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Author(s): Scott J. Steppan and Ulyses F. J. Pardiñas
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TWO NEW FOSSIL MUROIDS (SIGMODONTINAE: PHYLLOTINI) FROM THE EARLY PLEISTOCENE OF ARGENTINA: PHYLOGENY AND PALEOECOLOGY

SCOTT J. STEPPAN[1] and ULYSES F. J. PARDIÑAS[2]
[1]Division of Mammals and Laboratory of Molecular Systematics, MRC 534, Smithsonian Institution, Washington DC 20560;
[2]Departmento Científico Paleontología Vertebrados, Museo de La Plata, Paso del Bosque s/n, 1900 La Plata, Argentina.

ABSTRACT—Two new species and genera of extinct muroid rodents are described from fossil material dating to the early Pleistocene of Argentina (Sanandresian Substage/Subage). They are both tetralophodont forms belonging to the tribe Phyllotini (Sigmodontinae) and are assigned to *Ichthyurodon ameghinoi,* gen. et sp. nov., and *Olympicomys vossi,* gen. et sp. nov. Phylogenetic analyses involving extant phyllotines, the two new species, and two other newly discovered extinct phyllotines result in a refined and expanded concept of the clade consisting of *Loxodontomys* and the *Reithrodon* generic group. The generic diversity of this clade is thus doubled from four to eight. Several of the fossil genera appear to represent transitional forms, although *Ichthyurodon,* gen. nov., possesses dental traits unique among the members of the subfamily Sigmodontinae. The significance of the new species and their faunal context for our understanding of the paleoecology of the southern cone of South America is discussed.

RESUMEN—Se describen dos nuevos géneros y especies de roedores muroideos extinguidos sobre la base de material fósil del Pleistoceno temprano (Subpiso/Subedad Sanandresense) de Argentina. Ambos son formas tetralofodontes pertenecientes a la tribu Phyllotini (Sigmodontinae), siendo asignados a *Ichthyurodon ameghinoi,* gen. et sp. nov. y *Olympicomys vossi,* gen. et sp. nov. Los análisis filogenéticos que incluyen filotinos vivientes, las dos nuevas especies aquí descriptas y otros dos filotinos extintos nuevatente descubiertos, dan por resultado una redefinición y expansión del clado conformado por *Loxodontomys* y del grupo *Reithrodon.* De esta manera, la diversidad de este clado se amplía de cuatro a ocho géneros. Algunos de los géneros extintos parecen representar formas transicionales, aunque *Ichthyurodon,* gen. nov. posee rasgos dentarios únicos entre los Sigmodontinae. Además, se discute la significación de las dos nuevas especies y la fauna asociada en nuestra comprensión de la paleoecología del cono sur sudamericano.

INTRODUCTION

The history of our understanding of the fossil murids from South America can be divided into three major periods. The first encompassed the pioneering works of Burmeister (1879) and Ameghino (1889), in which numerous fossil species were described and the records for the living forms presented. The second, from 1900 until the 1970s, was characterized by a marked silence with minimal contributions; this period includes the description of only two new species and some nomenclatural changes (Rusconi, 1931; Hershkovitz, 1955, 1962, 1966a). The third and last period is characterized by a rejuvenated interest in these rodents, focused on four fundamental aspects: 1) scenarios that discussed centers of differentiation and episodes of dispersal; 2) new descriptions of genera and species; 3) taxonomic reviews of older collections; and 4) the paleoecological significance of the recognized communities (Reig, 1972, 1975, 1978, 1980, 1981a, b, 1984, 1986, 1987; Baskin, 1978, 1986; Tonni and Fidalgo, 1978, Marshall, 1979, Jacobs and Lindsay, 1984; Tonni et al., 1988; Voss and Myers, 1991; Braun, 1993; Fejfar et al., 1993, Pardiñas, 1993, 1995a, b; Steppan, 1993, 1995, 1996a; Voss, 1993; Voss and Carleton, 1993; Pardiñas and Lezcano, 1995). Despite the increasing interest in recent years, our limited knowledge of the paleodiversity of this group contrasts strongly with its current diversity, approached by only the Microchiroptera in the Neotropics.

In this context, Phyllotini is one of the tribes that merits a greater investigation of its paleontological record. What we know of this group principally derives from the Cenozoic deposits of the Argentine pampas and is restricted to two extinct species, *Graomys dorae* Reig, 1978 and *Auliscomys formosus* Reig, 1978 (both from the late Pliocene), and to some of the more common members of the current fauna (e.g., *Calomys, Reithrodon auritus*).

During the last five years, detailed excavations have been carried out with emphasis on recovering microvertebrate remains (Pardiñas, 1995a). Many of the excavated localities correspond to the classic deposits along the Atlantic coast of Buenos Aires Province. The province is famous in the South American paleomammalogical literature for its wealth of fossils. The abundant remains of muroids, particularly phyllotines, permit us to draw a more complex view concerning the diversity of this tribe.

In this paper, we describe two new genera and species of extinct phyllotines dating to the early Pleistocene of the Necochea region (in the southeast of Buenos Aires province; Fig. 1). We have included them in a phylogenetic analysis and revised the phylogenetic hypothesis for the *Reithrodon* group from the most recent cladistic treatments (Braun, 1993, Steppan, 1993, 1995) or taxonomic diagnosis (Olds and Anderson, 1989). Also, we discuss the significance of the new taxa for the evolution of the environment in the middle latitudes of Argentina.

MATERIALS AND METHODS

The comparisons and discussion are based on specimens of living (Appendix 1) and fossil phyllotines (Museo de La Plata—**MLP**). The dental nomenclature corresponds to Reig (1977). Measurements were taken with an ocular micrometer attached to a binocular Wild M-5 microscope (only maximum dimensions are indicated). The illustrations were made using the same instrument.

The collecting localities of "Balneario Neptuno," Las Grutas, and Punta Negra correspond to cliffs to the south-southeast of the city of Necochea (38°34′S 58°45′W; county of Necochea, Buenos Aires Province; see Fig. 1). In all cases, the material was collected in the B level, referred to Sanandresian Substage/Subage of the Marplatan Stage, early Pleistocene (see Tonni and Cione, [1995] and Cione and Tonni [1995] for more details).

Abbreviations used in the text and in the tables: **M1**, **M2**,

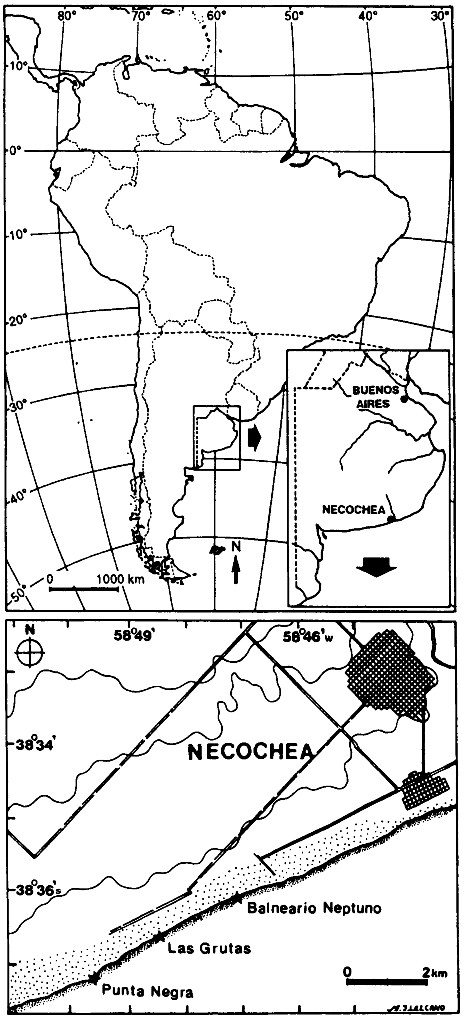

FIGURE 1. Geographic locations of the collecting localities.

