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A NEW GENUS AND SPECIES OF PHYLLOTINE RODENT FROM BOLIVIA

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A new species (Muridae, Sigmodontinae, Phyllotini), belonging to a new genus, is described on the basis of 2 specimens from 1 locality in the mountain forests of southeastern Bolivia. Diagnostic features are posteriorly divergent edges of supraorbital region, large and hypsodont molar teeth with somewhat prismatic pattern, and anterior zygomatic process not projecting as an overhanging point. The diploid chromosome number is 56 and the fundamental number is 76. Other external, cranial, dental, and karyologic characters in the tribe and new taxon are described, illustrated, and discussed. The hypothesized phylogenetic placement of the new genus based on gene-sequence, chromosomal, and morphologic data is presented relative to evolutionary relationships of selected phyllotine taxa.

Key words: Bolivia, new species, Phyllotini, rodent, Sigmodontinae, Yungas

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In July 1991, our Bolivian Expedition camped at an elevation of 1,500 m in humid forest at the village of Tapecua in the department of Tarija (Fig. 1). Here, the main east–west road in Tarija crosses a divide on the crest of 1 of 7 parallel ridges that lie between the arid high altiplano with its puna vegetation (Cabrera and Willink 1980) to the west and the lowland Gran Chaco with its xeric, thorn–scrub vegetation to the east.

At Tapecua, we captured 2 rats with dark areas on the tops of the hind feet. Their size and general appearance suggested *Andinomys edax*. However, the pelage seemed coarser and the ears slightly larger (in comparison to size of head and body). When we examined the uncleaned skulls in the field, the posterior divergence of the edges of the frontal bone in the supraorbital area and its greater width were unlike these features in *Andinomys*, and suggested *Graomys*. When the skulls were cleaned in the laboratory and the teeth were examined, their relatively large size, noticeable hypsodonty, and relatively prismatic form suggested a condition between the smaller, less-specialized teeth of *Graomys* and the larger, more acutely angled teeth of *Andinomys*. Subsequent chromosomal analysis revealed similarity to *Andinomys* in number of chromosomes, but not in number of chromosomal arms. A review of these and other genera of phyllotines revealed that no existing diagnosis of any phyllotine genus would accommodate the new rats without changing more than one-half of the statements about what characters were diagnostic.

The collection of 1991 included series of other phyllotine species of the region (e.g., *Phyllotis xanthopygus, P. osilae, P. caprinus, P. wolffsohni, Graomys domorum,* and *G. griseoflavus,* in addition to *A. edax*). The new rats were quite different from any of these and from *Andalgalomys*. Thus, a new genus is proposed for the new species. Steppan has studied cladistic relationships within the tribe Phyllotini, and in 1993 in-

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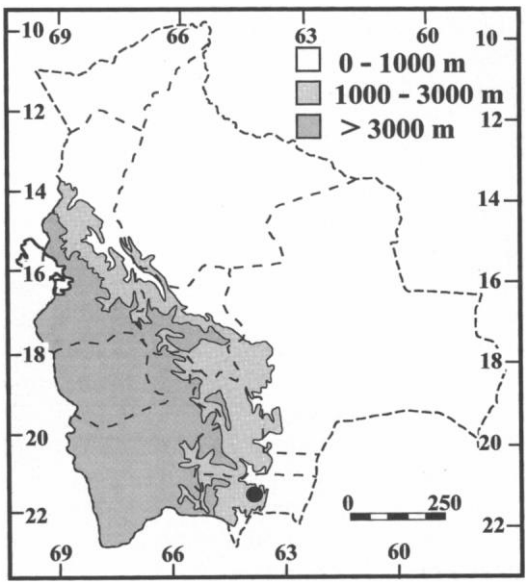

FIG. 1.—Map of Bolivia showing the location of Tapecua in relation to the major elevational belt between 1,000 and 3,000 m known as the Yungas and Valles Region.

cluded data provided by us on this new species (Steppan 1993). Another study (Braun 1993) on phenetic and cladistic relationships in the tribe was completed before discovery of this new species.

METHODS AND MATERIALS

Cranial measurements were taken with a stage craniometer as described by Anderson (1969). The midfrontal width was measured at the middle of the suture between the frontal bones as seen in dorsal view. We reviewed characters used in diagnosis and comparisons of *Andinomys, Graomys, Salinomys,* and *Andalgalomys* with other genera by various authors (Braun and Mares 1995; Gyldenstolpe 1932; Hershkovitz 1962; Olds et al. 1987; Osgood 1947; Thomas 1902). Most of these characters are included in the description or comparisons below.

We also attempted to code, for the new species, all characters used by Braun (1993) and Braun and Mares (1995). Although 21 of the 25 characters we used matched those of Braun (1993), the character states do not match for all characters. In addition, in the later paper (Braun and Mares 1995), even fewer states were used and ranges of values assigned to states do not match those of the earlier paper in all cases. This makes it difficult to compare scorings for character states in previous studies or to add taxa in subsequent studies. In a few cases, we were uncertain what exact dimensions were to be measured so some variation may be present between our scorings and those of these authors. Also, in assessing the state of genera in the cladogram, we believed it best to include more than 1 species for those that have more than 1. Thus, we added *Andalgalomys pearsoni, Calomys callosus,* and *Graomys domorum,* using data from Braun (1993) wherever possible. Our resulting character matrix is not reproduced here but is available on request.

Polymerase chain reaction and nucleotide sequencing.—Total genomic DNA was isolated from frozen liver tissue following Hillis et al. (1996). The cytochrome-*b* gene of the mitochondrial DNA was amplified using the polymerase chain reaction (PCR). The primers used to amplify the cytochrome-*b* gene were light-strand (*Mus* 14095) 5′ GAC ATG AAA AAT CAT CGT TGT AAT TC 3′ and heavy-strand (*Mus* 15398) 5′ GAA TAT CAG CTT TGG GTG TTG RTG 3′. Double-stranded DNA (dsDNA) products were obtained with PCR amplification using *Taq* DNA polymerase (Saiki et al. 1986, 1988); PCR amplifications were performed in 25-μl reactions. Samples were denatured at 95°C for 45 s, primers were annealed at 50°C for 40 s, and segments were extended at 70°C for 2 min with 4 s added to each extension for 40 cycles; 2.5 μl of reaction buffer (500 mM KCl; 100 mM Tris-HCl, pH 8.4–8.7; 25 mM $MgCl_2$; 0.5 μl bovine serum albumin), 4 μl deoxynucleoside triphosphates (2 mM of each deoxyadenosine triphosphate, deoxycytidine triphosphate, deoxyguanosine triphosphate, and deoxythymidine triphosphate in 10 mM Tris-HCl, pH 7.9), and 2 pmole of each primer was added to every reaction. The efficiency of the amplification was verified by visualizing 5 μl of the dsDNA product on a 0.8% agarose gel stained with ethidium bromide.

Primers used to amplify the cytochrome-*b* gene also were used in the sequence reaction. In addition, 2 internal primers (light-strand 5′ GTT GAA TGA ATC TGG GGC GG 3′ and heavy-strand 5′ AAC GAC AAG GTT AGC GAT AAA GG 3′) were used to sequence the entire gene. Specimens were sequenced on an Applied Biosystems 377 DNA Sequencer (Perkin-Elmer

Applied Biosystems, Foster City, California). Sequences were attained using the *Taq* DyeDeoxy™ Terminator Cycle Sequencing Kit (Perkin-Elmer Applied Biosystems, Warrington, United Kingdom) and following protocols provided therein. Sequences reported in this paper were deposited in the GenBank database (accession numbers AF159283–AF159294).

Data analyses.—Maximum parsimony was used to derive a phylogeny from the nucleotide-sequence data and separately from morphologic data. All maximum-parsimony analyses were conducted using PAUP, version 3.1.1 (Swofford 1993). In the morphologic analysis, characters were treated as unordered, weighted equally, and that analysis was performed using the exhaustive-search option. In the analysis of nucleotide-sequence data, characters were treated as unordered, discrete characters with four possible states (A, C, G, and T). Analyses were performed using the branch-and-bound search option. An unequal weighting scheme was used in the parsimony analyses and involved use of transversions only in 3rd position, total substitutions at 1st and 2nd positions, except 1st-base positions that coded for leucine, which were coded as Y for pyrimidine only (Honeycutt et al. 1995). Homoplasy in the parsimony analyses was evaluated using the consistency index (Kluge and Farris 1969) and the retention index (Farris 1989). Length of tree was used to determine the most-parsimonious solution, and support for individual clades was evaluated using both the decay index, which is the number of extra steps needed to collapse a node (Bremer 1988), and bootstrap resampling using 500 replications (Felsenstein 1985). The Jukes–Cantor (Jukes and Cantor 1969) distance measure was performed using the MEGA program (Kumar et al. 1993).

