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Cytogenetics and karyosystematics of phyllotine rodents (Cricetidae, Sigmodontinae)

II. Chromosome multiformity and autosomal polymorphism in *Eligmodontia*

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Abstract

Studied the bone-marrow and gonadal karyotypes, and the G- and C-banding of phyllotine mice of the genus *Eligmodontia* from different localities in Argentina. Twenty-eight specimens from Chasico, southern Buenos Aires Province, and from different localities of north eastern, south eastern and central Chubut showed a karyotype of $2n = 44$, $FN_a = 44$ comprised of one pair of large metacentric, 20 pairs of much smaller telocentric autosomes and a X-Y sexual system. One out of twelve individuals from Chasico, showed a $2n = 43$ Robertsonian variant of the same karyotype. Three specimens from Los Lagos, Neuquen, showed a quite different and polymorphic karyotype of $2n = 32-33$, $FN_a = 32$, consisting at the homozygous state of 14 pairs of telocentric, 1 pair of metacentric autosomes and the sexual pair. Additionally, the karyotype of $2n = 50$, $FN_a = 48$ from Peru, formerly briefly described by PEARSON and PATTON (1976), is illustrated and compared with the other two. The hypothesis is advocated that these three different cytotypes or chromosomal forms represent three different species. Thus, *Eligmodontia*, classically treated as a monotypic genus, is considered to be polytypic. The names *Eligmodontia typus*, and *E. puerulus* are provisionally proposed for the Buenos Aires-Chubutian, and the Peruvian cytotypes, respectively. The name to apply to the Neuquenian cytotype is discussed, but is considered unsolvable at the present state of knowledge.

Introduction

Eligmodontia is a genus of South American cricetids belonging to the phyllotine radiation (REIG 1986) which is striking because of its adaptations to life in arid biomes (MARES 1975, 1977). These long tailed and long eared mice with a long and silky fur are widespread in the southern cone of South America, from south of Peru to Tierra del Fuego.

The systematics of *Eligmodontia* is considered very simple since HERSHKOVITZ's (1962) revision, which only recognizes a single species with two subspecies: *E. typus typus* Cuvier, 1837, and *E. typus puerulus* Philippi, 1896, from seven allegedly different species described previously. In view of the widespread distribution and diversity of habitats of *Eligmodontia* populations, one is tempted to surmise that HERSHKOVITZ went too far in synonymizing all proposed species of this genus in just one species with two subspecies.

To test the alternative monotypic or polytypic hypotheses of species diversity in *Eligmodontia*, the karyological information can be an efficient tool. Unfortunately, chromosome information is almost nil in *Eligmodontia*. The few published data are the mention by PEARSON and PATTON (1976) of a karyotype of $2n = 50$, $FN_a = 48$ for *Eligmodontia typus* from southern Peru, and the preliminary account of the chromosomes of a population from Chasico that we further discuss in this paper (HURTADO DE CATALFO and WAINBERG 1977).

As a result of our current karyotyping of cricetids captured as a by-product of other research interests, the present authors found two extremely different karyotypes in samples of *Eligmodontia* from Argentina which differ from that reported by PEARSON and PATTON. We decided to join our results presenting the evidence gathered so far, which cogently favor the polytypic hypothesis.

Material and methods

We studied the chromosomes of 32 individuals (21 males, 11 females) from six localities in southern Argentina (Fig. 1): Pampa de Salamanca, Puerto Madryn, Paso de Indio, 28 de julio (Chubut Province); Los Lagos (Neuquen Province), and Chasicó (Buenos Aires Province). The animals were captured with Sherman live traps, and processed in our laboratories in Buenos Aires and La Plata. Skin and skull voucher specimens were deposited in the collection of Mammals of the Municipal Museum of Natural History at Mar del Plata (MMP), the Museum of Zoology, University of Wisconsin (MZW) and the Museum of La Plata (MLP).