M3, m1, m2, m3: notations for the upper and lower molars. **L**: length. **W**: width.

Phylogenetic Analysis

Specimens of the new species described here, in addition to representative living phyllotines, were scored for 40 of the morphological characters utilized in Steppan (1995), maintaining the same numbering scheme for ease of comparison (characters 1–98 are discussed in more detail in that publication). The recently described *Panchomys steppani* (Pardiñas, in press) from the late Pliocene of southeastern Bueno Aires Province, Argentina, and the currently undescribed genus "T" (Ortiz, et al., unpubl. data) from the late Pleistocene of Tafí del Valle, Argentina, were also included because of their possible relatedness to the species described in this paper. Characters 99–103 were added to the data matrix to incorporate the additional variation present in the fossil material. The data matrix in Table 1 highlights only those characters identifiable in one or more of the fossil taxa, and their character state definitions are given in Appendix II. Examined specimens are listed in Appendix I.

Sixteen extant species along with the four extinct species were included in the phylogenetic analysis. The broad diversity of phyllotines was included to test alternative placements of the fossil taxa and more accurately estimate character evolution in those taxa. Taxon sampling focused on those genera that shared some characters in common with any of the extinct species: all members of the *Reithrodon* group, *Loxodontomys, Graomys, Auliscomys,* and *Phyllotis. Calomys callosus* and *C. laucha* were designated as outgroups in accordance with the findings of Steppan (1993, 1995) and conventional opinion (e.g., Hershkovitz, 1962). The data were subjected to Wagner parsimony analysis using PAUP 3.1.1 (Swofford, 1993) with the following conditions: heuristic search with 20 random addition replicates, tree bisection-reconnection branch swapping. A 200-replicate bootstrap analysis was conducted as a non-parametric estimate of confidence in each node.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowditch, 1821
Superfamily MUROIDEA Miller and Gidley, 1918
Family MURIDAE Illiger, 1815
Subfamily SIGMODONTINAE Wagner, 1843
Tribe PHYLLOTINI Vorontsov, 1959

ICHTHYURODON, gen. nov.
(Fig. 2)

Type Species—*Ichthyurodon ameghinoi,* new species.

Type Locality—"Balneario Neptuno," 3 km southwest of Necochea, Necochea District, Buenos Aires Province, Argentina.

Geographic Distribution and Chronology—Region of Necochea (southeastern Buenos Aires province, Argentina); Sanandresian Substage/Subage, Marplatan Stage (early Pleistocene).

Diagnosis—Medium-sized mouse of the tribe Phyllotini distinguished from other phyllotines by large posteriorly directed paralophule on M3, paralophule subequal in size to paracone, posteroflexus a shallow notch, posteroloph small and indistinct, probably lost with wear, mure long and distinct, M3 not greatly simplified relative to M2, with protoflexus absent, deep anteroflexus; M2 with small paraloph directed posterolabially, distinct and narrow procingulum extending almost to paracone; M1 procingulum short, anteromedian flexus absent, cusps opposite, not alternate; enamel of opposing lophs overlap near the midline, do not connect; molars weakly hypsodont.

Etymology—*Ιχθυσ* (ichthys), fish; *ουρα* (ura), tail; *δοντοσ* (dontos), tooth (molar), referring to the distinctive conformation of the paracone and paralophule on M3.

Description—The procingulum of M1 is rounded, short, lacks an anteromedian flexus, and has a medial bulge. Cusps are opposite, mures are oriented at approximately 15–20° to long axis of toothrow. Enamel of opposing flexi overlaps near the midline, but does not connect. Apices of labial flexi curve posteriorly, while apex of hypoflexus curves anteriorly. Posterior region is broad with a large metacone. Mesolophs are absent from all teeth. Lingual root is large; presence of labial root is unknown.

M2 has a small paralophule directed posterolabially. Procingulum is distinct and narrow, extending almost to the paracone. Flexi are less curved than in M1, but similarly rotated relative to the midline. Protocone is smaller in area than hypocone.

M3 is slightly smaller than M2 (subequal or larger than M2 in *Loxodontomys*), not greatly simplified relative to M2. Protoflexus is absent; the anteroflexus is deep. The large paralophule is directed posteriorly, subequal in size to the paracone. Metaflexus is large and broadened into two arms along the mure, one arm directed anteriorly, the other posterolingually. Posteroflexus is a shallow notch that is lost with wear. Mure is long and distinct.

Measurements are provided in Table 2.

Comments—The key diagnostic structures of *Ichthyurodon*, unique among sigmodontines, are a very large paralophule on

TABLE 1. Character matrix for phylogenetic analysis, including only those characters which are preserved in the fossils. All characters were used in the analysis. Character state descriptions in Appendix II. See Steppan (1995) for complete data matrix for extant species.