Results

Family Muridae Illiger, 1815

Subfamily Sigmodontinae Wagner, 1843

See Musser and Carleton (1993) for taxa, authors, dates, and references of categories above tribe or in lower categories, except when detailed treatment is involved. Because of the general availability of this publication, we have chosen not to include all of that information here as recommended (International Commission of Zoological Nomenclature 1985). See Olds and Anderson (1989) for Vorontsov's tribal reference.

Tribe Phyllotini Vorontsov, 1959

The tribe was diagnosed by Olds and Anderson (1989) and Steppan (1995). In their diagnosis of the tribe Phyllotini, Olds and Anderson (1989) included the following combination of characters: 1, heel hairy; 2, ears moderate to large; 3, palate long (except in *Irenomys*); 4, incisive foramina long; 5, parapterygoid fossa relatively broader than mesopterygoid fossa (except in *Punomys*); 6, sphenopalatine vacuities large; 7, supraorbital region never evenly curved in cross section; 8, interparietal well developed; 9, zygomatic notch deeply excised (less so in *Irenomys*); 10, teeth tetralophodont; 11, M3 50% the length of M2.

All phyllotines (with exceptions noted) have this combination of characters but no character is unique to phyllotines. The 2 specimens of the new species exhibit all of these characters.

The following genera were included by Olds and Anderson (1989) in the tribe Phyllotini: *Andalgalomys, Andinomys, Auliscomys, Calomys, Chinchillula, Eligmodontia, Euneomys, Galenomys, Graomys, Irenomys, Neotomys, Phyllotis, Punomys,* and *Reithrodon.* Steppan (1993, 1995) excluded *Punomys* from the tribe. Fossil genera were not reviewed by Olds and Anderson (1989) or by Steppan (1993, 1995). The species *Auliscomys boliviensis* was placed in a new genus, *Maresomys,* by Braun (1993). Subsequently, *Maresomys boliviensis* was returned to *Auliscomys* by Steppan (1995). Recognition of *Maresomys* as a subgenus of *Auliscomys* would be consistent with Steppan's (1995) phylogeny. An additional genus (and species) of phyllotine, *Salinomys delicatus,* was described by Braun and Mares (1995). They considered *Salinomys* to be a sister group of a clade including *Andalgalomys* and *Graomys. Salinomys* is small and most of its diagnostic features (Braun and Mares 1995) suggest that it is

related more closely to *Andalgalomys* and *Graomys* than to the new genus, which may be the sister group of the *Andalgalomys–Graomys–Salinomys* clade (see discusion below). The new specimens from Tapecua clearly represent a new species and its assignment to a new genus seems warranted.

Tapecomys primus, new genus and species

Holotype.—Adult male, Colección Boliviana de Fauna (CBF), La Paz, Bolivia, 2414, skin (with distal part of tail missing) and skeleton, prepared by A. Nuñez Quiroz, field number 21, 14 July 1991. Frozen tissues (heart, liver, both kidneys) and cell suspension (New Mexico Kyrovoucher number [NK] 23413) are deposited in the University of New Mexico, Museum of Southwestern Biology, Albuquerque, New Mexico.

Additional specimens.—One: a young adult male, American Museum of Natural History (AMNH) 264448, prepared by T. L. Yates, field number 1501, skin, skeleton, frozen tissues (NK 23399), 13 July 1991, also from the type locality. Samples from the 2 specimens of blood, feces, gastrointestinal contents, ectoparasites, and endoparasites are at the University of Nebraska, Manter Laboratory of Parasitology, Lincoln.

Type locality.—Tapecua, 1,500 m, 21°26′S, 63°55′W, Department of Tarija, Bolivia.

Diagnosis.—A relatively large phyllotine rodent with brownish-agouti pelage dorsally and a ochraceous hue ventrally. The tail is bicolored, not penicillate, and is slightly longer than head and body. The manus is white. The pes is relatively large, brownish, and with a darker spot on top near bases of the toes. Edges of the supraorbital region are divergent posteriorly, sharply angled, slightly beaded, and continue as a distinct temporal ridge across the parietal bone. Hypsodont molar teeth are with somewhat prismatic pattern. Anterior zygomatic process is not projecting as an overhanging point.

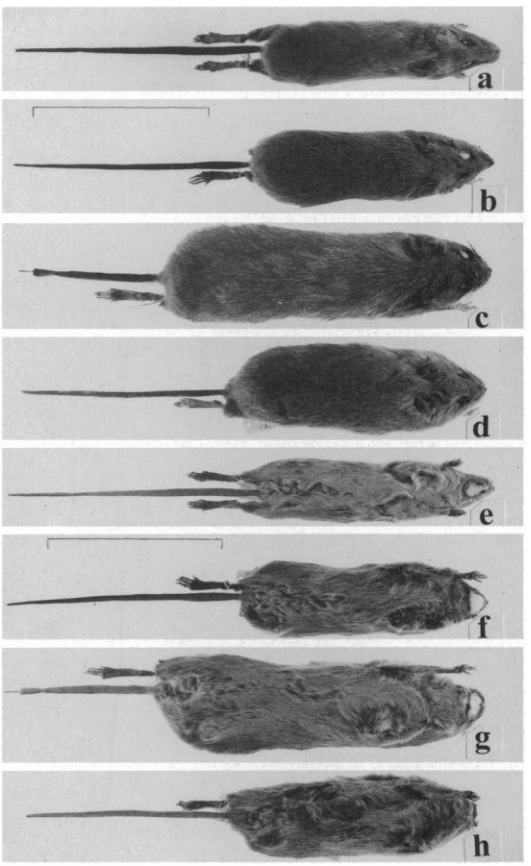

FIG. 2.—Dorsal and ventral views of skins; from top to bottom, a) and e) AMNH 268940, *Graomys domorum*; b) and f) AMNH 264448, *Tapecomys primus*; c) and g) holotype of *T. primus*; d) and h) AMNH 268939, *Andinomys edax*. Scale represents 100 mm.

Description.—A rat of medium size (larger than most phyllotines, see measurements), with tail and ears of moderate length. This rodent has no conspicuous color markings; in fact its drabness is impressive (dorsal and ventral views of skins in Fig. 2). The ventrum is paler than the dorsum and has an ochraceous wash. The color changes gradually from dorsum to ventrum, without a sharp line of demarcation on sides of the head or body. In contrast, a sharp line of demarcation exists on each side of the bicolored tail. Hairs on top of the hind foot near the bases of toes 2–4 are somewhat darker than hairs on other parts of the foot,

but not nearly so dark or conspicuous as the larger black areas on feet of *Rhipidomys*. Hairs on most or all of the top of the manus are white. Pollex has a broad nail, and other toes have claws. The most noteworthy feature is the broad supraorbital region with lateral edges sharply angled as noted in the Diagnosis. The molar teeth are relatively large, high-crowned, and prismatic. The diploid number of chromosomes (2n) is 56 and the fundamental number (FN) is 76.

Comparisons.—Olds and Anderson (1989) reported 16 characters and their states in 33 species of rodents, among which were 14 phyllotines. *Andinomys* was shown to differ from *Graomys* in relatively shorter tail, hind feet, and ears (all in relation to length of head and body). In 2 of these characters, length of tail and ears, the new genus agrees with *Andinomys* rather than *Graomys*. In relative length of hind feet it exceeds both *Andinomys* and *Graomys* (Fig. 3).

Forefeet are relatively larger in *Andinomys* than in *Tapecomys* (Fig. 4). Forefeet are small in *Andalgalomys*.

Although ears are fairly large in both *Tapecomys* and *Andinomys,* in proportion to size of body, they are smaller than in *Phyllotis* and *Graomys* (see ratios in Fig. 3). Ears are closely haired and brown outside and inside; *Tapecomys* and *Andinomys* are not noticeably different in these features. Ears of *Graomys* differ with species and locality but generally are blackish. In *G. domorum* a blackish spot may be evident on the external surface. In *Andalgalomys pearsoni,* the interior surface of the pinna has brownish hair and hairs on the external surface are slightly darker. Edges of ears differ; ears of *Tapecomys* have no pale border, whereas edges are whitish or grayish in *Andinomys*. Some *G. domorum* show pale edges of ears; *G. griseoflavus* and *A. pearsoni* do not.

