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Cytogenetic diversity and evolution of Andean species of *Eligmodontia* (Rodentia, Muridae)

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Abstract

The standard and G-banded chromosomes of northern species of the phyllotine genus *Eligmodontia* were investigated. *E. puerulus* showed 2n = 50, NFa = 48 in bone marrow cells of three males and four females from northern Chile, and *E. moreni* 2n = 34, NFa = 48 in three males from northern Argentina. Comparisons showed extensive conservation of G-band patterns, including those of 15 telocentric chromosomes of the former with the arms of eight metacentrics of the latter; these characteristics suggest seven centric fusions and one pericentric inversion in *E. moreni*. C-bands were small in *E. puerulus*, as well as in the related *Andinomys edax* 2n = 54, NFa = 54 (two males and one female from northern Chile). All these northern species have chromosome arm sizes smaller than 9 % of the total karyotype, in contrast to some longer arms reported in the southern *E. typus* and *E. morgani*; the latter were probably derived by tandem fusions. Thus, southern species comprise a derived phyletic line, probably evolved from a primitive northern ancestor having 2n = 50 and NFa = 48. The role of geographic and cytogenetic factors in this speciation pattern, similar to that of the related *Auliscomys* species living in the same area, is discussed.

Introduction

Among the nine genera included in the tribe Phyllotini of South American murid rodents, *Eligmodontia* is clearly distinct and specialized, given its adaptations to life in arid zones. Although it was considered monotypic by some authors, two recent cytogenetic studies (Ortells et al. 1989; Kelt et al. 1991) support the idea that at least three species should be distinguished, on the basis of striking chromosomal differences. These are: *Eligmodontia puerulus*, 2 n = 50, NFa = 48 (Pearson and Patton 1976; Ortells et al. 1989), reported for populations living in the Altiplano (the highlands of southern Peru, Bolivia and northern Argentina); *E. typus*, 2n = 44, NFa = 44 (Ortells et al. 1989) for populations from central Argentina; and *E. morgani*, 2n = 32, NFa = 32 (Ortells et al. 1989; Kelt et al. 1991) for those from southern Argentina. A cytologically unknown fourth species from northern Argentina, *E. moreni*, has also been included in the most recent world species list (Musser and Carleton 1993), but these authors stated (p. 701) that "The differentiation of *moreni* from *morgani* in the S Andes and from *typus* in the Pampas warrants further study".

We present here cytogenetic data on specimens of this fourth species. We also compare all standard chromosomes described for these four species, as well as the G-banded karyotypes of *Eligmodontia puerulus* from northern Chile and *E. moreni* from northern Argentina. In addition, we present C banded karyotypes of the first species and those of the karyotypically related phyllotine *Andinomys*, both from northern Chile, to date not yet described in these terms. The latter is a monotypic genus of the Altiplano, considered to be primitive on the basis of protein electrophoresis (Spotorno 1986).

Material and methods

Specimens

All animals were collected in the field. Skulls and skins were prepared as voucher specimens and deposited in the collection of the Laboratorio de Citogenética, Facultad de Medicina, Universidad de Chile (LCM).

Taxa (taxonomic names according to MUSSER and CARLETON 1993), original localities, number and sex of specimens (LCM numbers in parenthesis) were as follows. *E. puerulus*: Parinacota, 110 km NE Arica, I Región de Tarapacá, CHILE, 1 male (LCM 650); Choquelimpie, 114 km NE Arica, I Región de Tarapacá, CHILE, 2 males (LCM 1183–1193) and 4 females (LCM 1184–1283–1438–1439). *E. moreni*: Cauchari, Provincia de Salta, ARGENTINA, 3 males (LCM 1702–1703–1704). *Andinomys edax*: Murmuntani, 110 km E Arica, I Región de Tarapacá, Chile, 1 male (LCM 243); Pampa Yuscuni, 100 km NE Arica, I Región de Tarapacá, Chile, 1 male and 1 female (LCM 678–677).

Chromosome analysis

Chromosomes were obtained from bone marrow cells using the conventional in vivo colchicine hypotonic technique, preceded by a yeast injection to improve the mitotic index (LEE and ELDER 1980). Total chromosome counts per cell were made in at least five good quality metaphases per specimen. NFa is the number of visible autosomal arms per cell.

Chromosome measurements were based on photographic enlargements, using the best single chromatid per pair (best meaning easiest to measure). Values were transformed to percentages of the total haploid female set. Relative values, together with those from idiograms already published, were displayed in a scatter diagram, which we have called the karyo-idiogram (SPOTORNO et al. 1987); each chromosome is represented by a single point according to its arm lengths. This is a useful device which allows the simultaneous description, comparison and eventual distinction of all chromosomes from many species. Two derived morphological variables can be evaluated: total chromosome size (short arm plus long arm lengths) and centromeric index (100 times short arm length divided by total chromosome length). Such a procedure assumes that the total genome size is conserved among the species compared. Although this assumption is generally true for mammals, it may be validated by C-banding techniques, which detect heterochromatin-containing satellite DNA, or by the use of marker chromosomes when available (SPOTORNO et al. 1987).

Chromosomes were classified according to morphology (centromere position) using the nomenclature of LEVAN et al. (1964), and also according to size. We distinguished large, medium or small chromosomes when their relative lengths were $> 9\,\%$, 9–5.5 % or $< 5.5\,\%$ of the female haploid set, respectively (see MASSARINI et al. 1991).

