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Revision of the Tribe Phyllotini (Rodentia: Sigmodontinae), with a Phylogenetic Hypothesis for the Sigmodontinae

Scott J. Steppan

February 28, 1995
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Revision of the Tribe Phyllotini (Rodentia: Sigmodontinae), with a Phylogenetic Hypothesis for the Sigmodontinae

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**Accepted July 11, 1994
Published February 28, 1995
Publication 1464**

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

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Library of Congress Catalog Card Number: 94-62054

ISSN 0015-0754

PRINTED IN THE UNITED STATES OF AMERICA

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Revision of the Tribe Phyllotini (Rodentia: Sigmodontinae), with a Phylogenetic Hypothesis for the Sigmodontinae

Scott J. Steppan

Abstract

The phylogenetic relationships of the South American rodents of the tribe Phyllotini are reviewed, considering both the phylogenetic relationships of the phyllotines to the other sigmodontine tribes and the relationships within the phyllotines. Cladistic analysis of 40 morphological characters for 28 sigmodontine taxa provides a working hypothesis of sigmodontine phylogenetics, phyllotine monophyly, and likely sister-groups to the phyllotines. Five Old World and six New World cricetid taxa represent outgroups, and together they root the sigmodontine tree within a paraphyletic thomomyine group. The analysis corroborates the recent proposal of a monophyletic oryzomyine group that includes the tetralophodont genera *Holochilus*, *Pseudoryzomys*, and *Zygodontomys*. A supratribal clade is indicated that includes the Akodontini, Phyllotini, Scapteromyini, and *Punomys*. The distinctiveness and monophyly of the Central American tylomyine group is strongly supported. The taxonomic distribution of and variation in morphological characters of the dentition, skull, skeleton, and soft anatomy are discussed. Apparent biases in the evolutionary polarity of reductive characters are identified in detail from a broad taxonomic survey (174 species) for intra- and interspecific variation in number of vertebrae, as well as from optimization of other characters on the phylogenetic hypotheses. Conflicting results from various phylogenetic studies suggest that *Sigmodon* be considered Sigmodontinae *incertae sedis*. *Pseudoryzomys* and *Punomys* are removed from the phyllotines, and Phyllotini is diagnosed. A cladistic analysis of 35 phyllotine taxa using 98 morphological characters is presented, and the taxonomy of the phyllotine genera is revised. Species of *Andalgalomys* are referred to *Graomys*. Removal of *micropus* from *Auliscomys* to the genus *Loxodontomys* is supported. The two most species-rich genera, *Phyllotis* and *Calomys*, appear to be paraphyletic, but their species relationships are insufficiently resolved to justify modifying their taxonomy at this time.

Introduction

The phyllotines constitute one of the principal radiations of the New World muroids. Frequently the most abundant mammals in their range, phyllotine species are concentrated among the pastoral habitats of the Andes, stretching from Ecuador to Tierra del Fuego, and from the Pacific coast of Peru and Chile east through Patagonia to southeastern Brazil. Maximum diversity is achieved in the altiplano, with 44% of the phyllotine species

inhabiting the puna, an alpine steppe community (Reig, 1986).

This study presents a cladistic analysis of evolutionary relationships among members of the tribe Phyllotini. It then provides a taxonomic revision of the tribe with diagnoses of recognized genera within this phylogenetic context. An impediment to any such cladistic analysis within tribes is that intertribal relationships among Neotropical sigmodontine rodents, and even tribal monophyly, are poorly resolved. This lack of understanding of

TABLE 1. Species included in sigmodontine analysis. (Taxonomy follows Musser and Carleton [1993], with modifications noted.)

Old World "cricetids" ^a
Subfamily Calomyscinae
<i>Calomyscus baluchi</i>
Subfamily Cricetinae
<i>Cricetulus migratorius</i>
<i>Mesocricetus auratus</i>
<i>Phodopus sungorus</i>
Subfamily Mystromyinae
<i>Mystromys albicaudatus</i>
New World "cricetids"
Subfamily Tylomyinae ^b
<i>Nyctomys sumichrasti</i>
<i>Tylomys nudicaudus</i>
Subfamily Neotominae ^c
<i>Neotoma floridana</i>
<i>Ochrotomys nuttalli</i>
<i>Peromyscus leucopus</i>
<i>Scotinomys teguina</i>
Subfamily Sigmodontinae
Tribe Akodontini ^d
<i>Akodon albiventer</i>
<i>Akodon boliviensis</i>
<i>Oxymycterus hispidus</i>
Tribe Ichthyomyini
<i>Anotomys leander</i>
<i>Ichthyomys hydrobates</i>
<i>Neusticomys monticolus</i>
Tribe Oryzomyini ^e
<i>Holochilus brasiliensis</i>
<i>Neacomys spinosus</i>
<i>Nectomys squamipes</i>
<i>Oligoryzomys fulvescens</i>
<i>Oryzomys capito</i>
<i>Oryzomys palustris</i>
<i>Pseudoryzomys simplex</i>
<i>Zygodontomys breviceauda</i>
Tribe Phyllotini
<i>Calomys callosus</i>
<i>Graomys griseoflavus</i>
<i>Neotomys ebriosus</i>
<i>Phyllotis darwini</i>
<i>Reithrodon auritus</i>
Tribe Scapteromyini
<i>Kunsia tomentosus</i>
<i>Scapteromys tumidus</i>
Tribe Sigmodontini
<i>Sigmodon hispidus</i>
Tribe Wiedomyini
<i>Wiedomys pyrrhorhinos</i>
Thomasomyine group ^f
<i>Chilomys instans</i>
<i>Rhipidomys latimanus</i>
<i>Thomasomys aureus</i>
<i>Thomasomys baeops</i>
<i>Thomasomys rhoadsi</i>
Sigmodontinae incertae sedis
<i>Punomys lemminus</i>

higher-level relationships significantly reduces confidence in hypotheses of character polarities and specific membership within tribes. Better estimates of outgroups to the phyllotines are needed. Therefore, this study also presents a cladistic analysis for the subfamily Sigmodontinae (*sensu* Reig, 1980) in order to provide a provisional hypothesis of outgroup relationships to be applied to the phyllotine analysis, and a revised diagnosis of Phyllotini. These two nested analyses will be referred to as the sigmodontine and phyllotine analyses.

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*, *Galeomys*, *Graomys*, *Irenomys*, and *Phyllotis*. Problematic taxa have included *Euneomys*, *Holochilus*, *Neotomys*, *Pseudoryzomys*, *Punomys*, *Reithrodon*, *Sigmodon*, and *Zygodontomys*. "Problematic taxa" are those that at various times have been included within the phyllotine group as well as genera hypothesized to have been derived from a phyllotine ancestor. The phyllotine analysis examines representatives of all phyllotine genera, as defined by the results of the sigmodontine analysis. All formally or informally recognized supergeneric groups are represented in the sigmodontine analysis, as are all "problematic taxa" except *Euneomys*.

Evolutionary Relationships within Sigmodontinae

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 "cri-

^a Informal designation of Old World and New World "cricetids" reflects historical usage and serves to distinguish them from murines and arvicolines, but little support has been presented for the monophyly of either group.

^b *Sensu* Reig (1984). The distinctiveness of this group and its basal position relative to the North American neotomine-peromyscines and South American sigmodontines has also been noted by Carleton (1980).

^c *Sensu* Reig (1980).

^d Sigmodontine tribes regarded as informal groups by Musser and Carleton (1993) are here recognized in their formal tribal designations, *sensu* Vorontsov (1959).

^e Contents per Voss and Carleton (1993).

^f Monophyly and tribal status argued against by Voss (1993).

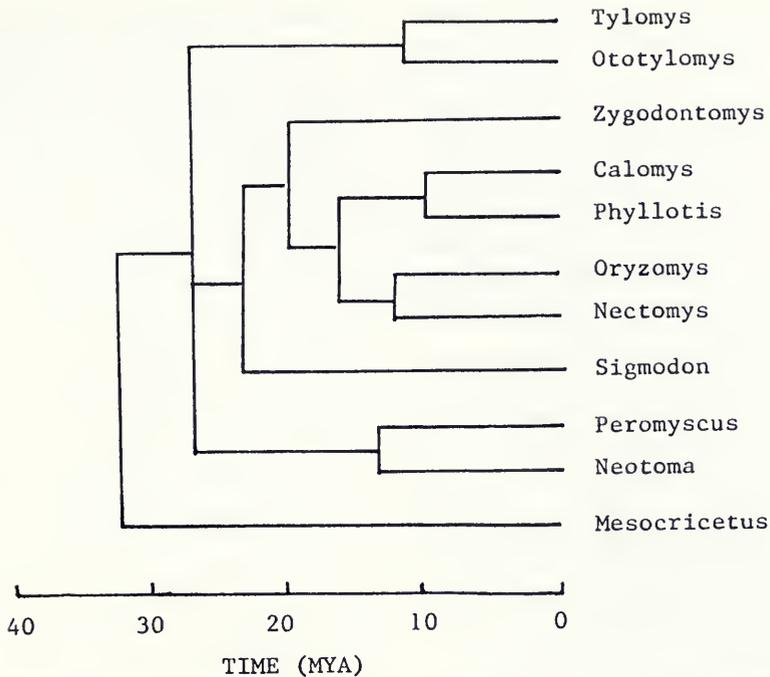


FIG. 1. Albumin immunological dendrogram of New World muroids (modified from Sarich, 1985).

cetids," the neotomine-peromyscines (Carleton & Musser, 1984; Musser & 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" or "complex" penis types, respectively (Hershkovitz, 1966b; Hooper & Musser, 1964). The subfamily Sigmodontinae is here considered to be limited to the predominantly complex-penis, largely Neotropical species in accordance with the taxonomy of Reig (1980) and evolutionary scenarios of Hershkovitz (1962, 1966a), excluding the Central American genus *Nyctomys*. The taxonomy of muroid rodents used in this paper is presented in Table 1. Cricetidae was not recognized by Musser and Carleton (1993), and in this paper I use the term "cricetid" for the assemblage of subfamilies sharing the dental morphology associated with earlier definitions of Cricetidae (Simpson, 1945).

Sigmodontinae (as was defined to include the North American neotomine-peromyscines) was one of only two muroid subfamilies that Carleton and Musser (1984, p. 300) were unable to diagnose, owing to their "immense heterogeneity." Monophyly of the Neotropical "complex penis" sigmodontines has not been clearly demonstrated,

but the few available molecular or cladistic studies are consistent with monophyly (Carleton, 1973; Catzeflis et al., 1993).

While Carleton cautioned that assuming monophyly of the complex-penis sigmodontines ("South American cricetines") "as presently constituted" was premature (1980, p. 140), his distance Wagner tree (1980, Fig. 41) does support monophyly of the Neotropical sigmodontines provided they are not defined as identical with "complex penis" murids and the Central American *Nyctomys* is excluded. The distinctiveness of *Nyctomys* from the other "complex penis" forms has been noted repeatedly for several aspects of the male reproductive system (Arata, 1964; Hershkovitz, 1966b; Hooper & Musser, 1964; Voss & Linzey, 1981). Sarich (1985) presented an albumin immunological dendrogram for New World "cricetids" (Fig. 1). The South American sigmodontines as defined in this study were a monophyletic branch in an unresolved trichotomy with the Central American *Tylomys* (which Carleton [1980] found to be most closely related to *Nyctomys*) and the North American *Peromyscus* and *Neotoma*. Catzeflis et al. (1993) reported a DNA hybridization study that clearly distinguishes the North and South American groups as separate lineages and referred

them to the subfamilies Neotominae and Sigmodontinae, following Reig (1980). Neotominae was represented by *Neotoma* and *Peromyscus* while Sigmodontinae was represented by *Sigmodon*, *Oryzomys*, *Zygodontomys*, *Akodon*, and *Phyllotis*. Catzefflis et al.'s (1993) analysis and review of previous DNA hybridization studies not only support the monophyly of the South American Sigmodontinae relative to the Neotominae, but also relative to other "cricetid" groups: cricetines and arvicolids. Molecular data sets thus support the definition of Sigmodontinae used in this paper.

Additional support for a monophyletic Sigmodontinae comes from distributions of ectoparasites and endoparasites. Wenzel and Tipton (1966) found that mites and lice (as well as the less host-specific ticks) found on complex-penised "cricetids" (sigmodontines) belonged to a radiation of South American origin. Congruently, Slaughter and Ubelaker (1984) found members of the nematode genus *Parastrongylus*, belonging to a species group largely restricted to Old World "cricetids," to be present in several oryzomyines and *Sigmodon*, but not in North American neotomine-peromyscines. The nematodes show strong host specificity and are not likely to have distributions strongly affected by climate, a criticism Carleton (1980) made of the flea data from Wenzel and Tipton (1966). Slaughter and Ubelaker (1984) argued that the neotomine-peromyscines had diverged from the lineage that later gave rise to the Old World "cricetids" and the sigmodontines prior to the complex-penised lineage having acquired the parasite.

Few hypotheses of relationships among the sigmodontines have been proposed, and only one has utilized phylogenetic methods (Carleton, 1980), wherein the analysis of the South American sigmodontines was peripheral to the principal objectives of the study. More comprehensive attempts (Gardner & Patton, 1976; Hershkovitz, 1962; Reig, 1986) have lacked the analytical rigor of cladistics. Nonetheless, the several scenarios and studies provide an important conceptual framework.

The group most commonly identified as the basal member of the sigmodontines has been the species-rich oryzomyines, which have often been portrayed as paraphyletic. The definition of "oryzomyines" has varied, either referring to oryzomyines *sensu stricto* (*Melanomys*, *Microrizomys*, *Neacomys*, *Nectomys*, *Nesoryzomys*, *Oecomys*, *Oligoryzomys*, *Oryzomys*, *Scolomys*, *Sigmodontomys* [Hershkovitz, 1962; Musser & Carleton, 1993]) or also including the thomasomyines (*Thomasomys*, *Rhipidomys*, *Delomys*,

Chilomys, *Aepeomys* [Reig, 1980]). Gardner and Patton (1976) derived all sigmodontine lineages from an *Oryzomys* karyotype. Reig (1986, 1987) considered oryzomyines to be the direct or indirect descendants [sic] of the ancestral *Oryzomys*-like sigmodontine. Carleton's (1980, Fig. 41) Wagner tree placed *Akodon* and *Oxymycterus* at the base of the South American lineage, while Sarich's (1985) immunological tree (Fig. 1) placed *Sigmodon* at the base of the South American branch, with *Zygodontomys* basal to the phyllotines and oryzomyines *sensu stricto*.

Hershkovitz (1962) envisioned two lineages arising from a pentalophodont (with complete mesolophostyle), *Thomasomys*-like stock: a thomasomyine group that gave rise to the oryzomyine group, and a tetralophodont lineage that gave rise to the paraphyletic akodontine group, from which radiated the ichthyomyine, phyllotine, and sigmodont groups (Fig. 2). Later, he presented the scapteromyines as the sister-group to the oxymycterines, and these together as part of the akodont radiation (Hershkovitz, 1966b). Vorontsov (1959) outlined what amounts to a monophyletic group consisting of his Phyllotini, *Euneomys*, and Sigmodontini (including *Reithrodon* and *Neotomys*). The Wagner tree generated by Carleton (1980) placed *Oxymycterus* as a basal South American genus and *Scapteromys* as highly derived, in contrast to his earlier noncladistic study of stomach morphology that hypothesized a sister-group relationship between these two (Carleton, 1973). The evolutionary scenario diagrammed by Gardner and Patton (1976) treats the akodontines and oxymycterines as sister-groups comprising an independent offshoot from *Oryzomys*. Other independent lineages include the thomasomyines, ichthyomyines, and a group composed of the phyllotines, sigmodonts, and scapteromyines.

Finally, Reig (1984, 1986) wove a complex biogeographic scenario for the South American "cricetids." He considered phyllotines to be most likely derived from akodontines, though he suggested that phyllotines could be independent offshoots from the oryzomyines. He also hypothesized that *Zygodontomys* was an independent oryzomyine offshoot of undetermined affinity and proposed the descent of ichthyomyines from a *Thomasomys*-like ancestor, scapteromyines from akodontines, and sigmodonts from the phyllotine *Neotomys*. Although there is no single point on which all of these authors agree, a consensus would place the oryzomyines or thomasomyines at the root of the sigmodontines.

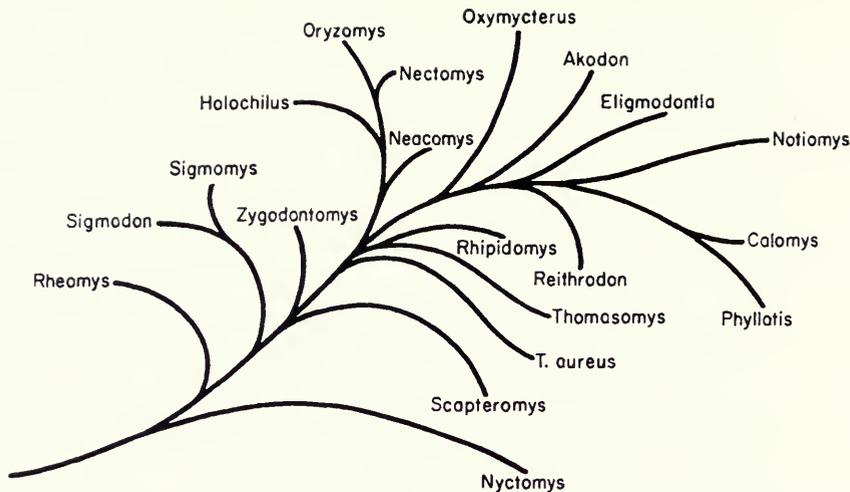


FIG. 3. Hypothesized relationships of South American "cricetines," based on phallic characters (from Hooper & Musser, 1964).

Taxonomic History of the Phyllotines

The following is a summary of the more recent taxonomic history of the phyllotines. Additional details, particularly of the period before 1962, can be found in Olds and Anderson (1989) and in Tate (1932a,b,c).

Herskovitz (1962, and Fig. 2) portrayed the phyllotines as a monophyletic group derived from akodont stock. In his detailed revision of the phyllotines and discussion of sigmodontine morphological evolution, Herskovitz included *Zygodontomys* (whose southern forms have since been removed to *Bolomys*) and *Pseudoryzomys* but excluded *Reithrodon* and *Neotomys* (which he considered to be sigmodonts along with *Sigmodon* and *Holochilus*), as well as *Euneomys*, *Irenomys*, and *Punomys*.

The glans penis of Neotropical "cricetids" was first systematically examined by Hooper and Musser (1964), who inferred evolutionary relationships among 19 genera based on estimates of overall similarity (Fig. 3). They found no diagnostic trait among the diverse phalli of five phyllotine genera. They seem to have excluded *Zygodontomys* (diagrammed near the base of the sigmodontine radiation; Fig. 3), although their discussion indicates that it could also be placed at the base of the phyllotines. The cited similarity between *Eligmodontia* and *Akodon* could lead to the interpretation of *Eligmodontia* as either a basal phyllotine or akodontine. They suggested that *Holo-*

chilus was best placed with the oryzomyines. *Reithrodon* was placed as a basal phyllotine; *Neotomys* and *Pseudoryzomys* were not examined. Inexplicably, *Geoxus* ("*Notiomys*") was diagrammed as part of a phyllotine lineage, though in the text it was described as allied to akodontines, *Oxymycterus*, and phyllotines.

Phyllotines have commonly been viewed as a paraphyletic group. Gardner and Patton (1976) diagrammed their view of evolutionary relationships among Neotropical "cricetids" based primarily on karyotypic data. They showed sigmodonts and scapteromyines as derived from primitive phyllotines. Pearson and Patton (1976) and Gardner and Patton (1976) agreed on the inclusion of *Andinomys*, *Auliscomys*, *Calomys*, *Chinchillula*, *Eligmodontia*, *Neotomys*, *Phyllotis* (including *Graomys*), and *Reithrodon* as phyllotines. Their analysis relied on similarity in number and form of unbanded chromosomes. They explicitly excluded *Zygodontomys* but did not examine the genera *Andalgalomys* (first described in 1978 as a *Graomys*), *Euneomys*, *Galenomys*, *Irenomys*, *Pseudoryzomys*, or *Punomys*.

Reig (1980, 1986) viewed all the major sigmodontine tribes as paraphyletic and stated that the phyllotines most likely evolved "directly from the oryzomyines through the akodontines" (Reig, 1986, p. 426). Reig (1986) also suggested that both sigmodont genera, *Holochilus* and *Sigmodon*, were (independently?) derived from a *Neotomys*-like ancestor in Peru.

Spotorno (1986) explored the akodontine and

phyllotine radiations (which he viewed as sister-groups) using banded karyotypes, electrophoresis, glans penis and bacular morphology, and cranial morphometrics. He argued that the phyllotines were monophyletic, citing simplification and planation of their molars, differentiation of the distal baculum, and a poorly developed base of the proximal baculum as characteristic features. Like Hershkovitz (1962) and Reig (1986), Spotorno considered the phyllotines to be derived from an akodontine ancestor. Though he drew no definite conclusions about phylogenetic relationships between genera, his concept of the phyllotines included *Andinomys*, *Auliscomys*, *Calomys*, *Chinchillula*, *Eligmodontia*, *Euneomys*, *Graomys*, *Irenomys*, *Phyllotis*, and *Reithrodon*. Spotorno did not explain why he considered *Reithrodon* a phyllotine but *Neotomys* a sigmodont. *Punomys* was listed as *Sigmodontinae incertae sedis* and not analyzed. *Pseudoryzomys* and *Zygodontomys* were omitted.

Olds and Anderson (1989) presented the first formal diagnosis of Phyllotini and the first implicitly cladistic treatment of the group, providing a foundation for this examination of phyllotine monophyly and tribal relationships. They included *Punomys* and excluded *Pseudoryzomys* and *Zygodontomys*. In their survey of 33 sigmodontine genera (14 phyllotine and 19 nonphyllotine), they could not find any 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 & Anderson, 1989, p. 63.)

Determining whether these characters are actually synapomorphies for the phyllotines requires a phylogenetic hypothesis for the subfamily. Olds and Anderson (1989) incorporated into their diagnosis characters that "may be synapomorphic" and recognized the difficulty of diagnosing the phyllotines given the current knowledge of tribal relationships by describing the diagnosis as a "hypothesis for future testing and elaboration" (p. 63). I will test their hypotheses of phyllotine monophyly and associated synapomorphies by conducting a more broadly based cladistic analysis for the subfamily.

Olds and Anderson (1989) also identified and diagnosed a distinct "Reithrodon-group" that included *Euneomys* and *Neotomys*. They alluded to a relationship of this group to the remaining sigmodonts but left this relationship unspecified.

Braun (1993) generally agreed with Olds and Anderson (1989) on the composition of Phyllotini but additionally included *Pseudoryzomys* as the most basal phyllotine. She did not recognize a *Reithrodon* group but instead found support for a generic group that included *Reithrodon*, *Euneomys*, *Neotomys*, and *Auliscomys* along with *Andinomys*, *Chinchillula*, *Galenomys*, *Irenomys*, and *Punomys*. Braun also elevated *Auliscomys boliviensis* to *Maresomys*, reinstated *Paralomys* for *Phyllotis gerbillus*, additionally including *Phyllotis amicus* in the reinstated genus, and resurrected *Loxodontomys* for *micropus*, which she removed from *Auliscomys*.

In an earlier version of this study (Steppan, 1993), using nearly the same phyllotine data set (see Materials and Methods), I excluded *Punomys* from the phyllotines. *Phyllotis* was found to be paraphyletic, but the internal nodes were very poorly resolved. *Calomys* was also paraphyletic, with *C. sorellus* as the sister-species to all remaining phyllotines. Confirmation was found for the *Reithrodon* group, which was most closely related to *Auliscomys*, *Galenomys*, and the resurrected *Loxodontomys*. *Graomys* appeared paraphyletic with respect to *Andalgalomys*, but character support was not strong. *Eligmodontia* was most closely related to *Graomys*, and this group appeared to be derived from *Phyllotis*.

Materials and Methods

Taxa and Characters Examined

Two separate but nested phylogenetic analyses were conducted: one on the Sigmodontinae and one on the Phyllotini. The sigmodontine analysis included 29 ingroup species representing all named tribes or major generic-groups. Eleven outgroup taxa included *Nyctomys* and *Tylomys* (Central American genera of uncertain affinities to the sigmodontines and neotomine-peromyscines), the terminal neotomine-peromyscines *Neotoma* and *Peromyscus*, the basal neotomine-peromyscines *Ochrotomys* and *Scotinomys* (Carleton, 1980), and the Old World "cricetids" *Calomyscus*, *Cricetulus*, *Mesocricetus*, *Phodopus*, and *Mystromys*. Rela-

TABLE 2. Species included in phyllotine analysis.

Thomasomyine group
<i>Thomasomys bacops</i>
Tribe Oryzomyini
<i>Holochilus brasiliensis</i>
<i>Nectomys squamipes</i>
<i>Pseudoryzomys simplex</i>
<i>Zygodontomys brevicauda</i>
Tribe Ichthyomyini
<i>Ichthyomys hydrobates</i>
Tribe Akodontini
<i>Akodon albiventer</i>
<i>Akodon boliviensis</i>
<i>Chroemys andinus</i>
<i>Oxymycterus hispidus</i>
Tribe Scapteromyini
<i>Scapteromys tumidus</i>
Sigmodontinae incertae sedis
<i>Punomys lemminus</i>
Tribe Phyllotini
<i>Andalgalomys pearsoni</i>
<i>Andinomys edax</i>
<i>Auliscomys boliviensis</i>
<i>Auliscomys pictus</i>
<i>Auliscomys sublimis</i>
<i>Calomys callosus</i>
<i>Calomys hummelincki</i>
<i>Calomys laucha</i>
<i>Calomys lepidus</i>
<i>Calomys sorellus</i>
<i>Chinchillula sahamae</i>
<i>Eligmodontia morgani</i>
<i>Euneomys chinchilloides</i>
<i>Euneomys petersoni</i>
<i>Galenomys garleppi</i>
<i>Graomys domorum</i>
<i>Graomys griseoflavus</i>
<i>Irenomys tarsalis</i>
<i>Loxodontomys micropus</i> ^a
<i>Neotomys ebriosus</i>
<i>Phyllotis amicus</i>
<i>Phyllotis andium</i>
<i>Phyllotis caprinus</i>
<i>Phyllotis darwini</i>
<i>Phyllotis definitus</i>
<i>Phyllotis gerbillus</i>
<i>Phyllotis haggardi</i>
<i>Phyllotis magister</i>
<i>Phyllotis osilae</i>
<i>Phyllotis wolffsohni</i>
<i>Phyllotis xanthopygus rupestris</i>
<i>Phyllotis xanthopygus xanthopygus</i>
<i>Reithrodon auritus evae</i>
<i>Reithrodon auritus pachycephalus</i>
<i>Reithrodon typicus</i>

^a Removal of *micropus* from *Auliscomys* to *Loxodontomys* recommended by Braun (1993) and Steppan (1993).

tionships among the Old World "cricetids" are unclear, but in a recent treatment (Musser & Carleton, 1993) these five taxa represented the murid subfamilies Calomyscinae, Cricetinae, and Mys-

tromyinae (see Table 1, with subfamily and tribal classification). Estimates of the number of phyllotine species vary with group limits and specific status of taxa, with most estimates between 40 and 45. The phyllotine analysis included 35 phyllotine OTUs representing 33 putative species in 14 phyllotine genera, in addition to 12 species belonging to 11 outgroup genera (Table 2).

Character assessments were made from direct examination of museum specimens (Field Museum of Natural History, Chicago, FMNH; Museum of Vertebrate Zoology, University of California, Berkeley, MVZ; National Museum of Natural History, Smithsonian Institution, Washington, D.C., USNM; University of Michigan Museum of Zoology, Ann Arbor, UMMZ; Museo Nacional de Historia Natural, Santiago, Chile, MNHN; The Museum, Michigan State University, East Lansing, MSU; specimens examined listed in the Appendix). Phallic measurements for some species were measured from published illustrations (Hooper & Musser, 1964; Spotorno, 1986). Evidence of two pairs of preputial glands was gathered from the literature (Voss & Linzey, 1981) for some species. Stomach and some hyoid data are from Carleton (1980), gallbladder data are from Voss (1991), and mammae number is from Gyldenstolpe (1932), Hershkovitz (1955, 1959, 1962, 1966b), and Olds (1988). Dental nomenclature follows Reig (1977, and Fig. 4).

A broad survey of characters from varied anatomical systems was conducted, resulting in 40 characters for the sigmodontine analysis and 98 characters in the phyllotine analysis covering dental, cranial, postcranial, external, gastrointestinal, and male reproductive tract systems. Seventeen characters were shared by the two analyses, but 5 of the 17 were coded differently in each. Many of those 17 were included in the phyllotine analysis to help define outgroup relationships. Previous surveys have found little variation in soft anatomy among phyllotines that was not already evidenced in the skeleton (Carleton, 1973; Voss & Linzey, 1981; Voss, 1991). The 40 sigmodontine characters represent 114 character states and a minimum of 74 character state transitions. The 98 phyllotine characters represent 265 character states and a minimum of 167 character state transitions. Character state descriptions were defined so as to be more objective or quantitative than they have been in the past. Ambiguous terms such as "relatively broad," "large," or "well developed" were generally but not entirely avoided. Quantitative characters or those with quantitative components were

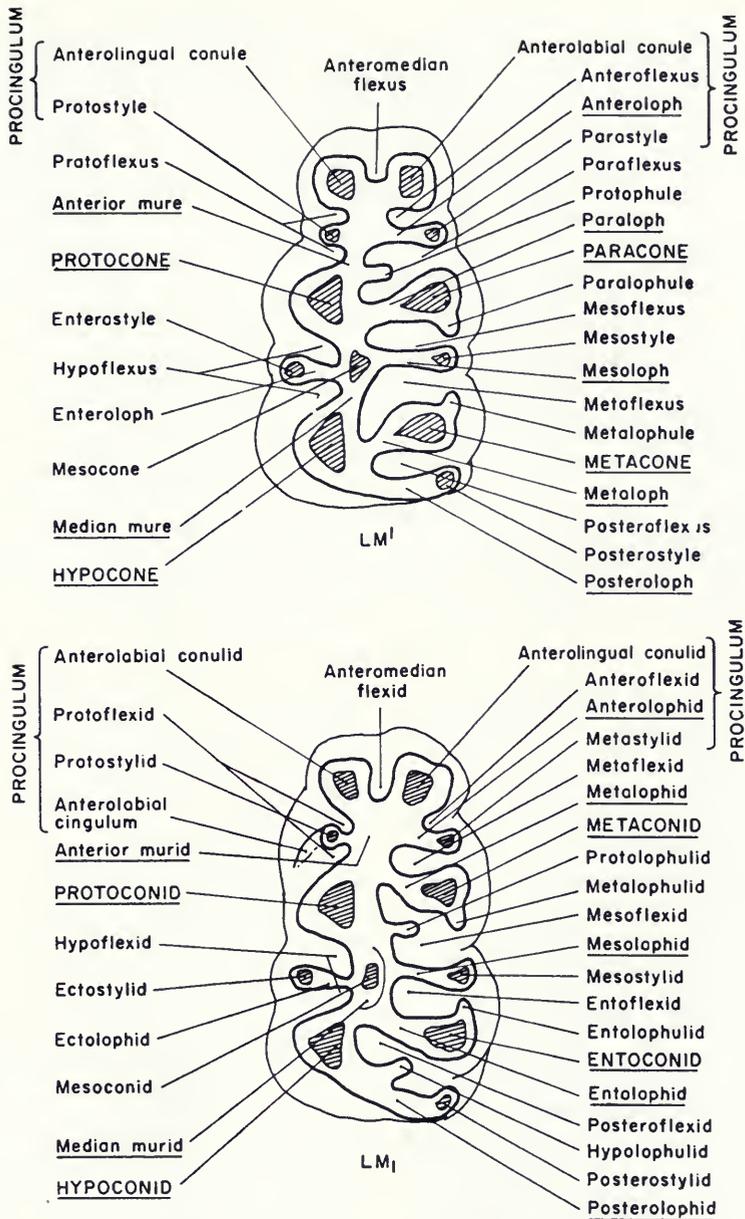


FIG. 4. Master plan of the occlusal surfaces of idealized first upper and lower molars of a cricetid rodent. All possible elements are shown with their corresponding names (from Reig, 1980).

measured using a digital caliper precise to ± 0.005 mm and values were rounded to the nearest 0.1 mm for coding. External measurements were recorded from specimen tags. Character polarities were determined by outgroup rooting within the parsimony analysis rather than *a priori*, so ple-

siomorphic character states are not always designated "0." Characters were treated as ordered unless otherwise noted.

Outgroup taxa in the phyllotine analysis were selected to include representatives of each of the sigmodontine tribes and major generic groups (ex-

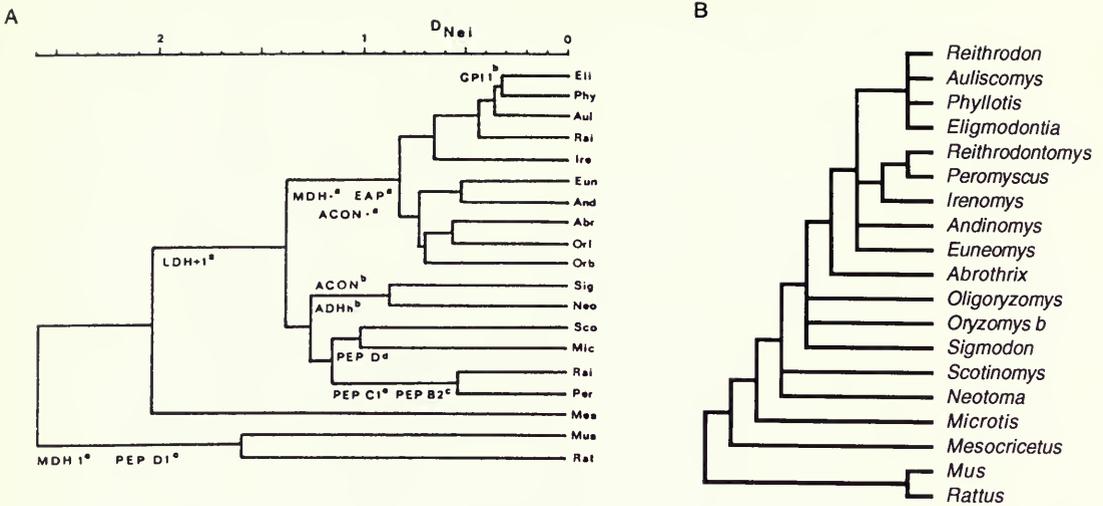


FIG. 5. A. UPGMA dendrogram of electrophoretic similarities (from Spotorno, 1986). B. Seventy percent majority-rule consensus tree of 141 equally most-parsimonious trees derived from the original allele data. In cladistic reanalysis, individual alleles were treated as character states, proteins as characters. Character states were unordered in a cladistic analysis using PAUP. A strict consensus of the most-parsimonious trees is completely unresolved.

cept the monotypic Wiedomyini). Both analyses 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 sigmodontine network was rooted by designating the Old World "cricetids" as outgroups. The phyllotine network was rooted in accordance with the results from the sigmodontine phylogeny and consistent with the common estimate of basal sigmodontines (Hershkovitz, 1962; Reig, 1980, 1986; Voss, 1993; Voss & Carleton, 1993). *Sigmodon* was not included in the final phyllotine analysis because previous molecular and morphological phylogenies were highly discordant on its position among sigmodontines. DNA hybridization has been reported to show *Sigmodon* to be the basal member of a Neotropical group, outside a group that included the oryzomyines, *Akodon*, and *Phyllotis* (Catzeffis et al., 1993), though the data were not presented. Likewise, albumin immunological distances placed *Sigmodon* outside a clade that included oryzomyines, akodontines, phyllotines, and ichthyomyines (Sarich, 1985). *Sigmodon* was clustered with the North American neotomine-peromyscines in phenetic (Spotorno, 1986, and Fig. 5A) and cladistic (Fig. 5B; reanalysis of data in Spotorno, 1986) analyses of electrophoretic data, and its inclusion resulted in three discordant and unconventional tree topologies with

this data set (see Discussion under Phylogenetic Relationships within Sigmodontinae).

Quantitative Character Coding

Quantitative characters, in this case the four ratio characters (M3 length/M2 length, M2 width/M2 length, ear/body, interparietal/parietal), were coded using a minor variation on segment-coding (Chappill, 1989). In segment-coding, itself a variation of range-coding (Colless, 1980), the total range of mean values for the taxa is divided into a number of equal-length segments. Segment-coding categorizes an ordered series of OTUs into discrete character states by creating a discriminant criterion that is a multiple of the pooled within-group standard deviation. Thus, the extent to which OTUs are grouped together is objectively determined by the actual observed variability within each of the OTUs. This characteristic of segment-coding and similar techniques, such as generalized gap-coding (Archie, 1985), is justified by the argument that the ease with which an evolutionary unit can evolve from one character state to another (e.g., response to selection) is a function of the amount of genetic variance present for that trait (Farris, 1966; Kluge & Farris, 1969; Archie, 1985).

