Chromosome divergence of *Octodon lunatus* and *Abrocoma bennetti* and the origins of Octodontoidea (Rodentia: Histricognathi)

Divergencia cromosómica de *Octodon lunatus* y *Abrocoma bennetti* y los orígenes de los Octodontoidea (Rodentia: Histricognathi)

ANGEL E. SPOTORNO [1], LAURA I. WALKER [1], LUIS C. CONTRERAS [2], JUAN C. TORRES [3], RAUL FERNANDEZ-DONOSO [1], M. SOLEDAD BERRIOS [1] and JUANA PINCHEIRA [1]

[1] Departamento de Biología Celular y Genética, Facultad de Medicina, Universidad de Chile, Casilla 70061, Santiago 7, Chile.
[2] Comisión Nacional de Medio Ambiente, Av. B. O' Higgins 949, P. 13, Santiago, Chile.
[3] Museo Nacional de Historia Natural, Interior Quinta Normal, Santiago, Chile.

ABSTRACT

Octodontoidea have 2n from 10 to 102, and NF from 16 to 202, the largest ranges known for a mammal family group. Although 4 out of the 7 genera have very similar karyotypes to the one found in *Octodon degus* 2n=58, NF=116, other two genera are extremely divergent ones. We describe and compare here the undescribed chromosome data from seven specimens of *Octodon lunatus* 2n=78, NF=128, and of thirteen specimens of *Abrocoma bennetti* 2n=64, NF=114, from the related monogeneric Abrocomidae. Karyotype and chromosome analysis based on shape, size, and G-, C-, and AgAs bands detected 20 and 7 telocentric pairs respectively. Most of these characters were previously unknown in non-*Ctenomys* octodontoids. Some large metacentric chromosomes differed among species, and the differences in G bands were more abundant than what would be expected from their 2n and NF. C bands were very heterogenous within karyotypes. The general cytogenetics features of *Abrocoma* were nearer to those of 4 octodontid genera than to those of *Chinchilla*, and consistent with the classical position of Abrocomidae within Octodontoidea. Given that *Abrocoma* is a predominantly northern genus, as it is *O. lunatus* among chilean Octodontidae, the northern origin of the whole group is suggested.

Key words: evolution, karyo-idiogram, karyograph, Chinchilloidea

RESUMEN

Los Octodontoidea tienen 2n entre 10 y 102, y NF entre 16 y 202, los más grandes intervalos conocidos para un grupo mamífero de nivel familiar. Aunque 4 de los 7 géneros de Octodontidae tienen cariotipos similares al de *Octodon degus* 2n=58, NF=116, los otros 3 géneros son extremadamente divergentes. Describimos y comparamos aquí datos cromosómicos no analizados de 7 especímenes de *Octodon lunatus* 2n=78, así como los de 13 especímenes de *Abrocoma bennetti* 2n=64, NF=114, perteneciente a la familia relacionada Abrocomidae, monogenérica. Los análisis cariotípico y cromosómico, basados en la forma, tamaño, y bandas G, C y AgAs detectaron 20 y 7 pares telocéntricos; éstos son caracteres previamente desconocidos dentro de octodontoides no *Ctenomys*. Algunos cromosomas metacéntricos grandes eran distintos entre especies, y las diferencias en bandas G fueron más abundantes que lo esperado a partir de de sus 2n y NF. Las bandas C fueron muy heterogéneas dentro de los cariotipos. Las características citogenéticas de *Abrocoma* fueron más similares a las de 4 géneros de Octodóntidos que a las de *Chinchilla*, lo que es consistente con la clásica posición de Abrocomidae dentro de Octodontoidea. Dado que *Abrocoma* es un género predominantemente del Norte, como lo es *Octodon lunatus* entre los *Octodon* chilenos, se sugiere un origen nortino para el grupo.

Palabras clave: evolución, cario-idiograma, cariógrafo, Chinchilloidea

INTRODUCTION

One of the major events in the evolution of South American mammals was the radiation of Southern Andean Octodontoidea, the second most diverse clade among the twelve endemic families of New World histricognath rodents (Patterson & Pascual 1972). Although the diversification of such monophyletic group (Nedhal et al 1994) seems to be linked to the rise of the Andes, details are largely unknown, since most of the species from its morphologically well distinct families have been poorly studied by molecular or other modern methods.

At a first glance, we might expect that such large divergences might be associated with large chromosomal divergences.

Nevertheless, as four divergent living genera of the most diverse Octodontidae were known to have species with very similar karyotypes to that of *Octodon degus* 2n=58 and NF=116, it was suggested "that diversification of the main adaptatively different lineages of octodontines took place without major chromosome repatterning" (Reig 1989).

With the recent descriptions of the highest chromosome and arm numbers for a mammal karyotype, 2n=102, NF=202 in the octodontid *Tympanoctomys barrerae* (Contreras et al. 1990), of the C-banding karyotypes in some Octodontoids (Gallardo, 1992), and of the *Ctenomys steinbachi* karyotype of 2n=10, NF=16 (Anderson et al. 1987), the situation have been reversed. The superfamily now exhibits the largest range of 2n and NF values known for a mammalian family group.

We report and analyze here the chromosomes of two rare species from Central Chile, *Octodon lunatus* and *Abrocoma bennetti*. The latter belongs to Abrocomidae, traditionally considered a closely related family to Octodontidae and Ctenomyidae. All are usually included within the superfamily Octodontoidea (Patterson & Pascual 1972). Nevertheless, it has been recently suggested that Abrocomidae might belong to the more recent superfamily Chinchilloidea (Glanz & Anderson 1990).

The chromosome analyses of both species, further cytogenetic data from the related octodontids *Octodon degus*, *Spalacopus cyanus* and *Tympanoctomys barrerae*, and morphological and biogeographic information, will demonstrate that the karyotypes of *Octodon lunatus* and *Abrocoma bennetti* represent intermediate conditions between two divergent extremes: *Tympanoctomys* and the rest of Octodontoidea (Contreras et al. 1990). This have been called a bidirectional trend in karyotype evolution (Gallardo 1992). It will be also shown that those data are consistent with the traditional position of Abrocomidae within Octodontoidea, suggesting a northern origin and a southern diversification of Octodontidae along the Andes.

MATERIALS AND METHODS

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

Taxa, original localities, altitude above sea level (in meters), and number of examined specimens with LCM numbers (in parenthesis) are as follows. ABROCOMIDAE, *Abrocoma bennetti*: 2 km SE Las Tacas, IV Region, 50 m (1: 287); 3 km NE Aucó, IV Region, ca. 1050 m (2: 443, 444); Las Breas, IV Region, ca 2000 m (2: 368, 442); La Dehesa, E Santiago, RM, ca. 850 m (8: 001, 005,.007, 303, 418, 421, 422, 423). OCTODONTIDAE, *Octodon degus*: Los Molles, IV Región, 50 m (2: 184, 1619); La Dehesa, RM, ca. 850 m (12: 267, 268, 310-316, 320-323). *O. lunatus*: 5 km NE Aucó, IV Región (2: 1032, 1286); 2 km NE Peñuelas, V Región (5: 1617-1619, 1676, 1677). *Spalacopus cyanus*: 10 km W Catapilco, V Región (6: 269, 270, 272-275); Farellones, RM, ca. 2800 m (5: 336, 630, 767, 837, 838); Lagunillas, RM, ca. 2600 m (1: 340). *Tympanoctomys barrerae*: Salinas 40 km N of Desaguadero, Mendoza, Argentina, ca 500 m (1: 1076).

