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New data on the systematics and karyology of *Podoxymys roraimae* (Rodentia, Cricetidae)

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Abstract

Sixty years after its first description by H. E. Anthony, the second record of the monotypic akodontine cricetid *Podoxymys roraimae* was obtained at the type locality, the summit of the Roraima tepui, Venezuela. It was a juvenile female with little tooth wear. The new specimen permitted an updated description of the species, and a more precisely characterization of its molar teeth, which have clearly defined bunodont cusps and well developed mesolophids. *Podoxymys* is more closely related to *Microxus bogotensis* than to species of *Oxymycterus*. The concept of an oxymycterine group is discussed and rejected on the basis of recent electrophoretic results. Thus, the similarities between *Podoxymys* and *Oxymycterus* are better considered as a result of convergence. Analysis of standard metaphase chromosomes of the new individual resulted in a particularly low-numbered karyotype of 2n = 16. The occurrence of low-numbered karyotypes in different groups of eutherian mammals indicates that genome condensation in a few chromosome pairs occurred independently in different phylads. In the Akodontini, two such phylads occur, one involving Brasilian forms, and another comprising a group of species of *Akodon* from the northern Andes. *Podoxymys* is more likely to belong to the latter, both by biogeographical reasons, and because of its close resemblance with the Venezuelan *Microxus bogotensis*.

Introduction

The tepuis are tableland high elevations that rise abruptly interspersed within the forests and savannas of northeastern South America. They lodge a unique flora and fauna which has long attracted the attention of naturalists by the high frequency of generic and specific andemisms (Mayr and Phelps 1967; Steyermark, 1986; Ochoa and Gorzula 1992). Among mammals, one outstanding example of such an endemism is *Podoxymys roraimae*, a species of a monotypic genus of akodontine cricetid mice only known from the summit of the Roraima tepui, which rises up to above 2700 m in the southeastern corner of Bolivar State (Venezuela). This species was described by Anthony (1929) on the basis of 5 specimens. Up to now no additional specimens have been found. Apart from the original brief description by Anthony, those specimens were the basis of further partial descriptions of its anatomy by Gyldenstolpe (1932), Carleton (1973), and Hinojosa et al. (1987). Recently, one individual was obtained during a brief expedition organized by the La Salle Natural History Museum of Caracas (MHNLS) in June, 1989. The new specimen allowed to advance in the knowledge of the anatomy and systematics of this rare mouse, and the acceptably successful preparation of chromosomes in the field permitted to report for the first time its standard karyotype.

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Material and methods

The single specimen of *P. roraimae* reported herein was a young female obtained during the night or early morning of June 1, 1989. It was captured on a line of 100 Sherman live-traps laid at 2628 m a. s. l. at the summit of the Roraima mountain. The trap line was set for six nights on a surface covered by a carpet of the moss *Sphagnum* sp. in which various small cavities were scattered. The overall yield was one *P. roraimae* and four *Rhipidomys macconnelli.* Skins and skulls of all specimens were deposited in the MHNLS, Caracas, were those of *P. roraimae* bear cataloque number MHNLS-8860. This specimen was compared with notes and drawings of original specimens of *P. roraimae* taken previously by one of the authors (OAR) at the American Museum of Natural History. Direct comparisons have also been made with specimens of *Akodon, Oxymycterus, Microxus,* and other South American cricetids from different collections. Fur and hair colors follow Smithe (1975). Standard body and cranial measurements were taken with a Vernier calliper (app. 0.1 mm) and the eye piece of a stereomicroscope (app. 0.01 mm). All measurements are given in mm. Nomenclature of enamel components of the molar teeth, follows Reig (1977). Metaphase chromosomes were obtained in the field by the bone marrow method (Reig et al. 1971), and stained with Giemsa. Ten karyotypes were constructed from enlarged photographic prints, and the lengths of chromosomes and chromosome arms were measured, averaged and expressed as a percentage of the total length of the female haploid set (LHS) (Table) (Reig et al. 1971). Chromosome nomenclature follows Levan et al. (1964), Chromosomes were also assorted into size classes as follows: large-sized equal those > 9 % of LHS; medium-sized, those between 5.5 and 9 %, and small-sized those between 2 and 5.5 %.

