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Phylogenetic Relationships Among the Phyllotini (Rodentia: Sigmodontinae) Using Morphological Characters

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Thirty-three species representing all 14 genera of the South American rodent tribe Phyllotini and 5 problematic genera are surveyed for 96 multistate and binary dental, cranial, skeletal, external, and male reproductive tract characters. Wagner parsimony analysis confirms *Calomys* as the most basal phyllotine genus, and as currently constituted it is likely paraphyletic. The results are consistent with the exclusion of *Pseudoryzomys* from the phyllotines and the separation of *Reithrodon* and *Neotomys* from *Holochilus* at the tribal level. Several highly differentiated generic groups that include a radiation of altiplano endemics centered on *Auliscomys* and the largely southern Andean/Patagonian *Reithrodon* group appear to form a clade. A *Graomys* generic group that includes *Andalgalomys* and *Eligmodontia* is also apparent, but its relationships to other phyllotines are obscured by poorly resolved internal nodes in the more species-rich and probably paraphyletic genus *Phyllotis*. The significance and consequences of more intensive taxonomic sampling are discussed. The taxonomic consequences of the phylogeny are presented.

KEY WORDS: Phyllotini; phylogenetics; South America; rodents; morphology.

INTRODUCTION

Morphologically diverse and ecologically prominent, the mice and rats of the tribe Phyllotini comprise the most tractable taxon for phylogenetic analysis of the major radiations of muroid rodents in South America. Phyllotine species boundaries and interspecific relationships are better delimited than in the two other major radiations of the Neotropical subfamily Sigmodontinae, the oryzomyines and the akodontines. However, despite many studies on phyllotine taxonomy, karyology, and ecology, their phylogeny remains poorly resolved. A robust phylogeny should yield important insights into the complex but poorly known biogeographic history of the Andes and the arid regions of South America. This paper presents a comprehensive phylogenetic analysis for all phyllotine genera and most of the 40 to 45 species by broadly surveying morphological systems.

Debates on the evolution of the phyllotines have focused on four issues: (1) the

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proper identification of those members belonging to the phyllotine group, (2) the phylogenetic relationships among the species of this clade, (3) the relationship of phyllotines to the other sigmodontine rodents, and (4) identifying the continent on which the phyllotines originated. Phyllotine membership and defining characters have fluctuated among studies, but nearly all workers have recognized the following taxa as phyllotines: *Andalgalomys*, *Andinomys*, *Auliscomys*, *Calomys*, *Chinchillula*, *Eligmodontia*, *Galenomys*, *Graomys*, *Irenomys*, and *Phyllotis*. Problematic taxa have included *Euneomys*, *Holochilus*, *Neotomys*, *Pseudoryzomys*, *Punomys*, *Reithrodon*, *Sigmodon*, and *Zygodontomys*. The phylogeny of the phyllotines proper is the principal objective of this paper, and nearly all phyllotine species are included in the analysis. This study does not constitute a robust test of phyllotine monophyly because outgroups are much less thoroughly sampled than the phyllotines, and characters were chosen principally for their variation among phyllotines rather than among the tribes of the Sigmodontinae. The latter two issues are not directly addressed here. Paleontologists have been more active that neontologists in addressing the fourth issue on continental origins. Fossil teeth and mandibles, purportedly phyllotine, from the late Miocene of North America have been pivotal to polarizing commonly espoused sigmodontine biogeographic scenarios (Baskin, 1978; Czaplewski, 1987; Jacobs and Lindsay, 1984) and potentially the Great American Interchange (Marshall *et al.*, 1982).

Native muroid rodents are represented in South America exclusively by the subfamily Sigmodontinae Wagner 1843. Debate continues as to whether this taxon includes the North American cricetines, the neotomine–peromyscines (Carleton and Musser, 1984; Musser and Carleton, 1993), or is limited to the predominantly South American species *sensu* Reig (1980, 1986). The northern and southern continental groups have also been characterized as having "simple" and "complex" penis types, respectively (Hershkovitz, 1966; Hooper and Musser, 1964). In this paper, I adopt the taxonomy of Reig (1986).

The sigmodontines are conventionally subdivided into a set of tribes, first formalized by Vorontsov (1959), or referred to informally as "generic groups." Reig (1980) recognized seven tribes, ordered here from largest to smallest by estimated number of species (after Musser and Carleton, 1993): Oryzomyini (oryzomyine group, 85; thomasomyine group, 48), Akodontini (77), Phyllotini (46), Ichthyomyini (14), Sigmodontini (14), Scapteromyini (6), and Weidomyini (1), plus four small genera *incertae sedis* (5). The thomasomyine group within the Oryzomyini and the oxymycterine group within the Akodontini are sometimes elevated to equal rank with the tribes. The sigmodontines are ecologically diverse, occupying sylvan, pastoral, fossorial, and aquatic habitats from sea level to over 5000 m (Pearson, 1958).

Hershkovitz (1962, Fig. 2) portrayed the phyllotines as a monophyletic group derived from an akodont stock. In his detailed revision of the phyllotines and commentary on sigmodontine morphological evolution, he included *Zygodontomys* and *Pseudoryzomys* but excluded *Reithrodon*, *Neotomys* (both of which he considered sigmodonts along with *Sigmodon* and *Holochilus*), *Euneomys* (closely related to both phyllotines and sigmodonts), *Irenomys*, and *Punomys*. He identified the "primitive" *Calomys* section, with *Calomys*, *Eligmodontia*, and *Zygodontomys*. In the "advanced" *Phyllotis* section, in one lineage he placed *Pseudoryzomys* as the sister taxa to *Galenomys* and *Phyllotis*

(encompassing *Auliscomys* and *Graomys*), and in the other lineage he placed *Andinomys* and *Chinchillula*.

The glans penis of neotropical cricetines was first examined systematically by Hooper and Musser (1964), who inferred evolutionary relationships from their qualitative estimates of overall phallic similarity. They diagrammed *Zygodontomys* outside the phyllotines near the base of the sigmodontine radiation (1964, Fig. 8), although their discussion suggests that it could also be placed at the base of the phyllotines. The similarity of *Eligmodontia* and *Akodon* could lead to the interpretation of *Eligmodontia* as either a basal phyllotine or an akodontine. They suggested that *Holochilus* was best placed with the oryzomyines. *Reithrodon* was placed as a basal phyllotine. *Neotomys* and *Pseudoryzomys* were not examined.

Pearson and Patton (1976) and Gardner and Patton (1976) included within the phyllotines *Andinomys*, *Auliscomys*, *Calomys*, *Chinchillula*, *Eligmodontia*, *Neotomys*, *Phyllotis* (including *Graomys*), and *Reithrodon*. Their analyses relied on similarity in number and form of unbanded chromosomes. They explicitly excluded *Zygodontomys* and did not examine the genera *Andalgalomys* (member species first described in 1977), *Euneomys*, *Galenomys*, *Irenomys*, *Pseudoryzomys*, and *Punomys*. A diagram of evolutionary relationships (Pearson and Patton, 1976, Fig. 5) placed two groups, *Graomys* and *Reithrodon* + *Auliscomys*, within a *Phyllotis* lineage. *Eligmodontia*'s position is unclear, but *Neotomys* was far removed from *Reithrodon*.

Spotorno (1986) explored the radiations of the akodontines and phyllotines (which he viewed as sister groups) using banded karyotypes, electrophoresis, glans penis and bacular morphology, and cranial morphometrics. Though he drew no definite conclusions about phylogenetic relationships among genera, he included in parts of his analysis *Andinomys*, *Auliscomys*, *Calomys*, *Chinchillula*, *Eligmodontia*, *Euneomys*, *Graomys*, *Irenomys*, *Phyllotis*, and *Reithrodon*. Spotorno did not explain why he placed *Reithrodon* in the phyllotines but placed *Neotomys* in the sigmodonts. *Punomys* was listed as Sigmodontinae *incertae sedis* but not analyzed. *Pseudoryzomys* and *Zygodontomys* were not addressed.

The first formal diagnosis and the most implicitly cladistic treatment of the phyllotines was presented by Olds and Anderson (1989). They included *Punomys* and excluded *Pseudoryzomys* and *Zygodontomys*. In surveying 33 sigmodontine genera (14 phyllotine and 19 nonphyllotine), they found no unique synapomorphies for the phyllotines. All phyllotines were found to have the following combination of characters: "hairy heel, ears moderate to large, palate long (except in *Irenomys*), incisive foramina long, parapterygoid fossa relatively broader than mesopterygoid fossa (except in *Punomys*), sphenopalatine vacuities large, supraorbital region never evenly curved in cross section, interparietal well developed, zygomatic notch deeply excised (less so in *Irenomys*), teeth tetralophodont, M3 more than half the length of M2" (Olds and Anderson, 1989, p. 63).