	Character number																																												
Species	1	2	3	4	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	38	43	44	45	74	99	100	101	102	103
Calomys callosus	0	0	0	2	0	1	1	1	1	1	1	0	2	0	1	0	0	2	0	2	1	2	0	1	0	1	1	1	0	0	0	0	0	2	0	1	1	1	0	1	?	1	0	1	0
Calomys laucha	0	0	0	2	0	1	1	1	1	1	1	1	2	0	1	1	0	2	0	2	1	1	0	1	0	1	1	1	0	0	0	0	0	2	0	1	1	1	0	1	1	1	0	1	0
Calomys sorellus	0	1	0	2	0	1	?	?	1	1	0	0	2	1	1	1	0	2	0	2	1	2	2	0	1	1	1	1	0	0	0	?	0	1	0	1	1	1	0	1	1	1	0	1	?
Graomys pearsoni	0	1	0	2	0	1	1	1	1	0	0	0	1	0	1	3	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0	1	2	1	0	1	1	1	0	1	?
Graomys griseoflavus	0	1	0	2	0	1	1	0	0	0	0	2	2	1	2	3	0	2	0	2	1	0	0	0	0	1	1	0	0	1	0	0	2	2	0	1	2	0	0	1	0	1	1	1	0
Euneomys chinchilloides	2	1	2	0	0	0	0	0	0	0	0	2	0	0	0	2	1	2	1	1	0	0	1	0	1	0	0	0	0	0	1	1	1	1	1	1	1	0	1	0	2	0	0	0	0
Euneomys petersoni	2	1	2	0	0	0	0	0	0	0	0	2	0	0	0	2	1	2	1	1	0	0	1	0	1	0	0	0	0	0	1	0	2	1	1	1	1	0	1	0	2	0	0	0	?
Reithrodon typicus	3	0	?	?	?	?	?	?	0	0	0	2	1	0	2	2	0	2	0	3	1	?	?	?	?	?	0	0	0	0	?	0	1	1	1	3	3	?	1	0	0	1	1	1	?
Reithrodon auritus	3	0	2	2	0	1	1	0	0	0	0	2	1	0	2	2	0	2	0	3	1	0	0	0	0	0	0	0	0	0	1	0	1	2	1	3	3	1	1	0	0	1	1	1	1
Neotomys ebriosus	4	0	2	0	0	0	1	1	0	0	0	2	1	0	2	3	0	2	0	3	0	0	1	0	0	0	1	0	0	0	2	1	2	1	2	0	3	1	1	0	0	1	0	1	1
Phyllotis osilae	0	1	0	2	0	1	1	0	0	0	0	0	2	1	1	3	0	1	0	0	0	1	2	1	1	0	2	1	0	0	0	0	0	2	1	1	1	0	0	2	1	1	?	1	?
Phyllotis xanthopygus	0	1	0	2	1	1	?	0	0	0	0	1	2	1	2	?	0	1	0	1	1	1	2	0	1	1	1	1	0	0	0	0	0	1	1	1	1	0	0	2	1	1	1	1	0
Phyllotis andium	0	1	0	2	0	1	1	0	0	0	0	1	2	1	1	?	0	1	0	2	1	1	1	0	1	1	1	1	0	0	0	0	0	1	0	1	1	1	0	2	1	1	?	1	?
Auliscomys sublimis	2	2	1	1	0	1	0	0	0	0	0	0	2	1	1	3	0	2	0	2	1	0	0	0	0	1	2	1	1	0	1	1	0	1	1	2	0	0	0	1	?	0	0	1	?
Auliscomys pictus	2	?	1	1	0	?	0	0	1	0	0	1	1	0	1	2	0	2	0	2	1	1	1	0	0	1	1	1	1	0	1	1	0	1	1	2	0	0	0	1	1	1	0	1	?
Loxodontomys micropus	0	0	2	?	1	1	0	0	0	0	1	2	2	0	0	?	0	2	0	3	1	1	1	1	0	1	1	1	0	0	1	0	0	1	1	2	1	1	0	0	1	0	0	0	0
Olympicomys vossi	?	?	?	?	?	1	?	1	?	?	?	?	2	1	1	0	0	1	0	?	0	?	?	?	?	?	0	0	0	?	?	0	0	?	?	?	?	?	?	?	?	?	1	0	?
Ichthyurodon ameghinoi	?	?	?	?	?	?	?	?	0	0	0	1	?	?	?	?	?	?	?	2	?	0	1	0	0	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?
Panchomys steppani	?	?	?	?	?	1	?	?	0	0	0	2	0	0	1	0	0	2	0	2	0	?	?	?	?	?	0	0	0	?	?	?	?	?	1	?	?	?	1	?	1	0	2	0	1
Genus "T"	2	1	2	2	0	1	0	0	0	0	0	1	0	?	0	0	0	1	0	1	0	0	1	0	0	0	2	0	0	0	1	0	0	1	1	1	2	1	0	0	2	1	0	0	?

FIGURE 2. Holotype of *Ichthyurodon ameghinoi* MLP 91-VI-25-166, right maxilla with M1–3. Scale bar = 1 mm.

M3 and small corresponding paralopule on M2. Although only a single specimen is known, the size of these structures lies far outside the range of intraspecific variation observed in any living phyllotine species. We interpret these structures to be paralophules arising from the paracone rather than a mesoloph partially fused with the paracone because they are directed posteriorly rather than laterally, which is usually the case with fused mesolophs. Also, the paralophule in *Ichthyurodon* is most developed on M3, small on M2, and absent on M1. This polarity is contrary to the typical pattern of the mesoloph, whether partially fused or entire, where the mesoloph is most developed on M1 and least developed or even lost on M3. Distinguishing between paralophules and fused mesolophs can be difficult even with Recent material and age-structured samples (Hershkovitz, 1966b, 1993), and homology assessments should always be tested with better ontogenetic data should such material be discovered.

ICHTHYURODON AMEGHINOI, sp. nov.

Holotype—MLP 91-IV-25-166, right maxilla with M1–3.

Hypodigm—Includes only the holotype.

Diagnosis—The same as for the genus by monotypy. Measurements in Table 2.

Etymology—In honor of Florentino Ameghino, (1854–1911), father of Argentine paleontology.

OLYMPICOMYS, gen. nov.
(Fig. 3)

Type Species—*Olympicomys vossi*, new species.

Type Locality—Punta Negra, Necochea District, Buenos Aires Province, Argentina.

Geographic Distribution and Chronology—Region of Necochea (southeastern Buenos Aires Province, Argentina); Sanandresian Substage/Subage, Marplatan Stage (early Pleistocene).

Diagnosis—Phyllotine resembling *Loxodontomys* (Fig. 4) in occlusal pattern of lower molars, but larger and more robust, with lingual accessory root of m1 undivided, anteromedian flexid absent, procingulum of m1 moderately rotated and with rhomboidal shape, protoflexid of m1 a lake, posterolophid of m1 indistinct, cusp arrangement intermediate between opposite and alternate; protoflexid of m2 smaller than m3; m3 not sim-

TABLE 2. Upper and lower dental measurements for the two new genera and other members of the *Reithrodon* group sensu lato. Abbreviations: L: length, W: width. Standard deviations in parentheses.

	Measurement	*Ichthyurodon ameghinoi* (n = 1)	*Olympicomys vossi* (n = 4)	*Loxodontomys micropus* (n = 7)	*Reithrodon auritus* (n = 12)	*Neotomys ebriosus* (n = 3)	*Euneomys chinchilloides* (n = 3)
M1	L	2.80		2.47 (0.09)	3.19 (0.07)	2.55 (0.10)	2.57 (0.12)
	W	1.82		1.68 (0.06)	2.03 (0.06)	1.85 (0.05)	1.84 (0.06)
M2	L	1.64		1.60 (0.03)	1.93 (0.07)	1.43 (0.02)	1.65 (0.02)
	W	1.68		1.53 (0.07)	1.89 (0.13)	1.83 (0.07)	1.72 (0.06)
M3	L	1.40		1.49 (0.11)	1.85 (0.11)	1.60 (0.00)	1.32 (0.09)
	W	1.52		1.34 (0.11)	1.51 (0.09)	1.59 (0.08)	1.36 (0.03)
M1–3	L (alveolar)	6.28		6.00 (0.14)	7.47 (0.18)	5.83 (0.14)	5.80 (0.14)
m1	L		2.71 (0.08)	2.38 (0.11)	3.07 (0.17)	2.55 (0.10)	2.43 (0.13)
	W		1.68 (0.09)	1.53 (0.04)	1.75 (0.05)	1.67 (0.05)	1.65 (0.05)
m2	L		1.72 (0.07)	1.63 (0.06)	1.73 (0.06)	1.73 (0.02)	1.63 (0.05)
	W		1.67 (0.05)	1.58 (0.05)	1.83 (0.07)	1.84 (0.00)	1.67 (0.08)
m3	L		1.96 (0.10)	1.89 (0.06)	1.77 (0.11)	1.81 (0.08)	1.72 (0.09)
	W		1.60 (0.08)	1.40 (0.04)	1.50 (0.11)	1.63 (0.02)	1.44 (0.03)
m1–3	L (alveolar)		6.69 (0.16)	5.94 (0.14)	7.09 (0.20)	5.93 (0.18)	6.38 (0.14)

plified, longer than m2, with mesoflexid of moderate size, and three roots.