Chromosome analysis. Chromosomes were obtained from bone marrow cells using the conventional in vivo colchicine, hypotonic method, preceded by yeast injection to improve the mitotic index (Lee & Elder 1980). Some metaphase cells were stained with 2% Giemsa, or treated with C (Crossen 1972, Sumner 1972) and G banding techniques (Chiarelli, 1972). The nucleolar organizing regions were detected by silver staining procedures (Quack & Noel 1977).

Giemsa stained chromosomes were first measured on photographic enlargements and their relative lengths calculated as percentages the female haploid set (FHS; see Reig & Kiblisky 1969, Massarini et al. 1991). They were classified as large, medium or small sized, when their relative lenghts were > 9%, 9 - 5.5% or < 5.5% of

FHS, respectively. This standard procedure assumes a constancy in the DNA amount per cell. When substantial interspecific variations in C bands were detected later, we also compared absolute chromosome lengths and displayed them within a karyo-idiogram, a bivariate plot allowing detailed chromosome comparisons (Spotorno et al. 1985).

Some G-banded karyotypes were compared from selected metaphases of male and female specimens from each taxa. Chromosome pairs were classified according to their G band pattern similarities as totally corresponding (homologous), partially corresponding (homeologous) or unique among the different taxa (Walker et al. 1992).

RESULTS

The karyotype of *Octodon lunatus* was strikingly asymmetric in the size and shape of its elements (Fig. 1). Among its 78 chromosomes, 20 pairs were small and telocentric in shape, with no visible short arms, and the other 20 were small sub-telocentric, submetacentric or metacentric ones. Since the largest chromosome (5.1% of the female haploid set) was a single submetacentric element in males and were 2 in females, they probably are the X; the pressumed Y was a very small one (1.44% of the FHS). The submetacentric pair 22 (3.6% of the FHS) exhibited a distinct interstitial secondary constriction at its long arm (Fig. 1).

The 64 small chromosomes of *Abrocoma bennetti* also exhibited a certain asymmetry in shape. Only 7 pairs were totally telocentric ones, the remaining 25 pairs having all other possible shapes (Fig.1). The largest chromosome (5.9% of the FHS) was also the presumptive X, and the probable Y had a 2.6% FHS, with a metacentric shape. The single secondary constriction was consistently observed in the autosome pair 12 (3.5% FHS). These features are basically similar to those described by Gallardo 1992, with some differences in the size of the second telocentric (number 26 in his Fig. 3).

There were many similarities, as well as striking differences, between these karyotypes and those described for *Octodon degus, Spalacopus cyanus* (Fernández-Donoso 1968, Reig et al. 1972) and *Tympanoctomys barrerae* already reported (Contreras et al. 1990). Such similarities in size and shape are shown in the comparative karyo-idiogram of Fig. 2.

On the other hand, the 7 and 20 wholly telocentric chromosomes here found in *Octodon lunatus* and *Abrocoma bennetti* respectively, were completely absent as such in the karyotypes of all the other species. Moreover, we expected that many metacentric and submetacentric chromosomes would overlapped in the karyo-idiogram, since they were abundant in karyotypes having very similar 2n and NF. Nevertheless, most chromosomes were distributed all over this area of the karyo-idiogram (Fig. 2). For example, chromosome 1 from *O. degus* was much larger than the largest autosome of *O. lunatus* (number 21 in Fig. 2), and both were very different than the nearest in *A. bennetti* (number 8).

G bands allowed reasonable identifications of some chromosomes and chromosome arms between karyotypes (Fig. 3). Clear examples are the almost complete similarities in kind and sequence of G-bands shown by: a) the X chromosomes of the four species (being *Spalacopus* the most divergent); b) the chromosomes bearing the secondary constriction in all the four karyotypes (chromosome numbers as follows: *lunatus* 23, *bennetti* 12, *degus* 4 and *cyanus* 5); and c) *A. bennetti* 1 and *O. lunatus* 3 and also with the long arm of *O. degus* 3 (Figs. 3 and 5). In concordance with the divergent morphologies of the abundant metacentric chromosomes, we were not able to establish reasonable correspondences among most of these elements when compared in detail.

C-bands were relatively constant among different cells and individuals within a species. Since nominal subspecies have been described for *Spalacopus cyanus* from the mountains and the coast of Chile, we examined individuals from two such different populations. No differences in C-
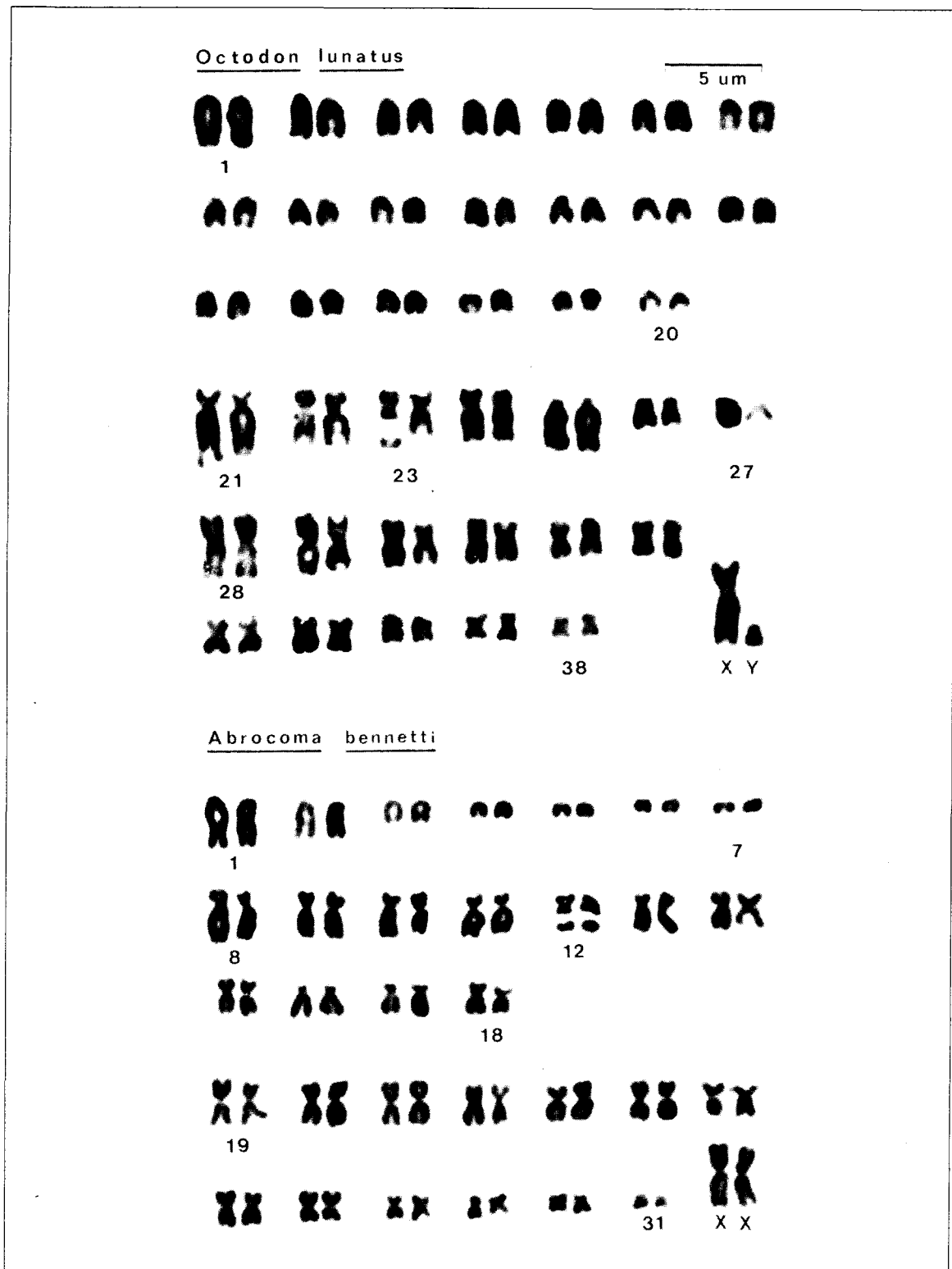
Fig. 1. Chromosomes of *Octodon lunatus* male, specimen LCM 1032 (upper); and *Abrocoma bennetti* female, LCM 287 (lower).