Olds and Anderson (1989) also diagnosed a distinct "*Reithrodon* group" that included *Euneomys* and *Neotomys*. They alluded to a relationship of this group to the remaining sigmodonts (*Holochilus* and *Sigmodon*) but left this relationship unspecified. From phenetic and cladistic analyses, Braun (1993) considered *Pseudoryzomys* to be the most basal phyllotine but did not recognize a *Reithrodon* group. Instead, she found

support for including the members of the putative *Reithrodon* group in a clade with *Auliscomys*, *Andinomys*, *Chinchillula*, *Galenomys*, *Irenomys*, and *Punomys*. She also found *Calomys* and *Eligmodontia* to occupy basal positions and that both *Phyllotis* and *Auliscomys* were paraphyletic.

This study follows Olds and Anderson (1989) in defining phyllotine taxa, with the exception of *Punomys*. A cladistic analysis of 28 sigmodontine taxa provides a provisional hypothesis of sigmodontine relationships and phyllotine monophyly (Steppan, unpublished manuscript). That analysis includes characters not part of this study that support the monophyly of Phyllotini and other tribes (e.g., mesoloph, hemal arch, mammae). The sigmodontine phylogeny indicates that *Punomys* lies outside the phyllotines, near the base of a phyllotine–akodontine–scapteromyine radiation. Putative synapomorphies supporting this definition of Phyllotini are the moderate to large ears (>0.16 head and body length), the parapterygoid fossa being broader than the mesopterygoid fossa (narrower in *Punomys*), the very open sphenopalatine vacuities (partially constricted in *Punomys*), and the complete loss of a mesoloph (present in *Punomys*). Plesiomorphic characters for the phyllotines that serve to distinguish them from other sigmodontines include the presence of eight or more mammae, a long palate, the incisive foramina reaching the molars, a deeply excised zygomatic notch, the absence of a hemal arch at the base of the tail, and the presence of a gall bladder. The tribal affinities of *Punomys* have usually been treated with uncertainty (Musser and Carleton, 1993; Osgood, 1943, 1947; Reig, 1980; Spotorno, 1986), with it often being classified as Sigmodontinae *incertae sedis*. Reig (1986) suggested that *Punomys* was descended from protophyllotine stock or an independent oryzomyine offshoot.

Pseudoryzomys, *Zygodontomys*, and *Holochilus*, three genera that have at times been included in or proposed to be derived from the phyllotines, are considered here to be oryzomyines. Voss and Carleton (1993) include these three genera in their diagnosis of the Oryzomyini. The hypothesis of sigmodontine relationships used in this study is in full agreement, hypothesizing the following characters as oryzomyine synapomorphies: the presence of 12 thoracic rib pairs, the presence of a hemal arch, the absence of a gall bladder, the presence of eight or more mammae, and a long palate (except *Holochilus*). Importantly, these tribal definitions were not codified into *a priori* constraints on the phylogenetic analysis.

MATERIALS AND METHODS

Estimates of the number of phyllotine species vary with group limits and specific status of taxa, with most estimates between 40 and 45. This study included 37 taxa representing 33 putative species in 14 phyllotine genera, in addition to 12 species belonging to 11 outgroup genera (see Table I, with tribal classification). Character assessments were made from direct examination of museum specimens (Field Museum of Natural History, FMNH; Museum of Vertebrate Zoology, MVZ; U.S. National Museum, USNM; University of Michigan Museum of Zoology, UMMZ), with the exception of the undescribed species from Tapecua, Bolivia. For this taxon, most characters were coded by Dr. S. Anderson and the remaining characters assessed from photographs in consultation with Dr. S. Anderson. Phallic measurements for some species were taken from published illustrations (Hooper and Musser, 1964; Spotorno, 1986). Evidence of

Table I. Character Matrix and Tribal Classification for Species Included in Phylogenetic Analysis

	1	10	20	30	40	50	60	70	80	90	96
Thomasomyines:											
Thomasomys baeops	010???????1	1222102022	3112100000	0110021111		0110011200	0221113?01	1101010300	1110020207	??10112000	??????
Oryzomyines:											
Nectomys squamipes	0107101802	1022002022	3110000000	0110010?02		0021002300	0200020101	0100000100	1110001?02	0010?02010	000??0
Holochilus brasiliensis	01?2001110	0022?12020	31?????000	0?10011102		002?001300	002?010107	0002107300	117001????	??01?02010	000??0
Pseudoryzomys simplex	00020?1113	1021002021	1110100010	01100111{0,1}1		0031001300	01?0101101	1100200100	0100001???	??00101000	?????0
Zygodontomys brevicauda	0100000113	1021002021	1110100010	0110011112		0011002300	0110011101	0100110100	1100101202	0000100010	000??0
Akodontines:											
Akodon albiventer	0107121000	1002011011	2121100100	0010000120		0001001100	0003103101	1100201310	0201310000	0010100100	?00000?
Akodon boliviensis	0107101001	1102011021	2121100010	0010000120		0001001000	0030101100	2100201300	1200310000	0010100120	0?0??1
Chroeomys andinus	0100001??0	1102011010	2121111000	0010010111		0001001100	0030202101	2100300100	1200310001	0010101110	??????
Oxymycterus hispidus	0117110001	0111011010	11????0?000	0011000211		?001001200	011001{1,2}101	0100017300	1210307???	???1210011	?????1
Scapteromyines:											
Scapteromys tumidus	0211001110	1111010021	2?22111000	0000000{0,1}11		0020001100	0110012117	1{0,1}0?21?200	0110307???	??21??2100	??0??1
Sigmodontinae incertae sedis:											
Punomys lemminus	010???????1	1202001020	2110000110	0211000011		1100011200	1230121101	1012201101	1021300107	?0201111100	??????
Ichthyomyines:											
Ichthyomys hydrobates	0100020000	0000000000	0011000000	0001000001		00?00?1000	0000010?01	0100000000	0110020217	??10?02200	010001
Phyllotines:											
Andalgalomys pearsoni	0102001111	0001013010	1000000000	1100020211		0021002300	0230102007	2110310100	0121311207	??10010000	?????1
Andinomys edax North	012???????0	0012021020	3202000210	0?11001111		1121010201	2210112111	1101300310	1011300102	0?10110200	000??1
Andinomys edax South	0101011000	0012021020	3202000210	0?11001111		1131010201	2211112112	1101300310	1011200102	0010110200	?????1
Auliscomys boliviensis	121101???0	0001017020	2000001211	0111110011		0200010200	0111213001	2100300110	0111300101	0?10011200	000???
Auliscomys pictus	2?11007001	0011012020	2111001111	0111011021		0100011200	012?212000	2101300100	0111200101	0?20110100	010021
Auliscomys sublimis	2211001000	0002113020	2100001211	0111011021		0100000100	0121112000	2100300100	0111030000?	?120110100	?1002?
Calomys callosus	0002001111	1102010020	2120101110	0010020111		0011002300	0130111101	2100300000	0111301001	0010111100	100??1
Calomys hummelincki	0102001111	1?02010020	2110700010	00000101{1,2}1		0011002300	0237111101	2100300000	0111301??	??10011000	??????
Calomys laucha	0002001111	1112011020	2110101110	0010020?11		0011002300	0131112001	2100300100	0101300001	0?10011100	100???
Calomys lepidus	0102001111	1112011020	1110111111	0011010211		0010011200	0122113000	2110300010	0211300001	0010012100	?????0
Calomys sorellus	0102001??1	1002111020	2122011110	0017010211		0011001200	0221112000	2100300100	0111300101	0?10011110	100017
Chinchillula sahamae	0112021100	1002117000	0101000110	0011011011		0200011210	02?1112111	1100300200	7111320101	0020011200	000??1
Eligmodontia morgani	0002001110	0001023020	2120101211	0010130211		0111002200	0231113000	2110300110	0201310101	0121?20100	000?21
Euneomys c. chinchilloides	2120000000	0020002121	1001010000	0111111111		0210111211	0211212111	2001300110	0011220011	1010010110	1??????
Euneomys c. petersoni	2120000000	0020002121	1001010000	0110211111		0210111211	0211212111	2001300110	0011220011	1011011110	?????1
Galenomys garleppi	0212071?11	0002117010	1110001210	0111020011		0100011200	0231112001	2100300100	0211200001	0?10?22200	??????
Graomys griseoflavus	0102001100	0022123020	2100001100	1000220211		0120002300	0221102001	2100310110	0101311101	1010000100	100?21
Graomys domorum	0102001?00	0022123020	2120111100	0000121211		0121002300	0221113001	2100310110	0101311107	??10010100	?????1
Irenomys tarsalis	3010000000	0012002000	0200000110	0211101121		1111011200	1231223011	1100300300	1011210201	0110002100	0?0?21
Loxodontomys micropus	0027111000	0122007020	3111101110	0110011121		0111011100	0211112001	2000300110	?0103001?1	0010011011	000???
Neotomys ebriosus	4020000110	0021023020	3001000100	0211212201		2231111201	1131112112	2002300311	0021100?02	0010110211	?????1
Phyllotis amicus	01?200?100	0012117020	2112111210	0010120211	0{0,1}20002200	0222123001		2101300110	0211207???	??10010000	000021
Phyllotis andium	0102001100	0012117010	2111011110	0010010111		0111001200	0221113001	2100300110	0211200201	0110000100	000021
Phyllotis caprinus	01020?????0	0012127020	1112011110	0100117?11		0110001200	0222112001	2100300110	0171300207	??10010100	2011??
Phyllotis darwini	0102011100	0012127010	1112111210	0101121111		0120001201	0222112001	2100300110	0211300101	0110010100	201?21
Phyllotis definitus	0112071?00	0072117010	??12111110	0110120011		0110011200	0222213000	2110300100	0211207????	??10010111	10?0??
Phyllotis gerbillus	0172011100	0012121020	1122110210	0010130211		0111002200	0231113001	2100300110	0211200107	?210112000	00????
Phyllotis haggardi	0102001000	0002127010	0121110210	0011020111		0110001200	0221123002	2100300000	0221200177	??10011100	10????
Phyllotis magister	0102001000	0012127010	1112111210	0010121111		0110011200	0211223000	2100300100	0101207??1	0?10100101	20112?
Phyllotis osilae	0102001100	0002113010	0012110210	0000021111		0110001100	0222113007	2200300110	1201300101	0110010101	{1,2}000?1
Phyllotis wolffsohni 01	{0,1}2001000	0012127010	1102100110	0100017?11		0121011300	0221212001	1100300100	0111200201	0000010101	000???
Phyllotis x. xanthopygus	0102011?00	0012127010	1112011110	0010011111		0110001200	0222112001	2100300100	027?300101	0110010100	20117?
Phyllotis x. rupestris	0102011100	0002127010	1012011110	0010121111		0111001200	0221112001	2100300100	0211300101	0110010200	20112?
Reithrodon auritus evae	30????????0	0021027020	31?????000	0?10121131		123?111211	0221023001	2022400211	0012011177	?011?27200	1?0?2?
Reithrodon a.pachycephalus	3022001100	0021022020	3100000000	0110121131		1231111211	0221023?01	2022400111	0012011171	0011?11100	100021
Reithrodon typicus	30????????0	0021022020	31?????000	0?10111131		123?111211	0221023?01	2022400111	0012017???	??11?17?7?	??????
species nova 01020	{0,1)1000	0010027022	?101101100	127011?2{0,1}1		012?002300	027011201?	2101307?7?	1110{2,3)20102	0010100011	??????

