

A NEW FOSSIL PHYLLOTINE (RODENTIA: MURIDAE) FROM NORTHWESTERN ARGENTINA AND RELATIONSHIPS OF THE *REITHRODON* GROUP

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We describe an extinct murid, assigned to the tribe Phyllotini, from the late Pleistocene (Taffí del Valle Formation) of La Angostura (26°55'30"S, 65°41'50"W; 1,900 m elevation) in northwestern Tucumán Province, Argentina. The new genus is characterized by very hypsodont molars with flat crowns and simplified occlusal structure, upper incisors with a mediolateral groove, a straight premaxillary–maxillary suture, and high zygomatic plate with a small spine on its anterodorsal edge. Phylogenetic analyses including fossil and living members of the *Reithrodon* group show that the new genus is the sister taxon to the *Reithrodon–Neotomys–Euneomys* clade. The paleoenvironmental and paleogeographic significance of the new genus is discussed within the context of the climatic changes that occurred during the late Pleistocene in southern South America. The new phyllotine would have lived in high-elevation grasslands, which today occur >1,000 m higher under cold and dry climatic conditions than those of the last glacial maximum.

Key words: Argentina, paleoenvironment, phylogeny, Pleistocene, Sigmodontinae, taxonomy

Until recently, knowledge of the extinct genera of sigmodontine rodents from the Pliocene and Pleistocene of South America was restricted to *Dankomys* Reig, 1978 (Akodontini) and *Cholomys* Reig, 1980 (Wiedomyini). New field work at several outcrops in central Argentina has increased the diversity of known muroids with the discovery of 3 new genera of fossil phyllotines related to the *Reithrodon* group (Pardiñas 1997; Steppan and Pardiñas 1998). The best known sigmodontine paleofaunas come from the Argentinean pampas (Pardiñas 1995a; Reig 1987), the Minas Gerais region, Brazil (Voss and Myers 1991; Winge 1887), and recently from

northern Ecuador (Fejfar et al. 1993, 1996) and Bolivia (Pardiñas and Galliari 1998; Steppan 1996). In Argentina, the paleontological record mostly is restricted to middle latitudes and low elevations, which hinders formulating empirically supported hypotheses concerning the original differentiation (sensu Reig 1986) and primary dispersive and cladogenetic events of the sigmodontines. The sigmodontine fauna of Buenos Aires Province seems, in general, to reflect evolutionary events that took place outside the pampas (Pardiñas 1995a, 1995b). The generic and, to a certain extent, the species composition of present muroid communities were established towards the early–middle Pleistocene (Ensenadan; Pardiñas

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1995a, 1999). Reig (1984, 1986) suggested that centers of differentiation for the Akodontini and Phyllotini occurred in the Andean puna (13–27°S), with dispersal outward to lowlands of eastern and south-central South America. It is necessary to widen our knowledge of the fossil sigmodontines of other regions of Argentina, particularly the northwestern Andean region, to understand sigmodontine evolution, dispersal, and differentiation. Unfortunately, the fossil record of these rodents within the northwestern region is poorly known, although recent microvertebrate excavations in Quaternary sediments are promising (Collantes et al. 1993; Ortiz et al. 1998). We describe the 1st Argentine extinct sigmodontine from outside the pampas, recovered from late Pleistocene deposits. Phylogenetic relationships of this new genus are evaluated with respect to extant and fossil members of the *Reithrodon* group. Paleobiogeographic considerations are discussed to evaluate the paleoenvironmental significance of the new phyllotine and are related to oscillations in the late Pleistocene climate.

MATERIALS AND METHODS

Specimens were collected by P. Ortiz and collaborators and were curated in the fossil vertebrates collection of the Instituto Miguel Lillo Institution (PVL). Remains were from an accumulation generated by the feeding activity of owls (Ortiz et al. 1998). This assemblage includes 13 other species of extant rodents (*Ctenomys*, *Cavia*, *Galea musteloides*, *Akodon* cf. *A. spegazzinii*, *Abrothrix* cf. *A. illutea*, *Necromys* cf. *N. lactens*, *Oxymycterus* cf. *O. paramensis*, *Oligoryzomys* sp., *Andinomys edax*, *Calomys*, *Neotomys ebriosus*, *Phyllotis xanthopygus*, and *Reithrodon auritus*). The Late Pleistocene age (Lujanian) of the assemblage was established by biostratigraphic indicators (Collantes et al. 1993) and accelerator mass spectrometry radiocarbon dating on loess (Zinck and Sayago 1999), which established an age of about 10,000–30,000 years ago. The material was obtained through wet sieving with a 0.1-mm mesh.

Tooth crown-surface terminology followed

Reig (1977). Measurements in millimeters were obtained using manual calipers and a micrometer eyepiece included in a binocular microscope. The maximum length and width of molars were assessed. Microphotographs were processed in the Electronic Microscopic Laboratory of northwestern Argentina (San Miguel de Tucumán, Argentina).

The new taxon was included in a phylogenetic analysis with other members of the *Reithrodon* group, both living and extinct, and a sampling of other phyllotine species. Those genera included extant *Euneomys*, *Neotomys*, and *Reithrodon*, and 3 recently described extinct genera, *Pancho-mys* (Pardiñas 1997), and *Ichthyurodon* and *Olympicomys* (Steppan and Pardiñas 1998). Dental and cranial characters used were largely those discussed by Steppan (1995), with several additional characters described by Steppan and Pardiñas (1998). Characters states for the new genus are listed in Appendix I. Phylogenetic analyses were performed using maximum parsimony, with the computer program PAUP (Swofford 1993). One hundred bootstrap resamplings (Felsenstein 1985) were used to estimate the robustness of hypothesized clades. Characters were ordered. A complete description of the analysis was presented by Steppan and Pardiñas (1998).

RESULTS

Tafimys, new genus

Type species.—New species described herein.

Included species.—Only the type species.