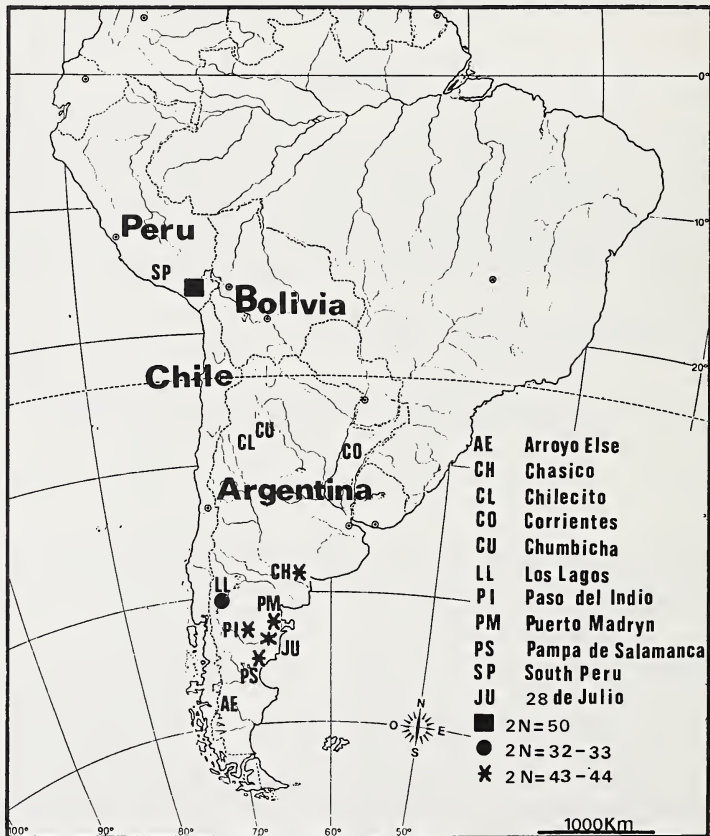


Fig. 1. Map showing where samples of *Eligmodontia* studied in this paper were collected and localities cited in the text. Diploid numbers are indicated for the former

We processed the bone marrow chromosomes following the techniques described in ROTHFELS and SIMINOVITCH (1958) and in REIG et al. (1971). G- and C-banding were obtained using the techniques of SEABRIGHT (1971) and SUMNER (1972), respectively. Male meiosis was studied in testicular direct preparations (EVANS et al. 1964). We followed LEVAN et al. (1964) for the nomencla-

ture of chromosomes according to the centromere position. Idiograms of each karyotype were constructed by measuring at least 10 enlarged metaphase prints. FNa are autosomal numbers. For the assortment of chromosomes in size classes, we called large those chromosomes measuring $> 9\%$ of the length of the female haploid complement; medium-sized those ranging from 5.5 to 9.0, small those ranging from 2 to 5.5%, and microchromosomes those measuring $< 2\%$ of the female haploid chromosomal length.

Results

Twelve individuals from Chasico and 16 individuals from the four localities in Chubut Province showed an identical $2n = 44$, FNa = 44 karyotype (Fig. 2). One female individual from Chasico showed a $2n = 43$, FNa = 44 variant of the same karyotype. The animals

Table 1. Mean values (\bar{x}), standard deviation (SD) and number of metaphases (N) measured of chromosomes of *Eligmodontia typus*, expressed as a percentage of the female haploid set. Arm ratio = long arm/short arm

Chromosome	N	Total \bar{x}	Length SD	Arm \bar{x}	Ratio SD
1	11	17.6	.91	1.1	.05
2	11	6.6	.26	∞	
3	11	6.0	.22	∞	
4	11	5.2	.17	∞	
5	11	4.9	.10	∞	
6	11	4.7	.11	∞	
7	11	4.4	.07	∞	
8	11	4.1	.19	∞	
9	11	3.9	.15	∞	
10	11	3.8	.11	∞	
11	11	3.7	.22	∞	
12	11	3.5	.18	∞	
13	11	3.3	.15	∞	
14	11	3.2	.13	∞	
15	11	3.0	.21	∞	
16	11	3.0	.17	∞	
17	11	2.9	.17	∞	
18	11	2.8	.11	∞	
19	11	2.6	.21	∞	
20	11	2.4	.24	∞	
21	11	1.9	.32	∞	
X	11	6.8	.57	1.30	.25
Y	11	3.5	.41	5.00	1.87