two pairs of preputial glands was adopted from the literature (Voss and Linzey, 1980) for some species. Gall bladder data are from Voss (1991).

A broad survey of characters from varied anatomical systems was conducted, resulting in 96 characters covering dental, cranial, postcranial, external, and male reproductive tract systems. Previous surveys have found little variation in soft anatomy among phyllotines that was not already evidenced in the skeleton (Carleton, 1973; Voss and Linzey, 1980; Voss, 1991). These 96 characters represent 268 character states and a minimum 172 character state transitions. Character state descriptions (Appendix) were defined so as to be more objective or quantitative than they have been in the past. Ambiguous terms such as "relatively broad," "large," and "well developed" were generally but not entirely avoided. Quantitative characters or those with quantitative components were measured using a digital caliper precise to ± 0.005 mm and values were rounded to the nearest 0.1 mm for coding. Character polarities were determined by outgroup rooting within the parsimony analysis. Characters were treated as ordered unless otherwise noted in the Appendix.

Outgroup taxa were selected to include representatives of each of the tribes and major generic groups (except the monotypic Weidomyini) of Sigmodontinae. This analysis used the preferred method of Maddison *et al.* (1984) when outgroup relationships are not well resolved, by simultaneously resolving ingroup and outgroup relationships under global parsimony. The resulting network was then rooted between *Thomasomys* and the oryzomyines, in accordance with an hypothesis of sigmodontine phylogeny (Steppan, unpublished manuscript) and consistent with the common estimate of basal sigmodontines (Hershkovitz, 1962; Reig, 1980, 1986; Voss, 1993; Voss and Carleton, 1993). *Sigmodon* was not included in the final analysis because previous molecular and morphological phylogenies were highly discordant on its position among sigmodontines. Albumin immunological distances placed *Sigmodon* outside a clade which included oryzomyines, akodontines, phyllotines, and ichthyomyines (Sarich, 1985), clustered it with the North American neotomines in phenetic (Spotorno, 1986) and cladistic (Steppan; unpublished reanalysis of data of Spotorno, 1986) analyses of electrophoretic data, and resulted in a highly unconventional tree topology when included in this data set (*Holochilus* and *Sigmodon* annectant between oryzomyines and *Graomys*; akodontines descended from a derived phyllotine genus, *Auliscomys*). Its phylogenetic position is thus highly problematic and the characters and taxonomic scope of this study are inappropriate to resolve the issue.

Phylogenetic hypotheses were generated under the principle of Wagner parsimony using the computer program PAUP, Version 3.1 (Swofford, 1993). Heuristic tree search algorithms were employed rather than the exact methods of exhaustive search or branch-and-bound, which required prohibitively long computer runs with the many taxa included in this study. Minimum-length trees were accumulated from multiple replicate analyses, each starting with a different random tree. Experience with this data set demonstrated that with this many taxa (>40), most single replicates will *not* find trees of the minimum length. Consensus trees were produced from distinctive subsets of the accumulated minimum length trees. The sensitivity of the resulting topology was tested by multiple runs in which particularly interesting or pivotal taxa or characters were excluded. Additionally, a 118-replicate bootstrap analysis was performed on the standard data set to provide nonparametric estimates for the confidence to be placed in each node of the tree. Bootstrapping randomly resamples the characters in the data set with replacement (Felsenstein, 1985). The tree search algorithm of PAUP can be constrained so that it retains

only those trees conforming to an *a priori* tree topology. The difference in tree length between the most parsimonious trees overall and the constrained trees provides additional information in evaluating alternative phylogenetic hypotheses. Twenty such hypotheses were evaluated, with as many as 54 replicate analyses run under a single constraint. Only unequivocal character state changes are reported as hypothetical synapomorphies. Consistency and retention indexes were calculated for each character. The consistency index (c.i.) is the minimum possible number of character state transformations divided by the number of times that character is hypothesized to change across a tree. The retention index (r.i.) is related to the c.i. and can be thought of as an estimate of the informativeness of a character in regard to groupings (Farris, 1989, p. 418).

Information on the specimens examined for this study, including specimen numbers and localities, can be obtained from the author upon request.

RESULTS

One hundred twenty equally most parsimonious trees were found. Each tree is 817 steps long, with an overall c.i. of 0.208 and an r.i. of 0.538. Most variation between trees involved minor branching shifts within *Phyllotis*, but two distinct subsets are apparent. Eighty-eight of the trees place *Punomys* as the sister taxon to the phyllotines (75% majority-rule consensus shown in Fig. 1), while the remaining 32 place it in a derived phyllotine clade with *Andinomys* and *Irenomys* (strict consensus shown in Fig. 2, pruned of branches to simplify viewing). The consensus trees of each subset are nearly identical to each other in both ingroup and outgroup topology, with the exception of where *Punomys* attaches to the trees. The hypothesis of sigmodontine phylogeny referred to in this study (Steppan, unpublished manuscript), whose broader survey of nonphyllotines and selection of characters make it a more appropriate estimator of phyllotine membership, places *Punomys* basal to the phyllotines. Because the inclusion of *Punomys* has no effect on hypotheses of phyllotine relationships outside of one terminal branch, and because the hypothesis of sigmodontine phylogeny closely matches the majority subset summarized in Fig. 1, that majority subset will constitute the preferred hypothesis discussed in the remainder of this paper. Selected nodes are numbered in Fig. 1 for references in the text.

When only the 37 phyllotine taxa are considered, the pruned trees are 542 steps long, with c.i. = 0.279 and r.i. = 0.567. The 88 most parsimonious trees of the preferred subset differ in the branching sequence of the basal nodes of *Phyllotis* and in the position of *Scapteromys* relative to the akodontine (*Akodon* to *Oxymycterus*) and phyllotine branches joining at node 1. The c.i. values for both the complete and the pruned data sets are in the middle of the observed range for published trees with similar numbers of taxa (Archie, 1989). Consistency indexes are inversely correlated with the number of taxonomic units (Archie, 1989). The 118-replicate bootstrap consensus tree is shown in Fig. 3, pruned of outgroups to highlight the phyllotines. Below each node the numbers indicate the percentage of replicates including those particular nodes. The mean percentage for the nodes (including outgroups) is 41%. When a character is referred to in the text, it is followed by a parenthetic reference giving its character number and its c.i., calculated from the 75% majority-rule consensus of the 88 equally most parsimonious trees presented in Fig. 1, excluding nonphyllotine species. Character descriptions are listed in the Appendix.

Fig. 1. Seventy-five percent majority-rule consensus tree of the 88 equally most parsimonious trees which place *Punomys* outside the phyllotines. Each tree is 817 steps long, with c.i. = 0.208 and r.i. = 0.538. The tree is rooted between *Thomasomys* and the oryzomyine group containing *Nectomys*. Numbers identify nodes that are referred to in the text. The node labeled 2 defines the tribe Phyllotini.

The ichthyomyines are thought to be an isolated branch of the Sigmodontinae, not closely related to any other sigmodontine group (Voss, 1988). The placement of *Ichthyomys* among the akodontines is likely due to convergence on simplified molar structure in the two groups.