Diagnosis.—A member of the tribe Phyllotini, subfamily Sigmodontinae, family Muridae. Size medium, similar to *Phyllotis darwini* or *Loxodontomys micropus*, characterized by highly hypsodont and very simplified molars, M1 trilophodont with unique accessory labial root, m1 with anteriorly acuminate procingulum without anterolabial cingulum, m3 with vestigial mesoflexid; cranium with high zygomatic plate with parallel edges and small hook-shaped anterodorsal spine, straight premaxillary–maxillary suture, and very short rostrum.

Description.—See below.

Etymology.—Refers to the geographic (Tafí del Valle; Tafi Valley) and stratigraphic

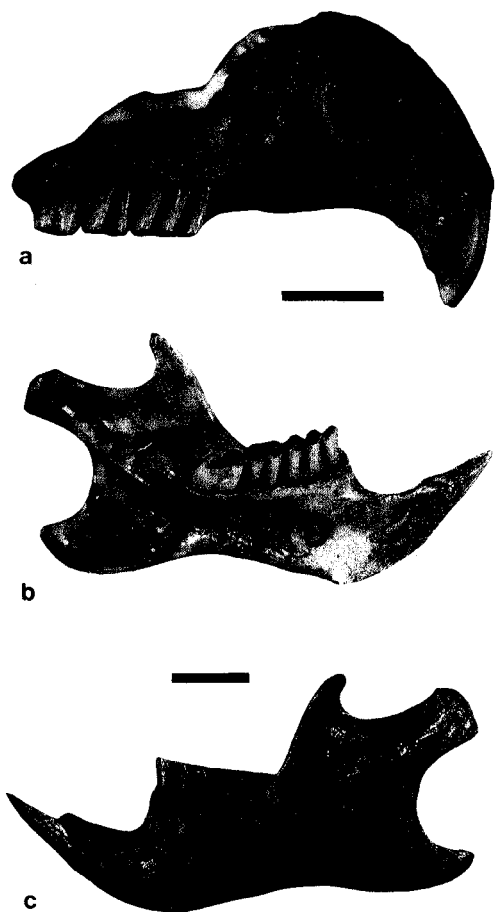


FIG. 1.—Holotype and paratype of *Tafimys powelli* (Phyllotini: Upper Pleistocene. Argentina): a) PVL 4825, anterior portion of skull in lateral view (holotype) and b–c) PVL 4920, left mandible (paratype). Scale bar = 3 mm.

ic (Tafí del Valle Formation) occurrence of the fossil. Tafí: corruption of the aymara *thaa* (cold) and *uí* (place), literally “a very cold place” (Lizondo Borda 1938), and *mys* (mouse).

Tafimys powelli, new species

Holotype.—PVL 4825, anterior fragment of the skull with incisors and both molar tooththrows (excluding left M2–3; Figs. 1a and 2).

Paratypes.—PVL 5450, left maxilla with zygomatic plate, incisor and M1 (Fig. 3); PVL 4830, incomplete left lower jaw, with

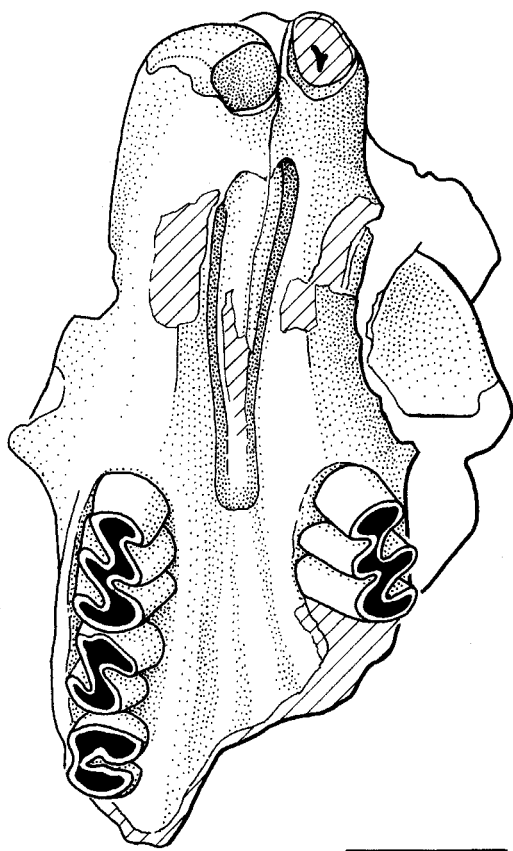


FIG. 2.—Holotype of *Tafimys powelli* (Phyllotini: Upper Pleistocene. Argentina): PVL 4825, anterior portion of skull in palatal view. Scale bar = 3 mm.

m1–2; PVL 4841, incomplete palate with both molar tooththrows (excluding right M3); PVL 4842, right maxilla with complete zygomatic plate and M1–2; PVL 4855, fragment of right zygomatic plate with a complete upper molar tooththrow (Fig. 4); PVL 4920, complete left lower jaw with m1–3 (Fig. 4); PVL 4921, incomplete right lower jaw with m1–3; PVL 4922, fragment of right maxilla with M1–2; PVL 5272, incomplete left lower jaw with m1–3 (Fig. 4).

Hypodigm.—The holotype, the paratypes, and a number of cranial–dental remains and isolated molars and incisors (PVL 4825–4882, PVL 4920–4924, PVL 5120–5438, and PVL 5619). Includes 47 right maxilla, 58 left maxilla, 136 right lower jaws, and