Results

Morphology

The data obtained from the new specimen, combined with our data from the original specimens and published information on the stomach (Carleton 1973) allow us to compose the following description of *P. roraimae:*

Size small (head and body about or less than 100 mm) Tail long, as long as or a little longer than head and body. Front claws moderately long (third claw 2.5–3 mm), slender and pointed: claws of the hind feet as in *Akodon*. Fur dense, lax and moderately long, back and sides of head and body, hind feet and tail uniformly dusky-brown (color 19). Hairs long (10 mm on the back), soft and very abundant, blackish (color 82) in most of the length from the base and cinnamon (color 123-A) at the tip. Pelage shortest at the head and the ventral region, where the cinnamon staining is more evident. Eyes very small; ears of small size but clearly visible, although pinnae are partially covered by the dense pelage. Skull (Fig. 1) narrow and slender, with long and narrow muzzle, rather broad interorbital region without trace of supraorbital beading, and a long, deep, moderately inflated and evenly rounded brain case. Upper profile of skull sloping forward from the frontoparietal suture. Nasals shorter than frontals and rather narrow, with posterior ends well behind the frontomaxillary suture. Anterior borders of nasals and premaxillae moderately projected forward beyond the incisors. Parietals short, less than half the length of frontals. Interparietal reduced. Incisive foramina noticeably long, longer than the cheek tooth row and extending backwards to the hypocone of the first molars. Palate short and broad, extending backward to the level of last molars; cheek-tooth rows divergent to the front. Pterygoid region long; mesopterygoid fossa open in front and parellel-sided. Zygomatic plate reduced, narrow and low and markedly sloping backwards. Zygomatic arches week and thread-like at the middle, scarcely flaring beyond brain-case and gradually diverging backward. Interorbital region broad, smooth and rounded, with supraorbital edges rounded and moderately convergent backward. Bullae slightly inflated and moderate in size. Mandible slender, elongate and proodont, though less so than in *Oxymycterus,* with a short coronoid process and small capsular projection. Upper incisors opisthodont and relatively narrow. Molars rather small and broad, bunodont and brachyodont (Fig. 2). Upper molars with lophs almost completely transverse. In M1 and M2 the main external cusps are subequal, the para- and metaflexus are oriented backward, and enterostyle is missing. M1 with somewhat reduced procingulum, with visible anteromedian flexus and anteroflexus in moderately worn teeth, mesoflexus very narrow but present, and mesoloph strongly reduced but not fully fused with paraloph. M2 with mesoloph well developed but low, separated from paraloph by a deep mexoflexus; mesostyle absent. M3 strongly reduced, about ½ the length of M2. Unworn lower molars with opposing cusps somewhat oblique in position, the lingual ones more anterior than the labial ones, tending to a simple prismatic pattern with wear. Procingulum of m1 narrow and simple, without anteromedian flexid. Mesolophid and mesoflexid well developed but low in m1 and m2, and mesostylid absent. Ectolophid and ectostylid may be present in m1, but are absent in m2–m3. Third lower molar moderately reduced, about ¾ the length of m2. Stomach unilocular-hemiglandular, with reduced area of glandular epithelium. Caecum well developed, but very reduced, reaching only 4.4 % of the total intestine length. Large intestine also short.

