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SYSTEMATICS OF *OXYMYCTERUS* WITH DESCRIPTION OF A NEW SPECIES FROM URUGUAY

FEDERICO G. HOFFMANN,* ENRIQUE P. LESSA, AND MARGARET F. SMITH

Laboratorio de Evolución, Facultad de Ciencias, Montevideo 11400, Uruguay (FGH, EPL)
Department of Biological Sciences and Museum, Texas Tech University, Lubbock, TX 79409-3131 (FGH)
Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720 (MFS)

The taxonomic status of the genus *Oxymycterus* in Uruguay is assessed through morphologic, morphometric, and molecular comparisons with other species in the genus. Our analyses uncover the existence of a previously undescribed species, described herein, and restrict *O. nasutus* to SE Uruguay and SE Brazil. Uruguayan species are morphologically similar but differ substantially in sequences of the mitochondrial cytochrome-*b* gene. In contrast, *O. rufus* was found to be morphologically distinct from *O. nasutus* and the new species but genetically similar to the new species. Phylogenetic analyses lack resolution at the base of the genus but suggest well-supported relationships between *O. amazonicus* and *O. delator*, *O. quaestor* and *O. judex*, and *O. rufus* and the new species.

Key words: cytochrome *b*, DNA sequence, morphology, new species, *Oxymycterus*, Uruguay

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The genus *Oxymycterus* has a complex taxonomic history, reviewed in Oliveira (1998). Hershkovitz (1994) organized information for the genus based on published accounts and specimens available at the Field Museum of Natural History (FMNH, Chicago, Illinois), listing 23 named forms. Oliveira (1998) conducted a comprehensive survey of cranial morphometric variability throughout the geographic range of the genus and established 10 species groups to provide a framework for understanding morphological variation in *Oxymycterus*. *O. amazonicus*, *O. angularis*, *O. delator*, *O. inca*, *O. nasutus*, and *O. rufus* were each included in their own group. *O. dasytrichus*, *O. hispidus*, and *O. roberti* were included in the dasytrichus group; *O. judex*, *O. misionalis*, and *O. quaestor* in the judex group; *O. juliacae*, *O. nigrifrons*, and *O. hiska* in the juliacae group; and *O. paramensis* and *O. hucucha* in the paramensis group. Twenty-two of the 23 names from Hershkovitz (1994) were incorporated, and 5 additional species plus 13 additional subspecies were added. One form from Hershkovitz (1994) that was not included was *O. iheringi*, which was elevated to a new genus, *Brucepattersonius*, by Hershkovitz (1998).

The systematic status of the genus *Oxymycterus* in Uruguay is also confusing. Darwin collected what became the type specimen of *O. nasutus* in Maldonado, Uruguay. Vaz Ferreira (1960) recognized *O. nasutus* as a subspecies of *O. rufus* (type locality: Entre Ríos, Argentina), whereas Ximénez et al. (1972) assigned *O. nasutus* to *O. rutilans* (a junior objective synonym of *O. rufus* according to Hershkovitz 1994). In contrast, Langguth (1976) and Langguth and Anderson (1980) considered *O. nasutus* to be a junior synonym of *O. rufus* that did not warrant subspecific status. Despite these differences in nomenclature, authors agreed on the presence of only a single species of long-nosed mouse in the country. More recently, however, Hershkovitz (1994) treated

* *Correspondent: fhoffman@ttacs.ttu.edu*

O. nasutus as a valid species and, based on Vaz Ferreira (1960), mentioned the potential presence in Uruguay of a 2nd, larger species that he considered to be *O. rufus*.

This study focused on 3 topics: assessing the taxonomic status of Uruguayan samples of *Oxymycterus*, presenting cytochrome-*b* (cyt-*b*) data for 9 of the 10 species groups defined by Oliveira (1998), and assessing systematic relationships among these species groups and zoogeographical implications.

Materials and Methods

Morphological analyses.—Specimens of 16 species of *Oxymycterus* were included in morphological analyses: *O. amazonicus* ($n = 2$), *O. angularis* ($n = 9$), *O. dasytrichus* ($n = 49$), *O. delator* ($n = 44$), *O. hiska* ($n = 1$), *O. inca* ($n = 23$), *Oxymycterus* sp. n. ($n = 67$), *O. judex* ($n = 32$), *O. juliacae* ($n = 13$), *O. misionalis* ($n = 14$), *O. nasutus* ($n = 42$), *O. nigrifrons* ($n = 21$), *O. paramensis* ($n = 49$), *O. quaestor* ($n = 18$), *O. rufus* ($n = 32$), and *Oxymycterus* sp. *B* ($n = 1$). A list of all specimens examined and their geographic localities is given in Appendix I.

The following 29 cranial measurements were taken, adapted from Patterson (1992b): greatest skull length, least distance from posterior border of supraoccipitals to tip of nasals; condylobasal length, least distance from posterior margin of occipital condyles to anteriormost projection of premaxillae; basal length, least distance from anterior margin of foramen magnum to posteriormost margins of incisive alveoli; zygomatic breadth, greatest distance across zygomatic arches perpendicular to longitudinal axis of cranium; braincase breadth, greatest distance across braincase; mastoid breadth, greatest distance between mastoid processes; palatilar length, distance from anteriormost margin of palate to posteriormost margins of incisive alveoli; length of incisive foramina, distance between anteriormost and posteriormost margins of incisive foramina; width of incisive foramina, greatest distance between labial margins of paired incisive foramina perpendicular to longitudinal axis of cranium; diastema, distance between posterolateral margin of incisive alveolus and anteromedial margin of M1 alveolus; length of maxillary toothrow, distance from anterior margin of M1 alveolus to posterior margin of M3 alveolus; palatal width at M1, greatest distance between labial alveoli of M1 perpendicular to longitudinal axis of cranium; palatal width at M3, greatest distance between labial alveoli of M3 perpendicular to longitudinal axis of cranium; width of zygomatic plate, width of zygomatic plate dorsal to insertion on skull, parallel to longitudinal axis of skull; nasal length, greatest length of nasal bones from posteriormost projection of frontal suture to tip; nasal width, greatest distance between margins of paired nasal bones at incisive insertion; rostral width, greatest rostrum width across incisive capsules; incisive width, greatest width of paired incisor tips; width of nasal opening, greatest distance between exterior margin of nasal-premaxillary cylinder; width of frontal sinus, distance across skull immediately posterior to maxillary arms of zygomata; interorbital breadth, least distance across frontal bones; frontal length, length at midline from nasal to parietal sutures; parietal length, length at midline between frontal and interparietal sutures; interparietal length, length at midline between parietal and supraoccipital sutures; interparietal width, least distance between left and right parietal–supraoccipital sutures; mandibular length, distance between median margin of lower incisor alveolus and mandibular condyle; condylar length, distance between posterior margin of m3 alveolus and mandibular condyle; process height (MPH), distance from superior border of coronoid process to bottom of angular process; ramus depth, distance between labial margin of m1 alveolus and ventral border of dentary. Dental terminology follows Reig (1977) for enamel pattern and Hershkovitz (1962) in all other cases.