Cromosomas de *Octodon lunatus* macho, espécimen LCM 1032 (arriba); y *Abrocoma bennetti* hembra, LCM 287 (abajo).

bands (Fig. 4b) nor in G-bands (not illustrated) were detected among them.

C bands also revealed an heterogenous distribution of constituve heterochromatin within some karyotypes. Small but clear C-bands were present at the centromeric region of many chromosomes from *Octodon degus* and *Spalacopus cyanus* (Fig. 4), but they were absent in ten chromosomal pairs of the former and six ones of the latter. Most of the latter were subtelocentric ones, and their centromeric region exhibited stained G-bands (Fig. 3). Conversely, most metacentric chromosomes with centromeric C bands showed light G-bands in the centromeric regions.

The C-bands of *Octodon lunatus* and *Abrocoma bennetti* were also pericentromeric and of small sizes (male 1032 and female 287, respectively, not illustrated here). The exception was a single chromosome in *Octodon lunatus*, probably the Y, with a large pericentromeric C-band in the proximal region of the long arm.

Some homeologies between species chromosomes were evident through G- and C-band comparisons. For instance, the short arm of autosome 1 of *Spalacopus cyanus* corresponded with the long arm of the autosome 1 of *Octodon degus* (Fig. 5). This band sequence was also identical to those shown by the telocentric autosome 1 of *Octodon lunatus* (Fig. 4). We were not able to identify this chromosomal portion in the *Abrocoma* genome.

A large and unique C band was evident in the subcentromeric region of *Spalacopus* 1 long arm (Fig. 4b; see also Gallardo 1992). The staining of this band was lighter than that of the small centromeric one, suggesting differences in condensation or base composition. This feature was not evident in the previous description mentioned, a difference probably derived from the different technique used. This particular portion of heterochromatin exhibited distinct G banding (Fig. 4b and 5).

AgAs-stained bands were consistently present in a single chromosome pair having similar size and shape among all karyotypes (Fig. 2 and 6). They are at the same place where secondary constrictions appeared under other staining procedures. This AgAs-positive band was usually larger in the homologue with a greater length, probably representing a functional condition.

DISCUSSION

After the cytogenetic description of almost all species from all genera of Octodontoidea s.s., a general picture on the chromosome evolution of the three most diverse families seems to emerge. This can be seen graphically by means of two synthetic diagrams: the taxic curve (Fig. 7) and the karyograph (Fig. 8).

The taxic curve shows the diversity in number of species of the different clades of Octodontoidea s.s.; the diploid numbers have been added in this particular case. An asymmetrical hollow curve distribution is observed, which is one of the most remarkable characteristic on the distribution of intrataxonomical diversity of many living organisms (see full discussion in Reig 1989). Although a very similar curve was obtained by such author for Octodontidae genera (including *Ctenomys*), his interpretation of chromosomal variation in this group was limited to four non-*Ctenomys* species karyotypes by that time. Now we have information for eleven species included in such a graph.

After his discussion of the 2n=58 karyotype as the probable primitive one, and as an exception to his main thesis, Reig (1989) concluded: "These data also suggest that diversification of the main adaptively different lineages of octodontines took place without major chromosomal repatterning, and show that chromosomal invariance in them is related to absence or poverty in species differentiation" (p. 264). Further species additions, and particularly the large increase in diploid number ranges and variations described for *Octodon* (present report) and *Aconaemys* species (Gallardo & Reise 1992), as well as the gross G-band divergences among 2n=58 karyotypes here detected, strongly suggest that much more genome diversity is included among the Octodontoidea lineages. Our data thus reinforces the main thesis

of Reig (1989) that morphological and ecological diversification took place in association with major chromosomal changes.

The karyograph of Fig. 8 displays most of the known diploid and fundamental numbers of Octodontoidea species. Most exhibit predominantly metacentric karyotypes (towards the upper diagonal in Fig. 7). The telocentric chromosomes of *Octodon lunatus* and *Abrocoma bennetti* represent a striking departure of such gene-

Fig. 2. Comparative karyo-idiogram of chromosome lengths from *Spalacopus cyanus* (some chromosomes), *Octodon degus*, *O. lunatus* and *Abrocoma bennetti*. Chromosome nomenclature according to Levan et al. 1964; i= centromeric index. Some chromosomes of interest are marked with numbers, sex chromosomes with X or Y, and NOR bearing chromosomes with arrow-heads.

Cario-idiograma comparativo de las longitudes cromosómicas de *Spalacopus cyanus* (algunos cromosomas), *Octodon degus*, *O. lunatus* y *Abrocoma bennetti*. La nomenclatura cromosómica sigue a Levan et al. 1974; i= índice centromérico. Algunos cromosomas de interés están marcados con números, cromosomas sexuales con X o Y, y cromosomas portadores de NOR con puntas de flechas.

ral tendency, demanding a detailed comparison and explanation.

Telocentric chromosomes like those present in *A. bennetti* and *O. lunatus* karyotypes, probably represent primitive conditions within Octodontoidea. First, they are actually present in Abrocomidae, a family usually considered as the most related outgroup of present Octodontidae and Ctenomyidae (Patterson & Pascual 1972). Second, they are also present in all the three families, since telocentric chromosomes have been also described in a few species of the Ctenomyidae phyletic line, for instance *Ctenomys torquatus* (Reig & Kiblisky 1969) and *C. sociabilis* (Gallardo 1991). Third, although metacentric chromosomes are the most frequent condition within octodontids (Contreras et al. 1990), a closer analysis shows that some exhibit divergent morphologies (Figs. 2 and 5), demonstrating they are not homologous elements, i.e. they were not inherited as such from a recent common ancestor. In short, metacentric chromosomes seem to have evolved independently in two or perhaps the three phyletic lines, probably through parallel centric fusions of the pressumptive ancestral telocentric elements. This point of view has been also suggested for ctenomyids (Ortells 1990), octodontids (Contreras et al. 1994), and for two genera of muroid rodents living in the same regions, *Eligmodontia* and *Auliscomys* (Spotorno et al. 1994).

