

# Satellite DNA and Chromosomal Evolution in *Ctenomys* Rodents: A Necessary Clarification

M.S. Rossi

Departamento de Fisiología, Biología Molecular y Celular, IFIBYNE-CONICET, Universidad de Buenos Aires, Buenos Aires, Argentina

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*Ctenomys* is a quite large group of South American subterranean rodents (more than 60 species) that exhibits the widest range of karyotype diversity in mammals with chromosomal diploid numbers ( $2n$ ) ranging from 10 to 70. *Ctenomys* has been considered as an example of explosive cladogenesis triggered by chromosomal repatterning [for a comprehensive classical review on *Ctenomys*, see Reig et al., 1992]. Chromosomal repatterning has been related to factors that reach from the population down to the genomic level. Recurrent contractions and expansions of repetitive Pvull *Ctenomys* sequence (RPCS), the major heterochromatic satellite DNA present in these genomes, have been related to chromosomal evolution in *Ctenomys* [Rossi et al., 1995; Slamovits et al., 2001].

Recently, *Cytogenetic and Genome Research* published an article by Novello et al. [2010] that, among other points, analyzes the relation between heterochromatin content, chromosomal diploid and fundamental number (FN) in 7 populations belonging to the Uruguayan species of the *Ctenomys*. After expressing heterochromatin content as the percentage of C-positive areas of entire metaphases, the authors performed a linear-regression test between these percentages and  $2n$  and NF values. Since the regression values resulted low, they concluded that in the case of the Uruguayan *Ctenomys* populations,

heterochromatin is not involved in chromosomal rearrangements. This conclusion seems to conflict with our previous work in which we showed that expansion and contractions of RPCS are associated with changes in karyotypes, whereas stasis of RPCS correlated to chromosomal stability [Slamovits et al., 2001]. However, these 2 papers differ in the group of studied species and, actually the main point, in their experimental approaches.

The role heterochromatin RPCS (and satellite DNAs in general) plays in chromosomal architecture does not rely merely on its copy number but, instead, on its dynamics of expansion, contraction and intragenomic movement. For this reason, we were convinced that it was essential to evaluate the evolution of RPCS through the cladogenetic process in *Ctenomys*. From this perspective, we employed phylogenetic approaches not only to estimate the evolutionary relationship among lineages (that in our case were quite divergent), but also to examine the relationship between dynamics of RPCS and karyotype variability. We employed the following approach: first, we obtained the cytochrome b-based phylogeny of 28 *Ctenomys* species that represent almost all main lineages of the genus. Then, we estimated the RPCS copy number by dot-blot hybridization, and, considering it as a continuous character, we reconstructed its hypothetical states in all

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María Susana Rossi, Laboratorio de Fisiología y Biología Molecular  
Departamento de Fisiología, Biología Molecular y Celular (IFIBYNE-CONICET)  
Universidad de Buenos Aires, Ciudad Universitaria, Pabellón II, 2° piso  
Buenos Aires EHA1428 (Argentina)  
Tel. +54 11 4576 3386/68, E-Mail srossi@fbmc.fcen.uba.ar

nodes of the tree, using maximum-likelihood algorithms. With these data, we then evaluated the relationship between RPCS stability and chromosomal evolution through the cladogenesis of the species. We found several events of gains and losses of RPCS copy number along the tree. Important variations in RPCS copy number (either expansion or contraction) between closely related species were accompanied by karyotype repatterning. In contrast, stasis of RPCS copy number occurred within karyotypically stable groups [Slamovits et al., 2001]. These results clearly suggested that the dynamics of RPCS is associated with chromosomal evolution in *Ctenomys* lineages.

The work by Novello et al. [2010] include 7 Uruguayan populations, belonging to 2 closely related species, *C. pearsoni* (2n = 56, 64, 66, 70) and *C. torcuatus* (2n = 44), and to *C. rionegrensis* (2n = 50) which belongs to a divergent, cohesive and well-known group of species named *mendocinus* group. As can be seen, the phylogenetic range analyzed in this work is much more restricted than that studied in Slamovits et al. [2001]. According to the authors, the range of variation of heterochromatin among the *C. pearsoni* karyomorphs varies between 7.0% and 0.8% [see table 1 in Novello et al., 2010]. ~~With certainty, the quantitative measurement of C heterochromatin is subjected to inaccuracies. However, according to the criteria employed by Slamovits et al. [2001], these errors are moderate.~~

Recently, we found that moderate changes in RPCS copy number occur among individuals from the same population that share the same karyotype [Caraballo et

al., 2010]. The affirmation that RPCS would not be related to chromosomal variability, for instance in the case of *C. pearsoni*, could be true if the differences in copy number between the closely related karyomorphs resulted quite low or even moderate. We believe that phylogenetic approaches are necessary to explore any aspect of chromosomal evolution, especially in the case of divergent karyomorphs of the genus' main lineages, but also in the case of the Uruguayan species that show a broad range of chromosomal variation, particularly in the case of the 4 karyomorphs of *C. pearsoni*.

Another point that I would like to emphasize refers to the authors' claim: 'the occurrence of unequal crossing-over may be hampered since RPCS lack repeated nucleotide inside monomer sequences' [Novello et al., 2010, p 159]. Unequal crossover has been claimed to be one of the major mechanisms of change in satellite DNA copy number. Together with gene conversion it is also responsible for horizontal spreading of new variants [see Ugarkovic and Plohl, 2002]. In the first case, the result of the recombination event could be the gain or loss of thousands or millions of monomer units of the satellite DNA. Unequal crossover is rather an intermonomeric than an intramonomeric event. After this clarification, it is worth noting that RPCS monomers contain several 5'CAGG3' and 5'GAGG3' sequences (and/or its complements) that promote recombination, first described in Jeffrey's microsatellites, in recombinational points of the major histocompatibility murine complex [Steinmetz et al., 1986] as well as in other satellite DNA sequences [Bogenberger et al., 1987].

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