Etymology—Named in honor of the centennial of the modern Olympic games.

Description—Based primarily on the holotype, but includes the rest of the known material. Jaw is more robust than that of *Loxodontomys* or representatives of *Auliscomys.* Diastema is abrupt, its length less than the length of m1–2 combined, with its lowest point below the alveolar plane. Superior branch of the masseteric crest presents a sharp border (visible as a shelf in dorsal view) and extends from the middle of m3 to the anterior border of m1, and to the level of the mental foramen, merging with a very short inferior branch. Mental foramen is partially visible in lateral view. Capsular projection is enlarged and angled toward the base of the robust coronoid process.

Lower dentition largely conforms to the generalized phyllotine pattern. All molars are moderately hypsodont (somewhat less than in *Loxodontomys*), occlusal surface is planar (sensu Hershkovitz, 1962), and cusp positions are alternate to intermediate (i.e., not opposite).

The m1 is rounded and lengthened. The procingulum is rhomboid and mildly attenuated anteriorly, without an anteromedian flexid. In the specimens with strong occlusal wear, the terminal anterolabial cingulum contacts the protoconid, creating a protofossetid. The protoconid and hypoconid are transversely oriented, well developed, and subequal in size. The transversely directed hypoflexid penetrates midway into the tooth and its apex is slightly behind that of the mesoflexid. The posteroflexid is reduced and lost in the oldest individuals. The labial accessory root is well developed and undivided. A lingual accessory root is present.

The m2 is rectangular in outline. Its murid is oblique to the midline because the apex of the mesoflexid is rotated anteriorly and the hypoflexid posteriorly. Only a vestige of the protoflexid (smaller than in *Loxodontomys micropus*) is preserved in the paratype. Three roots are present.

The m3 is incipiently sigmoidal, with overlapping lophids and an enlarged posterior region. Hypoflexid is notably well developed, extending across two thirds of the occlusal surface of the tooth. The mesoflexid is reduced, though persisting with its apex shifted anteriorly.

Measurements are provided in Table 2.

Comments—Although *Olympicomys* lacks autapomorphic features, its mosaic suite of characters prevents its inclusion in any other known genus. Nonetheless, in this short description of *Olympicomys,* it has been unnecessary to compare it to the multitude of living phyllotines, most of which are clearly distinct from and not closely related to the new form. It is more simplified, hypsodont, and lophate than the more plesiomorphic *Calomys* and *Eligmodontia,* more robust and laminate than the reduced dentitions of *Chinchillula* and *Galenomys,* and lacks any of the diagnostic features characterizing *Andinomys, Irenomys, Ichthyurodon,* the *Reithrodon* group sensu lato, or an undescribed genus from the Holocene of northern Ecuador (Mezzabotta and Steppan, unpubl. data). With its generalized phyllotine dentition, *Olympicomys* is superficially similar to *Graomys, Phyllotis, Loxodontomys,* and *Auliscomys.* The last genus once included *L. micropus* (Simonetti and Spotorno, 1980; Reig, 1986; Musser and Carleton, 1993) until Braun (1993) formally resurrected *Loxodontomys,* originally proposed as a subgenus of *Phyllotis* by Osgood (1947). *Olympicomys* does not appear to be congeneric with *Ichthyurodon* because the second and third molars show no evidence of the complexity seen in the later genus, the third molar is not similarly enlarged, the first molar is elongate rather than rounded, and the toothrow is more hypsodont. The two genera have not been recovered from the same formation. The large m3 of *Olympicomys* distinguishes it from all other phyllotines except *Loxodontomys* and the *Reithrodon* group. Thus, in overall dental morphology, and in such features as degree of hypsodonty, enlarged m3, and cusps more rounded than triangular, it most closely resembles *Loxodontomys.* However, it shares other features with *Graomys* that distinguish it from *Loxodontomys,* primarily the shape of the procingulum, the hypoflexid not shifted posteriorly, and cusps not arranged oppositely.

OLYMPICOMYS VOSSI, sp. nov.

Holotype—MLP 91-IV-25-179, incomplete right mandible with incisor and m1–m3 (adult individual). Collected by Dr. E. Tonni and collaborators.

Paratype—MLP 91-IV-25-108, incomplete right mandible with m1–m3 and the interalveolar portion to the incisor (old adult). Collected by Dr. G. Vucetich and collaborators in Las Grutas.

Hypodigm—The type, paratype and MLP 91-IV-25-80, fragment of right mandible with m1–m2 (old adult), collected by Dr. E. Tonni and collaborators in Punta Negra, and MLP 95-XII-1-20, fragment of left mandible with incomplete m2 and m3 (adult), collected by Dr. Noriega and collaborators in Punta Negra.

Diagnosis—The same as for the genus by monotypy.

Etymology—Dedicated to Dr. Robert Voss of the American Museum of Natural History, for his contributions to our understanding of sigmodontine evolution and ecology.

FIGURE 3. Holotype of *Olympicomys vossi* MLP 91-VI-25-179, right mandible with m1–3. Scale bar = 1 mm.

Phylogenetic Analysis

Parsimony analysis results in three most parsimonious trees of 283 steps excluding uninformative characters. One of these trees is arbitrarily chosen for presentation (Fig. 5). The other two trees differ only in the relationships of *Ichthyurodon* and new genus "T" relative to the *Reithrodon* group sensu stricto, node "B" (one branch has zero length in Fig. 5). Most of the fossil species are placed in the *Reithrodon* group sensu lato, node "A." *Ichthyurodon* is placed along with new genus "T" as possible sister groups to the *Reithrodon* group sensu stricto. Branch lengths leading to these two species are short, as expected from the limited number of dental characters.

Olympicomys vossi is placed by this analysis within *Graomys,* a result that contrasts with the qualitative similarity in size and shape of cusps between *Olympicomys* and *Loxodontomys.* In fact, trees only two steps longer place *O. vossi* at the base of the *Reithrodon* group sensu lato, as does the bootstrap majority-rule consensus tree (not shown). This instability probably reflects the few cladistically informative characters present in lower dentitions and the composite appearance of the dentition of *O. vossi.*

Bootstrap percentages for interior nodes are generally low (Fig. 5). The best supported node directly involving a fossil species is that defining the sister group to *Loxodontomys* at 30%. Node "A", just below it, is only supported at 24%. However, because *Olympicomys* has these two nearly equally parsimonious placements, all nodes between these two positions are prevented from having high bootstrap values. When *Olympicomys* is removed from the analysis, the remaining topology is unaffected while bootstrap values increase significantly. For example, node "A" increases to 57%, and the nodes immediately basal and distal to it increase from 25% to 63% and from 30% to 62%, respectively. Nearly every other bootstrap value in the tree increases as well, especially that for *Graomys,* from 27% to 83%.