The phyllotines form a monophyletic group (node 2) relative to the problematic taxa *Pseudoryzomys*, *Zygodontomys*, and *Holochilus*, corresponding with the results of

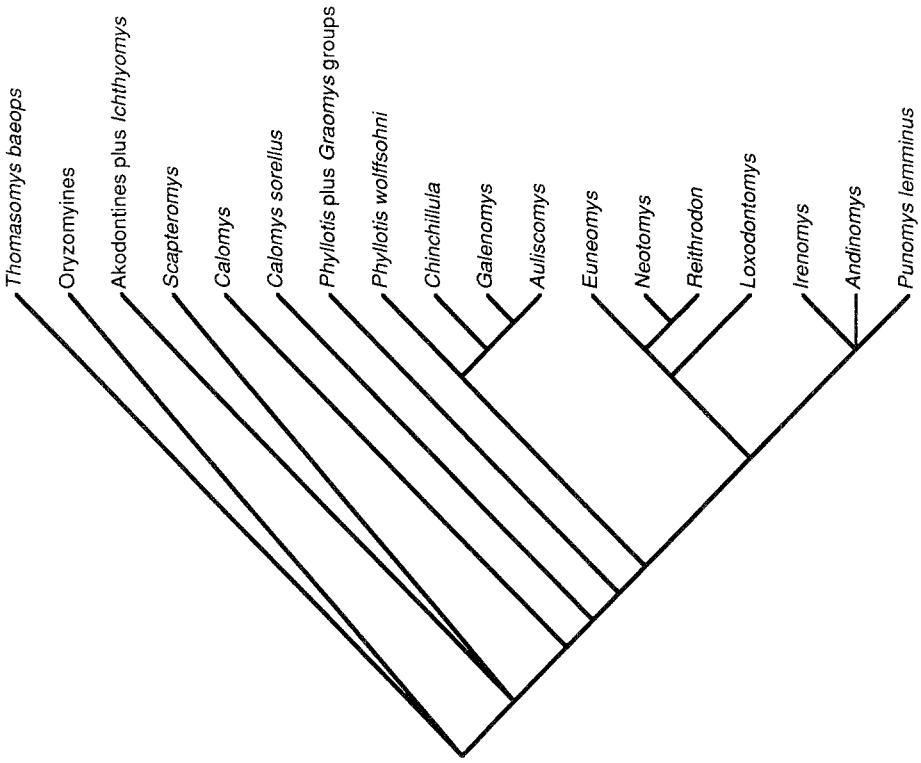

Fig. 2. Strict consensus of the 32 equally most parsimonious trees that place *Punomys* within the phyllotines. Each tree is also 817 steps long, with c.i. = 0.208 and r.i. = 0.538. Terminal taxa have been consolidated into genera or generic groups to simplify the topology. All consolidated portions of the tree are identical to Fig. 1. Only the position of *Punomys* differs between the two consensus trees.

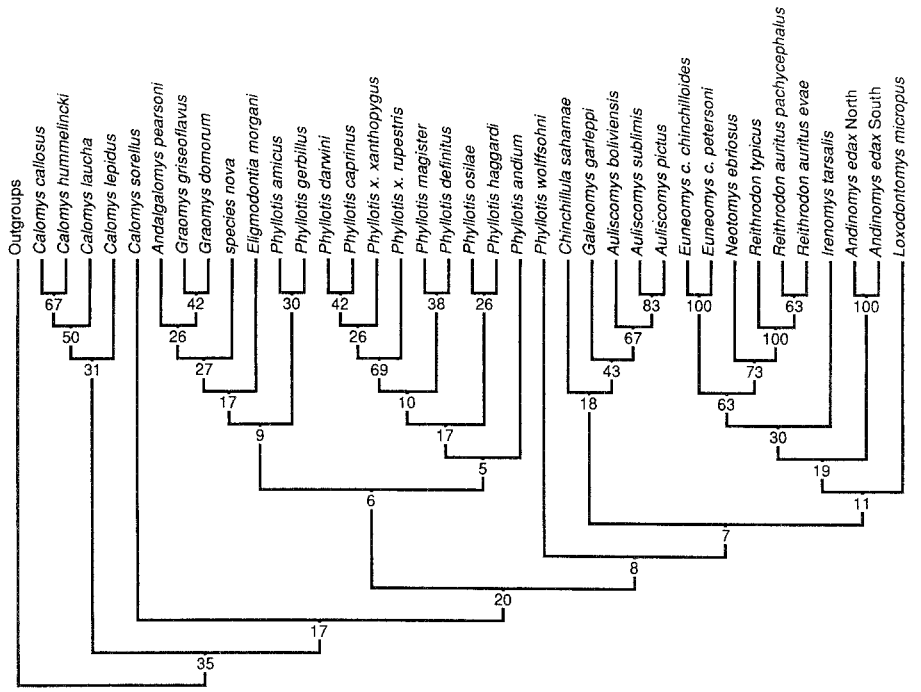

Fig. 3. Bootstrap consensus tree of 118 bootstrap replicates, pruned of outgroups. Numbers below nodes indicate the percentage of bootstrap replicates containing the indicated clades.

a broader taxonomic survey of sigmodontine relationships (Steppan, unpublished manuscript). The shortest trees found placing *Pseudoryzomys* with the phyllotines (even as the most basal member) and not with any of the outgroups is 12 steps longer than the shortest tree overall. *Holochilus* has in the past been associated with *Reithrodon*, *Neotomys*, and *Sigmodon* in the sigmodont group (Hershkovitz, 1955, 1962). The shortest tree conforming to this hypothesis is 19 steps longer than the most parsimonious trees. Excluding the situation with *Punomys*, the shortest tree wherein the phyllotines are not monophyletic (*Akodon* and *Chroeomys* placed distal from *Calomys*) is six steps longer than the most parsimonious trees.

Calomys appears paraphyletic with *C. sorellus* as the sister taxon to the remaining phyllotines. The placement of *C. sorellus* with the remaining phyllotines (node 3) is supported by a ventral pair of preputial glands (No. 95, c.i. = 1.0), loss of the parastyle/anteroflexus M1/ (No. 12, c.i. = 0.50), more than 25 caudal vertebrae (No. 78, c.i. = 0.25), and a long interparietal (No. 52, c.i. = 0.25). It should be noted here that the taxonomy of *Calomys* is particularly unstable and can result in some confusion, with different studies utilizing different nomenclatures.

Monophyly of the taxa terminal from *Calomys*, including *Phyllotis* and *Reithrodon*, which are referred to as "post-*Calomys*" (node 4), is supported by a moderate to large medial–ventral pair of preputial glands (No. 95, c.i. = 1.0), loss of the small mesostyle (except in *Chinchillula*; No. 11, c.i. = 0.50), the apparent infolding and near-loss of the anteromedian flexid M/1 (No. 17, c.i. = 0.38), and the premaxillaries not being behind the anterior edge of the incisors as in *C. lepidus* and *C. sorellus* (No. 38, c.i. = 0.33). The post-*Calomys* taxa comprise two similarly sized clades (nodes 5 and 6) in the most parsimonious trees. The clade including *Reithrodon* and *Auliscomys* (node 5) is much more highly differentiated, as reflected in the greater generic diversity as currently recognized (nine genera versus four). *Phyllotis wolffsohni* is placed near the base of the more diverse clade that includes *Reithrodon* and *Auliscomys*, but some trees only one to two steps longer than the most parsimonious place it within a *Phyllotis* grade. Characters supporting the inclusion of *P. wolffsohni* in the *Reithrodon* and *Auliscomys* clade (node 5) include a "y"- or comma-shaped fissure in the upper incisors (No. 3, c.i. = 0.40), premaxillaries terminating behind the anterior edge of the incisors (No. 38, c.i. = 0.33), and subequal mesopterygoid and parapterygoid fossae widths (No. 61; the condition found in all the basal taxa within the clade; c.i. = 0.33).

Two generic groups can be recognized within the diverse clade (node 5). The best supported is the *Reithrodon* group (node 7), previously defined by Olds and Anderson (1989), consisting of *Reithrodon*, *Neotomys*, and *Euneomys*. Maintaining the semiformal nomenclature employed by Olds and Anderson (1989), the other clade is the *Auliscomys* group (node 8), which includes *Galenomys* and *Chinchillula* but not *Loxodontomys micropus* [usually considered an *Auliscomys* (Musser and Carleton, 1993; Simonetti and Spotorno, 1980)]. While *L. micropus* is relatively well supported as the sister taxon to the *Reithrodon* group in the most parsimonious trees, it is placed outside of *Andinomys* in the bootstrap consensus tree. Sensitivity analyses reveal that these two placements are the two principal alternative hypotheses for *micropus* favored by this data set. Additionally, the shortest tree that includes *micropus* within a monophyletic *Auliscomys* is seven steps longer than the shortest tree overall. Thus this data set does not support the inclusion of *micropus* within an *Auliscomys* clade. Inclusion of *L. micropus* with the *Reith-*

rodon group is supported by a relatively parallel-sided parapterygoid fossa (No. 62, c.i. = 1.00), a tripartite fissure in the upper incisors (No. 3, c.i. = 0.40), and a narrow mesopterygoid fossa (No. 61, c.i. = 0.33).