Segment-coding proceeds by first calculating the pooled within-group standard deviation (s_p) for the set of taxa and then choosing a value for the

multiplier (c). This size of the multiplier determines the percentage of overlap between the distributions of two OTUs (e.g., $1s_p = 31\%$ overlap between two populations, $3s_p = 7\%$ overlap) (Archie, 1985). Use of larger multipliers represents a more conservative estimate of the number of biologically significant state transitions. Characters that vary little between taxa but show high intraspecific variability would be subdivided less than characters with relatively little intraspecific variation. The OTUs are then ordered (usually ascending) by the magnitude of their means. Starting at one end of the series, all those OTUs that fall within a group bounded by cs_p are joined in a "segment." This step is repeated for each subsequent segment. The process is repeated until the last OTU in the series has been joined into a segment. These subsets are then converted to codes by increasing the code value by 1 for each segment transition. The size of the segments is determined *a priori* as a multiple, c , of the pooled within-group standard deviation, s_p . In this way, the number of character states is determined by the amount of infraspecific variation relative to interspecific variation.

One drawback of generalized gap-coding and its related techniques is that the position of one end of a subset is strongly influenced by the distribution of OTU values at the other end. Nearly identical OTUs can be categorized into two different states because of the specific value of the OTU at the other end of the subset. In other words, taxon sampling can significantly affect a generalized gap-coding scheme and the addition of even a single taxon can require a recoding of all others. Traditional gap-coding techniques place state transitions at large gaps but have a series of other shortcomings. The number of character states increases with the number of OTUs in generalized gap-coding, independent of the range and multiplier value (the number often decreases in gap-coding). With a large number of OTUs, there will be a large number of character states. If the magnitude of the multiplier is increased to compensate for this effect, the result is to concentrate the transitions toward the extremes of the series, decreasing the phylogenetic information content. Standardizing segment (group) lengths *a priori* minimizes or eliminates these shortcomings. For more detailed discussions and critiques of the various quantitative coding techniques, the reader is referred to prior studies (Archie, 1985; Chappill, 1989; Mickovich & Farris, 1981) and references therein.

The modification used in this study is to allow

the segments, whose lengths were calculated *a priori*, to shift as a group so that segment boundaries could fall within the largest available gaps. The segments were not allowed to shift more than one-half a segment. The objective of this shift was to avoid arbitrarily splitting two taxa with very similar values and placing them into different character states. The multiplier used for all four quantitative characters was 4, chosen to yield an overlap between OTUs of less than 5% (Archie, 1985). This is larger than that recommended by Chappill (1989), who preferred $\frac{1}{4}$ or $\frac{1}{2}$ (yielding overlaps of 45% and 40%, respectively), but those small multiplier values would result in dozens of character states for each character, raising the likelihood of excessive influence by the quantitative characters on the phylogenetic analysis. A multiplier of 4 is commonly used with generalized gap-coding and its related techniques.

Analytical Methods

Phylogenetic hypotheses were generated under the principle of Wagner parsimony using the computer program PAUP, version 3.1.1 (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 these data sets demonstrated that with this many taxa (>40), most single replicates will *not* find trees of the minimum length. Consensus trees were produced from the accumulated minimum-length trees. The sensitivity of the resulting topologies was tested by multiple runs in which particularly interesting or pivotal taxa or characters were excluded. Additionally, 100 (sigmoidontine) and 200 (phyllotine) replicate bootstrap analyses were performed on the data sets to provide nonparametric estimates for the confidence to be placed in each node of the trees. 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 tree provides additional information in evaluating alternative phy-

TABLE 3. Data matrix for sigmodontine analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Oryzomys capito</i>	2	1	0	0	0	0	0	2	1	1	2/3	0/1	2	0	1	0
<i>Oryzomys palustris</i>	2	1	0	1	0	0	0	2	0/1	1	3	1	1	0	1	0
<i>Oligoryzomys fulvescens</i>	2	1	0	0	0	0	0	1/2	0	1	2	0	1	0	1	0
<i>Nectomys squamipes</i>	2	1	0	0	0	0	0	2	0	2	3	1	1	0	1	0
<i>Neacomys spinosus</i>	2	1	1	0	0	0	0	1	0	1	3	0/1	1	0	1	0
<i>Zygodontomys breviceauda</i>	1	1	1	1	0	0	0	2	0	1/2	3	0	1	0	1	0
<i>Pseudoryzomys simplex</i>	1	1	0	0/1	0	0	0	2	0	1	3	0	1	0	1	0
<i>Holochilus brasiliensis</i>	0	2	1	0	0	0	0	2	0	1	3	0	0	0	1	0
<i>Akodon boliviensis</i>	1	0	0	2	0	1	0	2	1	2	1	0	0	0	0	0
<i>Akodon albiventer</i>	1	0	0	2	0	1	0	2	1	2	1/2	0	0	0	0	0
<i>Oxymycterus hispidus</i>	1	0	0	1	0	1/2	0	2	1	2	2	0	0	0	0	0
<i>Anotomys leander</i>	1	0	0	0	0	1	1	0	0	1/2	1	0	0	0	0	0
<i>Ichthyomys hydrobates</i>	0	0	?	0	0	0	1	0	0	2	0	2	0	0	0	0
<i>Neusticomys monticolus</i>	0	0	0	0	0	0/1	1	0	0	2	0	?	0	0	0	0
<i>Chilomys instans</i>	2	0	0	0	0	1	0	1	1	0	1	0/1	1	0	0	0
<i>Rhipidomys latimanus</i>	2	1	0	0/1	1	0	0	1	1	1	3	0/1	1	0	0	0
<i>Thomasomys aureus</i>	2	1	0	1	1	0/1	0	1	1	1	2	1	1	0	0	0
<i>Thomasomys baeops</i>	2	1	0	0/1	1	0	0	1	1	0/1	2	1	1	0	0	0
<i>Thomasomys rhoadsi</i>	2	1	0	0	0	0/1	0	1	0	2	1	0	1	0	0	0
<i>Wiedomys pyrrhorhinos</i>	2	1	0	0/1	0	0	0	1/2	1	0	2/3	0	1	0	0	0
<i>Kunsia tomentosus</i>	?	1	1	1	0	0	0	2	1	2	3	0	2	0	0	1
<i>Scapteromys tumidus</i>	1	1	0	1	0	1	0	2	0	2	1	0	0	0	0	0
<i>Calomys callosus</i>	0	1	0	1	0	0	0	2	0	1	3	0	1	0	0	0
<i>Graomys griseoflavus</i>	0	1	1	1	1	0	0	2	1	1	3	0	1	0	0	0
<i>Phyllotis darwini</i>	0	1	1	1	1	1	0	2	0	1	2	0	1	0	0	0
<i>Neotomys ebriosus</i>	0	2	1	0	2	1	0	2	0	1	2	?	1	0/1	0	0
<i>Reithrodon physodes</i>	0	1	0	3	2	1	0	2	1	1/2	2	1	2	0	1	0
<i>Punomys lemminus</i>	1	1	0	1	1	2	0	2	0	2	2	1	1	0	0	0
<i>Sigmodon hispidus</i>	0	1	1	1	0/1	0	0	2	1	0	3	1	1	0	0	0
<i>Nyctomys sumichrasti</i>	2	1	0	0	0/1	0	0	1	1	0	3	0	2	1	0	1
<i>Tylomys nudicaudus</i>	1	1	0	0	1	0	0	1	1	1	3	0	2	1	0	1
<i>Ochrotomys nuttalli</i>	2	0	0	0	1	0	0	0/1	1	1	1	0/1	1	0	0	0
<i>Scotinomys teguina</i>	?	1	0	0/1	0	1	1	1	0/1	1	2	0	1	0	0	0
<i>Neotomys floridana</i>	0	1	0	0	1	1	0	1/2	1	0	2/3	0	2	0	0	1
<i>Peromyscus leucopus</i>	2	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0
<i>Calomyscus baluchi</i>	0	0	0	0	0	0	0	1	1	0	2	0	2	0	0	0
<i>Cricetulus migratorius</i>	0	1	0	0	0/1	0	0	0	1	0	2	0	1	0	0	0
<i>Mesocricetus auratus</i>	0	2	0	0	?	0/1	0	0	0	0	2	?	1	0	0	0
<i>Mystromys albicaudatus</i>	0	0	0	2	1	0/1	0	2	0	1/2	2	0	0	0	1	0
<i>Phodopus sungorus</i>	0	1	0/1	0	1	0	0	1	0	0	1/2	0	1	0	0	0

logenetic hypotheses. Twenty such phyllotine and nine sigmodontine hypotheses were evaluated, with as many as 54 replicate analyses run under a single constraint. Character transformations were optimized assuming both delayed transformation, which favors parallelisms over reversals, and accelerated transformation, which favors reversals over parallelisms. Only unequivocal character state changes are reported as hypothetical synapomorphies. Consistency and retention indexes among ingroup taxa were calculated for each character. The consistency index (CI) 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 (RI) is related to the CI and can be thought of as an estimate of the informativeness of a character in regard to groupings (Farris, 1989, p. 418).

The sigmodontine analysis was also conducted with the inclusion of a weighted dummy variable so as to bias the analysis toward the *a priori* assumption of sigmodontine monophyly. This allows a larger set of trees to be considered than while employing topological constraints, increasing the likelihood of finding the most-parsimonious trees. The sigmodontine analysis was not meant as a test of monophyly, and both constrained and unconstrained analyses were compared. Previous studies generally supported sigmodontine monophyly (Carleton, 1980; Catzeffis

TABLE 3. Extended.

17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
0/1	0	1	0	0	1	0	?	1	2	3	1	0	0	1	1	0	3	2	0	1	0	0	0	
1	1	1	1	0	0	0	2	1	2	2	2	0	0	1	1	0	2	2	0	1	0	0	0	
?	1/2	1	1	1	1	0	2	1	2	2	1/2	0	?	?	1	0	3	2	0	0	0	0	0	
2	0	2	0	1	0	0	2	1	2	2	2	0	0	?	?	0	2	2	0	1	0	0	0	
0	0	0	1	1	2	0	?	1	1	2	1	0	0	?	?	?	3	2	0	1	0	0	0	
1	0	1	1	1	1	0	?	1	2	2/3	2	?	?	1	1	0	1	2	0	1	0	0	0	
0/1	1	1	1	1	0	0/2	?	1	2	3	2	0	?	?	?	0	2	2	0	?	0	0	0	
1	0	1	1	3	0	2	2	1	2	2/3	1/2	0	?	?	1	?	1	3	0	1	0	0	0	
0	2	1	2	3	2	2	2	1	1	3	0	0	0	?	?	0	2	2	0	1	1	0	0	
0	1	1	2	3	2	2	2	1	1	3	0	0	0	1	1	1	2	2	0	?	1	0	0	
1	0	?	0	1	2	?	?	1	1	3	0	0	0	1	1	1	3	2	0	2	1	3	0	
2	0	0/1	0	1/2	1	2	2	1	0	2	?	?	?	?	?	0	0	1	1	1	1	1	1	
2	0	1	0	3	1	2	2	1	1	2	?	?	?	?	?	0	0	1	0	1	0	1	1	
2	0	1	0	3	2	2	2	1	1	2	0	0	0	?	?	0	1	1	0	1	1	1	1	
0	0	1	0	1	0	0	?	1	1	0/1	0	0	?	?	?	0	3	1	?	1	1	0	0	
0/1	0	0	0/1	3	0	2	?	1	1	1	0	0	1	?	?	?	2	1	?	?	0	0	0	
0	0	0	1	3	0	2	?	1	1	0	0/1	0	0	?	?	1	2	1	0	?	?	1	1	0
0	1	0/1	1	3	0	2	?	1	1	0/1	0/1	?	?	?	?	1	3	1	?	1	1	0	0	
0	0	0	0	3	2	2	?	1	1	?	0	?	?	?	?	1	2	1	?	0	1	0	0	
0	1/2	1	1/2	3	2	0	?	1	2	1	1/2	?	?	?	?	1	3	1	?	?	?	?	?	
2	0	1	2	2	2	2	?	?	?	?	?	?	?	?	?	1	2	2	0	?	1	?	?	
0	0/1	0	2	2	2	0	?	1	1	3	0	0	?	?	?	1	2	2	?	1	1	2	0	
0	2	2	3	0	2	0/2	2	1	2	4	0	0	0	1	1	1	3	3	0	1	1	0	0	
0	2	2	3	1	2	2	2	1	2	2	0	0	?	?	?	1	0	3	2	0	2	1	0	0
0	2	2	3	1	2	0	2	1	1	2	0	0	0	1	1	1	3	2	0	2	1	0	0	
0	2	2	3	3	1	0	?	1	1	?	0	0	0	?	?	1	2	2	0	2	1	0	0	
0	2	2	3	1	0	2	?	1	2	4	0	0	0	?	?	2	3	2	0	2	1	0	0	
0	1	2	2	1	2	0	?	?	?	?	?	?	?	?	?	1	2	?	0	?	?	?	?	
1	2	0	3	2	0	2	2	1	2	4	1	0	0	1	1	1	2	3	0	2	1	0	0	
2	0	0	1	3	0/1	2	1	0	1	1	0	1	1	?	0	?	2	0	?	2	0	0	0	
2	0	0	0	3	1	2	0	0	0	2	0	1	1	0	0	?	2	0	1	1	0	0	0	
0	2	0	1/2	3	2	2	1	1	1	3	0	0	1	?	0	?	3	1	1	1	0	1	0	
0	1	0	1	3	0	2	1	1	1	3	0	0	0	?	1	1	3	0	1	1	1	0	0	
1	0	0	1	3	1	2	1	0	1	2/3	0	1	0	0	0	?	2	0	1	0	1	2	0	
0	2	1	2	3	2	2	1	1	1	3	0	1	1	1	0	?	3	1	1	0	1	2	0	
1	2	1	3	2	2	0	?	0	1	3	1	1	1	?	?	1	3	?	0	?	?	0	0	
1	1	1	2	3	2	2	1	0	1	4/5	0	1	1	?	0	2	2	2	0	0	0	0	0	
2	1	?	2	2	2	2	0	0	1	5	0	0	1	0	1	?	?	2	0	0	1	0	0	
?	2	?	2	1	2	2	?	?	1	4	0	?	?	?	?	?	?	?	0	?	?	?	?	
1	2	?	1/2	2	?	2	?	1	1	5	0	1	1	0	1	?	2	?	0	?	?	?	?	

et al., 1993; Hooper & Musser, 1964), but the issue has not been explicitly tested cladistically.

The data set used in the phyllotine analysis is generally the same as that published previously (Steppan, 1993, Table 1), with several changes. Five characters were added (42P, 46P, 47P, 54P, 55P), several were redescribed and recoded to better describe the observed variation (e.g., 59P, 76P, 77P), four were deleted after additional data demonstrated higher infraspecific variability, and typographical errors were corrected. Additionally, the undescribed species from Tapecua, Bolivia, collected by Sydney Anderson, that was referred to in Steppan (1993) is not included in this study, pending a formal description.

Comparative Morphology

For the characters discussed below, numbers preceded by "S" and "P" refer to their numbers in the sigmodontine and phyllotine analyses, respectively, as listed in the two data matrixes (Tables 3, 4). Several characters without numbers are discussed because they are autapomorphies or are systematically valuable even if they were phylogenetically uninformative within the context of this phylogenetic analysis.

Character states were treated in the analysis as ordered, except where noted otherwise. Transformation series were generally hypothesized to be linear, but orderings of the character states do not

TABLE 4. Data matrix for phyllotine analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Thomasomys baeops</i>	0	1	0	?	?	?	?	?	?	1	1	2	2	2	1	0	2	0	2	2
<i>Ichthyomys hydrobates</i>	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Holochilus brasiliensis</i>	0	1	?	2	0	0	1	1	1	0	0	0	2	2	?	1	2	0	2	0
<i>Nectomys squamipes</i>	0	1	0	?	1	0	1	0	0	2	1	0	2	2	0	0	2	0	2	2
<i>Pseudoryzomys simplex</i>	0	0	0	2	0	?	1	1	1	3	1	0	2	1	0	0	2	0	2	1
<i>Zygodontomys brevicauda</i>	0	1	0	0	0	0	0	1	1	3	1	0	2	1	0	0	2	0	2	1
<i>Akodon albiventer</i>	0	1	0	?	1	2	1	0	0	0	1	0	0	2	0	1	1	0	1	1
<i>Akodon boliviensis</i>	0	1	0	?	1	0	1	0	0	1	1	1	0	2	0	1	1	0	2	1
<i>Chrocomys andinus</i>	0	1	0	0	0	0	1	?	?	0	1	1	0	2	0	1	1	0	1	0
<i>Oxymycterus hispidus</i>	0	1	1	?	1	1	0	0	0	1	0	1	1	1	0	1	1	0	1	0
<i>Scapteromys tumidus</i>	0	2	1	1	0	0	1	1	1	0	1	1	1	1	0	1	0	0	2	1
<i>Punomys lemminus</i>	0	1	0	?	?	?	?	?	?	1	1	2	0	2	0	0	1	0	2	0
<i>Calomys callosus</i>	0	0	0	2	0	0	1	1	1	1	1	1	0	2	0	1	0	0	2	0
<i>Calomys hummelincki</i>	0	1	0	2	0	0	1	1	1	1	1	?	0	2	0	1	0	0	2	0
<i>Calomys laucha</i>	0	0	0	2	0	0	1	1	1	1	1	1	1	2	0	1	1	0	2	0
<i>Calomys lepidus</i>	0	1	0	2	0	0	1	1	1	1	1	1	1	2	0	1	1	0	2	0
<i>Calomys sorellus</i>	0	1	0	2	0	0	1	?	?	1	1	0	0	2	1	1	1	0	2	0
<i>Andalgalomys pearsoni</i>	0	1	0	2	0	0	1	1	1	1	0	0	0	1	0	1	3	0	1	0
<i>Graomys domorum</i>	0	1	0	2	0	0	1	?	0	0	0	0	2	2	1	2	3	0	2	0
<i>Graomys griseoflavus</i>	0	1	0	2	0	0	1	1	0	0	0	0	2	2	1	2	3	0	2	0
<i>Eligmodontia morgani</i>	0	0	0	2	0	0	1	1	1	0	0	0	0	1	0	2	3	0	2	0
<i>Galenomys garleppi</i>	0	2	1	2	0	?	1	?	1	1	0	0	0	2	1	1	?	0	1	0
<i>Auliscomys boliviensis</i>	1	2	1	1	0	1	?	?	?	0	0	0	0	1	0	1	?	0	2	0
<i>Auliscomys pictus</i>	2	?	1	1	0	0	?	0	0	1	0	0	1	1	0	1	2	0	2	0
<i>Auliscomys sublimis</i>	2	2	1	1	0	0	1	0	0	0	0	0	0	2	1	1	3	0	2	0
<i>Euneomys chinchilloides</i>	2	1	2	0	0	0	0	0	0	0	0	0	2	0	0	0	2	1	2	1
<i>Euneomys petersoni</i>	2	1	2	0	0	0	0	0	0	0	0	0	2	0	0	0	2	1	2	1
<i>Reithrodon auritus evae</i>	3	0	?	?	?	?	?	?	?	0	0	0	2	1	0	2	?	0	2	0
<i>Reithrodon auritus pachycephalus</i>	3	0	2	2	0	0	1	1	0	0	0	0	2	1	0	2	2	0	2	0
<i>Reithrodon typicus</i>	3	0	?	?	?	?	?	?	?	0	0	0	2	1	0	2	2	0	2	0
<i>Neotomys ebriosus</i>	4	0	2	0	0	0	0	1	1	0	0	0	2	1	0	2	3	0	2	0
<i>Loxodontomys micropus</i>	0	0	2	?	1	1	0	0	0	0	1	2	2	0	0	?	0	2	0	0
<i>Irenomys tarsalis</i>	3	0	1	0	0	0	0	0	0	0	0	0	1	2	0	0	2	0	0	0
<i>Andinomys edax</i>	0	1	0	1	0	1	1	0	0	0	0	0	1	2	0	2	1	0	2	0
<i>Chinchillula sahamae</i>	0	1	1	2	0	2	1	1	0	0	1	0	0	2	1	1	?	0	0	0
<i>Phyllotis amicus</i>	0	1	?	2	0	0	?	1	0	0	0	0	1	2	1	1	?	0	2	0
<i>Phyllotis andium</i>	0	1	0	2	0	0	1	1	0	0	0	0	1	2	1	1	?	0	1	0
<i>Phyllotis caprinus</i>	0	1	0	2	0	?	?	?	?	0	0	0	1	2	1	2	?	0	2	0
<i>Phyllotis darwini</i>	0	1	0	2	0	1	1	1	0	0	0	0	1	2	1	2	?	0	1	0
<i>Phyllotis definitus</i>	0	1	1	2	0	?	1	?	0	0	0	0	?	2	1	1	?	0	1	0
<i>Phyllotis gerbillus</i>	0	1	?	2	0	1	1	1	0	0	0	0	1	2	1	2	1	0	2	0
<i>Phyllotis haggardi</i>	0	1	0	2	0	0	1	0	0	0	0	0	0	2	1	2	?	0	1	0
<i>Phyllotis magister</i>	0	1	0	2	0	0	1	0	0	0	0	0	1	2	1	2	?	0	1	0
<i>Phyllotis osilae</i>	0	1	0	2	0	0	1	1	0	0	0	0	0	2	1	1	3	0	1	0
<i>Phyllotis wolffsohni</i>	0	1	0/1	2	0	0	1	0	0	0	0	0	1	2	1	2	?	0	1	0
<i>Phyllotis xanthopygus rupestris</i>	0	1	0	2	0	1	1	1	0	0	0	0	0	2	1	2	?	0	1	0
<i>Phyllotis xanthopygus xanthopygus</i>	0	1	0	2	0	1	1	?	0	0	0	0	1	2	1	2	?	0	1	0

imply polarity (i.e., "0" is not necessarily primitive).

General cranial features referred to in the character discussions are diagrammed in Figures 6–8.

Dentition

1P. INCISOR GROOVES—Grooves on upper incisors—5 states (Fig. 9).

0 = absent

1 = fine striae

2 = 1 mediolateral shallow groove

3 = 1 mediolateral deep groove; 1 small shallow groove on midline

4 = 1 involuted groove on lateral corner

Although incisor grooves are unusual in other muroids, groove morphologies are relatively di-

TABLE 4. Extended.

21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	
3	1	1	2	1	0	0	0	0	0	0	1	0	0	2	1	1	1	1	0	1	0	1	0	0	1	0/1	1	1	
0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	?	0	0	0	2	?	1
3	1	?	?	?	?	?	0	0	0	0	?	0	0	1	1	1	0	2	0	0	0	0	2	?	0	0	0	0	1
3	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	?	0	2	0	0	0	0	2	1	0	0	2	0	2
1	1	1	0	1	0	0	0	1	0	0	1	0	0	1	1	1	0/1	1	0	0	0	0	3	1	0	0	0	0	1
1	1	1	0	1	0	0	0	1	0	0	1	0	0	1	1	1	1	2	0	0	0	0	1	1	0	0	0/2	0	2
2	1	2	1	1	0	0	1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	1	0	1	0	1	2	0	1
2	1	2	1	1	0	0	1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	1	0	1	0	1	2	0	1
2	1	2	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0/1	0	1	0	0	2	0	1
1	1	?	?	?	?	?	0	?	0	0	0	0	1	0	0	0	2	1	1	?	0	1	0	1	0	1	2	0	1
2	?	2	2	1	1	1	0	0	0	0	0	0	0	0	0	0/1	1	1	0	0	1	2	0	0	0	0	2	0	1
2	1	1	0	0	0	1	1	0	0	2	1	0	0	0	0	0	1	1	1	1	1	2	0	0	0	0	2	1	1
2	1	2	0	1	0	1	1	1	0	0	0	0	0	2	0	1	1	1	0	0	0	0	1	1	0	0	0	0	2
2	1	1	0	?	0	0	0	1	0	0	0	0	0	1	0	1	1/2	1	0	0	0	0	1	1	0	0	0	0	2
2	1	1	0	1	0	1	1	1	0	0	0	0	0	2	0	?	1	1	0	0	0	0	1	1	0	0	0	0	2
1	1	1	0	1	1	1	1	1	1	0	0	1	0	1	0	2	1	1	0	0	0	1	1	0	0	0/1	0/1	1	1
2	1	2	2	0	1	1	1	1	0	0	0	?	0	1	0	2	1	1	0	0	0	0	1	1	0	0	0	0	1
1	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0	2	1	1	0	0	0	0	2	1	0	0	2	0	2
2	1	2	0	1	1	1	1	0	0	0	0	0	1	2	1	2	1	1	0	1	0	2	1	0	0	0/1	0	0	2
2	1	0	0	0	0	1	1	0	0	1	0	0	2	2	0	2	1	1	0	1	0	2	0	0	1	0	0	0	2
2	1	2	0	1	0	1	2	1	1	0	0	0	1	3	0	2	1	1	0	1	0	1	0	1	1	0	0	0	2
1	1	1	0	0	0	1	2	1	0	0	1	1	0	2	0	0	1	1	0	1	1	1	0	0	0	0	2	1	1
2	0	0	0	0	0	1	2	1	1	0	1	1	1	1	0	0	1	1	0	2	1	0	0	0	0	0	2	1	0
2	1	1	1	0	0	1	1	1	1	0	1	1	0	1	1	0	2	1	0	1	1	1	0	0	0	0	2	1	1
2	1	0	0	0	0	1	2	1	1	0	1	1	0	1	1	0	2	1	0	1	1	0	0	0	0	0	0/2	0	0
1	0	0	1	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1	0	2	0	1	0	1	0	2	1	1	1
1	0	0	1	0	1	0	0	0	0	1	0	2	1	1	1	1	1	1	0	2	0/1	1	0	1	0	0	0	1	1
3	1	?	?	?	?	?	0	0	0	0	?	0	1	2	1	1	3	1	1	2	1	3	?	1	1	0	0	1	1
3	1	0	0	0	0	0	0	0	0	0	1	0	1	2	1	1	3	1	1	2	1	3	1	1	1	0/2	1	1	1
3	1	?	?	?	?	?	0	0	0	?	0	1	1	1	1	1	3	1	1	2	1	3	?	1	0	2	1	1	1
3	0	0	1	0	0	1	0	0	0	2	1	2	1	2	2	2	0	1	2	2	1	3	1	1	0	0	0	1	1
3	1	1	1	0	1	1	1	0	0	1	0	0	1	1	1	1	2	1	0	1	1	1	1	1	0	0	0	1	1
0	2	0	0	0	0	0	1	1	0	0	2	1	1	0	1	1	2	1	1	1	1	1	1	1	0	0	0	1	1
3	2	0	2	0	0	0	2	1	0	0	?	1	0	0	1	1	1	1	1	1	1	3	1	0	0	0/2	1	0	1
0	1	0	1	0	0	0	1	1	0	0	0	1	0	1	1	0	1	1	0	2	1	0	0	0	0	0	0	1	1
2	1	1	2	1	1	1	2	1	0	0	0	0	0	1	2	0	2	1	1	0	0/1	0	2	0	0	0	0	0	2
2	1	1	1	0	1	1	1	1	0	0	0	0	0	1	0	1	1	1	0	1	0	1	1	0	0	0	0	0	1
1	1	1	2	0	1	1	1	1	0	0	1	0	1	1	?	1	1	1	0	1	1	1	0	0	0	0	0	0	1
1	1	1	2	1	1	1	2	1	0	0	1	1	1	2	1	1	1	1	0	1	1	1	2	0	0	0	0	0	1
?	?	1	2	1	1	1	1	1	0	0	1	0	1	2	0	0	1	1	0	1	0/1	1	0	0	0	0	0	1	1
1	1	2	2	1	1	0	2	1	0	0	0	0	1	3	0	2	1	1	0	1	0	1	1	0	0	0	0	0	2
0	1	2	1	1	1	0	2	1	0	0	0	1	0	2	0	1	1	1	0	1	1	1	0	0	0	2	0	1	1
1	1	1	2	1	1	1	2	1	0	0	0	0	0	1	2	1	1	1	0	1	1	1	1	0	0	0	0	1	1
0	0	1	2	1	1	0	2	1	0	0	0	0	0	2	1	1	1	1	0	1	1	1	0	0	0	2	0	1	1
1	1	0	2	1	0	0	1	1	0	0	1	0	0	1	1	?	1	1	0	1	0/1	2	1	0	0	0	0	1	1
1	0	1	2	0	1	1	1	1	0	0	0	0	1	2	1	1	1	1	0	1	1	1	1	0	0	0	0	0	1
1	1	1	2	0	1	1	1	1	0	0	0	0	0	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	1

verse among phyllotines and are present in *Auliscomys*, *Euneomys*, *Irenomys*, *Neotomys*, and *Reithrodon*. Grooves are not found among other New World muroids except for *Sigmodon alstoni* and the neotomine-peromyscine *Reithrodontomys*. Fine, not always consistent striae are found in *Auliscomys boliviensis*. The other two species of *Auliscomys*, *sublimis* and *pictus*, exhibit fine, shallow grooves, although those of *sublimis* (Fig.

9A) are less pronounced than those of *pictus* (Fig. 9B) and usually require magnification to identify. The grooves in *Euneomys* (Fig. 9C) are distinct, while those of *Irenomys* (Fig. 9D) and *Reithrodon* (Fig. 9E) are still more pronounced and easily visible to the naked eye. The grooves in *Neotomys* (Fig. 9F) are the most developed, being invaginated with a prominent valley retained on the labial corner of the tooth. The position of the grooves

TABLE 4. *Continued.*

	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70
<i>Thomasomys baeops</i>	2	0	0	0	1	0	2	1	0	0	3	?	0	1	1	1	0	1	0	1	3
<i>Ichthyomys hydrobates</i>	0	0	0	0	2	1	0	0	0	0	0	?	0	1	0	1	0	0	0	0	0
<i>Holochilus brasiliensis</i>	3	0	0	0	0	0	0	?	1	0	0	1	0	?	0	0	0	2	1	0	3
<i>Nectomys squamipes</i>	3	0	0	0	1	0	2	0	1	0	0	1	0	1	0	1	0	0	0	0	1
<i>Pseudoryzomys simplex</i>	3	0	0	0	0	0	1	0	1	0	1	1	0	1	1	1	0	0	2	0	1
<i>Zygodontomys brevicauda</i>	3	0	0	0	0	0	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1
<i>Akodon albiventer</i>	1	0	0	0	0	0	0	0	0	0	3	1	0	1	1	1	0	0	2	0	3
<i>Akodon boliviensis</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	1	0	0	2	0	3
<i>Chroecomys andinus</i>	1	0	0	0	0	0	0	0	0	0	2	1	0	1	2	1	0	0	3	0	1
<i>Oxymycterus hispidus</i>	2	0	0	0	0	0	1	0	0	0	1/2	1	0	1	0	1	0	0	0	1	3
<i>Scapteromys tumidus</i>	1	0	0	0	0	0	1	0	0	0	2	1	1	?	1	0/1	0	?	2	1	2
<i>Punomys lemminus</i>	2	0	0	1	1	?	2	0	0	0	1	1	0	1	1	0	1	2	2	0	1
<i>Calomys callosus</i>	3	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	0	0	3	0	0
<i>Calomys hummelincki</i>	3	0	0	0	0	0	2	?	0	0	1	1	0	1	2	1	0	0	3	0	0
<i>Calomys laucha</i>	3	0	0	0	0	0	1	1	0	0	2	0	0	1	2	1	0	0	3	0	1
<i>Calomys lepidus</i>	2	0	0	0	0	0	1	2	0	0	3	0	0	0	2	1	1	0	3	0	0
<i>Calomys sorellus</i>	2	0	0	0	0	0	2	1	0	0	2	0	0	0	2	1	0	0	3	0	1
<i>Andalgalomys pearsoni</i>	3	0	0	0	0/1	0	2	0	0	1	2	0	0	?	2	1	1	0	3	1	1
<i>Graomys domorum</i>	3	0	0	0	0	0	2	1	0	1	3	0	0	1	2	1	0	0	3	1	1
<i>Graomys griseoflavus</i>	3	0	0	0	0	0	2	1	0	1	2	0	0	1	2	1	0	0	3	1	1
<i>Eligmodontia morgani</i>	2	0	0	0	0	0	2	1	0	0	3	0	0	0	2	1	1	0	3	0	1
<i>Galenomys garleppi</i>	2	0	0	0	0	0	2	1	0	0	2	0	0	1	2	1	0	0	3	0	1
<i>Auliscomys boliviensis</i>	2	0	0	0	0	0	1	1	0	0	3	0	0	1	2	1	0	0	3	0	1
<i>Auliscomys pictus</i>	2	0	0	0	0	0	1	?	0	0	2	0	0	0	2	1	0	1	3	0	1
<i>Auliscomys sublimis</i>	1	0	0	0	0/1	0	1	1	0	0	2	0	0	0	2	1	0	0	3	0	1
<i>Euneomys chinchilloides</i>	2	1	1	0	0	0	2	1	0	0	2	1	1	1	2	0	0	1	3	0	1
<i>Euneomys petersoni</i>	2	1	1	0	0	0	2	1	0	0	2	1	1	1	2	0	0	1	3	0	1
<i>Reithrodon auritus evae</i>	2	1	1	0	1	0	2	1	1	0	3	0	0	1	2	0	2	2	4	0	2
<i>Reithrodon auritus pachycephalus</i>	2	1	1	0	1	0	2	1	1	0	3	?	0	1	2	0	2	2	4	0	1
<i>Reithrodon typicus</i>	2	1	1	0	1	0	2	1	1	0	3	?	0	1	2	0	2	2	4	0	1
<i>Neotomys ebriosus</i>	2	0	1	1	0/1	0	1	1	0	0	2	1	1	2	2	0	0	2	3	0	3
<i>Loxodontomys micropus</i>	1	0	0	0	0	0	2	1	0	0	2	0	0	1	2	0	0	0	3	0	1
<i>Irenomys tarsalis</i>	2	0	0	1	1	1	2	1	0	0	3	0	1	1	1	1	0	0	3	0	3
<i>Andinomys edax</i>	2	0	1	2	1	1	2	1	0	0	2	1	1	2	1	1	0	1	3	0	3
<i>Chinchillula sahamae</i>	2	1	0	0	1	1	2	1	0	0	2	1	1	1	1	1	0	0	3	0	2
<i>Phyllotis amicus</i>	2	0	0	0	0	0	2	2	0	0	3	0	0	1	2	1	0	1	3	0	1
<i>Phyllotis andium</i>	2	0	0	0	0	0	2	1	0	0	3	0	0	1	2	1	0	0	3	0	1
<i>Phyllotis caprinus</i>	2	0	0	0	0	0	2	2	0	0	2	0	0	1	2	1	0	0	3	0	1
<i>Phyllotis darwini</i>	2	0	1	0	0	0	2	2	0	0	2	0	0	1	2	1	0	0	3	0	1
<i>Phyllotis definitus</i>	2	0	0	0	0	0	2	2	0	0	3	0	0	0	2	1	1	0	3	0	1
<i>Phyllotis gerbillus</i>	2	0	0	0	0	0	2	1	0	0	3	0	0	1	2	1	0	0	3	0	1
<i>Phyllotis haggardi</i>	2	0	0	0	0	0	2	1	0	0	3	0	0	2	2	1	0	0	3	0	0
<i>Phyllotis magister</i>	2	0	0	0	0	0	2	1	0	0	3	0	0	0	2	1	0	0	3	0	1
<i>Phyllotis osilae</i>	1	0	0	0	0	0	2	2	0	0	3	0	0	?	2	2	0	0	3	0	1
<i>Phyllotis wolffsohni</i>	3	0	0	0	0	0	2	1	0	0	2	0	0	1	1	1	0	0	3	0	1
<i>Phyllotis xanthopygus rupestris</i>	2	0	0	0	0	0	2	1	0	0	2	0	0	1	2	1	0	0	3	0	1
<i>Phyllotis xanthopygus xanthopygus</i>	2	0	0	0	0	0	2	2	0	0	2	0	0	1	2	1	0	0	3	0	1

on the incisors is down the middle of the tooth, with two exceptions. Pearson and Christie (1991) found that the position of the groove, either medial or positioned asymmetrically toward the lateral margin, distinguished two species of *Euneomys*. In *Neotomys*, the groove is shifted to the lateral margin, leaving the anterior surface of the tooth smooth and slightly concave.

2P. INCISOR PROCUMBENCY—4 states.