The tail is well-haired in both Tapecomys and *Andinomys,* but *Tapecomys* has noticeably finer, shorter, and ventrally grayer hair and smaller scales, which, because of the reduced coverage of hair, are more visible (Fig. 5). The tail is not penicillate in *Tapecomys, Andalgalomys,* or *Andinomys*; however, distal tufts of longer hair occur in *Graomys, Eligmodontia,* and *Salinomys*.

Fur seems to average shorter in *Tapecomys* than in *Andinomys* (dorsal hairs 10–20 mm in length in *Andinomys*), but this is difficult to quantify. Fur seems coarser in *Tapecomys* than in *Andinomys,* where it is fine, soft, and not woolly. This also is difficult to quantify. Dorsum is brownish, dull buffy, or fulvous buffy, and lined with black in both *Andinomys* and *Tapecomys*. The sides of *Tapecomys* do not differ in color from the dorsum so much as in some *Andinomys*.

Ventral color is not sharply delineated from that of dorsum in either *Tapecomys* or *Andinomys,* in contrast to sharp delineation in *Graomys* and *Andalgalomys*. Venter has an ochraceous wash in *Tapecomys,* is buffy white in *Andinomys,* and is white in *Graomys, Andalgalomys,* and *Salinomys*. As in most other phyllotines, hairs are basally slate colored in both *Tapecomys* and *Andinomys*. Basally white hairs occur in *Graomys,* especially *G. griseoflavus,* and in *Andalgalomys* and *Salinomys*.

As in most phyllotines, head is like body in color. *Tapecomys* has blackish hairs around eyes, and *Andalgalomys* has paler hairs around eyes.

Feet are well-haired on upper surfaces in both *Tapecomys* and *Andinomys,* but hair seems longer, coarser, and more conspicuous in *Andinomys*. Hair of the ends of the digits is silvery white and extends beyond the claws in both genera, but number of hairs and their length seem more evident in *Andinomys*. The 5th hind toe, not including the claw, reaches only to the 1st phalanx in *Tapecomys* but reaches the middle of the 2nd phalanx of the 4th toe or at least to its base in *Andinomys*. Palmar pads are smaller in *Tapecomys* than in *Andinomys* (Fig. 4). Pads are rounded, but not exactly circular, in both genera. The unguis of the pollex is blunt as in other phyllotines; in contrast,

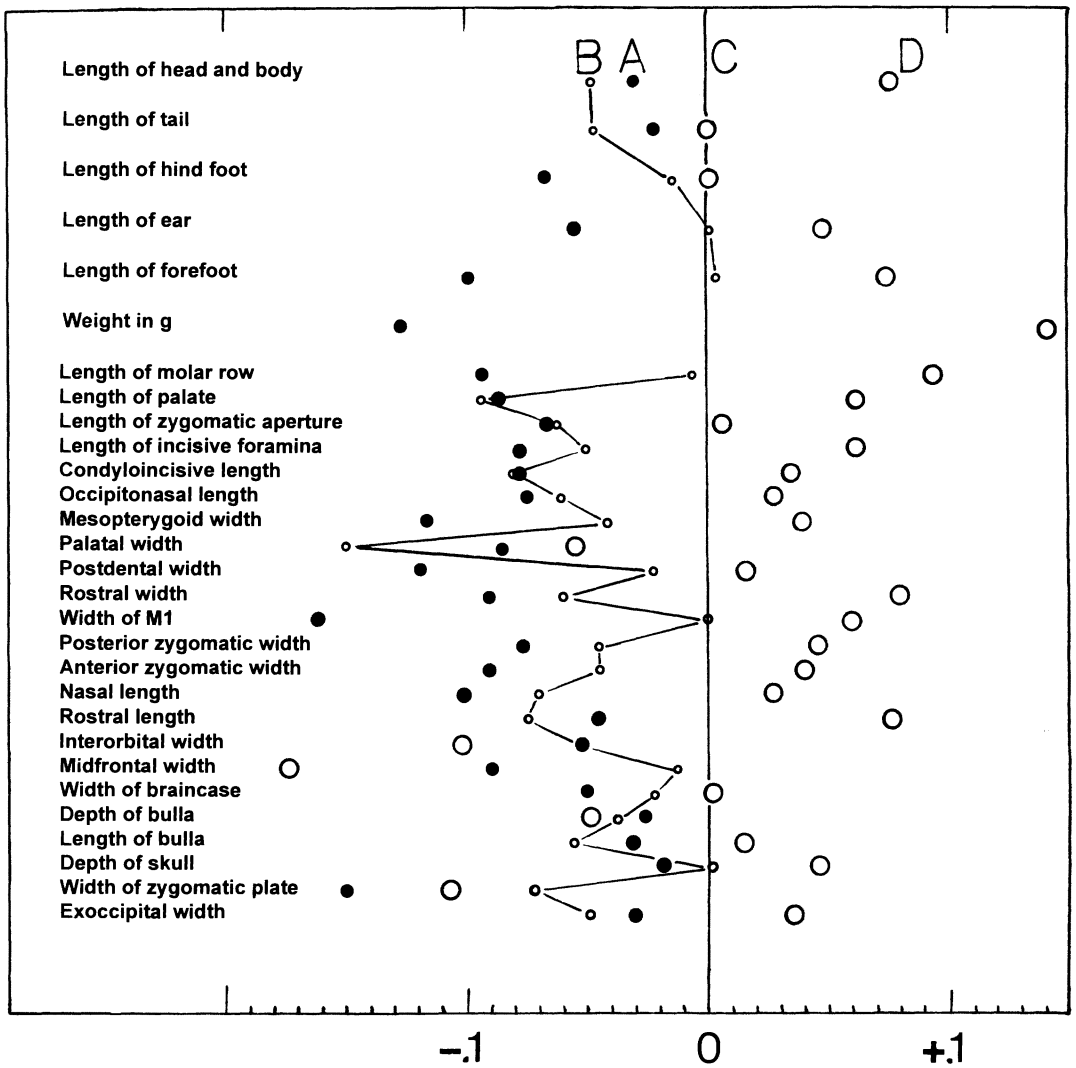

FIG. 3.—Ratio diagram, a) AMNH 246789, *Graomys griseoflavus*; b) AMNH 264448, *Tapecomys primus,* c) standard for comparison holotype of *T. primus,* and d) AMNH 262771, *Andinomys edax.* For references and discussion of ratio diagrams see Anderson (1972).

Oxymycterus (not a phyllotine) has a sharp claw.

The number and position of mammae are unknown. The 2 specimens of *Tapecomys* are males and mammae are not visible on the dried skins.

Upper incisors, nasals, and other parts of the rostrum of the skull in most phyllotines, including *Tapecomys,* are slender, in contrast to the more robust muzzle of *Andinomys* (Fig. 6 and, for dentaries, Fig. 7). The supraorbital borders are farther apart, posteriorly divergent, and sharply edged or ridged in *Tapecomys, Graomys,* and *Andalgalomys,* in contrast with *Andinomys* and many other phyllotines such as *Phyllotis, Galenomys, Auliscomys,* and *Chinchillula.* In these genera, a narrow and almost parallel-sided interorbital region is concave in the middle line and has the concavity bordered by low, rounded, and inconspicuous ridges. These do not overhang the orbit or

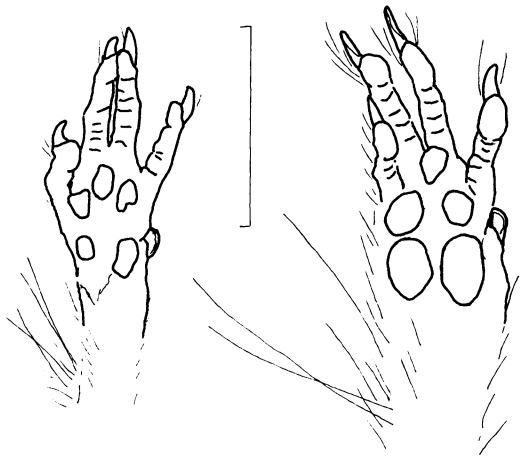

FIG. 4.—Forefeet, at left, of AMNH 264448, *Tapecomys primus,* and at right, AMNH 262771, *Andinomys edax.* Scale represents 10 mm. Both are drawn to same scale to show relative sizes of the feet and the shapes and sizes of pads.

