

## KARYOTYPIC AND MEIOTIC EVIDENCE FOR A ROBERTSONIAN CHROMOSOME POLYMORPHISM IN THE LIZARD *Liolaemus fuscus* (TROPIDURIDAE, SAURIA)

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### ABSTRACT

A population chromosome polymorphism due to a single centric fission of pair four in the lizard *Liolaemus fuscus* ( $2n=32$ ) from northern Chile, is described. Metaphase II analysis of heterozygote males showed a regular meiotic segregation (97%). This supports hypotheses that centric fission rearrangements are involved in this lizard's karyotypic diversity and that the meiotic effects of fission heterozygotes are nearly neutral in most populations.

### INTRODUCTION

The origin of chromosome diversity in many vertebrate taxa is determined by Robertsonian type chromosome rearrangements. Chromosome number polymorphisms such as those found at the inter or intrapopulation level are also determined by this type of translocation (Swanson *et al.*, 1981).

Single or multiple centric fissions are the main chromosome rearrangement found in the evolution of lizard karyotypes, including *Anolis*, *Sceloporus grammicus* and *Liolaemus* (Webster *et al.*, 1972; Lamborot *et al.*, 1981; Sites, 1983; Lamborot, 1991). The chromosome number of the extensive *Liolaemus* genus ranges from  $2n=30$  to  $2n=44$  with a mode of  $2n=32$  (Lamborot and Alvarez-Sarret, 1989). There are also species with a high chromosome number, with alterations in the macrochromosome domain of the karyotype. Centric fissions and pericentric inversions are mainly involved in these chromosome changes (Lamborot *et al.*, 1979; Navarro *et al.*, 1981; Lamborot and Alvarez-Sarret, 1989).

There is well documented evidence for intraspecific chromosome polymorphism in *S. grammicus* and in *L. monticola*, which have shown considerable chromosome variations in several populations examined. Intrapopulation polymorphism is generally over 10% in *S. grammicus*, while in *L. monticola* it is around 50% (Lamborot *et al.*, 1981; Porter and Sites, 1985; Lamborot, 1991).

*Liolaemus fuscus* is a small sized oviparous lizard, distributed in Chile from Concepción ( $36^{\circ}47'S - 73^{\circ}04'W$ ) to Coquimbo ( $29^{\circ}50'S - 71^{\circ}15'W$ ) (Donoso-Barros, 1966). This region has a mediterranean climate tendency, with decreasing humidity from southern to northern latitudes. *L. fuscus* also shows a geographic distribution along an altitudinal gradient, ranging from 500 to 1300 m (Veloso and Navarro, 1988). The karyotype of *L. fuscus* is  $2n=32$ , with 12 macrochromosomes and 20 microchromosomes (Lamborot *et al.*, 1979; Navarro *et al.*, 1981).

Chromosome polymorphism was studied in a population of *L. fuscus*.

### MATERIAL AND METHODS

Karyotypes were determined from 17 adult specimens (13 males and four females) of *L. fuscus* from Culimó, IV Región ( $32^{\circ}04'S - 71^{\circ}14'W$ ), 390 m and six specimens (four males, two females), from Quebrada de Macul, Región Metropolitana, Santiago ( $33^{\circ}38'S -$

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70°23'W), 630 m. Samples were obtained during 1988, 1989 and 1991.

Metaphase plates were obtained by the squash method, from previously colchicized specimens. The intestines, spleen and testes were sampled. Slides were stained with 4% Giemsa pH 7.2. Chromosome number was determined by direct counting under a microscope. Macrochromosomes of 14 metaphase plates, from eight specimens from Culimó were measured. The Centromeric Index (*i*) was calculated in order to establish the chromosome morphology (Levan *et al.*, 1964). The size of each macrochromosome was calculated as a percentage of the total diploid macrochromosome length, which extends from pair one to pair six.

The number and morphology of macrochromosomes from spermatocytes II of the germ line (Metaphase II) were determined for three reproductively active males. All karyotyped specimens are deposited in the Herpetological Collection from the Faculty of Medicine, Universidad de Chile (DBGUCH).

## RESULTS

Eleven specimens from Culimó and all the specimens from Quebrada de Macul, showed  $2n=32$ . Pairs 1, 3, 4, 5, and 6 were metacentric and pair 2 submetacentric ( $i = 33.5$ ) with a distinct secondary constriction in the telomeric region of the long arm. The number of microchromosomes in all individuals was 20. At the microchromosome domain, pairs 7 and 9 were metacentric and pair 8 corresponded to the sexual pair, which is heteromorphic in males (XY). The X chromosome is metacentric and the Y chromosome is telocentric. The rest of the microchromosomes had a dot shape. (Figure 1A). The size of the macrochromosomes decreased progressively, except for pair 6, which was 50% of the 5th pair.