- 0 = hyper-opisthodont
- 1 = opisthodont
- 2 = orthodont
- 3 = proodont

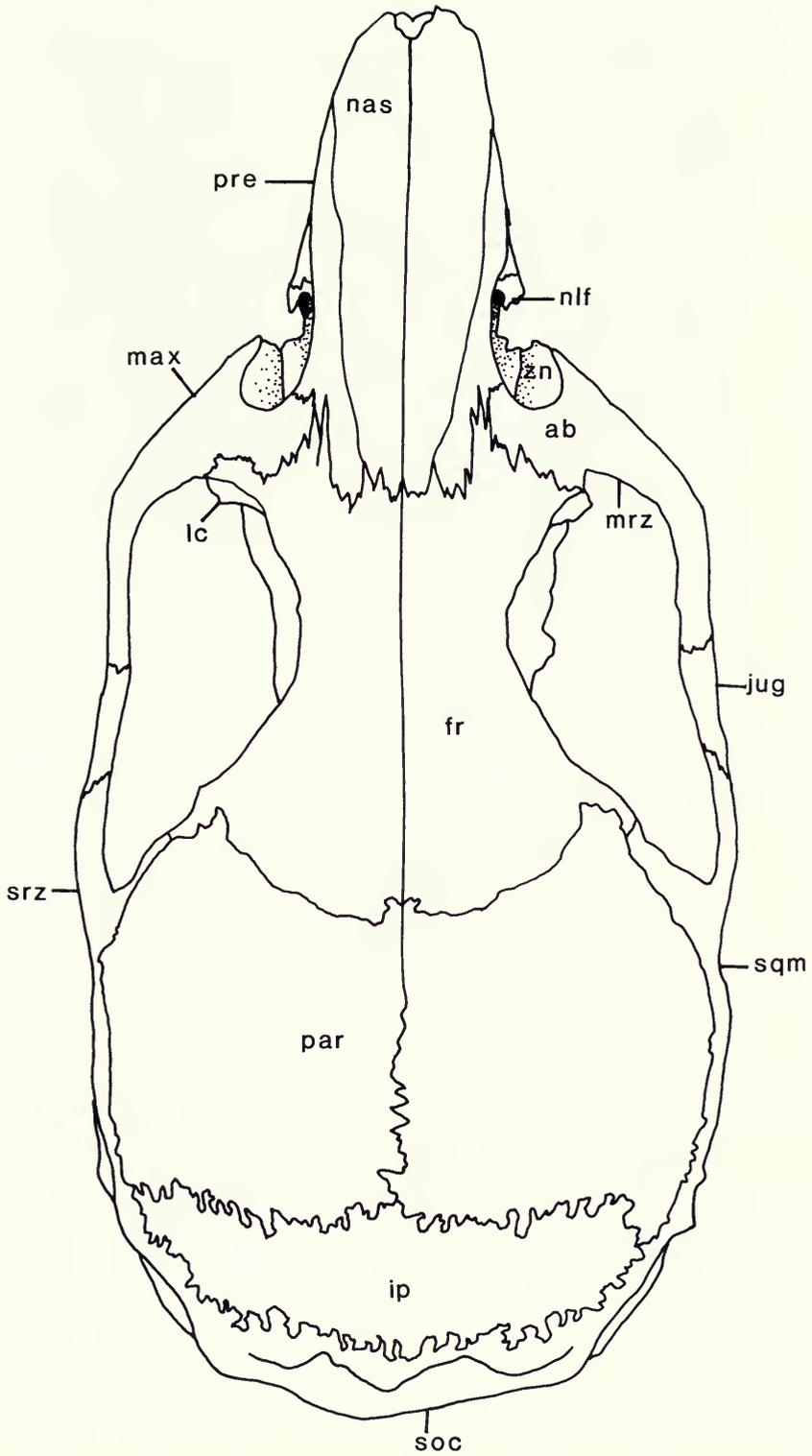
Upper incisor procumbency is usually subdivided into three categories (e.g., Hershkovitz, 1962,

TABLE 4. *Continued.*

71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98		
0	0	1	1	0	2	?	2	0	2	0	?	?	?	1	0	1	1	2	0	0	0	?	?	?	?	?	?		
0	0	0	1	0	2	?	2	0	2	1	?	?	?	1	0	?	0	2	2	0	0	0	1	0	0	0	1		
0	0	1	1	0	2	?	2	0	?	?	?	?	?	0	1	?	0	2	0	1	0	0	0	0	?	?	0		
0	0	1	1	0	2	?	0	1	2	0	2	0	0	1	0	?	0	2	0	1	0	0	0	0	?	?	0		
0	0	0	1	0	2	?	0/2	1	1	?	?	?	?	?	0	0	1	0	1	0	0	0	?	?	?	?	0		
0	0	1	1	0	1	?	0	1	2	0	2	0	0	0	0	1	0	0	0	1	0	0	0	?	?	?	0		
1	0	0	2	1	0	0	2	0	0	0	0	0	0	1	0	1	0	0	1	0	0	?	?	0	0	0	?		
0	0	1	2	0	0	0	2	0	0	0	0	0	0	1	0	1	0	1	0	1	2	0	?	?	?	?	1		
0	0	1	2	0	0	0	0/2	0	0	0	1	0	0	1	0	1	0	1	1	1	0	?	?	?	?	?	?		
0	0	1	2	0	0	0	?	0	1	?	?	?	?	2	1	2	1	0	0	1	1	?	?	?	?	2	1		
0	0	0	1	0	0	0	0	0	1	?	?	?	?	2	1	?	?	2	1	0	0	?	?	?	?	?	1		
0	1	1	0	1	0	0	0	0	1	?	?	?	?	0	2	0	1	1	1	1	0	0	?	?	?	?	?		
0	0	0	1	1	0	0	0/1	1	0	0	1	0	0	1	0	1	1	1	1	1	0	0	1	0	0	?	?		
0	0	0	1	1	0	0	0	1	0	?	?	?	?	?	1	0	0	1	1	0	0	0	?	?	?	?	?		
0	0	0	1	1	0	0	0/2	0	0	0	1	0	?	?	1	0	0	1	1	1	0	0	1	0	0	?	?		
1	0	0	2	1	0	0	0	0	0	0	1	0	0	1	0	0	1	2	1	0	0	?	?	?	?	?	?		
0	0	0	1	1	0	0	0	0	1	0	1	0	?	?	1	0	0	1	1	1	1	0	1	0	0	0	1	?	
0	0	0	1	1	0	0	2	1	2	0	?	?	?	?	1	0	0	1	0	0	0	0	?	?	?	?	2	1	
1	0	0	1	1	0	0	2	1	2	0	?	?	?	?	1	0	0	1	0	1	0	0	?	?	?	?	?	1	
1	0	0	1	1	0	0	2	1	2	0	1	1	0	?	?	1	0	0	0	1	0	0	1	0	0	?	?	1	
1	0	0	2	1	0	0	2	0	1	0	1	0	1	2	1	?	2	0	1	0	0	0	0	0	0	?	?	1	
0	0	0	2	1	0	1	0	0	0	0	1	0	?	?	1	0	?	2	2	2	0	0	?	?	?	?	?	?	
1	0	0	1	1	0	0	0	0	1	0	1	0	?	?	1	0	0	1	1	2	0	0	0	0	0	?	?	?	
0	0	0	1	1	0	1	0	0	1	0	1	0	?	?	2	0	1	1	0	1	0	0	0	1	0	0	2	1	
0	0	0	1	0	0	0	0	0	0	?	?	?	?	1	2	0	1	1	0	1	0	0	?	?	1	0	?	?	
1	0	0	0	1	0	1	1	0	0	1	1	1	0	1	0	0	1	0	1	0	1	1	0	1	?	?	?	?	
1	0	0	0	1	0	1	?	0	0	1	1	1	0	1	1	0	1	1	1	1	1	0	?	?	?	?	?	1	
1	1	0	0	2	2	?	2	1	0	?	?	?	?	0	1	?	2	?	2	0	0	1	?	?	?	?	?	?	
1	1	0	0	2	2	?	2	1	?	?	?	?	?	?	1	?	?	1	?	1	?	?	?	?	?	?	?	?	
1	1	0	0	2	2	?	2	?	?	?	?	?	?	?	1	1	?	1	?	1	?	?	?	?	?	?	?	?	
1	1	0	0	1	1	1	0	0	?	?	?	?	?	?	0	2	0	0	1	0	1	1	0	2	1	1	?	?	
1	0	?	0	0	0	0	0/1	0	1	0	1	0	0	1	0	0	1	0	0	1	1	0	1	1	0	0	?	?	
0	0	1	0	1	0	?	2	0	2	0	1	0	1	1	0	0	0	2	1	0	0	0	?	?	?	?	?	1	
1	0	1	0	1	0	1	0	0	1	0	2	0	0	1	0	1	1	0	2	0	0	?	?	?	?	?	?	1	
0	0	?	1	1	0	0/1	?	0	?	?	?	?	?	?	0	1	0	0	2	0	0	1	1	2	0	0	?	?	
1	0	0	2	1	0	1	0	0	2	?	?	?	?	?	1	0	0	1	0	0	0	0	0	0	0	0	0	2	1
1	0	0	2	1	0	1	0	0	2	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2	1
1	0	0	1	1	0	0	0	0	2	0	?	?	?	?	1	0	0	1	0	1	0	0	2	0	1	1	?	?	
1	0	0	2	1	0	0	0	0	2	0	1	0	1	1	0	0	1	0	0	1	0	1	0	0	2	0	1	?	?
0	0	0	2	1	0	1	0	?	?	?	?	?	?	?	1	0	0	1	0	1	1	1	1	1	0	?	?	?	
1	0	0	2	1	0	1	0	0	1	0	?	?	?	?	0	1	0	1	1	2	0	0	0	0	0	0	?	?	
0	0	0	2	1	0	1	0	0	1/2	?	?	?	?	?	?	1	0	0	1	1	1	0	0	1	0	?	?	?	
0	0	0	1	1	0	1	0	?	?	?	?	?	?	?	1	0	1	0	0	1	0	1	2	0	1	1	2	?	
1	0	1	2	1	0	0	0	0	2	0	1	0	1	1	0	0	1	0	1	0	1	0	1	1/2	0	0	0	?	?
0	0	0	1	1	0	1	0	0	2	0	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	?	?	?
0	0	0	2	1	0	0	0	0	2	0	1	0	1	1	0	0	1	0	1	0	2	0	0	2	0	1	1	2	?
0	0	0	2	1	0	0	0	0	2	0	1	0	1	1	0	0	1	0	1	0	1	0	0	2	0	1	1	?	?

Fig. 19): opisthodont (recurved), orthodont, and proodont (extended forward). Because of the diversity of opisthodont forms among phyllotines, this category was further divided into opisthodont and hyper-opisthodont. The categories are defined by the position of the cutting edge of the incisor relative to the vertical-incisive plane. The vertical-incisive plane passes through the anterior alveolar border and is perpendicular to the basal-incisive

plane. In proodont teeth, the cutting edge lies anterior to the vertical-incisive plane. In orthodont teeth the cutting edge lies along the vertical-incisive plane, while in opisthodont and hyper-opisthodont teeth it lies posterior to the plane. Hyper-opisthodont teeth are distinguished from opisthodont teeth by the cutting edge lying posterior also to the posterior alveolar border of the incisor. Proodont incisors are not found in any phyllotine,



but this observation depends on how much variation is subsumed within the orthodont category. Hershkovitz (1962) described *A. boliviensis* and *Galenomys* as having proodont incisors, but my observations of many of the same specimens that he examined led me to categorize them as orthodont, as are *A. sublimis* and *A. pictus*. The lower incisors of *Galenomys* are also highly proodont, and Hershkovitz (1962) reported that *Galenomys* is more pronounced in this regard than any other "cricetine."

Most of the remaining phyllotines have opisthodont incisors. Hyper-opisthodont incisors are limited to *C. callosus* and *C. laucha*, *Eligmodontia*, *Reithrodon*, *Neotomys*, *Irenomys*, and *Loxodontomys*.

3P. UPPER INCISOR DENTINE FISSURE—3 states (Fig. 10).

0 = long straight slit

1 = short, not quite linear slit, "comma"-shaped

2 = tripartite, "Y"-shaped

In most phyllotines and other sigmodontines, the dentine of the incisor is cleaved anteroposteriorly into a long, straight slit (Fig. 10C). Members of the *Reithrodon*, *Auliscomys*, and *Andinomys* generic-groups are characterized by modifications of this condition. The genera *Auliscomys*, *Chinchillula*, *Galenomys*, and *Irenomys* show a shorter slit that becomes rounded or "comma"-shaped at the anterior end (Fig. 10B). This condition can also be found in *P. definitus* and in some specimens of *P. wolffsohni*. In the third condition, the anterior end splits in two, becoming tripartite or "Y"-shaped (Fig. 10A). This condition is found in the *Reithrodon* generic-group, in *Loxodontomys*, and in northern *Andinomys edax*. The tripartite condition is best developed in *Loxodontomys* and has not been observed by me outside the phyllotines. This trait often shows some variability within species (most notably in *Andinomys*, which exhibits both states "0" and "2"), and wear patterns can make it difficult to determine whether the straight or "comma"-shaped condition is present.

4P 5P. LABIAL ROOT OF M1—4 states, 2 sub-characters.

00 = absent

10 = present, small, set medially

20 = present, medium to large, set laterally

?1 = 2 lateral roots

The character states and transition series match Carleton (1980) with the exception that Carleton hypothesized that two lateral roots were derived directly from roots absent, while I allow two roots to be derived from any of the states in a single step. Carleton hypothesized the absence of labial roots to be plesiomorphic for neotomine-peromyscines, but a large lateral root is the widespread and possibly plesiomorphic condition among phyllotines. *Auliscomys* and *Andinomys* have a small medial root, while *Euneomys*, *Neotomys*, and *Irenomys* lack it altogether. The condition in *Loxodontomys* is unclear because it possesses a second root along the lateral border, which may be a modification of the primitive condition.

MOLAR ROOTS OF M2—Not coded. The widespread condition among phyllotines is a single large lingual root in addition to the anterior and posterior roots. *Reithrodon auritus pachycephalus* and possibly *Euneomys chinchilloides* have a partially bifurcated lingual root. The condition in other species of those genera is not known. *Chinchillula* lacks the lingual root entirely, consistent with the general reduction in the number of molar roots in that genus.

6P. MOLAR ROOTS OF M3—3 states.

0 = 3 roots

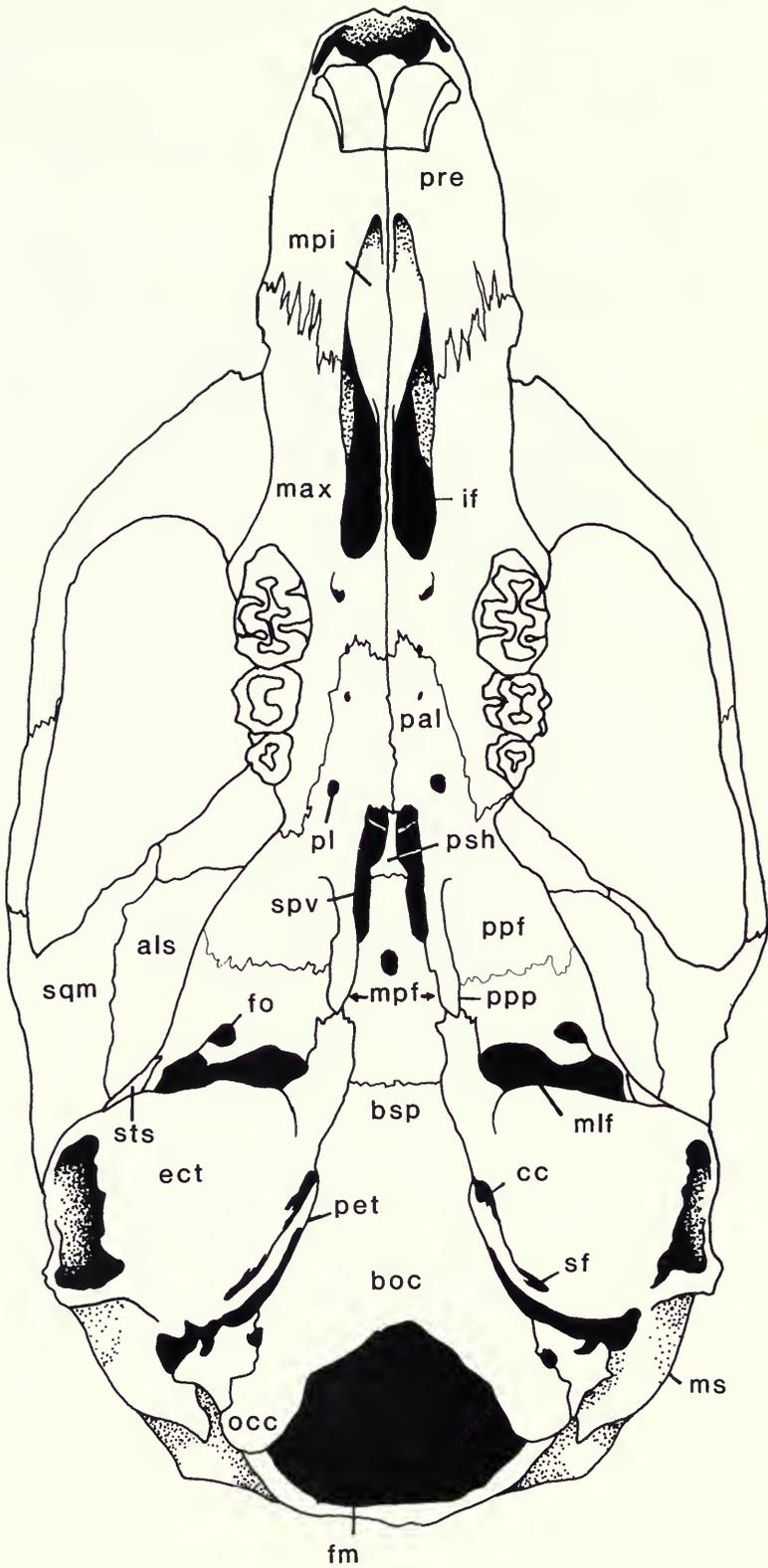
1 = 2 roots

2 = 1 root

Phyllotines show one, two, or three roots in the third upper molar, with three roots the common condition. Carleton (1980) considered three roots to be plesiomorphic for the neotomine-peromyscines. Reduced numbers occur in *Andinomys*, *Chinchillula*, *Loxodontomys*, *A. boliviensis*, *Phyllotis gerbillus*, *P. darwini*, and *P. xanthopygus*. All these examples have two roots except for *Chinchillula*, which has the most highly derived condition of a single root.

7P. LABIAL ROOT OF M1—2 states.

←
FIG. 6. Dorsal view of a generalized *Phyllotis* cranium. ab, antorbital bridge; fr, frontal; ip, interparietal; jug, jugal; lc, lachrymal; max, maxillary; mrz, maxillary root of zygomatic arch; nas, nasal; nlf, nasolacrimal foramen; par, parietal; pre, premaxillary; soc, supraoccipital; sqm, squamosal; srz, squamosal root of zygomatic arch; zn, zygomatic notch.



- 0 = absent
1 = present

Carleton (1980) considered absence of the labial root to be plesiomorphic for the neotomine-peromyscines, but the presence of a labial root is the widespread condition among phyllotines. Only *Euneomys*, *Neotomys*, and *Irenomys* lack this root. These are the same species that lack the labial root on M1. The intermediate condition found in some M1s (presence of a small, medially positioned root) is not observed in the m1 of any phyllotine.

8P. MOLAR ROOTS OF M2—2 states.

- 0 = 2 roots
1 = 3 roots

Three roots is the widespread condition, again in apparent contrast to Carleton's (1980) hypothesis that two roots was plesiomorphic for the neotomine-peromyscines. The derived reduced state is again found in *Euneomys* and *Irenomys*, but not in *Neotomys*. Two roots are also found in *Andinomys*, *Auliscomys*, and *Loxodontomys* as well as *P. magister*, *P. haggardi*, and *P. wolffsohni*. However, sample sizes are usually one or two, so individual variation is difficult to assess.

9P. MOLAR ROOTS OF M3—2 states.

- 0 = 2 roots
1 = 3 roots

Again, the widespread state among the phyllotines is for the full complement of three roots. Two roots were found in *Andalgalomys*, *Eligmodontia*, *Galenomys*, and *Neotomys*. It is unknown if three roots are found in the unexamined species of *Andalgalomys* and *Eligmodontia*.

10P. ANTEROMEDIAN FLEXUS M1—4 states.

- 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

Character states "0" and "3" are difficult to distinguish because both represent absence of the anteromedian flexus but are at opposite ends of the

transformation series. In some outgroup taxa that superficially appear to lack the anteromedian flexus (e.g., *Pseudoryzomys*, *Zygodontomys*), the remnant enamel island from a fully infolded and cutoff flexus can be seen in relatively unworn teeth. Cutoff flexi can also be clearly seen at all ages in many oryzomyines. There is thus the distinct possibility that the absence of an anteromedian flexus could be a secondary loss from a derived, infolded condition rather than from reduction of the flexus depth. Additionally, enamel islands, sometimes connected to the flexus, can be seen in slightly worn teeth of some phyllotine species. The condition for species lacking this ontogenetic information is conservatively coded as unknown, "?". A distinct anteromedian flexus is found in *Andalgalomys*, *Calomys*, *Galenomys*, and *Auliscomys pictus*.

1S. MESOLOPH(-ID)—3 states.

- 0 = mesoloph(-id) joined with mesostyle(-id): (pentalophodont)
1 = small mesoloph or mesolophid present, does not join with mesostyle(-id), or partially fused with paracone
2 = absent: (tetralophodont)

Hershkovitz (1993) pointed out the potential for mistaking a paralophule (arising from the paracone) with a mesoloph (arising from the mure). Mesoloph is weakly developed in some akodontines and *Anotomys* and usually partially fused to paracone when present; there may be either a well-developed mesoloph or paralophule in *Scapteromys* (a partially fused mesoloph seems most likely). Among sigmodontines, complete mesolophostyles (mesoloph fused with the mesostyle) are found only in oryzomyines and thomasomyines. The pentalophodont condition is conventionally hypothesized to be plesiomorphic (e.g., Hershkovitz, 1962, 1966b, 1993; Carleton, 1980). However, placement of the root to the sigmodontine tree can strongly affect this polarity assignment. Mesolophs are entirely absent in phyllotines and most ichthyomyines.

ENTEROLOPH, ECTOLOPHID—Not analyzed. The absence of an enteroloph or ectolophid was listed

FIG. 7. Ventral view of a generalized *Phyllotis* cranium. als, alisphenoid; boc, basioccipital; bsp, basisphenoid; cc, carotid canal; ect, ectotympanic part of auditory bulla; fm, foramen magnum; fo, foramen ovale; if, incisive foramen; max, maxillary; mlf, middle lacerate foramen; mpf, mesopterygoid fossa; mpi, medial process of incisive foramen; ms, mastoidal capsule; occ, occipital condyle; pal, palatines; pet, petrosal part of auditory bulla; pl, posterolateral palatal pit; ppf, parapterygoid fossa; ppp, parapterygoid process; pre, premaxillary; psh, presphenoid; sf, stapedial foramen; spv, sphenopalatine vacuity; sqm, squamosal; sts, stapedial spine of auditory bulla.

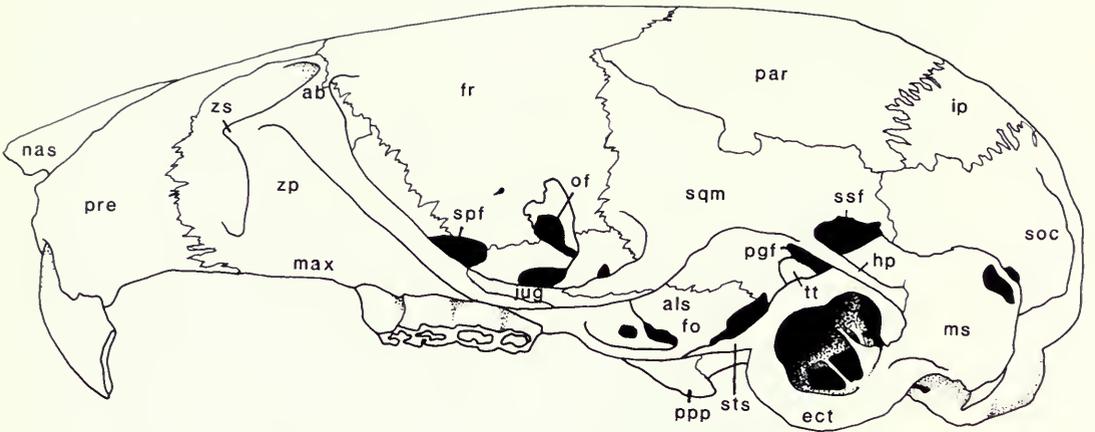


FIG. 8. Lateral view of a generalized *Phyllotis* cranium. ab, antorbital bridge; als, alisphenoid; ect, ectotympanic part of auditory bulla; fo, foramen ovale; fr, frontal; hp, hamular process of squamosal; ip, interparietal; jug, jugal; max, maxillary; ms, mastoidal capsule; nas, nasal; nlf, nasolacrimal foramen; of, optic foramen; par, parietal; pfg, postglenoid foramen; ppp, parapterygoid process; pre, premaxillary; soc, supraoccipital; spf, sphenopalatine foramen; sqm, squamosal; ssf, subsquamosal foramen; sts, stapedial spine of auditory bulla; tt, tegmen tympani; zp, zygomatic plate; zs, zygomatic spine.

by Olds and Anderson (1989) as a possible phylotine synapomorphy, but they chose not to include it in the diagnosis. Olds and Anderson implied that it shows a parallel pattern to the mesoloph(-id) and cited Carleton's (1980) general concept of the derived and concerted simplification of various enamel structures. However, while most sigmodontines have a mesoloph(-id), among surveyed species only *Punomys* has a distinct enteroloph and ectolophid. It is therefore phylogenetically uninformative within the context of this study.

11P. MESOSTYLE M1—2 states.

- 0 = absent
- 1 = present

A small mesostyle on the labial border, unconnected to a mesoloph, is found in *Calomys* and *Chinchillula*. All other phyllotines lack the mesostyle.

12P. PARASTYLE/ANTEROFLEXUS M1—3 states.

- 0 = absent
- 1 = present, indistinct
- 2 = present, distinct

An indistinct parastyle and shallow anteroflexus are found in *Calomys* and *Loxodontomys* and may be plesiomorphic for the phyllotines. Both are absent in *C. sorellus* and all remaining phyllotines. The problematic *Punomys* has a well-developed parastyle.

13P. FLEXUS PENETRATION M1—3 states.

- 0 = flexi from opposite sides do not reach each other
- 1 = enamel overlaps, or flexi meet at midline
- 2 = flexi cross beyond each other

This character varies strongly with age, and the characterizations here are for adults with moderately worn teeth. Wear reduces the apparent penetration, so that in many taxa (e.g., *Phyllotis*), the flexi of well-worn molars do not overlap. Taxa with highly involuted molars, the "sigmodont" condition of Hershkovitz (1955), include *Euneomys*, *Reithrodon*, and *Neotomys*. Less strongly involuted but still overlapping flexi are found in *Graomys* and *Loxodontomys*. Nonoverlapping flexi occur sporadically among the phyllotines and can be found in species of *Calomys*, *Phyllotis*, *Andalgamys*, *Eligmodontia*, and *Auliscomys* in addition to some of the monotypic genera.

14P. ANTEROLABIAL CINGULUM M1—3 states.

- 0 = anterolabial cingulum absent
- 1 = anterolabial cingulum weakly developed, lost with wear
- 2 = anterolabial cingulum distinct

A distinct anterolabial cingulum that is present at all ages is the common condition in phyllotines. There is considerable variation in length and width that is discussed under protoflexid. Variation is also associated with the size, shape, and overall

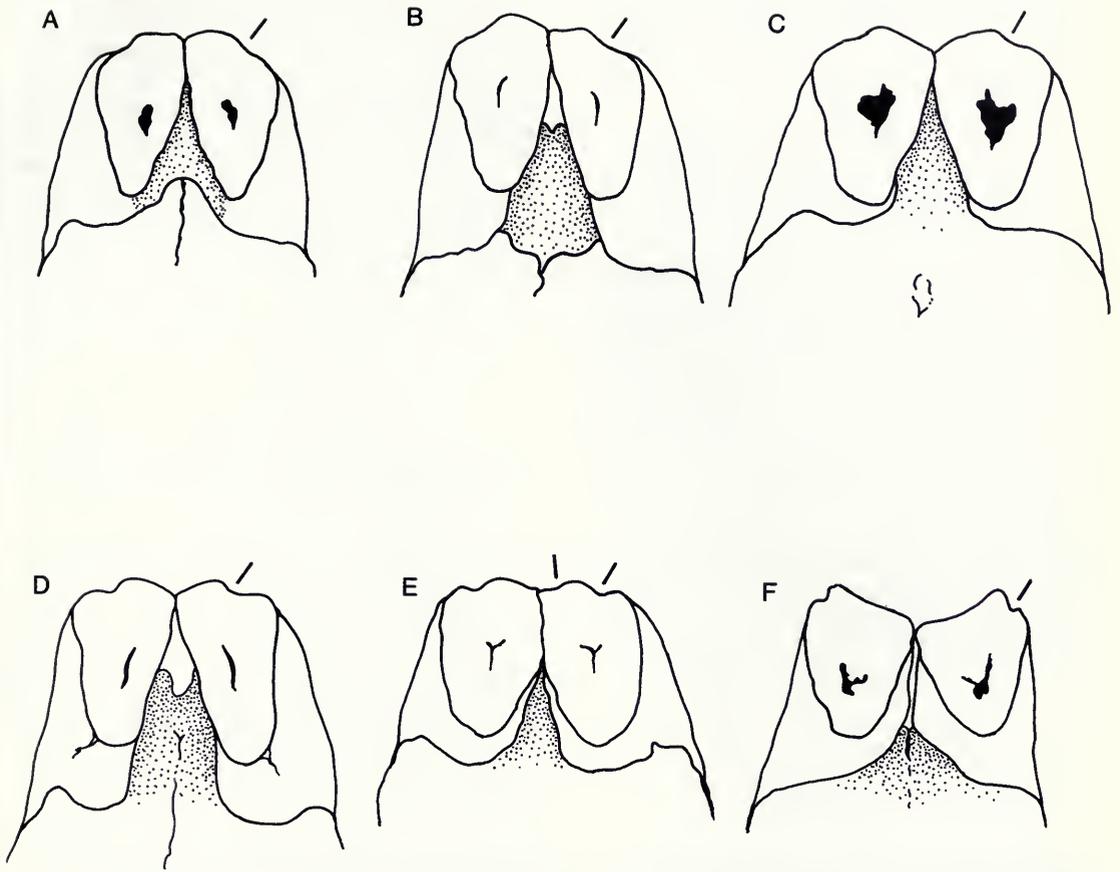


FIG. 9. Variation in incisor grooves among phyllotines; pointers identify grooves. A, *Auliscomys sublimis* (FMNH 107711); B, *Auliscomys pictus* (FMNH 64344); C, *Euneomys chinchilloides* (FMNH 50600); D, *Irenomys tarsalis* (FMNH 124057); E, *Reithrodon auritus* (FMNH 134228); F, *Neotomys ebriosus* (FMNH 24777).

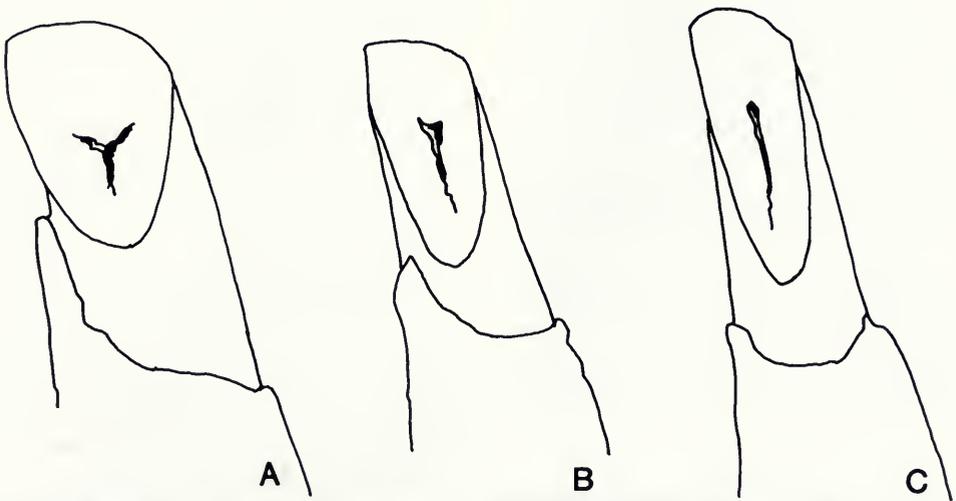


FIG. 10. Upper incisor dentine lake. A, tripartite, *Loxodontomys micropus* (FMNH 23237); B, curved, *Irenomys tarsalis* (FMNH 133164); C, straight, *Graomys griseoflavus* (FMNH 50923).

complexity of the procingulum. Reduction of the anterolabial cingulum occurs in *Andalgalomys*, *Eligmodontia*, *Auliscomys*, *Reithrodon*, and *Neotomys*, while it is completely absent in *Euneomys*.

15P. PROTOFLEXID M1—2 states.

- 0 = short anterolabial cingulum, which may curl toward protoconid; simple protoflexid
- 1 = long anterolabial cingulum, fusing with protoconid and leaving protoflexid as lake

A medium to short anterolabial cingulum that may curve toward the protoconid but that does not fuse is widespread among sigmodontines and thus appears to be plesiomorphic for the phyllotine. In the derived condition, which was not observed in the outgroups, the anterolabial cingulum is very long and fuses with the protoconid at least basally, leaving the protoflexid as a lake. The derived condition is found in all *Phyllotis*, *C. sorellus*, *Chinchillula*, *Galenomys*, *A. sublimis*, and *Graomys*. The protostylid may be made distinct by a pinching of the cingulum proximally or may be unrecognizable within the gradual thinning of the anterolabial cingulum. The protoflexid lake is most pronounced in almost all species of *Phyllotis*.

16P. CUSP ARRANGEMENT M1—3 states.

- 0 = primary cusps opposite in position
- 1 = primary cusps intermediate
- 2 = primary cusps alternate

Primary cusps can be positioned so that the labial and lingual pairs are each opposite each other, with no anterior or posterior shift. In the alternate arrangement, the metacone is situated across from the hypoflexid, produced by a posterior shift of the lingual conids relative to the labial conids. Carleton (1980) tentatively hypothesized opposite cusps as plesiomorphic, but the intermediate condition is most widespread among the phyllotines. Opposite cusps are found in *Euneomys*, *Irenomys*, and *Loxodontomys*. Close attention to ontogenetic series is needed to verify cusp homology among the "sigmodont" genera in order to score this character.

17P. ANTEROMEDIAN FLEXID M1—3 states.

- 0 = absent or limited to shallow groove
- 1 = prominent
- 2 = infolded to form lake, which may be lost with wear

Variation in this trait parallels that in M1. Addressing the oryzomyines where the lake is highly developed, Voss and Carleton (1993) described the lake as an "internal enameled pit" and cited

the same uncertainties as I do; they did not hypothesize an ancestral condition. Carleton (1980) considered the absence of the flexid (undivided anterocone) to be primitive, but at a much more inclusive taxonomic level. The taxonomically scattered occurrence of a faint remnant of the lake in young individuals of some *Graomys*, *Phyllotis*, and *Auliscomys* raises the likelihood that the observed absence in most *Phyllotis* and *Auliscomys* is a secondary loss. Many of the species, particularly most *Phyllotis*, have been coded as unknown to reflect that uncertainty. Prominent anteromedian flexids are found in most *Calomys*, *Andinomys*, and *P. gerbillus*. An infolded lake is found in *Euneomys*, *Reithrodon*, and *Irenomys*.

18P. PROCINGULUM SEPARATION M1—2 states.

- 0 = procingulum attached by anterior mure
- 1 = procingulum separated, mure cut by opposing flexids

The procingulum in *Euneomys* (Fig. 40D) is entirely separate from the primary cusps by the absence of a connecting mure. This condition persists even in highly worn teeth. This trait is unique to *Euneomys* among the phyllotines and among all examined sigmodontines. The separation of the procingulum in the fossil *Bothriomys* was presumably important to Hershkovitz's decision to synonymize it with *Euneomys* (Hershkovitz, 1962). However, the procingulum is distinctly triangular in *Bothriomys*, similar to *Reithrodon* and *Neotomys*, rather than the equally distinct round procingulum in *Euneomys*.

19P. POSTEROLOPHID/STYLID M1—3 states.

- 0 = absent
- 1 = intermediate, posteroflexid present as groove, or obvious in juvenile, absent with strong wear
- 2 = distinct at all ages

The posterolophid is never highly developed and large in phyllotines but ranges from a prominent lophid to absence. The intermediate condition is common, where the posteroflexid may be prominent in juvenile teeth but then lost with strong wear. The widespread condition among phyllotines is for a prominent lophid to be present at all ages. Posterolophids are entirely absent only in the prismatic molars of *Irenomys* and *Chinchillula*. The intermediate condition is found in *Andalgalomys*, *Galenomys*, and all *Phyllotis* except *P. gerbillus*, *P. amicus*, and *P. caprinus*.

20P. POSTEROLOPHID/STYLID M3—3 states.

- 0 = absent

- 1 = intermediate, posteroflexid present as groove, or obvious in juvenile, absent with strong wear
- 2 = distinct at all ages

The range of variation among sigmodontines in this structure is largely the same as for m1, although in general the third molar is less complex than the first molar. Reflecting this, no posterolophid is found in most phyllotines. The only exceptions are bud-like posterolophids in *Euneomys* and the occasional remnant of a posteroflexid in *Neotomys*.

21P. PROCINGULUM M2—4 states.

- 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

The procingulum on the second molar is physically constrained by the first molar and is much less complex than the procingulum on the first molar. For example, anterior conules are always absent. In phyllotines, it usually appears compressed against the first molar. Nonetheless, development of the procingulum on M2 exhibits relatively high variability between individuals of the same species. Complete loss of the anteroflexus and procingulum is found in *Irenomys*, *Chinchilla*, *P. osilae*, and *P. haggardi*. A well-developed procingulum is found in *Reithrodon*, *Neotomys*, *Loxodontomys*, and *Andinomys*. The comparative presence or absence of accessory anterior or posterior lophs is diagnostic among the “sigmodont” genera. Among them, only *Neotomys* has a posteroloph (on M3), and *Euneomys* lacks the procingulum on both M2 and M3 that is seen in *Reithrodon* and *Neotomys*.