Placement of *Panchomys* with *Reithrodon* and *Neotomys* is supported by two putative synapomorphies: primary cusps of m1 positioned intermediate or alternate, and ventral swelling at the premaxillo-maxillary suture. Characters unequivocally supporting these three taxa as the sister clade to *Euneomys,* forming the *Reithrodon* group sensu stricto, are deeply interpenetrating flexi, m3 mesoflexid not reduced, and a sharply angled premaxillo-maxillary suture. The last trait is not found in any other New World muroid. The condition of this trait is unknown in *Ichthyurodon* and *Olympicomys.* New genus "T" possesses the plesiomorphic condition, with the suture not sharply angled. The placement of *Ichthyurodon* and the new genus "T" as possible sister taxa to the *Reithrodon* group is supported by incisor grooves (condition unknown in *Ichthyurodon*), m1 anterolabial cingulum absent (weakly present in young *Reithrodon* and *Neotomys*), m2 procingulum absent (weakly present in young *Reithrodon*), M3 flexi axes unrotated relative to those of M2, M3 hypoflexus not reduced, and m3 mesoflexid not shifted in position. Additional characters unequivocally supporting the inclusion of the fossil species in the *Reithrodon* group sensu lato, node "A," are a tripartite dentine fissure in the upper incisors and m3 longer than m2 (smaller in *Reithrodon* and *Neotomys*).

DISCUSSION

Systematics and Phyllotine Diversity

Ichthyurodon appears to be a basal member of the *Reithrodon* group sensu lato. Examination of near-most parsimonious trees and bootstrap frequencies indicates that the placements of genus "T" as a member of the *Reithrodon* group sensu lato and of *Panchomys* in the *Reithrodon* group sensu stricto are more robust. The greater confidence in the placement of *Panchomys* and genus "T" is primarily due to the preservation of important cranial features in these two taxa. *Olympicomys* is only represented by several lower jaws, while *Ichthyurodon* is only known from an upper tooth row. Furthermore, the particular instability of *Olympicomys* is due to its generally plesiomorphic dentition and the mosaic nature of its dental traits for characters that are relatively homoplastic across the tree. It also lacks many synapomorphies among characters that exhibit relatively low homoplasy. This situation is common with fossil muroids, which are often represented only by lower molars or jaws. Lower molars are more stereotyped than upper molars among phyllotines. The most variable and diagnostic molar is M3 (cf. Fig 4) and thus it is the most informative for systematics. This study illustrates the difficulty of building phylogenetic hypotheses based primarily on fossil material where most characters are missing. In this case, the extant species are principally responsible for providing the underlying tree structure.

The inclusion of fossils strengthens the hypothesis of a close

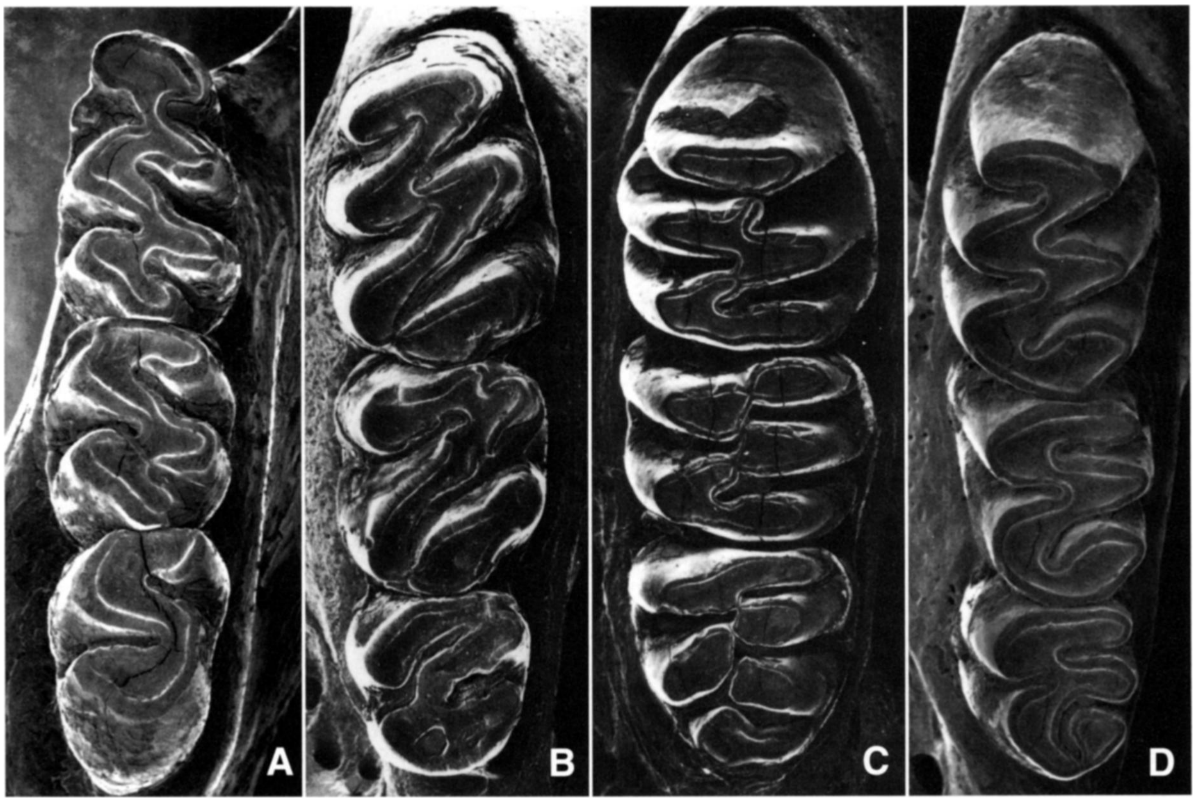

FIGURE 4. Lower toothrow of (**A**) *Loxodontomys.* Upper toothrows of (**B**) *Euneomys,* (**C**) *Neotomys, and (***D**) *Reithrodon.* Figures not to same scale.

relationship between the *Reithrodon* group and *Loxodontomys* suggested previously by Steppan (1993, 1995) by providing intermediate morphologies—especially genus "T" (Ortiz et al., unpubl. data)—between the extant taxa. The low bootstrap values give little support to that contention, but they are caused by the relatively small number of characters preserved in the fossils and by the particularly unstable behavior of *Olympicomys.* Because *Olympicomys* has two nearly equally parsimonious placements—sister to *Graomys* or in the *Reithrodon* group sensu lato—all nodes subtending these two positions will necessarily be supported at less than about 50%, no matter how much character support there may be for the individual nodes. Given the above statements and the overall similarity between *Olympicomys* and *Loxodontomys, Olympicomys* most likely joins the tree near node "A" as a basal member of the *Reithrodon* group sensu lato or basal to that clade. Additional material is clearly needed to test this tentative hypothesis.