Therefore, it appears that chromosome rearrangements have been much more frequent and complex than what was initially suggested by the apparent similarities in the 2n and NF exhibited by the three families. This agrees with paleontological data that indicate a relatively long time of divergence for the group (Patterson & Pascual 1972).

The Octodontoidea genomes have been accumulating different amounts and kinds of heterochromatin, here detected through C bands, in many phyletic lines. The small centromeric C-bands observed in the primitive *Abrocoma* as well as in *Ctenomys sociabilis* (Gallardo 1991 and 1992) contrast with the well marked and large ones detected in most of the chromosomal
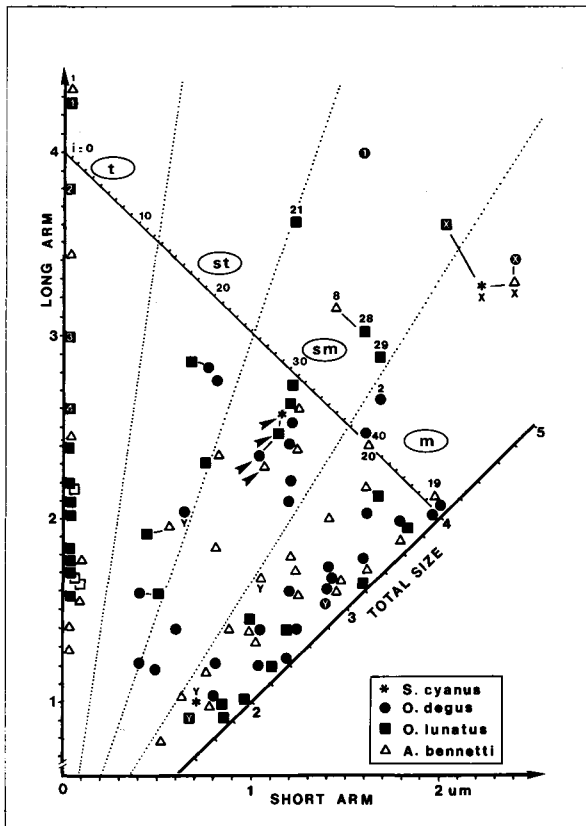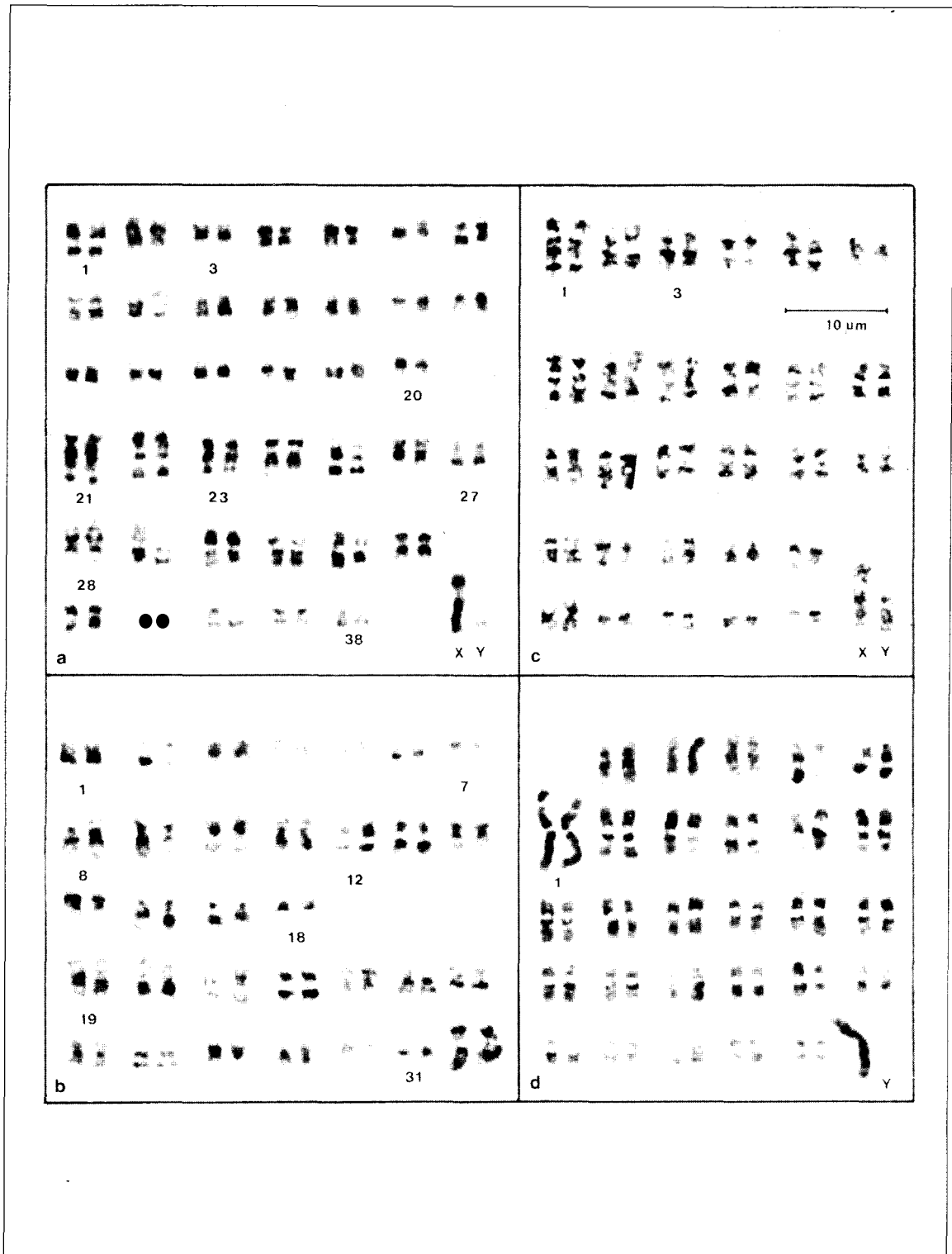
Fig. 3. G-banded chromosomes of: a. *O. lunatus* male, LCM 1032; b. *Abrocoma bennetti* female, LCM 287; c. *Octodon degus* male, LCM 253 ; and d. *Spalacopus cyanus* male, LCM 340. Chromosomes numbers are from the original karyotype descriptions.