22P. PROCINGULUM M2—3 states.

- 0 = absent
- 1 = protoflexid appears as groove; if pronounced in juvenile, then wears away with age
- 2 = procingulum well developed

Development of the procingulum on m2 also exhibits relatively high variability among individuals of the same species. The common condition for phyllotines is a weakly developed procingulum in which the protoflexid appears as a groove and, if pronounced in juveniles, wears away with age. Absence of a procingulum at all ages is found in

Andalgalomys, *Auliscomys boliviensis*, *P. osilae*, *Euneomys*, and *Neotomys*. The more developed but still bud-like procingulum appears in *Irenomys* and *Andinomys*.

23P. HYPOFLEXUS REDUCTION M3—3 states.

- 0 = no reduction relative to M2
- 1 = reduced relative to M2
- 2 = highly reduced relative to M2, to absent

This character and the several following (24–30) describe the complex but subtle variation in the shape of the third molars. General descriptions of shape (e.g., “S”-shape, “C”-shape) were tried initially, drawing from the descriptions in Carleton’s (1980) character 5. These generalities, however, did not adequately describe the independent variation among the dental elements, among other things making state determinations problematic. Therefore, shape was broken down into its specific elements so that they could be more precisely defined. Although this runs the risk of overinflating the taxonomic importance of potentially interrelated characters, I did not find objective grounds for reducing the weight of these characters in the analysis. For each multistate character in this group, character states were treated as ordered.

24P. REDUCTION OF MESOFLEXUS M3—3 states.

- 0 = no reduction relative to M2
- 1 = reduced relative to M2
- 2 = highly reduced relative to M2, or absent

25P. POSTERIOR SHIFT OF MESOFLEXUS M3—2 states.

- 0 = no shift relative to M2
- 1 = posterior shift relative to M2

26P. HYPOFLEXUS LAKE M3—2 states.

- 0 = hypoflexus present, no lake
- 1 = hypoflexus pinched to form lake

In some phyllotines, the hypoflexus appears to have been pinched off to form a lake. The hypoflexus lake is sometimes extended anteroposteriorly orthogonal to the general orientation of the hypoflexus, as in *P. osilae*. A hypoflexus lake is found in some *Calomys*, *Euneomys*, *Graomys domorum*, and all *Phyllotis* except *P. wolffsohni*. The widespread condition among sigmodontines and most phyllotine genera is an intact hypoflexus.

27P. ROTATION OF FLEXUS AXES M3—2 states.

- 0 = no rotation of hypoflexus and mesoflexus axes relative to M2
- 1 = axes rotated relative to M2

28P. MESOFLEXID REDUCTION M3—3 states.

- 0 = no reduction relative to m2
- 1 = reduced relative to m2
- 2 = highly reduced relative to m2, or absent

29P. ANTERIOR SHIFT OF MESOFLEXID M3—2 states.

- 0 = no shift relative to m2
- 1 = anterior shift relative to m2

30P. POSTERIOR SHIFT OF HYPOFLEXID M3—2 states.

- 0 = no shift relative to m2
- 1 = posterior shift relative to m2

31P. FUSION OF OPPOSING FLEXI IN M3—2 states.

- 0 = flexi do not meet
- 1 = flexi meet, median mure cut

The widespread condition among both outgroups (sigmodontines) and phyllotines is for the opposing flexi not to meet at the midline. In *Irenomys*, they meet and the enamel from opposing flexi fuse but remain intact; the flexi are not continuous (Fig. 40). This is the condition for all pairs of flexi and flexids in *Irenomys*. In three species, *Andalgalomys pearsoni* and *Graomys griseoflavus* as well as *Andalgalomys ologi* (according to published photos [Olds et al., 1987]), the opposing flexi in M3 do in fact fuse and become continuous. *Graomys domorum* is variable for this trait. Most but not all individuals of *Graomys griseoflavus* exhibit fused flexi. In *Andalgalomys*, the flexi are fused in M2 as well.

32P. RATIO OF M3 LENGTH TO ALVEOLAR LENGTH OF MOLAR TOOTH ROW—3 states.

- 0 = < 0.205
- 1 = 0.205–0.25
- 2 = > 0.25

The occlusal length of M3 was compared to the alveolar length of the maxillary tooth row. Among those taxa with enlarged molars, two classes are recognized: most have moderate molars (< 0.25 tooth row length) while large molars (> 0.25 tooth row length) are found in *Irenomys* and *Neotomys*.

2S. LENGTH M3—3 states.

- 0 = < 0.63 length M2
- 1 = 0.63 to 0.96 length M2
- 2 = > 0.96 length M2

Character state values were determined using segment-coding with a multiplier of 4. Olds and

Anderson (1989) considered an M3 more than half the length of M2 to be diagnostic of the phyllotines. My observations of the taxonomic distribution of this character disagree with that reported by Olds and Anderson. I find that virtually all sigmodontines (26 of 28 surveyed) possess this condition. The source of this systematic discrepancy is unknown but may be due to measurement criteria. They stated that “phyllotines seem broadly plesiomorphic in this regard” (p. 62), yet included it in the diagnosis.

3S. SHAPE M2—2 states.

- 0 = width < 0.91 length
- 1 = width > 0.91 length

Width was measured at the widest point, rather than the occlusal surface, to avoid variation due to wear. Character state values were determined using segment coding with a multiplier of 4. Generalized gap-coding with a criterion variable of 4 results in the same state definitions. Olds and Anderson (1989) reported that the width in phyllotines at the posterior half is $\frac{2}{3}$ or more of the greatest length of the tooth, in contrast to the narrower teeth of oxymycterines, akodontines, scapteromyines, and ichthyomyines. They suggested that phyllotines probably possess the plesiomorphic condition. As with the ratio of M3/M2, my survey disagrees: no sigmodontine examined has a tooth narrower than $\frac{2}{3}$ proportion. Width of the occlusal surface, as was measured by Olds and Anderson (1989), is strongly affected by wear, and these differences in definition and age criteria may account for the differences in coding.

Cranium and Mandible

33P. CAPSULAR PROJECTION OF MANDIBLE—2 states.

- 0 = distinct capsule, or elevation of superior masseteric ridge, usually ventral to the coronoid process
- 1 = indistinct or absent

In many murids, a distinct capsule forms around the root of the lower incisor; this capsule then projects out from the body of the mandible. This character can vary among individuals, so moderate sample sizes are needed for coding.

34P. HEIGHT OF CORONOID PROCESS—3 states.

- 0 = above maximum height of mandibular condyle

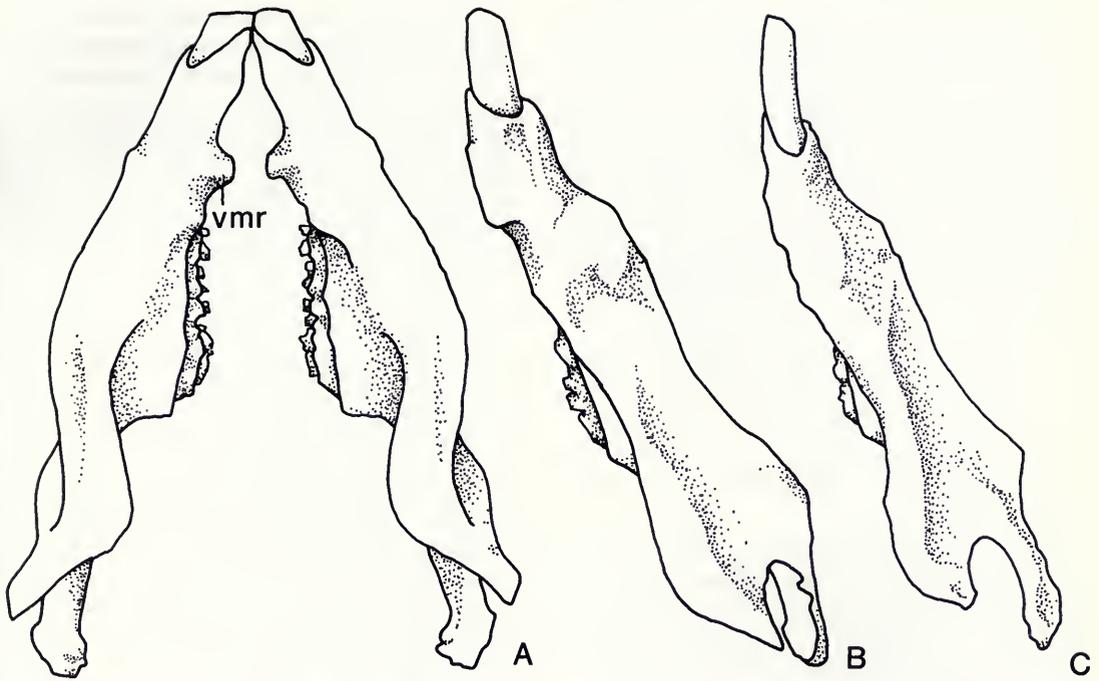


FIG. 11. Ventromedial process of the mandibular ramus (vmr). A, process distinct, *Neotomys ebriosus* (FMNH 24775); B, process weakly present, ramus sharply angled, *Loxodontomys micropus* (FMNH 124393); C, process absent, ramus rounded, *Phyllotis andium* (FMNH 19468).

- 1 = subequal
- 2 = below mandibular condyle

Coronoid processes that rise above the maximum height of the mandibular condyle, relative to the basal plane of the mandible, are common among phyllotines and were found among all surveyed outgroups.

35P. ANTERIOR MASSETERIC RIDGE POSITION—4 states.

- 0 = anterior edge not formed into a knob, well ventral to dip of diastema
- 1 = knob slightly below dorsal edge of mandible
- 2 = knob just reaches dorsal edge of mandible
- 3 = knob exceeds dorsal edge

The anteriormost extent of the masseteric ridge is usually enlarged into a small knob or swelling, and the ridge varies between taxa in its dorsal/ventral position as well as in anterior/posterior position relative to the mental foramen and the ventral curvature of the diastema. This character is surprisingly stable within species. A knob just below the dorsal edge of the mandible at the diastema is common among the phyllotines. In *Irenomys* and *Andinomys*, the knob is below and

well posterior to the ventral curvature of the diastema. The knob just reaches the dorsal edge of the mandible in *C. callosus*, *C. laucha*, *Andalgalomys*, *Graomys*, most *Phyllotis*, *Galenomys*, and *R. auritus*. The most extreme condition, which appears derived in reference to its absence among other sigmodontines, has the knob exceeding the dorsal edge of the mandible and is found only in *Eligmodontia* and *P. gerbillus*.

36P. MEDIOVENTRAL PROCESS OF MANDIBULAR RAMUS—3 states (Fig. 11).

- 0 = process absent, ramus rounded when viewed ventrally or not sharply angled
- 1 = process weakly present, or ramus sharply angled, near 90°
- 2 = process distinct

At the posterior terminus of the symphysis, the ventral surface of the ramus curves so that the two halves of the mandible diverge. The radius of curvature at this point is variable among taxa. It ranges from smoothly curved, to sharply angled ($\approx 90^\circ$), to the presence of a distinct pair of processes nearly rejoining at the midline (Fig. 11). Greater development of this trait is generally associated with robustness of the jaw. Intraspecific variation

can sometimes cross over the categorical boundary between smoothly and sharply rounded. The more widespread condition among sigmodontines is smoothly rounded (Fig. 11C). The sharply angled condition (Fig. 11B) is found in *G. domorum*, the remaining *Phyllotis*, and all other genera except *Neotomys*. The condition in *Neotomys* is further modified into distinct processes (Fig. 11A), diagnostic for the genus, although some individuals of *Andinomys* have moderately developed processes.

37P. PREMAXILLARY PROTRUSION—3 states.

- 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

This character is defined by the point at which the anterior edges of the premaxillaries terminate relative to the most anterior margin of the upper incisors. This character is structurally associated with incisor procumbency, but most variation appears to be independent of that dental character.

4S 38P. POSTERIOR EXTENT OF INCISIVE FORAMINA—4 states.

- 0 = not reaching anterior margin of anterolabial and anterolingual conules of M1
- 1 = level with anterolabial and anterolingual conules
- 2 = extending to level of paracone and protocone
- 3 = extending to level of hypocone and metacone

This character is often imprecisely but conveniently designated as “length” of the incisive foramina. Among sigmodontines, foramina that do not reach the first molars are characteristic of the ichthyomyines, many oryzomyines, and some thomomyines. Most other sigmodontines exhibit state “1” where the incisive foramina reach the anterior conules. The widespread presence of state “0” (“short foramina”) among the outgroups surveyed in this study suggests that condition as the plesiomorphic condition for sigmodontines, but Voss and Carleton (1993) considered the plesiomorphic state as unknown. The most extensive foramina are found among some akodontines and phyllotines.

The widespread condition among phyllotines is for the incisive foramina to terminate approximately medial to the anterior conules of M1. Foramina that do not reach the anterior alveoli of the molars are found among phyllotines only in *Neotomys*. Foramina extend to the paracone and proto-

cone in *Irenomys*, *Loxodontomys*, *Auliscomys sublimis*, and *A. pictus*. Even longer foramina that extend to the hypocone and metacone are diagnostic of *Reithrodon*. The fossil *Proreithrodon* (Rovert, 1914), which was synonymized by Hershkovitz (1955) with *Reithrodon*, appears to have much less extensive incisive foramina than any living *Reithrodon*, raising questions about its proper taxonomic placement.

39P. MAXILLARY SEPTUM OF INCISIVE FORAMINA—3 states.

- 0 = length $\leq \frac{1}{2}$ incisive foramina
- 1 = length $\frac{1}{2}$ – $\frac{3}{4}$ incisive foramina
- 2 = length $> \frac{3}{4}$ incisive foramina

The length of the maxillary septum, which is visible in the incisive foramina, can vary independently of the posterior extent of the incisive foramina. The phyllotines show little variation for this character, with all species surveyed having septa that extend between $\frac{1}{2}$ and $\frac{3}{4}$ the length of the incisive foramina. *Calomys hummelincki* has septa that may be less than $\frac{1}{2}$ the foramina length. Greater variation in this trait occurs outside the phyllotines, where most akodontines have very short septa ($< \frac{1}{2}$) and most oryzomyines have septa that exceed $\frac{3}{4}$ the incisive foramina length.

40P. ORIENTATION OF INCISIVE FORAMINA—2 states.

- 0 = separation of anterior apices $< 80\%$ separation of posterior apices
- 1 = separation of anterior apices 80–100% of posterior apices

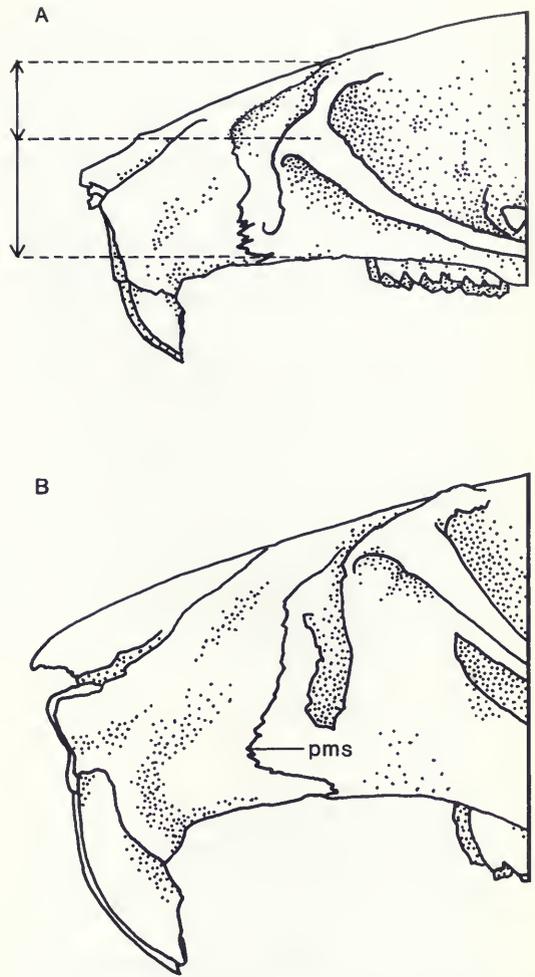
Among sigmodontines, the posterior apices of the incisive foramina are typically more widely set apart than the anterior apices. Among some phyllotines, the anterior region is more robustly excavated. In *Reithrodon*, *Irenomys*, and *Andinomys*, the anterior apices are separated by a distance between 80 and 100% that separating the posterior apices. In *Neotomys*, the anterior apices are most robust, being as broadly separated as the posterior apices.

5S 41P. DORSOVENTRAL POSITION OF ANTERIOR ROOT OF ZYGOMATA—3 states (Fig. 12).

- 0 = antorbital bridge lying well below dorsal surface of rostrum ($\frac{1}{4}$ – $\frac{1}{2}$ less than rostrum height, as measured from the midpoint between height of zygomatic spine and anteriormost border of orbit)
- 1 = antorbital bridge below rostrum (displaced $< \frac{1}{4}$ rostrum height)

2 = insertion high, close on dorsal surface rostrum ($< 1/8$) or posterior surface of bridge joins at dorsal level of surface

In sigmodontines, the anterior root of the zygomatic arch rests upon the zygomatic plate, which leans out from the rostrum. The structure connecting the dorsal surface of the zygomatic plate with the rostrum is the antorbital bridge. The dorsoventral position of the antorbital bridge was measured at the midpoint between the zygomatic spine and the anteriormost margin of the orbit (Fig. 12). The widespread condition among sigmodontines and the likely plesiomorphic condition among phyllotines is for the antorbital bridge to lie well below the dorsal surface of the rostrum, between $1/2$ and $1/4$ the depth of the rostrum below the dorsal surface (Fig. 12A). This condition characterizes *Calomys* and *Andalgalomys*, although some individuals of *P. amicus* have low-lying antorbital bridges. Most phyllotines have the condition where the antorbital bridge is displaced between $1/4$ and $1/8$ the rostral depth below the dorsal surface. A still more extreme condition, where the antorbital bridge lies close on the dorsal surface of the rostrum ($< 1/8$ the rostral depth), is found in *Chinchillula*, *Euneomys*, *Neotomys*, *Reithrodon*, and *Auliscomys boliviensis*. In *Euneomys*, the bridge actually inserts onto the dorsal surface of the rostrum (Fig. 12B).



6S 42P. POSTERIOR MARGIN OF ZYGOMATIC PLATE—2 states.

- 0 = anterior to M1 alveolus
- 1 = subequal or anterior to alveolus

This character was judged by the position of the posterior margin of the zygomatic plate (equivalent to the anterior margin of the orbit when viewed ventrally) relative to the anterior alveolus of the first upper molar. Both states are present among “cricetid” outgroups, but state “0” appears to be the more common.

7S. MASSETERIC TUBERCLE—2 states.

- 0 = absent
- 1 = present

The tendon of the superficial masseter attaches at the bases of the inferior zygomatic root. Among ichthyomyines and to a lesser extent *Scotinomys*, the point of insertion is on a distinct bony spur (Voss, 1988, Fig. 12) projecting out from the zygomatic root, rather than being marked by a patch of rugose bone. Absence of the masseteric tubercle is widespread among New World murids and like-

FIG. 12. Position of the anterior root of the zygomatic, with measurement positions indicated; pms, premaxillo-maxillary suture. A, $1/4$ – $1/2$ below dorsal surface of rostrum, *Calomys laucha* (FMNH 29246); B, inserting high on the rostrum, *Euneomys chinchilloides* (FMNH 133088).

ly plesiomorphic (Voss, 1988). The only other taxon identified with a masseteric tubercle is the peromyscine *Megadontomys* (Voss, 1988).

8S. ZYGOMATIC NOTCH—3 states.

- 0 = absent
- 1 = shallow, depth $< 1/2$ width of notch, and notch less than half length of zygomatic plate
- 2 = deep, well developed

Carleton (1980) concluded that an absent or barely described zygomatic spine was the primitive condition for North American neotomine-peromyscines and other nonsigmodontine murid rodents, and Olds and Anderson (1989) cited

Carleton (1980) as justification for their polarization of "no notch" as primitive in phyllotines. However, Carleton's observation is weakly informative for phyllotine systematics without a strong phylogenetic hypothesis. Carleton's character 25 actually referred to both the zygomatic notch and zygomatic spine, with emphasis on the spine, not the notch. He viewed these two aspects of the maxillary root of the zygomata as highly correlated, in a data set dominated by neotomine-peromyscines. However, within the phyllotines, as an example, the spine (which defines the anterior portion of the notch) can vary greatly between relatively closely related species with little variation in the posterior development of the notch. The development of the spine is primarily controlled by the degree of excavation of the ventral body of the zygomatic plate, in addition to the overall breadth of the plate. These two aspects of the zygomatic plate need to be distinguished when discussing the sigmodontines. Deep notches are found in most sigmodontines except ichthyomyines, many thomasomyines, and some oryzomyines.

43P. DEVELOPMENT OF ZYGOMATIC SPINE—4 states.

- 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

The range of variation for this character in the phyllotines equals or exceeds that found among all other sigmodontines. The length of the spine is influenced by the width of the dorsal region of the zygomatic plate and the degree of excavation in the ventral body of its anterior border (see Fig. 8). Voss and Carleton (1993) considered a non-spinous plate to be primitive for sigmodontines, and the common condition among sigmodontines surveyed in this study is for the anterior border of the zygomatic plate to be flat and oriented nearly vertically. Flat margins of the zygomatic plate or weakly developed spines are the widespread conditions among phyllotines. Zygomatic spines are most developed in *Reithrodon*, where their length is greater than the width of the zygomatic plate at the plate's narrowest point. *Auliscomys*, *Chinchilla*, and *Galenomys* lack spines and have a reduced dorsal body of the zygomatic plate, producing a convexly rounded anterior border that recedes dorsally (e.g., Fig. 34).

44P. INCLINATION OF ZYGOMATIC PLATE—2 states.

- 0 = $< 20^\circ$ (in frontal view)
- 1 = $\geq 20^\circ$

The lateral inclination of the zygomatic plate out from the rostrum varies moderately among phyllotines ($\approx 10\text{--}40^\circ$) but also shows significant variation within species. Zygomatic plates that are inclined greater than 20° from the vertical are widespread among sigmodontines and most likely plesiomorphic for the phyllotines.

45P. PREMAXILLO-MAXILLARY SUTURE ORIENTATION—2 states.

- 0 = $90\text{--}135^\circ$ angle formed relative to palatine plane by the suture on the lateral surface of rostrum and below antorbital foramen
- 1 = suture nearly horizontal at ventral end, sharply angled ($\geq 90^\circ$) in middle of rostrum

In most phyllotines and all other sigmodontines, the premaxillo-maxillary suture on the side of the rostrum is oriented essentially dorsoventrally and forms a $90\text{--}135^\circ$ angle with the ventral edge of the rostrum as it passes around to the ventral side. *Euneomys*, *Neotomys*, and *Reithrodon* are the only sigmodontine genera possessing a suture that makes a sharp bend ($\geq 90^\circ$) in the middle of the rostrum and is nearly horizontal when it passes around to the ventral side (Fig. 12). The extinct *Proreithrodon* (Ameghino, 1908) does not appear to possess this clearly derived condition.

9S 46P. POSTERIOR EXTENSION OF NASALS—2 states (Fig. 13).

- 0 = posteriormost terminus lies clearly posterior to the dorsal maxillary-frontal suture at its contact with the lachrymal
- 1 = terminus lies subequal with or anterior to the maxillary-frontal suture

The extension of the nasals was evaluated against the point at which the maxillary-frontal suture, running along the dorsal surface of the rostrum, reaches the edge of the rostrum and contacts the lachrymal. Nasals often extend further in adults than in juveniles, but ontogenetic variation among adults does not seem significant. The nasals do not extend posterior to the suture contact (Fig. 13A) in most "cricetid" outgroups, except some Old World "cricetids." Within the sigmodontines, occurrence of "long" nasals (Fig. 13B) is scattered, with both conditions being found within several tribes.

"Long" nasals are widespread among phyllotines, with shorter nasals limited to *Graomys* and *Reithrodon*.

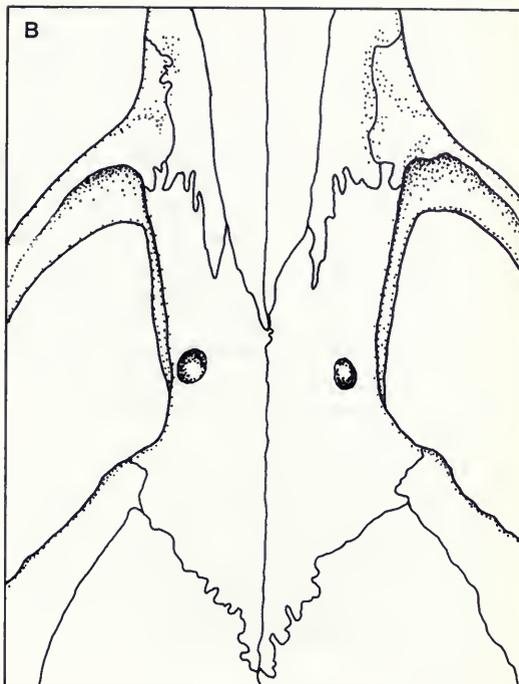
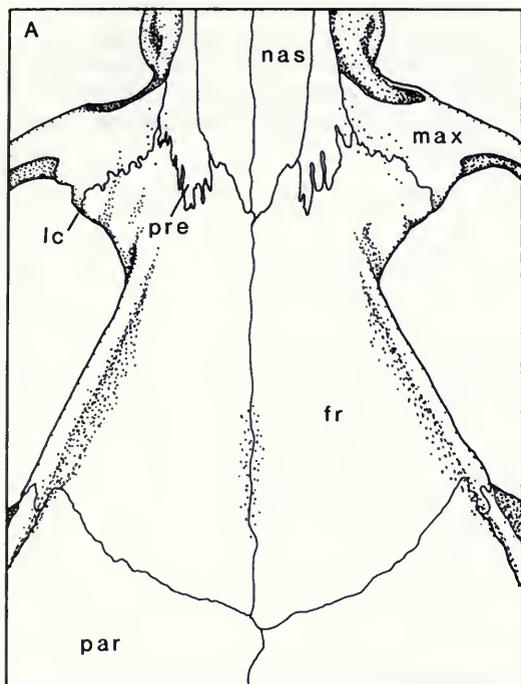


FIG. 13. Dorsal views of interorbital region. **A**, *Nyctomys sumichrasti* (FMNH 35185); **B**, *Ichthyomys hydrobates* (FMNH 90293).

10S 47P. POSTERIOR EXTENSION OF PREMAXILLARIES—3 states (Fig. 13).

- 0 = posterior terminus of premaxillaries extends posterior to the terminus of the nasals
- 1 = terminus of premaxillaries subequal to terminus of nasals
- 2 = terminus of premaxillaries lies anterior to terminus of nasals

Premaxillaries that lie anterior to (“shorter” than) nasals (Fig. 13B) were not observed among the “cricetid” outgroups, and subequal premaxillaries (Fig. 13A) were found only in basal neotomine-peromyscines. “Long” premaxillaries thus may be plesiomorphic for the sigmodontines. Premaxillaries that extend subequally to nasals were found among many oryzomyines, phyllotines, and thomatomyines, with “short” premaxillaries common among other groups.

No phyllotine was observed to have premaxillaries that clearly extended posterior to the nasals.

48P. NASAL WIDTH—2 states.

- 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

Narrow nasals, defined relative to the minimum interorbital distance on the dorsal surface of the rostrum, are widespread among the sigmodontines and likely plesiomorphic for the phyllotines. Greatest nasal width exceeds the interorbital constriction in *Andinomys*, *Auliscomys* (except *sublimis*), *Chinchillula*, *Euneomys*, *Galenomys*, *Irenomys*, *Neotomys*, *Reithrodon*, and some *Phyllotis*. Most of these genera also have relatively constricted interorbital regions, but expansion of the anterior nasals is obvious.

49P. INTERORBITAL SHAPE—3 states.

- 0 = interorbital ridge anteriorly divergent, narrowest region in posterior half
- 1 = narrowest point of interorbital region centrally situated within orbital region, as bounded by the frontals
- 2 = supraorbital ridge posteriorly divergent, narrowest region anterior

This character describes the shape of the supraorbital region and the position of the maximum constriction when viewed dorsally. The widespread condition among sigmodontines is where the maximum constriction is situated centrally within the region bounded by the frontals. This condition is sometimes called “hourglass”-shaped

and was considered plesiomorphic for neotomine-peromyscines (Carleton, 1980) and sigmodontines (Voss, 1993). Two modifications of the plesiomorphic condition can be easily recognized. In one condition commonly seen among other muroid rodents, the maximum constriction is anterior and the supraorbital region diverges posteriorly. *Andalgalomys*, *Graomys*, *Eligmodontia*, *Calomys* (*C. callosus*, *C. laucha*, *C. hummelincki*), *P. gerbillus*, and *P. amicus* share this condition, which is associated with ridged and overhanging supraorbitals. Another derived condition, where the maximum constriction is situated posteriorly and the supraorbital region diverges anteriorly, is found in *Andinomys* and two species of *Auliscomys*, *A. boliviansis*, and *A. sublimis*.

Carleton (1980) combined this and the following character into a single character, "supraorbital shape and temporal ridges." Among species that I surveyed, the two characters are associated in that posteriorly divergent supraorbitals are always overhanging and anteriorly divergent supraorbitals are not, but multiple combinations were observed.

11S 50P. SUPRAORBITAL EDGE—4 states.

- 0 = supraorbital region smoothly rounded when viewed in cross-section
- 1 = weakly angled at edge of dorsal surface, or angled for half the length of the supraorbital region
- 2 = distinctly angled ($\approx 90^\circ$), but not overhanging
- 3 = sharply angled into overhanging shelf, at least posteriorly

The variety of supraorbital morphologies exhibited by sigmodontines makes it difficult to provide precise definitions of character states. Olds and Anderson (1989) followed Hershkovitz (1962) in describing the diagnostic condition for phyllotines as "supraorbital region never evenly curved in cross section." The edge can vary from smoothly rounded, to being distinctly but obtusely angled, to acutely angled into an overhanging shelf. The widespread condition for phyllotines is for the supraorbital edges to be angled along nearly the entire supraorbital region. A possibly derived condition where only the posterior region is weakly angled is found in *Loxodontomys*, *A. sublimis*, and *P. osilae*. Care must be taken in scoring the character because the ridge becomes more sharply defined with age. The sharply ridged, overhanging condition is found in some *Calomys* (*C. callosus*, *C. laucha*, *C. hummelincki*), *Andalgalomys*, *Gra-*

omys, and (weakly) *P. wolffsohni*. The overhanging supraorbital is also characteristic of many oryzo-myines. Because it is unclear which states might be adjacent to overhanging supraorbitals in a transformation series, this character was conservatively treated as unordered.

51P. SUPRAORBITAL RIDGE—2 states.

- 0 = absent or directed laterally
- 1 = lateral edges of supraorbital ridged and directed dorsally

This character distinguishes those supraorbital edges that are raised into dorsally directed ridges from those with no or overhanging ridges. The condition, widespread among sigmodontines and likely plesiomorphic for the phyllotines, is to lack any dorsally directed ridges. Dorsally directed ridges are found in *Euneomys*, *Reithrodon*, and *Chinchillula*.

52P. SUPRAORBITAL KNOBS—2 states.

- 0 = absent
- 1 = small swellings or knobs on anterior supraorbital region, just posterior to lachrymal

In some phyllotines that otherwise show a slight medial trough along the midline of the supraorbital region (i.e., similar to weak ridging of the supraorbital edges), bony processes of the frontals are found along the supraorbital margins just posterior to the lachrymal bones. Supraorbital knobs are unrelated to the inflated frontals found in oxy-mycterines. The widespread condition is for no such swellings. Supraorbital knobs are found in *P. darwini*, *Andinomys*, *Euneomys*, *Neotomys*, and *Reithrodon*.

53P. MEDIODORSAL FUSION OF FRONTALS—3 states.

- 0 = complete
- 1 = partially open or vascularized
- 2 = distinct and consistent fontanelle

The widespread condition among sigmodontines and clearly the plesiomorphic condition for phyllotines is for the frontals to be completely fused along the midline. In *Irenomys*, *Neotomys*, and *Andinomys*, that fusion is not complete for most individuals. In *Irenomys* and *Neotomys*, the gap usually is associated with what appears to be a sinus emerging from within the frontals. In some individuals, channels in the bone indicate that a vessel loops up from the frontals and back down into the frontals or cranium. A distinct fontanelle

is present in *Andinomys* as noted by previous workers (e.g., Hershkovitz, 1962). More than 90% of *Andinomys* individuals examined (≈ 50) possess a fontanelle, and several have a second fontanelle in the posterior region of the frontals as well.

12S 54P. SHAPE OF FRONTOPARIETAL SUTURE—2 states (Fig. 13).

- 0 = rounded, edge of frontal convex
- 1 = straight or slightly sigmoidal to concave

The shape of the frontoparietal suture was evaluated for the body of the suture, excluding the lateral margins, which usually curve anteriorly to “horn”-shaped extensions of the parietal: the horns are present in taxa exhibiting either condition. Convex, rounded sutures (Fig. 13A) are found in all surveyed outgroups, are widespread among sigmodontines, and thus are likely the plesiomorphic sigmodontine condition. *Ichthyomys* (Fig. 13B) possesses the more extreme condition where the frontal edge of the suture is concave.

Convex sutures are likewise widespread among phyllotines, with the presumptively derived condition limited to *Andinomys*, *Chinchillula*, *Irenomys*, and *Reithrodon*. This coding scheme does not apply well to *Neotomys*, whose frontals are very rounded and sometimes “heart”-shaped, and so *Neotomys* was coded as unknown.

55P. ANGLE OF FRONTOPARIETAL SUTURE—2 states (Fig. 13).

- 0 = obtuse angle
- 1 = acute or right angle

The angle was evaluated by judging the orientation along the body of the sutures. In cases with strong curvature, particularly near the medial apex, the condition was evaluated by extending lines joining the medial apex to the triple junctures of the frontals, parietals, and squamosals on both sides. In the majority of cases without strong curvature, these two criteria are congruent. Obtusely angled sutures (Fig. 13A) are widespread among sigmodontines and phyllotines and are thus likely plesiomorphic for the phyllotines. This character was not phylogenetically informative among the nonphyllotines surveyed for this study.

13S. RATIO OF INTERPARIETAL/PARIETAL LENGTH—3 states.

- 0 = < 0.43
- 1 = $0.43\text{--}0.70$
- 2 = > 0.70

Character state values were determined using segment-coding with a criterion variable of 4. Descriptions of interparietal size or shape are often imprecise (e.g., “well developed, at least transversely” [Olds & Anderson, 1989], “small, triangular, or irregularly oblong” [Voss, 1988]) due partially to high intraspecific variability in both attributes. I chose to define one aspect of size and shape as the length of the interparietal relative to the parietal, measured along the midsagittal line. Because this character is variable within most of the recognized tribes as well as in the outgroups, polarity is difficult to determine and easily affected by tree topology. This character appears to be more informative within tribes rather than between. Olds and Anderson (1989) included a “well developed” interparietal in their differential diagnosis of the phyllotines. They described a well-developed interparietal as plesiomorphic for the phyllotines in their character review and thus did not list it with the likely synapomorphies.

56P. MEDIAL LENGTH OF INTERPARIETAL/PARIETAL—3 states.

- 0 = < 0.33
- 1 = $0.33\text{--}0.45$
- 2 = > 0.45

A separate coding scheme was used for the phyllotine analysis because the range of variation was less than among the sigmodontines, but taxonomically significant variation could still be recognized. As with character 11S, lengths of the interparietal and parietal were measured along the midline. The common condition among phyllotines is for a long interparietal (state “2”), but the plesiomorphic condition is unclear with all instances of short interparietals among other sigmodontines. A moderate interparietal (between 33 and 45% the medial length of the parietal) is found in most *Calomys* except *C. sorellus*, which, like most other phyllotines, has a larger interparietal that is greater than 45% of the parietal length. Moderate interparietals are also found in *Auliscomys* and *Neotomys*. Although not coded in this study because of the difficulty in coding the complex variation observed, shape of the interparietal may be a useful character at other taxonomic levels. For example, my observations indicate that despite substantial individual variation, particular shapes characterize and distinguish species, subspecies, and even populations within the *Phyllotis darwini* complex.

14S. PARIETAL/OCCIPITAL CONTACT—2 states (Fig. 14).

