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The Chromosomes of Some Octodontids with Special Reference to *Octodontomys* (*Rodentia; Hystricomorpha*)

Wilma George and Barbara J. Weir

Lady Margaret Hall, Oxford and Wellcome Institute
of Comparative Physiology, Zoological Society of London, London

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Abstract. The chromosomes of three species (*Octodontomys gliroides*, *Octodon degus* and *Ctenomys talarum*) of octodontid hystricomorph rodents are compared. — The diploid numbers are 38, 58 and 48 respectively. No polymorphic chromosomes were noted in the specimens available. The sex chromosomes are heteromorphic and pair end to end in meiosis. — The karyotypes are compared on the basis of the extreme specialisation of the habitat of the three species. The asymmetric karyotype of *Octodontomys* can be compared more readily with that of a *Ctenomys* ancestor than with that of its present-day relative, *Octodon*.

Introduction

There is a considerable diversity of opinion on the exact groupings of species and families of the rodent suborder *Hystricomorpha* (*s. l.*: Simpson, 1945). Although Ellerman (1940), Simpson (1945) and Cabrera (1957–1961) consider that the tuco-tucos are a distinct family, the *Ctenomyidae*, Pascual *et al.* (1965) place them as a subfamily (*Ctenomyinae*) of the family *Octodontidae*. In the genus *Ctenomys* the diploid chromosome number ranges from 22 to 68 (Kiblisky and Reig, 1966) and the usefulness of these chromosome data for analysis of the systematics and evolution of this genus has been discussed by Reig and Kiblisky (1969). The chromosomes of the degu (*Octodon degus*: subfamily *Octodontinae* of Pascual *et al.*, 1965 or family *Octodontidae* of most authors) have been discussed by Fernández (1968). In 1970 three specimens of the chozchoz (*Octodontomys gliroides*), a monotypic genus, were obtained. As far as we are aware, no reports on the chromosomes of any other octodontids have been published.

The karyotype of the chozchoz was therefore elucidated and compared with that of the degu (*Octodon degus*) and the tuco-tuco (*Ctenomys talarum*) from the colonies maintained at the Institute (Weir, 1970; Wise *et al.*, 1968). We will refer to all three species as octodontids.

Materials and Methods

The identification of specimens was determined from study of the literature and matching of skulls against the type specimens in the British Museum (Natural

History) of London. The type specimen came from Potosi, Bolivia (Thomas, 1902) but our chozchoris were caught 4 km N.E. of Humahuaca, Province of Jujuy, Argentina. Our animals conformed to the details of *Octodontomys* given in the literature and a prepared skull matched the type specimen (2.2.2.2.) in the British Museum.

The degu were derived from the colony at the Instituto de Medicina, Santiago de Chile and are of the same stock as that studied by Fernández (1968). Skull preparations confirm that the species is *Octodon degus*.

The tuco-tuco were caught 20 km S.E. Magdalena, Province of Buenos Aires, Argentina. This was about 4 km from the area where Reig and Kiblisky (1969) obtained their specimens.

Blood was removed from one male and two female chozchoris by a retrobulbar technique (Riley, 1960) under halothane anaesthesia. No more than 300 µl were removed at any one time from each animal. The blood sample was prepared according to the technique described by Hungerford (1965) and the air-dried slides were stained in lacto-propionic orcein and mounted in Euparal. Few metaphase plates with countable chromosomes were found, but these were well spread.

When the male chozchoz was killed a preparation of seminiferous tubules was made according to the method of Meredith (1969). The best results were obtained with tissue kept at room temperature for 15 minutes in 1% hypotonic sodium citrate. Several good metaphase plates and meioses were found.

Micropreparations of blood were made by the method described above from 10 male and 10 female *Octodon degus*. Meiotic metaphases were obtained from testis preparations from four animals.

Meiotic and mitotic plates from the testes of two *Ctenomys talarum* were studied, and bone marrow squashes were prepared from one of them using the technique described by Tjio and Whang (1962) and Ford (1966).

During analysis of the chromosomes the position of the centromere was estimated by a modification of the method described by Levan *et al.* (1964) and used by Reig and Kiblisky (1969) for *Ctenomys*. No differentiation was made between acrocentrics and telocentrics. The *nombre fondamental*, NF (Matthey, 1945), was calculated by counting each arm of the metacentric, submetacentric and subacrocentric chromosomes and only the one arm of acrocentrics.