Cromosomas bandeados G de: a. *O. lunatus* macho, LCM 1032; b. *A. bennetti* hembra, LCM 287; c. *Octodon degus* macho, LCM 253; y d. *Spalacopus cyanus* macho, LCM 340. Números cromosómicos son los de la descripción cariotípica original.
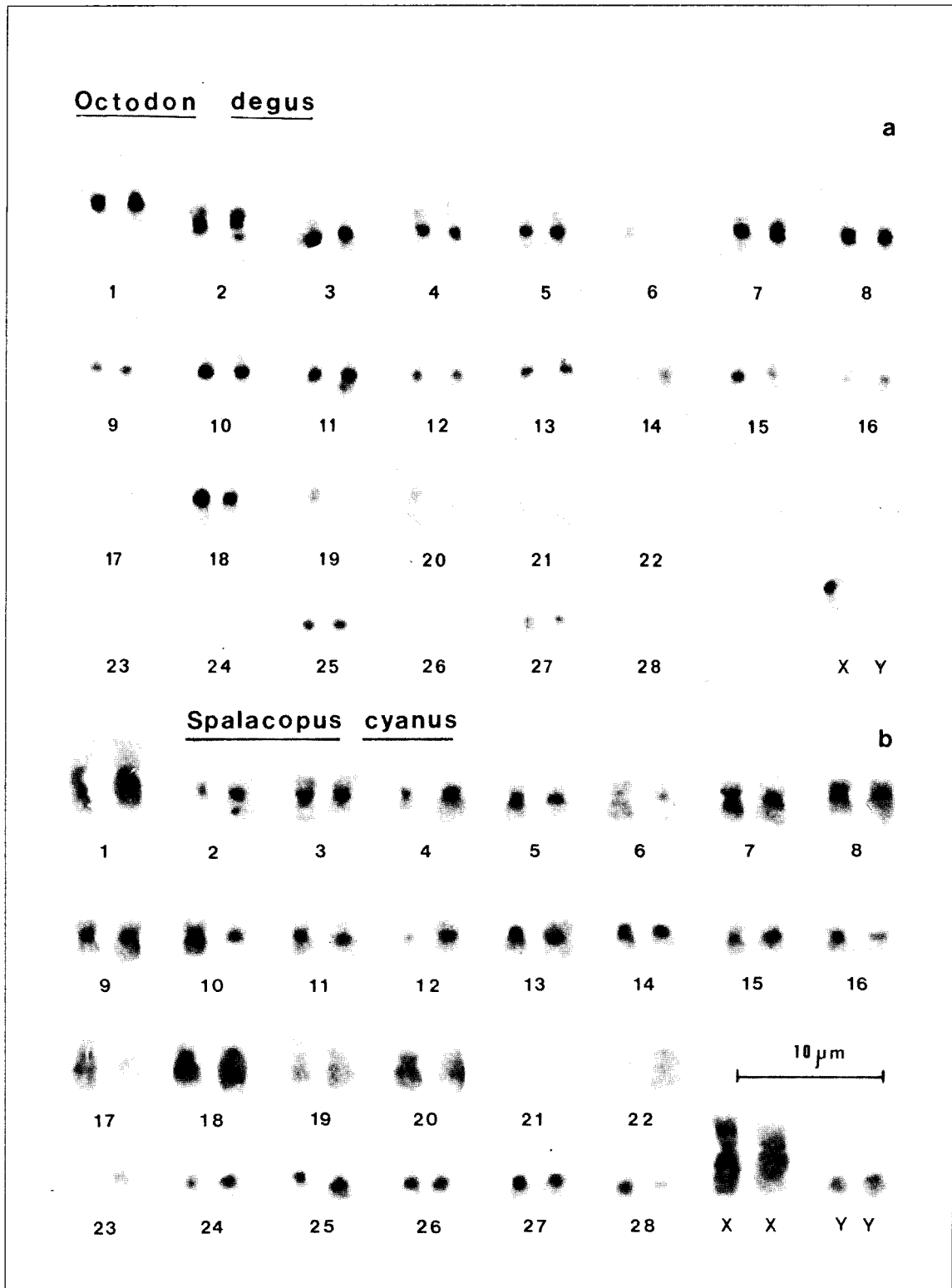
Fig. 4. C banded metaphases of: a. *Octodon degus*, male, LCM 267; b. *Spalacopus cyanus*, two males; in every pair, left chromosome is from LCM 751, and right one, from LCM 340.

Metafases bandeadas C de: a. *Octodon degus*, macho, LCM 267; b. *Spalacopus cyanus*, dos machos; en cada par, el cromosoma izquierdo es del LCM 751, y el derecho, de LCM 340.

short arms of *Tympanoctomys barrerae* (Contreras et al. 1990), and also in the pericentromeric region of some chromosomes of many species, such as *Octodon degus*, *Spalacopus cyanus* (Fig. 4 and Gallardo 1991), *Ctenomys opimus*, *Octodontomys gliroides* (Gallardo 1991) and other *Ctenomys* species (Massarini et al. 1991). Sometimes, such heterochromatin involved many whole short arms, as in four species of *Ctenomys* (Massarini et al. 1991).

It is most probable that the main mechanism of such heterochromatin increases was the amplification of the same short sequences of repetitive DNA, given that a DNA probe from a species of *Ctenomys* hibridized with differing amounts of the DNA extracted from other *Ctenomys* and *Octodontomys* species (Rossi et al. 1990), In situ hybridization of the same DNA probe with different chromosomes of other Octodontoidea would be a definitive proof of this hypothesis.
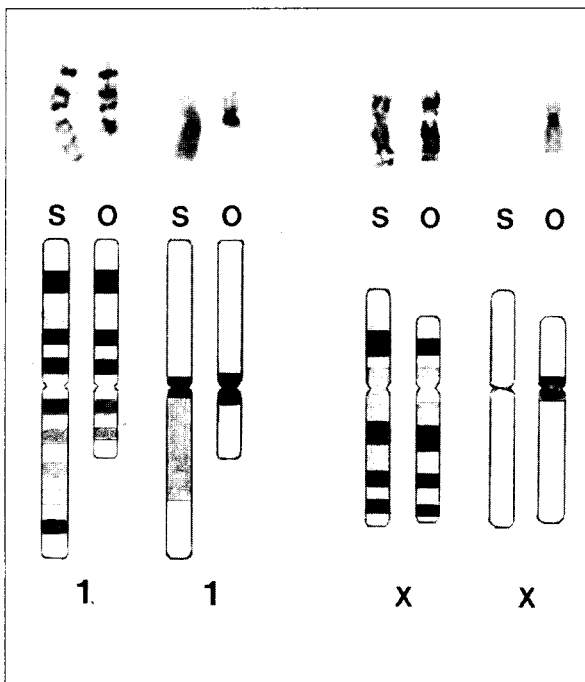

Fig. 5. Comparative G- and C-banded idiograms of autosome 1 and the X chromosome of *Spalacopus cyanus* (S) and *Octodon degus* (O).

Idiogramas bandeados G y C del autosoma 1 y del cromosoma X de *Spalacopus cyanus* (S) y *Octodon degus* (O).

In any case, amplifications of DNA sequences to give whole heterochromatic arms seem to have ocurred independently in *Tympanoctomys barrerae* and in a few *Ctenomys* genomes, thus increasing the total number of chromosome arms in these octodontid and ctenomyid phyletic lines. Since these new arms would increase the total number of chromosome arms, this would explain some of the extreme high NF values, as shown in Fig. 7.

Although many chromosomes seem to have been affected in such a process of heterochromatin amplification, a few regions remained unaffected in different genomes. The lack of heterochromatin actually shown by only some submetacentric chromosomes here observed in *Octodon*, *Spalacopus* (Fig. 4) and in a few *Ctenomys* species (Gallardo 1992; Massarini et al. 1991), in contrast with the usual amplification to all the chromosomes of a karyotype (an example in Walker et al. 1979), suggests an incomplete process (for instance, Walker et al. 1991), or more probably, the existence of some constraints in the diffusion or fixation of heterochromatin accumulation. Interchromosomic associations, like those described for *O. degus* and *C. opimus* (Fernández-Donoso & Berríos 1993), might be one of the mechanisms favouring differential diffusion or isolation of heterochromatic portions within particular genomes.