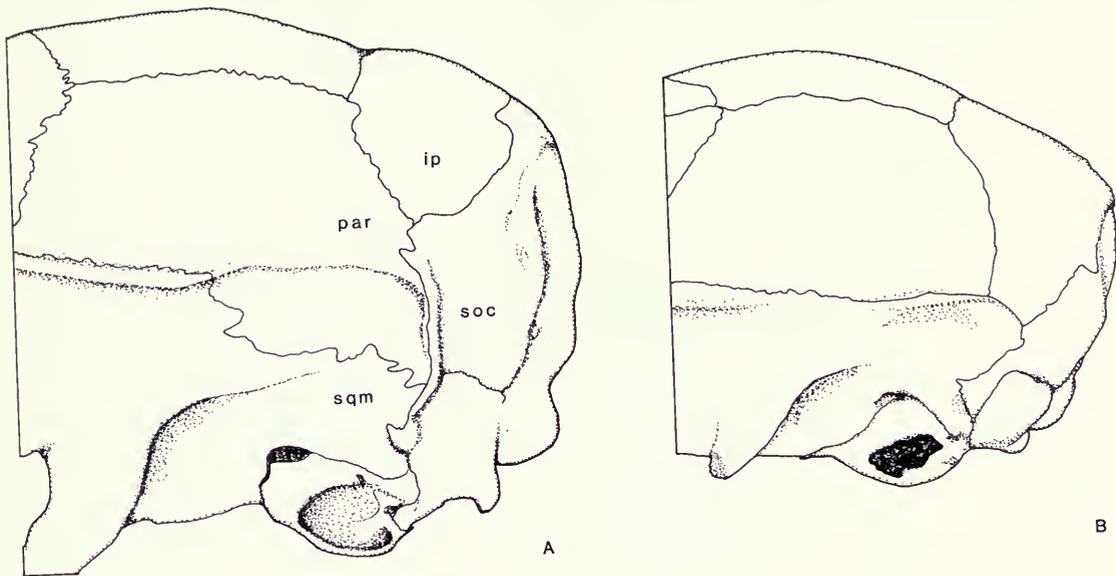


FIG. 14. Dorsolateral views of posterior cranium. **A**, parietal and occipital in contact, *Nectomys squamipes* (FMNH 141633); **B**, interparietal and squamosal in contact, *Nyctomys sumichrasti* (FMNH 35186).

0 = parietal and occipital in contact with each other, interparietal and squamosal not in contact

1 = interparietal and squamosal in contact with each other, parietal and occipital not in contact

The widespread condition seen in sigmodontines and outgroups is for the posterolateral margins of the parietal to contact the anterolateral corners of the occipital (Fig. 14A), even in species with well-developed interparietals. This parietal/occipital contact may be little more than a millimeter in length but precludes any contact between the lateral margins of the interparietal and the posteromedial corners of the squamosal. Only tytomysines have interparietals that are broadly in contact with the squamosals (Fig. 14B), precluding contact between parietals and occipitals. *Neotomys* is polymorphic for this character, with all four bones nearly meeting at a single vertex.

57P. ORIENTATION OF ANTERIOR BORDER OF AUDITORY BULLA—3 states.

0 = oblique (viewed ventrally)

1 = transverse

2 = rounded

This character largely describes the degree of anterior inflation in the bulla. The widespread condition among sigmodontines is oblique (un-

inflated: sloping posterolaterally), but because this condition is so restricted among phyllotines, transverse (moderately inflated) may be a phyllotine synapomorphy. An oblique bulla is found in *C. callosus*, *Andalgalomys*, and some *Andinomys*. A rounded anterior border to the bulla is found in *C. lepidus* and many *Phyllotis*.

15S 58P. TEGMEN TYMPANI—2 states.

0 = tegmen tympani contacts posterior suspensory process of squamosal across middle lacerate foramen

1 = tegmen tympani does not contact squamosal

In most sigmodontines, the tegmen tympani, also known as the periotic portion of the petrosal, crosses the middle lacerate foramen to contact the posterior suspensory process of the squamosal (Voss, 1993, Fig. 8). Voss (1993) and Voss and Carleton (1993) considered this to be the plesiomorphic condition. Voss and Carleton (1993) also proposed that the absence of this contact, and in particular the absence of the suspensory process, is a synapomorphy of the tribe Oryzomyini, but their sample of sigmodontine genera was limited. Absence of the contact was found in all surveyed oryzomyines, including the tetralophodont *Holochilus*, *Pseudoryzomys*, and *Zygodontomys*, in the phyllotine *Reithrodon*, and in the Old World cricetine *Mystromys*.

59P. SHAPE OF STAPEDIAL SPINE OF AUDITORY BULLA—2 states (Fig. 15).

- 0 = circular to ovoid in cross-section
- 1 = laterally appressed against auditory bulla, not smoothly rounded in cross-section

The lateral compression may be a consequence of the high degree of inflation of the auditory bulla in *Andalgalomys* and *Graomys*, the only taxa in which this character has been observed (Fig. 15B). The stapedial spine is bounded medially and/or laterally by the stapedial artery or its subsidiary branches, the supraorbital and infraorbital.

16S. SQUAMOSAL FOLD—2 states.

- 0 = absent
- 1 = present

The squamosal fold is a thickening along the anterior border of the postglenoid foramen, with the dorsal edge nearly folded over the anterior margin, strongly obscuring a large tegmen tympani and small postglenoid foramen. A squamosal fold has only been observed in *Kunsia*, *Tylomys*, and *Nyctomys*.

17S. SUBSQUAMOSAL FORAMEN—3 states.

- 0 = present, well developed
- 1 = reduced to slit, little or no exposure to occipital
- 2 = absent

Carleton (1980) considered the absence of the subsquamosal foramen to be plesiomorphic for New World murids, despite the more widespread occurrence of state "0." The various conditions are dispersed throughout the sigmodontines, but all phyllotines have a well-developed subsquamosal foramen.

60P. THICKNESS OF HAMULAR PROCESS OF SQUAMOSAL—4 states.

- 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

The presence and thickness of the hamular process of the squamosal is dependent on the presence of the subsquamosal foramen. The most frequent condition among phyllotines is for a thin, fragile

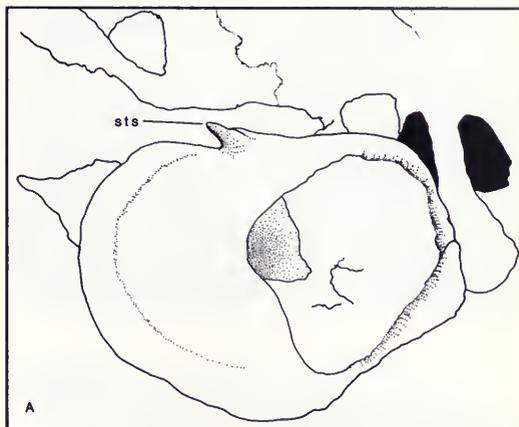


FIG. 15. Stapedial process of bulla (sts). A, rounded, *Phyllotis xanthopygus* (FMNH 20115); B, laterally appressed, *Graomys griseoflavus* (FMNH 50927).

hamular process that widens where it joins the mastoid, thus appearing flattened. The distinction between this state ("2") and one where the posterior terminus is thin also and does not appear flattened ("3") does not seem to be taxonomically informative among genera; both states can be found in *Calomys*, *Graomys*, *Phyllotis*, and *Auliscomys* in nearly equal frequency. A reduced subsquamosal foramen and thick hamular process are found in *C. callosus* and *C. hummelincki*, as well as in several outgroups. The absence of both foramen and process is found in ichthyomyines and some oryzomyines.

61P. POSITIONS OF TEMPORAL VACUITIES—2 states.

- 0 = subsquamosal and postglenoid foramina positioned essentially dorsoventrally

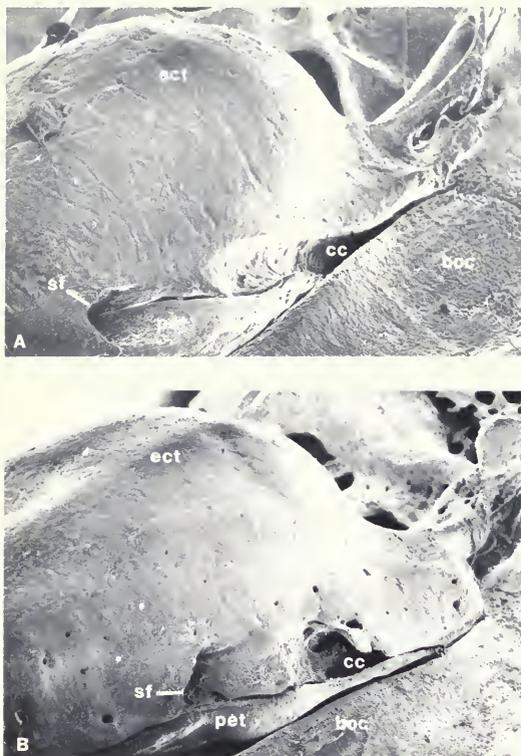


FIG. 16. Medial views of auditory bulla and internal carotid canal. **A**, internal carotid bounded by both basioccipital and ectotympanic, *Phyllotis andium* (FMNH 81249); **B**, internal carotid bounded by petrosal and ectotympanic portions of auditory bulla, *Neotomys ebriosus* (FMNH 24775). boc, basioccipital; cc, carotid canal; ect, ectotympanic part of auditory bulla; pet, petrosal part of auditory bulla; sf, stapedial foramen.

1 = postglenoid foramen distinctly anterior to subsquamosal foramen

This character is a simplified description of a complex trait that depends on the orientation and thickness of the hamular process of the squamosal, as well as the size, shape, orientation, and relative positions of the temporal vacuities: the subsquamosal foramen and the postglenoid foramen. The anterior extent of each is particularly influential in determining state assignments. The common condition among phyllotines is for the vacuities to be positioned essentially dorsoventrally. The common condition among the outgroups is for the vacuities to be positioned distinctly anteroposteriorly, with the postglenoid foramen more anterior than ventral to the subsquamosal foramen. This condition is found in *C. callosus* and *C. humme-*

lincki, *Euneomys*, *Neotomys*, *Andinomys*, and *Chinchillula*.

62P. INTERNAL CAROTID CANAL—2 states (Fig. 16).

- 0 = bounded by both basioccipital and the ectotympanic portion of auditory bulla
- 1 = bounded entirely (or nearly so) by petrosal and ectotympanic portions of auditory bulla

The widespread condition among sigmodontines and probably the plesiomorphic condition for phyllotines is for the carotid canal to be bounded by both the auditory bulla and the basioccipital bone as the internal carotid artery passes between them to enter the braincase (Fig. 16A). The alternate condition differs in having a flange of the petrosal extend between the basioccipital and the internal carotid artery, thus along with the ectotympanic portion of the bulla entirely or almost entirely forming the carotid canal (Fig. 16B). This condition is found in *Andinomys*, *Chinchillula*, *Euneomys*, *Irenomys*, and *Neotomys*.

63P. EXTENSION OF EUSTACHIAN TUBE—3 states.

- 0 = tube does not reach posterior lobe of pterygoid process
- 1 = tube subequal to posterior lobe of pterygoid process, does not extend anterior to the base of process
- 2 = tube extends anteriorly past base of pterygoid process

The widespread condition among phyllotines and sigmodontines, and most likely plesiomorphic for the phyllotines, is for the anterior flange of the eustachian tube to be subequal with the pterygoid process, reaching the posterior lobe of the process, but not extending anterior to the base of the process. This is the intermediate state in the transition series represented among the phyllotines. The eustachian tubes of many *Andinomys* have lanciolate projections that can extend up to 2 mm anterior to the bases of the pterygoid processes.

18S 64P. RELATIVE WIDTH OF MESOPTERYGOID FOSSA—3 states.

- 0 = distinctly broader than adjacent parapterygoid fossae
- 1 = subequal
- 2 = distinctly narrower than adjacent parapterygoid fossae

Previous studies have not always specified a criterion for evaluating the size of the two fossae.

This is particularly important because both fossae may converge or diverge posteriorly to different degrees, and thus the relative proportions will vary. Olds and Anderson (1989) evaluated mesopterygoid breadth at the posterior margin of the zygomatic aperture. I chose to make the comparison at the basisphenoid–presphenoid suture, believing that this would be a more stable reference landmark. The different criteria may be the explanation for the differences in coding (i.e., *Holochilus*, *Pseudoryzomys*). Olds and Anderson (1989) considered that a parapterygoid fossa relatively broader than the mesopterygoid fossa was diagnostic for the phyllotines.

The condition is variable among sigmodontines, but within the phyllotines the widespread condition is for the mesopterygoid fossa to be distinctly narrower than the parapterygoid fossa. The two fossae are subequal in breadth in *Chinchillula*, *P. wolffsohni*, *Irenomys*, and *Andinomys*. Broad mesopterygoid fossae are found in several outgroup taxa (*Holochilus*, *Nectomys*, *Oxymycterus*, and *Zygodontomys*).

65P. PARAPTERYGOID SHAPE—3 states.

- 0 = posterior width < 1.5 times anterior width
- 1 = 1.5–2.4 times anterior width
- 2 = > 2.4 times anterior width

This character describes the degree of posterior divergence in the parapterygoid fossa. The common condition among surveyed sigmodontines and the widespread condition among phyllotines is for the posterior breadth to be 1.5–2.4 times the anterior breadth. The probably derived condition where the posterior breadth is less than 1.5 times the anterior breadth is found in *Euneomys*, *Loxodontomys*, *Neotomys*, and *Reithrodon*. The parapterygoid fossa diverges more strongly only in *P. osilae*.

19S. SHAPE OF MESOPTERYGOID FOSSA—3 states.

- 0 = posteriorly convergent, “horseshoe”-shaped
- 1 = parallel sided, “U”-shaped
- 2 = posteriorly divergent, “V”-shaped

The coding of this character for the two analyses differs to reflect the greater range of variation among sigmodontines than among phyllotines. Most outgroups are either convergent or parallel-sided. All phyllotines are divergent, although some are nearly parallel-sided.

66P. SHAPE OF MESOPTERYGOID FOSSA—3 states.

- 0 = posterior width < 1.5 times anterior width
- 1 = 1.5–2.4 times anterior width

2 = > 2.4 times anterior width

The categorical values are the same as for the parapterygoid fossa. Here the common condition in phyllotines is a relatively parallel-sided mesopterygoid fossa (“0”). Moderate posterior divergence (1.5–2.4 anterior breadth) is found in *Calomys lepidus*, *Andalgalomys*, *Eligmodontia*, and *P. definitus*. The most posteriorly divergent condition is found in *Reithrodon*.

67P. PARAPTERYGOID FOSSA DEPTH—3 states.

- 0 = flat, even with bony palate
- 1 = slightly to moderately excavated above level of bony palate
- 2 = deeply excavated above level of bony palate

The widespread condition among sigmodontines and phyllotines is for a shallow parapterygoid fossa, essentially even with the bony palate. A parapterygoid fossa excavated slightly beyond the level of the bony palate is found in *Euneomys* and *Andinomys*. *Reithrodon* and *Neotomys* share a well-excavated parapterygoid fossa. Depth and breadth of the parapterygoid fossa may be functionally correlated with hypsodont grinding molars because the internal pterygoids originate in the parapterygoid fossae (Kesner, 1980; Rinker, 1954), and Carleton (1980) accordingly considered a deep fossa as derived.

20S 68P. SPHENOPALATINE VACUITIES—5 states.

- 0 = absent, roof of mesopterygoid fossa wholly ossified
- 1 = narrow slit encompassing presphenoid–basisphenoid juncture, wholly visible within mesopterygoid fossa
- 2 = vacuity distinct but constricted, orbital wings of presphenoid not fully separated posterior to medial pterygoid processes
- 3 = vacuity large, medial pterygoid processes fully anterior to orbital wings of presphenoid, not visible in mesopterygoid fossa, no large projections of lateral margins into the vacuity
- 4 = vacuity very large, orbital wings of presphenoid filamentous, very large optic foramen

The ancestral condition for this character is difficult to determine. All states except the most open vacuities seem to be common among other “critetids.” Carleton (1980) considered a wholly ossified roof of the mesopterygoid fossa to be primitive for neotomine–peromyscines, and Olds and Anderson (1989) considered “large” sphenopala-

tine vacuities (following the description in Carleton [1980]) to be a synapomorphy for phyllotines. With the additional character states used in this study, very open sphenopalatine vacuities (states "3" and "4") are only found in the phyllotines and in *Sigmodon*. Voss (1991) reported significant but discrete variation for this trait among *Zygodontomys brevicauda*. The open sphenopalatine vacuity that he illustrated for some populations would be categorized as state "2" under my coding scheme rather than state "3," as characterizes the phyllotines.

Variation in the extent of excavation in the sphenopalatine vacuities is much greater among sigmodontines than within the phyllotines. All phyllotines have large sphenopalatine vacuities that are fully exposed within the mesopterygoid fossa. *Reithrodon* is characterized by especially large sphenopalatine vacuities in addition to large optic and anterior lacerate foramina. The convergence of the foramina and vacuities in *Reithrodon* has resulted in filamentous orbital wings of the presphenoid. State "4" is subsumed in state "3" in the sigmodontine analysis because it is represented only in *Reithrodon*, making it uninformative in the analysis.

69P. POSITION OF ORBITAL WINGS OF PRES-PHENOID—2 states.

- 0 = wings anterior to a distinct constriction of the presphenoid
- 1 = wings posterior to maximum constriction

The widespread and almost certainly plesiomorphic condition in phyllotines is for the wings to join the presphenoid anterior to the sharp constriction that occurs just anterior to the basisphenoid. Among phyllotines, the derived condition, where the wings join equal with or posterior to the maximum constriction, is found only in *Andalgalomys* and *Graomys*. The derived condition is largely due to the gradual thinning of the presphenoid in those two genera, rather than the abrupt constriction present in the other phyllotines.

21S 70P. POSITION OF ANTERIOR BORDER OF MESOPTERYGOID FOSSA—4 states.

- 0 = lying ≥ 1 M3 tooth-length posterior to M3
- 1 = lying between $\frac{1}{2}$ and 1 tooth-length posterior to M3
- 2 = lying between 0 and $< \frac{1}{3}$ tooth-length posterior to M3
- 3 = reaching posterior plane of paired M3s ("short palate")

The position of the mesopterygoid fossa was evaluated relative to the line connecting the posterior borders of the upper third molars. This character has sometimes been referred to as "palate length." I used the same criterion for coding "short" palates as did Olds and Anderson (1989), namely, that the mesopterygoid fossa extend anteriorly beyond the posterior edge of M3, but my observations disagree with their coding ("long" palates) for *Ichthyomys*, *Holochilus*, and *Neotomys*. Hershkovitz (1962) regarded a "short palate" as primitive for the sigmodontines.

The widespread condition among phyllotines is for the anterior border of the mesopterygoid fossa to be within $\frac{1}{3}$ to 1 tooth-length (M3) posterior to the posterior alveoli. A shorter palate, with the mesopterygoid fossa within $\frac{1}{3}$ of a tooth-length, is found in some *Reithrodon auritus* and *Chinchillula*. The mesopterygoid actually reaches the posterior plane of the third molars in *Irenomys*, *Neotomys*, and *Andinomys*.

71P. MEDIAL PROCESS OF POSTERIOR PALATE—2 states.

- 0 = absent
- 1 = present

The common condition among sigmodontines and the phyllotines is for there to be no medial process from the posterior margin of the palate.

72P. POSTERIOR PALATINE RIDGE—2 states.

- 0 = absent or indistinct
- 1 = present, a longitudinal ridge formed by convergence of parallel channels arising from palatine foramina

The posterior palatine ridge is a distinct ridge running down the midline of the palate, most pronounced posteriorly. It is usually, but not always (e.g., *Punomys*), continuous with a median process of the posterior palate. The ridge appears to be formed principally by the near coalescence of two channels running along the palate. Among phyllotines, the posterior palatine ridge is found only in *Reithrodon* and *Neotomys*.

73P. POSTEROLATERAL PALATAL PITS—2 states.

- 0 = anterior to mesopterygoid fossa
- 1 = posterior to anterior border of mesopterygoid fossa

A pair of pits are always found among phyllotines in the posterior region of the palate framing the anterior border of the mesopterygoid fossa.

The widespread condition is for these pits to be just anterior to the mesopterygoid fossa. Alternatively, the pits are displaced posteriorly into the anterior region of the parapterygoid fossae. This condition is found in *Irenomys*, *Andinomys*, and *P. osilae*. Of these three species, only *P. osilae* has a "long" palate; that is, two of three phyllotines with pits posterior to the edge of the mesopterygoid fossa have a mesopterygoid fossa that extends far anteriorly. However, the two traits are not as highly correlated as that observation suggests. Among outgroup taxa surveyed, four out of seven with pits posterior to the mesopterygoid fossa in fact have "long" palates where the mesopterygoid is greater than $\frac{1}{3}$ of a tooth-length from the molars.

74P. ORIENTATION OF MAXILLARY TOOTH ROWS—3 states.

- 0 = posteriorly divergent
- 1 = parallel
- 2 = convergent

The orientation of the maxillary tooth rows is estimated by lines passing through the apexes of the alveoli. Akodontines generally have convergent tooth rows, oryzomyines generally parallel, but *Punomys* has divergent tooth rows. Thus, the plesiomorphic condition for phyllotines is unclear.

75P. SPHENOPALATINE FORAMEN—3 states.

- 0 = absent or nearly ossified
- 1 = present, small to moderate size
- 2 = present, large

The common condition among sigmodontines is for the sphenopalatine foramen to be absent or constricted, but the widespread condition among phyllotines is for a distinct and moderate-sized foramen to be present. The constricted condition also occurs in *Auliscomys sublimis* and *Loxodontomys*. A particularly large sphenopalatine foramen is found in *Reithrodon*, consistent with the general high degree of fenestration in its basal cranium.

22S 76P. CAROTID CIRCULATION—3 states.

- 0 = both stapedial and sphenofrontal foramina present, squamosal–alisphenoid groove present
- 1 = stapedial foramen present, but sphenofrontal foramen absent, no squamosal–alisphenoid groove
- 2 = both stapedial and sphenofrontal foramina absent, no squamosal–alisphenoid groove

Coding largely follows Carleton (1980), who followed Bugge's (1970) polarity. Readers are directed to Bugge (1970) for discussion of the carotid system in muroid rodents and to Brylski (Brylski, 1990; geomyoids), Carleton (1980; New World "cricketines"), Voss (1988; ichthyomyines), Carleton and Musser (1989; oryzomyines), and Voss and Carleton (1993; oryzomyines) for more detailed descriptions of this character in New World muroids. Each of these workers considered a complete stapedial system (state "0") to be primitive for the group they were discussing. In the primitive condition, the carotid artery splits into the internal carotid and the stapedial artery. The stapedial artery passes into the auditory bulla, through the stapes, and into the cranium. After a split of the stapedial, the supraorbital branch passes along the internal surface of the squamosal and alisphenoid bones, leaving a groove as evidence of its passage, and eventually emerges through the sphenofrontal foramen. The "primitive" condition, with functional stapedial foramen, sphenofrontal foramen, and squamosal groove all present, is found in this survey in basal ichthyomyines (Voss, 1988), some thomasomyines, *Wiedomys*, some oryzomyines, akodontines, scapteromyines, *Punomys*, and virtually all phyllotines. Also common among sigmodontines in this survey are those conditions considered to be derived. These derived conditions are characterized by loss of the sphenofrontal foramen and loss of the supraorbital branch of the stapedial artery. Further loss of the infraorbital branch of the stapedial artery results in the reduction of the stapedial foramen. These derived conditions are found in many oryzomyines, some thomasomyines, terminal ichthyomyines (according to Voss, 1988), *Sigmodon*, and among phyllotines in *Reithrodon* and *Neotomys*. Voss (1991) reported that *Zygodontomys brevicauda* shows well-defined discrete geographic variation for this trait, with one set of populations having a complete stapedial circulation and the other set lacking a complete stapedial circulation. It is interesting that this species shows geographic variation for two traits that are otherwise conserved at the generic or even tribal level.

77P. SQUAMOSAL FENESTRA—2 states.

- 0 = squamosal fenestra present where masticatory–buccinator nerve passes over the squamosal–alisphenoid groove
- 1 = squamosal fenestra absent

Where the squamosal–alisphenoid groove crosses the trough formed on the exterior of the alisphenoid

noid by the masticatory–buccinator nerve, a fenestra often appears. Squamosal fenestrae were only observed in individuals with a squamosal–alisphenoid groove (i.e., complete stapedial system), which is likely a structural necessity for the bone to be thin enough for the fenestra to occur. Under this argument, a fenestra cannot be present in animals with a derived stapedial system. This character was therefore coded as unknown in taxa with the derived stapedial system, which still allows the potential for incongruent ancestral state assignments under parsimony, but this should be unimportant to the analysis if it should happen. Polarity of this character is uncertain. Most phyllostines have the squamosal fenestra, although there is significant individual variation. Taxa with the complete supraorbital circulation that generally lack the fenestra include *Galenomys*, *Euneomys*, *Irenomys*, southern *Andinomys*, most *Phyllotis*, and *Auliscomys pictus*. A reduced supraorbital circulation, where the stapedial foramen in the auditory bulla is present but constricted, and both the sphenofrontal foramen and squamosal–alisphenoid groove are absent, is found among phyllotines only in *Neotomys*. *Reithrodon* is the only phyllotine without a stapedial artery.

23S 78P. ALISPHENOID STRUT—3 states.

- 0 = absent or filamentous
- 1 = consistent dorsal process, but does not fully cross foramen ovale
- 2 = present and bony

The absence of an alisphenoid strut is widespread among the phyllotines, but some individual variation is apparent. Voss (1993) and Voss and Carleton (1993, Fig. 10) considered presence of the alisphenoid strut to be plesiomorphic for sigmodontines. Among phyllotines, a complete and consistent alisphenoid strut is found in *Andalgalomys*, *Eligmodontia*, *Graomys*, *Irenomys*, and *Reithrodon*. In an intermediate condition, at the usual position of the strut, a process of the alisphenoid extends into the foramen ovale from the dorsal side. This condition is found in *Euneomys* and *Chinchillula*. Because there is no direct indication that a dorsal process is the intermediate state in transformations between absence and presence, the character states are treated as unordered.

24S. HYOID—3 states.

- 0 = entoglossal process long and attenuate, basihyal arched, thyrohyal long
- 1 = entoglossal process a small knob, basihyal arched, thyrohyal long

- 2 = entoglossal process absent, basihyal straight, thyrohyal short

Transformation series and state descriptions follow Carleton (1980, Fig. 11), from which most of the data were gathered, but coding order was modified to allow linear ordering of the character states for the analysis. Carleton considered the intermediate condition, with entoglossal process small, to be plesiomorphic for most muroid groups he surveyed. All sigmodontines surveyed by Carleton (1980) or myself lack an entoglossal process.

Postcranial Skeleton

25S. ARTICULATION OF FIRST RIB—2 states.

- 0 = first rib articulates with first thoracic vertebra only
- 1 = first rib articulates with transverse process of seventh cervical vertebra in addition to first thoracic vertebra

Articulation with the seventh cervical vertebra is recognized by the presence of a faceted articulation surface on the vertebra's transverse process, in addition to apparent contact (Carleton, 1980, Fig. 15). Carleton (1980) considered dual articulation as derived within neotomine–peromyscines. The presence of both states among nonsigmodontines and the universal dual articulation among sigmodontines suggests that dual articulation may be a synapomorphy for the sigmodontines.

26S. NUMBER OF THORACIC AND LUMBAR VERTEBRAE—3 states.

- 0 = 14 thoracic and 5 or 6 lumbar
- 1 = 13 thoracic and 6 lumbar
- 2 = 12 thoracic and 7 lumbar

Thoracic vertebrae were defined as having complete pairs of fully formed and articulating thoracic ribs. Supernumerary ribs are easily distinguished from complete ribs because they never articulate with the preceding vertebra (as do complete ribs), are always shorter and thinner, may diverge at odd angles, and often exhibit enlarged and deformed heads. Supernumerary ribs that lack these conditions were considered to be associated with lumbar vertebrae. Carleton (1980) considered 13 thoracic and 6 lumbar vertebrae to be plesiomorphic for the New World muroids. The number of vertebral elements was surveyed across various taxa in addition to those included in the phylogenetic anal-

ysis (Table 5, 179 species total). The Central American tylomyines, of uncertain affinities to the sigmodontines or neotomine-peromyscines, generally have more thoracic vertebrae (13, 14, or 15) while maintaining the six lumbar vertebrae. Thirteen thoracic and six lumbar vertebrae appear to be the widespread conditions among sigmodontines and are found in thomasomyines, ichthyomyines, akodontines, phyllotines, and scapteromyines. The apparent consistency of this character among generic groups suggests that it may be highly informative regarding oryzomyine relationships (Table 6). This trait appears more labile among the phyllotines than among the other sigmodontines (Steppan, 1993).

A consistent pattern is observed among species that are polymorphic for the number of thoracic rib pairs and vertebral number. Of the 57 species found to be polymorphic for rib pairs, only 13 have minority variants with fewer than the modal number of thoracic ribs. In all other species, the minority variant has an additional pair of either complete ribs (31 species) or incompletely formed supernumerary ribs (24 species) (the numbers of species just listed do not add up to 57 because some species have three or four conditions present). Only 6.3% of the 978 individuals examined differ from their species' modal count for true ribs.

79P. NUMBER OF THORACIC RIB PAIRS—2 states.

- 0 = 13 thoracic ribs
- 1 = 12 thoracic ribs

The coding for the phyllotine analysis differs from the sigmodontine analysis in not including more than 13 ribs. The widespread and probably plesiomorphic condition among phyllotines is 13 ribs. Twelve ribs are found in *Andalgalomys*, *Graomys*, *Reithrodon*, and some *Calomys*.

Some of these observations differ from published counts and deserve further discussion. Both Carleton (1980) and Olds (1988) reported that *C. callosus* has the plesiomorphic 13 ribs. Nineteen of the 20 skeletons of *callosus* examined in this study clearly had only 12 ribs and one had a thin, short thirteenth pair that did not articulate with the twelfth thoracic vertebra. Of the 11 skeletons examined by Carleton (1980), I could find only one individual that had more than 12 ribs (and the degree of articulation was unclear). Carleton (1980) also reported that both *Graomys griseoflavus* and *Sigmodon hispidus* possess the plesiomorphic condition. Of the 13 skeletons of *G. griseoflavus* examined, 11 had 12 ribs, with no evidence that the thirteenth pair had been broken

off; one appeared to have 12 ribs, but two additional disarticulated ribs were found with this skeleton; and only one had a complete thirteenth pair. Of the two skeletons examined by Carleton (1980), one was too damaged for an accurate count by me, and the other was not found. In *G. domorum*, not previously reported, seven skeletons clearly had the derived condition, one had an extra thoracic pair (13T [thoracic] + 7L [lumbar]), one was missing a lumbar vertebra (12T + 6L), and three had the plesiomorphic condition (13T + 6L). Ten of 13 skeletons of *Sigmodon hispidus* examined had the derived 12 thoracic and 7 lumbar rib pairs, as was observed by Voss (1992) in his revision of the South American species of *Sigmodon*. Three of the five skeletons examined by Carleton (1980) were reexamined by me; one had 13 rib pairs, one had a supernumerary pair, and one had a single supernumerary rib. This variation does not appear to be a preparation artifact. None of the specimens in species with moderate to large series and characterized as having 13 rib pairs were observed to have lost the last pair without leaving some evidence on the vertebrae. Additionally, the second lumbar vertebra can be recognized by an enlarged transverse process relative to those on the thoracics. This enlarged process would have obstructed an additional rib, if a rib had been present.

27P. NUMBER OF CAUDAL VERTEBRAE—6 states.

- 0 = > 40
- 1 = 36–40
- 2 = 30–35
- 3 = 24–29
- 4 = 20–23
- 5 = 11–19

Coding was derived from a histogram of all surveyed sigmodontine species (Table 5). Vertebral counts show limited variation in well-preserved specimens, typically with 80% of specimens within a range of two, with a few notable exceptions (*Holochilus brasiliensis*, 25–34; *Microryzomys minutus*, 27–38; *Oecomys concolor*, 32–38; *Oligoryzomys microtis*, 31–38; *Macrotarsomys bastardi*, 30–40). This variation within species may reflect currently unrecognized taxonomic diversity or misidentification of specimens. Carleton (1980) was unable to reliably estimate polarity for this character. Nearly the entire range of variation is found among the outgroups, from state "1" in *Nyctomys* to state "5" in some "cricetids," but the extremes are likely to be derived in both sigmodontines and outgroups.

TABLE 5. Vertebral counts among Neotropical sigmodontines and selected muroids.

Taxon ^a	N ^b	Thoracic ^c	Lumbar ^d	Caudal ^e
Tribe Akodontini				
<i>Akodon (Abrothrix) longipilis</i>	10	13	6	26–29 (28)
	1	13	5	
<i>A. (Abrothrix) sanborni</i>	7	13	6	24–27
<i>A. (Akodon) aerosus</i>	8	13	6	27–29
<i>A. albiventer</i>	7	13	6	23–25
<i>A. azarae</i>	2	13	6	26
	1	13 + 1	6	> 24
<i>A. boliviensis</i>	5	13	6	24–26
	1	13 + 1	6	
	1	13	7	24–25
<i>A. cursor</i>	11	13	6	27–28
<i>A. mollis</i>	4	13	6	28
<i>A. neocenus</i>	3	13	6	24–25
<i>A. olivaceus</i>	15	13	6	25–27
	2	12	7	25
<i>A. puer</i>	4	13	6	24–26
	1	14	6	25
<i>A. puer lutescens</i>	2	13	6	21–22
<i>A. subfuscus</i>	7	13	6	24–27
<i>A. torques</i>	8	13	6	28–30
	1	14	5	30–31
<i>A. urichi</i>	5	13	6	24–27
<i>A. xanthorhinus</i>	11	13	6	22–23 (22)
	1	13 + 1		
<i>A. (Deltamys) kempii</i>	2	13	6	29–30
<i>A. (Microxus) bogotensis</i>	1	12	7	25
	1	14	5	25–26
<i>A. (M.) mimus</i>	10	13	6	27–30
	2	12 + 1	7	
	1	12	7	30
	1	12	6	> 24
<i>A. (Thaptomys) nigrita</i>	6	13	6	23–24
<i>Bolomys amoenus</i>	8	13	6	23–26 (26)
	1	13 + 1	7	26
<i>B. lasiurus</i>	4	12	7	23–25
	1	?	6	> 19
<i>B. obscurus</i>	1	13	6	
<i>B. temchuki</i>	1	13	6	27
<i>Chelemys macronyx</i>	9	13	6	20–22
<i>Chroeomys andinus</i>	3	13	6	22–23
<i>C. jelskii</i>	12	13	6	23–26 (25)
<i>Geoxus valdivianus</i>	9	13	6	21–23 (22)
<i>Notiomys edwardsii</i>	1	13	6	18
<i>Oxymycterus delator</i>	6	13	6	27–29 (28)
<i>O. inca</i>	9	13	6	25–26
	1	13 + 1	6	25–26
	1	14	6	25
<i>O. platensis</i>	4	13	6	26–27
<i>O. rufus</i>	8	13	6	26
	1	13	7	25
<i>Thalpomys lasiotis</i>	1	13	6	19
Tribe Ichthyomyini				
<i>Anotomys leander</i>	7	14	6	33–34 (33)
<i>Chibchanomys trichotis</i> ^f	3	14	5	30–33
	1	13	6	
<i>Ichthyomys hydrobates</i>	1	13	6	≥ 25
<i>I. pittieri</i> ^f	1	13	6	30–33

TABLE 5. *Continued.*

Taxon ^a	N ^b	Thoracic ^c	Lumbar ^d	Caudal ^e
<i>I. tweedii</i>	4	13	6	32–34
<i>Neusticomys monticolus</i>	7	13	6	29–30
<i>N. venezuelae</i> ^f	2	14	5	30–33
<i>Rheomys mexicanus</i> ^f	8	13	6	> 33
	1	14	6	
<i>R. raptor</i>	4	13	6	32–33
<i>R. thomasi</i>	12	13	6	> 30
	1	14	5	33
	1 ^f	14	6	
<i>R. underwoodi</i>	2	13	6	30–33
Tribe Oryzomyini				
<i>Holochilus brasiliensis brasiliensis</i> ^g	8	12	7	25–34 (25–26, 29–30, 34)
	7	12	7	29–32
	1	11	7	29
<i>H. brasiliensis vulpinus</i>	4	12	7	33–35
<i>H. chacarius</i>	6	12	7	29–32
	2	11	7	29
<i>Lundomys molitor</i>	2	12	7	36
<i>Melanomys caliginosus</i>	9	12	7	28–29
	1	13	6	28
<i>Microroryzomys altissimus</i>	2	12	7	37
	1	12	6	
<i>M. minutus</i>	2	12	7	37–38
	1	12	?	27
	1	12	6	
	1	13	6	
<i>Neacomys guianae</i>	5	12	7	29–31
<i>N. spinosus</i>	10	12	7	32–35
	1	12	8	
	1	13	6	> 33
<i>N. tenuipes</i>	3	12	7	32–33
	1	13	6	33–34
<i>Nectomys squamipes</i>	8	12	7	31–32
<i>Nesoryzomys indefessus indefessus</i>	1	13	6	> 25
<i>N. indefessus narboroughi</i>	2	12	7	≥ 25
	1	13	6	27
<i>Oecomys bicolor</i>	11	12	7	34–37 (36)
	3	12 + 1	7	35
<i>O. concolor</i>	1	12	7	32–33
	2	12	7	36, 38
<i>O. mamorae</i>	1	12	7	
<i>O. paricola</i>	1	12	7	38
<i>O. roberti</i>	4	12	7	37–39
	1	12 + 1	7	37
<i>O. superans</i>	2	12	7	38–39
	1	13	7	
<i>O. trinitatis</i>	3	12	7	37–38
	1	12 + 1	7	37
<i>Oligoryzomys andinus</i>	1	12	7	> 34
	1	12 + 1	7	
	1	13	6	36
<i>O. chacoensis</i>	7	12	7	32–35 (34)
	2	12 + 1	7	35
<i>O. delticola</i>	2	12	7	35–36
	1	12 + 1	7	35
	1	13	7	
<i>O. destructor</i>	2	12	7	35–36
	1	13	6	