Chromosome bands were obtained by treating metaphase cells with G-banding (CHIARELLI et al. 1972) and C-banding techniques (CROSSEN 1972; SUMNER 1972). Comparisons of G-banded karyotypes were made in at least three selected metaphases from each taxon. Using shared G-band patterns, chromosomes from two or more species were classified as totally corresponding, partially corresponding or unique (WALKER et al. 1979).

Results

The karyotypes of the two main geographic populations were clearly different. All the specimens of *E. puerulus* from Chile exhibited cells with 2n = 50 and NFa = 48. All chromosomes were telocentric, with no visible short arms (Fig. 1a). This karyotype was essentially identical to those described for populations from Peru, Bolivia and northern Argentina (ORTELLS et al. 1989; KELT et al. 1991). Chromosome sizes graded from medium to small. The largest telocentric chromosome (pair 1) was clearly identified by size, amounting to 8.3 % of the total karyotype length. Pairs 3 and 8 showed a secondary constriction in the middle of their long arms (arrows in Fig. 1a), although the latter was not clearly visible in short metaphases. Sex chromosomes were difficult to identify in standard Giemsa karyotypes; the X was the third largest and the Y was among the many small chromosomes.

All the *Eligmodontia moreni* specimens from northern Argentina consistently showed karyotypes with 2n = 34 and NFa = 48 (Fig. 1b). The eight largest chromosomes displayed metacentric or submetacentric shapes, with pairs 3 and 6 exhibiting a clear secondary

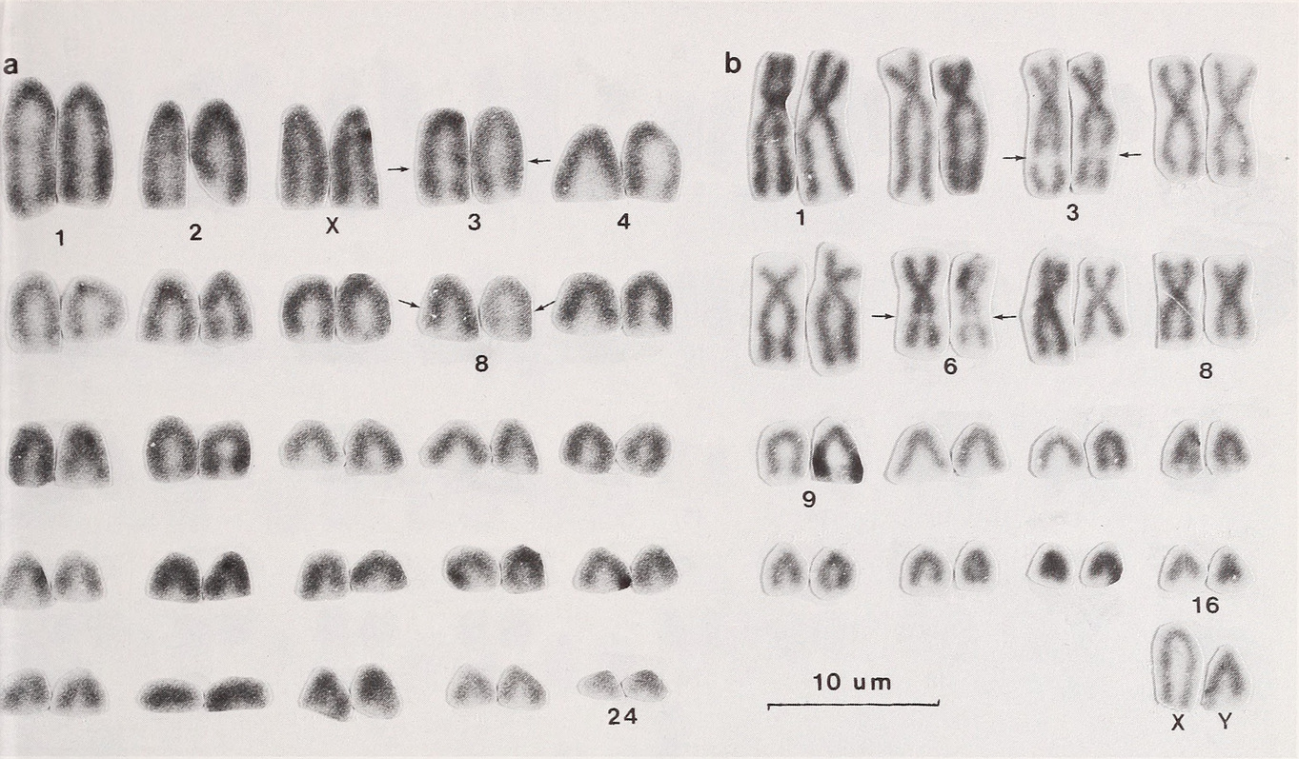

Fig. 1. Standard karyotypes of: a) *Eligmodontia puerulus* female (LCM 1193), X chromosome localized according to its size; and b) *E. moreni* male (LCM 1704). Arrows point to secondary constrictions

constriction in the middle of their long arms (arrows in Fig. 1b). The largest chromosome arm comprised 8.5 % of the karyotype length. The X chromosome was the largest telocentric, and the Y a small telocentric with an extremely short arm.