Six specimens (four males and two females) from Culimó had  $2n=33$ , with 13 macrochromosomes. The conservative NF24 and the chromosome measurements, allowed us to conclude that one of the homologues corresponding to pair 4, is fissioned. The other homologue is metacentric ( $i = 45.83$ ). The resulting telocentric chromosomes have a slightly different size, 6.66% and 5.74%, respectively (Figure 1B). The other chromosome pairs of this karyotype correspond to the  $2n=32$  standard karyotype.

Meiotic diakinesis analysis of macrochromosomes revealed that all  $2n=33$  males had five bivalents and one trivalent, which is consistent with a heterozygote fission centric rearrangement (Figure 1C). Analysis of 100 metaphase II cells of three heterozygote males showed that 97 gave the expected, under regular segregation: 46 secondary spermatocytes with six

metacentric chromosomes and 51 cells with five metacentric and two telocentric chromosomes (Figure 1D and E). Only 3% of the metaphase II plates were aneuploids at the corresponding macrochromosomes domains.

## DISCUSSION

Heterozygotes for a single centric fission of pair 4 were found only in specimens from Culimó, which corresponds to the northern border of the distribution of *L. fuscus*. All specimens from Quebrada de Macul, were homomorphic, with six pairs of macrochromosomes and 20 microchromosomes. The homomorphic condition of the southern populations was also shown in previous papers (Lamborot *et al.*, 1979; Navarro *et al.*, 1981). Both sampling localities are geographically separated by about 150 km in a straight line, with geographic barriers represented by the Aconcagua River and areas of strong anthropogenic disturbance.

*L. fuscus* populations are small and can be found in various types of habitats. It has been suggested that the principal chromosome diversity found in *Liolaemus* corresponds to xeric environments, north to Maipo River (33°S) (Lamborot, 1991). Xeric environment, which are also found in Culimó, have climatic instability, with severe episodic drought conditions. During drought periods, vegetation can persist but is restricted to a few places. Normal climatic conditions correspond to an expansion of the vegetation, in this situation *L. fuscus*, is also found again. This continuous expansion and retraction of the vegetation can explain the isolated and small populations at the border of the distribution of *L. fuscus*. The small population size may increase the chance of fixation of chromosomal rearrangement in this species.

Chromosome fusion and fission are alternative explanations for our findings in *L. fuscus*. We stress fission rearrangement because there is considerable evidence that the more common karyotype in *Liolaemus* is comprised of six pairs of banded macrochromosomes which presumably correspond to the ancestral condition (Lamborot *et al.*, 1979; Navarro *et al.*, 1981, Lamborot and Alvarez-Sarret, 1989). *L. pseudolemniscatus*  $2n=44$  (24,20) is also present in Culimó. All its macrochromosomes have telocentric morphology (Navarro *et al.*, 1988). In this locality there is a cytotype not previously described for *L. monticola*,  $2n=36$  (16,20) with two pairs of telocentric chromosomes and only 20 microchromosomes, which is similar to the "northern race" of Lamborot *et al.* (1981) and Lamborot (1991). It has been suggested that in both species, derived telocentric macrochromosomes originate from centric fissions rearrangements (Navarro *et al.*, 1988; Lamborot, 1991).

The type of chromosome rearrangement we found in *L. fuscus*, is new evidence that centric fissions are a