All measurements were taken using dial calipers to the nearest 0.1 mm. All specimens were included in morphometric analyses. Specimens were assigned to species based on their cranial morphology before performing morphometric tests. Taxonomic arrangement follows Oliveira (1998).

Multivariate statistical analyses of morphometric data were performed using Matlab (The Mathworks Inc., Natick, Massachusetts). A principal-components analysis was used to explore variation in data. Multivariate analysis of variance was used to compare variation within and among species, and ''size-free'' discriminant-function analysis was used to sort variation in relation to species. In the case of the multivariate

analysis of variance, results were bootstrapped 10,000 times in order to obtain a null distribution and circumvent the assumption of multinormality. Finally, observations were reclassified based on minimum and size-adjusted Mahalanobis distances, with 1,000 bootstrap replicates used to estimate frequency distributions of classification. Missing values for specimens where some data were missing were estimated via maximum likelihood following Little and Rubin (1987); species assignment was not taken into account at this stage so as to obtain conservative estimates. Data were log-transformed in all cases, and males and females were analyzed together on the basis of preliminary results and apparent lack of sexual dimorphism (Oliveira 1998). All data will be provided upon request.

Molecular analyses.—Ten species of *Oxymycterus* were included in phylogenetic analyses: *O. amazonicus* ($n = 1$), *O. dasytrichus* ($n = 4$), *O. delator* ($n = 3$), *O. hiska* ($n = 1$), *Oxymycterus* sp. n. ($n = 2$), *O. judex* ($n = 2$), *O. nasutus* ($n = 2$), *O. quaestor* ($n = 1$), *O. paramensis* ($n = 1$), and *O. rufus* ($n = 3$). *Akodon boliviensis*, *Thaptomys nigrita*, *Bolomys amoenus*, and *Juscelinomys huanchacae* were included as outgroups. DNA was extracted from either frozen or alcohol-preserved liver tissue using sodium dodecyl sulfate–proteinase K–NaCl extraction and alcohol precipitation (Maniatis et al. 1992; Miller et al. 1988). Purified mitochondrial DNA was obtained from frozen liver tissue by a rapid method based on an alkaline lysis procedure, using Promega Wizard Minipreps (Promega, Madison, Wisconsin—Beckman et al. 1993). The complete mitochondrial cyt-*b* DNA was amplified via polymerase chain reaction using primer MVZ 05 with MVZ 14 (Smith and Patton 1993), in 30 cycles of double-stranded amplifications, denaturing at 93°C for 1 min, annealing at 45°C for 1 min, and extension at 72°C for 1 min. Strands were separated using Dynal Dynabeads M-280 Streptavidin (Dynal Biotech, Lake Success, New York) and sequenced with a combination of external and internal primers, including light-strand primers MVZ 05, MVZ 11, MVZ 45, MVZ 23 (Smith and Patton 1993), and MVZ 67 (Patton et al. 1996) and heavy-strand primers MVZ 06 and MVZ 04 (Smith and Patton 1993). Detailed procedures for amplification and manual sequencing followed those in Smith and Patton (1991). Sequences were also generated on an automated DNA sequencer using the *Taq* FS cycle sequencing kit (model 377, Applied Biosystems Inc., Foster City, California). One additional sequencing primer was used on the automated sequencer, MVZ 103 (5′-CACCCTAAC[A/C]CGCTTCTTCGC-3′). Sequences were edited using the Sequence Navigator software (Applied Biosystems Inc.). Compared with the 1,140-bp cyt-*b* gene of *Akodon*, *Oxymycterus* has an extra codon at the end of the sequence, followed by a T, which is presumably polyadenylated to form a stop codon, as in the cyt-*b* gene of *Mus* (Bibb et al. 1981:175). The first 1,137 bp of cyt *b* were used for phylogenetic analyses.

Uruguayan specimens from the Laboratorio de Evolución, Montevideo, Uruguay, were classified according to skull morphology, and species assignment was double-checked by digesting the complete cyt-*b* fragment with the restriction enzyme *Alu*I (which only digests samples from *O. nasutus*). In all cases, the correspondence between morphological and molecular diagnoses was complete (see Appendix I for list of all specimens examined). All DNA sequences are available in GenBank; accession numbers are as follows: *A. boliviensis* M35691, *T. nigrita* AF108666, *B. amoenus* M35711, *J. huanchacae* AF133667, *O. amazonicus* AF454765, *O. delator* U03525, AF454766–7, *O. dasytrichus* AF454768–71, *Oxymycterus* sp. nov. AF175286–7, *O. judex* AF454773–4, *O. hiska* U03542, *O. nasutus* AF175288–9, *O. paramensis* U03536, *O. quaestor* AF454772, *O. rufus* AF454775–7.

Pairwise distances were calculated using the uncorrected percentage of sequence divergence. Three different methods were used to estimate phylogenetic relationships: neighbor joining, maximum parsimony, and maximum likelihood. All analyses were carried out in PAUP* (version 4.02—Swofford 1999). Sequence divergence for neighbor-joining analysis (Saitou and Nei 1987) was calculated using Tamura–Nei (1993) distance, which allows for unequal proportions of bases and independent rates for different types of nucleotide substitutions. In the case of parsimony analyses, 4 different transition–transversion ratios (2:1, 5:1, 6:1, and 10:1) were applied to explore sensitivity of results to variation in the substitution model. Heuristic searches were performed with 10 random additions of taxa. Support for the nodes was evaluated by bootstrap analyses, with 1,000 replicates. In the case of likelihood analyses, different models of nu-

cleotide substitution were evaluated following Huelsenbeck and Crandall (1997). An initial tree was generated using neighbor joining; this tree was used to estimate the likelihood of the following models: Jukes–Cantor (Jukes and Cantor 1969), Kimura 2-parameter (Kimura 1980), and Hasegawa–Kishino–Yano (Hasegawa et al. 1985), which in turn can be used in their simplest forms or with gamma rates. Parameter values were then set to those of a complex model (HKY+Γ) that optimized the following parameters: proportion of each base, transition–transversion ratio, and shape (alpha) of gamma distribution. A maximum-likelihood heuristic search with 10 random additions of taxa was then performed. Additional details are presented in the ''Results'' section.