The cytogenetic features of *Abrocoma* are of some interest since the phylogenetic position of the monogeneric Abrocomidae have been recently changed from the superfamily Octodontoidea to the Chinchilloidea (Glanz & Anderson 1990). Although a detailed chromosome comparison among all these taxa should wait the description of chinchillids G-bands, the general cytogenetic features of *Abrocoma bennetti* are more near to those of 4 Octodontidae genera than to those of *Chinchilla* (Fig. 7). This argues in favour of the classical position of Abrocomidae within Octodontoidea.

A few hints about the probable northern origin of the main phyletic lines of Octodontoidea arise from these data. First, *Abrocomidae* is a rather northern family, having three of the four living species
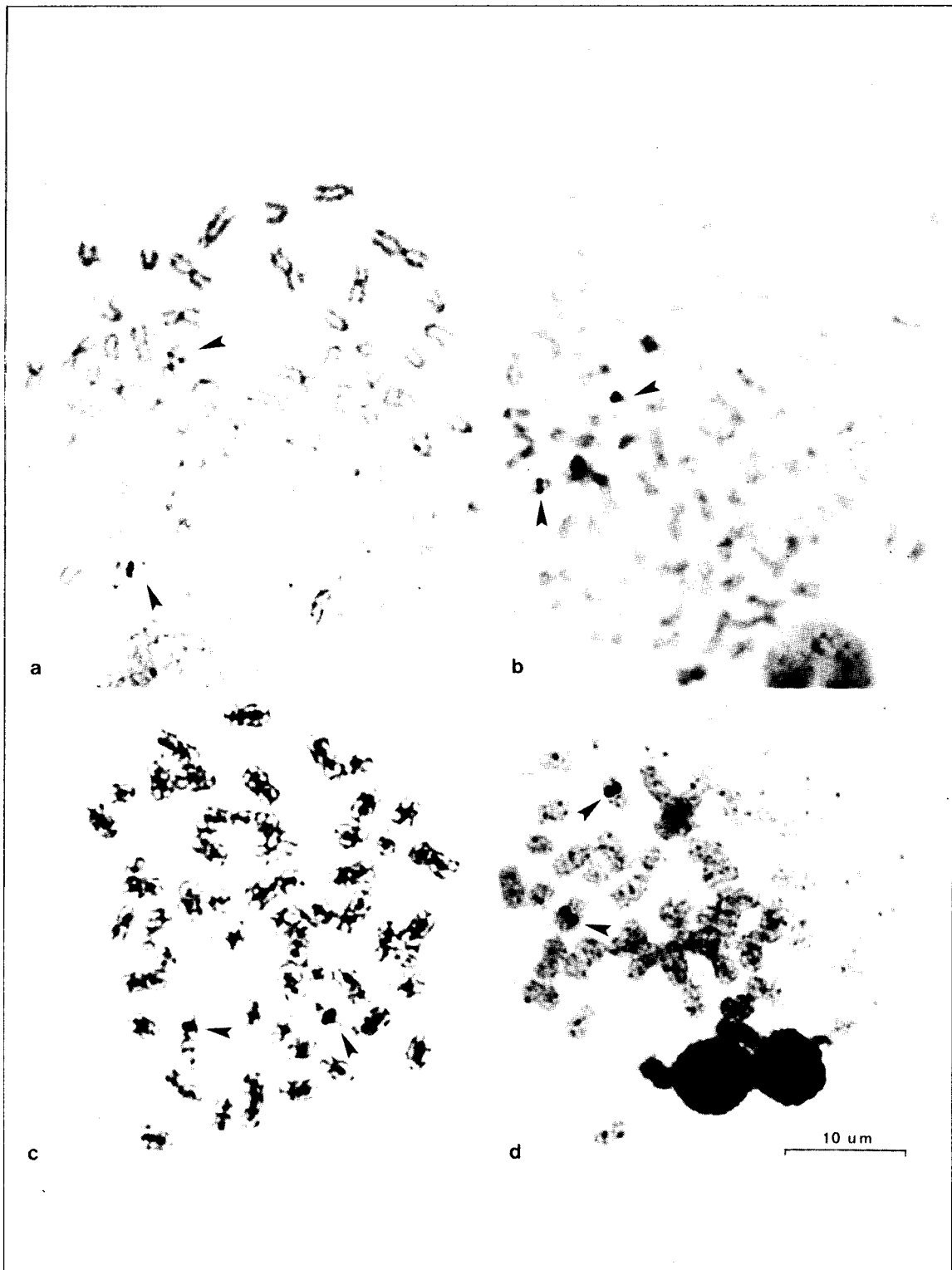
Fig. 6. AgAs NOR metaphases from: a. *Octodon lunatus* male, LCM 1286; b. *Tympanoctomys barrerae* male, LCM 1076; c. *O. degus* male, LCM 429; d. *Spalacopus cyanus* male, LCM 340. NOR bearing chromosomes marked with arrow-heads.

Metafases AgAs NOR de: a. *Octodon lunatus* macho, LCM 1286; b. *Tympanoctomys barrerae* macho, LCM 1076; c. *O. degus* macho, LCM 429; d. *Spalacopus cyanus* macho, LCM 340. Cromosomas portadores NOR marcados con puntas de flechas.

distributed in the Altiplano subregion (Glanz & Anderson 1990). Second, the whole group of Ctenomys species with the primitive condition of symmetric sperm heads, which is also shared by the rest of Octodontoidea, have also northern distributions; the remaining Ctenomys with the derived condition of asymmetric sperm heads, have southern distributions (Gallardo 1991, Roldan et al. 1992). Third, among the Octodontidae s.s., O. lunatus, having a primitive karyotype, lives in Cen-