Results

Octodontomys gliroides

Mitosis. Metaphase plates (Fig. 1) from two male and two female chozchoris were counted in 90 cells. In 77 the count was 38 and in 8 the count was 37. The remaining cells had 36 and 35 and were probably short of chromosomes as a result of the comparatively violent spreading technique. We conclude that $2n = 38$ in *Octodontomys gliroides*.

The chromosomes are grouped as three pairs of long, each forming more than 9% of the total haploid length of the karyotype, three pairs of medium length (between 5.5% and 9%), nine pairs of small (between 2.0 and 5.5%) and three pairs of microchromosomes (less than 2.0%).

Metacentric and submetacentric chromosomes represent 60% of the karyotype, the rest is composed of acrocentrics and subacrocentrics (Fig. 3). The NF for *Octodontomys* was 68.

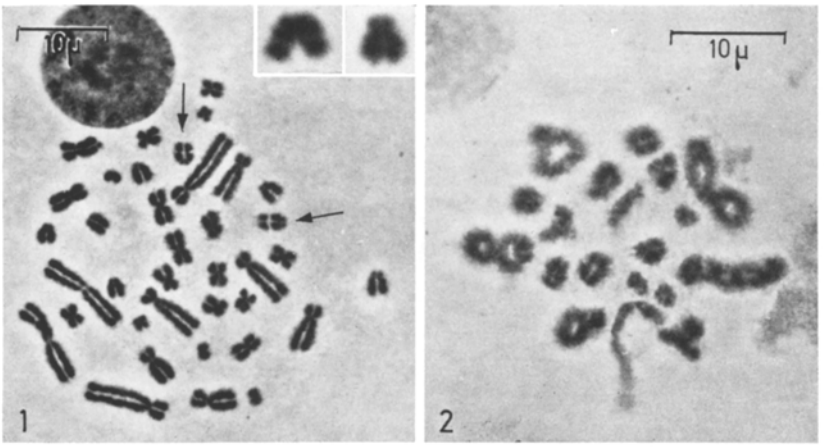

Fig. 1. A metaphase spread of a female *Octodontomys gliroides*. The satellited chromosome pair 12 can be clearly seen (arrowed). (Leucocyte, lactopropionic orcein stain.) The inset at upper right shows a member of chromosome 12 (left) and the Y-chromosome (right) from a male *O. gliroides*

Fig. 2. A meiotic spread from a male *O. gliroides*. (Testis squash, lactopropionic orcein stain)

The X-chromosome (the sixth largest) is a medium metacentric chromosome forming 6% of the total haploid length. The Y-chromosome is a submetacentric small chromosome (Fig. 1). Autosome pairs 1 and 2 are very long (14% and 12% of the total haploid length respectively) and they stand out from the rest of the karyotype. Chromosome 1 is metacentric and chromosome 2 is subacrocentric. The remaining pair (3) of long subacrocentric chromosomes is marginally bigger than the following three pairs of medium metacentric and submetacentrics. The small chromosomes are made up of five pairs of indistinguishable metacentrics and four pairs of acrocentric, or just subacrocentric, chromosomes. The longest of these acrocentrics (pair 12) bears a well marked secondary constriction on its long arm.

The karyotype of *Octodontomys* (Fig. 3) is strikingly asymmetrical, or heterogeneous, both in contrast of chromosome sizes and in the distribution of metacentrics and acrocentrics.

Meiosis. From the testis preparations there were 65 good meiotic metaphases (Fig. 2). Four of these were multiple, giving counts of from 69 to 76 bivalents. It was difficult to tell whether these were polyploid cells or a fusion of the chromosomes of two neighbouring spermatocytes that were dividing synchronously. Forty-nine of the dividing spermatocytes contained 19 bivalents and in the remainder, the number varied from 17 to 18. There seems no reason to doubt that $n = 19$, which confirms the estimate for the diploid number of 38.