run back as distinct temporal ridges onto the parietals, except that in some *Andinomys* weak ridges continue onto the parietals. Temporal ridges are conspicuous and overhang the orbit in *Tapecomys, Andalgalomys,* and *Graomys.* A slitlike opening, often present in *Andinomys* between the frontals near the center of the interorbital region (in 10 skulls examined) is not present in either of the 2 skulls of *Tapecomys.*

Posterior parts of the zygomatic arches project more widely than anterior parts in most murids; the difference between the anterior and posterior expansions is less in *Tapecomys* than *Andinomys.* Among phyllotines, the anterior part bows outward most noticeably in *Galenomys.*

In *Tapecomys,* the frontoparietal sutures meet at an angle that is obtuse or scarcely evident as part of a broad curve rather than as a right or acute angle as in *Andinomys.* Distance across frontoparietal sutures on the dorsal surface is more than greatest width across frontomaxillary sutures and more than alveolar length of molar row in *Tapecomys*; the reverse is true in *Andinomys.*

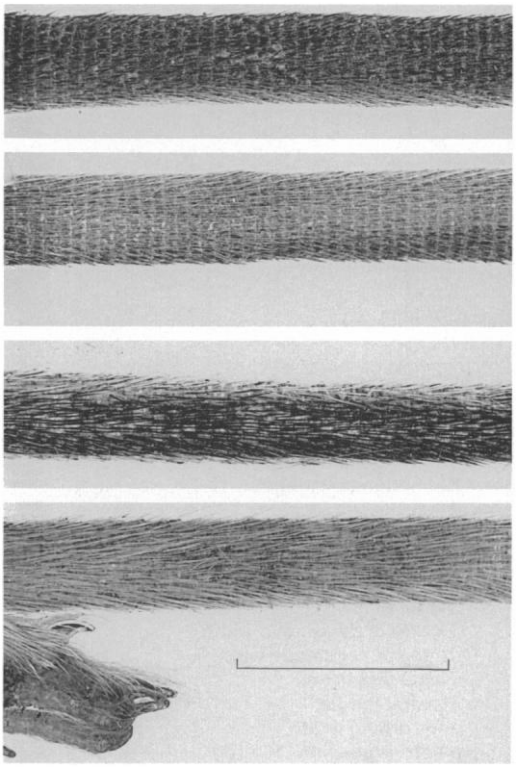

FIG. 5.—View of tails; from top to bottom, dorsal and ventral views of AMNH 264448 *Tapecomys primus,* and dorsal and ventral views of AMNH 268939, *Andinomys edax.* Scale represents 10 mm. Note finer and shorter hairs and greater visibility of scales in *Tapecomys.*

The palatal (= incisive) foramina were said (Thomas 1902) to have sharply defined edges in *Andinomys.* The sharpness is not greatly different in *Tapecomys* and *Andinomys,* but may be slightly more extreme in these 2 genera than in other phyllotine genera.

The mesopterygoid fossa is comparatively broad, but to a lesser degree in *Tapecomys* than *Andinomys.* This fossa is parallel-sided to a greater degree in *Tapecomys* than in *Andinomys.* Parapterygoid fossae are shallower in *Tapecomys* than in *Andinomys, Andalgalomys,* and *Graomys.* In comparison, these fossae are even deeper in the *Reithrodon* group.

The anterior margin of zygomatic plate is concave; this concavity is less extreme in

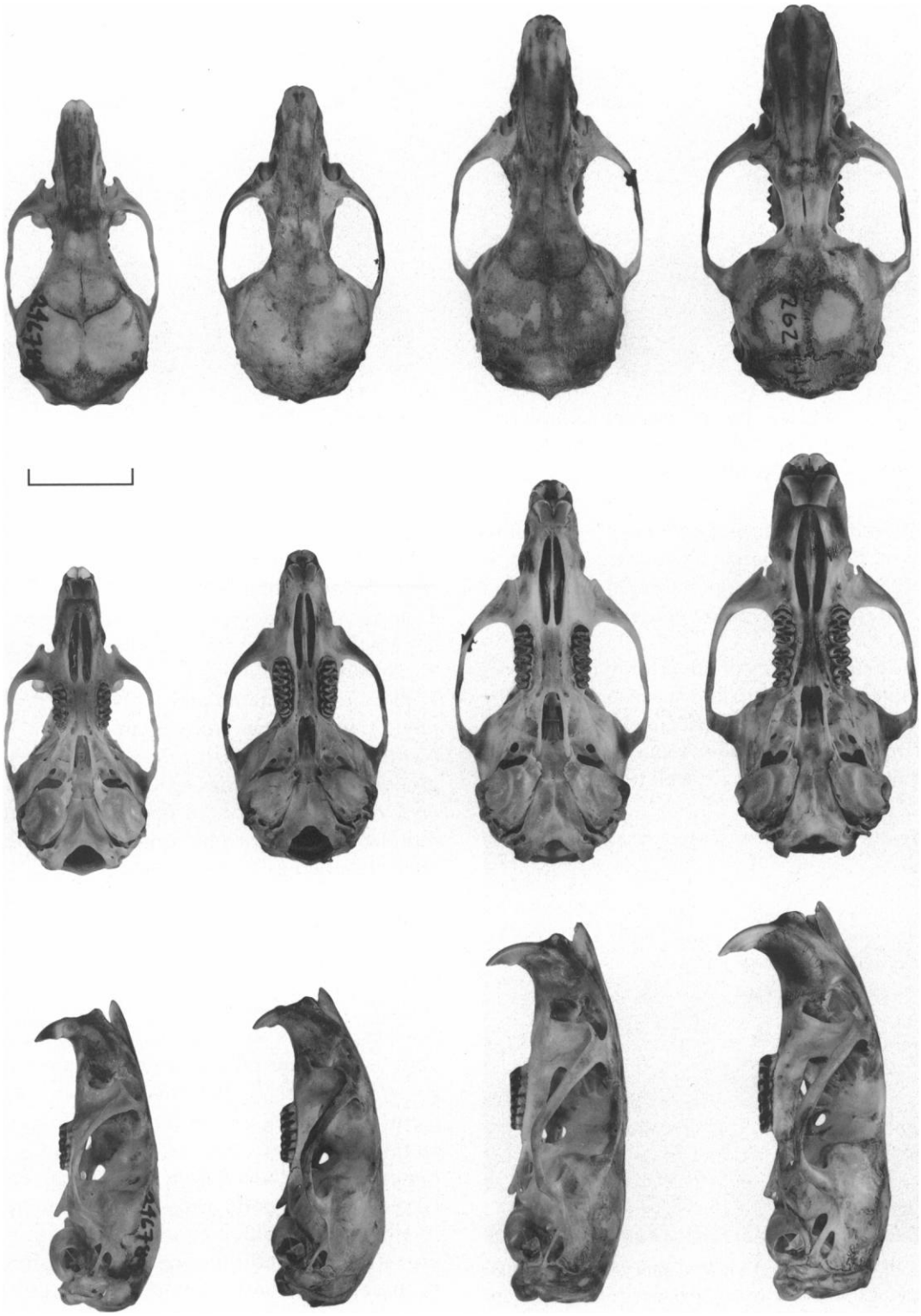

FIG. 6.—Skulls in dorsal, ventral, and lateral views; left to right, AMNH 246789, *Graomys griseoflavus*; AMNH 264448, *Tapecomys primus*; holotype of *T. primus*; AMNH 262771, *Andinomys edax*. Scale represents 10 mm.

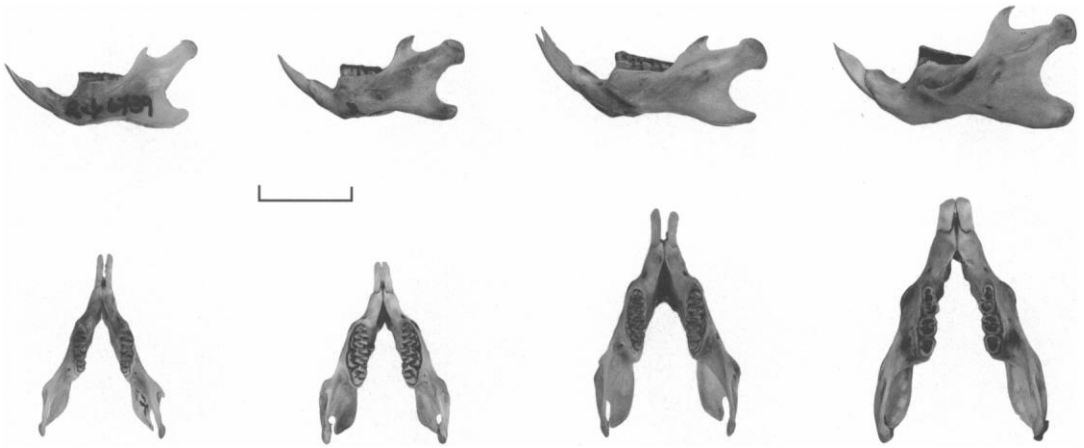

FIG. 7.—Lower jaw and teeth in occlusal and lateral views, left to right; AMNH 246789, *Graomys griseoflavus*; AMNH 264448, *Tapecomys primus*; holotype of *T. primus*; AMNH 262771, *Andinomys edax*. Scale represents 10 mm.