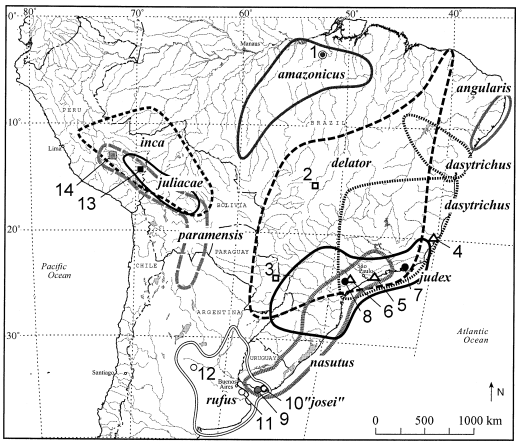

FIG. 1.—Geographic distribution of species groups included in genus *Oxymycterus* based on maps in Oliveira (1998). Numbers correspond to localities from samples used in molecular analyses.

RESULTS

Oxymycterus josei, new species

Holotype.—An adult male specimen consisting of skin, skull, skeleton, and glans penis in formalin, MNHN 3838 (CA687), has been deposited at Museo Nacional de Historia Natural (MNHN), Montevideo, Uruguay. Frozen tissues of holotype (liver, kidney, and heart) and liver in alcohol have been deposited in Laboratorio de Evolución, Facultad de Ciencias, Montevideo, Uruguay.

Type locality.—West margin of Arroyo Tarariras, Balneario Las Flores, Departamento de Maldonado, Uruguay.

Distribution.—Known from southwestern Uruguay, south of the Río Negro, in the Departamentos de Soriano, Colonia, San José, Canelones, and Maldonado (33–35°S, 55–58°W). *O. josei* occurs sympatrically with *O. nasutus* at Las Flores and at Barra de Maldonado (type locality of *O. nasutus*) in Departamento de Maldonado (Fig. 1).

Etymology.—We name this species after Joseph ''José'' A. Cook (currently at Idaho State University, Pocatello, Idaho), who has worked hard for the development of Uruguayan mammalogy.

Diagnosis.—A ''medium-sized'' species of *Oxymycterus* (see Hershkovitz [1994] and Hinojosa et al. [1987] for a review of characteristics of the genus) with reddish to dark-brown pelage and occasional white spots in underparts. Hind feet large and strong with long claws and 6 plantar pads, forefeet small with small claws and 5 plantar pads. Skull long, narrow, medium-sized sensu Hershkovitz (1994); nasals thin, rounded at tip, and projecting with premaxillae anteriorly to incisors, forming the trumpet-like nose characteristic of the genus; broad and strong zygomatic plate; lacrimals small; zygomatic arches broader than braincase; frontal sinuses inflated, broader than interorbital constriction; interorbital region with rounded margins; incisive foramina elongated and ovate, extending beyond anterior conule of 1st molar; interparietal reduced; braincase walls parallel and not rounded; supraoccipital and lamboidal ridges well developed; incisors yellowish, short, and opisthodont; molars small and hypsodont; M1 tetralophodont with a well-developed anteromedian flexus and M3 greatly reduced; M1 clearly longer than M2; 1st upper molar with well-developed protostyle, and enteroloph well developed with clearly marked enterostyle; enamel pattern in lower 1st molar analogous to that in upper 1st molar.

Morphological Comparisons

Oxymycterus josei can be distinguished from larger species of the genus (*O. angularis*, *O. dasytrichus*, *O. inca*, *O. judex*, *O. misionalis*, *O. quaestor*, and *O. rufus*) by its smaller size. The rostrum of *O. josei* is more slender, the zygomatic arches are narrower, and the molar toothrow is shorter than in *O. amazonicus*, *O. angularis*, *O. delator*, *O. dasytrichus*, *O. inca*, *O. judex*, *O. misionalis*, *O. quaestor*, and *O. rufus*. *O. paramensis* differs from *O. josei* in having shorter and darker pelage; a longer palate, which extends behind posterior plane of 3rd molar; and a thinner angular process; and in lacking an enteroloph in 1st molar. *O. rufus*, the closest species at the molecular level, differs from *O. josei* in having a bigger, more slender skull, stronger mastoid processes, a wider palate, and stronger molar teeth, and in lacking an enterostyle (enterostylid) in 1st molar. In addition, *O. rufus* presents a shorter, thicker baculum than does *O. josei*, which presents a more elongated one that is also more delicately built.

Oliveira (1998) presented a detailed comparison of the species in the genus, defining species groups and comparing them. He included Argentinean samples from Buenos Aires, Córdoba, and Entre Ríos in the rufus group, and he recognized the specific status of *O. judex*, *O. quaestor*, and *O. dasytrichus*, all of which he distinguished from Uruguayan specimens by their larger size. His discriminant-function analysis clearly distinguished these units from his ''nasutus'' group, where both Uruguayan species were included.

The species most similar in morphology to *O. josei* is *O. nasutus*, which coexists sympatrically with *O. josei* in the eastern part of its range. Although *O. josei* reaches larger size than *O. nasutus*, the 2 species cannot be distinguished externally; a similar situation has been reported in other sympatric congeneric species of sigmodontine rodents (Voss 1991).

Oxymycterus josei has a somewhat stronger skull than *O. nasutus*. The most conspicuous differences are in the zygomatic plate and in the 1st molar of upper and lower toothrows: *O. josei* presents a wider, stronger zygomatic plate and a stronger superior maxillary root of the zygomatic arch, whereas zygomatic plate and superior maxillary root are smaller in *O. nasutus* (Fig. 2). Differences in the 1st molar of upper and lower rows are easily detected, but they can only be studied in juvenile specimens because of the fact that the enamel pattern is soon worn down with age in these species. In *O. josei* M1 presents a protosyle and a well-marked enterostyle with an enteroloph, whereas in *O. nasutus* M1 lacks a protostyle and shows a reduced enteroloph without enterostyle; m1 shows analogous species differences (Fig. 3).