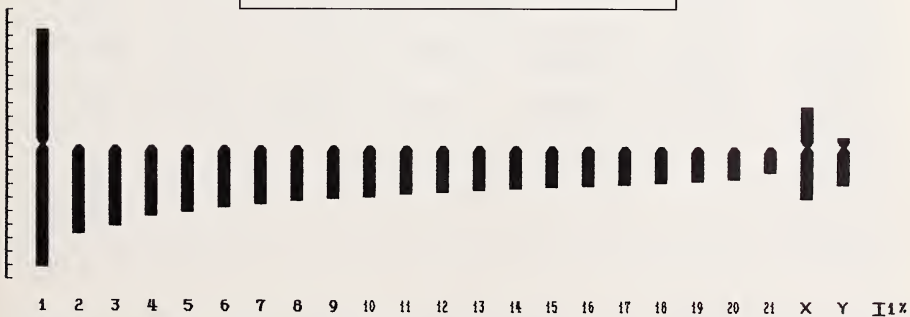


Fig. 2. Idiogram of *Eligmodontia typus*, $2n = 44$, FNa = 44

from Los Lagos, Neuquen, showed a quite different karyotype: one female and one male showed a karyotype of $2n = 33$, $FNa = 32$, and one male a $2n = 32$, $FNa = 32$ variant.

The autosomal set of the $2n = 44$ karyotype shows a pair of large (17.6 %) metacentric ($r = 1.06$) chromosomes followed by 20 pairs of telocentric chromosomes grading in size from medium-sized (pair 2–4), to small (pairs 5–19) and microchromosomes (pairs 20–21) (Table 1, Figs. 2 and 3). The X is a medium sized (6.5 %) metacentric, and the Y is a small (3.5 %) subtelocentric chromosome. G-bands allow us to correctly establish the homologies of all chromosomes (Fig. 4). C-banding (Fig. 5) showed a pericentromeric C-positive region on all autosomal pairs. The X chromosome also shows pericentromeric heterochromatin, but in addition two C-positive lighter bands are present in the long arm. The Y is fully C-positive. The $2n = 43$ karyotype of the single female individual from Chasico (Fig. 6) differs from the above described $2n = 44$ karyotype in having a medium sized odd banded autosome and two odd small-sized telocentric autosomes. We failed to obtain good G-banding in this individual, but chromosomal measurements allow us to infer that the short and the long arm of the odd metacentric correspond to one chromosome of autosomes pairs 5 and 18, respectively of the $2n = 44$ karyotype. Thus, a Robertsonian fusion/fission translocation is here in case. $2n = 44$ chromosomes are also present in the studied spermatogonial metaphases. In diakinesis and metaphase I cells we recognized 21 autosomal bivalents and the sexual bivalent. X and Y chromosomes show a meiotic end-to-end pairing. Pair I bivalent is obviously much larger than the remaining, and it usually shows three (Fig. 7) and less frequently only two chiasmata. The remaining bivalents show just one chiasma.

We have been unsuccessful in obtaining banding chromosomes in specimens from Los Lagos. As represented by one male individual, the “normal” karyotype of this form of 14 pairs of telocentric and one pair of metacentric autosomes and an X–Y sexual system (Fig. 8 and 9). There is a rather abrupt size gap between pairs 1–6 and the remaining autosomal pairs (Table 2). Pairs 1–5 are large, pair 6 medium-sized, but chromosomes of this group decrease gradually in size. Pair 7 is a medium sized metacentric. Pairs 8 to 15 are all telocentric chromosomes gently decreasing in size from medium sized to small. A clear-cut secondary constriction is evident on autosomal pairs 4 and pair 9, similar to those present in the karyotype of the Peruvian form reported by PEARSON and PATTON (1976) (Fig. 10). The X is a medium sized (5.8 %) telocentric, and the Y is a small metacentric chromosome.