Tapecomys than in *Andinomys, Andalgalomys,* and *Graomys*. Zygomatic process is not an overhanging point in *Tapecomys,* but is in *Andinomys, Andalgalomys, Salinomys,* and *Graomys*.

Posterior nares (= anterior margin of mesopterygoid fossa) are more or less at the level of the back of M3 in *Andinomys* and *Tapecomys*. In *Graomys* and *Andalgalomys,* the posterior nares are well posterior of M3.

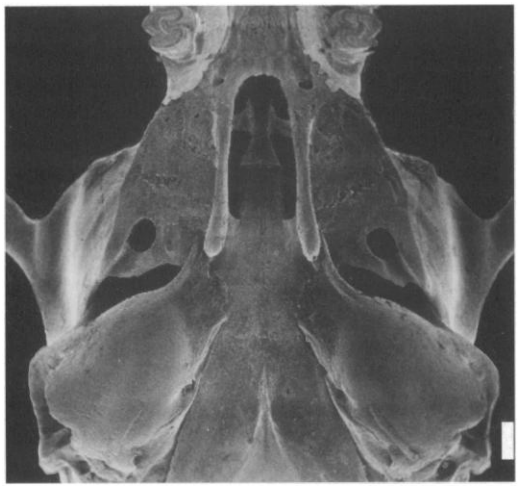

FIG. 8.—Ventral view of pterygoid and bullar regions of skull (scanning electron microscope photo) of holotype of *Tapecomys primus*. Scale at lower right is 1 mm.

Bullae are about the same size in larger skulls of *Andinomys* and in *Tapecomys* (Fig. 8), so bullae are relatively larger in *Tapecomys*. *Graomys* and *Andalgalomys* have bullae that are relatively larger than in *Tapecomys* or *Salinomys*.

Incisors are smooth anteriorly, as in most phyllotines; strong grooves are present in *Neotomys* and *Reithrodon,* and weak grooves occur in some species of *Auliscomys*. Anterior surfaces of upper incisors are rounded as in most phyllotines, not somewhat flattened as in *Andinomys*.

Upper molar rows are more or less parallel in *Tapecomys,* and are divergent posteriorly in *Andinomys*. The M1 has 5 roots of various sizes in the holotype of *T. primus* (Fig. 9), and is 3-rooted in *Andinomys*. The m1 has 2 roots in *Andinomys*; 6 roots of various sizes are present in the holotype of *T. primus* (Fig. 9). We have not extracted teeth to examine molar roots in *Graomys* and *Andalgalomys*. Molars are large in *Andinomys* and *Chinchillula,* somewhat enlarged in *Tapecomys* (Fig. 9), and smaller in other genera, although there is a range of crown heights and other dental dimensions in these. Enlargement could have occurred independently in more than 1 phyllotine lineage. Molars are highly hypsodont in *An-*

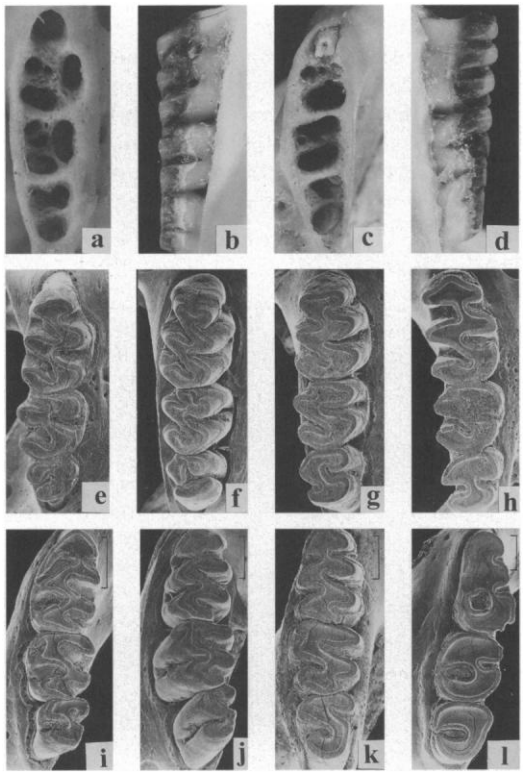

FIG. 9.—Holotype of *Tapecomys primus,* from left to right; a) right upper molariform alveoli, b) left upper molariform tooth row in labial view, c) left lower molariform alveoli, d) right lower molariform tooth row in lingual view; note hypsodonty and numbers of roots, and upper and lower molar tooth rows. Scanning electron microscope photos; e) and i) AMNH 246789, *Graomys griseoflavus*; f) and j) AMNH 264448, *Tapecomys primus*; g) and k) holotype of *T. primus*; and h) and l) AMNH 262771, *Andinomys edax.* Scales (different for each specimen) represent 1 mm.

dinomys and *Chinchillula,* slightly less so in *Tapecomys,* only slightly hypsodont in *Graomys* and *Phyllotis,* and quite brachydont in *Andalgalomys, Eligmodontia,* and *Calomys.*

The enamel pattern has an almost microtine appearance in the young specimen (this refers to the presence of closed triangular columns). The occlusal pattern of teeth is more complicated than is apparent after the wear of adult life; the lateral angles are much more acute when less worn and become comparatively blunt in old age. Angularity is more extreme in *Andinomys* than in *Tapecomys.* The spaces (i.e., reentrant angles on either side of the tooth) more or less alternate in *Andinomys, Tapecomys,* and most other phyllotines (in contrast to the tendency in *Chinchillula* for inside and outside angles to be opposite). The occlusal surface of molars is flat from earliest stages of wear in both *Tapecomys* and *Andinomys.*

Other comparative data for *Andalgalomys, Graomys, Eligmodontia,* and *Calomys* can be found in Olds et al. (1987) and for phyllotines in general in Olds and Anderson (1989), Braun (1993), and Steppan (1993). *Tapecomys* (as species nova) was scored for as many of the 96 characters as possible in Steppan's (1993) table 1. A comparison of those scorings and the list of characters in Steppan's (1993) appendix II will provide additional characters of *Tapecomys.* As noted in the Discussion, most of the characters in the matrices of Steppan (1993) and Braun and Mares (1995) are different.

As a 1st approximation and to simplify comparisons of various proportions, a ratio diagram (Fig. 3, of 4 representative individuals) was prepared; some differences deserve comment. Comparative data for most of these measurements (in a series of 11 *Graomys domorum* and 12 *Graomys griseoflavus*) are available in Olds et al. (1987: table 2). Data also are given there for 2 species of *Andalgalomys.* Means, standard deviations, minima, and maxima are included for those who wish to test the significance of differences more explicitly. In Table 1, we have cited the minimum and maximum values for the 2 species of *Graomys* together. We also include, for *Andinomys edax,* minimum and maximum values for external measurements of a series of 6 adults (3 males, 3 females) from near Camataqui, Bolivia, and cranial measurements of a series of 1 male and 3 females from Sama, Bolivia. Notice that the individual selected for the ratio diagram is a male that is larger than those included in the series that pro-

TABLE 1.—Measurement of 4 specimens of 3 of phyllotines (in mm, except weight graphed in Fig. 2). Under each entry for *Andinomys* and *Graomys,* we included the minimum–maximum range of the given measurement in a sample of 6 adult *Adinomys* and 23 adults of both species of *Graomys* (*G. domorum* and *G. griseoflavus,* see text). Additionally, we have placed an asterisk (*) after each measurement of the adult *Tapecomys* in our table that falls outside of the minimum–maximum range for both species of *Graomys* together. The single specimen (AMNH 246789) is of *G. griseoflavus.*[a]