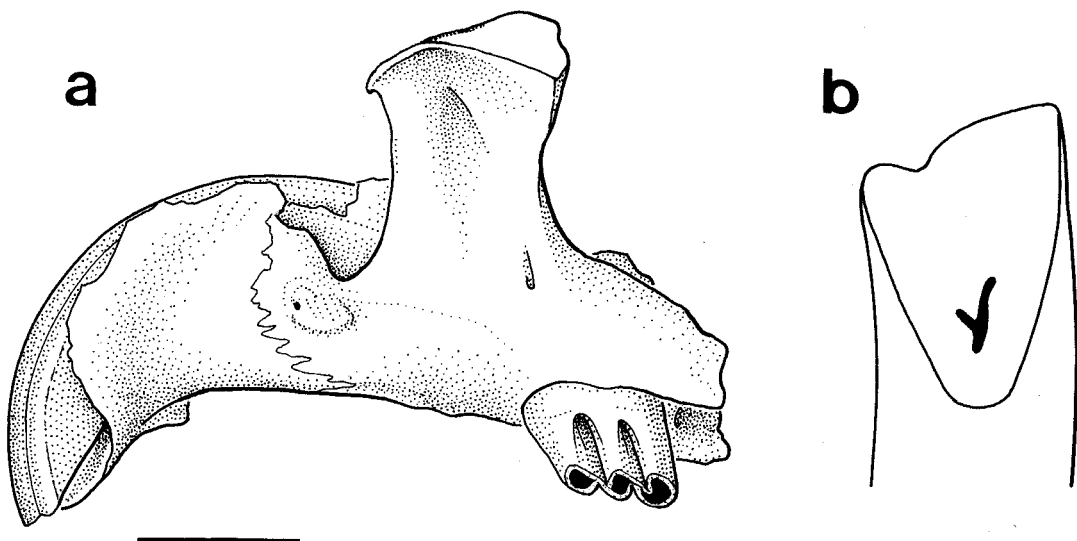


FIG. 3.—Paratype of *Tafimys powelli* (Phyllotini: Upper Pleistocene. Argentina): a) PVL 5450, right maxilla in lateral view and b) PVL 5619, schematic upper incisor groove and dentine fissure. Scale bar = 3 mm.

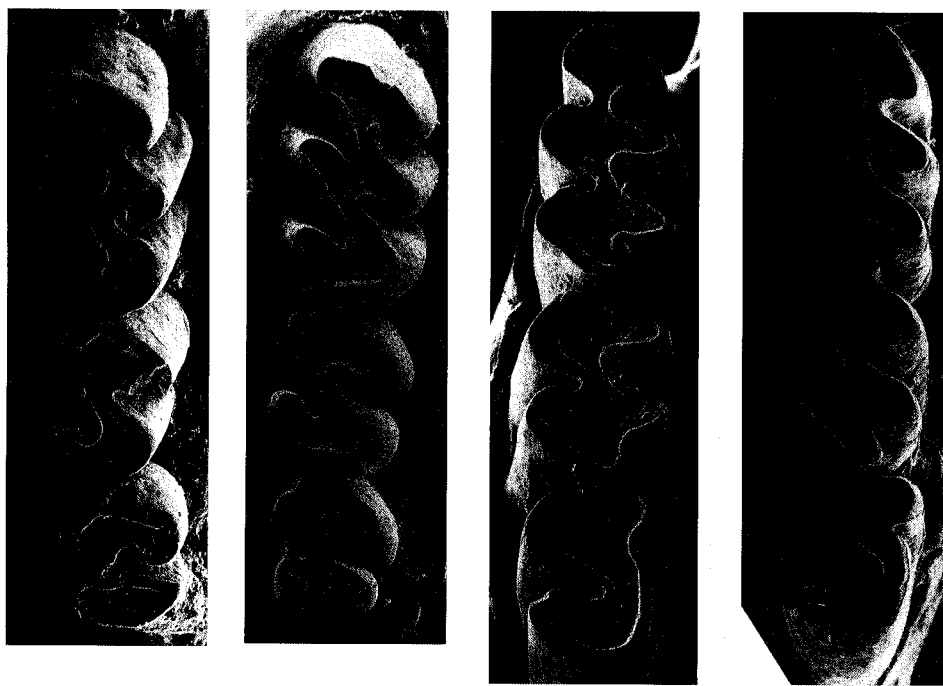


FIG. 4.—Upper and lower molars of *Tafimys powelli* (Phyllotini: Upper Pleistocene. Argentina): left to right, PVL 4825 (holotype. M1-3, coronal length = 5.1 mm), PVL 4855 (M1-3, 4.7 mm), PVL 4920 (m1-3, 5.7 mm), and PVL 5272 (m1-3, 5.5 mm).

TABLE 1.—Cranial and dental measurements (mm) for *Tafimys powelli*, new genus and species (Phyllotini: Upper Pleistocene, Argentina).

| Character | Sample | Mean | SD | Range |
|-----------------------------|--------|-------|-------|-----------|
| Length of upper diastema | 1 | 6.80 | | |
| Length of incisive foramina | 1 | 15.70 | | |
| Width of zygomatic plate | 6 | 3.11 | 0.277 | 2.8–3.5 |
| Incisor–M3 length | 1 | 13.80 | | 13.8 |
| Width of palate between M1 | 2 | 2.10 | | 2.10 |
| Alveolar length of M1–3 | 15 | 5.70 | 0.165 | 5.5–6.0 |
| Coronal length of M1–3 | 7 | 5.01 | 0.285 | 4.6–5.3 |
| Length of M1 | 15 | 2.16 | 0.120 | 4.0–2.4 |
| Width of M1 | 15 | 1.55 | 0.102 | 1.4–1.7 |
| Length of M2 | 16 | 1.41 | 0.078 | 1.3–1.5 |
| Width of M2 | 16 | 1.36 | 0.069 | 1.3–1.5 |
| Length of M3 | 8 | 1.26 | 0.122 | 1.1–1.4 |
| Width of M3 | 8 | 1.19 | 0.060 | 1.1–1.3 |
| Width of upper incisor | 2 | 1.25 | | 1.2–1.3 |
| Depth of upper incisor | 2 | 1.60 | | 1.5–1.7 |
| Total length of mandible | 6 | 18.75 | 0.254 | 17.3–19.9 |
| Depth of mandible below m1 | 29 | 4.84 | 0.158 | 4.5–5.1 |
| Alveolar length of m1–3 | 30 | 6.16 | 0.185 | 5.8–6.7 |
| Coronal length of m1–3 | 22 | 5.85 | 0.227 | 5.4–6.3 |
| Length of m1 | 30 | 2.42 | 0.143 | 2.2–2.9 |
| Width of m1 | 30 | 1.42 | 0.067 | 1.3–1.6 |
| Length of m2 | 28 | 1.61 | 0.100 | 1.4–1.8 |
| Width of m2 | 28 | 1.46 | 0.110 | 1.2–1.7 |
| Length of m3 | 22 | 1.65 | 0.147 | 1.4–2.0 |
| Width of m3 | 22 | 1.27 | 0.085 | 1.1–1.5 |
| Width of lower incisor | 6 | 1.20 | 0.097 | 1.1–1.3 |
| Depth of lower incisor | 4 | 1.47 | | 1.4–1.5 |
| Length of lower diastema | 8 | 3.27 | 0.159 | 2.6–3.8 |
| Incisor–m3 length | 8 | 12.07 | 0.262 | 11.0–13.3 |

135 left lower jaws, and >350 isolated molars and incisors, belonging to ≥ 188 individuals.