Fig. 1. Skull and lower jaw of a juvenile female of *Podoxymys roraimae* (MHNLS-8860) from the type locality (Roraima mountain, SW of Bolivar State, Venezuela). *Above:* dorsal view of the skull; *middle:* ventral view of the skull; *below:* lateral view of the skull and mandible (enlarged × 2.8)

Measurements of female MHNLS-8860 and of the type specimen, female, AMNH 75586 (in parentheses; omitted when unavailable): Total length 150.0 (196.0); head and body, 72.0 (101.0); tail, 78.0 (95.0); hind foot 21.5 (23); ear, 13.4; greatest length of skull, 24.7 (27.5); length of nasal, 8.5 (11.0); zygomatic breadth, 11.2 (12.3); interorbital breadth, 5.6 (6.0); breadth of rostrum at mid-point, 4.1 (4.2); breadth of brain case, 11.4 (12.3); incisive foramen (length × breadth) 5.8 × 1.7 (7.2 × 2.1); diastema length, 5.9 (6.9); length upper molar row, 4.14 (4.38); length of lower molar row, 4.50 (4.27); M1, 1.79 × 1.24 (2.14 × 1.21); M2, 1.32 × 1.10 (1.40 × 1.21); M3, 0.69 × 0.77 (0.83 × 0.91); m1, 1.79 × 1.18 (1.85 × 1.24); m2, 1.24 × 1.10 (1.31 × 1.19); m3, 1.07 × 0.77 (1.07 × 0.94); total length small intestine, 414.0; total

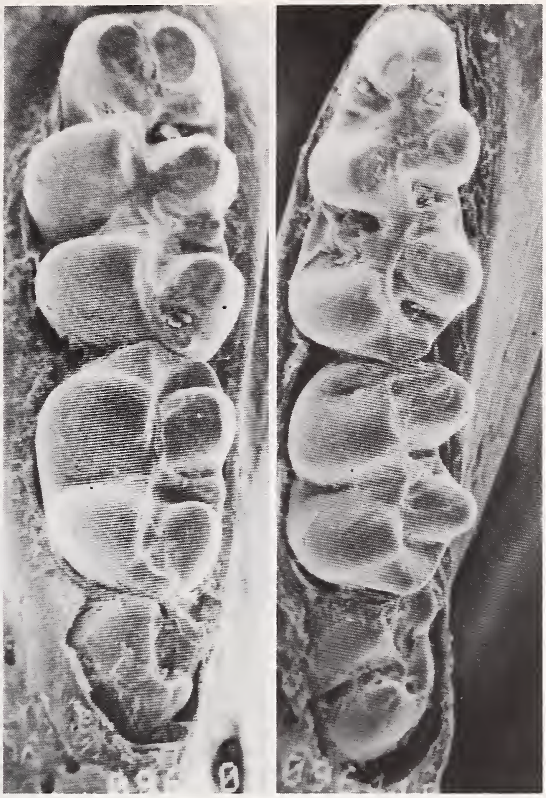

Fig. 2. Scanning electron microphoto of upper (left), and lower (right) molar teeth of the juvenile female specimen of *Podoxymys roraimae* (MHNLS-8860) from the type locality (Roraima mountain, SW of Bolivar State, Venezuela)

transverse length, blind intestine, 22.0; total measured length, large intestine, 53.0 (actual length must be a little longer, as a small unmeasured cut-off portion must be added); body weight, 10 g.

Cytogenetics

The karyotype of *P. roraimae* is striking by the very low diploid and fundamental (including sex chromosomes) numbers of 2n = 16 and FN = 26 (Fig. 3). The karyotype is formed by five pairs of large biarmed, and three pairs of teleocentric chromosomes. As arranged by size, pair 1 is made by very large metacentrics (Table) separated from the following four elements by a sharp size gap. Pairs 2 and 3 are similar in size, the former being submetacentric and the other metacentric. Pairs 4 and 5 are similarly-sized submetacentrics. A large size gap separates pair 5 from the medium-sized telocentric pair 6, whereas pairs. 7 and 8 are small chromosomes. Therefore, each chromosome pair is very distinctive in size and morphology. As the single studied individual was a female, it is only tentative to identify the X chromosomes. Based on the similarity between the karyotype of *P. roraimae* and that of *Akodon "arviculoides"* (see later) we tentatively identify the chromosomes of pair 7 as the female sex chromosomes.