The remarkable taxonomic pattern documented here is the concentration of fossil diversity within the *Reithrodon* group, just a small branch among current sigmodontine diversity. Our study is just part of a sudden expansion in knowledge of past sigmodontine diversity. Prior to 1995, the number of extinct sigmodontine taxa recognized in South America consisted of no more than nine species and the two genera *Cholomys* (Reig, 1980) and *Dankomys* (Reig, 1978) (the remaining extinct species are in the extant genera *Akodon, Graomys,* and *Auliscomys* [=*Loxodontomys*]). Some Holocene fossils described by Winge (1887) from cave deposits could be added to the list pending a long overdue critical reexamination of the material (Voss and Myers, 1991; Voss and Carleton, 1993). Overall, the number of extinct forms contrasts sharply with present diversity, which stands at over 300 species and 64 genera (Musser and Carleton, 1993; Steppan, 1996b). Ongoing and recently published paleontological investigations will add at least nine species and seven genera, thus doubling the number of species and quadrupling the number of genera (Fejfar et al., 1996; Steppan, 1996a; Bond et al., in press; Pardiñas, in press; Carleton and Olson, unpubl. data; Mezzabotta and Steppan, unpubl. data; Ortiz et al., unpubl. data). These recent discoveries indicate that paleontological excavations that specifically screen for the micro-mammal fauna can add greatly to our understanding of sigmodontine evolution.

Paleoecology

Today, the moderate- to large-sized phyllotines (adult weight between 50 and 120 g) dominate the xeric habitats in the middle latitudes of Argentina. In contrast, the small phyllotines (10 to 50 g) are abundant in humid and grassland regions. The first group dominated the pampean region, which are predominately grasslands today, for much of the Plio–Pleistocene (Pardiñas and Tonni, 1993; Pardiñas, 1995a). This situation could be explained by a more severe climate during that time. The samples from the early Pleistocene of Necochea appear to be dominated by *Reithrodon auritus* and *Olympicomys vossi,* along with *Ichthyurodon ameghinoi.* This diversity of moderate to large phyllotines, added to the poor representation of other major tribes (e.g., Akodontini), suggests a climate with lower temperatures, moderate rainfalls, and greater potential evapotranspiration due to an increase in the continentality. Such a climate is also indicated for extra-glacial areas during the glacial advances in the patagonian mountain chain. Thus, Rabassa and Clapperton (1990:172) argued that "the greatest Patagonian glaciation developed during the Early Pleistocene, contrary to the global pattern which saw the most extensive ice volumes developing during the last 800 ka. In southern Patagonia, glaciers advanced up to 200 km east of the mountain front and reached the Atlantic continental shelf. . ." (see also Rabassa et

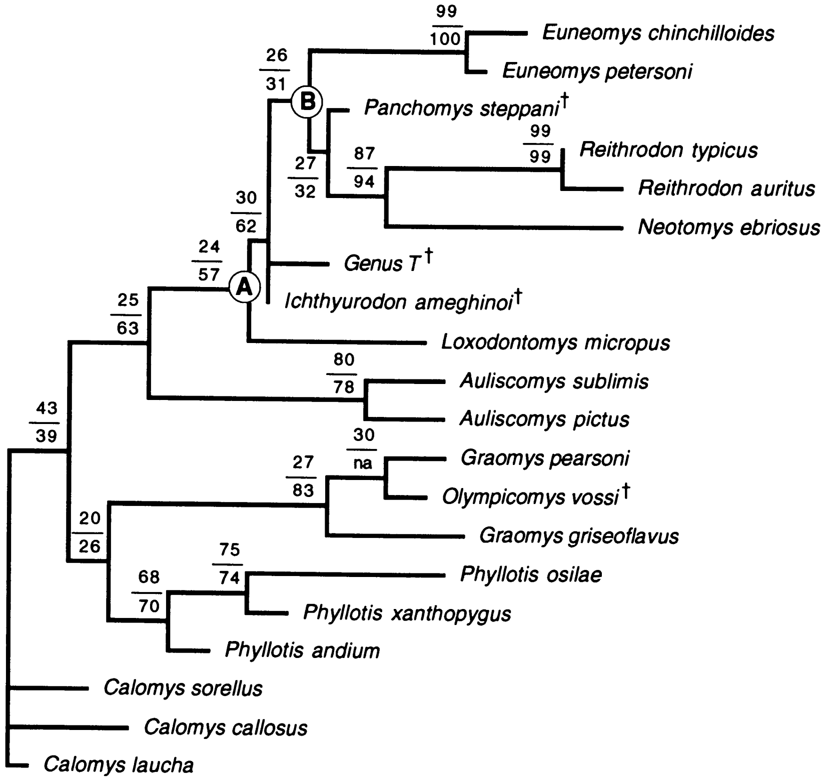

FIGURE 5. Phylogram of one of three most parsimonious trees from the phylogenetic analysis. The other two trees differ only in the relationships of *Ichthyurodon* and genus "T" relative to node "B." Branch lengths are proportional to the number of unambiguous character state changes. Node "A" defines the *Reithrodon* group sensu lato, node "B" defines the *Reithrodon* group sensu stricto. Numbers to the left of nodes are the bootstrap percentages: numbers above the lines found in 200 replicates with the complete data set (although topology of majority-rule bootstrap consensus tree may not be congruent); numbers below the lines are from bootstraps excluding *Olympicomys.*

al., 1986). Other faunistic elements present in the Necochea samples strengthen the hypothesis of a very dry, cold climate, including *Lestodelphys,* a marmosine marsupial currently distributed in central Patagonia (Tonni and Cione, 1995), and the notable abundance of ctenomyine rodents.

The geographic distributions of the members of the *Reithrodon* group sensu lato have shifted from the Pliocene to the Recent. The current distributions of *Euneomys* and *Loxodontomys* more or less circumscribe the Andean region of Patagonia in Argentina and Chile, while *Neotomys* occupies the high elevation grasslands in isolated areas from southern Peru to northern Argentina. Uniquely, *Reithrodon auritus* and *R. typicus* show a distribution extended into the lowlands of southern and central Argentina and Uruguay. The fossil record shows high diversity in the pampean region (today inhabited only by *R. auritus*), correlated with the development of microherbivore lineages adapted to open habitats. This expansion of the *Reithrodon* group in the pampas occurred from the late Pliocene until the middle Pleistocene, the period during which the basic generic composition was established that with few variations persists until the present time (Pardiñas, 1995b).

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APPENDIX I

Recent Specimens Examined—Museum abbreviations are as follows: Field Museum of Natural History, **FMNH**; Museum of Vertebrate Zoology, University of California, Berkeley, **MVZ**; National Museum of Natural History, Smithsonian Institution, **USNM**; University of Michigan Museum of Zoology, **UMMZ**; Museo Nacional de Historia Natural, Santiago Chile, **MNHN**; The Museum, Michigan State University, **MSU**.

Calomys callosus—ARGENTINA. Catamarca: La Merced (MSU 19235, 19237). Jujuy: Calilegua (FMNH 22235, 23373). Tucumán: Concepción (FMNH 30167–30173). BOLIVIA. El Beni: San Juan (FMNH 118807, 118808); San Joaquín (FMNH 117123); Yuatre (FMNH 118296); Yutiole (FMNH 118605, 118610, 118294). Santa Cruz: San Miguel Rincon (AMNH 260686–260690). Tarija: Villa Montes (FMNH 34238). PARAGUAY. Chaco: Fortin Madrejon, WNW (UMMZ 125466, 125468–125477). Presidente Hayes: Juan de Zalazar, 8 km NE (UMMZ 133915–133922). Total: 35.