Known distribution.—La Angostura, 26°55'30"S, 65°41'50"W, 1,900 m elevation, Departamento Tafí del Valle, Tucumán Province, Argentina. Tafí del Valle Formation (late Pleistocene, Lujanian Age).

Diagnosis.—As for the genus by monotypy.

Measurements.—See Table 1.

Description.—Based on the whole hypodigm.

Skull (Figs. 1, 2, and 3) has rostrum proportionately shorter than any other extant species of the *Reithrodon* group (sensu Olds and Anderson 1989); diastema and incisive foramina reduced in extension; premaxillary–maxillary suture (Fig. 3a)

straight (sensu Stepan 1995), similar to *L. micropus*, and not angled as in extant members of the *Reithrodon* group and *Pancho-mys* (Pardiñas 1997:549, figure 5; Stepan 1995:29, figure 12b); zygomatic plate similar to most phyllotines: high, anterior and posterior edges parallel and vertically oriented, with a small hook-shaped spine at the anterodorsal angle (with its apex downwards inflex; Fig. 3a); insertion area of the masseter lateralis pars profunda well defined; incisive foramina narrow and extended posteriorly to the anterior border of M1 (Fig. 2); palate broad (sensu Hershkovitz 1962); molar tooththrows posteriorly divergent.

Mandible (Figs. 1b and 1c) is similar in morphology and robustness to *L. micropus*; height of the horizontal ramus at the middle

of the m1 greater than the length of the diastema; symphysis short and high with its anterior point slightly below the alveolar row plane; masseteric crest with a small but marked inferior ridge, this one starts at the angular process and it elevates until it becomes noticeable at the level of the hypoconid of m1, fusing to the upper ridge to produce a broader ridge of rounding edges, which ends immediately at the anterior border of the m1 and at the level of the mental foramen (from which it remains clearly separated, as distinguished from *R. auritus*); mental foramen medium size, visible in lateral view; coronoid process well developed, almost vertically oriented (similar to *Euneomys chinchilloides*), its apex exceeds the maximum height of mandibular condyle; sigmoid notch wide; angular process shorter than the condyle; angular notch similar to that of *N. ebriosus*; condyle shorter than in living representatives of the *Reithrodon* group, at the same level as the coronoid process; capsular projection, just visible in juveniles, weak with a similar morphology to *L. micropus*, located between coronoid process and condyle.

Upper incisors narrow (Fig. 3b) with conspicuous mediolateral longitudinal groove, similar in size and shape to that of *Euneomys*; dentine fissure tripartite, Y-shaped (Steppan 1995:23, figures 9 and 10); enamel orange; opisthodont.

Molars flat crowned (Fig. 4) with very simplified occlusal design, even in individuals with relatively unworn teeth, and show a hypsodonty comparable to that of *R. auritus*; main cusps opposite, perimetrical enamel thick with very deep lateral grooves (Fig. 3a).

The M1 is anteroposteriorly enlarged with a trilophodont pattern; loph and flexi are oblique in juveniles, with a tendency to a more transverse position in adults; procingulum anteroposteriorly compressed and retains no traces of an anteromedian flexus; anterior mure slightly oblique, defined by a penetrating protoflexus in the occlusal plane; metaloph and paraloph well devel-

oped and similarly extended; bases of the mesoflexus and hypoflexus alternating, forming an oblique median mure; small accessory labial root, medially positioned.

The M2 is rectangular with a bilophodont pattern due to limited development of the paraflexus; loph more transversely oriented than M1; hypocone region more developed than the protocone; posteroloph absent; large lingual root present in addition to the anterior and posterior root.

In the M3, although highly simplified, juveniles retain an occlusal design unique among known phyllotines. In individuals with little wear, an incipient paraflexus has been preserved, an open mesoflexus framed by the paralophule and metalophule of moderate size; the hypoflexus is deeply penetrating and its base changes direction in a 90° angle. With wear, a mesofossette is generated, which sometimes meets the hypoflexus, while every trace of the paraflexus disappears. The anterior root is larger than the posterior root and partially forked at the distal end.

The m1, like M1, is enlarged but with a tetralophodont pattern; procingulum with asymmetric rhomboidal outline, stretched toward the lingual edge, and lacks any trace of an anteromedian flexid or anterolabial cingulum; metaflexid transversely oriented with its base opposite that of the protoflexid, forming a short anterior murid of medial position; posterior murid somewhat oblique; metalophid and entolophid similarly developed and transversely positioned; posterolophid very short and oblique; some molars with 2 small accessory roots at the labial edge.

The m2 has protoflexid absent; mesoflexid with its based oriented slightly forward, near the hypoflexid, forming a slightly oblique murid; posterolophid, proportionally more developed than m1 and well defined by a moderate distoflexid (sensu Hershkovitz 1993) points backwards; very large anterior and posterior roots.