Statistics of mean lengths of entire chromosomes (T.L.) mean lengths their long (L.L.A.) and their short arms (L.S.A.), and arm ratio (r) and their standard deviations (SD) of *Podoxymys roraimae* from Mount Roraima, Bolivar State, Venezuela

The lengths are expressed as a percentage of the total chromosome length of the female haploid set

Chromosome	T.L.		L.L.A.		L.S.A.		r	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	23.73	.64	12.69	.22	11.14	.38	1.14	.004
2	18.50	.32	12.80	.76	5.51	.14	2.37	.004
3	17.48	.84	9.72	.17	7.91	.50	1.25	.002
4	12.81	.72	7.78	.42	5.03	.35	1.59	.090
5	12.09	.35	7.71	.26	4.38	.09	1.78	.025
6	7.16	.16	7.16	.16	–	–	–	–
7	4.35	.27	4.35	.27	–	–	–	–
8	3.85	.11	2.15	.22	–	–	–	–

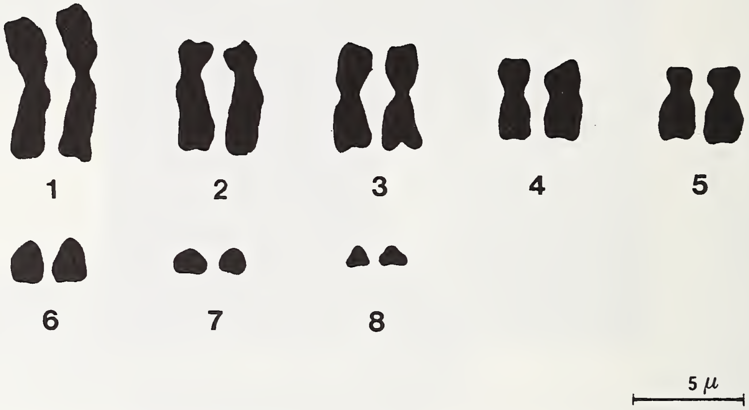

Fig. 3. Giemsa-stained bone-marrow karyotype of *Podoxymys roraimae,* the same specimen of Figs 1 and 2

Discussion

The new specimen matches well enough the holotype and the original description of *P. roraimae* (Anthony 1929) as no casting doubts to its species identification. The differences found in size and morphology reflect the fact that the holotype was an adult with advanced tooth wear, whereas MHNLS-8860 is a juvenile. This allowed us to examine in more detail the molar structure, which resulted peculiar for akodontine standards by the well-developed mesoloph-lophids and the bunodont cusps. However, both in the craneo-dental and digestive system characters, *P. roraïmae* fits well with the diagnosis of the tribe Akodontini (Reig 1987).

Of the eleven recognized extant genera of the Akodontini (Reig 1987), *Podoxymys* was reported to be alike *Oxymycterus* (Anthony 1929) and *Microxus* (Ellerman 1941). Hershkovitz (1966) proposed to distinguish within the akodont rodents an "oxymycterine group", including *Oxymycterus, Podoxymys, Lenoxus, Microxus,* and *Abrothrix* (Hershkovitz considered *Microxus* to be a synonym of *Abrothrix,* but Reig, 1987, found no reasons for such a synonymy). The concept of an oxymycterine group has been recently discussed by Hinojosa et al. (1987), who concluded that it is unclear. Recent electrophoretic data strongly indicate that *Microxus* is more closely related to *Akodon* than to

Oxymycterus, and that the latter is not close to *Lenoxus* (Patton et al. 1989). Besides, *Abrothrix* together with *Chelemys* and *Geoxus* make a subclade of its own clearly differentiated in genetic distance from the remaining Akodontini (Spotorno 1986; Barrantes et al. 1992).