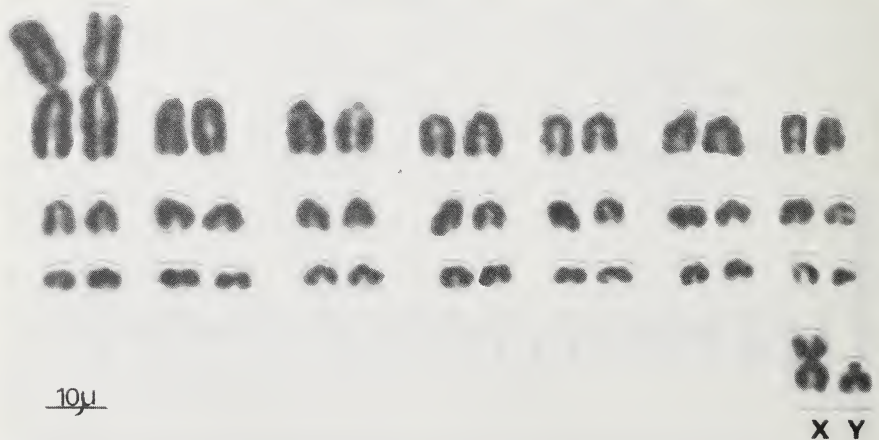


Fig. 3. Bone marrow standard Giemsa staining karyotype of *Eligmodontia typus* from Puerto Madryn, Chubut Province, Argentina, $2n = 44$; $FNa = 44$

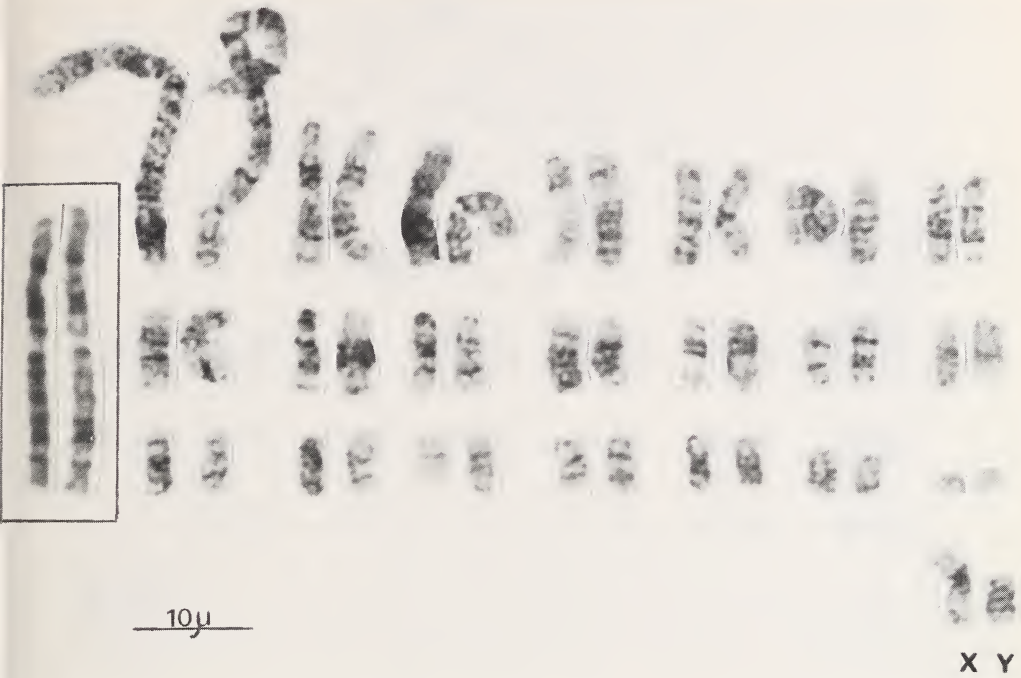


Fig. 4. G-banded karyotype of *Eligmodontia typus* from Puerto Madryn, Chubut Province, Argentina. $2n = 44$; $FN_a = 44$. In the rectangle, elongated first pair of autosomes of another metaphase of the same animal is included to better appreciate the G-banding pattern

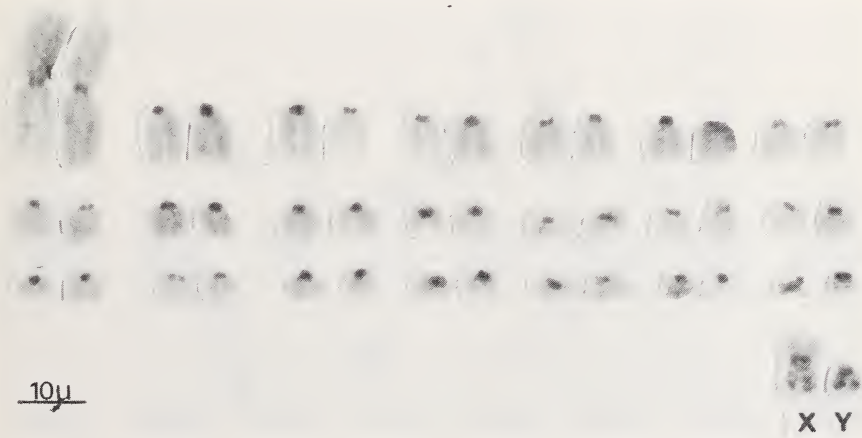


Fig. 5. C-banded karyotype of *Eligmodontia typus* from Puerto Madryn, Chubut Province, Argentina. $2n = 44$; $FN_a = 44$