The m3 is almost as long as m2; vestigial mesoflexid even in individuals with rela-

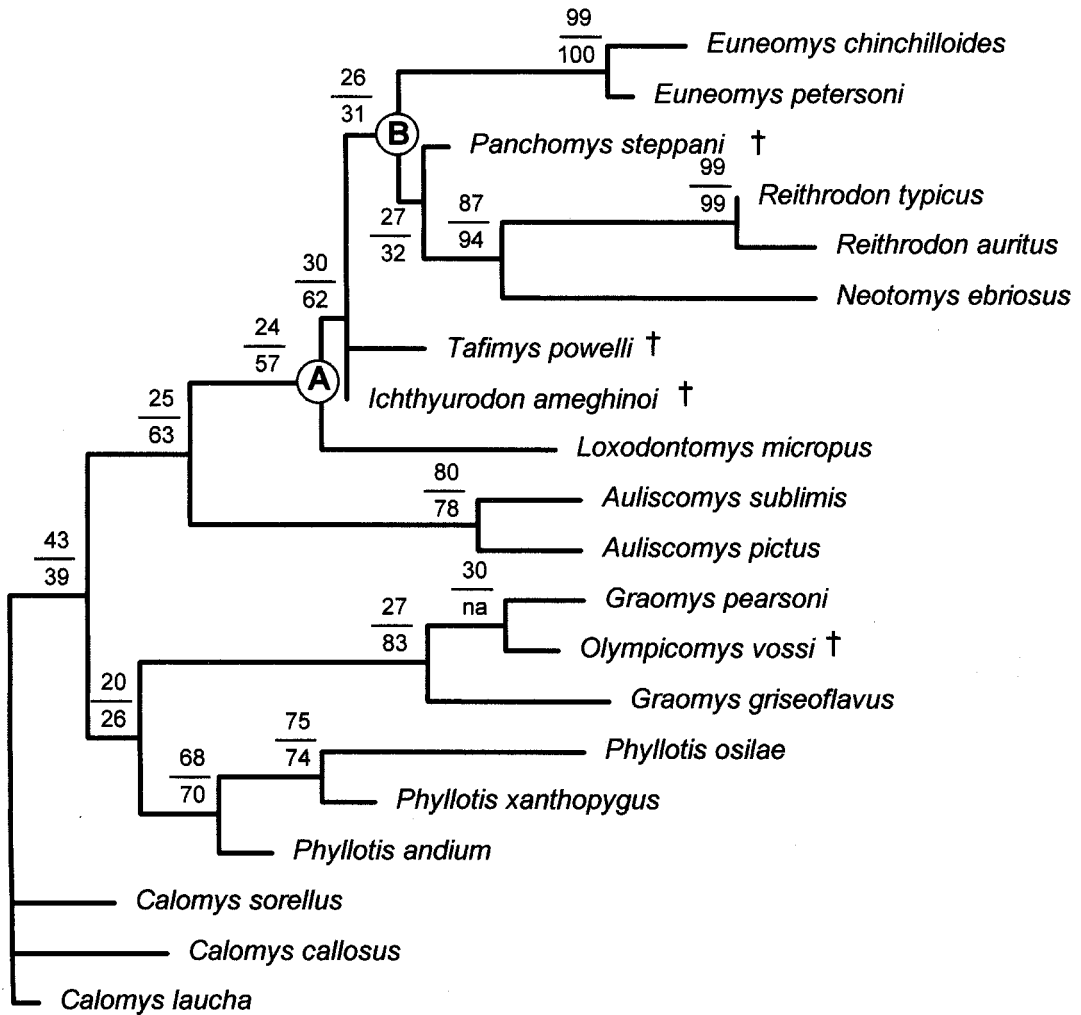


FIG. 5.—Phylogram of 1 of 3 most-parsimonious trees from the phylogenetic analysis. Branch lengths are proportional to the number of unambiguous character state changes. Node A defines the *Reithrodon* group sensu lato and node B defines the *Reithrodon* group sensu stricto (Steppan and Pardiñas 1998). Numbers to the left of nodes are the bootstrap percentages, including (above) and excluding (below) *Olympicomys*.

tively unworn teeth, which causes loss of the sigmoid pattern; hypoflexid deeply penetrating in the occlusal plane, more than the $m1-2$; anterior and posterior roots of equal size.

Etymology.—In honor of Jaime Powell, for his contributions to the development of vertebrate paleontology in northern Argentina.

Phylogenetic analysis.—The phylogenetic analysis yielded 3 most-parsimonious

trees, each 283 steps long. In all 3 trees, *Tafimys* was placed within the *Reithrodon* group sensu lato (node A, Fig. 5). The 3 trees differ in their placement of *Tafimys* within this group. In 1 tree, *Tafimys* is the sister group to the *Reithrodon* group sensu stricto (node B), whereas in the other trees it is either sister to *Ichthyurodon*, or basal to the clade formed by *Ichthyurodon* and the *Reithrodon* group sensu stricto. Bootstrap support for placement of *Tafimys*

within the *Reithrodon* group sensu lato initially seems low (30% for *Tafimys* + node B and 24% for node A), but uncertainty regarding relationships in this region of the tree are due to the paucity of phylogenetically informative characters preserved in *Ichthyurodon* or *Olympicomys* (Steppan and Pardiñas 1998). *Olympicomys* lacks many synapomorphies and has a composite suite of traits that makes estimation of its relationships particularly unstable (Steppan and Pardiñas 1998). Bootstrap percentages calculated when *Olympicomys* is excluded rise to 62% and 57%, respectively. *Ichthyurodon* is similarly plesiomorphic for most dental traits but does have several distinctive autapomorphies (excluded from analysis because they are not parsimony informative) that allow for its unequivocal definition. When *Ichthyurodon* is also excluded from the analysis, bootstrap percentages increase to 84% and 69%, respectively.

DISCUSSION

Phylogenetic relationships.—The phylogenetic analyses place *Tafimys* within the *Reithrodon* group sensu lato with moderate to high confidence. Uncertainty regarding its precise phylogenetic relationships comes primarily from *Ichthyurodon*, for which several key characters have not been preserved; for example, upper incisor grooves and fissures, angled premaxillary–maxillary suture, procingula on lower molars. Given the very hypsodont molars of *Tafimys* that it shares with the *Reithrodon* group and the uncertainty regarding *Ichthyurodon*, our preferred hypothesis is that *Tafimys* is the sister group to the *Reithrodon* group sensu stricto.