The *Reithrodon* group (node 7) is supported by a sharply angled premaxillo-maxillary suture (No. 45; unique within the Sigmodontinae; c.i. = 1.00), sigmoidal molars, *sensu* Hershkovitz (1955) (represented here by multiple characters), the lack of anterior shift by the mesoflexid M/3 (No. 29, c.i. = 0.50), distinctly grooved incisors (No. 1, c.i. = 0.44), an anterior root of the zygomata that inserts high, close to the dorsal surface of the rostrum (No. 42, c.i. = 0.40), a moderately large distal baculum relative to the proximal baculum (No. 91, c.i. = 0.40), the absence of labial root M/1 (No. 7, c.i. = 0.33), lateral ridges of the supraorbital region that are raised dorsally (No. 49, c.i. = 0.33), and supraorbital knobs (No. 50, c.i. = 0.33). The close relationship of *Reithrodon* with *Neotomys* is supported by a deeply channeled posterior palate with a distinct median ridge (No. 70, c.i. = 1.00), the loss of the supraorbital branch of the stapedial artery (No. 75, c.i. = 0.27 overall; but this character state is unique among the phyllotines), well-separated anterior apexes of the incisive foramina (No. 41, c.i. = 0.67), deeply grooved incisors (No. 1, c.i. = 0.44), strongly developed zygomatic spines (No. 43, c.i. = 0.33), and deeply excavated parapterygoid fossae (No. 64, c.i. = 0.33).

Auliscomys pictus, *A. sublimis*, *A. boliviensis*, *Galenomys*, and *Chinchillula* together comprise the *Auliscomys* group (node 8). The bootstrap consensus tree (Fig. 3) indicates that less confidence should be placed in the more basal nodes. Sister-species status for *A. pictus* and *A. sublimis* (83% of the bootstrap replicates) is supported by a medial digit of the baculum that is much longer than the lateral digits (No. 92, c.i. = 1.0), the incisive foramina extending to the level of the paracone and protocone (No. 39, c.i. = 0.50), the ventral surface of the foreclaws forming a distinct keel (No. 83, c.i. = 0.50), and lightly grooved upper incisors (No. 1, c.i. = 0.44). The genus *Auliscomys*, excluding *micropus*, is characterized by upper incisors with fine striae or shallow grooves (No. 1, c.i. = 0.44), an anteriorally divergent supraorbital region (No. 47, c.i. = 0.40), a reduced labial root M1/ (No. 4, c.i. = 0.33), a posterior shift of hypoflexid M/3 (No. 30, c.i. = 0.33), and a moderately short interparietal (No. 52, c.i. = 0.25). Supporting the node joining *Galenomys* with *Auliscomys* are orthodont to weakly proodont incisors (No. 2, c.i. = 0.29 overall; but the character state is unique among phyllotines) and a narrow mesopterygoid fossa (No. 61, c.i. = 0.33). This clade is no longer monophyletic in some trees that are three steps longer than the most parsimonious. This analysis does not support the suggested association between *Galenomys* and *A. boliviensis* (Braun, 1993): these two taxa are sister species in only 5% of bootstrap replicates. Less stable is the position of *Chinchillula*. Support for its placement at the base of the *Auliscomys* group comes from the anterior border of the zygomatic plate being rounded or receding dorsally (No. 43, c.i. = 0.33 overall; but the character state is unique among the phyllotines) and premaxillaries that terminate behind the anterior plane of the incisors (No. 38, c.i. = 0.33). *Chinchillula* can be found outside the *Auliscomys* group in trees only one step longer than the most parsimonious tree; in this alternative hypothesis, *Chinchillula* is immediately basal to the clade joining the *Reithrodon* group with *Andinomys* and *Irenomys* (node 9).

The most parsimonious trees (Fig. 1) place two genera not generally recognized by previous workers as closely related: *Andinomys* and *Irenomys*. Their grouping together

is supported by an anterior masseteric ridge that is below and well posterior from the diastema (No. 36, c.i. = 0.27 overall; but the character state is unique among the phyllotines), relatively widely separated anterior apexes of the incisive foramina (No. 41, c.i. = 0.67), frontals that are incompletely fused or apparently vascularized along the midline (No. 51, c.i. = 0.67), and posterolateral palatal pits in the anterior pterygoid fossa (No. 71, c.i. = 0.33). The bootstrap consensus tree (Fig. 3) differs from the most parsimonious consensus tree by placing *Irenomys* as the sister taxon to the *Reithrodon* group, with *Andinomys* one node basal from that. The bootstrap tree represents the hypothesis that moderate to deeply grooved incisors evolved only once, raising the c.i. of character No. 1 to 0.57. The shortest tree that does not join *Andinomys* with *Irenomys* is three steps longer than the shortest tree overall. The topology of this longer tree matches the bootstrap consensus tree with regard to *Andinomys* and *Irenomys*. The node joining *Loxodontomys* with the *Reithrodon* and *Andinomys* groups (node 9) is supported primarily by posteriorally divergent maxillary toothrows (No. 72, c.i. = 0.29 overall; but the character state is unique among the phyllotines).

The second major post-*Calomys* clade consists of *Phyllotis*, *Eligmodontia*, *Graomys*, *Andalgalomys*, and the undescribed species from Tapecua designated here *species nova* (node 6). Complete loss of the anteromedian flexid M/1 (No. 17, c.i. = 0.38) and posteriorally convergent maxillary toothrows (No. 72, c.i. = 0.29) provide limited support for this clade. The basal branches of this clade are clearly occupied by members of *Phyllotis*, but the sequence of internal branching is poorly resolved: bootstrap values for internal nodes are typically less than 20%. The clade consisting of *Graomys*, *Andalgalomys*, and *species nova* (node 10) is supported by the loss of an anterior shift of the mesoflexid M/3 (No. 29, c.i. = 0.50), orbital wings of the presphenoid that are posterior to the maximum constriction of the presphenoid (No. 66, c.i. = 0.50), a small but distinct zygomatic spine (No. 43, c.i. = 0.33), a sharply ridged, overhanging supraorbital region (No. 48, c.i. = 0.33), and parallel maxillary toothrows (No. 72, c.i. = 0.29). The most parsimonious trees indicate that *Graomys* is paraphyletic, while the bootstrap consensus tree indicates that it is monophyletic in 42% of the replicates. Within this *Graomys* clade on the most parsimonious trees, the node joining *G. griseoflavus* with *Andalgalomys* and *species nova* is supported principally by the fusion of opposing flexi in M3/ (No. 31, c.i. = 1.0). Two additional steps are needed for a monophyletic *Graomys*.

The *Graomys*/*Andalgalomys* clade (node 10) is placed as the sister group to *Eligmodontia*, though this grouping is not as well supported as the *Graomys*/*Andalgalomys* clade. *Phyllotis gerbillus* and *P. amicus* next join successively to this group in the shortest trees (Fig. 1) or as a sister clade in the bootstrap consensus tree (Fig. 3). This more inclusive clade is supported by a posteriorally divergent supraorbital (No. 48, c.i. = 0.40) and premaxillaries that protrude well anterior from the incisive plane (No. 38, c.i. = 0.33).

The deeper-level relationships within *Phyllotis* are the most poorly resolved aspect of this study. The consensus tree in Fig. 1 shows *Phyllotis* to be paraphyletic. The highest bootstrap percentage for a node also found in Fig. 1 is 69% for the clade consisting of *P. darwini*, *P. caprinus*, and the two subspecies of *P. xanthopygus*. Character support for this *xanthopygus* species group is provided principally by three phallic characters: hooks on the lateral mounds (No. 95, c.i. = 1.00), dorsal knobs on the lateral

mounds (No. 94, c.i. = 1.00), and a large distal baculum relative to the proximal baculum (No. 91, c.i. = 0.40). The bootstrap percentage is 38% for the clade of *P. magister* and *P. definitus*, two very restricted and geographically distant taxa that had been considered conspecific by Pearson (1958). Specific character support is weak but includes nasals that are slightly broader than the minimum interorbital distance (No. 46, c.i. = 0.25 overall; but the character state is unique within the *Phyllotis* clade), large tegmen tympani (No. 55, c.i. = 0.29), and pectoral streaks (No. 91, c.i. = 0.17).

DISCUSSION

Few studies have made explicit statements about phyllotine relationships, so it is difficult to compare the results of this study. Some of the earlier studies (e.g., Hooper and Musser, 1964) make pairwise statements of similarity that are difficult to translate into a hierarchical phylogenetic hypothesis. In his revision of *Phyllotis*, Pearson (1958) found consensus with Ellerman (1941) and Osgood (1947) and recognized four subgenera: *Graomys*, *Auliscomys*, *Loxodontomys*, and *Phyllotis*. The basis for his taxonomy was not detailed, as the focus was on species-level issues, but grew out of his fieldwork and observations of museum skins and skulls. The species composition of these subgenera coincides with the nomenclature and results of this study with the exception of *P. gerbillus*, which Pearson (1958) removed to the related genus *Paralomys*. The phylogenetic relationships implied by placing these subgenera under *Phyllotis* is consistent with this study with regard to *Graomys* being closely related to *Phyllotis* but is incongruent with regard to *Auliscomys* and *Loxodontomys*, which this study show to be more closely related to other genera. Pearson (1958) also did not recognize *Eligmodontia* as part of a *Phyllotis* group.