G-bands allowed the identification and comparison of every chromosome from both karyotypes. The X of *E. puerulus* was the third in size (Fig. 2a), showing two dark bands in the middle of its arm, a pattern already described for most mammals (Pathak and Stock 1974). It was almost identical to the X of *E. moreni* (Figs. 2b and 3). The Y chromosomes from both species were also very similar in bands and size, except for the presence of a short arm unique to *E. moreni* (Fig. 3).

When G-banded karyotypes were compared side by side (Fig. 3), all chromosomes or chromosome arms were found to correspond in bands and sizes. The single exception was chromosome 13 from *E. puerulus*, which appears to be unique. In particular, the arms of the largest seven metacentric chromosomes of *E. moreni* had corresponding telocentric chromosomes in *E. puerulus*, suggesting the occurrence of Robertsonian fusion/fission processes during the evolution of these species. The remaining metacentric pair 8 corresponded in bands and size to the single telocentric pair 5 from *E. puerulus*, suggesting the occurrence of a pericentric inversion.

C-bands were very small and confined to centromeric positions in most, if not all, the chromosomes of both *E. puerulus* (Fig. 4a) and *Andinomys edax* (2n = 56, NFa = 56, Fig. 4b). The latter karyotype was very similar to that reported for a single female from northern Argentina (Pearson and Patton 1976), with the exception that only pairs 1, 27 and Y had short arms in these Chilean specimens. A faint intercalar C-band was observed in the middle of pair 8 in *Andinomys*, and at a similar site of pair 3, or perhaps 4, in *E. puerulus*; this happens to be the usual localization of secondary constrictions in its Giemsa standard chromosomes (Fig. 1a).

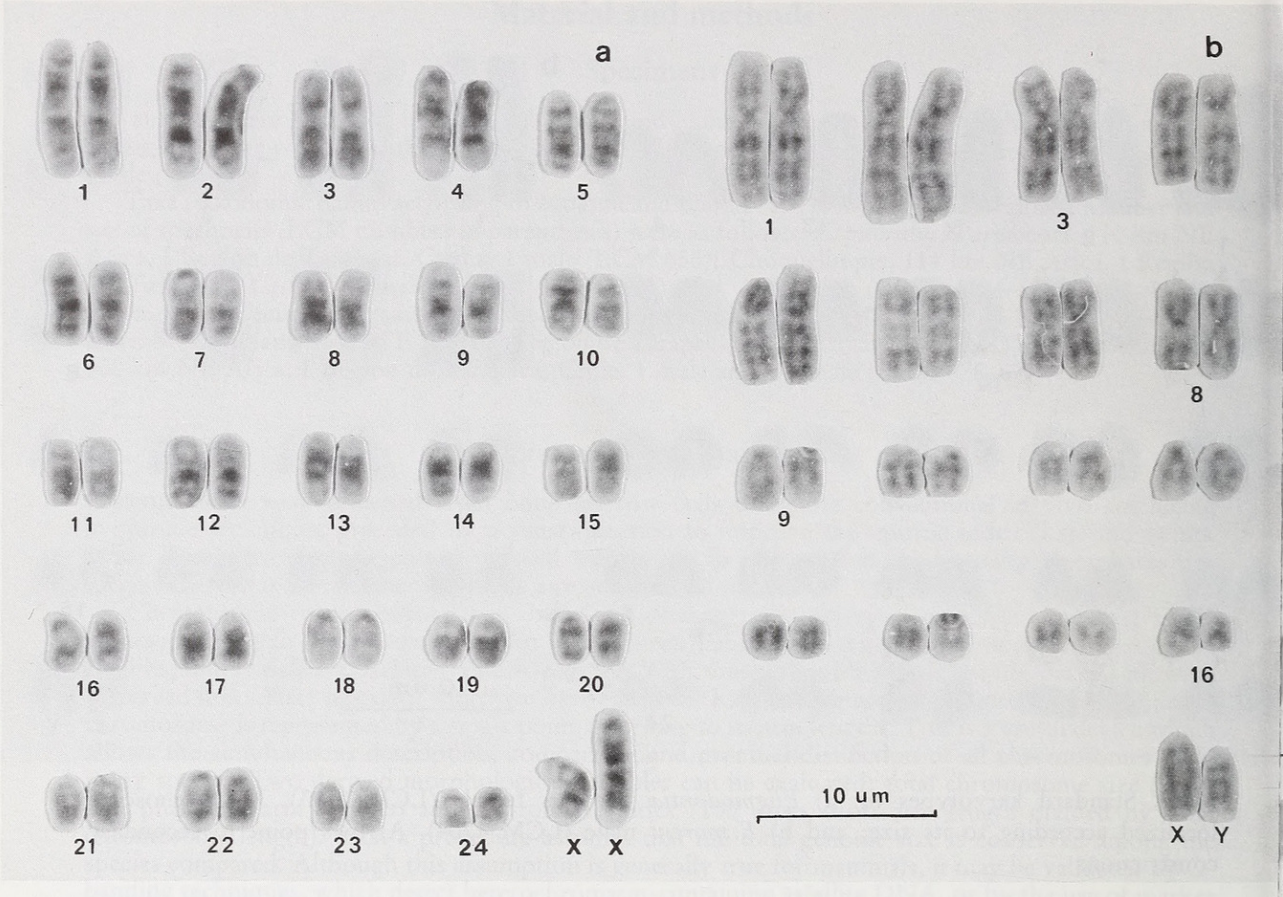

Fig. 2. G-banded karyotypes of: a) *Eligmodontia puerulus* female (LCM 1283); and b) *E. moreni* male (LCM 1704). Arrows point to secondary constrictions