TABLE 5. *Continued.*

Taxon ^a	N ^b	Thoracic ^c	Lumbar ^d	Caudal ^e
<i>O. eliurus</i>	1	12	7	37
<i>O. flavescens</i>	5	12	7	34
<i>O. fulvescens</i>	4	12	7	32-33
	1	12 + 1	7	32-33
	1	13	7	32
<i>O. longicaudatus</i>	6	12	7	33-35
	1	13	6	35
<i>O. magellanicus</i>	2	12	7	≈ 31
<i>O. microtis</i>	3	12	7	31-33
	1	12	8	
	1	13	7	32
	1	11	7	
<i>O. microtis fornesi</i>	3	12	7	34-38
	2	13	6	31-32
<i>O. nigripes</i>	6	12	7	31-36
	1	12 + 1	7	> 28
	1	13	7	35
<i>Oryzomys albigularis</i>	4	12	7	37
	2	12 + 1	7	≥ 34
<i>O. alfaroi</i>	4	12	7	36-37
<i>O. bolivaris</i>	1	12	7	
<i>O. buccinatus</i>	3	12	7	38-40
<i>O. capito</i>	10	12	7	27-28
	2	13	6	> 28
<i>O. chapmani</i>	3	12	7	32-33
<i>O. couesi</i>	3	12	7	> 30, 33
<i>O. intermedius</i>	6	12	7	29-31
<i>O. keaysi</i>	5	12	7	36-37
<i>O. melanotis</i>	4	12	7	30-32
<i>O. nitidus</i>	1	12	7	31
<i>O. palustris</i>	8	12	7	32-33
	1	12 + 1	7	
<i>O. polius</i>	2	12	7	35-36
	1	12	8	35
<i>O. ratticeps</i>	4	12	7	37-39
<i>O. subflavus</i>	3	12	7	35-36
<i>O. talamancae</i>	6	12	7	29
	1	12 + 1	7	> 28
<i>Pseudoryzomys simplex</i>	1	12	7	29-30
	1	12	8	
<i>Sigmodontomys alfari</i>	4	12	7	33-36
<i>Zygodontomys brevicauda</i>	5	12 ^h	7	> 26, 34
"Thomasomyine group"				
<i>Aepeomys lugens</i>	1	13	6	≈ 38
<i>Chilomys instans</i>	1	13	6	> 36
	1	12	7	> 33
<i>Delomys dorsalis</i>	1	13	6	30
	1	12 + 1	7	> 27
<i>D. sublineatus</i>	2	13	6	30
<i>Rhipidomys couesi</i>	5	12	7	≈ 38
	2	13	6	37
<i>R. fulviventris</i>	1	13	6	35
<i>R. latimanus</i>	4	13	6	35-37
<i>R. macconnelli</i>	1	13	6	40
<i>R. mastacalis</i>	2	12	7	38-41
	1	12 + 1	7	
<i>R. nitela</i>	1	12	7	
<i>R. scandens</i>	1	12	7	> 38

TABLE 5. *Continued.*

Taxon ^a	N ^b	Thoracic ^c	Lumbar ^d	Caudal ^e
<i>R. venezuelae</i>	3	12	7	39–42
	1	12	6	39–40
<i>R. venustus</i>	1	13	6	
<i>Thomasomys aureus</i>	5	13	6	41–43
	1	13	7	41
<i>T. baeops</i>	5	13	7	37–41
<i>T. cinereus</i>	2	13	6	
	1	14	6	42
<i>T. daphne</i>	2	13	6	41
<i>T. gracilis</i>	1	13	6	38
<i>T. hylophilus</i>	2	13	6	41
<i>T. oreas</i>	1	13	6	38
<i>T. paramorum</i>	6	13	6	35–39 (38)
<i>T. pyrrhonotus</i>	1	13	7	> 38
	1	13 + 1	7	39
<i>T. rhoadsi</i>	1	13	6	
<i>Wiedomys pyrrhorhinos</i>	6	12	7	39
Tribe Phyllotini				
<i>Andalgalomys pearsoni</i>	2	12	7	31
<i>Andinomys edax</i>	7	13	6	28–30 (30)
<i>Auliscomys boliviensis</i>	6	13	6	25–27
<i>A. pictus</i>	4	13	6	22–26
	1	14	5	27
<i>A. sublimis</i>	4	13	6	24–25
<i>Calomys bolivae</i>	4	12	7	≈ 25
<i>C. callosus</i>	19	12	7	22–25 (23–24)
	1	12 + 1	7	
	2	12	6	
	1	13	7	25
<i>C. hummelincki</i>	5	12	7	21–23
	2	12	6	21–22
	1	13	6	
<i>C. laucha</i>	9	13	6	21–23
	1	12 + 1	7	
<i>C. lepidus</i>	4	13	6	20–22
<i>C. musculus</i>	7	13	6	27–28
	1	13	6	24–26
	2	12	7	
	1	? + 1	7	
	1	14	5	29
<i>C. sorellus</i>	11	13	6	27–28
	2	13	6	30–31
	1	14	6	29
<i>C. tener</i>	1	12	7	24
<i>C. venustus</i>	1	12	7	22
	1	13	7	25
<i>Chinchillula sahamae</i>	1	13	6	> 21
<i>Eligmodontia morgani</i>	6	13	6	25–26
<i>E. puerulus</i>	1	13	6	26
<i>Euneomys chinchilloides</i>	10	13	6	22–24 (22)
<i>Galenomys garleppi</i>	6	13	6	17–19
<i>Graomys domorum</i>	6	12	7	31–32, 35
	3	13	6	32–34
	1	13	7	
	1	12	6	
<i>G. griseoflavus</i>	12	12	7	32–35
	1	13	6	35

TABLE 5. *Continued.*

Taxon ^a	N ^b	Thoracic ^c	Lumbar ^d	Caudal ^e
<i>Irenomys tarsalis</i>	8	13	6	34–39
	1	13 + 1	6	
<i>Loxodontomys micropus</i>	6	13	6	28–29
	1	13	7	> 26
<i>Phyllotis amicus</i>	1	13	6	35–36
<i>P. andium</i>	3	13	6	34
<i>P. caprinus</i>	2	13	6	33–34
<i>P. darwini</i>	10	13	6	28–35 (32)
<i>P. gerbillus</i>	1	13	6	27
	1	13 + 1	7	30
<i>P. haggardi</i>	3	13	6	> 27
<i>P. osilae</i>	19	13	6	31–34 (32, 33)
<i>P. wolffsohni</i>	6	13	6	36 [n = 1]
<i>P. xanthopygus rupestris</i>	6	13	6	32–33
	1	13 + 1	6	34
<i>P. xanthopygus xanthopygus</i>	29	13	6	29–33 (31)
	1	12	7	
<i>Reithrodon auritus</i>	9	12	7	24
	1	13	6	25–26
Tribe Scapteromyini				
<i>Scapteromys tumidus</i>	7	13	6	28–30 (29)
	1	12	7	> 26
Tribe Sigmodontini				
<i>Sigmodon alleni</i>	3	12	7	25
	1	12	8	
<i>S. fulviventer</i>	2	12	7	
<i>S. hispidus</i>	9	12	7	23–25
	1	12 + 1	7	23
	1	13	6	24
	1	13	7	23
<i>S. leucotis</i>	1	12	7	25
	1	13	6	> 19
<i>S. ochrognathus</i>	4	12	7	25–27
Tylomyines				
<i>Nyctomys sumichrasti</i>	7	13	6	36–37
	2	13	7	37
	1	12	7	
<i>Ototylomys phyllotis phyllotis</i>	6	15	6	30–33
<i>O. phyllotis fumeus</i>	1	14	6	33–36
<i>Tylomys fulviventer</i>	4	14	6	35–40
	1	14 + 1	6	
<i>T. mirae</i>	2	14	6	33
<i>T. nudicaudus</i>	9	14	6	≈ 33
	3	13	7	35–36
	1	15	6	32
<i>T. panamensis</i>	4	14	6	35–36
<i>T. watsoni</i>	1	14	6	
Neotomine–Peromyscines				
<i>Baiomys musculus</i>	1	13	6	> 23
<i>Ochrotomys nuttalli</i>	1	13	6	26
<i>Scotinomys teguina</i>	3	13	6	26
Nesomyines				
<i>Brachytarsomys albicauda</i>	3	13	7	≈ 35
<i>Brachyuromys ramirohitra</i>	1	13	7	24

TABLE 5. *Continued.*

Taxon ^a	N ^b	Thoracic ^c	Lumbar ^d	Caudal ^e
<i>Eliurus myoxinux</i>	1	13	7	27–30
<i>Gymnuromys roberti</i>	2	13	7	> 27
<i>Macrotarsomys bastardi</i>	4	13	7	33, 37, 39, 40
	1	12 + 1	8	≈ 30
<i>Nesomys audeberti</i>	2	13	7	≈ 30
<i>N. rufus</i>	4	13	7	29–31
Old World "cricetids"				
<i>Calomyscus baluchi</i>	5	13	6	28–30
<i>Cricetulus barabensis</i>	1	13	6	16
<i>C. longicaudatus</i>	4	13	6	17
	1	13 + 1	6	17
<i>Cricetus cricetus</i>	4	13	6	16–17
<i>Mesocricetus auratus</i>	2	13	6	12
<i>Mystromys albicaudatus</i>	1	13	6	24
<i>Phodopus sungorus</i>	5	13	6	11
	1	13	7	9
<i>Tscherskia triton</i>	1	13	6	22

^a Specific and generic taxonomy follows Musser and Carleton (1993).

^b Number of skeletons examined for each vertebral count category.

^c Number of thoracic ribs as defined by pairs of fully formed thoracic ribs. Number after plus sign indicates the number of pairs of supernumerary ribs.

^d Number of lumbar vertebrae, including vertebrae with supernumerary ribs.

^e Numbers in parentheses indicate modal counts for species with sufficiently large sample sizes.

^f Data from Voss (1988, Table 10).

^g Associating *Holochilus* with the oryzomyines rather than with *Sigmodon* has been suggested based on several organ systems and presented by Voss and Carleton (1993).

^h One individual has a supernumerary rib that arises from the seventh cervical vertebra.

TABLE 6. Distribution of selected characters among oryzomyine and thomasomyine genera.

Taxon	Gallbladder ^a	Ribs	Mammæ ^b	Hemal arch	Zygomatic notch
<i>Thomasomys</i>	Present	13	6	Present at low frequency	Shallow
<i>Chilomys</i>	Present	13	6	Absent	Shallow
<i>Delomys</i>	Present	13	6–8	Absent	Deep
<i>Nesoryzomys</i>	Absent	13	?	Absent	Deep
<i>Neacomys</i>	Absent	12	6	Square	Shallow
<i>Oecomys</i>	Absent	12	8	Square	Shallow
<i>Microryzomys</i>	Absent	12	8	?Spinous?	Shallow
<i>Melanomys</i>	Absent	12	8	Spinous	Medium
<i>Nectomys</i>	Absent	12	8	Spinous	Deep
<i>Oligoryzomys</i>	Absent	12	8	?Spinous?	Deep
<i>Oryzomys</i>	Absent	12	8	Spinous	Deep
<i>Pseudoryzomys</i>	Absent	12	8	Spinous	Deep
<i>Zygodontomys</i>	Absent	12	8	Spinous	Deep
<i>Holochilus</i>	Absent	12	10	Spinous	Deep

^a Voss (1991).

^b Gyldenstolpe (1932), Hershkovitz (1955), and Voss (1993).

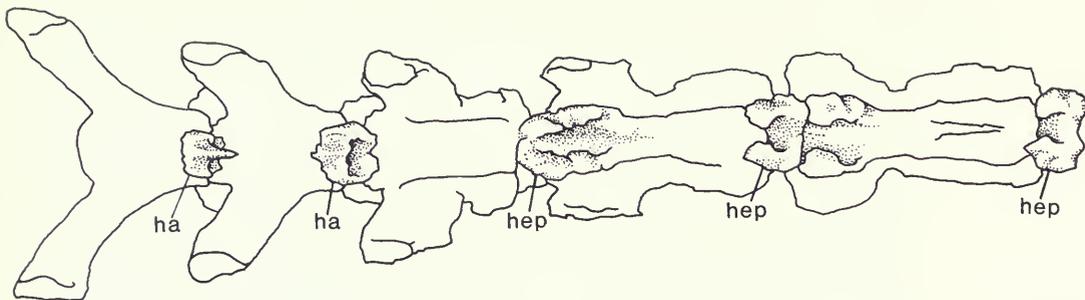


FIG. 17. Ventral view of caudal vertebrae 1-5 in *Nectomys squamipes* (FMNH 14163), indicating the hemal arches (ha) and hemal processes (hep).

80P. NUMBER OF CAUDAL VERTEBRAE—3 states.

- 0 = < 25
- 1 = 25-30
- 2 = > 30

TAIL LENGTH—Not analyzed. Tail length is highly correlated with number of caudal vertebrae and provides the more common definition of this general trait. Olds and Anderson (1989) described tail length as variable within Phyllotini, but they nonetheless chose to include it in their data matrix. While indeed being quite variable within the phyllotines (ranging from 0.33 to 1.4 times head and body length), tail length seems to be more conserved and therefore informative outside the phyllotines. Most sigmodontines (oryzomyines, thomomyines, ichthyomyines) have moderate to long tails (> 0.85 head and body length). Olds and Anderson (1989) agreed with Hershkovitz (1962, p. 54) that short and long tails are derived from moderate-length tails. It is unclear in both works whether this polarity only refers to sigmodontines in general or is also a statement about the ancestral condition in phyllotines.

81P. NEURAL SPINE OF SECOND THORACIC VERTEBRA—2 states.

- 0 = longest spine present on T2 (at least twice as long as nearby spines)
- 1 = short on T2, instead longest on T3

All sigmodontines except the ichthyomyines have a greatly enlarged neural spine on the second vertebra that acts as the site of attachment for the nuchal ligament (Voss, 1988). Voss reported that in ichthyomyines the spine of the third thoracic is both enlarged and the attachment site for the ligament. An enlarged spine on the second thoracic vertebra is plesiomorphic and widespread for the phyllotines just as in the sigmodontines. However, *Euneomys* also has an enlarged spine on the third thoracic. The only other occurrence of this derived

condition among phyllotines is in *Reithrodon*. In 16 skeletons of *Reithrodon auritus pachycephalus*, one had a longer spine on the third thoracic vertebra and five had second and third spines of approximately equal length.

82P. HEIGHT OF NEURAL SPINE OF SECOND CERVICAL VERTEBRA—3 states.

- 0 = not significantly enlarged
- 1 = enlarged, distinct knob
- 2 = very enlarged into distinct keel, "plow"-shaped, may overlap C3

The widespread condition among phyllotines is for the neural spine on the second cervical vertebra to be enlarged into a distinct knob, usually wider than long. In the likely derived condition, the knob is further enlarged into a distinct plow-shaped keel that may overlap the third cervical vertebra. This condition is found in *Andinomys* and *Neotomys*. The least developed condition was found by this survey only in *Akodon*.

83P. LENGTH OF NEURAL SPINE OF SECOND CERVICAL VERTEBRA—2 states.

- 0 = does not overlap C3
- 1 = does overlap C3, excluding situation where height is very enlarged

Among phyllotines without a greatly enlarged neural spine on the second cervical vertebra, the widespread condition is for that spine to not overlap the third cervical vertebra. Alternatively the knob is angled posteriorly and overlaps the third cervical. This condition is found in *Andalgalomys*, *Euneomys*, and some *Graomys griseoflavus*.

28S. HEMAL ARCH—3 states (Fig. 17).

- 0 = absent
- 1 = present, with simple posterior border
- 2 = present, with spinous posterior border

In the majority of sigmodontines, the median coccygeal artery, which passes along the ventral

side of the tail, is bounded by hemal processes at the vertebral junctions, usually starting between the second and third, becoming most pronounced between the fourth and fifth, and then diminishing along the next five to ten vertebrae. The hemal arch is a complete bony ring enclosing the artery and is typically located at the joint between the second and third caudal vertebrae (Fig. 17). Hemal arches are commonly found among other mammalian orders. In species with additional arches between the first and second and/or the third and fourth caudal vertebrae, the arch between the second and third is usually the most complex or most developed. Among surveyed pentapododont genera with 12 thoracic vertebrae (Table 6), all appear to possess a "ring"-shaped hemal arch (except *Wiedomys*). The posterior edge of the arch is extended into a distinct spinous process in *Necotomys*, *Pseudoryzomys*, *Zygodontomys*, most *Oryzomys*, and possibly *Microrizomys*. An unmodified hemal arch is found in *Oecomys*, *Neacomys*, *Oryzomys albigularis*, *O. capito*, and possibly *O. xanthaeolus*, as well as sporadically among some thomomysines, but sample sizes are small and arches are often damaged. I observed a hemal arch in only two tetralophodont genera, *Andinomys* and *Sigmodon* (in both cases, the arch lacked a spinous process).

84P. POSITION OF DELTOID TUBEROSITY—2 states.

- 0 = < 59%, measured from condyle of humerus to notch of deltoid tuberosity relative to total length
 1 = ≥ 59%

The position of the deltoid tuberosity on the humerus is measured as the percentage of total humerus length from the condyle to the notch of the tuberosity. The widespread condition for phyllotines is for the tuberosity to be less than 59% of the total length from the condyle.

29S. ENTEPICONDYLAR FORAMEN—2 states.

- 0 = present
 1 = absent

The presence of an entepicondylar foramen, located above the medial epicondyle of the humerus and next to the supertrochlear foramen (Carleton, 1980, Fig. 13), was considered by Carleton (1980) to be primitive for neotomine-peromyscines. It is present in tylomyines (*sensu* Carleton, 1980), most neotomine-peromyscines and Old World "crice-tids," but absent in all sigmodontines examined.

30S. SUPERTROCHLEAR FORAMEN—2 states.

- 0 = absent
 1 = present

Polarity of this character is difficult to determine, but most outgroup taxa lack it. All sigmodontines have a supertrochlear foramen except *Rhipidomys latimanus*. Carleton (1980) did not report on this character.

31S. PROXIMAL EXTENT OF FIFTH METATARSAL—2 states.

- 0 = peroneal process of fifth metatarsal equal with or proximal to the distal edge of calcaneum (articular surface with the cuboid)
 1 = fifth metatarsal not proximal to cuboid/calcaneum articulation

Taxonomic coverage is limited, but a "long" peroneal process (state "0") was found only among the outgroups.

32S. TROCHLEAR PROCESS OF CALCANEUM—2 states.

- 0 = level with posterior articular facet, process broad and shelf-like
 1 = gap between proximal edge of process and posterior articular facet, process shorter and less shelf-like

Coding for this character largely follows Carleton (1980), except that his state "2" was not observed among species I surveyed and is not included. Carleton (1980) considered the most proximal position of the process (state "0") to be plesiomorphic for the neotomine-peromyscines, but that is unlikely to be true also for the sigmodontines, among which I did not observe state "0." Both character states were found among the outgroups.

External Morphology

85P. VENTRAL SURFACE OF CLAWS (MANUS)—3 states.

- 0 = open basally
 1 = closed basally, without strongly developed keel
 2 = fused, forming distinct keel

The widespread condition among phyllotines is for claws to be closed basally, without developing a distinct keel. In *Eligmodontia*, *Chinchillula*, *Auliscomys pictus*, and *A. sublimis* the claw is strongly fused basally, forming a distinct keel. *Phyllotis wolffsohni*, alone among phyllotines, has a claw that is not closed basally.

86P. LENGTH OF D1 RELATIVE TO D5 (PES)—2 states.

- 0 = D1 distinctly shorter than D5
- 1 = D1 and D5 subequal in length, not extending past first interphalangeal joint of D2–4

The widespread condition among phyllotines is for digit 1 to be distinctly shorter than digit 5. Reduction in the length of D5 so that it is subequal in length with D1 and does not extend past the bases of D2–4 is present in *Reithrodon* and *Eligmodontia*. Outside the phyllotines, such short outer digits are also seen in genera with varying locomotor modes: *Oxymycterus*, *Sigmodon hispidus*, *Kunsia*, *Bolomys*, *Akodon (Thaptomys)*, *Holochilus*, and *Scapteromys*.

87P. POSITION OF HYPOTHENAR PAD—2 states.

- 0 = hypotenar extending distally beyond proximal base of the first interdigital pad
- 1 = intermediate to first interdigital and thenar pads

The widespread condition among phyllotines is for the hypotenar to extend distally beyond the base of the first interdigital pad. This is in contrast to the widespread condition among surveyed outgroups, where the hypotenar is intermediate between the first interdigital and thenar pads without significantly overlapping the position of either. The hypotenar is absent in the highly derived hindfeet of *Eligmodontia*.

33S 88P. FURRING OF SOLES OF FEET (PES)—3 states.

- 0 = sparse hair only on heels
- 1 = heels furred, distal pads naked
- 2 = heel and distal pads furred

Olds and Anderson (1989) listed this character among the possible phyllotine synapomorphies and included it in the diagnosis but did not include it in their data matrix (1989, Table 1). Their discussion implied that it is a widespread condition among sigmodontines while among phyllotines it is characterized by species-specific adaptations to local environments. Furred heels are found in thomomyines, akodontines, and some phyllotines.

Furring of the soles of the hindfeet in phyllotines varies from sparse lateral fur that extends toward the sole, to more extensive furring around and onto the sole of the heel, to furring among the distal pads. The third condition is easily distinguished from the first two, which have no hair at all in the broad distal portion of the sole.

34S. EAR (PINNA) SIZE—4 states.

- 0 = < 0.068 combined head and body length
- 1 = 0.069–0.108 combined head and body length
- 2 = 0.108–0.150 combined head and body length
- 3 = > 0.150 combined head and body length

Character state values were determined using the segment-coding technique on log-transformed ratios as described in the Materials and Methods section. There are minor differences between Olds and Anderson (1989) and this study in the size estimation and coding of several species. These differences may be a product of sampling. Four of the five species with the relatively largest ears sampled belong to phyllotines.

89P. COUNTERSHADING OF TAIL—3 states.

- 0 = distinctly bicolored
- 1 = indistinctly bicolored
- 2 = monocolored

Both distinctly and indistinctly bicolored tails are common among phyllotines and sigmodontines, making polarity equivocal. Indistinctly bicolored tails have a weak but noticeable contrast between the darker dorsum and lighter underside. Distinctly bicolored tails have a sharp contrast between the dorsal and ventral sides. Monocolored tails are found scattered among the phyllotines.

90P. FURRING OF TAIL DORSUM—3 states.

- 0 = sparsely furred, scales evident
- 1 = furred, scales visible but indistinct
- 2 = densely furred, scales scarcely visible

Moderately furred tail is the most common character state among phyllotines.

91P. BODY PELAGE PATTERN—3 states.

- 0 = distinctly countershaded
- 1 = indistinctly or not countershaded

The widespread condition among phyllotines is for the dorsum and sides of the body to be a contrasting color and tone from the undersides. No phyllotine is considered to be monocolored, but *Euneomys* and *Neotomys* are indistinctly bicolored.

92P. PECTORAL STREAKS—2 states.

- 0 = absent
- 1 = present

Only a minority of phyllotine species possess pectoral streaks, and those few are concentrated

in the genus *Phyllotis*. A pectoral streak is usually an ocher coloration to the fur along the midline in the pectoral region, approximately circular to longitudinal in shape, often presenting a subtle contrast to the predominantly neutral color of the undersides and usually limited to a streak rather than spreading laterally toward the shoulders. Pectoral streaks are found in *Neotomys*, *Loxodontomys*, *P. osilae*, *P. magister*, *P. definitus*, *P. wolffsohni*, and at small to moderate frequencies in some populations of *P. xanthopygus*.

35S. MAMMAE NUMBER—4 states.

- 0 = 4
- 1 = 6
- 2 = 8
- 3 = 10 or more

Four pairs of pectoral, postaxial, abdominal, and inguinal mammae constitute the widespread condition among the Sigmodontinae. Six mammae (postaxial, abdominal, and inguinal) are found in the thomasmomyines (e.g., *Thomasomys*, some *Delomys*, *Rhipidomys*), all ichthyomyines, some oryzomyines (just *Neacomys*), *Wiedomys*, and the “problematic” *Rhagomys* (Reig, 1980). Voss (1993) considered six mammae to be plesiomorphic for the sigmodontines. Mammae number may be intraspecifically variable in *Delomys dorsalis* (6–8; Voss, 1993), but sharp geographic segregation of the mammary counts suggests that two species may be present. More than eight mammae are found only in some *Calomys*, *Sigmodon*, and *Holochilus*. Thus, eight mammae is likely plesiomorphic for the phyllotines, but the presence of six versus eight mammae may be highly informative for pentalophodont sigmodontines (Table 6).

Characters of the Phallus and Soft Anatomy

36S. BACULAR COMPLEXITY—2 states.

- 0 = lateral bacular mounds present
- 1 = lateral bacular mounds absent

The complex penis with lateral bacular mounds present has conventionally been considered primitive for most muroids (Hooper & Musser, 1964; Hershkovitz, 1966b). Carleton (1980) hypothesized that the simple penis was primitive for the neotomine–peromyscines. I coded taxa with highly reduced and peculiar lateral mounds (*Nyctomys*, *Scapteromys*) as unknown given this simplified

coding scheme. Spotorno (1992) considered reduced or absent lateral mounds to be derived for New World murids and linked with a suite of traits partially controlled by hormonal levels.

93P. DISTAL/PROXIMAL BACULAR LENGTH—3 states (Fig. 18).

- 0 = < 0.63
- 1 = 0.63–0.77
- 2 = > 0.77

The landmarks chosen to define this character are from the distal tip of the medial digit of the distal baculum to the distal tip of the proximal and from the tip of the proximal to the line connecting the widest points of the base. The common condition for phyllotines is for an intermediate-sized distal baculum, 63–77% the length of the proximal baculum. A large distal baculum, ranging from 79 to 105% the proximal length, characterizes most members of the *P. xanthopygus* species group (*P. xanthopygus*, *P. darwini*, *P. magister*, and *P. caprinus*; Steppan, 1993). No sigmodontines outside *Phyllotis* have such relatively large distal bacula (Hooper, 1962; Hooper & Musser, 1964; Hershkovitz, 1966b; Spotorno, 1986; this study).

94P. LENGTH OF LATERAL MOUNDS RELATIVE TO MEDIAL MOUND—2 states.

- 0 = > 2/3
- 1 = < 2/3

The widespread and likely plesiomorphic condition among phyllotines is for the lateral mounds to be greater than 2/3 the length of the medial bacular mound. *Auliscomys sublimis* and *A. pictus* share the derived condition where the lateral mounds are less than 2/3 the medial length. *Andinomys* is unusual in having lateral mounds that are longer than the medial (Spotorno, 1986).

95P. HOOKS ON LATERAL MOUNDS—2 states (Fig. 18).

- 0 = absent
- 1 = present, pointing basally

The widespread condition among sigmodontines and phyllotines, and thus likely the plesiomorphic condition among phyllotines, is for the lateral mounds of the distal baculum to be simple and unmodified. The presence of basally directed hooks projecting from the tips of the lateral mounds is unique to the *Phyllotis xanthopygus* species-group (Fig. 18). The condition in *P. definitus* is unclear; while Spotorno (1986, Fig. 5.9) indicates

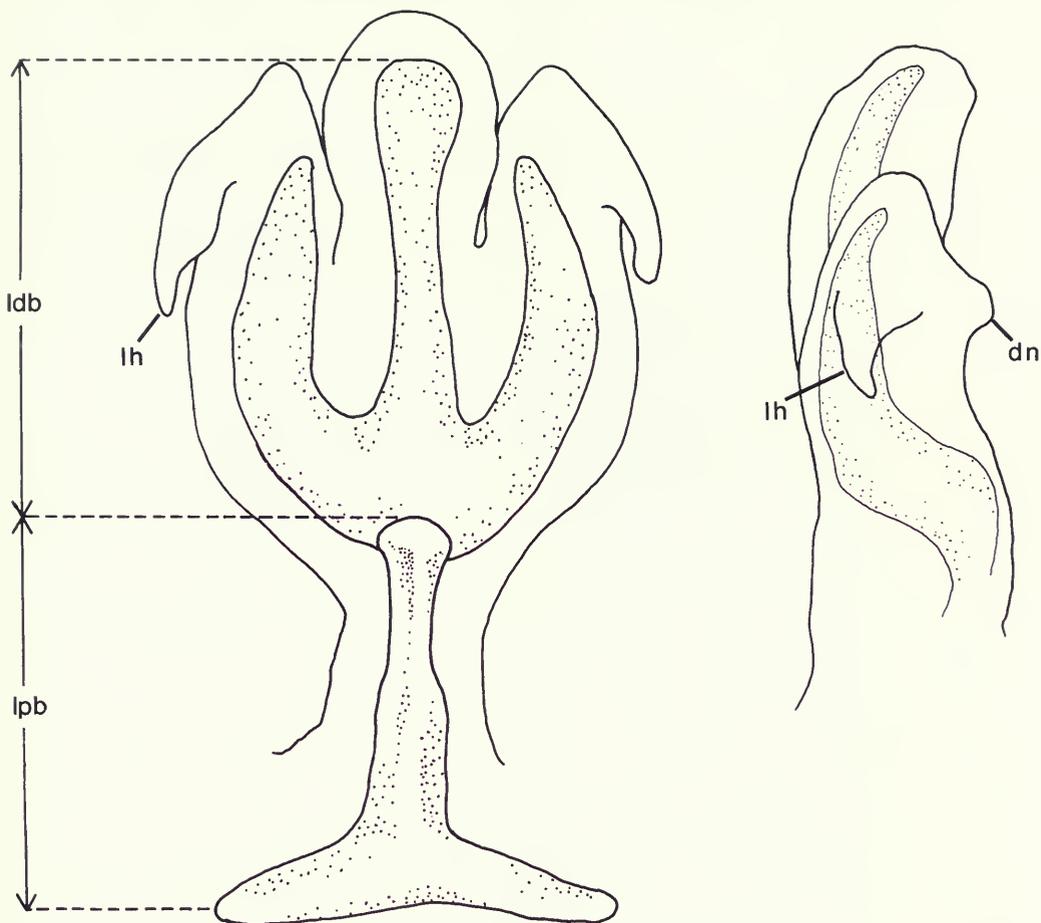


FIG. 18. Ventral and lateral views of bacular apparatus in *Phyllotis magister* (FMNH 107469). dn, dorsal knob of lateral mounds; ldb, length of distal baculum; lh, lateral hooks; lpb, length of proximal baculum.

the presence of small hooks, species similarly drawn in that publication do not possess hooks among FMNH specimens examined by me. Preparation differences are probably the cause of the differing observations.

96P. KNOB ON DORSAL SURFACE OF LATERAL MOUNDS—2 states (Fig. 18).

0 = absent
1 = present

Small knobs project from the middorsal surface of the lateral mounds in the species *Phyllotis xanthopygus*, *P. caprinus*, and *P. magister* (Fig. 18). Suitably prepared phalli of *P. darwini* were not available for examination. All other examined species lacked the dorsal knobs.

37S. PREPUTIAL GLANDS—3 states.

0 = absent
1 = one pair present
2 = two pairs present

Data and character coding are adapted from Voss and Linzey (1981). Male accessory glands show little phylogenetically informative variation among the sigmodontines (Voss & Linzey, 1981). The exceptions are ventral prostrates, which vary only among akodontines, and the number of preputial glands. At least one species in each major generic-group possesses a single pair, with the exception of the oxymycterines and *Sigmodon*. A single pair or no preputials are both widespread among other muroids (Carleton, 1980), but absence of preputials is found only in several oryzomyines and thomomyines (4 of 17 species surveyed). Two pairs were not reported by Carleton (1980) or Voss and Linzey (1981) outside the South American Sig-

modontinae. The plesiomorphic state for sigmodontines therefore appears to be one pair. Two pairs of preputials occur in *Chroeomys jelskii* (my observations suggest small third or even fourth pairs), oxymycterines (sometimes raised to tribal status, otherwise treated as a subgroup within the akodontines), *Sigmodon*, and most phyllotines.

97P. PREPUTIAL GLANDS—3 states.

- 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 (2–4 mm) medial pair

Two sources of data on preputial glands were available for this study: Voss and Linzey's (1981) study on male accessory glands in New World murroids and my observations of partially cleared and stained phalli. The coding was adjusted to reflect the range of variation observed in phyllotines as compared to sigmodontines. Voss and Linzey (1981) found one pair (\approx 10 mm) in *Calomys* (*C. callosus* and *C. laucha*), while the rest of the surveyed phyllotines (*Andalgalomys pearsoni*, *Eligmodontia typus*, *Graomys griseoflavus*, *P. darwini*, and *P. osilae*) had a second smaller ventral pair (2.5–3.5 mm). The material examined by Voss and Linzey (1981) consisted of phalli dissected from fluid-preserved carcasses stored in 70% alcohol. I examined phalli that had been partially cleared and stored in glycerin. With microscopic examination of dissected and backlit phalli, I found that greater detail could be observed than with un-cleared alcohol-preserved specimens. My observations of species of *Akodon*, *Chroeomys*, *Calomys*, *Phyllotis*, *Auliscomys*, *Irenomys*, and *Neotomys* all support the observations of Voss and Linzey (1981). However, *C. sorellus* was found to have a very small ventral pair of glands in exactly the same position and with the same texture and shape as the ventral pair in the other phyllotines. This ventral pair is so small, 0.5–0.8 mm, that it is possible that Voss and Linzey would not have recognized it using their methods had they examined *C. sorellus*. Because I did not have access to appropriately cleared phalli of *C. callosus* and *C. laucha* to confirm the absence of such a small ventral pair of glands, these two species were coded as unknown ("?"). All nine specimens of *P. xanthopygus chilensis* examined by me have an additional third pair, 1 mm long and situated between the lateral and medial pairs.

38S 98P. GALLBLADDER—2 states.

- 0 = absent
- 1 = present

Carleton (1980) and Voss (1993) considered the presence of a gallbladder to be plesiomorphic among New World "cricetids." Voss (1991) examined 93 species of sigmodontine rodents for the presence of a gallbladder. This character shows little variation within tribes or major generic groups. The only exceptions seem to be characteristic of unrelated scattered genera. A gallbladder is present in all surveyed akodontines except *Lenoxus* and *Akodon cursor*, all ichthyomyines except *Ichthyomys*, all thomasomyines except *Rhipidomys*, all phyllotines, the scapteromyines, and *Sigmodon* (*Punomys* was not examined). It is absent in all oryzomyines, including *Pseudoryzomys*, *Zygodontomys*, and *Holochilus*. All 16 surveyed phyllotines have a gallbladder (Voss, 1991).

39S. GASTRIC EPITHELIUM I—4 states.

- 0 = hemiglandular
- 1 = intermediate, reduction in glandular zone around antrum
- 2 = discoglandular
- 3 = pouched

40S. GASTRIC EPITHELIUM II—2 states.

- 0 = hemiglandular
- 1 = intermediate, reduction in glandular zone along greater curvature

Data and coding are slightly modified from Carleton (1973). Character 40S is treated as a separate character to distinguish the intermediate condition found in ichthyomyines from that found in *Thomasomys* and *Scapteromys*. The large majority of sigmodontines possess the hemiglandular condition.

Phylogenetic Relationships within Sigmodontinae

Results

When the analysis includes the dummy variable to favor sigmodontine monophyly, 28 equally most-parsimonious trees result, the strict consensus of which is presented in Figure 19. Each of the most-parsimonious trees (including outgroups) is 287 steps long with a CI of 0.26 and RI (Farris, 1989) of 0.61. When only the sigmodontines are considered, the respective values are 195 steps, CI

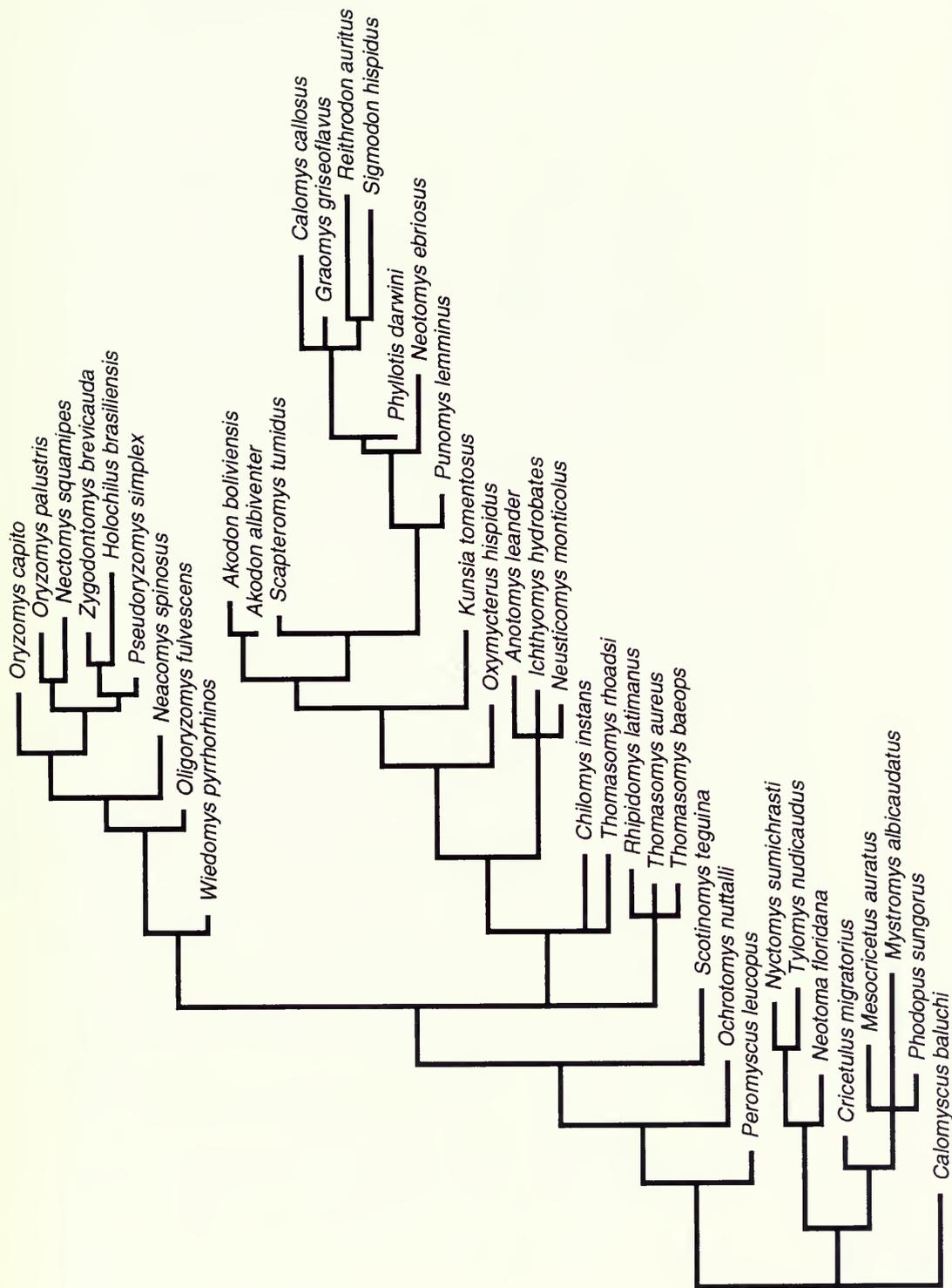


Fig. 19. Strict consensus cladogram of the 28 equally most-parsimonious trees for the South American Sigmodontinae, with a dummy variable included to favor sigmodontine monophyly. For the sigmodontine portion of the tree, each most-parsimonious tree is 195 steps long. CI = 0.33, RI = 0.63. Branch lengths are proportional to the number of hypothesized character state transitions, excluding the dummy variable.