Hershkovitz (1962) revised the phyllotines and recognized a *Calomys* section, which could be a clade or a grade, and a *Phyllotis* section, which should translate as a clade. The *Calomys* section was distinguished from the *Phyllotis* section primarily by the crested (bunodont) rather than flat or terraced molars. *Zygodontomys* from his *Calomys* section and *Pseudoryzomys* from his *Phyllotis* section have since been removed from the phyllotines. The remainder of his *Calomys* section consists of *Calomys* and *Eligmodontia*. Like Pearson (1958), he included *Auliscomys* and *Graomys* within the genus *Phyllotis* and indicated that *Euneomys* and the sigmodonts (*Reithrodon*, *Neotomys*, *Holochilus*, and *Sigmodon*) might be considered the sister groups to the phyllotines.

Pearson and Patton (1976) and Spotorno (1986) have diagrammed hypotheses of evolutionary relationships based on karyotypic data. Species that share the same diploid and fundamental numbers are generally also found by this analysis to be closely related; e.g., *Auliscomys pictus* with *A. sublimis*, and *Phyllotis xanthopygus* and *P. darwini* with *P. caprinus*. However, *P. amicus* and *P. magister* also share the same karyotypic formula but are morphologically quite distinct. Similarly, *P. haggardi* and *P. gerbillus* share their karyotypic formulas with the *xanthopygus* species group. Higher-order relationships show less comparability across the two data sets. For example, Spotorno (1986) places *Andinomys* at the base of the phyllotine radiation, while the karyotypes of *Reithrodon*, *Euneomys*, and *Neotomys* are as diverse as those of the phyllotines as a whole and give no indication of their close relationship. In fact, Spotorno (1986, p. 22) explicitly acknowledged that the gross karyotype is a poor estimator of homology, concluding

from G-banding patterns that the close similarity of the *P. xanthopygus* and *Euneomys* karyotypes "represent[s] independent acquisitions within each taxon." Spotorno (1986) also screened electrophoretic alleles. His PRIM network separates *Andinomys*, *Irenomys*, and *Euneomys* from *Reithrodon* and *A. micropus* by placing them near the base of the tree. A cladistic reanalysis of the same data set (Steppan, unpublished) is very different from the published phenetic analyses at the generic level and includes such unlikely species pairs as *P. xanthopygus* with *Andinomys* and *Reithrodon* with *Eligmodontia*. The electrophoretic data set of Spotorno (1986) does not seem to be highly informative for the phyllotines, although the results are generally consistent with current taxonomy at the tribal through family levels.

Reig (1986) presented a biogeographic scenario for the diversification of phyllotines and other sigmodontine groups. His scenario drew upon molar morphology and its dietary correlates, ecology, karyology, biogeography, and the limited fossil evidence. Paraphrasing in cladistic terminology, Reig (1986) visualized the brachyodont *Calomys* as the most basal and generalized phyllotine genus and *C. sorellus*, with its "primitive karyotype," as the most basal member of either a *Calomys* or a post-*Calomys* clade. His view of the lowland *Calomys* (e.g., *C. callosus* and *C. laucha*) as derived or terminal species is consistent with this study. *Phyllotis* and an herbivorous *Neotomys–Sigmodon–Holochilus* complex constitute the basal members among the remaining phyllotines and evolved in the central and southern altiplano. *Auliscomys*, *Galenomys*, and the sister taxa *Chinchillula* and *Andinomys* are then hypothesized to be independently evolved from a highly paraphyletic *Phyllotis*. In sharp contrast to the results of this study, Reig (1986) hypothesized that *Graomys* and *Auliscomys* are sister taxa. *Andalgalomys*, *Pseudoryzomys*, and *Eligmodontia* would be independently derived from *Calomys*. Finally, *A. micropus* and *Euneomys* are independent southern offshoots of a paraphyletic *Auliscomys*. Thus *Graomys* would be closely related to *Euneomys* and unrelated to *Andalgalomys*, while *Reithrodon*, *Neotomys*, and *Euneomys* are unrelated to each other.

Braun (1993) recently reported results of phenetic and cladistic analyses of the phyllotines based on 36 craniodental and 10 external characters. Her cladogram shows some similarities to mine, although the robustness of her cladistic results are unknown due to software limitations and the procedures used, and because confidence estimates (e.g., bootstrap values or additional steps required to break up clades) were not reported. Character support for clades was not generally reported either. A principal conclusion was that *Pseudoryzomys* was the sister taxon to the phyllotines and, thus, may be the basal phyllotine. The inclusion of only the phyllotines, two akodonts, and *Pseudoryzomys* in the actual numerical analysis, without any oryzomyines, precluded testing the tribal status of *Pseudoryzomys*. The results of this study indicate that *Pseudoryzomys* is not a phyllotine, nor is it within a clade that includes the phyllotines and akodontines.

The status of *Pseudoryzomys* in these two studies highlights the importance of taxonomic sampling in phylogenetic studies. Without selecting representatives of all likely outgroups, as well as sampling the variation within outgroups, a robust statement of monophyly cannot be made. Regions of the more inclusive tree must be explored by the data set to allow putative ingroup taxa a sufficient number of alternative attachment locations and avoid being misled by homoplasy. Insufficient sampling may unintentionally constrain taxa into the ingroup, where more complete sampling of character evolution, and therefore homoplasy, provides many more alternative positions. Like any

study, this analysis has had to sacrifice taxonomic resolution (primarily in the outgroups) in a trade-off with time in order to make the study practicable. Thus, while this analysis has greater power to test phyllotine monophyly than Braun's (1993), that power is limited primarily to testing whether a taxon should be excluded from the ingroup, rather than including an outgroup or problematic taxon. For example, the placement of a single akodontine within the ingroup might be less convincing evidence for rejecting phyllotine monophyly than the placement of a phyllotine among the akodontines. This is directly analogous to issues of unequal sampling in statistics, although regions of a branching hierarchy are being sampled rather than within-group variation per se. Thus the placement of *Pseudoryzomys* with oryzomyines is interpreted as evidence that it is not a phyllotine, while the placement of *Punomys* as a phyllotine in some trees can more easily be interpreted as due to convergence (collateral data are, of course, important to both interpretations).

One consequence of more thoroughly sampling a phylogeny is that as the number of taxa increases, the mean c.i. of characters decreases (Archie, 1989). Across all taxa in Fig. 1, the average character state transition (forward or back) occurs five times. Thus by conventional assessments, most characters in this study are highly homoplasious. This would seem to reduce confidence in some of the results, because characters would seem to be less informative. However, the greater confidence inspired by the lower apparent homoplasy in smaller data sets would be illusory. The power of an analysis to estimate a phylogeny would logically increase as the branches of that phylogeny are more finely sampled. While decreasing the c.i. of characters by discovering previously unknown homoplasy, the addition of more taxa may also discover the evidence for character evolution that allows that very recognition of homoplasy which is necessary for accurate phylogeny reconstruction. The trade-off is that the number of items being estimated (i.e., clades) increases also, and thus the power to estimate each node accurately may not improve. This trade-off may be reflected in the observation that average bootstrap values are inversely (but weakly) correlated with the number of taxa for random subsets of this data set.

As for character evaluation, most characters should lower in c.i. with increasing number of taxa. This is to be expected and should not, in general, lower the confidence in a character. However, if a character's c.i. drops more than expected on average, then perhaps the information content of that character was overestimated in the smaller analyses. On the other hand, if its c.i. drops less than expected, then confidence in the informativeness of that character should increase. Either way, the assessment should be more accurate.

Two notable examples of this process of character evaluation from this study are the numbers of thoracic ribs and incisor grooves. My initial survey of rib number found it to be polymorphic in some species and to be variable between genera. Thirteen ribs is the widespread condition and 12 ribs are found in four phyllotine genera: *Reithrodon*, *Andalgalomys*, *Graomys*, and some *Calomys*. This pattern requires at least three independent losses on the most parsimonious trees. With greater taxonomic sampling among outgroups, this character appears more conservative. With data on an additional 90 sigmodontine species (Steppan, unpublished manuscript), 12 ribs are found to occur in four more groups: among oryzomyines, *Sigmodon*, and *Wiedomys* and in the thomasomyine genus *Rhipidomys*. Similarly, grooved incisors among New World muroids have been

found in *Sigmodon alstoni*, the peromyscine *Reithrodontomys*, and three clades of phyllotines: shallow grooves in *Auliscomys* and deep grooves in *Irenomys* and the *Reithrodon* group. The groove in *Neotomys* presents an additional transition to an involuted and pinched condition on the lateral corners rather than the open longitudinal depressions down the front surface found in the other deep-grooved forms. It is unclear why these two distinctive characters should be so much more variable among the phyllotines, which contain more than half the evolutionary transitions among sigmodontines for these two characters, while containing only 15% of sigmodontine species.