tral Chile, occupying a more northern territory than those of O. bridgesi and O. pacificus (Hutterer 1994). Fourth, among all Octodontoidea, only the southern Octodontidae s.s. species share the derived condition of 2-2 penial spikes (Contreras et al. 1994), with the relatively northern Octomys and Tympanoctomys retaining the primitive 1-1 condition. Therefore, the geographic distribution of many independent characters suggest a northern origin for an initial radiation in the central Andes,
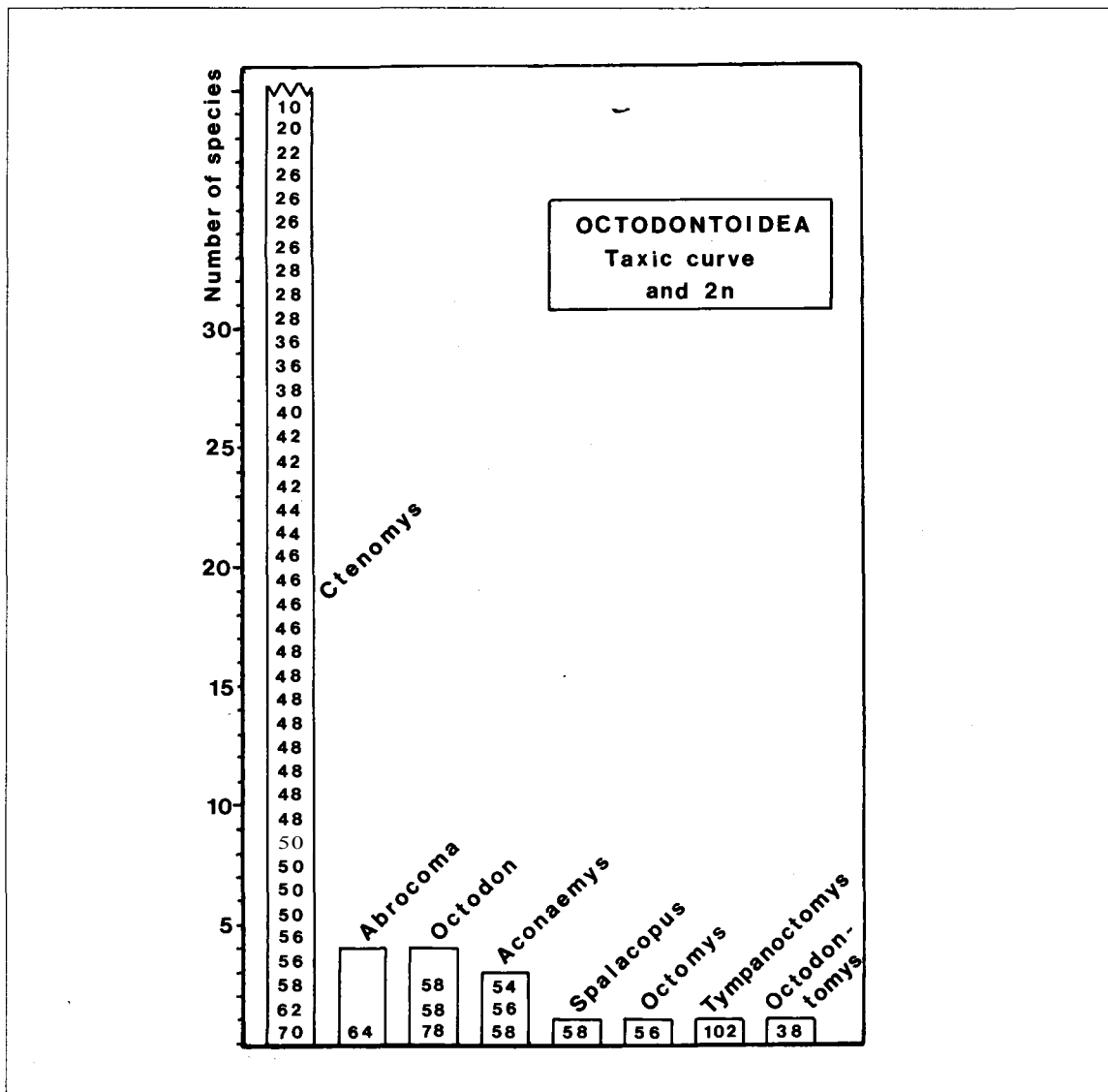

Fig. 7. Taxic curve having an asymmetric distribution of living species diversity in extant genera of Octodontoidea (data from Reig 1989, Ortells et al. 1990, Contreras et al. 1990 and further additions here reported).

Curva táxica con una distribución asimétrica de la diversidad de las especies vivas en los actuales géneros de Octodontoidea (datos de Reig 1989, Ortells et al. 1990, Contreras et al. 1990, y adiciones aquí reportadas).

through which the three main Octodontoidea phyletic lines arose, and a later expansion to the xeric environments of the southern Andes (Spotorno 1979, Contreras et al. 1987). The recent description of the earliest South American hystricomorph rodent in a Tinguiririca fauna from Central Chile (Wyss et al. 1993) suggests that such drier habitats are much older than what was previously thought.

ACKNOWLEDGEMENTS

LITERATURA CITED

ANDERSON S, TL YATES & JA COOK (1987) Notes on Bolivian mammals 4: The genus *Ctenomys* (Rodentia, Ctenomyidae) in the eastern lowlands. American Museum Novitates 2891: 1-20.

CHIARELLI BA, M SARTI-CHIARELLI & DA SHAFER (1972) Chromosome banding with trypsin. Mammalian Chromosomes Newsletters 13: 44-45.
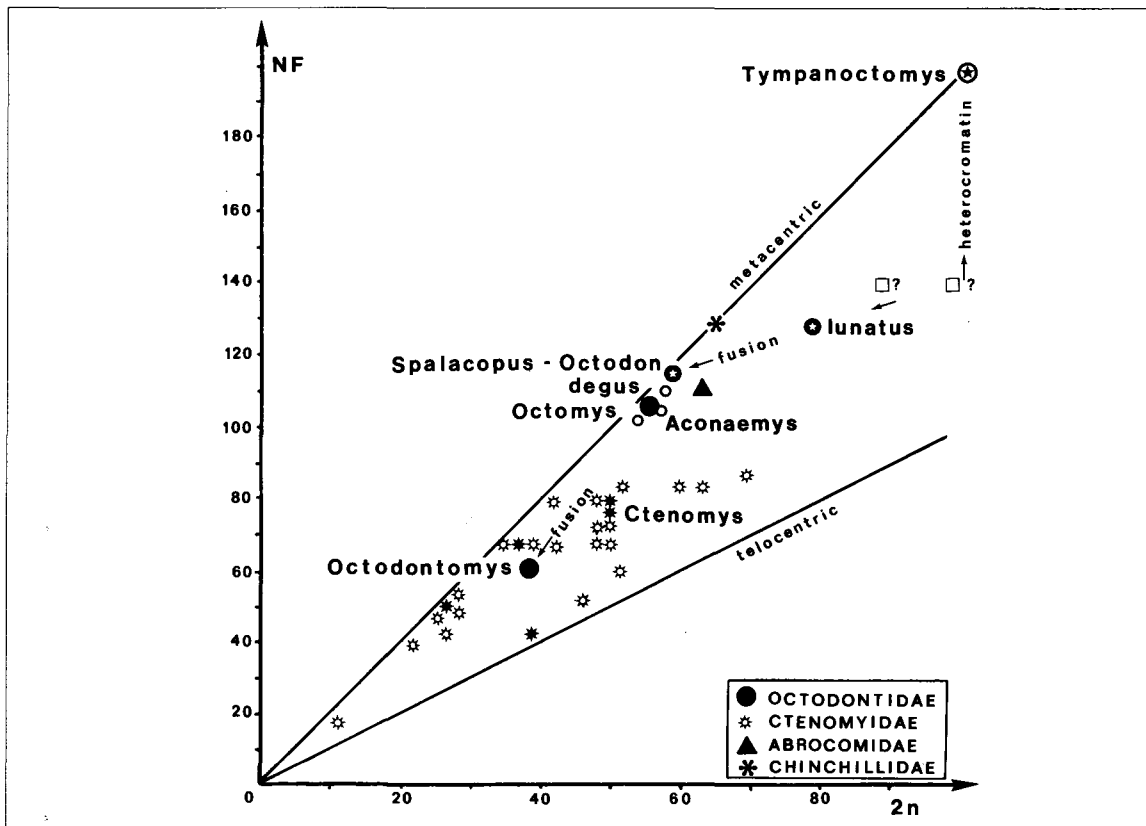

Fig. 8. Karyograph of known karyotypes of Octodontoidea. Limits for possible values indicated by the two diagonals; karyotypes with only metacentric chromosomes fall on the upper diagonal. Arrows show possible directions of chromosome change. Black *Ctenomys* signs mark species with asymmetrical sperms (from Roldan et al. 1992). The value for *Chinchilla lanigera* included for comparison. (modified from Contreras et al. 1990, with further data from Anderson et al. 1987, and Gallardo & Reise 1992).