TABLE 7. Consistency and retention indexes for sigmodontine characters.

Number	Character name	CI ^a	RI ^a
1.	Mesoloph(-id)	0.333	0.733
2.	Length M3	0.333	0.429
3.	Shape M2	0.167	0.286
4.	Posterior extent of incisive foramina	0.429	0.636
5.	Dorsoventral position of anterior root of zygomata	0.400	0.625
6.	Posterior margin of zygomatic plate	0.333	0.556
7.	Masseteric tubercle	1.000	1.000
8.	Zygomatic notch	0.667	0.857
9.	Posterior extension of nasals	0.143	0.500
10.	Posterior extension of premaxillaries	0.333	0.636
11.	Supraorbital edge	0.300	0.462
12.	Shape of frontoparietal suture	0.400	0.500
13.	Ratio of interparietal/parietal length	0.333	0.556
14.	Parietal/occipital contact	[1.000] ^b	[1.000] ^b
15.	Tegmen tympani	0.500	0.875
16.	Squamosal fold	[0.500]	[0.667]
17.	Subsquamosal foramen	0.333	0.500
18.	Relative width of mesopterygoid fossa	0.250	0.500
19.	Shape of mesopterygoid fossa	0.286	0.545
20.	Sphenopalatine vacuities	0.600	0.875
21.	Position of anterior border of mesopterygoid fossa	0.231	0.265
22.	Carotid circulation	0.200	0.429
23.	Alisphenoid strut	0.200	0.636
24.	Hyoid	[0.667]	[0.833]
25.	Articulation of first rib	[0.500]	[0.800]
26.	Number of thoracic and lumbar vertebrae	0.500	0.818
27.	Number of caudal vertebrae	0.444	0.500
28.	Hemal arch	0.667	0.875
29.	Entepicondylar foramen	[0.500]	[0.833]
30.	Supertrochlear foramen	[0.333]	[0.750]
31.	Proximal extent of fifth metatarsal	[1.000]	[1.000]
32.	Trochlear process of calcaneum	[0.500]	[0.800]
33.	Furring of soles of feet (pes)	0.333	0.636
34.	Ear (pinna) size	0.300	0.462
35.	Mammae number	0.400	0.700
36.	Bacular complexity	[0.333]	[0.500]
37.	Preputial glands	0.400	0.500
38.	Gallbladder	0.333	0.778
39.	Gastric epithelium I	0.750	0.667
40.	Gastric epithelium II	1.000	1.000

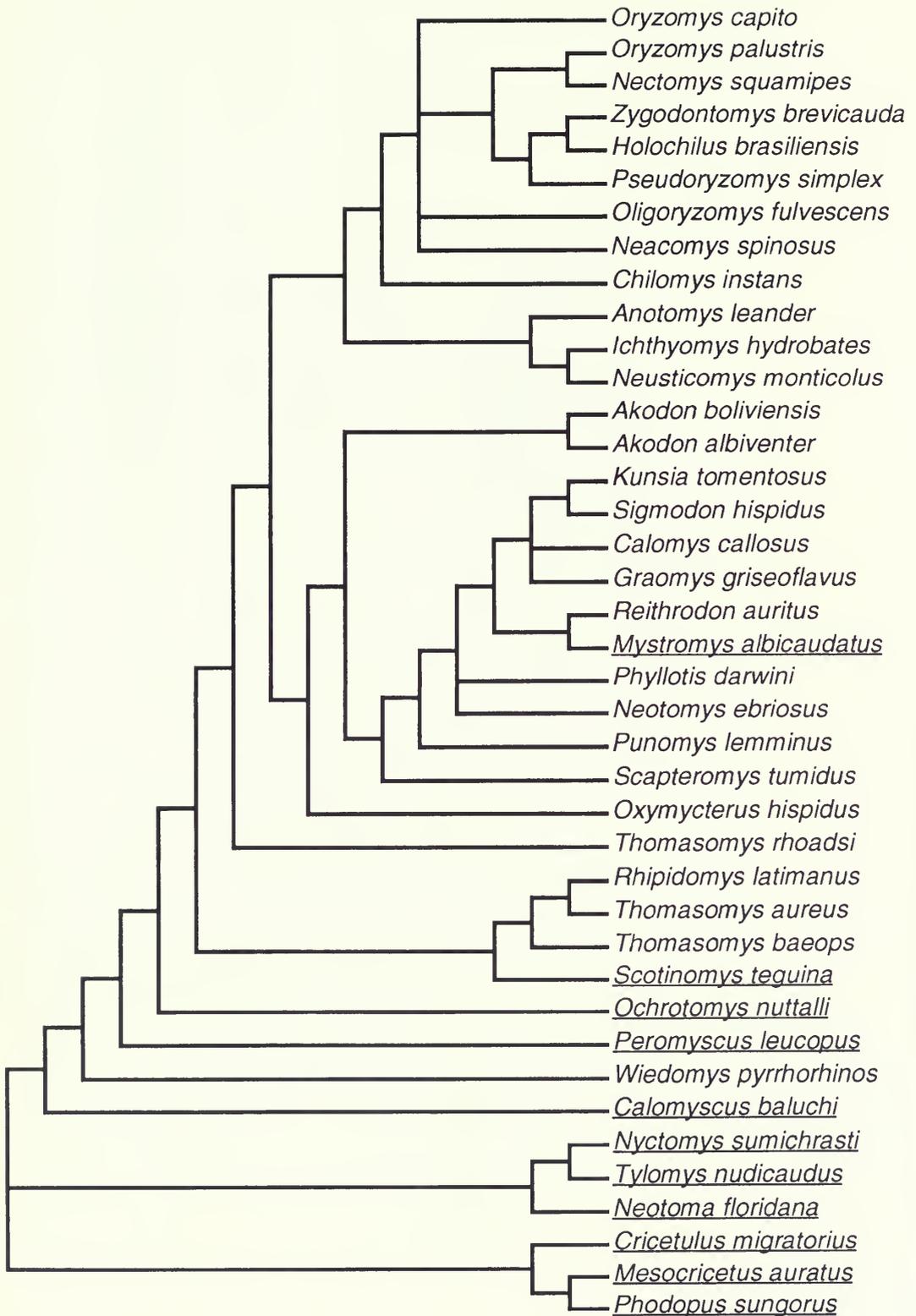
^a Character indexes calculated over the sigmodontine portion only of the strict consensus tree in Figure 19.

^b Indexes in brackets (e.g., [0.500]) were calculated over the entire tree, including outgroups, because the character was invariant or uninformative within the sigmodontines.

= 0.33, and RI = 0.63. The CIs are at or slightly below the values expected for the number of taxa, based on a survey of other published studies (Archic, 1989; Sanderson & Donoghue, 1989), and well within the range of surveyed studies. All analyses designated the Old World "cricetids" as the outgroups. Table 7 lists CIs and RIs for each character.

The tree in Figure 19 was produced by including a dummy variable: all outgroups coded as "0," all sigmodontines coded as "1." The dummy variable had to be weighted four times the standard weight

before a monophyletic Sigmodontinae was among the most-parsimonious trees. When no dummy variable was included, the trees in Figure 20 resulted (strict consensus of 18 trees, each 282 steps long). The deviations from monophyly in Figure 20 are the inclusion of the South African *Mystromys* within the phyllotines as the sister taxon to *Reithrodon*, the placement of the neotomine-peromyscine *Scotinomys* at a basal position within the sigmodontines, and *Wiedomys* dropping down into the neotomine-peromyscines. Only one step is needed to remove *Scotinomys* from the sig-



modontines and place *Wiedomys* among them, but all four steps are needed to remove *Mystromys*. The seemingly unlikely placement of *Mystromys*, both on conventional systematic and biogeographic grounds, leads me to prefer the weighted tree with the monophyletic Sigmodontinae. Characters that unequivocally support a monophyletic Sigmodontinae given the outgroup topology in Figure 19 (*Scotinomys* as the sister-group to Sigmodontinae) include complex baculum and entoglossal process of hyoid absent. Other possible sigmodontine synapomorphies given different outgroup topologies (e.g., monophyletic neotomine-peromyscines) would include dual articulation of the first rib with the transverse processes of the seventh cervical and first thoracic vertebrae, fifth metatarsal not posterior to cuboid/calcaneum articulation, entepicondylar foramen of humerus absent, supertrochlear foramen of humerus present, and a gap between trochlear process and articular facet of the calcaneum.

Neither the weighted nor the unweighted analyses show a monophyletic Neotominae, but they do strongly support a monophyletic tylomyine group *sensu* Carleton (1980) and Reig (1984), *Nyctomys* and *Tylomys*. This pairing is found in 92% of bootstrap replicates (Fig. 21) and is supported by the following putative synapomorphies: no parietal/occipital contact, squamosal fold, preputial glands present, overhanging supraorbital, subquamosal foramen absent, stapedia branch of the carotid artery reduced or absent, more than 30 caudal vertebrae, and gallbladder absent. All these character states are found in *Ototylomys* as well except a squamosal fold; the presence of preputials and gallbladder in *Ototylomys* is unknown. *Otonyctomys* was not examined. Absence of subquamosal foramen and reduction of carotid circulation can also be found in *Neotoma*. Four steps are required to collapse the branch joining the tylomyines and forming a trichotomy with *Neotoma*.

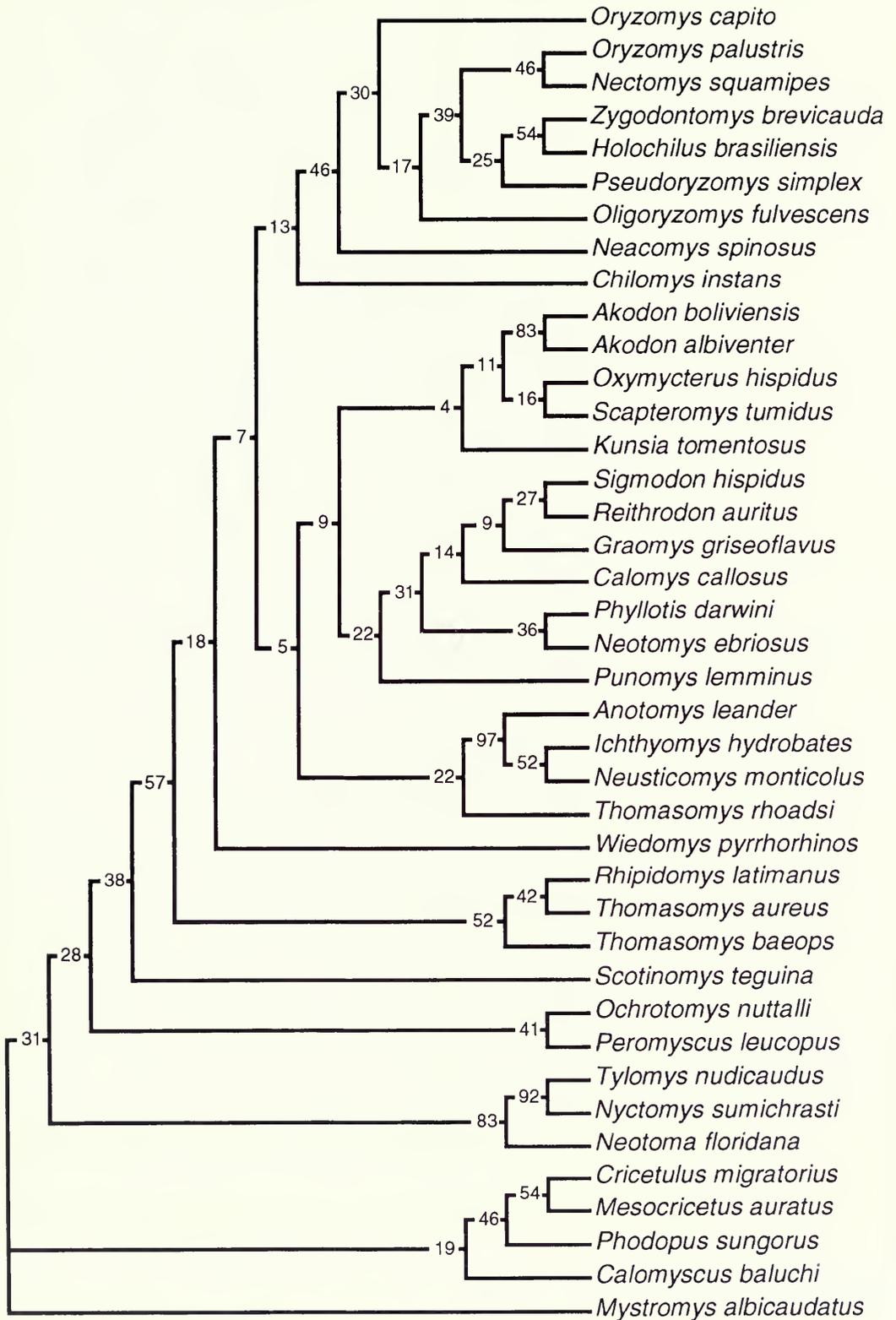
The phylogenetic analysis identifies two well-defined branches within the Sigmodontinae tree, ichthyomyines and the oryzomyines *sensu* Voss and Carleton (1993), including the tetralophodont genera *Holochilus*, *Pseudoryzomys*, and *Zygodon-*

tomys (Fig. 19). Monophyly of the ichthyomyines has already been established (Voss, 1988), but this study more directly tests monophyly by placing the ichthyomyines in a broader cladistic analysis. In the bootstrap analysis weighted to favor sigmodontine monophyly (Fig. 21), Ichthyomyini is found in 97% of replicates. Trees five steps longer than the most-parsimonious trees (with or without a dummy variable) must be examined before a nonmonophyletic Ichthyomyini is found. Ichthyomyine monophyly is supported by nasals that extend posterior to lachrymal, masseteric tubercles, small or very small pinnae, and reduced gastric glandular epithelium. Sensitivity analyses demonstrate that, although the ichthyomyines are most commonly placed in a clade with other tetralophodont groups, the akodontines and phyllotines, the sister-group to the ichthyomyines is sometimes the oryzomyines or a thomasomyine. It appears that the ichthyomyines occupy a relatively basal position in the sigmodontine tree.

The oryzomyine taxa, exclusive of the thomasomyines, form the second major clade. Supporting the oryzomyines *sensu stricto* are the putative synapomorphies of nasals extending posterior to lachrymal (except in some *Oryzomys*), alisphenoid strut absent, long palate (except in *Holochilus*), eight or more mammae, 12 thoracic vertebrae (except in *Neacomys*), fewer than 36 caudal vertebrae, hemal arch present, and gallbladder absent. The distribution of some of these potentially diagnostic characters is explored in greater taxonomic detail in Table 6. The most-parsimonious trees given sigmodontine monophyly (Fig. 19) place *Wiedomys* as the sister-group to the oryzomyines. In this hypothesis, absence of the alisphenoid strut, 12 ribs, and possibly presence of the hemal arch (weakly developed in *Wiedomys*) would be synapomorphies of the more inclusive clade. However, the bootstrap consensus places *Chilomys* as the sister taxon to Oryzomyini, indicating that the sister-group to Oryzomyini is unresolved. Two additional steps are needed to draw the putatively basal oryzomyines (*Oligoryzomys* or *Neacomys*) out of the oryzomyines. Three additional steps are needed to disrupt oryzomyine monophyly when

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FIG. 20. Strict consensus cladogram of the 28 equally most-parsimonious trees of the South American Sigmodontinae, without a dummy variable. Overall length for each tree is 282 steps. The South African-endemic *Mystromys* is placed among the phyllotines, and the neotomine-peromyscine *Scotinomys* is placed near the base of the sigmodontines. Outgroup taxa are underlined.



Oligoryzomys and *Neacomys* are excluded from the analysis.

The root of the sigmodontine tree is placed within the thomasomyines, which appear to be highly paraphyletic. However, the bootstrap percentages are lowest for this region of the tree (Fig. 21). This analysis suggests that *Thomasomys* is also paraphyletic and its members occupy basal positions on the tree. Four additional steps are needed to join *T. rhoadsi* with its congeners in a monophyletic *Thomasomys*. However, placement of the sigmodontine root is unstable because most characters that are variable within the sigmodontines are also variable among the outgroups. The result of this is that character polarities determined by outgroup criteria are only as accurate as the outgroup topology. Sensitivity analyses (not illustrated) demonstrated that shifts in outgroup relationships had significant impact on the placement of the sigmodontine root. Among these various analyses, the topological relationships within the sigmodontine portion of the unrooted network were relatively stable. It was the placement of the root within that network that was most unstable. Thus, if the neotomine-peromyscines and tylomyines were sister-groups and the Old World "cricetids" were paraphyletic, then the morphology of the ancestral sigmodontine would most closely resemble the Old World "cricetids," and the sigmodontine root would be placed just outside the phyllotine group. If the tylomyines were the sister-group to the sigmodontines, then the root would be placed near the base of the oryzomyines. In most rooting alternatives, though, the thomasomyines were still paraphyletic and generally basal.

The remaining branch with the most character support is that consisting of akodontines, scapteromyines, phyllotines, *Sigmodon*, and *Punomys*, and is the sister-group to the ichthyomyines in Figure 19. I will refer to it by the shorter name of the tetralophodont tribal-group because it is comprised by most of the taxa hypothesized by Hershkovitz to be derived from tetralophodont stock (i.e., lacking a complete mesolophostyle). The issue of *Sigmodon* is addressed separately below. This clade is supported by the following putative synapomorphies, as hypothesized from the mapping of character transformations on the tree: incisive foramina extending to the molars, deep

zygomatic notch, reduction to fewer than 30 caudal vertebrae (with hypothesized subsequent increase), and eight or more mammae. If the ichthyomyines are not the immediate sister-group to the tetralophodont tribal-group, then reduction or partial fusion of the mesolophostyle would also be a supporting character. The tetralophodont tribal-group is also generally characterized by the plesiomorphic presence of a gallbladder, a stapedia artery imparting a squamosal groove, moderately haired heels, nonoverhanging supraorbital surface, 13 thoracic rib pairs (with subsequent reduction), no hemal arch, and relatively small M3 (with enlargement among the phyllotines). Bootstrap percentages for this clade are very low (Fig. 21).

Within the tetralophodont tribal-group, Scapteromyini (Hershkovitz, 1966), which includes *Scapteromys* and *Kunsia*, appears polyphyletic, and an Akodontini that includes the oxymycterines (*sensu* Reig, 1987) without the scapteromyines may be either paraphyletic (bootstrap consensus tree) or polyphyletic (most-parsimonious trees). However, only one additional step is needed to be consistent with a monophyletic Akodontini (*Akodon* plus *Oxymycterus*). Two additional steps are needed for a monophyletic Scapteromyini. *Punomys* is placed as the sister taxon to the phyllotines plus *Sigmodon*.

Monophyly of the phyllotines as currently defined is not directly supported. This analysis places *Sigmodon* within the phyllotine radiation. Three additional steps are needed to bring *Sigmodon* down to the immediate sister taxon to the phyllotines. In that topology, *Punomys* is placed as the sister taxon to *Oxymycterus* in an akodontine clade. In the most-parsimonious trees (Fig. 19), *Sigmodon*, *Reithrodon*, and *Neotomys* have the longest branch lengths among the terminal sigmodontine taxa. Characters that support a phyllotine plus *Sigmodon* clade (or a phyllotine clade with *Sigmodon* excluded) include complete loss of the mesoloph, premaxillaries subequal in extent with nasals, large sphenopalatine vacuity, mesopterygoid narrower than parapterygoid, and large pinnae (except *Neotomys*). The clade of *Punomys* plus the phyllotines is supported by a zygomatic arch inserting at a moderate to high position on the rostrum and a moderately long interparietal.

Traditional notions of a Sigmodontini (Reig,

FIG. 21. Majority-rule bootstrap consensus tree (100 replicates) for the Sigmodontinae, including dummy variable weighted to favor sigmodontine monophyly. Numbers indicate percentage of replicates containing the specified clades.

1980) are not supported. The shortest trees that place *Sigmodon* and *Holochilus* as sister taxa are six steps longer than the most-parsimonious trees. Notably, those constrained trees move *Sigmodon* into the oryzomyines while leaving the rest of the tree nearly unchanged. The shortest trees that include a Sigmodontini *sensu* Hershkovitz (1955; *Sigmodon*, *Holochilus*, *Reithrodon*, *Neotomys*) are 11 steps longer. In those alternative trees, the weight of *Reithrodon* and *Neotomys* draws *Holochilus* into a terminal phyllotine branch.

Discussion

Three principal conclusions can be drawn from the sigmodontine analysis. First, the Oryzomyini (Voss & Carleton, 1993), which includes the tetralophodont genera *Holochilus*, *Pseudoryzomys*, and *Zygodontomys*, but which excludes the thomasomyines, is confirmed. Second, the phyllotines are members of a tetralophodont tribal-group that includes the akodontines, scapteromyines, and *Punomys*. Third, the root of the sigmodontines is placed within the thomasomyine group. Monophyly of the Sigmodontinae is indicated given reservations regarding *Mystromys* and *Scotinomys*. Additionally, the monophyly of the Ichthyomyini and Tylomyinae is strongly supported.

A problem for any sigmodontine phylogeny given the current state of muroid systematics is the rooting of the tree. Many workers have taken the position that the oryzomyines or thomasomyines are the basal sigmodontines (Gardner & Patton, 1976; Hershkovitz, 1962, 1993; Reig, 1980, 1986), partially because oryzomyines *sensu lato* are characterized by many traits considered widespread and potentially plesiomorphic among other cricetine or murid rodents. Phyllotines have been considered by neontologists to be highly derived (Hershkovitz, 1962; Reig, 1986). However, Jacobs and Lindsay (1984) concluded that phyllotines were primitive among sigmodontines, based almost entirely on the identification of *Bensonomys*, the oldest putatively sigmodontine fossils, as a subgenus of *Calomys*. Their hypotheses of primitive traits among sigmodontines are merely those of *Bensonomys* (Jacobs & Lindsay, 1984, Table 2) but are limited to molar and lower mandible characters, the only characters observable from the fossils. In contrast, this study found few dental characters (only three were included) that were informative at the tribal to subfamily level, and rooting of the

sigmodontine radiation based on a few dental characters seems prone to mislead. Additionally, most of the *Bensonomys* fossils cannot be a *Calomys* as the genus is currently defined (Steppan, 1993); they possess mesolophs that are entirely absent among all extant *Calomys* and in the sister-group to *Calomys*, the remaining phyllotines. This argument does not preclude the possibility that prephyllotine ancestors or their relatives may have possessed reduced mesolophs.

The placement of *Chilomys* is unstable, and in the past it has been placed either with the thomasomyines (Hershkovitz, 1966a; Voss, 1991) or with the oryzomyines *sensu stricto* (Reig, 1980, 1986; Voss & Linzey, 1981). The proper status of the Wiedomyini is difficult to assess from this analysis, but *Wiedomys* does not appear to be far derived from a basal "thomasomyine" grade.

Voss (1993) argued that formally maintaining genera in the tribe Thomasomyini was unjustifiable owing to their collective lack of unifying, apomorphic characters and the inability to assign individual "thomasomyine" genera to other demonstrable monophyletic groups. As an alternative, he recommended referring to thomasomyines formally as a "plesion," citing Wiley (1981) for comparison, to emphasize that they share primitive attributes. Wiley (1981, p. 219) explicitly reserved the nonranked category "plesion" for fossil taxa, allowing them to be classified with Recent taxa without revising established classifications for either the fossil or Recent taxa.

The study strongly supports a tylomyine group that includes *Nyctomys*, *Tylomys*, and *Ototylomys* (and presumably *Otonyctomys*, which was not examined). While this study groups the tylomyines with *Neotoma*, other studies indicate that the tylomyines are basal members of a New World radiation with no clear affinities to either the sigmodontines or neotomine-peromyscines (Carleton, 1980; Sarich, 1985; Haiduk et al., 1988; Catzeflis et al., 1993). Using G-banded chromosomes, Haiduk et al. (1988) suggested that *Nyctomys* was a basal member of a neotomine radiation after its separation from the South American sigmodontines. However, because the sigmodontines available for comparison constituted a taxonomically biased and incomplete sample, including only oryzomyines and *Sigmodon*, suggested relationships to the sigmodontines as a whole must be tentative at best. The monophyly and basal phylogenetic position of the tylomyines should be recognized formally. Tribal status as the Tylomyini (Carleton, 1980) would be most in keeping

with the results of this study (tylomysines as sister-group to *Neotoma*), but the available molecular studies suggest that elevating the tylomysines to an equal status with the sigmodontines and neotomine-peromyscines as the subfamily Tylomyinae (*sensu* Reig, 1984) would be more generally consistent.

This analysis is generally at odds with the relationships and evolutionary tendencies in chromosomal evolution proposed by Gardner and Patton (1976). They hypothesized that chromosome change was unidirectional, dominated by Robertsonian fusions that reduced diploid number. Partially as a consequence of their model, the genus *Oryzomys* was proposed to be the stem group from which all sigmodontines arose. This analysis clearly shows that *Oryzomys* is a member of a derived clade separated from all other sigmodontine tribes. Nor is *Oryzomys* the basal member of the oryzomyine clade, although the genus as currently constituted is probably not monophyletic. Gardner and Patton (1976) also hypothesized that *Holochilus* was derived from a phyllotine stock; it is clearly an oryzomyine. Akodontines were diagrammed as independently derived from *Oryzomys* (Gardner & Patton, 1976, Fig. 10), while this study indicates that the akodontines are related to the phyllotines and scapteromyines. Even a cursory mapping of diploid numbers on the trees from this study indicates that Robertsonian fusion cannot be used as the exclusive model of chromosomal evolution in sigmodontines. Gardner and Patton's model (which has also been proposed by Bianchi et al. [1971] and Pearson and Patton [1976]) has been salutary, but it has unfortunately sometimes been evoked as a phylogenetic axiom to polarize phylogenetic relationships (e.g., Vitullo et al., 1990).

The previous discussion has referred to *Sigmodon* as an entity separate from the phyllotines despite its placement in Figure 19. There are three reasons for believing that the results of the phylogenetic study shown in Figure 19 are misleading in regard to *Sigmodon*. First, three independent molecular data sets place *Sigmodon* outside any clade formed by the remaining sigmodontines. DNA hybridization places *Sigmodon* outside a clade that includes *Oryzomys*, *Zygodontomys*, *Akodon*, and *Phyllotis* (Catzeflis et al., 1993). Protein immunological distances place *Sigmodon* as the outgroup to all the other sigmodontines (Sarich, 1985), while the rest of the immunological tree (Fig. 1) is in general agreement with this study. Electrophoretic allele data analyzed phenetically

(Spotorno, 1986) (Fig. 5A) and cladistically (Fig. 5B, reanalysis of data in Spotorno, 1986) place *Sigmodon* among the North American neotomine-peromyscines. Second, when *Sigmodon* is included in the phyllotine data set (results not shown), three discordant alternative placements for *Sigmodon* are represented among the most-parsimonious trees. Sixty percent of most-parsimonious trees include *Sigmodon*, with 27% placing *Sigmodon* as the sister-taxon to the phyllotines plus akodontines and 13% placing *Sigmodon* as the basal oryzomyine. The last two alternatives push *Graomys* to a basal position among the phyllotines, in contrast to its typical terminal position (Steppan, 1993). The placement of *Sigmodon* among the phyllotines in the sigmodontine analysis may be due to the taxa sampled and the characters included. For example, three of the five phyllotines in this sigmodontine analysis possess 12 ribs (*Calomys*, *Graomys*, *Reithrodon*), which is most-parsimoniously hypothesized as a synapomorphy joining them with *Sigmodon*. However, this results from the improbable sampling of three independent rib losses from the both common and plesiomorphic phyllotine condition (Steppan, 1993). Likewise, *Sigmodon*, *Graomys*, and *Reithrodon* are associated in this analysis by the presence of an alisphenoid strut, but the strut appears to be independently evolved in *Graomys* and *Reithrodon* (Steppan, 1993). *Sigmodon* possesses the posteriorly divergent, ledged supraorbital region found in some oryzomyines, *Andalgalomys*, and *Graomys*, but that is very different from the narrow and vertically ridged supraorbitals of *Reithrodon* and *Neotomys*. Third, *Sigmodon* lacks an angled premaxillo-maxillary suture, a synapomorphy that joins *Reithrodon*, *Neotomys*, and *Euneomys* and is unique to them (Steppan, 1993), and also lacks grooved incisors (except *S. alstoni*), another putative synapomorphy of the *Reithrodon* group.

Sigmodon and some *Holochilus* are apparently the only sigmodontines other than *Calomys* with more than eight mammae. This would seem to support the Sigmodontini *sensu* Reig (1980). However, the remaining characters do not support the Sigmodontini, and this analysis places *Sigmodon* and *Holochilus* far apart on the tree (Fig. 19) and requires an additional six steps to unite them. Additionally, albumin immunological cross-reactions between *Sigmodon* and *Holochilus* are much lower than in other intratribal comparisons (Sarich, 1985).

On the basis of the results here, and consistent

with the frequently suggested but rarely acted upon observations of previous workers (Gardner & Patton, 1976; Hooper & Musser, 1964; Sarich, 1985; Voss & Myers, 1991), *Holochilus* should be removed from the Sigmodontini, leaving only *Sigmodon*. These various analyses disagree so strongly on the position of *Sigmodon* that it seems best to draw no conclusions at this time on its relationships. Thus, if Sigmodontini is retained as a separate tribe, it should be considered Sigmodontinae *incertae sedis*, or even Muridae *incertae sedis*.

An interesting series of patterns is developed with characters that involve gain or loss, and in particular gain or loss of discrete structures, as opposed to topological conformation of parts. Among characters that show significant homoplasy (i.e., multiple observations of evolutionary transformations), structures that are lost generally are not regained. Gallbladders, stapedial branch of the carotid artery, mesoloph(-id), and thoracic ribs all show a bias toward loss (or bias against reacquisition) based on character mapping and optimization (accelerated transformation, ACCTRAN, and delayed transformation, DELTRAN, options were both used). Unless otherwise noted, character transformations discussed below were hypothesized using both optimizations or by ACCTRAN, which *disfavors* the observation of directional bias in character transformations. Across the entire tree (and other records; Voss, 1991), the gallbladder is lost nine times (oryzomyines, *Ichthyomys*, *Rhipidomys*, *Ochrotomys*, tylomyines, *Cricetulus*, *Akodon cursor*, *Geoxus valdivianus*) but never regained. Mesolophs are reduced at least two times (tetralophodont tribal group plus ichthyomyines, ancestor of *Holochilus*, *Pseudoryzomys*, and *Zygodontomys*) and entirely lost three to four times (phyllotines, some ichthyomyines, *Sigmodon*, *Holochilus*), but (depending on phylogenetic resolution) only gained to a poorly developed condition in *Anotomys*, maybe some akodontines not included here, and originally in an ancestor to the sigmodontines. The stapedial branch of the carotid artery shows at least seven reductions or losses among sigmodontines (oryzomyines, *Thomasomys/Rhipidomys* clade, some ichthyomyines, *Reithrodon*, *Sigmodon*, *Neotomys*, *Chilomys*), but, depending on relationships within the oryzomyines and under ACCTRAN optimization, only three reversals (*Neacomys*, *Neusticomys*, *Zygodontomys*). Under DELTRAN optimization, there are nine reductions in carotid circulation and only one reversal (*Zygodontomys*).

Similarly, ribs show six losses (given phyllotine phylogeny of Steppan [1993] and data in Table 5; *Sigmodon*, *Calomys*, *Graomys*, *Reithrodon*, *Rhipidomys*, and oryzomyines plus *Wiedomys*) versus two gains (*Anotomys* and *Neacomys*).

In contrast, mammae number shows at least five increases (sigmodontines, tetralophodont tribal-group, oryzomyines, *Calomys*, *Holochilus*, *Sigmodon*) versus one to two reductions (*Scotinomys*, tylomyines plus *Neotoma*). Given this tree topology, alisphenoid strut (four gains, four losses) and caudal vertebrae (approximately five gains, five losses) do not show a bias. Somewhat surprisingly, the quantitative character pinna size shows seven to eight reductions versus one (phyllotines) to three (*Neusticomys*, *Thomasomys baeops*) enlargements, depending on resolution of polytomies. The preponderance of pinna reduction over enlargement may in part be an artifact of the particular selection of character states.

Phyllotine Monophyly

Because of the placement of *Sigmodon* within the phyllotines, this study does not provide strong support for the monophyly of the tribe Phyllotini. However, if the molecular studies are correct in placing *Sigmodon* in a basal position among the sigmodontines, then its placement among the phyllotines in this study may be due to convergence and the absence of any taxa along the *Sigmodon* lineage to provide evidence for character transformations, thus leaving *Sigmodon* with a very long branch length. Very long branches due to insufficient taxonomic sampling can lead to erroneous groupings (Felsenstein, 1978; Huelsenbeck & Hillis, 1993). Forced removal of *Sigmodon* does not affect the remaining hypothesized relationships. Therefore, I define the Phyllotini as the common ancestor of the following genera and all its descendants: *Andalgalomys*, *Andinomys*, *Auliscomys*, *Calomys*, *Chinchillula*, *Eligmodontia*, *Euneomys*, *Galenomys*, *Graomys*, *Irenomys*, *Neotomys*, *Phyllotis*, and *Reithrodon*. *Punomys* does not appear to be a phyllotine, but in a taxonomically more focused study (Steppan, 1993) *Punomys* is equivocally associated with some phyllotine taxa. I therefore agree with the conclusions of Olds and Anderson (1989) on the content of Phyllotini, with the single exception of not including *Punomys*. Diagnostic synapomorphies for the Phyllotini are moderate or large pinnae (> 0.15 head and body length), parapterygoid fossa rela-

tively broader than mesopterygoid fossa, very open sphenopalatine vacuities, complete loss of the mesoloph, posterior extensions of premaxillaries and nasals subequal, and (except *Calomys*) two pairs of preputial glands. In contrast, the following character states hypothesized by Olds and Anderson (1989) to be phyllotine synapomorphies instead appear to be plesiomorphic: hairy heel, palate long, incisive foramina long, supraorbital region never evenly curved in cross-section, interparietal well developed, zygomatic notch deeply excised, teeth tetralophodont (which includes vestigial mesolophs [Olds & Anderson, 1989]), and M3 more than half the length of M2. A formal diagnosis is presented in the Taxonomy section.

Although most recent studies have excluded *Pseudoryzomys* from the phyllotines (e.g., Olds & Anderson, 1989; Voss & Myers, 1991; Voss & Carleton, 1993), others have included it (Braun, 1993; Reig, 1986). I agree with Voss and Carleton (1993) on moving *Pseudoryzomys* to the Oryzomyini. Other oryzomyines (e.g., *Microakodontomys*, *Oligoryzomys* sp., Hershkovitz, 1993) exhibit reduction and loss of the mesoloph(-id) in association with the transition from forest to grassland and scrub communities (Hershkovitz, 1993). Braun (1993) concluded from a cladistic analysis that *Pseudoryzomys* is either the basal phyllotine or the sister taxon to the phyllotines. Her study included two oryzomyine and one thomasomyine species in the outgroups, but these were used to define ancestral states and were not included in the actual numerical analysis. Thus, intentionally or not, *Pseudoryzomys* was assumed *a priori* to be a member of a clade that included the phyllotines and the other outgroups, two species of *Akodon*. With only two closely related *Akodon* remaining as outgroups to the phyllotines, the analysis could not test the tribal relationships of *Pseudoryzomys* or the monophyly of the phyllotines. This analysis demonstrates that *Pseudoryzomys* is unrelated to the phyllotines: at least 10 additional steps are required to place it as a basal phyllotine or among the tetralophodont tribal-group.