The results of this study hold several taxonomic consequences. Most of the morphologically diverse group of taxa (e.g., *Reithrodon*, *Euneomys*, *Andinomys*, and *Chinchillula*; node 5) are unaffected in their binomial nomenclature. But two distinct generic groups can be recognized. *Reithrodon*, *Euneomys*, and *Neotomys* form the best supported of these groups, confirming the conclusion of Olds and Anderson (1989). The *Reithrodon* group is distributed in the southern Andes, Patagonia, and the grasslands of Argentina and Paraguay. If *Loxodontomys micropus* is indeed the sister taxon to the *Reithrodon* group, then the southern character of this clade is reinforced because *L. micropus* lives in the temperate forests of southern Chile.

This study is consistent with the removal of *Reithrodon* and *Neotomys* from the sigmodont group (Hooper and Musser, 1964; Pearson and Patton, 1976; Olds and Anderson, 1989). *Holochilus* is placed in an oryzomyine group, while the patristic distances between *Reithrodon* and *Neotomys*, on the one hand, and *Holochilus*, on the other, are moderate to large for this data set and suggest no close relationship. Trees joining *Holochilus* with *Reithrodon* and *Neotomys* are 19 steps longer than the most parsimonious trees.

The next most strongly defined clade is the *Auliscomys* group (node 8). Here the taxonomy should be modified, as this analysis demonstrates that *micropus* does not belong in *Auliscomys*. Instead, *micropus* appears to be the sister species to the *Reithrodon* group. Seven additional steps are needed to bring *micropus* into a strictly *Auliscomys* clade. Therefore, *micropus* should be elevated to generic status under the name *Loxodontomys*, originally erected by Osgood (1947) as a subgenus of *Phyllotis* and recently resurrected by Braun (1993). The *Auliscomys* group also includes *Galenomys* and *Chinchillula*. This clade is strikingly defined in both geography and external morphology. All five species have short or very short tails, have relatively stout bodies, and are endemic to the altiplano of central and southern Peru, western Bolivia, and far northern Chile. These external characters were not included in the analysis that produced the phylogenetic hypothesis and thus provide some independent support. Simonetti and Spotorno (1980) moved *micropus* from *Phyllotis* to *Auliscomys* because of its similar karyotype and proximity to *Auliscomys* species in an ordination analysis. The karyotypes are indeed similar and suggest a close association, but their multivariate analysis was based on only 4 external and 11 partially redundant molar measurements. Additionally, *micropus* was compared to *Auliscomys*, *Phyllotis*, and *Andinomys* but to none of those taxa to which this analysis indicates that it is related. Their multivariate analysis does not conflict with the results of this study. The exclusion of *L. micropus* from *Auliscomys* avoids the more complex biogeographic scenarios required to explain its disjunct southern forest distribution (Simonetti and Spotorno, 1980; Walker and Spotorno, 1992) and replaces them with a remarkable altiplano radiation that currently involves extensive sympatry.

The monophyly of *Phyllotis* presents the most problematic aspect of this study. This

question is closely linked to the phylogenetic positions of *Andalgalomys*, *Graomys*, and *Eligmodontia*, which might best be referred to as the *Eligmodontia* group. The results of this study do not support the conclusions of several studies which, in emphasizing dental and orofacial characters, suggested a close relationship between *Calomys* and members of the *Eligmodontia* group (Williams and Mares, 1978; Olds, 1988). However, the low bootstrap percentages for the internal nodes of *Phyllotis* suggest that these nodes should be collapsed. Thus, this important region of the phylogenetic history of the phyllotines remains unresolved. Therefore, no nomenclatural changes are suggested for the *Eligmodontia* group at this time, but it seems likely that either the content of *Phyllotis* will be expanded or *P. amicus* and *P. gerbillus* will need to be removed. Braun (1993) resurrected *Paralomys* to contain these two species, although her cladogram did not show them to be sister species. Her *Paralomys* is characterized by relatively large ears and interparietals, hairiness among interdigital pads, divergent interorbitals, and several other minor characters. The shortest trees in this study that contain a monophyletic *Phyllotis* are six steps longer than the most parsimonious trees, further reducing the likelihood of monophyly.

The most parsimonious trees suggest that, due to the paraphyletic nature of *Graomys*, the undescribed species from Tapecua and *Andalgalomys* should be subsumed within *Graomys*. However, the bootstrap consensus tree and examination of characters indicate that the paraphyletic status of *Graomys* is insufficiently supported to justify taxonomic changes at this time. From this analysis, *species nova* appears to be a more derived member of current *Andalgalomys*. These issues should prove fruitful for a more restricted phylogenetic analysis.

Finally, this analysis suggests that *Calomys* may be paraphyletic. However, the results of this analysis are best considered equivocal on this point, because a monophyletic *Calomys* can be found in trees only two steps longer than the most parsimonious trees. Further surveys of the relatively slowly evolving preputial glands in *Calomys* would be particularly important (No. 95, c.i. = 0.50 among all species in this study and 1.0 in phyllotines). *Calomys callosus*, *C. laucha*, and most outgroup species are reported to have one pair, while all other phyllotines have a second, smaller medial–ventral pair (Voss and Linzey, 1980). A second ventral pair is also found in *C. sorellus* in the same position as the second pair in the remaining phyllotines, but it is much smaller: 0.5 versus 2–3 mm. Even when preputial glands are excluded from the analysis, *C. sorellus* is placed as the sister group to the remaining phyllotines, supported by the loss of the parastyle/anteroflexus; the presence of more than 25 caudal vertebrae, and the longer interparietal.

APPENDIX: CHARACTER DESCRIPTIONS

Dental Characters

(1) Grooves on upper incisors
- 0 = absent
- 1 = fine striae
- 2 = 1 mediolateral, shallow
- 3 = 1 mediolateral to near-lateral deep groove; 1 small shallow on midline
- 4 = 1 involuted on lateral corner

(2) Incisor procumbency
0 = hyperopisthodont
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, 5) Labial root of M1/: 4 states, 2 subcharacters.
00 = absent
10 = present, small, set medially
20 = present, medium to large, set laterally
?1 = 2 lateral roots
(6) Molar roots M3/
0 = 3 roots
1 = 2 roots
2 = 1 root
(7) Labial root of M/1
0 = absent
1 = present
(8) Molar roots of M/2
0 = 2 roots
1 = 3 roots
(9) Molar roots of M/3
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 M/1
0 = anterolabial cingulum absent
1 = anterolabial cingulum weakly developed
2 = anterolabial cingulum distinct

(15) Protoflexid M/1
- 0 = anterolabial cingulum short, may curl toward protoconid; protoflexid simple
- 1 = anterolabial cingulum long, fusing with protoconid and leaving protoflexid as lake

(16) Cusp arrangement M/1
- 0 = primary cusps opposite in position
- 1 = primary cusps intermediate
- 2 = primary cusps alternate

(17) Anteromedian flexid M/1
- 0 = absent or limited to shallow groove
- 1 = prominent
- 2 = infolded to form lake

(18) Procingulum separation M/1
- 0 = procingulum attached by anterior mure
- 1 = procingulum separated, mure cut by opposing flexids

(19) Posterolophid/stylid M/1
- 0 = absent
- 1 = intermediate, posteroflexid present as groove; often absent with strong wear
- 2 = distinct at all ages

(20) Posterolophid/stylid M/3
- 0 = absent
- 1 = intermediate, posteroflexid present as groove; often 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 M/2
- 0 = absent
- 1 = protoflexid appears as groove; often 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 relative to M2/
1 = rotated relative to M2/
(28) Mesoflexid reduction
0 = no reduction relative to M/2
1 = reduced relative to M/2
2 = highly reduced relative to M/2 or absent
(29) Anterior shift of mesoflexid M/3
0 = no shift relative to M/2
1 = anterior shift relative to M/2
(30) Posterior shift of hypoflexid M/3
0 = no shift relative to M/2
1 = posterior shift relative to M/2
(31) Fusion of opposing flexi in M3/
0 = flexi do not meet
1 = flexi meet, median 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

Cranial Characters

(33) Masseteric ridge of the mandible, posterior
0 = indistinct
1 = distinct
(34) Capsular projection of mandible
0 = elevation of superior masseteric ridge
1 = indistinct or absent
(35) Height of the coronoid process
0 = above maximum height of mandibular condyle
1 = subequal
2 = below mandibular condyle
(36) Anterior masseteric ridge position
0 = anterior edge not formed into a knob
1 = knob slightly below dorsal edge of mandible
2 = knob just reaches dorsal edge of mandible
3 = knob exceeds dorsal edge
(37) Medioventral process of mandibular ramus
0 = process absent, ramus rounded
1 = process weakly present, ramus angled
2 = process distinct
(38) Premaxillary protrusion
0 = premaxillaries terminating behind the anterior plane of the incisors

1 = premaxillaries terminating at or slightly anterior to incisive plane
2 = premaxillaries produced well anterior to incisive plane