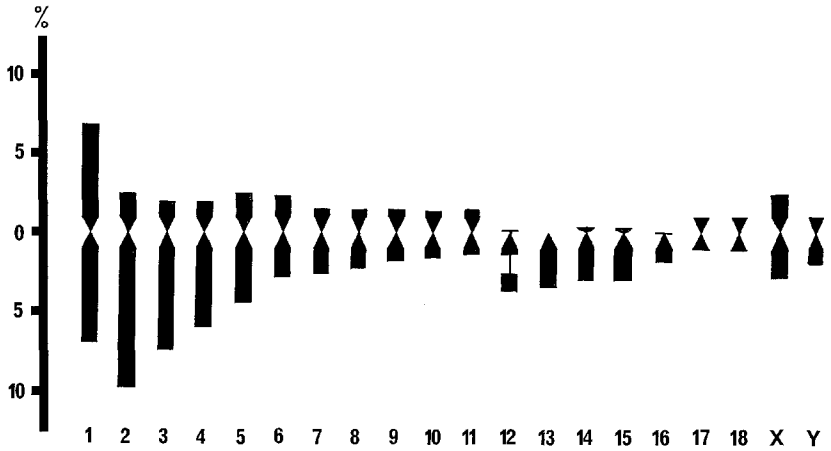

Fig. 3. Idiogram of a male *Octodontomys gliroides*. Chromosome lengths are expressed as percentages of the whole female set, and chromosomes are arranged in pair order but only one member of each pair is represented. X and Y are the sex chromosomes

Chromosome pair 1 had four or five chiasmata along its length in all the cells studied. The remaining long pairs varied from cell to cell in having two, three or sometimes four chiasmata. The average number of chiasmata per bivalent was 1.8 but, owing to the low chromosome number, the recombination index was only 53. This is a low figure compared with some other hystricomorphs studied (George and Weir, in preparation) but may be near average for other mammals (Ford, 1969).

Octodon degus

Mitosis. The karyotypes from the metaphase plates studied confirmed those of Fernández (1968). The diploid number is $2n = 58$.

We found that the majority of chromosomes were small metacentrics. There was only one medium-sized autosome which was submetacentric and formed about 6% of the total haploid length. There were no acrocentrics and only three pairs of subacrocentrics. Fernández (1968) found six pairs of subacrocentrics but it seems unlikely that this is a significant difference. Such discrepancies result from differences of interpretation, or of individual measurements, but these are important, only for estimation of the NF of a karyotype (see Discussion). It was confirmed that one pair of small acrocentrics has secondary constrictions or satellites. The X-chromosome is a medium metacentric. The Y-chromosome is submetacentric and in all our male degus we found it to be smaller than the Y-chromosome reported by Fernández (1968). The calculated NF of *Octodon degus* was 116.

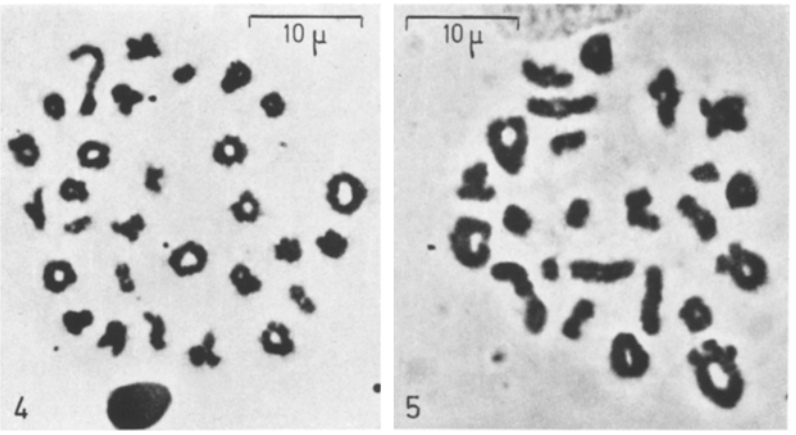

Fig. 4. A meiotic spread from *Octodon degus*. (Testis squash, lactopropionic orcein stain)

Fig. 5. A meiotic spread from *Ctenomys talarum*. (Testis squash, lactopropionic orcein stain)

Meiosis. The meiotic metaphase plates, like those described by Fernández (1968), show that the X- and Y-chromosomes pair end to end in the usual rodent formation and that the majority of bivalents have either one or two chiasmata (Fig. 4). The average chiasmata per bivalent of 1.6 gave a comparatively high recombination index of 73.

Ctenomys talarum

Mitosis. The results confirmed the detailed work of Reig and Kiblisky (1969) in that $2n = 48$. Our calculated NF was 78.

Meiosis. Reig and Kiblisky (1969) do not report on meiosis in *Ctenomys* and, therefore, in addition to comparing a few metaphase plates with those of *Octodontomys* we studied some meiotic chromosomes. The X- and Y-chromosomes pair end to end (Fig. 5). The majority of bivalents have only one chiasma so that the average number per chromosome pair is 1.4 and the recombination index averages 57.