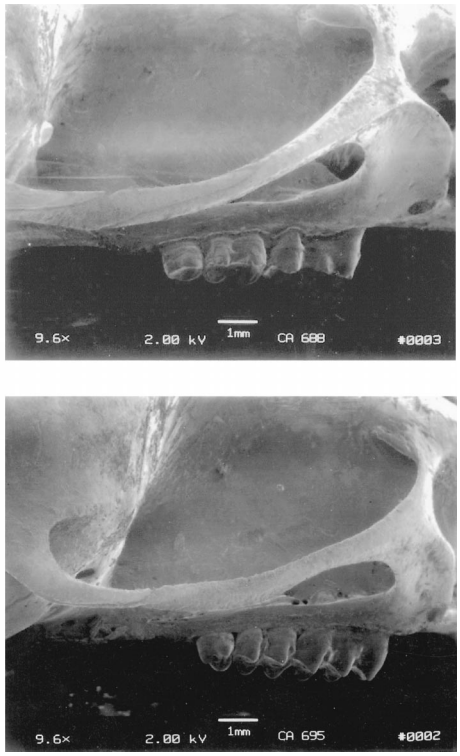

FIG. 2.—Lateral view of zygomatic plate of a) *O. josei* and b) *O. nasutus*.

Morphometric Comparisons

Different multivariate techniques were used to assess morphometric variation

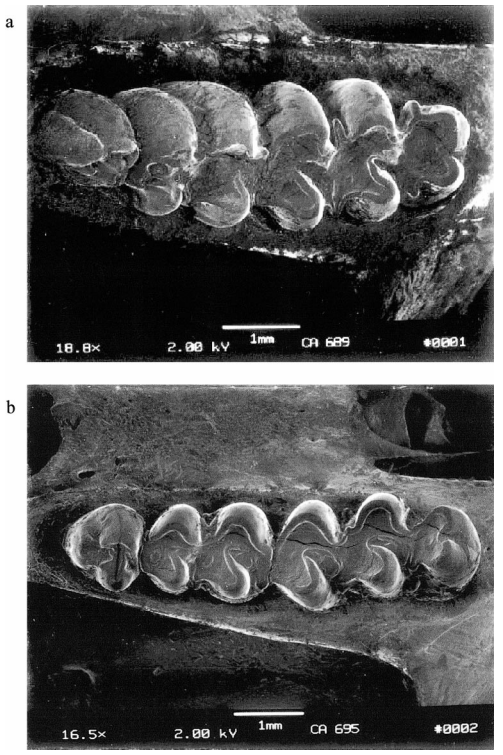

FIG. 3.—Upper molar toothrow plate of a) *O. josei* and b) *O. nasutus*.

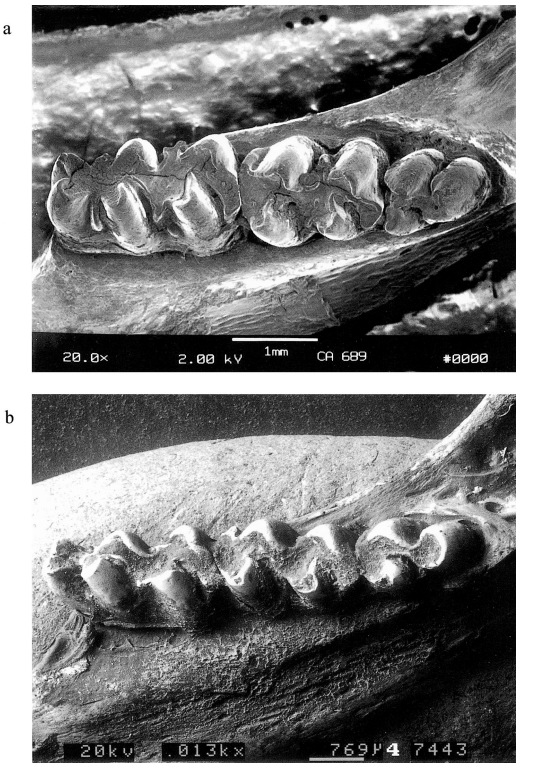

FIG. 4.—Lower molar toothrow plate of a) *O. josei* and b) type specimen of *O. nasutus*.

among species in this study: principal components analysis, multivariate analysis of variance, and size-free discriminant function analysis (where 1st principal components analysis axis is extracted, and discriminant function analysis is performed from here onward). The 1st step was to perform a principal components analysis on the covariance matrix (results not shown). Three components were extracted, accounting for 59.8%, 14.9%, and 5.0% of the variance. The 1st component extracted can be explained as a size component, with positive loadings on all variables, higher than 0.6 on all variables except interparietal length and interparietal width. This would suggest that size is the most important source of variation in the data set. The latter variables present high loadings on the 2nd component. The 2nd step was a multivariate analysis of variance with species as factors and 10,000 iterations. Results detected significant differences among groups ($F = 7.94$, $P \ll 0.001$). The next step was a size-free discriminant analysis including geographically relevant species: *O. delator, O. josei*, *O. judex*, *O. misionalis*, *O. nasutus*, *O. quaestor*, and *O. rufus*. As in principal components analysis, 3 axes were extracted, accounting for 45.7%, 29.2%, and 13.4% of the variance. Plots of individual scores grouped by species show 3 distinct clusters: *O. josei* and *O. nasutus*; *O. judex*, *O. misionalis*, and *O. quaestor*; and *O. delator* and *O. rufus* (Fig. 4). Finally, observations were reclassified on the basis of minimum, size-adjusted Mahalanobis distances and 1,000 bootstrap replicates to estimate frequency distributions of classification. Individuals classified as *O. josei* were reclassified as *O. rufus* with a frequency of 3.45%, whereas no individuals

TABLE 1.—Frequency matrix from the reclassification function, with results presented as percentages. Classifications given are presented in rows, reclassifications in columns.