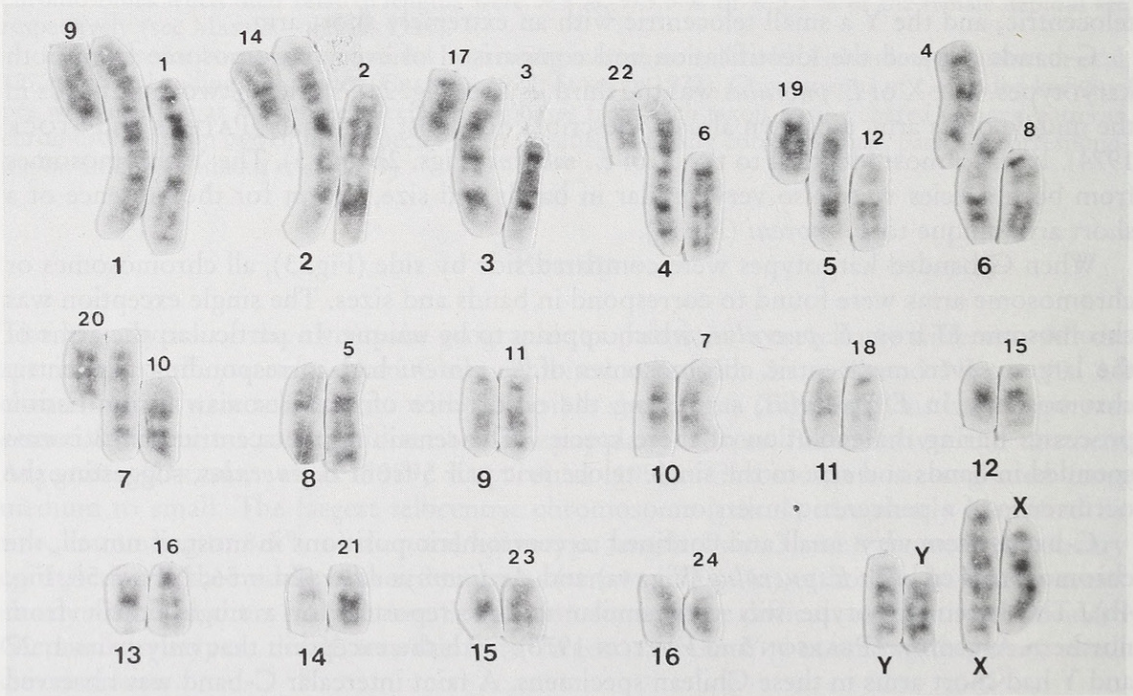

Fig. 3. Correspondence of G-band patterns between the chromosomes of *Eligmodontia moreni* (aligned large numbers at bottom) and *E. puerulus* (small numbers above). Chromosome 13 of the former not included, since it was difficult to match