Discussion

At first glance the chromosomes of *Octodontomys gliroides* (Table 1) show no obvious resemblance to those of other octodontids. The diploid number of 38 is comparatively low, though not outside the range found by Reig and Kiblisky (1969) for *Ctenomys* species (*C. magellanicus* has $2n = 36$, and *C. occultus* has $2n = 22$).

The NF varies considerably among octodontids, and one of the difficulties in comparing this value in different species and genera is that observers calculate it in different ways.

Table 1. A comparison of the chromosome data for three species of octodontid (*Hystricomorpha, Rodentia*)

A) Mitosis	$2n$	Autosomal pairs																Sex chromosomes		NF
		large >9%				medium 5.5–9%				small 2.0–5.5%				micro <2%				X	Y	$2(m+sm+sa)+a+2X$
		m	*sm*	*sa*	*a*	*m*	*sm*	*sa*	*a*	*m*	*sm*	*sa*	*a*	*m*	*sm*	*sa*	*a*			
Octodontomys gliroides	38	1	–	2	–	1	2	–	–	5	–	1	3	2	–	–	1	medium *m* 6%	small *sm* 1.9%	68
Octodon degus	58	–	–	–	–	–	1	–	–	16	5	2	–	1	2	1	–	medium *m* 5.9%	micro *m* 2%	116
Ctenomys talarum	48	–	–	–	1	–	1	3	1	3	–	4	6	1	–	2	1	medium *m* 5.8%	micro *a* 0.9%	78

B) Meiosis	n	XY pairing	Average No. chiasmata	Chiasmata/chromosome (Xta/n–1)	Recombination index (Xta+n)
Octodontomys gliroides	19	end to end	34	1.7	53
Octodon degus	29	end to end	44	1.6	73
Ctenomys talarum	24	end to end	33	1.4	57

Matthey (1966) gave a subjective definition for the position of the centromere in suggesting that a chromosome is metacentric if the swellings on the end of the short arms are of the same size as the swellings on the ends of the long arms. Anything shorter than this, or without swellings, is acrocentric. Levan *et al.* (1964) gave a quantitative method for assessing the position of the centromere. The application of their method tended to increase the estimated number of subacrocentrics (subtelocentrics in their terminology) since they classed a chromosome as subtelocentric when the arm ratio was 3 to 7. Wurster and Benirschke (1968) assessed their NF as twice the sum of the metacentrics and submetacentrics, plus the sum of the subacrocentrics and the acrocentrics, plus the X-chromosomes. Clearly the NF calculated in this way will depend on whether the centromere position is determined according to Matthey (1966) or to Levan *et al.* (1964). Wurster and Benirschke (1968) seem to have preferred to follow the suggestions of Matthey (1966).

In the present study, a method based on that of Levan *et al.* (1964) has been used because it is quantitative and has been used in descriptions of the chromosomes of some other hystricomorphs (Reig and Kiblisky, 1969; Fernández, 1968). We simplified the method by allocating the chromosomes into four categories: metacentric, submetacentric, subacrocentric and acrocentric. In this way the conventional method of estimating NF by grouping metacentrics, submetacentrics and subacrocentrics together and considering the acrocentrics as a separate group is more closely followed. Difficulties of measurement further complicate the problem and it is probably true to say that the NF of a group of animals is only useful within the confines of one author's calculations.

Our calculations give an NF of 68 for *Octodontomys gliroides* compared with 78 for *Ctenomys talarum* (for which Reig and Kiblisky, 1969, calculate 89). *Octodon degus* has an NF of 116, well out of the range of the other two species.

In almost all the *Ctenomys* species studied by Reig and Kiblisky (1969) a pair of small autosomes with secondary constrictions or satellites was found. We also found these chromosomes in *Octodontomys*, where they are small acrocentrics. In *Ctenomys* they are mainly metacentric or submetacentric, but sometimes appear as small acrocentrics. They are also found in *Octodon degus*, as a pair of small submetacentric or subacrocentric chromosomes. In all instances the secondary constriction is in the long arm or the chromosome and is on the proximal half of the long arm or near the centre, thus producing a comparatively long satellite. This is in marked contrast to the chinchillids (Nes, 1963; George and Weir, unpublished) but similar to *Proechimys guairae* (George and Weir, unpublished) and *Geocapromys brownii* (George and Weir, 1972).