	O. delator	*O. josei*	*O. judex*	*O. misionalis*	*O. nasutus*	*O. quaestor*	*O. rufus*
O. delator	90.48	2.38	0.00	2.38	0.00	0.00	4.76
O. josei	5.17	67.24	1.72	0.00	20.69	1.72	3.45
O. judex	0.00	0.00	70.00	3.33	3.33	20.00	3.33
O. misionalis	0.00	8.33	16.67	58.33	8.33	0.00	8.33
O. nasutus	2.44	17.07	0.00	0.00	78.05	0.00	2.44
O. quaestor	0.00	0.00	23.53	5.88	0.00	70.59	0.00
O. rufus	3.23	0.00	0.00	0.00	3.23	0.00	93.55

classified as *O. rufus* were reclassified as *O. josei* (Table 1).

MOLECULAR COMPARISONS

The first 1,137 bp of cyt *b* were used for all molecular comparisons, for reasons mentioned above. Of the 1,137 bp, 745 were identical in all samples, with 292 parsimony-informative sites. Of the 392 variable sites, 62, 29, and 301 were 1st, 2nd, and 3rd codon positions, respectively.

Nine (or 10 if we consider LG41 as *O. quaestor*) species of *Oxymycterus* are included in this section, representing 9 of the different species groups described by Oliveira (1998).

Pairwise uncorrected distances among species of *Oxymycterus* average 7.5% and range from 1.9% between *O. rufus* and *O. josei* to 9.6% between *O. rufus* and *O. amazonicus* (Table 2). Intraspecific comparisons range from 0% in *O. josei* and *O. judex* to 1.3% in *O. dasytrichus*. However, intraspecific comparisons were only possible for a subset of the species included. Average distance values between *Oxymycterus* and outgroups were 16.2%, 16.6%, 16.5%, and 10.2% with *A. boliviensis*, *T. nigrita*, *B. amoenus*, and *J. huanchacae*, respectively.

Neighbor-joining, maximum parsimony, and maximum likelihood were used to reconstruct the phylogeny of *Oxymycterus*. Evaluation of 10,000 random trees results in a significant signal-to-noise ratio ($g1 = -0.74$, $P < 0.01$) statistic. All analyses show strong support for sister-taxa relationships between *O. amazonicus* and *O. delator*, *O. quaestor* and *O. judex*, and *O. rufus* and *O. josei*. A neighbor-joining tree using the Tamura–Nei distance (tree not shown) sorts the species into 2 different groups, with *O. amazonicus*, *O. delator*, *O. dasytrichus*, and *O. nasutus* in 1 cluster and *O. hiska*, *O. paramensis*, *O. rufus*, *O. josei*, *O. quaestor*, and *O. judex* in the other. However, apart from the sister-taxa relationships noted previously, only the branch leading to *O. amazonicus* + *O. delator* + *O. dasytrichus* has a high bootstrap value (bs = 80). Parsimony analyses present the same topology, separating the species into 2 clades, with *O. amazonicus* + *O. delator* as sister clade to the remainder of the genus (Fig. 5). Changes in the transition–transversion ratio do not result in different topologies. Bootstrap values for most basal nodes are low (bs < 70); only the monophyly of the genus has a high bootstrap value (bs = 100). In the case of maximum-likelihood analyses, the strict consensus parsimony tree was used to evaluate the likelihood of different models of nucleotide substitution (Fig. 6). A maximum-likelihood analysis of the complete data set, with parameter values set to the HKY+Γ model of nucleotide substitution (Hasegawa et al. 1985), resulted in a tree that included *Juscelinomys* within *Oxymycterus* (empirical base frequencies, transition–transversion ratio = 7, and value of gamma shape parameter, $\alpha = 0.201$). This tree was not significantly different ($P > 0.44$ in a Kishino–Hasegawa test—Kishino and Hasegawa 1989) from a tree that constrained *Oxymycterus* to be monophyletic.

TABLE 2.—Pairwise uncorrected percentage of cytochrome-*b* sequence divergence among species of *Oxymycterus*, and the outgroups, *Akodon*, *Bolomys*, *Juscelinomys*, and *Thaptomys*.

	A. boliviensis	*T. nigrita*	*B. amoenus*	*J. huanchacae*	*O. amazonicus*	*O. delator*	*O. dasytrichus*	*O. nasutus*	*O. hiska*	*O. paramensis*	*O. josei*	*O. quaestor*	*O. judex*
A. boliviensis													
T. nigrita	13.5												
B. amoenus	15.6	14.4											
J. huanchacae	16.6	16.0	15.9										
O. amazonicus	16.1	16.1	15.8	9.2									
O. delator	16.2	16.3	16.3	9.3	2.9								
O. dasytrichus	16.1	16.8	16.5	10.7	6.3	6.1							
O. nasutus	16.0	17.6	16.2	10.5	7.8	7.7	6.9						
O. hiska	16.6	16.9	17.6	10.4	8.9	8.0	8.2	7.6					
O. paramensis	16.9	16.9	17.1	10.2	7.8	6.9	7.5	7.6	6.8				
O. josei	15.9	16.4	16.6	10.4	9.2	9.1	8.6	8.2	7.4	8.2			
O. quaestor	16.5	16.1	16.6	9.5	8.3	8.2	7.9	8.2	7.7	7.9	7.0		
O. judex	16.0	16.0	15.5	10.0	7.9	8	7.2	7.7	7.0	7.0	6.7	2.8	
O. rufus	16.3	16.9	17.2	11.1	9.6	9.5	8.8	8.1	7.3	8.6	1.9	7.2	6.9

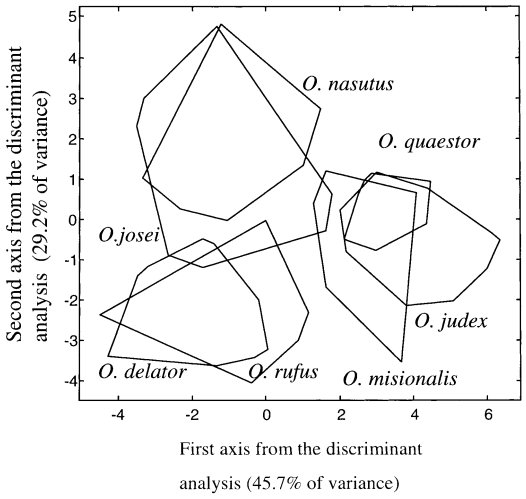

FIG. 5.—Size-free discriminant analyses of *O. delator*, *O. josei*, *O. judex*, *O. misionalis*, *O. nasutus*, *O. quaestor*, and *O. rufus*. Plot of species scores on first 2 axes.