	Tapecomys primus		*Andinomys edax*	*Graomys*
	CBF	AMNH	AMNH	AMNH
Dimension	2414	264448	262771	246789
Length of head and body	139	124	165	129
			134–149	111–159
Length of tail		143	160	152
			125–132	83–175
Length of hind foot	34*	33	34	29
			28–29	25–32
Length of ear	25	25	28	22
			24–25	20–28
Length of forefoot	13.0	13.1	15.5	10.3
Weight (g)	94	49	130	70
			66–80	
Length of molar row	6.7*	6.6	8.3	5.4
			6.8–7.3	4.69–5.88
Length of palate	6.6*	5.3	7.6	5.4
				5.07–6.50
Length of zygomatic aperture	11.0*	9.5	11.2	9.4
				8.61–10.40
Length of incisive foramina	8.4*	7.5	9.7	7.0
				6.26–8.17
Condyloincisive length	35.1*	29.1	38.0	29.2
				25.80–33.00
Occipitonasal length	37.7*	32.7	40.0	31.6
			32.1–35.6	28.80–35.90
Mesopterygoid width	2.1*	1.9	2.3	1.6
				1.27–1.89
Palatal width	3.4	2.4	3.0	2.8
				4.99–7.00
Postdental width	5.8*	5.5	6.0	4.4
			5.5–6.0	4.83–5.27
Rostral width	6.9	6.0	8.3	5.6
				5.01–7.03
Width of M1	1.9*	1.9	2.2	1.3
			1.9–2.0	1.44–1.86
Posterior zygomatic width	18.8*	16.9	20.9	15.7
			18.1–18.9	
Anterior zygomatic width	18.0*	13.0	16.3	12.1
				13.31–16.40
Rostral length	11.6	9.8	13.8	10.4
			11.0–12.2	8.67–11.90
Interorbital width	5.3	4.7	4.2	4.7
			3.8–4.2	4.41–5.79
Midfrontal width	6.5	6.4	4.4	8.0
Width of braincase	14.7	14.0	14.9	13.1
			13.1–14.5	12.0–14.74
Depth of bulla	4.7	4.3	4.2	4.4
				3.13–4.95
Length of bulla	5.8	5.1	6.0	5.4
				5.33–6.93

TABLE 1.—Continued.

Dimension	*Tapecomys primus* CBF 2414	*Tapecomys primus* AMNH 264448	*Andinomys edax* AMNH 262771	*Graomys* AMNH 246789
Depth of skull	11.2	11.3	12.5	10.7 11.10–13.30
Width of zygomatic plate	4.6*	3.9	3.6	3.2 2.90–4.02
Exoccipital width	10.2	9.1	11.1	9.5

[a] AMNH, American Museum of Natural History; CBF, Colacción Boliviana de Fauna.

vided the minimum and maximum values that are cited. The dimension labeled as palatilar length in Olds et al. (1987:PRL in table 2) was actually length of palate.

In external dimensions, *Tapecomys* has (relative to length of head and body) a tail that is shorter than in the reference specimen of *Graomys* and longer than that of *Andinomys*; however, both length of head and body and length of tail are sufficiently variable that differences in proportions are of uncertain significance. The hind foot and ear are longer than in *Graomys* or *Andinomys*. The most significant of these differences is that of the hind foot when *Tapecomys* and *Graomys* are compared. The forefoot and hind foot of the younger *Tapecomys* are relatively larger than in the older individual (as generally is true of rodents, and many other mammals), and the feet are relatively larger in both individuals of *Tapecomys* than in *Graomys*. Although this 1 measurement of the forefoot of the adult *Tapecomys* does not differ relative to length of head and body when compared with *Andinomys,* direct comparison reveals that feet are larger in *Andinomys* from Tarija that were compared. Other *Andinomys* from the Department of La Paz do not seem to have feet that are as large, so geographic variation may exist in the size of feet. Weight tends to vary as the cube of a linear measurement of size, such as length of head and body, so the wide spread seen in weights is expected. The weight of the younger *Tapecomys* would be completely off the diagram to the left.

In cranial and dental dimensions, the younger *Tapecomys* has (relative to occipitonasal length) a larger dentition as reflected in length of molar row and width of M1; palatal width is relatively less and the skull is relatively deep. These all reflect common ontogenetic changes. The most conspicuous differences of *Tapecomys* (based primarily on the adult) when compared with *Graomys* and *Andinomys* are smaller dentition than *Andinomys,* as reflected in length of molar row and lesser palatal width, lesser rostral width and length in *Tapecomys* than in *Andinomys,* greater interorbital width and midfrontal width, and greater width of zygomatic plate in *Tapecomys* and *Graomys* than in *Andinomys.*

The karyotype of *T. primus,* based on a single male (the holotype, NK 23413, CBF 2414), consists of 11 pairs of metacentric–submetacentric and 16 pairs of acrocentric autosomes, a large submetacentric X, and a small submetacentric Y (Fig. 10a). The diploid number (2n = 56) is the same as in *Andinomys edax,* but the number of autosomal arms differs (FN = 76 in *T. primus*; in contrast to 56–58 in *A. edax*).

Structurally, the karyotype of *T. primus* most closely resembles that of *Phyllotis wolffsohni* (Fig. 10b; Pearson and Patton 1976) and *P. definitus* (Pearson 1972). The karyotype differs from these 2 species of *Phyllotis* by the presence of an additional pair of submetacentric autosomes. The sex chromosomes also seem structurally similar. The Y chromosome is small and submetacentric in *P. wolffsohni* and *T. primus* and,

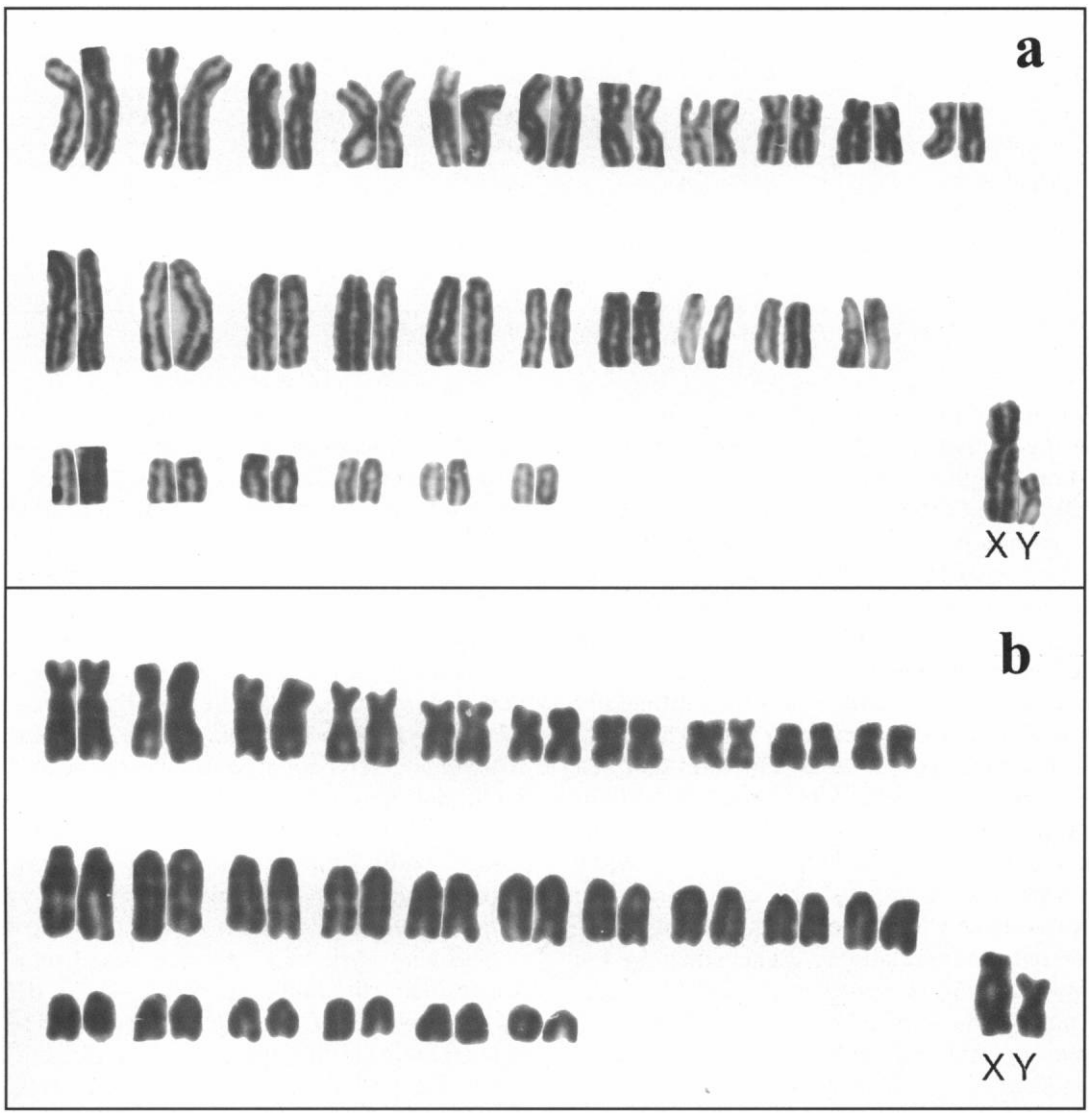

FIG. 10.—Karyotypes of a) the holotype of *Tapecomys primus* and b) a specimen of *Phyllotis wolffsohni* from Tarija, Bolivia (AMNH 268881). Chromosomal preparations were obtained directly from bone marrow in the field.