Calomys laucha—ARGENTINA. Buenos Aires: Dorrego (FMNH 50939, 50940, 50942–50945); Near Henderson (FMNH 23395); Partida Balcarce (MSU 16815, 16816, 16818, 16819); Urdampilleta (FMNH 23405). Rio Negro: Chimpay (FMNH 50932, 50937). BOLIVIA. Tarija: Villa Montes, 10 km E (AMNH 246668, 246674, 246841, 246849, 246867). PARAGUAY. Presidente Hayes: Juan de Zalazar, 8 km NE (UMMZ 133928) Total: 20.

Calomys sorellus—PERU. Ancash: Hda. Catoc (FMNH 81288, 81289); Nevado Quincayhuanca (FMNH 81276, 81287). Arequipa: Arequipa (FMNH 107795); Caraveli (FMNH 107399); Chivay (FMNH 107688, 107689, 107732); Ayacucho: Chunyacc (UMMZ 120286); Jawaymachay (UMMZ 120291); Pacaicasu (UMMZ 120288, 120289); Tambo, San Miguel (FMNH 75388, 75389); Tucumachay (UMMZ 120290). Cuzco: Huancarani (MVZ 171549–171554. La Libertad: mountains near Otuzco (FMNH 19209, 19210). Total: 24.

Graomys griseoflavus—ARGENTINA. Catamarca: Belén (FMNH 28423); Pta. Tinogasta (FMNH 29163). Río Negro: Chimpay (FMNH 50920, 50923–50928). BOLIVIA. Santa Cruz: Cordillera Guanacos (FMNH 21431, 21432). Tarija: Tablada (FMNH 29165, 29166); Tiquipa, Laguna Palmar (AMNH 246777, 246778); Villa Montes (AMNH 246773, 246779). PARAGUAY. Boquerón: Colonia Fernhéim (FMNH 54359, 54360); La Urbana (FMNH 34235). Alto Paraguay: Puerto Casado (FMNH 54407). Total: 21.

Graomys pearsoni—BOLIVIA. Santa Cruz: Robore, 29.5 km W (AMNH 260762). PARAGUAY. Nueva Asunción: km 620, Trans-Chaco road (UMMZ, uncataloged; [T.W. Nelson field numbers #184, 193, 201, 202, 233]). Total: 6.

Phyllotis andium—ECUADOR. Azuay: Valle de Yunguilla (FMNH 43311). PERU. Ancash: Mácate (FMNH 20914, 20915, 20923, 20938, 21145); Río Mosna (FMNH 129248, 129249). Libertad: Hac. Llagueda (FMNH 19464). Lima: Lima (FMNH 107361). Total: 10.

Phyllotis osilae—PERU. Puno: Chucuito (FMNH 51285, 51287; 107843, 107859); Ilave, 35 km S (FMNH 107860, 107870–107872, 107874, 107881, 107885, 107887, 107888, 107891, 107894–107896); Pucará, 6 km S (MVZ 173165); Santa Rosa, 12 km S (MVZ 173162); Yunguyo (FMNH 51269, 51270, 51274, 51278). Total: 23.

Phyllotis xanthopygus—ARGENTINA. Santa Cruz: Río Ecker (FMNH 124384–124388, 124436–124439). CHILE. Aisén: Chile Chico (FMNH 133940, 133943, 133944, 133947, 133958, 133973, 133979, 133982). Magallanes: Última Esperanza, Laguna Lazo (FMNH 50542). Total: 18.

Loxodontomys micropus—ARGENTINA. Río Negro: San Carlos de Bariloche (FMNH 23840–23842). Santa Cruz: Río Ecker (FMNH 124393, 124394, 124397, 124435). CHILE. Aisén: Pto. Ibáñez (FMNH 132705, 132706); Reserva Nac. Coihaique (FMNH 132874). Rio ñireguao (FMNH 22229, 23283–23285, 23287). Llanquihue: (FMNH 50647). Magallanes: Puerto Natales (FMNH 50614); Punta Arenas (FMNH 50615–50622; 127337). Malleco: Cerro Nahuelbuta (FMNH 50643–50645). Osorno: Refugio, Valle de la Picada (FMNH 127717–127720). Total: 33.

Auliscomys pictus—PERU. Arequipa: Cailloma (FMNH 49775, 107678, 107716) Cuzco: Machu Picchu, 20 km E (FMNH 107804, 107806, 107819). Junín: Carhuamayo (FMNH 54734–54742); Junín (FMNH 21132, 21133, 21135–21142—topotypes); Pachacayo (FMNH 20060); Tarma (FMNH 64344). Puno: Puno, Hac. Collacachi (FMNH 49751); Santa Rosa, 6 km W (FMNH 107918, 107920, 107922, 107925, 107926; 107968, 107975). Total: 34.

Auliscomys sublimis—PERU. Arequipa: Cailloma, Chivay (FMNH 107696, 107711); Laguna Salinas (FMNH 49542, 49543, 49546, 49547); Sumbay (FMNH 49536, 49537, 49539, 49540, 49544, 49545). Puno: (FMNH 51260); Huacullani (FMNH 52669–52671); Ilave, 35 km S (FMNH 107873); Laguna de Loriscota, 5 mi. N (MVZ 145613); Puno (AMNH 213596, 213597, 213601). Total: 20.

Euneomys chinchilloides—ARGENTINA. Tierra del Fuego: Lago Fagnano (FMNH 50736). CHILE. Aisén: Pto. Ibáñez (FMNH 133088, 133089, 134027; 134181–134184, 134186, 134233). Magallanes: Punta Arenas (FMNH 50600, 50601). Total: 12.

Euneomys petersoni—CHILE. Aisén: Coihaique Alto, 4.5 km E (FMNH 133082, 133083, 133085, 133086). Magallanes: Última Esperanza, Laguna Lazo (FMNH 50584–50586, 50588–50590, 50593, 50595–50599); Lago Sarmiento (FMNH 50583). Total: 18.

Neotomys ebriosus—ARGENTINA. Jujuy: Sierra de Zenta (FMNH 41282). PERU. Pasco: Chigrín (FMNH 24776–24778); La Quinua (FMNH 24775). Ancash: Recuay Ticapampa (FMNH 81283). Cuzco: Marcapata, Ccolini (FMNH 75580). Junín: Paccha (FMNH 64345). Puno: Hac. Collacachi (FMNH 49708); Ilave (FMNH 107824, 107842); Yunguyo (FMNH 51261, 51263). Total: 13.

Reithrodon auritus pachycephalus—CHILE. Aisén: Chile Chico (FMNH 134178; 134188, 134189, 134225, 134226, 134228, 134229, 134231, 134232, 134235); Coihaique Alto (FMNH 134187, 134192; 134196, 134202, 134204, 134205, 134207, 134210, 134213, 134222, 134224). Magallanes: Punta Arenas (FMNH 124426, holotype); Rio Verde (FMNH 50570–50576). Total: 29.