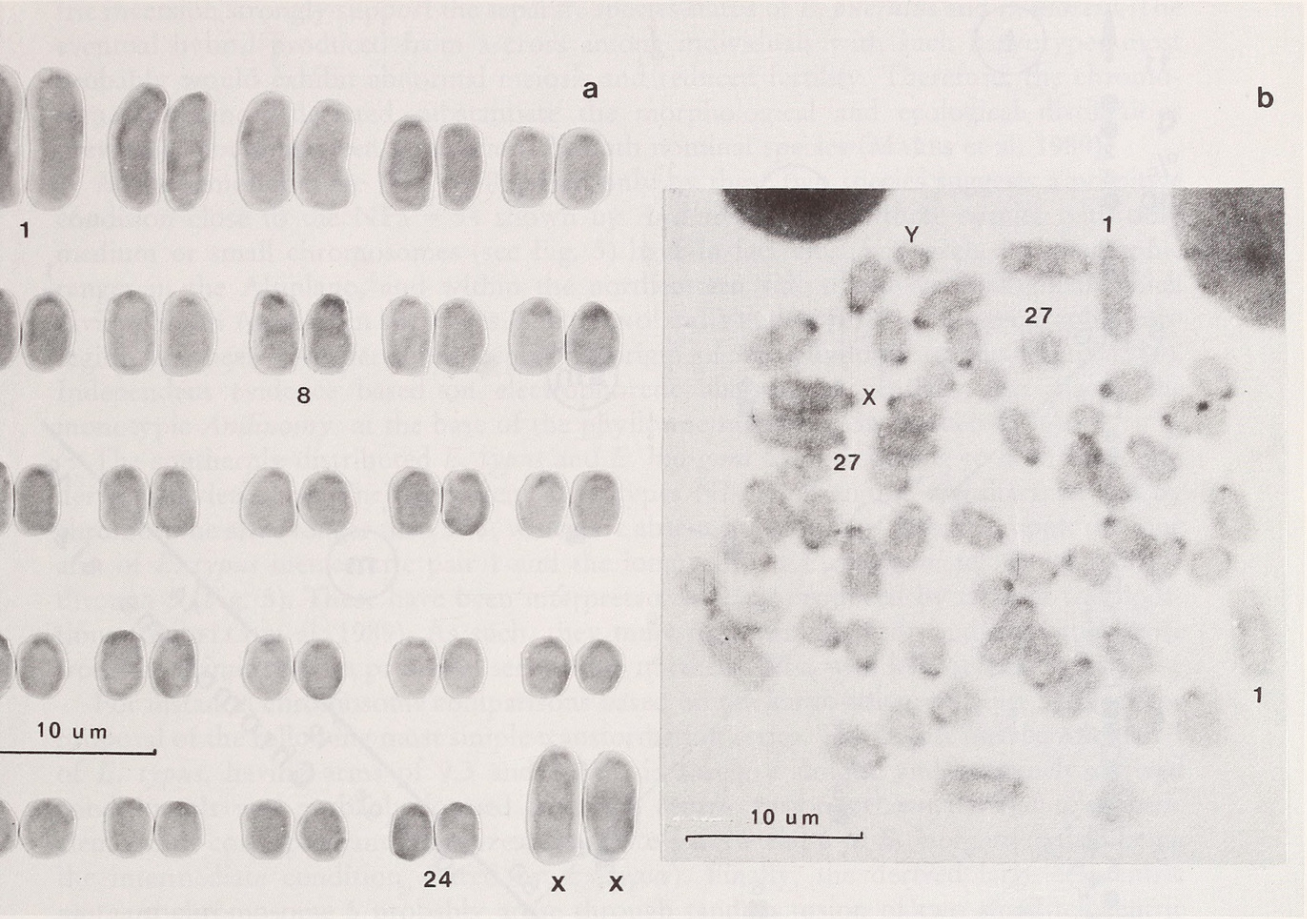

Fig. 4. C-banded metaphases of: a) *Eligmodontia puerulus* female (LCM 1283), and b) *Andinomys edax* male (LCM 678), with 2n = 56, NFa = 56. Sex chromosomes and the smallest metacentric autosome are indicated

Discussion

Our results provide data allowing for a reasonably complete view of the extreme cytogenetic diversity and the still obscure phylogenetic relationships of *Eligmodontia* species.

But firstly, we will now evaluate empirically the assumption that, despite the large changes in 2n and NFa, the total genome sizes of *Eligmodontia* species have been conserved since their last common ancestor. On the one hand, there are no large amounts of heterochromatin in *E. puerulus* NFa = 48, or in *E. typus* NFa = 44 (Ortells et al. 1989), or in the related phyllotine *Andinomys edax* NFa = 56. On the other hand, if relative lengths of all chromosomes from the five species are compared in a single karyo-idiogram, as shown in figure 5, at least two marker chromosomes, the X and Y, clearly retain their relative lengths at roughly 6 to 7% and 3.4 to 3.9%, respectively, despite the most probable pericentric inversion which gave rise to the derived *typus* X and Y, as well as the *morgani* Y chromosome. If large changes in total genome size had occurred, such length ranges should be expected to exhibit larger variations than those observed here. G-bands, where available, also document the size constancy of the identified sex chromosomes. In summary, gross constancy among genome sizes may be accepted as a reasonable assumption for further chromosome comparisons based on relative lengths.

Inferences about species distinctions, chromosomal changes and phylogenetic relationships can be made from our results when compared with those already published. It is immediately obvious that at least seven Robertsonian fissions or fusions and one pericen-