DISCUSSION

The monophyly of the genus *Oxymycterus* was supported in Smith and Patton's (1999) analysis, and the genus was consistently grouped with the Akodontine genera *Akodon*, *Thaptomys*, and *Bolomys*. There was no support for an ''oxymycterine group.'' Recent work on the genus has resulted in the description of 5 new species: *O. hiska* and *O. hucucha* (Hinojosa et al. 1987), *O. amazonicus* (Hershkovitz 1994), *O. caparaonense* (Hershkovitz 1998), and *O. josei* (current study). Furthermore, Oliveira's (1998) revision restricted *O. hispidus* and revived *O. dasytrichus*, *O. judex*, *O. juliacae*, *O. misionalis*, and *O. quaestor*, among others, as valid species on morphological grounds, grouping all forms into species groups. A comprehensive revision of the group is beyond the scope of this paper, and the reader is referred to the aforementioned work by Oliveira (1998).

Our morphometric, morphologic, and molecular analyses agree on the presence of 2 different species of *Oxymycterus* in southern Uruguay: *O. josei* and *O. nasutus*. Morphological differences between them are

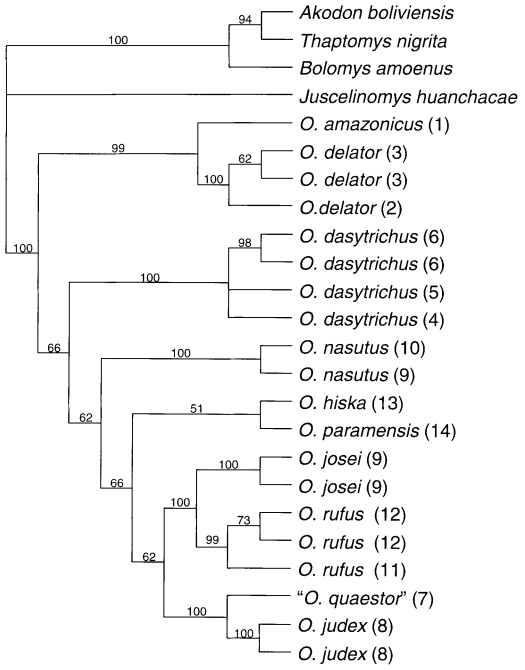

FIG. 6.—Most parsimonious tree from parsimony analyses of *Oxymycterus*, with transition–transversion ratios ranging from 1 to 10. Bootstrap values from the ''unweighted'' case are provided next to the corresponding nodes. Numbers correspond to localities in Fig. 1. *A. boliviensis*, *T. nigrita*, *B. amoenus*, and *J. huanchacae* were set as outgroups.

subtle. Differences in enamel pattern are evident but are lost in adult specimens. Differences in skull morphology are not as clear-cut, but they can be studied in adult specimens. Morphometric analyses classify correctly 67% of *O. josei* specimens and 78% of *O. nasutus* specimens. Both Uruguayan species can be distinguished from *O. rufus* on the basis of their skull and bacular morphology and morphometric analyses. In contrast to morphology and morphometrics, genetic distance analyses present *O. rufus* and *O. josei* as closely related, and both show high distance values relative to *O. nasutus*. Combining the 3 sets of analyses supports the view that *O. josei* and *O. rufus* are readily distinguishable at the morphological and morphometric levels, with differences similar to comparisons among different species. Molecular data point to the recent timing of separation between these 2 species. Detailed geographic sampling will be needed to understand processes that have led to such rapid morphological divergence.

Discovery of a new species of mammal in Uruguay, in a relatively well-studied region of the country, underscores the importance of combining molecular, morphometric, and morphological techniques in assessing biodiversity and conservation concerns. Even though both *O. josei* and *O. nasutus* had already been trapped sympatrically, they had not been distinguished, probably because of their close resemblance. Barlow's (1969) data on the biology of the 2 species need to be reevaluated and might reveal ecological differences between the species because they were considered as 1 species at the time.

Two alternative biogeographic scenarios have been advanced to account for the present distribution of the genus. Reig (1987) supported the idea that the area of original diversification was in the Andes, whereas Hershkovitz (1994) proposed the Atlantic forest in SE Brazil as the area from which the group spread. Although our study was limited in species and geographic localities, our phylogenetic analyses do not provide support for either an Andean or an Atlantic clade and suggest the need to advance more complex explanations for the zoogeography of the genus.

RESUMEN

Se presenta una evaluación del estatus taxonómico del género *Oxymycterus* en Uruguay, haciendo comparaciones morfológicas, morfométricas y moleculares con otras especies incluidas en el género. Nuestros análisis revelan la presencia de una especie no descrita, cuya descripción se presenta aquí, y restringen *O. nasutus* al SE de Uruguay y SE Brasil. Las especies uruguayas son muy similares en morfología, pero presentan diferencias sustanciales en la secuencia del gen mitocondrial del citocro-

mo *b. O. rufus* es morfológicamente distinta de *O. nasutus* y la especie nueva, y es genéticamente muy similar a la nueva especie. Los análisis filogenéticos carecen de resolución en la base del género, pero apoyan fuertemente los agrupamientos de *O. amazonicus* con *O. delator*, de *O. quaestor* con *O. judex*, y de *O. rufus* con la nueva especie.

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APPENDIX I

Specimens examined.—The 356 specimens examined belong to the following collections: Field Museum of Natural History (FMNH), Chicago; American Museum of Natural History (AMNH), New York; Museum of Zoology, University of Michigan (MZUM), Ann Arbor; Museu Nacional de Rio (MNR), Rio de Janeiro, Brazil; Museu de Zoologia (MZUSP), Universidade de Sao Paulo, Sao Paulo, Brazil; Museo Nacional de Historia Natural (MNHN), Montevideo; Laboratorio de Evolución, Facultad de Ciencias (CA and EV), Montevideo; Colección Zoología Vertebrados, Facultad de Ciencias (ZVC), Montevideo; Rijkmuseum Van Natuurlijke Histoire (RMHN), Stockholm; The Natural History Museum (NHM), London; and Museum of Vertebrate Zoology (MVZ), University of California, Berkeley. Field numbers are provided where Museum numbers were not available. Taxonomic arrangement follows Oliveira (1998). Specimens followed by a number were used in the phylogenetic analysis, and numbers in brackets correspond to locality numbers in Fig. 1.