Using the convention of deriving karyotypes from animals with a similar NF, we attempted to equate the karyotype of *Octodontomys* (NF = 68) with those of *Ctenomys talarum* (NF = 78) and *C. minutus* (NF = 78). In *Octodontomys* there are nine pairs of chromosomes smaller than the markers and eight pairs larger; in *Ctenomys talarum* there are eight smaller pairs and fourteen larger pairs.

In both genera, five pairs of the smaller chromosomes are metacentrics or submetacentrics and can be equated. The others are subacrocentrics and, if a small chromosome is borrowed from the other side of the marker in *Ctenomys*, four acrocentrics can be equated.

This leaves six pairs of metacentric or submetacentrics and two pairs of subacrocentrics in *Octodontomys* and one pair of submetacentrics and twelve pairs of subacrocentrics and acrocentrics in *Ctenomys talarum*. By a process of fusion the twelve pairs of sub- and acrocentrics could be converted into the six metacentric and submetacentrics of *Ctenomys talarum*. Pericentric inversions and translocations would adjust the details.

This does not necessarily infer that *Octodontomys* is a derivative of *Ctenomys* but suggests a possible relationship between the two groups, many species of *Ctenomys* showing a comparatively high number of acrocentric chromosomes and *Octodontomys* having fewer, longer and more heterogenous chromosomes. Reig and Kiblisky (1969) have shown that the same sort of possibilities exist within the genus *Ctenomys*.

Whatever level of taxon grouping has been used, it has always been agreed that *Octodon* and *Octodontomys* are more closely related to each other than either is to *Ctenomys*. And yet the chromosome relationship between *Octodon* and *Octodontomys* is obscure. Fifty of the chromosomes in the karyotype of *Octodon degus* are metacentric or submetacentric and there are only 6 subacrocentrics. The gentle grading in size from long chromosomes to short gives a very homogeneous karyotype. The derivation of the patterns of *Octodontomys gliroides* and *Octodon degus* from that of a common ancestor would require many complicated tandem fusions; further discussion is pointless until information on other species of octodontids becomes available.

It is interesting that Fernández (1968) remarks on the large size of the Y-chromosome in *Octodon degus* and contrasts it with the more usual very small Y-chromosome of hystricomorphs such as *Chinchilla laniger* (Nes, 1903) and species of *Cavia* (Cohen and Pinsky, 1966; Watson *et al.*, 1966). The length of 2.0% of the total haploid length found for the Y-chromosome in the present study conforms more closely to the range found in other hystricomorphs. It is unlikely that our degus were a different species from those of Fernández (1968), since they were derived from the same colony; we can offer no explanation of this discrepancy, although it may be significant that Reig and Kiblisky (1969) found considerable differences in the relative sizes of the Y-chromosome in different species of *Ctenomys*.

All the octodontid species occupy small areas, probably because they are closely tied to their ecological niches. Thus, many species of *Ctenomys* are isolated by their burrowing habit and this has allowed the build-up of divergent karyotypes (Reig and Kiblisky, 1969). The chozchoz lives in a specialised habitat at high altitude (3100 m above sea level)

in an area of cactus and acacia only (personal observation: B. J. Weir). The habitats of the other species have not been seen by us but the reports in the literature indicate that they are equally specialised.

The heterogeneous karyotype of *O. gliroides* suggests a long sequence of specialisation (Stebbins, 1971). Linkage groups have been built up to give the three pairs of surprisingly long chromosomes. The high rate of occurrence of chiasmata does not compensate for the small number of linkage groups and the resulting recombination index of 53 is low for a hystricomorph. The recombination index of *Ctenomys* (57) is also low compared with other hystricomorphs, including *Octodon degus* (73).

The increasing amount of information available for rodent karyotypes shows considerable diversity within a genus and even within species (Ford *et al.*, 1957; Wahrman *et al.*, 1969; Thaeler, 1968) so that without a full understanding of all the species in a genus, karyotype comparison provides little help in elucidating relationships between highly specialised genera. The chromosomes of the three octodontids studied here are highly specialised and the species appear to differ greatly in the ways in which they manage the gross mechanics of their hereditary mechanism.

The karyotype of *Octodontomys* suggests more affinity with that of *Ctenomys* than with *Octodon* but provides no help in establishing further relationships.

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Dr. Barbara Weir
Wellcome Institute of Comparative Physiology
The Zoological Society of London
Regent's Park
London NW1 4RY
England