Putative synapomorphies uniting *Tafimys* with the *Reithrodon* group sensu stricto are strongly grooved upper incisors, m1 anterolabial cingulum absent, m2 procingulum absent, M3 flexus axes unrotated relative to M2, M3 hypoflexus not reduced, m3 mesoflexid not shifted in position, and hypsodont molars. *Tafimys* shares a tripartite dentine fissure in the upper incisors with

Loxodontomys and the *Reithrodon* group, whereas it lacks the angled premaxillary–maxillary suture that is unique among New World muroids to the *Reithrodon* group sensu stricto.

Tafimys seems to possess a nearly transitional morphology between the generalized phyllotine condition and specialized morphologies in the *Reithrodon* group sensu stricto. Molars have become more simplified in structure while becoming more lophodont and hypsodont, changes associated with adaptation to grazing on abrasive vegetation (Hershkovitz 1955, 1962, 1993). *Tafimys* does not seem to have evolved any of the distinctive autapomorphic molar features that distinguish *Euneomys*, *Neotomys*, and *Reithrodon* from each other (Steppan 1995). The lack of highly derived autapomorphies suggests that *Tafimys* may have retained more plesiomorphic states in other characters.

Inclusion of *Tafimys* into phylogenetic analyses also strengthens support for the hypothesis that *Loxodontomys* is closely related to the *Reithrodon* group (Steppan 1995). Bootstrap values for the *Reithrodon* group sensu lato (node A) are higher when *Tafimys* is analyzed with the extant taxa than when only the extant taxa are studied (69% versus 35%; Steppan 1995), although fossil analyses do not include all phyllotine species. This again points out the value of combining fossil and living material in phylogenetic studies rather than looking at only one or the other. Most rodent fossils do not preserve enough character data to produce robust independent phylogenies, whereas living species represent just a subsample of the evolutionary history of the group, and less information about ancestral states.

Tafimys powelli during the late Pleistocene.—Taxonomic comparison of fossil mammalian faunas with extant ones is a common paleoecological method (Andrews 1995). Nonetheless, because ecological affinities of extinct species are unknown, mistaken paleoenvironmental inferences can be reached (Lister 1992). Because this is the

case with *T. powelli*, evaluating its functional morphology is appropriate. Specializations in the chewing apparatus of *T. powelli* include flat-crowned and highly hypsodont molars, simplification of the occlusal patterns, thick enamel, and deeply folded flexi and flexids. The degree of hypsodonty is greater than in *R. auritus*. Rensberger (1975) related hypsodonty to qualitative and quantitative differences in dietary composition. Among muroid rodents, brachydont forms eat seeds, fruits, and insects, whereas hypsodont taxa eat herbs, foliage, grass, or bark. Seed endosperm and fruit are less abrasive than stems and leaves of grass, with the latter containing higher percentages of silica (Bredon and Wilson 1963). Dental characteristics of *T. powelli* clearly suggest adaptation to a diet high in silica as is common in open grasslands.

Characteristics such as frequency of skeletal elements, preservation condition, and size of species indicate that remains of *T. powelli* formed part of a micromammalian fossil assemblage produced by owls, probably a predator similar in size to *Tyto alba* (P. E. Ortiz, in litt.). The agent of accumulation is of great importance regarding the paleoenvironmental reconstruction because it allows determination of contemporaneity of the taxa and their sympatry (although not syntopy). The associated fauna, 13 extant muroid and caviomorph rodents, contributes information about the local paleoecology. At the present time, the plant communities at the outcrop area (1,900 m elevation) are characterized by the dominance of high-altitude grasslands and mesophytic shrubs (*Cynodon dactylon*, *Poa annua*, *Sporobolus berterioanus*, *Bromus unioloides*, *Paspalum humboldtianum*, *Stipa*, and *Festuca*) in conditions of moderate moisture (Cabrera 1976; Meyer and Weyrauch 1966; Vervoort 1981, 1982). Nearby monospecific forests of alder ("aliso," *Alnus acuminata*) are found in areas on humid slopes with southern exposure (Bell 1991). Among sigmodontines that now live in the area, some species are exclusive to open en-

vironments (e.g., *Phyllotis xanthopygus*) and others inhabit high-altitude grasslands as well as moist forests located at a lower elevations (e.g., *Abrothrix illutea*, *Andinomys edax*, *N. lactens*, and *O. paramensis*). At present in the Tafí del Valle area, *R. auritus* is restricted to high-altitude grasslands >3,000 m elevation.

The taxa in the fossil sample suggest a general environment of open areas. The association of *Abrothrix* cf. *A. illutea*, *Necromys* cf. *N. lactens*, and *Andinomys edax* indicate an environment of high-elevation grasslands similar to that presently dominant in the upper level of the Yungas Phytogeographic Province (sensu Cabrera 1976). Furthermore, presence of *Calomys* and *R. auritus* supports the existence of open areas of grassland and herbaceous vegetation. Because of its highly restricted distribution *N. ebriosus* is the species that permits paleoenvironmental inferences with the highest degree of certainty. This sigmodontine inhabits highlands (Puna and High Andean Phytogeographic Province, sensu Cabrera 1976) of northwestern Argentina and southwestern Bolivia, and humid grasslands near streams >3,000 m in southern Peru (Bárquez 1983; Sanborn 1947).