Oxymycterus amazonicus.—BRAZIL: Pará, Marai, RMNH 7379; Xingu River, MZUSP 21317 [1].

Oxymycterus angularis.—BRAZIL: Alagoas, Viçosa, FMNH (VI 1854), FMNH (VI2198); Ceará, Sao Benedito, FMNH (IP 192); Guaraciaba do Norte, FMNH (IP 588), FMNH (IP 629); Pernambuco, Caruaru, FMNH (SNP 2571), FMNH (SNP 2495); Garanhuns, FMNH (SNP 321), FMNH (SNP 1120), FMNH (SNP 2286).

Oxymycterus dasytrichus.—BRAZIL: Espíritu Santo, Santa Tereza, FMNH (MNR 5330), FMNH (M 231), FMNH (M 307), MNR-ML 125 [4]; Minas Gerais, Além Paraíba, MNR 5473, MNR 7452; Ouro Preto, MNR 26134; Sao Paulo, Barra do Rio Junguía, FMNH 93064, FMNH 93065, FMNH 93066, FMNH 93067; Estaçao Boraceia, FMNH 145437, FMNH 145438, FMNH 145441, FMNH 145442, FMNH 145443, FMNH 145444, FMNH 145445, MVZ-JLP 16283 [5]; Fazenda Intervales, Capao Bonito, MVZ 183125 [6], MVZ 183126 [6], Itapepitinga, FMNH 136923; Primeiro Morro, FMNH 94525, FMNH 94526, FMNH 94527, FMNH 94528, FMNH 94530, FMNH 94531, FMNH 94532, FMNH 94533, FMNH 94534, FMNH 94535, FMNH 94537, FMNH 94538, FMNH 94539, FMNH 94540, FMNH 94541, FMNH 94542; Salto de Pirapora, FMNH 136924, FMNH 136925, FMNH 136926, FMNH 136927, FMNH 136928, FMNH 136929, FMNH 136930; Ubatuba, FMNH 53875, MNR 5303, MNR 5385, MNR 24436.

Oxymycterus delator.—PARAGUAY: Canindeyu, Curuguaty, MZUM 124289, MZUM 124290, MZUM 124291, MZUM 124292, MZUM 124293, MZUM 124294, MZUM 124295, MZUM 124296, MZUM 124297, MZUM 124298, MZUM 126085, MZUM 126086, MZUM 126087, MZUM 126088, MZUM 126089, MZUM 126091, MZUM 133937, MZUM 133938, MZUM 133939 [3],

MZUM 133941, MZUM 133942, MZUM 133943, MZUM 133973, MZUM 133974, MZUM 133978, MZUM 133979, MZUM 137077 [3]; Sapucay, NHM 3.4.7.18. BRAZIL: Matto Grosso, Serra do Roncador, NHM 80476, NHM 80477, NHM 80479, NHM 80480, NHM 80481, NHM 80482, NHM 80483, NHM 80484, NHM 80485, NHM 80486, NHM 80489, NHM 80491, NHM 80492, NHM 80493, NHM 80495; Fazenda Sao Luis, 30 km N Barra do Garcas, field number LPC 458 at the Universidade Federal de Minas Gerais, Brazil [2].

Oxymycterus hiska.—PERU: Puno, 14 km W Yanahuaya, MVZ 171518 [13].

Oxymycterus inca.—BOLIVIA: Santa Cruz, Santa Cruz de la Sierra, FMNH 22787; Buenavista, NHM 26.12.4.12; Cochabamba, Arani, FMNH 46151. PERU: Junín, Chanchamayo, FMNH 18186; La Paz, Mapirí, NHM 0.7.7.45, NHM 0.7.7.46, NHM 0.7.7.47, NHM 1.1.1.70, NHM 1.1.1.71, NHM 1.1.1.72, NHM 1.1.1.73, NHM 1.1.1.74, NHM 1.1.1.76, NHM 1.1.1.77, NHM 1.1.1.78, NHM 1.2.1.28.

Oxymycterus josei.—URUGUAY: Canelones, Arroyo del Bagre, ZVC (AL) 329, ZVC (AL) 422, ZVC (AL) 423, ZVC (AL) 426, ZVC (AL) 427, ZVC (AL) 428, ZVC (AL) 429, ZVC (AL) 888, ZVC (AL) 890, ZVC (AL) 891, ZVC (AL) 894; Arroyo Sarandí, MNHN 1519, MNHN 1526, MNHN 1553; Arroyo de la Tropa Vieja, MNHN 1190, AMNH 206166, AMNH 206167, AMNH 206168, Km. 36 Ruta Interbalnearia, AMNH 206169, AMNH 206170; Maldonado, Barra de Maldonado, AMNH 206182, AMNH 206183, AMNH 206184, AMNH 206185, AMNH 206186, AMNH 206187, AMNH 206188, CA 479 ?, CA 480 ?, CA 481 ?, MNHN 576, MNHN 577, MNHN 578, MNHN 579, MNHN 581, MNHN 2047, MNHN 2048; Las Flores, CA 599, CA 600, CA 601, CA 685, CA 686, CA 687, CA 688, CA 689, CA 690, CA 694, CA 696, CA 697, CA 701, CA 704, MVZ 183264 [10], MVZ 183265 [10]; Sierra de las Ánimas, MNHN 3046; San José, Ecilda Paullier, Estancia ''El Relincho,'' EV 986, EV 987, EV 988, EV 1002, EV 1003, EV 1004, EV 1005, EV 1020, EV 1021, EV 1022, EV 1023, EV 1024, EV 1025; Soriano, 3 km E de Cardona, AMNH 206205.

Oxymycterus judex.—BRAZIL: Santa Catarina, Florianopolis, NHM 2.8.25.1; Hansa, FMNH 35354, FMNH 35355, NHM 28.10.11.37, NHM 28.10.11.39, NHM 28.10.11.40, NHM 28.10.11.42, NHM 28.10.11.44, NHM 29.6.6.37, NHM 29.6.6.38, NHM 29.6.6.39, NHM 29.6.6.40, NHM 29.6.6.42, NHM 29.6.6.43, NHM 29.6.6.44, NHM 29.6.6.45, NHM 29.6.6.46, NHM 29.6.6.47; Joinville, FMNH 34374, FMNH 34375, FMNH 34377, FMNH 34378, FMNH 34380, FMNH 34383, NHM 13.7.8.4, NHM 13.7.8.5 ?, NHM 14.1.26.33, NHM 14.1.26.34, NHM 14.1.26.35, NHM 9.11.19.23; Sao Paulo, Fazenda Intervales, Capao Bonito, MVZ 183128 [8], MVZ 183129 [8].