As Ellerman (1941) surmised, *Podoxymys* is probably a close relative of *Microxus*. In fact a closer relationship of *Podoxymys* to *Microxus* than to *Oxymycterus* is expected by distribution, as *Microxus* is represented in the Venezuelan Andes, whereas species of *Oxymycterus* are mostly distributed in the south of South America. We have for comparison specimens referred to *M. bogotensis* from the Andes of Venezuela. Certainly, *M. bogotensis* and *P. roraimae* resemble each other more than any of them resembles species of *Oxymycterus*. They are similar in the relative forward extension of nasals and premaxillae, the degree of reduction of the zygomatic plate, the long frontals, the more reduced interparietal, and the deeper and shorter braincase. However, *M. bogotensis* has a shorter pelage, a much shorter incisive foramina that scarcely reaches the front of first upper molars, parallel cheek teeth rows, and much reduced third molars. Thus, *Podoxymys* may well be a close relative of *Microxus*, but its generic distinction seems to be well warranted.

The karyotype of *P. roraimae* is remarkable by its very low diploid number. Karyotypes with diploid numbers lower than 20 are common among marsupials (Hayman 1990), but they are a rarity (about 1 %) among placentals (Matthey 1973). An extreme case is that of the muntjak deer *Muntjacus muntjak*, with 2n = 6 and 2n = 8 in different subspecies (Wurster and Benirschke 1977; Wurster and Atkins 1972). A karyotype of 2n = 14, with polymorphic variants anf 2n = 15 and 2n = 16 has been described for a Brasilian akodontine erroneously referred to *Akodon arviculoides* (Maia and Langguth 1981; for its nomenclatorial status and references see Liascovich and Reig 1989). A monomorphic 2n = 18 karyotype occurs in the akodontine *Akodon urichi* (Reig et al. 1971), and polymorphic complements of 2n = 16–17 occur in *Nectomys palmipes* (Barros et al. 1992), whereas karyotypes of 2n = 17–18 with odd sex chromosome systems have been reported in the arvicolid voles *Ellobius lutescens* and *Microtus oregoni* (Matthey 1958), and 2n = 18 was also found in the murid *Nannomys* (Mattey 1964). Karyotypes of 2n = 16 are also known in some species of the leaf-nosed bats (Baker 1973).

There are good reasons to maintain that polarity in karyotype number among the Akodontini was from a high-numbered plesiomorphic to a low-numbered apomorphic state (Vitullo et al. 1986; Reig 1987). The same trend was found to be most likely in other tribes of South American cricetids (Gardner and Patton 1976), and in arvicolids (Matthey 1958; Moodi 1987). Thus, the process of condensing the karyotypes to a low number of chromosomes occurred independently in unrelated evolutionary phylads.

Karyotypes of Akodontini cover a wide range of diploid numbers, from 2n = 14 to 2n = 54 (Reig 1987, 1989; Liaskovich and Reig 1989). However, most of the 45 chromosomally known akodontine species have karyotypes within the 2n = 30–44 (42 %) or the 2n = 52–54 classes (Reig 1989). Of *Microxus*, only the karyotype *M. bogotensis* from the Venezuelan páramos is known (Barros and Reig 1979), which is polymorphic with 2n = 35–37. Actually, among the Akodontini, the karyotype of *P. roraimae* is only comparable at the level of chromosome number and gross morphology with the 2n = 14–16 karyotype of *Akodon "arviculoides"*, and that of 2n = 18 of *Akodon urichi*. It is remarkably similar to the 2n = 16 variant of *A. "arviculoides"* from Recife (Maia and Langguth 1981). Both share the same fundamental number, and differ mostly in the first autosomal pair, which is submetacentric in *A. "arviculoides"*, but metacentric in *P. roraimae*. As regards *A. urichi*, the differences are much greater and may involve several rearrangements. Unfortunately, we failed to obtain adequate G-banding karyotypes to test how far the resemblance between *P. roraimae* and *A. "arviculoides"* is due to actual arm sharing.