The presence of *Neotomys* and *Reithrodon* in the fossil sample suggests more severe local paleoenvironmental conditions, with lower temperature and less moisture than at present, and this is probably related to glacial events in the Late Pleistocene. The influence of the Upper Pleistocene glaciations extend through all South American Andes, including the tropical and subtropical regions (Simpson 1979). At the Tafí del Valle Formation, deposited during the last glacial events 10,000–30,000 years ago, geomorphologic and sedimentologic evidence indicates great climatic variability by the presence of paleosols interbedded with loess (Collantes et al. 1993; Sayago 1995; Zinck and Sayago 1999). The presence of loess in the sequence, in which the micromammal association was found, is related

to cold and dry periods (Collantes et al. 1993). In Tucumán Province, glaciers occupy the mountain ridges near Tafi Valley, such as Nevados del Aconquija (Rohmeder 1942), at present with permanent snow >5,250 m, and Cumbres Calchaquíes (Arcuri 1988; Halloy 1978). The extension of the glaciers in these areas was lowered to 4,000 m, and even to 3,800 m in protected places (Halloy 1978; Rohmeder 1942). This must have caused contraction and lowering of vegetation belts on mountain slopes, and an increase in the superficial extent of vegetative zones of the upper elevation, although this effect is difficult to quantify (Halloy 1978). The high-elevation micro-mammal communities must have responded to these environmental changes by following the descent of the vegetative zones, such as *Neotomys* and *Reithrodon* did.

A paleoenvironment of high-elevation grassland, which at present develops at ca. 3,000 m in the subtropical region, is consistent with the inferences from the specialization of the chewing apparatus of *Tafimys*. Although presence of *Neotomys* would directly imply existence of a Puna or High Andean environment, the association of *Neotomys* with other sigmodontines, particularly those that inhabit grasslands of upper elevations of the Yungas, better suggests an ecotonal community, as was suggested by Vervoort (1982).

Nevertheless, caution is necessary in using sigmodontines as paleoecological indicators because their distribution is linked tightly to the microenvironment. Factors such as environmental heterogeneity, vegetation patches, and probable presence of relictual species adapted to previous environmental conditions currently preclude extrapolating inferences to regional scales. Furthermore, the fossil sample of La Angostura could be a no-analogue assemblage (Graham and Grimm 1990), such as those detected in Pleistocene–Holocene beds of the Argentinean pampean region (Pardiñas 1999). More samples are needed to improve our knowledge of the Quaternary environ-

ment of northwestern Argentina and to evaluate the influence that climatic fluctuations of the late Pleistocene had on the distribution of sigmodontines.

Paleobiogeography of the Reithrodon group.—Given our new understanding of the diversity of this clade and the presumably adaptive origin of their highly derived dental and cranial features, considering the biogeographic context of the radiation is worthwhile. Few hypotheses have been proposed for the paleobiogeography of the living representatives of the *Reithrodon* group, due in part to the relatively recent proposal that *Euneomys*, *Neotomys*, and *Reithrodon* form a monophyletic group (Olds and Anderson 1989; Stepan 1993, 1995). Reig (1986) considered these genera to be derived from an ancestral stock that would have invaded the south Andean area in the early Miocene and later dispersed toward lowlands. Braun (1993:38) proposed a differentiation of *Neotomys* and *Reithrodon* in the “pampean ranges or in the ranges of the precordillera that developed in northwestern Argentina during the late Miocene and throughout the Pliocene,” whereas *Euneomys* would have had a separate origin from a *Phyllotis* ancestor in the Andean region. However, part of Braun’s (1993) hypothesis (e.g., the distributional hypothesis for *Euneomys* during the Pleistocene) was based on the identification of fossil remains (“*E. catenatus*”) that have since been recognized as *Graomys* (Pardiñas 1995b).

The *Reithrodon* group principally occupies the Southern Cone of South America, above 35°S (Fig. 6). *Reithrodon* and *Euneomys* occur in open areas, shrub steppes, herbaceous steppes, and ecotone areas bordering *Nothofagus* forests. *Loxodontomys* occupies similar habitats, although linked more to austral forests (Pearson 1995). North of 35°S in western Argentina, *Reithrodon* is found in a few isolated localities and restricted to high-elevation grasslands. *Reithrodon* also occupies the pampean prairie, reaching as far as Uruguay and southern tip of Brazil (Barlow 1969).

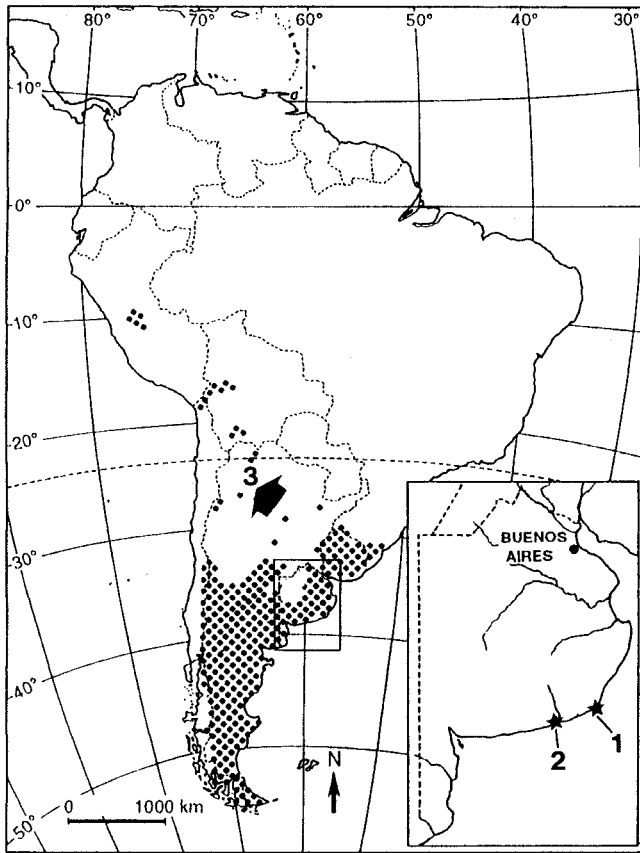


FIG. 6.—Approximate present distribution in South America of extant representatives of the *Reithrodon* group (dotted area) and type localities of the extinct phyllotines discussed in the text: 1) *Panchomys*; 2) *Olympicomys* and *Ichthyurodon*; 3) *Tafimys*.