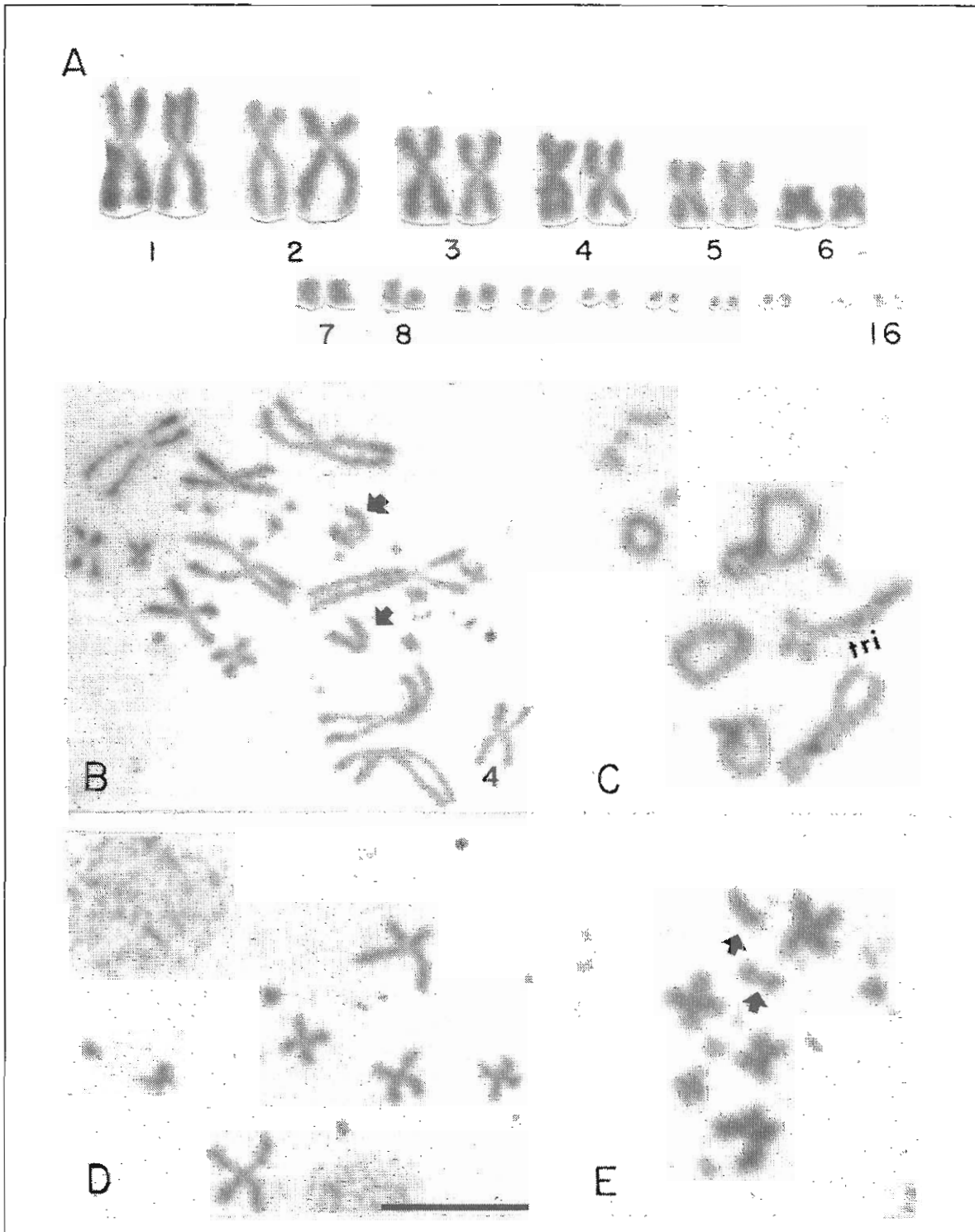


Figure 1 - A) Karyotype of *Liolaemus fuscus* ( $2n=32$ ). Pair 4 is metacentric, pair 7 is metacentric and pair 8 is the sex chromosome pair XY; B) Metaphase plate of *L. fuscus* from Culimó ( $2n=33$ ). The arrows indicate the fissioned telocentric chromosomes; C) Diakinesis array with a trivalent from a fissioned male heterozygote of *L. fuscus*; D) and E) Metaphase II of heterozygote *L. fuscus* for a pair 4 fission.

widespread mechanism for chromosome change in *Liolaemus*.

The lack of fissioned homozygotes could be due to the small sample size. The expected frequency for this kind of individuals is low ( $q^2 = .031$ ). We also cannot rule

out female meiotic drive or a lower viability of homozygotes for the rearrangement.

Most papers dealing with chromosome variation stress the importance of morphological chromosome changes at the somatic karyotype level to explain

relationships between chromosome changes and speciation. The meiotic segregation of heterozygotes for Robertsonian rearrangements in natural populations is also important in the same context. Due to meiotic assortment, aneuploidy can determine different levels of fertility in heterozygotes (Cappana *et al.*, 1976; Bianchi and Merani, 1980). We have not been able to assess the reproductive capacity of individuals with different karyotypes. However, analysis of secondary spermatocytes in *L. fuscus* heterozygotes revealed that at least in males, the chromosome meiotic segregation is normal, with a low prevalence of aneuploid gametes (3%), which is similar to that found in *Sceloporus grammicus*, with only one chromosome fission (Hall, 1973, in Porter and Sites, 1985).

Our results agree with Porter and Sites (1985) who suggested that at least in male lizards, Robertsonian rearrangements are not a strong meiotic barrier at the intrapopulation level.

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### RESUMO

Descreveu-se um polimorfismo cromossômico de população devido a uma única divisão cêntrica do par 4 do lagarto *Liolaemus fuscus* ( $2n=32$ ) do Norte do Chile. Análises da Metáfase II de machos heterozigotos mostraram uma segregação meiótica normal (97%). Tal evidência sustenta a hipótese que rearranjos da divisão cêntrica influenciam a diversidade do cariótipo do lagarto e os efeitos meióticos da divisão heterozigótica são quase neutros na maioria das populações.

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