain structural features characteristic for some taxonomic groups. Such structural features could be satellite DNA monomer length, A + T content, short sequence motifs or secondary and tertiary structures. Systematic analysis of a number of plant satellite monomers present in the database revealed a preferred length of ~165 bp and an A + T content >50% (Macas *et al.*, 2002). A short sequence motif known as the CENP-B box, characteristic of primate α -satellite DNA, represents the binding site for centromere protein B (CENP-B) (Kipling and Warburton, 1997). On α -satellite arrays that contain the CENP-B box, a centromere-specific chromatin complex is formed selectively (Ando *et al.*, 2002). Degenerate motifs related to the CENP-B box are found in a number of satellite DNAs from diverse mammalian species. Except for the CENP-B box, there is little sequence similarity between these satellite DNAs, pointing to its functional importance (Kipling and Warburton, 1997). An indication of the influence of selection on the CENP-B box during the evolution of α -satellite DNA has also been reported (Romanova *et al.*, 1996).

A comparative study of satellite DNAs found in species of the genus *Tribolium* (Insecta, Coleoptera) revealed a common structural feature, despite low sequence similarity among the satellites. All *Tribolium* satellites studied thus far have a 20–42 bp block of ~95% A + T nucleotides, flanked at one side by a stable inverted repeat (Ugarković *et al.*, 1996b). Similar structural features have been detected in centromeric satellite DNAs of *Saccharomyces cerevisiae* (Schulman and Bloom, 1991), and of the insect *Chironomus pallidivittatus* (Rovira *et al.*, 1993). Tertiary structures due to sequence-induced DNA curvature are characteristic for a number of satellite DNAs (Radice *et al.*, 1987; Fitzgerald *et al.*, 1994). All known *Palorus* satellites have the potential to form superhelical structures due to curvature of the DNA axis (Plohl *et al.*, 1998). It has been proposed that this structural feature could be important for tight packing of DNA and proteins in heterochromatin, and consequently be under selective pressure.

Conclusions

Extreme variation in the substitution rate combined with copy number change illustrates the complexity of satellite DNA evolution. The observed species specificity of satellite DNA profiles can be obtained by a change in

copy number of satellite DNAs present in the library without variance of their sequences (Meštrović *et al.*, 1998), by gradual sequence evolution without obvious quantitative change (Arnason *et al.*, 1992) or, as in most cases, by simultaneous change of both parameters (see, for example, Nijman and Lenstra, 2001). In addition, the content of the library also varies due to the emergence of new satellites and the decay of some repeats. In order to explain a complex pattern of satellite DNA evolution, elucidation of the molecular basis of turnover mechanisms affecting satellite DNA changes is necessary. Structural and biochemical studies of satellite DNA–protein complexes involved in heterochromatin and centromere formation could provide clues as to whether satellite DNA is important for the establishment of these domains. The study of satellite DNA evolution in natural populations could contribute to the understanding of evolutionary forces acting on its dynamics as well as the potential influence of satellite DNA dynamics on the evolution of species.

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