Fig. 6. Bone marrow standard Giemsa staining metaphase and karyotype of the polymorphic form of *Eligmodontia typus* from Chasico, Buenos Aires Province, Argentina. $2n = 43$; $FNa = 44$. The chromosomes involved in the postulated Robertsonian rearrangement are represented in the upper right corner

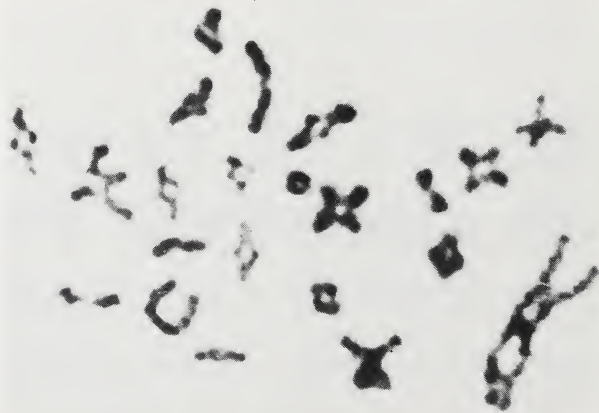


Fig. 7. Diacinesis of *Eligmodontia typus* from Chasico Buenos Aires Province, Argentina, showing the usual three chiasma configuration in pair one. $2n = 44$; $FNa = 44$

Table 2. Mean values (\bar{x}), standard deviation (SD) and number of metaphases (N) measured of chromosomes of *Eligmodontia* sp., expressed as a percentage of the female haploid set.
Arm ratio = long arm/short arm

Chromosome	N	Total \bar{x}	Length SD	Arm \bar{x}	Ratio SD
1	10	10.9	.71	∞	
2	10	10.9	.33	∞	
3	10	10.0	.18	∞	
4	10	9.4	.29	∞	
5	10	9.0	.17	∞	
6	10	8.0	.47	∞	
7	10	5.2	.22	1.1	.07
8	10	5.0	.21	∞	
9	10	4.5	.28	∞	
10	10	4.2	.36	∞	
11	10	4.0	.22	∞	
12	10	3.6	.16	∞	
13	10	3.3	.26	∞	
14	10	3.3	.43	∞	
15	10	3.2	.24	∞	
X	10	5.8	.45	∞	
Y	10	3.4	.34	1.4	.20



Fig. 8. Idiogram of *Eligmodontia* sp. $2n = 32$, $FN_a = 32$

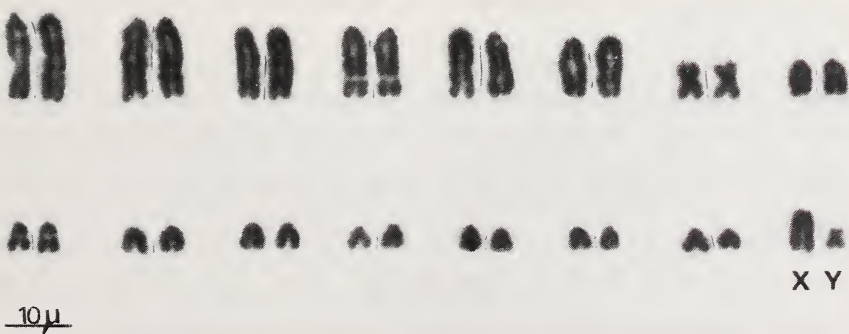


Fig. 9. Bone marrow standard Giemsa staining karyotype of *Eligmodontia* sp. from Los Lagos, Neuquen Province, Argentina. $2n = 32$; $FN_a = 32$