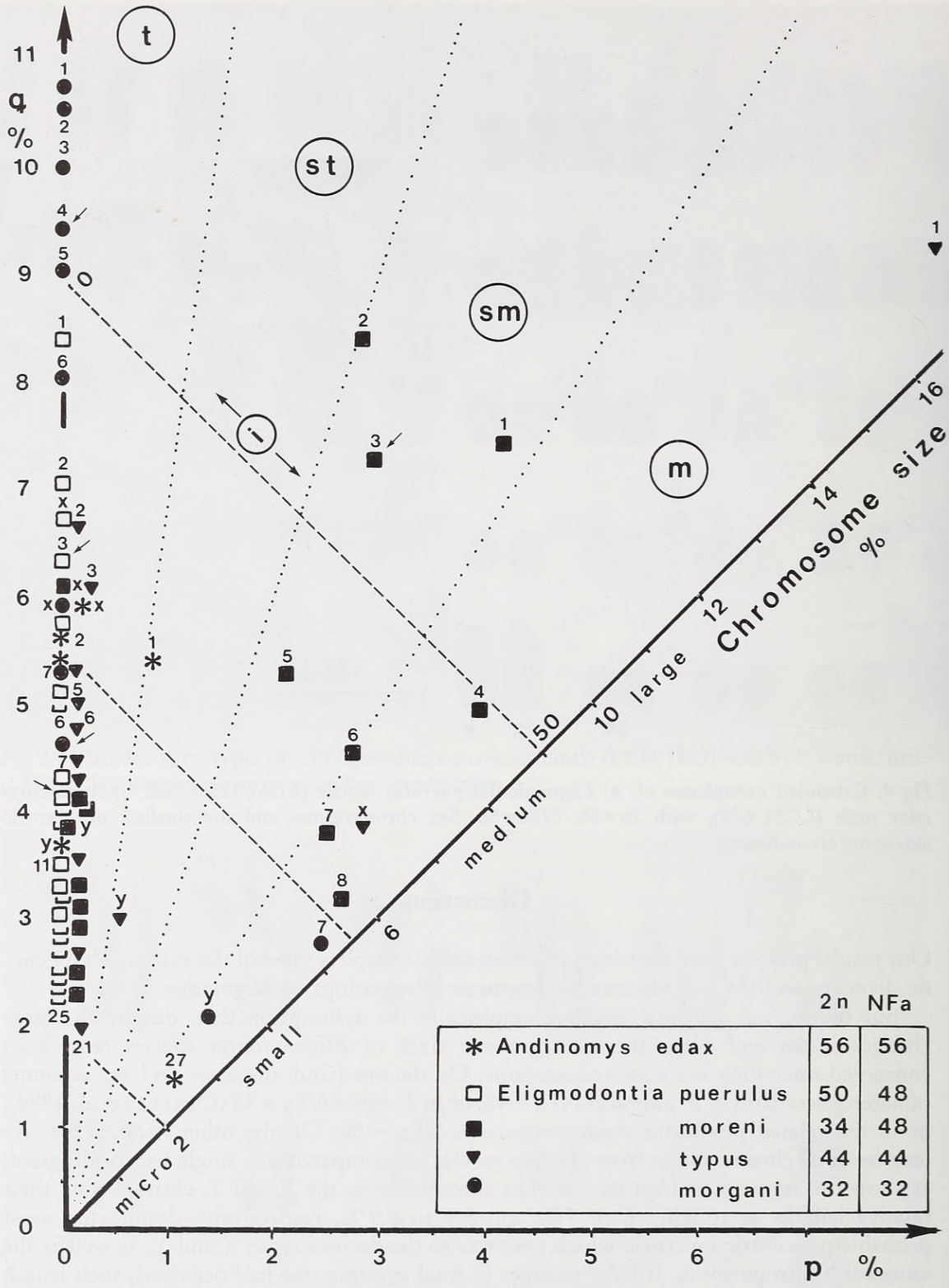

Fig. 5. Karyo-idiogram (bivariate plot) showing relative sizes of short arm (p) versus long arm (q) chromosomes from four *Eligmodontia* species and *Andinomys* (not all chromosomes actually shown). Total chromosome size may be read on the diagonal; chromosome classifications by morphology and size follow Levan et al. (1964) and Ortells et al. (1989), respectively. *Eligmodontia typus* and *E. morgani* data are from Ortells et al. (1989)

tric inversion strongly support the separate species status of *E. puerulus* and *E. moreni*. The eventual hybrid produced from a cross among individuals with such karyotypes most probably would exhibit abnormal meiosis and reduced fertility. Therefore, the chromosome differences detected substantiate the morphological and ecological distinctions previously noted between populations of both nominal species (MARES et al. 1989).

At the same time, the NFa = 48 shared only by these two species suggests a primitive condition close to the NFa = 54 shown by *Andinomys*. These three species with only medium or small chromosomes (see Fig. 5) have in fact close and exclusive geographic ranges in the Altiplano, and within the northeastern side of the xeric diagonal which divides South America in two parts (SPOTORNO and VELOSO (1989). This geographic subregion has been considered the center of origin of the phyllotine group (REIG 1986). Independent evidence based on electrophoretic analysis of proteins also placed the monotypic *Andinomys* at the base of the phyllotine radiation (SPOTORNO 1986).

The southernly distributed *E. typus* and *E. morgani* seem to belong to a different and derived phyletic line. Their divergent karyotypes NFa = 44 and 32 are characterized by chromosome arms longer than 9 %, which are absent in the NFa = 48 karyotypes: the long arm of *E. typus* metacentric pair 1 and the long arms of *E. morgani* telocentric pairs 1 through 5 (Fig. 5). These have been interpreted as being produced by tandem translocations (ORTELLS et al. 1989). As such, they must represent derived conditions that arose from the primitive ones presently seen in the northern NFa = 48 karyotypes.

For instance, chromosome comparisons based on the karyo-idiogram (Fig. 5) allow the proposal of the following most simple transformation series. The largest metacentric pair 1 of *E. typus*, having arms of 9.3 and 8.2 %, is surely a unique and extremely derived condition. It was probably formed from the centric fusion of two derived telocentric elements of correspondant large sizes, similar to pairs 5 and 6 of *E. morgani* (pair 5 being the intermediate condition shared by *E. typus*). Finally, the derived large telocentric *morgani* chromosome 5 probably arose through tandem fusion of two small telocentric elements such as those found in *E. puerulus* (the most ancestral condition, also shared by *Andinomys*), or in the small q arm of metacentric 1 of *E. moreni* (an additionally derived condition). Such a transformation series for this character may be linearly written through the following species tree: *([typus, morgani] puerulus [moreni])*. This topology is also a reasonable summary of cytogenetic data, as well as of geographic data, since it is consistent with the southern (*typus-morgani*) – northern (*puerulus-moreni*) axis of species distribution; therefore, it is a good candidate for a reasonable estimate of the real species phylogeny.

A strikingly similar northern-southern geographic pattern has been postulated for the chromosomal evolution of four related phyllotine species of the genus *Auliscomys* (WALKER and SPOTORNO 1993). Among them, "an ancestral telocentric karyotype would have undergone three consecutive tandem fusions" in southern species; later, three centric fusions probably occurred in northern species. The paleogeographic model proposed there, based on the assumption that actual biotic patterns in South America were determined by Quaternary geological and climatic changes (VUILLEMIER 1971), seems to be also valid for *Eligmodontia* species.