In fact, a parallel trend towards lower diploid numbers seems to occur within the Akodontini in two independent phylads. Reig (1987) recognized a northern Andean phylad probably derived from a primitive stock in the soutern puna region showing diploid numbers progressively, although irregularly, decreasing northwards. This phylad includes, among others, species and subspecies of *Akodon* such as *A. aerosus boliolus* (2n = 38), *A. prophilus* (2n = 26), *A. mollis* (2n = 22–23), *A. aerosus* ssp. (2n = 22), *A. torques* (2n = 22) *A. tolimae* (2n = 24), and *A. urichi* (2n = 18) (Reig 1987; Patton et al. 1990). *M. bogotensis* may represent a chromosomally more conservative offshoot of the same branch. As Reig (1987) suggested, *P. roraimae* is likely to be derived from the same stock. We now know that it exemplifies an extreme case of karyotypic reduction consistent with the general trend observed in the northern Andean phylad. But a trend in karyotypic condensation is also evident in an independent phylad which dispersed towards Brasil from a postulated north-central Argentinian dispersal sub-center, as represented by *A. cursor* of Misiones, Paraguay, and south of Brasil (2n = 24), and the karyomorphs of 2n = 14–16 referred to *A. "arviculoides"* from Sao Paulo, Rio de Janeiro and Recife (Liascovich and Reig 1989). The close similarity found between the karyotype of *P. roraimae* and the 2n = 16 karyomorph of *A. "arviculoides"* may be taken as suggesting a closer relation of the tepui akodont to this phylad. However, besides the general disaprowal of hypotheses on phylogenetic relations based on similarities among non-differentially stained karyotypes, there are other reasons to discard this alternative view. There is ample evidence that the tepuian fauna is closely linked to the Andean fauna (Mayr and Phelps 1967). Besides, the areas of distribution of *P. roraimae* and *A. "arviculoides"* are separated by the Amazonian Basin, a region thoroughly deprived of representatives of the Akodontini.

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Zusammenfassung

Neue Unterlagen über die Systematik und Karyologie von Podoxymys roraimae (Rodentia, Cricetidae)

Die akodontine Maus *Podoxymys roraimae,* von H. E. Anthony nach fünf Exemplaren beschrieben und 1929 einer monotypischen Gattung zugeordnet, wurde im Juni 1989 erstmals wieder an der Typuslokalität, dem Gipfel des Roraima tepui in Venezuela, gefangen. Anhand des juvenilen Weibchens und der Originalserie wird eine genauere Beschreibung der Gattung und Art gegeben. *Podoxymys* ist *Microxus bogotensis* ähnlicher als den Arten von *Oxymycterus.* Das Konzept einer oxymycterinen Gruppe innerhalb der Akodontini erscheint unwahrscheinlich und wird auf der Grundlage neuer elektrophoretischer Ergebnisse abgelehnt. Die Ähnlichkeit zwischen *Podoxymys* und *Oxymycterus* ist eher auf Konvergenz zurückzuführen. Die Analyse standardgefärbter Metaphasen des neuen Exemplares ergab eine bemerkenswert niedrige Zahl von 2n = 16 Chromosomen. Ein Vergleich niedriger Chromosomenzahlen bei Säugetieren zeigte, daß die Konzentration des Genoms in wenigen Chromosomenpaaren mehrfach in verschiedenen Stammbaumlinien erfolgte. Innerhalb der Akodontini lassen sich zwei Linien unterscheiden; die eine umfaßt brasilianische Arten, die andere eine Gruppe von *Akodon*-Arten der nördlichen Anden. *Podoxymys* scheint der letzteren nahezustehen, sowohl aus biogeografischen Gründen als auch wegen seiner großen Ähnlichkeit mit dem venezolanischen *Microxus bogotensis.*

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