Cariógrafo de los cariotypos conocidos de Octodontoidea. Límites de valores posibles indicados por las dos diagonales; cariotipos con sólo cromosomas metacéntricos caen en la diagonal superior. Las flechas marcan posibles direcciones de cambio. Signos negros en *Ctenomys* marcan las especies con espermios asimétricos (de Roldan et al. 1992). El valor para *Chinchilla lanigera* está incluido para comparación (modificado de Contreras et al. 1990, con datos adicionales de Anderson et al. 1987, y Gallardo & Reise 1992).

CONTRERAS LC, JC TORRES-MURA & JL YAIEZ (1987) Biogeography of Octodontid rodents: an eco-evolutionary hypothesis. Fieldiana: Zoology, New Series, 39: 401-412.

CONTRERAS LC, JC TORRES-MURA & AE SPOTORNO (1990) The largest known chromosome number for a mammal in a South American desert rodent. Experientia 46: 506-508.

CONTRERAS LC, JC TORRES-MURA, AE SPOTORNO & L WALKER (1994) The chromosomes of *Octomys mimax* and *Octodontomys gliroides* and the relationships of octodontid rodents. Journal of Mammalogy 75: 768-774.

CONTRERAS LC, JC TORRES-MURA, AE SPOTORNO & FM CATZEFLIS (1993) Morphological variations of the glans penis of South American Octodontid and Abrocomid rodents. Journal of Mammalogy 74: 926-935.

CROSSEN PE (1972) The crossen procedure. Mammalian Chromosomes Newsletters 13: 40.

FERNANDEZ-DONOSO R (1968) El cariotipo de *Octodon degus* (Rodentia, Octodontidae). Archivos de Biología y Medicina Experimentales 5: 33-37.

FERNANDEZ-DONOSO R & S BERRIOS (1993) Determinismo y azar en la arquitectura nuclear de los espermatocitos de mamíferos en la I profase de la meiosis. In: Becerra J, JM Pérez-Figares & P Fernández-Llebrez (eds) Progresos en Biología Celular: 69-73. Universidad de Málaga, Málaga.

GALLARDO MH (1991) Karyotypic evolution in *Ctenomys* (Rodentia, Ctenomyidae). Journal of Mammalogy 72: 11-21.

GALLARDO MH (1992) Karyotypic evolution in Octodontid rodents based on C-band analysis. Journal of Mammalogy 73: 89-98.

GALLARDO MH & D REISE (1992) Systematics of *Aconaemys* (Rodentia, Octodontidae). Journal of Mammalogy 73: 779-788.

GLANZ WE & S ANDERSON (1990) Notes on Bolivian mammals. 7. A new species od *Abrocoma* (Rodentia) and relationships of the Abrocomidae. American Museum Novitates 2991: 1-32.

HUTTERER R. (1994) Island rodents: a new species of *Octodon* from Isla Mocha, Chile (Mammalia: Octodontidae). Zeitscrift fur Saugetierkunde 59: 27-41.

LEE MR, PF ELDER (1980) Yeast stimulation of bone marrow mitoses for cytogenetic investigations. Cytogenetics and Cell Genetics 26: 36-40.

LEVAN A, K FREDGA & A SANDBERG. (1964): Nomenclature for centromeric position on chromosomes. Hereditas 52: 201-220.

MASSARINI AI, MA BARROS, MO ORTELLS & OA REIG (1991) Chromosomal polymorphism and small karyotypic differentiation in a group of *Ctenomys* species from Central Argentina (Rodentia, Octodontidae). Genetica 83: 131-144.

NEDBAL MA, MW ALLARD & RL HONEYCUTT (1994) Molecular Systematics of Hystricognath rodents: evidence from the mitochondrial 12S rRNA gene. Molecular Phylogenetics and Evolution 3: 206-220.

ORTELLS MO (1990) Biología evolutiva en el género *Ctenomys* (Rodentia, Octodontidae). Tesis para optar al grado de Doctor en Ciencias Biológicas, Universidad de Buenos Aires, 220 pp.

ORTELLS MO, JR CONTRERAS & OA REIG (1990) New *Ctenomys* karyotypes (Rodentia, Octodontidae) from north-eastern Argentina and from Paraguay confirm the extreme chromosomal multiformity of the genus. Genetica 82: 189-201.

PATTERSON B & R PASCUAL (1972) The fossil mammals of South America. In: Keast A, F Erk & B Glass (eds) Evolution, Mammals and Southern Continents: 247-310. State University of New York Press, Albany, New York.

QUACK B & B NOEL (1977) The XY chromosome pair in man and human spermatocytes visualized by silver staining. Nature 267: 431-433.

REIG, OA. (1989) Karyotype repatterning as one triggering factor in cases of explosive speciation. In: Fontdevila A (ed) Evolutionary Biology of transient unstable populations: 246-289. Springer Verlag, Berlin.

REIG OA & P KIBLISKY (1969) Chromosome multiformity in the genus *Ctenomys* (Rodentia, Octodontidae). Chromosoma 22: 201-244

REIG OA, A SPOTORNO, R FERNANDEZ (1972) A preliminary survey of chromosomes in populations of the Chilean burrowing rodent *Spalacopus cyanus* Molina (Caviomorpha, Octodontidae). Biological Journal of the Linnean Society, London 4: 29-38

ROLDAN ERS, M. GOMENDIO & AD VITULLO (1992) The evolution of eutherian spermatozoa and underlying forces: female selection and sperm competition. Biological Reviews 67: 551-593.

ROSSI MS, OA REIG & J ZORZOPULOS (1990) Evidence for rolling-circle replication in a major Satellite DNA from the South American rodents of the genus *Ctenomys*. Molecular Biology and Evolution 7: 340-350.

SPOTORNO A. (1979) Contrastación de la macrosistemática de roedores Caviomorfos por análisis comparativo de la morfología reproductiva masculina. Archivos de Biología y Medicina Experimentales 12: 97-106.

SPOTORNO AE (1985) Conceptos y métodos en cariología descriptiva y comparada. In: Fernández-Donoso R (ed) El núcleo: 5-165. UNESCO, Santiago.

SPOTORNO AE, J SUFAN & L WALKER (1994) Cytogenetic diversity and evolution of *Eligmodontia* Andean species. Zeitschrift fur Saugetierkunde 59: 299-308.

SUMNER AT (1972) A simple tecnique for demostrating centromeric heterochromatin. Experimental Cell Research 75: 304-306.

WALKER LI, AE SPOTORNO & J ARRAU (1984). Cytogenetic and Reproductive studies of two Nominal Subspecies of *Phyllotis darwini* and their experimental hybrids. Journal of Mammalogy 65: 220-230.

WALKER LI, AE SPOTORNO & J SANS (1991). Genome size variation and its phenotypic consequences in *Phyllotis* rodents. Hereditas 115: 99-107.

WALKER LI & AE SPOTORNO (1993) Tandem and centric fusions in the chromosomal evolution of the South American phyllotines of the genus *Auliscomys* (Rodentia, Cricetidae). Cytogenetics and Cell Genetics 61: 135-140.

WYSS AR, JJ FLYNN, MA NORELL, CC SWISHER, R CHARRIER, MJ NOVACEK & MC MCKENNA (1993) South America's earliest rodent and recognition of a new interval of mammalian evolution. Nature 365: 434-437.