Reithrodon typicus —URUGUAY. Lavalleja: Minas, Arroyo Polanco (FMNH 27707–27709). Rocha: Castillos (FMNH 27704). San Jose: Puerto Arazatí (FMNH 27653). Treinta y Tres: Quebrada de los Cuervos (FMNH 27705, 27706).Total: 7.

APPENDIX II

Character Descriptions—For detailed discussion of characters 1–98 the reader is referred to Steppan (1995).

1) Grooves on upper incisors: 0 = absent; 1 = fine striae; 2 = 1 medio-lateral, shallow groove; 3 = 1 medio-lateral deep groove; 1 small shallow groove on midline; 4 = 1 involuted groove on lateral corner.
2) Incisor procumbency: 0 = hyper-opisthodont; 1 = opisthodont; 2 = orthodont; 3 = proodont.
3) Upper incisor dentine fissure: 0 = long straight slit; 1 = short, not quite linear slit, 'comma' shaped; 2 = tripartite, "Y" shaped.
4) Labial root of M1: 0 = absent; 1= present, small, set medially; 2 = present, medium to large, set laterally.
6) Molar roots of M3: 0 = 3 roots; 1 = 2 roots; 2 = 1 root.
7) Labial root of m1: 0 = absent; 1 = present.
8) Molar roots of m2: 0 = 2 roots; 1 = 3 roots.
9) Molar roots of m3: 0 = 2 roots; 1 = 3 roots.
10) Anteromedian flexus M1: 0 = absent or limited to shallow groove; 1 = distinct or prominent; 2 = infolded to form lake; 3 = loss from state 2, with reduction of lake.
11) Mesostyle M1: 0 = absent; 1 = present.
12) Parastyle/anteroflexus M1: 0 = absent; 1 = present, indistinct; 2 = present, distinct.
13) Flexus penetration M1: 0 = flexi from opposite sides do not reach each other; 1 = enamel overlaps, or flexi meet at midline; 2 = flexi cross beyond each other.
14) Anterolabial cingulum m1: 0 = anterolabial cingulum absent; 1 = anterolabial cingulum weakly developed, lost with wear.; 2 = anterolabial cingulum distinct.
15) Protoflexid m1: 0 = short anterolabial cingulum, which may curl towards protoconid, simple protoflexid ; 1 = long anterolabial cingulum, fusing with protoconid and leaving protoflexid as lake.
16) Cusp arrangement m1: 0 = primary cusps opposite in position; 1 = primary cusps intermediate; 2 = primary cusps alternate.
17) Anteromedian flexid m1: 0 = absent or limited to shallow groove; 1 = prominent; 2 = infolded to form lake, which may be lost with wear.
18) Procingulum separation m1: 0 = procingulum attached by anterior mure; 1 = procingulum separated, mure cut by opposing flexids.
19) Posterolophid/stylid m1: 0 = absent; 1 = intermediate, posteroflexid present as groove, or obvious in juvenile, absent with strong wear; 2 = distinct at all ages.
20) Posterolophid/stylid m3: 0 = absent; 1 = intermediate, posteroflexid present as groove, or obvious in juvenile, absent with strong wear; 2 = distinct at all ages.
21) Procingulum M2: 0 = absent; 1 = anteroflexus appears as groove; 2 = protoflexus may appear also, if so procingulum poorly developed as broad, shallow projection with concave anterior edge; if not, then distinct antero- or paraflexus; 3 = procingulum distinct, well developed.
22) Procingulum m2: 0 = absent; 1 = protoflexid appears as groove; if pronounced in juvenile, then wears away with age; 2 = procingulum well developed.
23) Hypoflexus reduction M3: 0 = no reduction relative to M2; 1 = reduced relative to M2 ; 2 = highly reduced relative to M2, or absent.
24) Reduction of mesoflexus M3: 0 = no reduction relative to M2; 1 = reduced relative to M2 ; 2 = highly reduced relative to M2, or absent.
25) Posterior shift of mesoflexus M3: 0 = no shift relative to M2; 1 = posterior shift relative to M2.

26) Hypoflexus lake M3: 0 = hypoflexus present, no lake; 1 = hypoflexus pinched to form lake.
27) Rotation of flexus axes M3: 0 = no rotation of hypoflexus and mesoflexus axes relative to M2; 1 = axes rotated relative to M2
28) Mesoflexid reduction m3: 0 = no reduction relative to m2; 1 = reduced relative to m2 ; 2 = highly reduced relative to m2, or absent.
29) Anterior shift of mesoflexid m3: 0 = no shift relative to m2 ; 1 = anterior shift relative to m2.
30) Posterior shift of hypoflexid m3: 0 = no shift relative to m2; 1 = posterior shift relative to m2.
31) Fusion of opposing flexi in M3: 0 = flexi do not meet; 1 = flexi meet, mure cut.
32) Ratio of M3 length to alveolar length of molar tooth row: 0 = <0.205; 1 = 0.205–0.25; 2 = >0.25.
33) Capsular projection of the mandible: 0 = distinct capsule, or elevation of superior masseteric ridge, usually ventral to the coronoid process; 1 =indistinct or absent.
34) Height of the coronoid process: 0 = above maximum height of mandibular condyle; 1 = subequal; 2 = below mandibular condyle.
35) Anterior masseteric ridge position: 0 = anterior edge not formed into a knob, well ventral to dip of diastema; 1 = knob slightly below dorsal edge of mandible; 2 = knob just reaches dorsal edge of mandible; 3 = knob exceeds dorsal edge.
36) Medio-ventral process of mandibular ramus: 0 = process absent, ramus rounded when viewed ventrally or not sharply angled; 1 = process weakly present, or ramus sharply angled near 90°; 2 = process distinct.
38) Posterior extent of incisive foramina: 0 = not reaching anterior margin of anterolabial and anterolingual conules M1; 1 = level with anterolabial and anterolingual conules; 2 = extending to level of paracone and protocone; 3 = extending to level of hypocone and metacone.
43) Development of zygomatic spine: 0 = absent, anterior border of zygomatic plate rounded or receding dorsally; 1 = absent, anterior border nearly flat, vertical; 2 = moderate, anterior border weakly curved; 3 = strongly developed, pronounced concavity.
44) Inclination of zygomatic plate: 0 = <20° (in frontal view); 1 = ≥20°.
45) Premaxillo-maxillary suture orientation: 0 = 90–135° angle formed relative to palatine plane by the suture on the lateral surface of rostrum and below antorbital foramen; 1 = suture nearly horizontal at ventral end, sharply angled (=90°) in middle of rostrum.
74) Orientation of maxillary toothrows: 0 = posteriorly divergent; 1 = parallel; 2 = convergent.
99) Paraflexus M2: 0 = well developed; 1 = reduced; 2 = absent.
100) Orientation of the hypoflexus in M2: 0 = oblique, directed toward the paraflexus; 1 = transverse.
101) Torsion of m1 procingulum: 0 = no torsion; 1 = moderate torsion; 2 = strong torsion.
102) Reduction of m3: 0 = larger than or subequal to m2; 1 = small than m2.
103) Ventral swelling in the region of the premaxillo-maxillary suture: 0 = absent; 1 = present.