The earliest fossils for the generic group belong to *Reithrodon*. Presence of any diagnosable *Reithrodon* also indicates that lineages leading to all members of the generic group had diverged by that time. This is a consequence of the phylogeny in which *Reithrodon* is the most recently diverged lineage (Norell 1993; Norell and Novacek 1992). The earliest fossil record for *Reithrodon* is from Farola de Monte Hermoso (southwestern Buenos Aires province), with a middle-upper Pliocene age (Pardiñas and Tonni 1998). The earliest records for *Euneomys* and *Neotomys* are late Pleistocene in Patagonia and late Pleistocene in northwestern Argentina, respectively (Pardiñas 1999). *Panchomys*, *Ichthyurodon*, and *Taf-*

imys are from the late Pliocene of eastern Argentina, early Pleistocene of eastern Argentina, and late Pleistocene of northern Argentina, respectively. Thus, extensive ghost lineages (Norell and Novacek 1992) must be hypothesized for all these other genera. This produces a quandary regarding why so much of the fossil history is missing, given that at least 1 member of the group (*Reithrodon*) has an extensive fossil record. It may be that only *Reithrodon* occupied the habitats that produced the major fossil finds. If so, we can predict that after other geographic and stratigraphic horizons are sampled, other members of the generic group will have remains as old or older than *Reithrodon*.

Alternative explanations are that early fossils attributed to *Reithrodon* instead to earlier common ancestors. This would require that these ancestors had more extreme dentitions than some of their descendants, an unlikely prospect although not impossible. Finally, the phylogeny could be wrong. This alternative would be consistent with mitochondrial DNA phylogenies that indicate that *Reithrodon* is not nested within the phyllotines but may instead be a close relative (Engel et al. 1998; Smith and Patton 1993). Unfortunately, phyllotine sampling in those 2 studies was limited, and no other members of the *Reithrodon* generic group sensu lato were examined at all, so monophyly was not tested. Clearly, the addition of just a few new samples for DNA sequencing could have a significant impact on our interpretation of these fossils.

Evidence is insufficient to determine the original area of differentiation (sensu Reig 1986) for these phyllotines. However, biogeographic data and morphologic adaptations allow us to propose a model that might be tested by new data. The desertification of the southern end of South America, beginning at the start of the Miocene, caused the disappearance of the tropical-subtropical fauna that until then had characterized the Patagonian area, with more pronounced effects in the south (Pascual and Ortiz Jaureguizar 1990). Associated with this phenomenon, a group of distinctive akodontines and phyllotines may have evolved, mainly species-poor genera including the akodontines *Pearsonomys*, *Abrothrix*, *Chelemys*, *Geoxus*, and *Notiomys*, and the phyllotines *Loxodontomys*, *Irenomys*, *Ichthyurodon*, *Panchomys*, *Euneomys*, *Reithrodon*, and possibly *Tafimys*. The latter 4 show adaptations to grazing in grassland areas and herbaceous steppes, including increased hypsodonty, flat crowns, and shape and height of the zygomatic plates. Numerous glaciations starting in the Pliocene promoted expansion of these taxa toward the north and east. Dispersal of *Reithrodon* into the pampean region and

other sectors of central and northeastern Argentina could be considered an early, perhaps Pliocene, event within the context of a landscape similar to the patagonic steppe for most of the pre-Holocene history (Clapperton 1993; Tonni and Cione 1997).

Tafimys raises new questions about the sigmodontines of southern South America, because it is the only genus known to have gone extinct at the end of the Pleistocene. For middle latitudes in South America, no extinctions of muroid rodents were recorded in the last $0.7-0.5 \times 10^6$ years (Pardiñas 1995a, 1999). Still, it remains possible that *Tafimys* survives today in high-elevation refuges in northern Argentina and Bolivia, areas that are still little explored.

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APPENDIX I

Characters states for Tafimys used in the phylogenetic analysis.—See Steppan (1995) for detailed explanation: 1) deep mediolateral groove on upper incisors; 2) upper incisors opisthodont; 3) upper incisor dentine fissure tripartite, Y-shaped; 4) labial root of M1 present, small, set medially; 5) 2 roots in M3; 6) labial root of m1 present; 7) 2 roots in m2; 8) 2 roots in m3; 9) anteromedian flexus of M1 absent or limited to shallow groove; 10) mesostyle of M1 absent; 11) parastyle–anteroflexus of M1 absent; 12) flexi from opposite sides do not reach each other in M1; 13) anterolabial cingulum of m1 absent; 14) protoflexid of m1 absent; 15) primary cusps opposite in position in m1; 16) anteromedian flexid of m1 absent or limited to a shallow groove; 17) procingulum attached by anterior mure in m1; 18) posterolophid–stylid of m1 intermediate; 19) posterolophid–stylid of m3 absent; 20) anteroflexus of m2 appears as groove; 21) procingulum of m2 absent; 22) hypoflexus of M3 not reduced relative to M2; 23) mesoflexus of M3 highly reduced relative to M2; 24) mesoflexus of M3 not shifted relative to M2; 25) hypoflexus of M3 present, without to form a lake; 26) hypoflexus and mesoflexus of M3 not rotated relative to M2; 27) mesoflexid of m3 highly reduced relative to m2; 28) mesoflexid of m3 not shifted relative to m2; 29) hypoflexid m3 not shifted relative to m2; 30) flexi do not meet in M3; 31) ratio of M3 length to alveolar length of molar tooth row = 0.241; 32) capsular projection of mandible distinct; 33) height of coronoid process above maximum height of mandibular condyle; 34) anterior masseteric ridge

slightly below dorsal edge of mandible; 35) medioventral process of mandibular ramus weakly present; 36) posterior extent of incisive foramina reach level with anterolabial and anterolingual conules of M1; 37) posterior margin of zygomatic plate subequal to M1 alveolus; 38) moderate development of zygomatic spine; 39) in-

clination of zygomatic plate $> 20^\circ$; 40) premaxillary-maxillary suture oriented dorsoventrally, not sharply angled in middle of rostrum; 41) posteriorly divergent maxillary tooth rows; 42) hypoflexus of M2 oblique, directed toward the paraflexus; 43) no torsion of m1 procingulum; 44) m3 larger than m2.