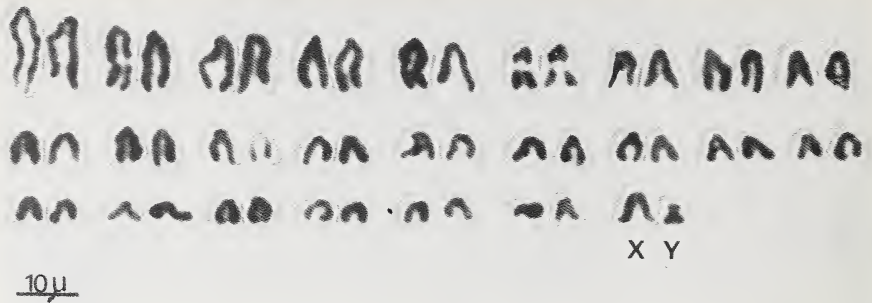


Fig. 10. Standard Giemsa staining karyotype of *Eligmodontia puerulus* from Ancomarca, Department of Puno, southern Peru. $2n = 50$; $FNa = 48$

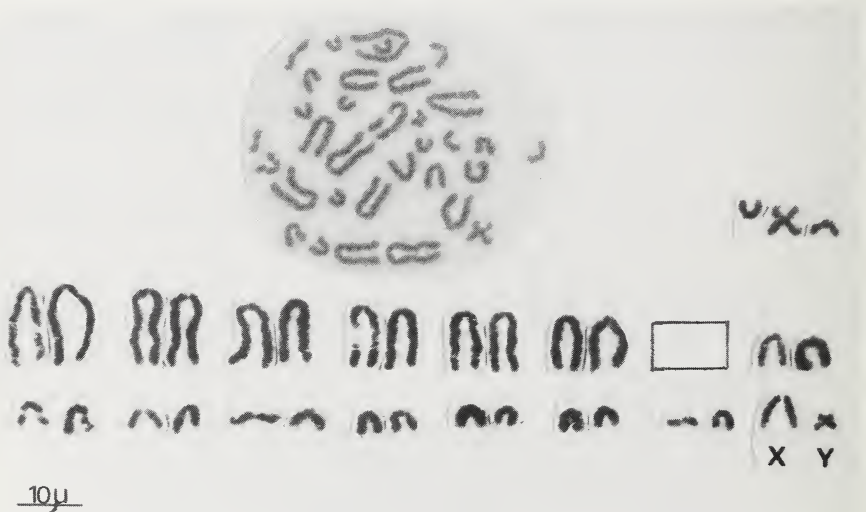


Fig. 11. Bone marrow standard Giemsa staining metaphase and karyotype of the polymorphic form of *Eligmodontia* sp. from Los Lagos, Neuquen Province, Argentina. $2n = 33$; $FNa = 32$. Other indications as in Figure 6

The $2n = 33$ karyotype shown by the remaining two individuals from Los Lagos has an extra pairs of telocentric and a single metacentric autosome. The sex chromosomes are as in the $2n = 32$ karyotype. The metacentric odd element matches in size chromosomes of pair 7 of the “normal” karyotype. Chromosomes of the extra pair measure 2.57 %, roughly matching, therefore the size of the arms of the single metacentric (Fig. 11; Table 2). We can here also infer that the differences between the two karyotypes are due to one Robertsonian rearrangement.

Discussion

Karyotypic differences and their evolutionary consequences

We have thus demonstrated that the supposedly monotypic genus *Eligmodontia* shows a remarkable karyotypic polytypy, with populations showing $2n = 32$ – 33 , $2n = 43$ – 44 and $2n$

= 50 chromosomes. This situation is not peculiar, as phyllotine genera are known by their extreme interspecific chromosomal heterogeneity (MASSOIA et al. 1968; PEARSON 1972; WAINBERG and FRONZA 1974; PEARSON and PATTON 1976; GARDENAL et al. 1977; SPOTORNO and WALKER 1979; WALKER et al. 1979, 1984; WILLIAMS and MARES 1978; FORCONE et al. 1980; VITULLO et al. 1984; PEREZ ZAPATA et al. 1986).