thus, differs from the acrocentric condition reported for *P. definitus,* although the morphology of the latter element was reported to be equivocal (Pearson 1972). The X chromosome in all 3 taxa is large and biarmed, although the figure by Pearson and Patton (1976) suggests that the condition in *P. wolffsohni* differs from the submetacentric condition found in the other 2 taxa by the presence of a metacentric X chromosome. Variation in the structure of sex chromosomes has been reported among other species of *Phyllotis* (Pearson and Patton 1976; Walker et al. 1979) and in the genus *Akodon* (Bianchi et al. 1976).

Published karyotypes for *Graomys domorum* and *G. griseoflavus* (Pearson and Patton 1976) differ significantly from that of *Tapecomys* with 2n = 28 and 36–38 in the former 2 taxa, respectively. Other spe-

cies of *Phyllotis* and *Auliscomys* also differ from *Tapecomys* in having lower diploid numbers.

We consider the general similarity between the karyotypes of *T. primus, P. wolffsohni,* and *P. definitus* to indicate convergence instead of recency of common ancestry because of striking differences in details of morphology. Based on the hypothesized ancestral phyllotine karyotype of 68 acrocentric autosomes proposed by Pearson and Patton (1976), both Robertsonian and non-Robertsonian numerical changes seem to have occurred in evolution of the *Tapecomys* cytotype. The minimum autosomal changes required to convert this hypothetical condition to that found in *Tapecomys* are 6 fusions to reduce the number of autosomes from 68 to 56 and 4 pericentric inversions to account for the additional 4 pairs of biarmed chromosomes present in the karyotype of *Tapecomys.* Further assessment of degree of homology among chromosomes of these taxa, and verification that these changes involve euchromatin, must await evaluation of banded karyotypes.

Therefore, we can add 3 chromosomal characters for *Tapecomys* to those summarized above. The 2n is 56 in *Tapecomys* and *Andinomys* but FNs are 76 and 56–58, respectively. The X chromosome is large and submetacentric in *T. primus,* large and telocentric in *A. edax,* large and metacentric in *P. wolffsohni,* submetacentric in *G. griseoflavus* (Pearson and Patton 1976), and large and acrocentric in *G. domorum* (Pearson and Patton 1976) and *A. pearsoni* (Olds et al. 1987). The Y chromosome is small and submetacentric in *T. primus* and *P. wolffsohni* and telocentric in *A. edax* (Spotorno et al. 1994), small and acrocentric in both species of *Graomys* (Pearson and Patton 1976), and a medium-sized acrocentric in *A. pearsoni* (Olds et al. 1987).

Etymology.—The generic name *Tapecomys* arbitrarily uses the first 5 letters of the name of the type locality, Tapecua, and an ending based on the Latin word for mouse, *Mus,* and is of masculine gender. The specific epithet, *primus,* is the Latin adjective for 1st.

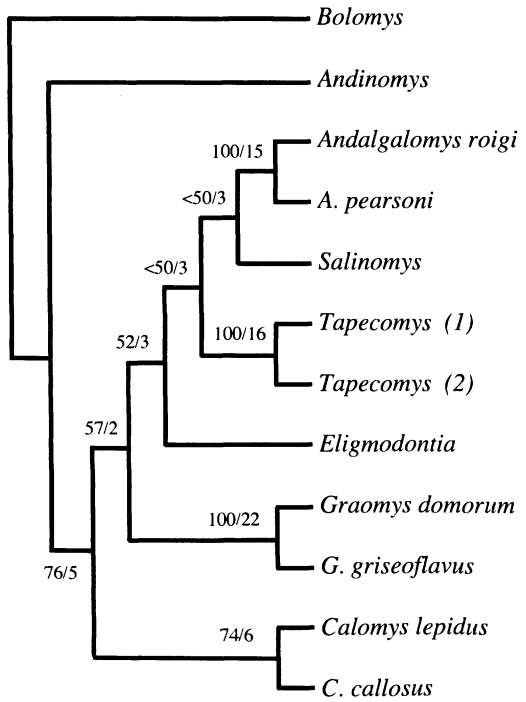

FIG. 11.—Phylogenetic relationships among selected genera of phyllotines based on parsimony analysis of nucleotide substitutions (length of tree = 506 steps; consistency index = 0.514; retention index = 0.427) among cytochrome-*b* sequences. Numbers to the left of the backslash are bootstrap values, whereas those on the right represent decay indices.

Phylogenetic analyses.—Transitions and transversions were plotted against the Jukes–Cantor (Jukes and Cantor 1969) distance. Neither transitions nor transversions revealed any apparent saturation effect relative to distances compared. However, more transition changes than transversion changes were present, especially at lower levels of divergence.

Parsimony analyses of the cytochrome-*b* gene-sequence data produced a single most-parsimonious tree (Fig. 11). The phyllotine genera *Calomys, Graomys, Eligmodontia, Salinomys,* and *Andalgalomys* formed a monophyletic assemblage that was strongly

supported by bootstrap analysis. Both specimens of *Tapecomys* formed a single monophyletic clade within this larger unit. Phylogenetically, *A. pearsoni* and *A. roigi* form a strongly supported clade to which *Salinomys* is the sister group. *Tapecomys* joins the tree, next followed by *Eligmodontia, Graomys,* and *Calomys,* in that order.

Discussion

In a cladistic analysis of morphologic characters of phyllotines, a *Graomys* group (node 10, containing *Graomys, Andalgalomys,* and the new species named here) was identified (Steppan 1993). This was based on his 75% majority-rule consensus tree of the 88 equally most-parsimonious trees, which placed *Punomys* outside the phyllotines. Node 10 was supported by the loss of an anterior shift of the mesoflexid of m3 (Steppan's character 29), orbital wings of the presphenoid that are posterior to the maximum constriction of the presphenoid (character 66), a small but distinct zygomatic spine (character 43), a sharply ridged, overhanging supraorbital region (character 48), and parallel maxillary toothrows (character 72). The new species also was placed as the sister group of *Andalgalomys,* principally because of the fusion of opposing flexi in M3 (character 31); however, *G. griseoflavus* also has this character state. We searched in the table (Steppan 1993:table 1) for possible synapomorphies. Only 2 of 96 characters showed a character state present in *Tapecomys* and *Andalgalomys* and not in *Graomys,* namely 15–0 and 54–0. These relate to the protoflexid of m1 and the anterior border of the auditory bulla. This support for a monophyletic clade including these 3 genera seems weak, but no alternative relationship is more strongly supported. A clade including *Graomys* and *Andalgalomys* has some support from other studies (Braun 1993; Olds et al. 1987). Our cytochrome-*b* data provide relatively strong support for such a monophyletic clade (which also includes *Calomys, Eligmodontia, Salinomys,* and *Andalgalomys*) and supports a close phylogenetic association between *Andalgalomys* and *Tapecomys.* These data place the new genus as a sister group to the *Salinomys–Andalgalomys* clade, although the exact placement of *Salinomys* relative to *Andalgalomys* is uncertain given the weak bootstrap support these nodes have in our tree.