Moreover, the extreme cytogenetic diversity of *Eligmodontia*, as well as the occurrence of tandem fusions rarely documented in mammals, suggest an active role of chromosomal changes in the speciation process. Although this has been a subject of renewed interest and controversy (CAPANNA 1982; PATTON and SHERWOOD 1983; BAKER and BICKHAM 1986; SITES and MORITZ 1987), recently REIG (1989) has contributed importantly to clarify such causal relationship; he suggested that explosive speciation processes were triggered by chromosomal rearrangements. However, fertility studies on the heterozygotes for different chromosomal rearrangements indicate that meiotic and evolutionary consequences are drastically different, depending upon the type of rearrangement. Thus, while single centric

fusions would have little or no reproductive isolation effects, because the fertility of heterozygotes is modified slightly or not at all (Bickham and Baker 1979; John 1981; Patton and Sherwood 1983), single tandem fusions would have drastic consequences, severely reducing the fertility of heterozygotes (White 1973; John 1981; for a recently reported case where tandem fusions are involved in hybrid infertility, see Ryder et al. 1989). The fact that both types of chromosomal changes have occurred independently within two different but related phyletic lines evolving within the same subregions, invites consideration of geographic factors in contrast to cytogenetic factors.

The following hypothetical sequence of events would be consistent with our cytogenetic data, the present species ranges and geography of the region. An ancestral, perhaps late Miocene species with NFa = 48, having a wide northern-southern range, was separated by the Plio-Pleistocene xeric diagonal. The northern ancestor would have evolved into the present *E. puerulus*, maintaining its karyotype morphology, and secondarily to *E. moreni*, mainly by centric fusions. Here, the ice barriers generated by cyclic glacial warming and freezing within the Andean valleys (Vuillemier 1971) would be an associated requirement for speciation processes that maintained the NFa = 48; i.e. geographic factors would be sufficient for biological isolation, and cytogenetic isolation was not required. By contrast, the populations on the flat landscapes of southern Argentina were less prone to be affected by such ice barriers. Here, tandem fusions, with drastic meiotic isolating consequences, could probably be sufficient to change NFa. In other words, geographic factors would be insufficient for isolation, and cytogenetic isolation was required in the southern subregion. A similar pattern of chromosome divergence seems to have occurred in the species of *Auliscomys* (Walker and Spotorno 1993). Therefore, the isolation required for speciation might be the product of subsidiary or complementary actions between extrinsic (geographic) factors and intrinsic (chromosome) mechanisms. These would explain the high degree of chromosomal divergence observed among these phyllotine rodents as well as within many mammalian groups.

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Zusammenfassung

Cytogenetische Vielfalt und Evolution von Eligmodontia-Arten in den Anden (Rodentia, Muridae)

Bei zwei Arten der Gattung *Eligmodontia* wurden Standard- und G-gebänderte Chromosomen aus Knochenmarkszellen untersucht. Drei Männchen und vier Weibchen von *E. puerulus* aus dem Norden Chiles zeigten 2n = 50, NFa = 48. Drei Männchen von *E. moreni* aus dem Norden Argentiniens zeigten 2n = 34, NFa = 48. Vergleichende Untersuchungen ergaben eine starke Konservierung der G-Bandenmuster. Bei insgesamt 15 telozentrischen Chromosomen von *E. puerulus* stimmten die Bandenmuster mit jenen von 8 metazentrischen Chromosomen von *E. moreni* überein. Dies kann als das Ergebnis von sieben zentrischen Fusionen und einer perizentrischen Inversion bei *E. moreni* interpretiert werden. Ähnlich wie bei der verwandten Art *Andinomys edax* (2n = 54, NFa = 54, zwei Männchen und ein Weibchen aus dem Norden Chiles untersucht), waren die C-Bänder von *E. puerulus* schmal. Im Gegensatz zu den südlichen Arten *E. typus* und *E. morgani* betrugen bei den nördlichen Arten die längsten Chromosomenarme weniger als 9 % des diploiden Karyotyps. Das Auftreten erheblich längerer Chromosomenarme bei den südlichen Arten deutet auf das Vorliegen von Tandemfusionen hin. Die südlichen Arten stellen demnach eine eigene phylogenetische Linie dar, die sich aus einem primitiven nördlichen Vorfahren mit 2n = 50 und NFa = 48 ableitet. Die Bedeutung geographischer und cytogenetischer Faktoren im Artbildungsprozeß bei *Eligmodontia* wird unter Bezugnahme auf *Auliscomys*-Arten aus demselben Verbreitungsgebiet diskutiert.

References

Baker, R. J.; Bickham, J. W. (1986): Speciation by monobrachial centric fusions. Proc. Natl. Acad. Sci. USA **83**, 8245–8248.

Bickham, J. W.; Baker, R. J. (1979): Canalization model of chromosomal evolution. Bull. Carnegie Mus. Nat. Hist. **13**, 70–84.

Capanna, E. (1982): Robertsonian numerical variation in animal speciation: *Mus musculus*, an emblematic model. In: Mechanisms of speciation. Ed by *C. Barigozzi*. New York: A. R. Liss. Pp. 155–177.