Oxymycterus juliacae.—BOLIVIA: Cochabamba, Charuplaya, NHM 2.1.1.95, NHM 2.1.1.96; Las Yungas, Locotal, RHNMS 204. PERU: Cuzco, Marcapata, FMNH 65706, FMNH 66404, FMNH 66405, FMNH 66407, FMNH 68617; Puno, Sandía, FMNH 78385, FMNH 78386; Segrario, FMNH 52621, FMNH 52622; Villa Carmen, FMNH 84365.

Oxymycterus misionalis.—ARGENTINA: Misiones, Caraguatay, FMNH 26753, FMNH 26754, FMNH 26755, FMNH 26757, FMNH 26841, FMNH 26856, FMNH 26857; Dos de Mayo, FMNH 122696; Goya, NHM 98.12.3.23, NHM 98.12.3.24; Puerto Aguirre, FMNH 23843; Puerto Bertoni, NHM 21.4.21.4; Puerto Gisela, NHM 24.6.6.50, NHM 24.6.6.51.

Oxymycterus nasutus.—URUGUAY: Cerro Largo, 6 km SE Melo, AMNH 206172, AMNH 206173, AMNH 206174, AMNH 206175, AMNH 206176; Río Tacuarí, 20 km SE Melo, AMNH 206177, AMNH 206178, AMNH 206179, AMNH 206180, AMNH 206181; Maldonado, Arroyo El Renegado E Pan de Azucar, CA 680; Barra del Arroyo Maldonado, CA 458 ?, MVZ 182701 [9]; Las Flores, CA 695 [10]; Rocha, Arroyo La Paloma, CA 614, CA 615, CA 616, CA 617, CA 618, CA 627, CA 629, CA 630; Santa Teresa, MNHN 1528, MNHN 1552, 22 km SE de Lascano, AMNH 206189, AMNH 206191, AMNH 206192, AMNH 206193, AMNH 206194, AMNH 206195, AMNH 206196, AMNH 206197, AMNH 206198, AMNH 206199, AMNH 206201, AMNH 206202, AMNH 206203, AMNH 206204. BRAZIL: Rio Grande do Sul, Sao Lorenço, NHM 85.6.26.19, NHM 88.11.30.13, BNMH 88.11.30.14.

Oxymycterus nigrifrons.—PERU: Puno, Limbani, FMNH 52476, FMNH 52623, FMNH 52624, FMNH 52625, FMNH 52626, FMNH 52627, FMNH 52628, FMNH 52630, FMNH 52631, FMNH 52632, FMNH 52633, FMNH

53136, FMNH 53144, FMNH 53145, FMNH 53146, FMNH 53147, FMNH 53148, FMNH 53149, FMNH 53150, FMNH 53151, FMNH 53152.

Oxymycterus paramensis.—BOLIVIA: Cochabamba, Arani, NHM 34.9.161, NHM 34.9.1.162, NHM 34.9.1.163, NHM 34.9.1.164, NHM 34.9.1.166, NHM 34.9.1.167; Ayopaca, FMNH 74892, FMNH 74893, FMNH 74894, FMNH 74895, FMNH 74896, FMNH 74897, FMNH 74898, FMNH 74899, FMNH 74900, FMNH 74901; Colomi, FMNH 51922, FMNH 51923, FMNH 51924, FMNH 51986, FMNH 51987, FMNH 51988; Choquecamata, NHM 2.1.1.90; Incachaca, FMNH 44682, FMNH 46152; Liruini, RMNH 358; Muellemuelle, FMNH 44863; Toncoma, FMNH 140811, RMNH 373, RMNH 375; Ucho Ucho, RMNH 387, RMNH 388, RMNH 390. ARGENTINA: Jujuy, Caimancito, FMNH 41280; Yala, FMNH 22234, FMNH 23316, FMNH 23317, FMNH 23318, FMNH 23319, FMNH 23320, FMNH 23321, FMNH 23322, FMNH 23323, FMNH 23324, FMNH 23325, FMNH 23326; Salta, Sierra de Aguaray, FMNH 35251. PERU: Allontayllando, NHM 22.1.1.99; Cuzco, 55.4 km by rd. N Calea, 3,560 m, MZUM 160535 [14].

Oxymycterus quaestor.—BRAZIL: Paraná, Roça Nova, NHM 3.7.1.80, NHM 3.7.1.81 ?; Rio de Janeiro, Teresópolis, FMNH 26585, FMNH 26586, FMNH 26587, FMNH 28588, FMNH 28590, FMNH 28591, FMNH 28592, FMNH 28593, FMNH 28594, FMNH 28595, MNR 6342, MNR 6346, MNR 10460, NHM 23.10.2.12, NHM 96.11.9.5; Sitio Xitaca, Nova Friburgo, LG 41 at the Museo Nacional de Rio, Rio de Janeiro, Brazil [7].

Oxymycterus rufus.—ARGENTINA: Buenos Aires, General Lavalle, FMNH 122697; Berisso, BAL 00-05-11 at the Museo de Historia Natural de la Plata [11]; La Plata, NHM 94.10.4.2, NHM 94.10.4.4, NHM 99.10.4.1; Pereira, FMNH 95138; Punta Lara, FMNH 95139, FMNH 98284, FMNH 98285, NHM 62.1925, NHM 64.751, NHM 64.752; Córdoba, Noetingen, NHM 17.1.25.35, NHM 17.1.25.36, NHM 17.1.25.37, NHM 17.1.25.38, NHM 17.1.25.39, NHM 17.1.25.40, NHM 17.1.25.41, NHM 17.1.25.74; Rio Cuarto, TK 49118 [12], TK 49121 [12]; Villa Dolores, NHM 16.1.6.32, NHM 16.1.6.33, NHM 16.1.6.34; Santa Fé, Delta del Paraná, NHM 20.3.14.17, NHM 20.3.14.18, NHM 20.3.14.19; Isla Ella, NHM 17.6.1.18, NHM 17.6.1.19, NHM 17.6.1.20, NHM 17.6.1.42.

Oxymycterus sp. B (in Patterson 1992a).—BOLIVIA: Cochabamba, Cochabamba, FMNH 51985.