Intragenetic karyotype heterogeneity in the Phyllotini is likely to be interpreted as following two different evolutionary patterns: mainly Robertsonian rearrangements and multiple type rearrangements. The first type is characteristic of *Phyllotis*, *Graomys* and *Auliscomys*, in which interspecific Robertsonian mutations leading to reproductive isolation (*Phyllotis*), or extensive Robertsonian polymorphisms (*Graomys*, see WAINBERG and FRONZA 1974) are the rule. Interspecific Robertsonian rearrangements are also an acting force in some species of *Calomys*, but they are in most cases superimposed on more complex chromosomal repatterning (VITULLO and MERANI, pers. comm.). In this case, chromosomal homologies are almost impossible to detect, as between *Calomys laucha* ($2n = 64$) and *Calomys musculinus* ($2n = 38$). As is well known, chromosomal rearrangements of the fusion/fission Robertsonian type may not lead to reproductive isolation in all cases, the origination through this mechanism of a sterility barrier depending on the number and type of chromosomes involved (SPIRITO et al. 1981; GROPP and WINKING 1981; GROPP et al. 1982) or of the establishment of meiotic compensation mechanisms (WHITE 1978). When pericentric inversions and other chromosomal mutations are superimposed, however, the isolating effect of karyotypic differentiation is much more effective (REIG et al. 1980).

Although small Robertsonian rearrangements have been found in two of the known karyotypes of *Eligmodontia*, it is evident that the overall chromosomal differences between the three different karyotypes of this genus could hardly be thought of as resulting alone from fusion/fission processes. Even when we are lacking relevant banding information from two of them, the karyotypic comparisons oblige us to assume a complex array of chromosomal rearrangements, involving a combination of pericentric inversions, tandem translocations, and presumably, euchromatic amplifications and deletions. The scarcity of C-banding, and the almost exclusive pericentromeric nature of the heterochromatin, precludes ascribing an effective role to heterochromatin. It is legitimate to infer, therefore, that the pattern of chromosomal differentiation involved is the outcome of a long and complex history of chromosomal evolution, resulting in karyotypes which are now fully incompatible with interfecundity. Thus, we have to conclude that each of these karyotypes belongs to a different species of *Eligmodontia*.

Systematics and nomenclature

The problem is the name to apply to each of these species. We can tentatively propose species names from available ones from regions close to the localities of the different karyotypes. TATE (1932) and HERSHKOVITZ (1962) afforded a detailed taxonomic history of the available names for species of *Eligmodontia*.

The karyotype of $2n = 50$ was referred by PEARSON and PATTON (1976) to *Eligmodontia typus*. As PEARSON (1951) had earlier referred specimens from southern Peru to *E. puerulus hirtipes*, this action meant the tacit acceptance of HERSHKOVITZ's (1962) lumping of *puerulus* Philippi as a subspecies of *typus*. However, both REISE (1973) and CORBET and HILL (1980) reestablished full species status for *puerulus* as OSGOOD (1943) and MANN (1945) did before. If we are to refer the $2n = 44$ karyomorph to *E. typus*, as discussed below, there is no doubt that the $2n = 50$ karyomorph of Peru has to be assigned to a species fully different from *typus*. The name *puerulus*, originally described from a specimen captured in San Pedro de Atacama, Antofagasta, Chile, at 3223 m a.s.l., would be indeed a reasonable option. As proposed by MANN (1945) and PEARSON (1951), other available

name from South of Peru, *E. hirtipes* Thomas 1902, is probably a mere subspecies of *puerulus*.

Of a more complex solution is the problem of the name to apply to the $2n = 44$ karyomorph found in Chasicó and localities of Chubut Province. Since Chasicó is only 60 kms from Bahía Blanca, and Bahía Blanca is the type locality of *elegans*, this might be an available name for this form. However, *elegans* has been repeatedly considered as a synonym of *typus*, which has priority (WATERHOUSE 1839; LESSON 1842; ALLEN 1905; HERSHKOVITZ 1962) and which was originally reported from "Buenos Aires". The further correction of the provenance of *typus* by D'ORBIGNY and GERVAIS (1847) as "province de Corrientes" was probably an error (CONTRERAS pers. comm). Therefore it is reasonable to apply the name *typus* to the $2n = 44$ karyomorph on the basis that one locality where it was found is close to the toptotypical locality of *elegans*, which is a putative junior synonym of *typus*. The study of chromosomes of specimens from other areas in Buenos Aires Province may be critical to corroborate this decision.