In regard to the possible relationship of *Andalgalomys* with *Tapecomys,* we note that the diploid numbers for these 2 genera are different. In *Andalgalomys olrogi, A. p. pearsoni,* and *A. p. dorbignyi,* 2n = 60, 78, and 76, respectively (Olds et al. 1987). Although not phylogenetically informative, these data suggest a fair amount of divergence between these genera. The same can be said for chromosomal differences between *Tapecomys* and *Graomys.* This group of rodents is characterized by large amounts of chromosomal variability even among phylogenetically close relatives. For example, several authors (Braun 1993; Olds et al. 1987; Steppan 1993) have suggested that *Graomys* and *Andalgalomys* are sister taxa. *A. pearsoni* and *G. griseoflavus* were regarded as sister taxa by Steppan (1995), then *G. domorum* as their sister group. On this basis, *Andalgalomys* was considered to be a synonym of *Graomys.* However, based on diploid numbers, *Graomys* and *Andalgalomys* are among the most divergent in the tribe Phyllotini. Our analyses of DNA are not consistent with placing *Andalgalomys* in synonomy with *Graomys,* and although these genera do seem to be closely related, they are not sister taxa. The monophyletic relationship of *A. pearsoni* and *A. roigi* is supported strongly by both bootstrap and decay analyses, as is the monophyletic relationship of the 2 species of *Graomys* examined by us.

Given these considerations and morphologic comparisons discussed above, *Tapecomys* seems likely to be closely related to *Graomys* and *Andalgalomys* and may represent the sister group to *Andalgalomys* or to a clade containing it and *Salinomys.* Recently, *Salinomys* was described and con-

sidered to be a sister group of the *Graomys–Andalgalomys* clade by Braun and Mares (1995). As noted above, our data are not consistent with this hypothesis, but these authors did not include *Tapecomys* in their study.

Several studies (Braun and Mares 1995; Steppan 1993) have suggested that *Graomys, Andalgalomys,* and *Eligmodontia* form a closely related group. Steppan (1993) also included *Tapecomys* (as species nova) and the most recent study has added the new genus *Salinomys* to the group. No analysis previously has included all of these genera. We compared characters used by Steppan (1993, 1995) and Braun and Mares (1995). Only 2 of the 25 characters used by Braun and Mares (1995) could be matched with characters in the set of 96 used by Steppan (1993), so it is encouraging that the different cladograms are similar. To provide further resolution to relationships in this group and to include all of these genera, we began with the character matrix of Braun and Mares (1995), added *Tapecomys* and *G. domorum,* and reanalyzed cladistic relationships based on these morphologic characters. A single most-parsimonious tree placed *Tapecomys* as the sister group of *Graomys* and placed *Andalgalomys* as a sister group to these 2 genera. *Eligmodontia* and *Salinomys* formed a clade at some distance from this group and species of *Calomys* did not form a monophyletic group. Boot-strap values for all branches in this tree were low (52–58).

Steppan (1993) suggested that these 3 genera should be subsumed under *Graomys,* the oldest name, or that *Tapecomys* should be treated as a more derived member of current *Andalgalomys.* These possible relationships were not sufficiently supported to justify taxonomic changes (Steppan 1993). In fact, our data do not support either idea. However, analysis of all of our data suggests that *Tapecomys* is a distinct taxon that is clearly related to these other genera.

The level at which the genus *Phyllotis* is related to the clade containing *Tapecomys* is less clear. *Phyllotis* was placed in a clade with *Chinchillula, Andinomys,* and *Irenomys,* and not closely related with the clade including other species of *Phyllotis* (Steppan 1995). This supports the interpretation that *Phyllotis,* as often recognized, is not strictly monophyletic, as suggested earlier by Braun (1993), who recognized the genus *Paralomys* for *P. haggardi* and *P. gerbillus* (see the discussion of relationships within *Phyllotis* by Steppan [1998]). Steppan (1995) did not include the new phyllotine from Tapecua in his analysis. In view of these unresolved questions, new karyologic data, the possibility of paraphyly within *Phyllotis* as now constituted, and especially the uncertain status of *P. wolffsohni,* further analyses within Steppan's post-*Calomys* (node 4) phyllotines are needed. Phylogenetic problems of this sort clearly do not lend themselves to easy solution (consider that Steppan's 1995 analysis involved 96 characters of 33 species representing all 14 genera of Phyllotini); consideration of multiple data sets often can prove useful in these complex groups.

The new genus probably is not confined to the type locality. The habitat around Tapecua is an interesting mixture of cloud forest vegetation and xerically adapted elements more characteristic of the Chaco at lower elevations to the east. This creates a mosaic of patches of columnar cacti and leguminous trees in open areas and broadleaf canopy trees and thick brush on hillsides and in ravines. The area is typical of the eastern foothills of the Andes Mountains in southern Bolivia and northern Argentina, with deep narrow canyons separating numerous low peaks. This type of habitat extends for many kilometers to the south and north, and *Tapecomys* likely occurs throughout this habitat. However, with the exception of the area in and around the type locality, the region is largely inaccessible by road. The specific place where the holotype was trapped was in a steep ravine a short distance below camp. The hillside was

strewn with moss-covered boulders and fallen logs. The trees formed a canopy of ca. 40% coverage and a number of large bushes grew in clumps under the trees. Judging by the large hind feet and long tail present in *Tapecomys* and the habitat of the type locality, it is possible that this species is at least somewhat arboreal.

Attempts by T. L. Yates and others to collect additional specimens in May 1993 at the type locality were unsuccessful. Whether this is indicative of a general rarity of this species, a low population level at that time, or our poor understanding of the habitat and habits of this species is unclear at present. Further exploration of this interesting region will help address this issue. We suspect that other taxa new to science remain to be discovered there.

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APPENDIX I

Specimens examined.—Acronyms for institutions are as follows: American Museum of Natural History (AMNH); British Museum (BM); Colección Boliviana de Fauna (CBF); Universidad Nacional de Tucumán, Colección de Mamiferos Lillo (Argentina; CML); University of New Mexico, Museum of Southwestern Biology (MSB); University of California, Berkeley, Museum of Vertebrate Zoology (MVZ); New Mexico kryovoucher number (NK); University of Oklahoma, Oklahoma Museum of Natural History (OMNH). Specimens, other than *Tapecomys,* are from the department of Tarija, Bolivia, unless noted otherwise. *Graomys domorum*: AMNH 268940, 11.5 km N, 5.5 km E Padcaya, 1,900 m, 21°47′S, 64°40′W. *Graomys griseoflavus*: AMNH 246789, 8 km S, 10 km E Villa Montes, 467 m, 21°19′S, 63°25′W. *Andinomys edax*: AMNH 262771, Rancho Tambo, 61 km by road E Tarija, 2,100 m, 21°27′S, 64°14′W; AMNH 268939, 4.5 km E Iscayachi, 3,750 m, 21°29′S, 64°55′W; MVZ 120227–120232, 25 km SSE of Camataqui, 3,760 m, 21°10′S, 65°03′W; BM 26.1.1.6, 26.1.1.10, 26.1.1.11, 26.1.1.14, Sama, 4,000 m, 21°29′S, 65°02′W. *Phyllotis wolffsohni*: AMNH 268881, 1 km E Tucumilla, 2,500 m, 21°27′S, 64°49′W.

Specimens used in the DNA sequence analyses (Fig. 11).—Specimens are from the Department of Tarija, Bolivia, unless noted otherwise. *Tapecomys primus*: CBF 2414, and AMNH 264448, Tapecua, 1,500 m, 21°26′S, 63°55′W. *Graomys domorum*: MSB 55291, Bolivia: Santa Cruz, 5 km SE (by road) of Comarapa, 1,695 m, 17°58′S, 64°29′W. *Graomys griseoflavus*: NK 23331, Bolivia: Santa Cruz: 26 km E Boyuibe, 800 m, 20°26′S, 63°02′W. *Bolomys amoenus*: MSB 67194, Serrania del Sama, 3,200 m, 21°27′S, 64°52′W. *Andinomys edax*: MSB 67192, 4.3 km E Iscayachi, 3,750 m, 21°29′S, 64°55′W. *Calomys lepidus*: MSB 57107, 1 km E

Iscayachi, Rio Tomayapo, 3,450 m, 21°29′S, 64°57′W. *Calomys callosus*: MSB 55985, Bolivia: Santa Cruz; 10 km N San Ramon, 250 m, 16°36′S, 62°42′W. *Eligmodontia puerulus*: MSB 70538, Bolivia: La Paz; 8.5 km W San Andrés de Machaca, 3,850 m, 16°59′4″S, 69°01′53″W. *Andalgalomys pearsoni*: MSB 55245, Bolivia: Santa Cruz; 29.5 km W Roboré, 475 m, 18°19′S, 60°2′W. *Andalgalomys roigi*: CML 3693, Argentina: Catamarca; Capayan, Chumbicha, 0.5 km E of Highway 38 along Highway 60, 1,500 feet. *Salinomys delicatus*: OMNH 23602, Argentina: San Luis; Capital, 15 km E Salinas del Bebedero, 1,350 feet.