(39) Posterior extent of incisive foramina relative to primary cusps of M1/
0 = not reaching plane of anterolabial and anterolingual conules
1 = level with anterolabial and anterolingual conules
2 = extending to level of paracone and protocone
3 = extending to level of hypocone and metacone

(40) Maxillary septum of incisive foramina
0 = length $\leq \frac{1}{2}$ incisive foramina
1 = length $\frac{1}{2}$–$\frac{4}{5}$ incisive foramina
2 = length $>\frac{4}{5}$ incisive foramina

(41) Orientation incisive foramina
0 = separation of anterior apexes $<80\%$ separation of posterior apexes
1 = separation of anterior apexes 80–100% of posterior apexes

(42) Dorsoventral position of anterior root of zygomata
0 = antorbital bridge laying well below dorsal surface of rostrum ($\frac{1}{4}$–$\frac{1}{2}$ less than rostrum height)
1 = antorbital bridge below rostrum (displaced $<\frac{1}{4}$ rostrum height)
2 = insertion high, close on dorsal surface rostrum

(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 ° (when viewed anteriorly)
1 = ≥ 20 °

(45) Premaxillo-maxillary suture orientation
0 = a 90–135 ° angle formed relative to palatine plane by the suture on the lateral surface of rostrum
1 = suture nearly horizontal at ventral end, sharply angled (≥ 90 °) in middle of rostrum

(46) Nasal width
0 = less than minimum interorbital distance of dorsal surface of rostrum
1 = greater than or equal to minimum interorbital distance of dorsal surface of rostrum

(47) Interorbital shape
0 = interorbital ridge anteriorly divergent, narrowest region in posterior half
1 = narrowest point of interorbital region centrally situated within orbital region bounded by frontals
2 = supraorbital ridge posteriorally divergent, narrowest region anterior

(48) Supraorbital edges
0 = smoothly rounded
1 = angled for approx. $\frac{1}{2}$ its length
2 = angled for all its length
3 = sharply ridged, overhanging

(49) Supraorbital ridge
0 = absent or directed laterally
1 = lateral edges of supraorbital ridged and directed dorsally
(50) Supraorbital knobs
0 = absent
1 = small swellings or knobs on anterior supraorbital region
(51) Mediodorsal fusion of frontals
0 = complete
1 = partially open or vascularized
2 = distinct and consistent fontanelle
(52) Medial length of interparietal/parietal
0 = <0.33
1 = 0.33–0.45
2 = >0.45
(53) Fenestra of the mastoidal capsule of the petrosal
0 = absent
1 = small, pinpoint
2 = medium
3 = large, easily seen with naked eye, $>\frac{1}{3}$ area of capsule
(54) Orientation of anterior border of auditory bulla
0 = oblique
1 = transverse
2 = rounded
(55) Tegmen tympani
0 = absent or poorly developed
1 = moderately developed, simple; contacts squamosal
2 = large; principal connection across fissure
(56) Stapedial process of bullae
0 = absent or weakly developed knob
1 = present, spinous; does not touch pterygoid ridge
2 = prominent; may touch pterygoid ridge
(57) Thickness of hamular process of squamosal
0 = process wholly absent (i.e., subsquamosal foramen absent)
1 = broad along entire length, subsquamosal foramen often reduced
2 = bridge reduced in thickness, posterior terminus appears flattened
3 = posterior end reduced as well, not greatly thicker than bridge
(58) Positions of temporal vacuities
0 = subsquamosal and postglenoid foramina positioned dorsoventrally
1 = postglenoid foramen distinctly anterior to subsquamosal foramen
(59) Internal carotid canal
0 = bounded by both occipital and ectotympanic portion of auditory bulla
1 = bounded entirely (or nearly so) by petrosal and ectotympanic portions of auditory bulla
(60) Extension of eustachian tube
0 = does not reach posterior lobe of pterygoid process
1 = subequal to posterior lobe
2 = tube extends anterior past base of process on lateral side

(61) Breadth of mesopterygoid fossa at presphenoid-basisphenoid suture
- 0 = distinctly broader than adjacent parapterygoid fossae
- 1 = subequal
- 2 = distinctly narrower than adjacent parapterygoid fossae

(62) Parapterygoid shape
- 0 = posterior width < 1.5 times anterior width
- 1 = 1.5–2.4 times anterior width
- 2 = > 2.4 times anterior width

(63) Shape of mesopterygoid fossa
- 0 = posterior width < 1.5 times anterior width
- 1 = 1.5–2.4 times anterior width
- 2 = > 2.4 times anterior width

(64) Parapterygoid fossa depth
- 0 = flat, even with bony palate
- 1 = recessed slightly above level of bony palate
- 2 = moderately excavated above level of bony palate
- 3 = deeply excavated above level of bony palate

(65) Sphenopalatine vacuities
- 0 = closed
- 1 = narrow slit surrounding presphenoid–basisphenoid juncture
- 2 = vacuity distinct but constricted, orbital wings of presphenoid not fully separated posterior to medial pterygoid processes
- 3 = medial pterygoid processes fully anterior to orbital wings of presphenoid
- 4 = orbital wings of presphenoid absent or very large optic foramen

(66) Position of orbital wings of the presphenoid
- 0 = wings anterior to a distinct constriction of the presphenoid
- 1 = wings posterior to maximum constriction

(67) Transpresphenoid foramen
- 0 = absent
- 1 = present

(68) Position of anterior border of mesopterygoid fossa
- 0 = lying ≥ 1 M3 tooth-length posterior to M3/
- 1 = lying between $\frac{1}{3}$ and 1 tooth-length posterior to M3/
- 2 = 0–$\frac{1}{3}$ tooth-length posterior to M3/
- 3 = reaching posterior plane of paired M3/

(69) Medial process of the posterior palate
- 0 = absent
- 1 = present

(70) Posterior palatine ridge
- 0 = absent or indistinct
- 1 = longitudinal ridge present

(71) Posterolateral palatal pits
- 0 = anterior to mesopterygoid fossa
- 1 = posterior to anterior border of mesopterygoid fossa

(72) Orientation of maxillary toothrows
- 0 = posteriorly divergent
- 1 = parallel
- 2 = convergent

(73) Posterior palatal foramen
0 = absent or closed
1 = present, tiny
2 = foramina large, distinct
(74) Sphenopalatine foramen
0 = absent or nearly ossified
1 = present, small to moderate size
2 = present, large
(75) Carotid circulation
0 = both stapedial and sphenofrontal foramen absent
1 = stapedial foramen present, but sphenofrontal foramen absent
2 = both foramina present
3 = both foramina and squamosal fenestra present
(76) Alisphenoid strut
0 = absent or filamentous
1 = consistent dorsal process, but does not fully cross foramen ovale
2 = present and bony

Skeletal Characters

(77) Number of fully articulating thoracic rib pairs
0 = 13 thoracic ribs
1 = 12 thoracic ribs
(78) Number of caudal vertebrae
0 = <24
1 = 24–30
2 = >30
(79) Neural spine on second thoracic vertebrae
0 = longest spine present on T2
1 = short on T2; instead longest on T3
(80) Height neural spine of second cervical vertebrae
0 = not significantly enlarged
1 = enlarged, distinct knob
2 = very enlarged into distinct keel
(81) Length neural spine of second cervical vertebrae
0 = does not overlap C3
1 = overlaps C3
(82) Position of deltoid tuberosity
0 = $<59\%$, measured from condyle of humerus to notch of deltoid tuberosity relative to total length
1 = $\geq 59\%$

External Characters

(83) Ventral surface of claws (manus)
0 = open basally
1 = closed basally
2 = fused, forming distinct keel

(84) Length of D1 relative to D5 (pes)
0 = D1 distinctly shorter than D5
1 = D1 and D5 subequal in length
(85) Position of basal tubercle of D5 (pes)
0 = subequal (overlapping) with distal tubercle of D1
1 = intermediate to distal and basal tubercles of D1
(86) Furring of soles of feet (pes)
0 = sparse hair only on heels
1 = heels furred, distal pad not
2 = distal pads furred
(87) Dorsoventral coloration of tail
0 = distinctly bicolored
1 = indistinctly bicolored
2 = monocolored
(88) Furring of tail dorsum
0 = sparsely furred, scales evident
1 = furred, scales visible but indistinct
2 = densely furred, scales scarcely visible
(89) Body pelage pattern
0 = distinctly bicolored or counter-shaded
1 = indistinctly bicolored
2 = monocolored
(90) Pectoral streaks
0 = absent
1 = present

Phallic Characters

(91) Distal/proximal bacular length (tip of distal to tip of proximal/tip of proximal to length at widest point of base)
0 = <0.63
1 = 0.63–0.77
2 = >0.77
(92) Relative length of lateral mounds to medial mound
0 = $>\frac{2}{3}$
1 = $<\frac{2}{3}$
(93) Hooks on lateral mounds, pointing basally
0 = absent
1 = present
(94) Knob on dorsal surface of lateral mounds
0 = absent
1 = present
(95) Preputial glands
0 = single large lateral pair
1 = single large lateral pair with very small ($<$ 1-mm) medial pair
2 = single large lateral pair with medium-length (2- to 4-mm) medial pair
(96) Gall bladder
0 = present
1 = absent

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