As regards the $2n = 32-33$ karyomorph from Los Lagos, Neuquen, its species assignment is a matter of serious doubt. The only available name in Patagonia for a species of *Eligmodontia* is *E. morgani* Allen 1901, from Arroyo Else, in north-western Santa Cruz. There is the antecedent that BIRABEN and SCOTT (1936) referred to *morgani* specimens found in Pilcaniyeu, Rio Negro, not very far from Los Lagos, Neuquen. However, specimens reported here from Pampa de Salamanca, which is closer to Arroyo Else than Los Lagos, showed the $2n = 44$ karyotype we assigned to *E. typus*, and the same happens with specimens from the intermediate locality of Paso del Indio. Additionally, it seems that a single species of *Eligmodontia* inhabits the south and the east central Patagonia, and therefore, *morgani* may be a junior synonym of *typus*. Assuming this, we prefer not to assign any specific name to the species living in Los Lagos, Neuquen, showing the peculiar $2n = 32-33$ karyotype which excludes its classification either as *E. puerules* or *E. typus*.

Acknowledgements

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Resumen

Multimorfismo cromosómico y polimorfismo autosómico en Eligmodontia (Cricetidae, Sigmodontinae)

Se estudiaron los cariotipos de médula ósea y de gonadas masculinas, y las bandas G- y C- en roedores filotinos del género *Eligmodontia* de diferentes localidades de Argentina. Veintiocho ejemplares de Chasicó, en el sur de la Provincia de Buenos Aires y del noreste, sudeste y centro de la provincia de Chubut mostraron un cariotipo de $2n = 44$, $F_n = 44$, constituido por un par de grandes metacéntricos y veinte pares de telocéntricos mucho más pequeños, y un sistema sexual X-Y. Un individuo de Chasicó mostró una variante robertsoniana del mismo cariotipo, de $2n = 43$ cromosomas. Tres ejemplares de Los Lagos, Provincia de Neuquen, demostraron poseer un cariotipo polimorfo completamente diferente del anterior, de $2n = 32-33$, consistente al estado homocigótico de 14 pares de autosomas telocéntricos, un par de metacéntricos pequeños y el par sexual. Se ilustra, además, el cariotipo de $2n = 50$, $F_Na = 48$ de Perú, dado a conocer someramente por PEARSON y PATTON, y se lo compara con los dos anteriores. Se sostiene la hipótesis de que estos tres diferentes citotipos corresponden a tres diferentes especies. De manera que *Eligmodontia*, clásicamente considerado un género momotípico, resultaría politépico. Se proponen provisionalmente los nombres de *Eligmodontia typus* para el citotipo de las provincias de Buenos Aires y Chubut, y de *Eligmodontia puerulus* para el

de Peru. Se discute el nombre que debería-corresponder al citotipo de Neuquen, considerandose que el problema no puede resolverse por ahora.

Zusammenfassung

Chromosomale Vielfalt und autosomaler Polymorphismus bei Eligmodontia (Cricetidae, Sigmodontinae)

Chromosomenbilder aus Knochenmark und Hoden von Nagern der Gattung *Eligmodontia* aus verschiedenen Gebieten Argentiniens wurden untersucht, zum Teil in Präparaten nach G- und C-Bandenfärbung. 28 Exemplare aus den Provinzen Buenos Aires und Chubut besaßen $2n = 44$ Chromosomen ($FN_a = 44$). Ein sehr großes Autosomenpaar war metazentrisch, die übrigen 20 Autosomenpaare waren sehr viel kleiner und telozentrisch. Ein Tier von Chasicó hatte offenbar als Folge einer Robertsonischen Fusion nur 43 Chromosomen. Drei Exemplare aus Los Lagos, Provinz Neuquen, zeigten einen ganz anderen Karyotyp: $2n = 32-33$; bei 32 Chromosomen waren 14 Autosomenpaare telozentrisch, ein kleines Paar metazentrisch. Bei dem Tier mit 33 Chromosomen entsprachen einem metazentrischen Autosom zwei kleine, bei den anderen Exemplaren nicht vorhandene telozentrische. Aus Peru ist ein weiterer Karyotyp ($2n = 50$; $FN_a = 48$) von PEARSON und PATTON (1976) beschrieben worden. Wir nehmen an, daß die drei Chromosomen-Typen drei verschiedenen Arten angehören, daß also *Eligmodontia* nicht nur eine Art enthält, wie bisher angenommen wurde, sondern mindestens drei. Wir beziehen den Namen *Eligmodontia typus* auf die Populationen mit 44 Chromosomen, *E. puerulus* auf den Typ mit 50 Chromosomen. Der Namen der Form mit 32 Chromosomen bleibt noch zu klären.

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