Crossen, P. E. (1972): The Crossen procedure. Mamm. Chrom. Newsl. **13**, 40.

Chiarelli, B. A.; Sarti-chiarelli, M.; Shafer, D. A. (1972): Chromosome banding with trypsin. Mamm. Chrom. Newsl. **13**, 44–45.

Kelt, D. A.; Palma, R. E.; Gallardo, M. H.; Cook, J. A. (1991): Chromosomal multiformity in *Eligmodontia* (Muridae, Sigmodontinae), and verification of the status of *E. morgani*. Z. Säugetierkunde **56**, 352–358.

John, B. (1981): Chromosome change and evolutionary change. In: Evolution and speciation. Ed. by W. R. Atchley and D. Woodruff. Cambridge: Cambridge Univ. Press. Pp. 23–51.

Lee, M. R.; Elder, F. F. B. (1980): Yeast stimulation of bone marrow mitoses for cytogenetic investigations. Cytogenet. Cell Genet. **26**, 36–40.

Levan, A.; Fredga, K.; Sandberg, A. (1964): Nomenclature for centromeric position on chromosomes. Hereditas **52**, 201–220.

Mares, M.; Ojeda, R. A.; Barquez, R. M. (1989): Guide to the mammals of Salta Province. Norman, USA: Univ. Oklahoma Press.

Massarini, A. I.; Barros, M. A.; Ortells, M. O.; Reig, O. A. (1991): Chromosomal polymorphism and small karyotypic differentiation in a group of *Ctenomys* species from Central Argentina (Rodentia: Octodontidae). Genetica **83**, 131–144.

Musser, G. G.; Carleton, M. D. (1993): Family Muridae. In: Mammal species of the world. Ed. by. D. E. Wilson and D. M. Reeder. Washington, London: Smithsonian Institution Press. Pp. 501–756.

Ortells, M. O.; Reig, O. A.; Weinberg, R. L.; Hurtado de Catalfo, G. E.; Gentile de Fronza, T. M. L. (1989): Cytogenetics and karyosystematics of phyllotine rodents (Cricetidae, Sigmodontinae). II. Chromosome multiformity and autosomal polymorphism in *Eligmodontia*. Z. Säugetierkunde **54**, 129–140.

Pathak, S.; Stock, A. D. (1974): The X chromosome in mammals: karyological homology as revealed by banding techniques. Genetics **78**, 703–714.

Patton, J. L.; Sherwood, S. W. (1983): Chromosome evolution and speciation in rodents. Ann. Rev. Ecol. Syst. **14**, 139–158.

Pearson, O. P.; Patton, J. L. (1976): Relationships among south american phyllotine rodents based on chromosome analysis, J. Mammalogy **57**, 339–350.

Reig, O. A. (1986): Diversity patterns and differentiation of high Andean rodents. In: High Altitude Tropical Biogeography. Ed. by. M. Monasterio and F. Vuilleumier. New York: Oxford Univ. Press. Pp. 404–439.

— (1989): Karyotypic repatterning as one triggering factor in cases of explosive speciation. In: Evolutionary biology of transient unstable populations. Ed. by A. Fontdevila. Heidelberg, Berlin: Springer-Verlag. Pp. 246–289.

Ryder, O. A.; Kumamoto, A. T.; Durrant, B. S.; Benirschke, K. (1989): Chromosomal divergence and reproductive isolation in dik-diks. In: Speciation and its consequences. Ed. by D. Otte and J. A. Endler. Sunderland, Massachusetts: Sinauer. Pp. 208–228.

Sites, J. W.; Moritz, B. (1987): Chromosomal evolution and speciation revisited. Syst. Zool. **36**, 153–174.

Spotorno, A. E. (1986): Systematics and evolutionary relationships of Andean phyllotine and akodontine rodents. Unpubl. Diss., Univ. California, Berkeley, USA.

Spotorno, A.; Brum, N.; Di Tomaso, M. (1987): Comparative Cytogenetics of South American deer. Fieldiana (Zool.) **84**, 473–483.

Spotorno, A. E.; Veloso, A. (1990): Flora and Fauna of the altiplano. In: Strategies in human adaptation to a rigorous environment: the Aymara. Ed. by. W. J. Schull and F. Rothhammer. Dordrecht: Kluwer Acad. Publ. Pp. 19–32.

Spotorno, A. E.; Walker, L. I. (1979): Analysis of chromosomal similarity according G banding patterns in four chilean species of *Phyllotis* (Rodentia, Cricetidae). Arch. Biol. Med. Exper. **12**, 83–90.

Sumner, A. T. (1972): A simple technique for demonstrating centromeric heterochromatin. Exp. Cell Res. **75**, 304–306.

Vuillemier, B. S. (1971): Pleistocene changes in the fauna and flora of South America. Science **173**, 771–780.

Walker, L. I.; Spotorno, A. E. (1993): Tandem and centric fusions in the chromosomal evolution of

the South American phyllotines of the genus *Auliscomys* (Rodentia, Cricetidae). Cytogen. Cell Genet. **61**, 135–140.

Walker, L. I.; Spotorno, A. E.; Fernandez-Donoso, R. (1979): Conservation of whole arms during chromosomal divergence of phyllotine rodents. Cytogen. Cell Genet. **24**, 209–216.

White, M. J. D. (1973): Animal cytology and evolution. Cambridge: Cambridge Univ. Press.

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