Phylogenetic Relationships within Phyllotini

Results

As should be expected, the results of this analysis conform closely to those produced earlier

(Steppan, 1993), using nearly the same data set (see Materials and Methods). While the most-parsimonious trees place *Punomys* in a clade with *Andinomys* and *Irenomys* (Fig. 22, strict consensus), trees only one step longer place *Punomys* outside the phyllotines (Fig. 23, 80% majority rule consensus). In Steppan (1993), these alternative topologies were equally parsimonious, and the nonphyllotine hypothesis for *Punomys* was preferred. The 200 replicate bootstrap analysis with this data set (Fig. 24) also places *Punomys* as the sister taxon to the phyllotines, the same as in the sigmodontine analysis. The root was placed between *Thomasomys* and the oryzomyines by designating *Thomasomys* as the outgroup.

Details of character support for specific nodes can be found in Steppan (1993). Differences between the two sets of analyses and principal areas of congruence will be highlighted here. Selected nodes are labeled on Figure 23 for references in the text.

This analysis results in 22 equally most-parsimonious trees, each 763 steps long, with a CI of 0.22 and an RI of 0.55 (Fig. 22, strict consensus). Excluding the outgroups, the trees are 525 steps long, CI = 0.29, RI = 0.57. Both sets of CIs are at the mean of the observed range of values for this many taxa (Archie, 1989) or somewhat below the "expected" value of 0.34 for 47 taxa (Sanderson & Donoghue, 1989). In each of the 121 equally most-parsimonious trees that do not include *Punomys* within the phyllotines (Fig. 23, 80% majority rule consensus), the respective values are 764 steps long, CI = 0.22, RI = 0.55 overall, and 498 steps long, CI = 0.30, RI = 0.58 excluding outgroups. Both sets of trees are of equal length when *Punomys* is pruned from the trees. Based on the arguments from the sigmodontine analysis and in Steppan (1993), the alternative hypothesis of a nonphyllotine *Punomys* will form the basis for the remaining analyses and discussion, as well as calculating CIs and RIs for individual characters (Table 8).

The differences between the preferred hypothesis from this analysis and Steppan (1993, Fig. 1) are minor and limited to several collapsed branches due to the greater number of trees in this analysis and the exclusion of two taxa (*species nova*, northern populations of *Andinomys edax*) included in the earlier study. The major difference between the two studies is greater character support in this analysis as reflected in higher average bootstrap percentages (46% in Fig. 24 versus 41% in Steppan [1993, Fig 3]).

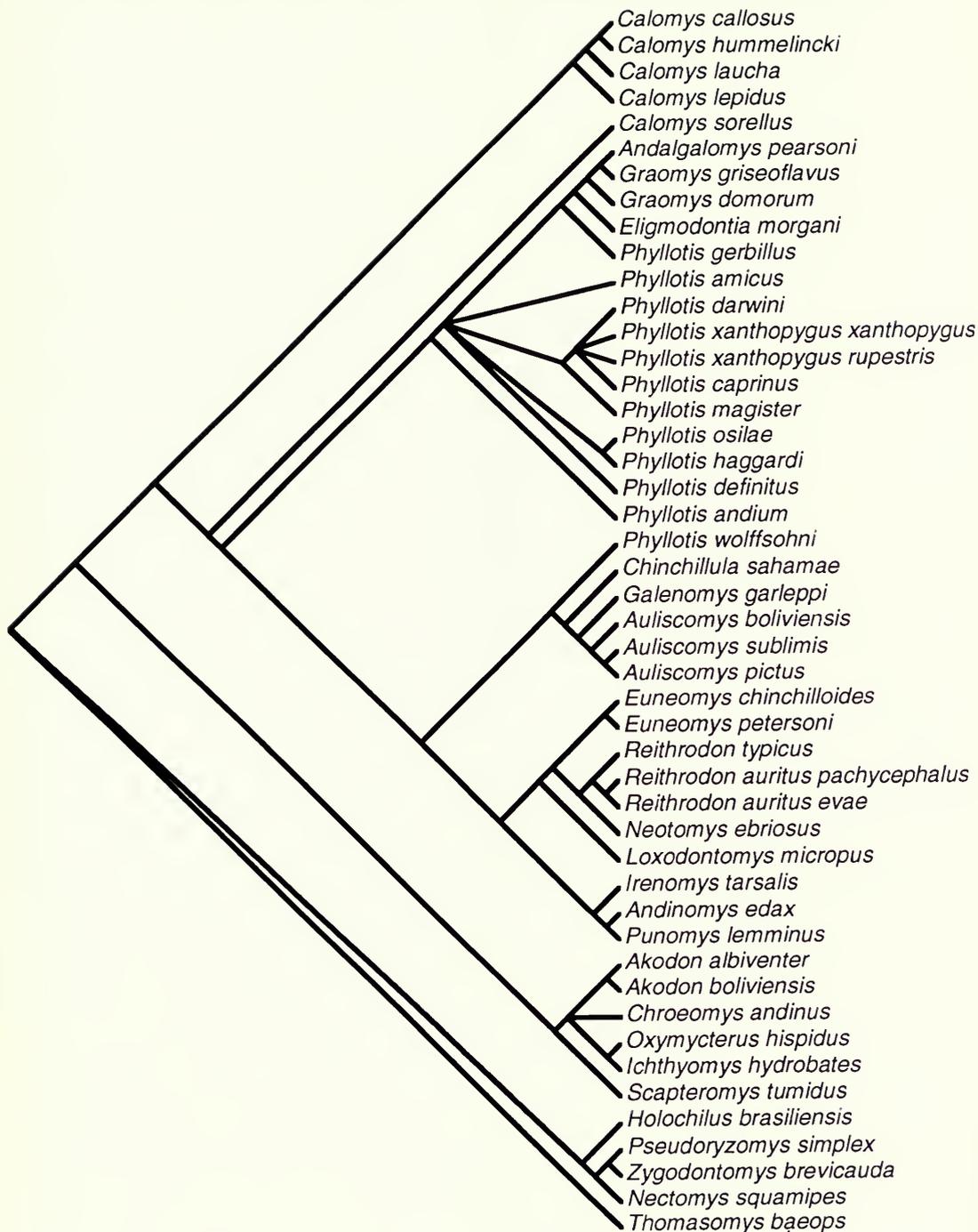


FIG. 22. Strict consensus cladogram of 22 equally most-parsimonious trees for the Phyllotini (763 steps long overall, CI = 0.22, RI = 0.55). *Thomasomys* and the four oryzomyine taxa (*Holochilus*, *Nectomys*, *Pseudoryzomys*, *Zygodontomys*) were designated as outgroups. *Punomys* is placed among the phyllotines with *Andinomys* and *Irenomys*.

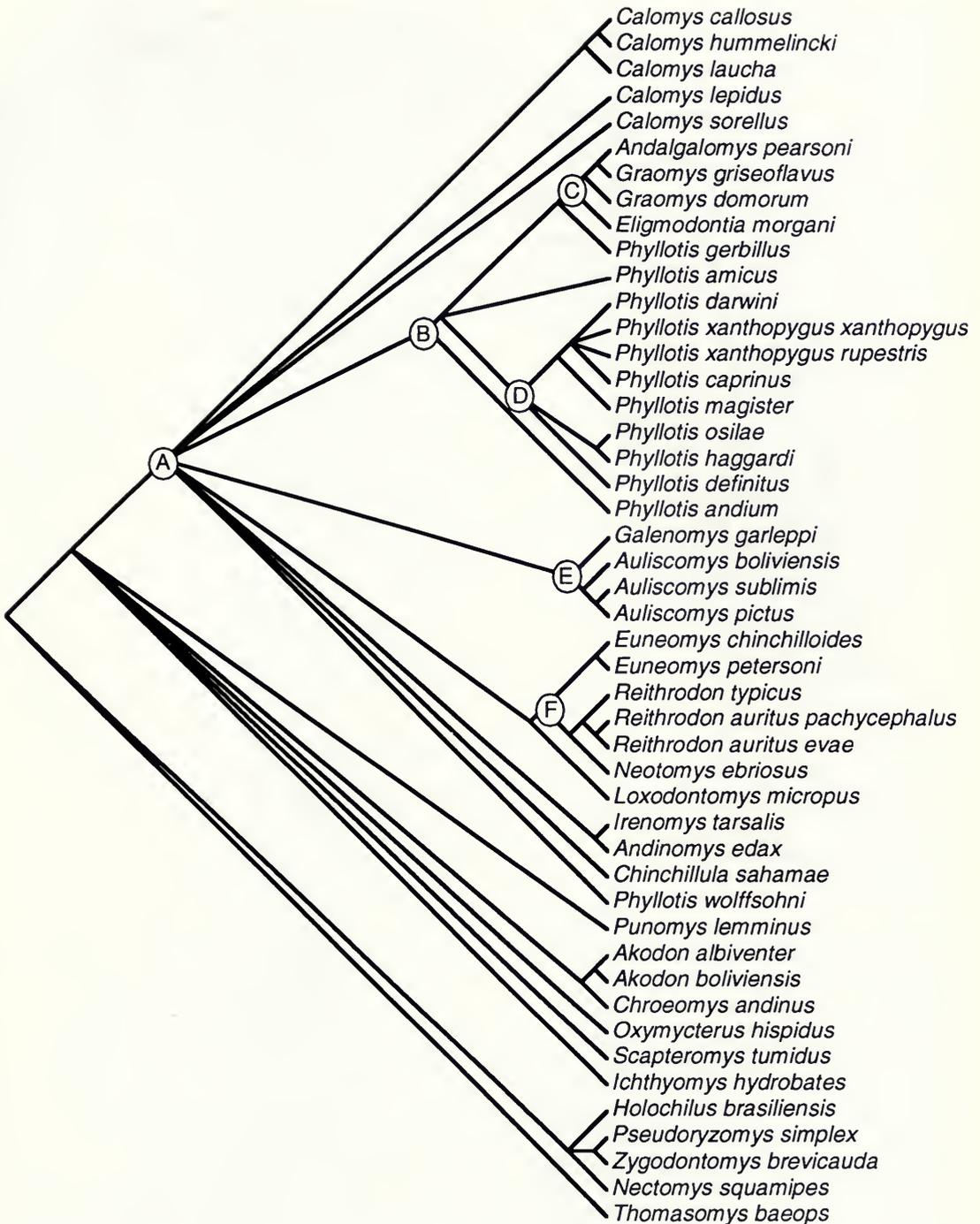


FIG. 23. Eighty percent majority-rule consensus tree of 121 equally most-parsimonious trees wherein *Punomys* is not a phyllotine. Each tree is one step longer than the most-parsimonious overall (764 steps long overall; excluding outgroups, each tree is 498 steps long, CI = 0.30, RI = 0.58). This topology represents the preferred hypothesis of phylogenetic relationships among the phyllotines. Labeled nodes are referred to in the text.

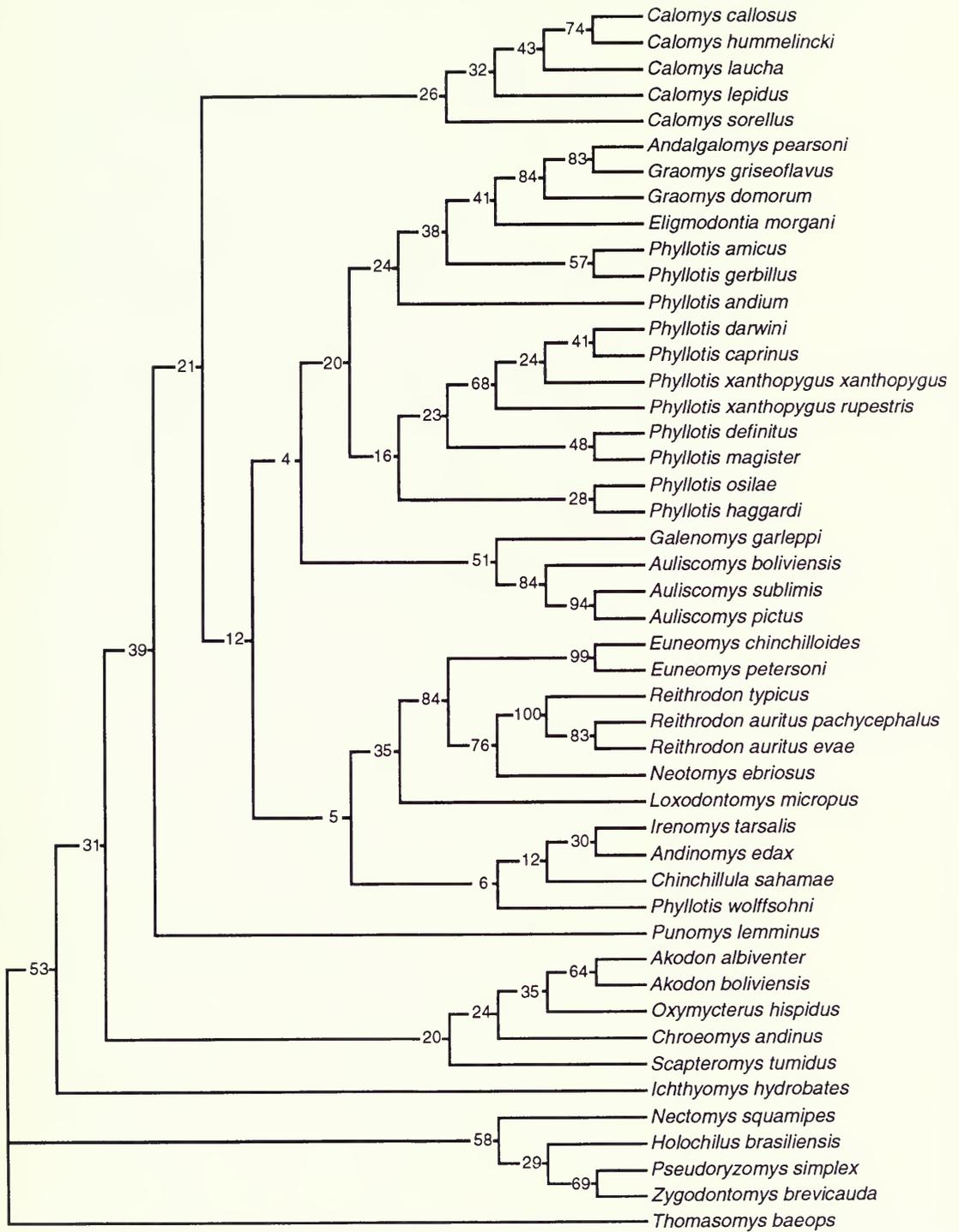


FIG. 24. Majority-rule bootstrap consensus tree (200 replicates) for the Phyllotini. Numbers indicate percentage of replicates containing the specified clades.

Calomys is paraphyletic in the majority of the most-parsimonious trees with *C. sorellus* as the sister taxon to the remaining phyllotines. The status of *Calomys sorellus* and *C. lepidus* is unresolved. Support for paraphyly (or monophyly) of *Calomys* is weak: the bootstrap tree (Fig. 24) indicates a monophyletic *Calomys* but in only 26% of bootstrap replicates. The placement of *C. sorellus* with the remaining phyllotines is supported by a ventral pair of preputial glands (97), loss of the parastyle/anteroflexus M1 (12), more than 25 caudal vertebrae (80), and long interparietal (56).

The basal nodes of the remaining phyllotines are unresolved in the preferred hypothesis (Fig. 23) but are resolved in the analysis with *Punomys* in the ingroup (Fig. 22) and in the previous analysis (Steppan, 1993). All analyses reveal four clades among the taxa terminal from *Calomys*. These include a *Phyllotis/Graomys* clade (node B), an *Auliscomys* group (node E), a clade including *Reithrodon* and *Loxodontomys* (node F), and the sister taxa *Andinomys* and *Irenomys*. The last three clades form part of the sister-group to the *Phyllotis/Graomys* clade in Figure 22. This clade, including *Reithrodon* and *Auliscomys*, is much more highly differentiated, as reflected in the greater generic diversity as currently recognized (nine genera versus four).

The bootstrap consensus tree joins *Phyllotis sensu stricto* with the clade containing *Graomys* and *Eligmodontia*, but this node is not fully resolved in the consensus of the most-parsimonious trees (Fig. 23, above node B). In any case, *Phyllotis* is shown to be polyphyletic. In addition to the core *Phyllotis* clade (node D), other species currently included in *Phyllotis* are basal members of clades with *Eligmodontia* and *Graomys* (*P. amicus*, *P. gerbillus*), *Auliscomys* and *Reithrodon* groups (*P. wolffsohni*), and a more inclusive clade (node B, *P. andium*). Bootstrap percentages for all these groupings are low, however, as *Phyllotis* occupies the most poorly resolved region of the tree. Eight additional steps are needed for a monophyletic *Phyllotis*. Furthermore, five additional steps are needed just to bring *andium* and *wolffsohni* into a *Phyllotis* clade while still leaving *amicus* and *gerbillus* at the base of the *Graomys* clade. Characters supporting the inclusion of *P. wolffsohni* at the base of the *Reithrodon* and *Auliscomys* groups include a nonlinear, "Y"- or "comma"-shaped fissure in the upper incisors (3), premaxillaries terminating behind the anterior edge of the incisors (37), and subequal mesopterygoid and parapterygoid fossae widths (64). Sensitivity analyses in-

dicate that despite low bootstrap percentages, *Phyllotis sensu stricto* (node D) is moderately stable. *Phyllotis sensu stricto* is supported by a moderate to large distal baculum (93) and a series of homoplasious characters.

The highest bootstrap percentage for any *Phyllotis* node that is also found in Figure 23 is 68%, for the clade consisting of *P. darwini*, *P. caprinus*, and the two subspecies of *P. xanthopygus*. Character support for this *xanthopygus* species-group is principally provided by three phallic characters: hooks on the lateral mounds (95), dorsal knobs on the lateral mounds (96), and a large distal baculum relative to proximal baculum (93). The bootstrap percentage is 48% for the clade of *P. magister* and *P. definitus*, two very restricted and geographically distant taxa that had been considered conspecific by Pearson (1958), but *P. magister* is placed as the sister-species to the *xanthopygus* species-group in the most-parsimonious trees (Figs. 22, 23). Specific character support for sister-species status is weak but includes nasals slightly broader than minimum interorbital distance (48, CI = 0.17 overall, but character state unique within the *Phyllotis* clade) and pectoral streaks (91, CI = 0.17).

The *Graomys/Andalgalomys* clade is placed as the sister-group to *Eligmodontia* (node C), though this grouping is not as well supported as the *Graomys/Andalgalomys* clade in the bootstrap tree. *Phyllotis gerbillus* and *P. amicus* next join successively to this group in the shortest trees (Fig. 23) or as a sister clade in the bootstrap consensus tree (Fig. 24). This more inclusive clade is supported by a posteriorly divergent supraorbital (50) and premaxillaries protruded well anterior to the incisive plane (37).

The clade consisting of *Graomys* and *Andalgalomys* is supported by orbital wings of the presphenoid posterior to maximum constriction of the presphenoid (69), a small but distinct zygomatic spine (43), a sharply ridged, overhanging supraorbital region (50), a laterally appressed stapedial spine (59), and 12 ribs (79). Paraphyly of *Graomys* with respect to *Andalgalomys* is strongly indicated as *G. griseoflavus* and *A. pearsoni* appear as sister-species. This pairing is found in 83% of bootstrap replicates and is supported by no hypoflexus reduction M3 (23), no posterior shift of mesoflexus M3 (25), fusion of opposing flexi M3 (31), and flattening of hamular process (60). Four additional steps are needed for a monophyletic *Graomys*, as the sister taxon to *Andalgalomys*.

Auliscomys pictus, *A. sublimis*, *A. boliviensis*, and *Galenomys* together compose the *Auliscomys* group

TABLE 8. Consistency and retention indexes for phyllotine characters.

Number	Character name	CI ^a	RI ^a
1.	Incisor grooves	0.444	0.762
2.	Incisor procumbency	0.286	0.500
3.	Upper incisor dentine fissure	0.333	0.733
4.	Labial root of M1	0.286	0.500
5.	Labial root of M1	1.000	0/0
6.	Molar roots of M3	0.286	0.286
7.	Labial root of m1	0.333	0.333
8.	Molar roots of m2	0.143	0.333
9.	Molar roots of m3	0.167	0.286
10.	Anteromedian flexus M1	0.167	0.286
11.	Mesostyle M1	0.250	0.400
12.	Parastyle/anteroflexus M1	0.333	0.333
13.	Flexus penetration M1	0.167	0.474
14.	Anterolabial cingulum m1	0.333	0.600
15.	Protoflexid m1	0.125	0.562
16.	Cusp arrangement m1	0.200	0.556
17.	Anteromedian flexid m1	0.300	0.462
18.	Procingulum separation m1	1.000	1.000
19.	Posterolophid/stylid m1	0.200	0.385
20.	Posterolophid/stylid m3	1.000	1.000
21.	Procingulum M2	0.200	0.478
22.	Procingulum m2	0.286	0.286
23.	Hypoflexus reduction M3	0.167	0.375
24.	Reduction of mesoflexus M3	0.154	0.522
25.	Posterior shift of mesoflexus M3	0.125	0.462
26.	Hypoflexus lake M3	0.167	0.667
27.	Rotation of flexus axes M3	0.125	0.417
28.	Mesoflexid reduction m3	0.167	0.375
29.	Anterior shift of mesoflexid m3	0.500	0.875
30.	Posterior shift of hypoflexid m3	0.333	0.500
31.	Fusion of opposing flexi in M3	1.000	1.000
32.	Ratio of M3 length to alveolar length of molar tooth row	0.200	0.467
33.	Capsular projection of mandible	0.125	0.364
34.	Height of coronoid process	0.200	0.556
35.	Anterior masseteric ridge position	0.300	0.611
36.	Medioventral process of mandibular ramus	0.222	0.500
37.	Premaxillary protrusion	0.250	0.538
38.	Posterior extent of incisive foramina	0.500	0.625
39.	Maxillary septum of incisive foramina	[0.667] ^b	[0.667] ^b
40.	Orientation of incisive foramina	0.667	0.800
41.	Dorsoventral position of anterior root of zygomatic	0.286	0.583
42.	Posterior margin of zygomatic plate	0.200	0.636
43.	Development of zygomatic spine	0.300	0.611
44.	Inclination of zygomatic plate	0.125	0.533
45.	Premaxillo-maxillary suture orientation	1.000	1.000
46.	Posterior extension of nasals	0.500	0.500
47.	Posterior extension of premaxillaries	0.200	0.429
48.	Nasal width	0.167	0.688
49.	Interorbital shape	0.333	0.600
50.	Supraorbital edge	0.333	0.500
51.	Supraorbital ridge	0.333	0.600
52.	Supraorbital knobs	0.333	0.714
53.	Mediodorsal fusion of frontals	0.667	0.500
54.	Shape of frontoparietal suture	0.333	0.600
55.	Angle of frontoparietal suture	0.500	0.500
56.	Medial length of interparietal/parietal	0.200	0.333
57.	Orientation of anterior border of auditory bulla	0.250	0.143
58.	Tegmen tympani	1.000	1.000
59.	Shape of stapedial spine of auditory bulla	1.000	1.000
60.	Thickness of hamular process of squamosal	0.250	0.600
61.	Positions of temporal vacuities	0.200	0.333

TABLE 8. *Continued.*

Number	Character name	CI ^a	RI ^a
62.	Internal carotid canal	0.250	0.400
63.	Extension of eustachian tube	0.222	0.125
64.	Relative width of mesopterygoid fossa	0.333	0.333
65.	Parapterygoid shape	1.000	1.000
66.	Shape of mesopterygoid fossa	0.333	0.500
67.	Parapterygoid fossa depth	0.400	0.727
68.	Sphenopalatine vacuities	1.000	1.000
69.	Position of orbital wings of presphenoid	1.000	1.000
70.	Anterior border of mesopterygoid fossa	0.333	0.333
71.	Medial process of posterior palate	0.100	0.400
72.	Posterior palatine ridge	1.000	1.000
73.	Posterolateral palatal pits	0.500	0.500
74.	Orientation of maxillary tooth rows	0.250	0.684
75.	Sphenopalatine foramen	0.667	0.667
76.	Carotid circulation	1.000	1.000
77.	Squamosal fenestra	0.111	0.333
78.	Alisphenoid strut	0.400	0.667
79.	Number of thoracic rib pairs	0.333	0.667
80.	Number of caudal vertebrae	0.200	0.579
81.	Neural spine of T2	1.000	1.000
82.	Height of neural spine of C2	0.500	0.500
83.	Length of neural spine of C2	0.500	0.500
84.	Position of deltoid tuberosity	0.200	0.429
85.	Ventral surface of claws (manus)	0.500	0.333
86.	Length of D1 relative to D5 (pes)	0.333	0.500
87.	Position of hypothenar pad	0.167	0.167
88.	Furring of soles of feet (pes)	0.286	0.000
89.	Countershading of tail	0.167	0.375
90.	Furring of tail dorsum	0.167	0.000
91.	Body pelage pattern	0.250	0.400
92.	Pectoral streaks	0.167	0.000
93.	Distal/proximal bacular length	0.333	0.692
94.	Length of lateral mounds relative to medial mound	1.000	1.000
95.	Hooks on lateral mounds	1.000	1.000
96.	Knob on dorsal surface of lateral mounds	1.000	1.000
97.	Preputial glands	0.667	0.000
98.	Gallbladder	[1.000]	[1.000]

^a Character indexes calculated over the phyllotine portion only of the consensus tree in Figure 23.

^b Indexes in brackets (e.g., [0.500]) were calculated over the entire tree, including outgroups, because the character was invariant or uninformative within the phyllotines.

(node E), which excludes *Loxodontomys micropus* (usually considered an *Auliscomys* [Musser & Carleton, 1993; Simonetti & Spotorno, 1980]). The shortest tree that includes *micropus* within a monophyletic *Auliscomys* is nine steps longer than the shortest trees overall. Thus, this data set does not support the inclusion of *micropus* within an *Auliscomys* clade. Sister-species status for *A. pictus* and *A. sublimis* (94% of bootstrap replicates) is supported by the medial digit of the baculum much longer than the lateral digits (94), incisive foramina extending to the level of the paracone and protocone (38), ventral surface of foreclaws forming distinct keel (85), and upper incisors lightly grooved (1). The genus *Auliscomys*, excluding *micropus*, is characterized by upper incisors with fine striae or

shallow grooves (1), supraorbital region anteriorly divergent (49), reduction of labial root M1 (4), and posterior shift of hypoflexid m3 (30). Supporting the node joining *Galenomys* with *Auliscomys* are orthodont to weakly proodont incisors (2, CI = 0.29 overall, but character state unique among phyllotines), posterior extent of premaxillaries terminating anterior to nasals (47), and narrow mesopterygoid fossa (64). 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): *boliviensis* is grouped with *Galenomys* in only 5% of bootstrap replicates versus 84% with *sublimis* and *pictus*.

Less stable is the position of *Chinchillula*. Support for its placement at the base of the *Auliscomys* group (Fig. 22) comes from the anterior border of the zygomatic plate rounded or receding dorsally (43) and premaxillaries terminating behind the anterior plane of the incisors (37). In the alternative hypothesis found in some of the most-parsimonious trees comprising Figure 23 and in the bootstrap consensus tree (Fig. 24), *Chinchillula* is basal to the *Andinomys* and *Irenomys* clade.

The best supported of the generic-groups is the *Reithrodon* group (node F), previously defined by Olds and Anderson (1989), consisting of *Reithrodon*, *Neotomys*, and *Euneomys*. Inclusion of *Loxodontomys* with the *Reithrodon* group is supported by a relatively parallel-sided parapterygoid fossa (65), a tripartite fissure in the upper incisors (3), and a narrow mesopterygoid fossa (64) and is found in 35% of bootstrap replicates.

The *Reithrodon* group is supported by a sharply angled premaxillo-maxillary suture (45, unique within the Sigmodontinae), sigmoidal molars, *sensu* Hershkovitz (1955) (represented here by multiple characters), no anterior shift by the mesoflexid m3 (29), distinctly grooved incisors (1), anterior root of the zygomata inserting high, close to dorsal surface of the rostrum (41), absence of labial root m1 (7), and supraorbital knobs (52). The close relationship of *Reithrodon* with *Neotomys* is supported by loss of supraorbital branch of the stapedia artery (76), a deeply channeled posterior palate with distinct median ridge (72), anterior apices of incisive foramina well separated (40), and deeply excavated parapterygoid fossae (67).

All the analyses 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 below and well posterior to the diastema (35, CI = 0.30 overall, but character state unique among the phyllotines), anterior apices of incisive foramina relatively widely separated (40), frontals incompletely fused or apparently vascularized along the midline (53), and posterolateral palatal pits in the anterior parapterygoid fossa (73). The bootstrap consensus tree (Fig. 24) groups the taxa in 30% of replicates.

Discussion

Comparisons between the results of this study and previous studies show only moderate agree-

ment regarding suprageneric relationships, and that discordance may be due in part to the strictly cladistic approach of this study in contrast to the evolutionary systematics of most prior studies. Some of the earlier studies (e.g., Hooper & Musser, 1964) make pairwise statements of similarity that are difficult to translate into a hierarchical phylogenetic hypothesis, and others implicitly rely on paraphyletic groups. In his revision of the genus *Phyllotis*, Pearson (1958) found consensus with Ellerman (1941) and Osgood (1947) and recognized four subgenera—*Graomys*, *Auliscomys*, *Loxodontomys*, and *Phyllotis*—and removed *P. gerbillus* to the related genus *Paralomys*. The phylogenetic relationships implied by placing these subgenera under *Phyllotis* is consistent with this study in regard to *Graomys* being closely related to *Phyllotis* but is incongruent in regard to *Auliscomys* and *Loxodontomys*, which this study shows 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 primarily distinguished from the *Phyllotis* section by 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* along with the sigmodonts (*Reithrodon*, *Neotomys*, *Holochilus*, and *Sigmodon*) might be considered the sister-groups to the phyllotines. Species-group assignments are more similar between Hershkovitz (1962) and this study; for example, Hershkovitz's *P. darwini* complex is almost identical to the *P. xanthopygus-magister* species-group seen in this study.

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—for example, *A. pictus* with *A. sublimis*, and *P. 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) placed *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 close relationship. In fact, Spotorno (1986; p. 22) explicitly acknowledged that 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 UPGMA dendrogram (Fig. 5A) separates *Andinomys*, *Irenomys*, and *Euneomys* from *Reithrodon* and *Loxodontomys* by placing them near the base of the tree. A cladistic reanalysis of the same data set (Fig. 5B) provides little resolution. The electrophoretic data set in Spotorno (1986) does not seem to be highly informative for the phyllotines.

Reig (1986) presented a biogeographic scenario for the diversification of the 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 *Calomys* as the most basal and generalized phyllotine genus, with *C. sorellus* as the most basal member of either a *Calomys* or phyllotines-minus-*Calomys* clade. His view of the lowland *Calomys* (e.g., *C. callosus*, *C. laucha*) as derived or terminal species is consistent with this study. *Phyllotis* and a *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, *Loxodontomys* 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* would be 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, recorded as 39 qualitative and 7 quantitative characters. Qualitative and quantitative characters were equally influential in the analyses because of the large number of character states in all the quantitative characters (8-10 each). 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. By only including the phyllotines, two akodonts, and *Pseudoryzomys* in the actual numerical analysis without any oryzomyines, the tribal status of *Pseudoryzomys* could not be tested. The results of this study indicate that *Pseudoryzomys* is not a phyllotine, nor is it within a clade that includes the phyllotines and akodontines.

From the results of these analyses, I propose several generic groups to provide an informal reference structure to communicate some of the better supported hypotheses. The informal nomenclature reflects the uncertainty regarding key nodes, some more inclusive than the generic-groups I propose, that would allow a proper cladistic allocation of monophyletic groups to formal subtribes. The groups I recognize are the *Graomys* group (node C) including *Andalgalomys*, *Graomys*, and *Eligmodontia*; the *Auliscomys* group (node E) including *Auliscomys* and *Galenomys*; the *Reithrodon* group (node F) including *Euneomys*, *Neotomys*, and *Reithrodon*; and the *Andinomys* group including *Andinomys* and *Irenomys*. The species *amicus* and *gerbillus*, currently assigned to *Phyllotis*, are most likely basal members of the *Graomys* group and should be assigned to it provided future studies confirm that hypothesis. *Loxodontomys* may well be a basal member of the *Reithrodon* group, but this study does not definitively demonstrate it. *Chinchillula* currently stands as *Phyllotini sedis mutabilis* for nearly equally parsimonious placements at the base of the *Auliscomys* or *Andinomys* groups. *Phyllotis* as currently recognized is almost certainly paraphyletic, but the relevant region of the phylogeny is not sufficiently resolved that I can confidently propose an alter-

native hypothesis with which to formally revise the taxonomy. Finally, more confidence can now be placed in my earlier suggestion (Steppan, 1993) that, due to the paraphyly of *Graomys*, *Andalgalomys* should be subsumed within it.

I will also suggest, but not diagnose, a more formal taxonomy, primarily as a hypothesis to be tested by further studies and as a possible aid to description of the phylogenetic hypotheses presented here. The most appropriate taxonomic category between genus and tribe would be the subtribe. To maximize information content and allow the use of both subtribes and generic groups in future taxonomies, recognized subtribes should be more inclusive than the generic groups that I just listed. In this scenario, the clade comprised minimally of *Phyllotis sensu stricto* and the *Graomys* group would be subtribe Phyllotina (node B). The sister-group to Phyllotina would be Reithrodonina and is expected to include the *Auliscomys*, *Andinomys*, and *Reithrodon* groups. Finally, the sister-group to the clade combining Phyllotina and Reithrodonina would be Calomyina, including only *Calomys*, unless *C. sorellus* were in fact the sister-group to Phyllotina-plus-Reithrodonina, in which case *sorellus* would have to receive its own genus and possibly subtribe.

Taxonomy

Numbers in parentheses listed in the diagnoses refer to the character number from the phylogenetic analysis of the phyllotines (Table 4). All diagnoses are phylogenetic in nature, in that they list character states hypothesized to be derived relative to a named, more inclusive taxon. Asterisk (*) signifies autapomorphy relative to the other phyllotines.

Tribe Phyllotini Vorontsov, 1959

TYPE GENUS—*Phyllotis*, by tautonymy.

INCLUDED TAXA—*Andinomys*, *Calomys*, *Chinchillula*, *Elignodontia*, *Euneomys*, *Galenomys*, *Graomys*, *Irenomys*, *Loxodontomys*, *Neotomys*, *Phyllotis*, and *Reithrodon*.

DIAGNOSIS—Members of the Neotropical subfamily Sigmodontinae (family Muridae) descended from a common ancestor with the following traits: moderate or large pinnae (> 0.15 head and body length), parapterygoid fossa relatively broad-

er than mesopterygoid fossa, very open sphenopalatine vacuities, complete loss of the mesoloph, posterior extensions of premaxillaries and nasals subequal, and (except in some *Calomys*) two pairs of preputial glands.

Calomys Waterhouse

(Figs. 25, 26)

Calomys Waterhouse, 1837. Proc. Zool. Soc. Lond., 1837:21.

Hesperomys Waterhouse, 1839. Zoology Voy. "Beagle," 2:75.

TYPE SPECIES—*Mus (Calomys) bimaculatus* (Waterhouse), 1837, by original designation.

INCLUDED SPECIES—The specific taxonomy of *Calomys* is less stable than the other phyllotine genera. Species have undergone numerous reassessments in recent years, principally due to the input of karyotypic data. The nomenclature used in the phylogenetic analysis largely followed Hershkovitz (1962), and nomenclatural uncertainties of certain specimens are indicated in the Appendix. In her unpublished revision of the genus, Olds (1988) recognized 10 species: *bimaculatus* Waterhouse, 1837, *callosus* Rengger, 1830, *hummelincki* Husson, 1960, *laucha* Olfers, 1818, *lepidus* Thomas, 1884, *murillus* Thomas, 1916, *musculus* Thomas, 1913, *sorellus* Thomas, 1900, *tener* Winge, 1888, and *venustus* Thomas, 1894. Vitullo et al. (1990) did not recognize *bimaculatus*, *murillus*, or *tener* but did recognize *fecundus* Thomas, 1926, and *callidus* Thomas, 1916. In contrast to Olds (1988), Musser and Carleton (1993) recognized nine species, among them *callidus*. They treated *fecundus* as a subjective synonym of *boliviae* Thomas, 1901, and synonymized *bimaculatus* and *murillus* with *laucha* and *musculus*, respectively. Whatever their rank, these taxa are properly included in *Calomys*, with reservations regarding *sorellus* as discussed under Comments.

DIAGNOSIS—Members of the tribe Phyllotini descended from a common ancestor with the following traits: no reduction in the mesoflexus M3 relative to M2 (24), posterior margin of zygomatic plate anterior to M1 (42), mesopterygoid fossa lying more than 1 tooth-length posterior to M3 (70), and length of distal baculum 63–77% of proximal length (93).

DISTRIBUTION—From central Peru at high elevations, through Bolivia, northern and central Ar-



FIG. 25. Cranium and mandible of *Calomys laucha* (FNMH 23405). Scale bar = 10 mm.

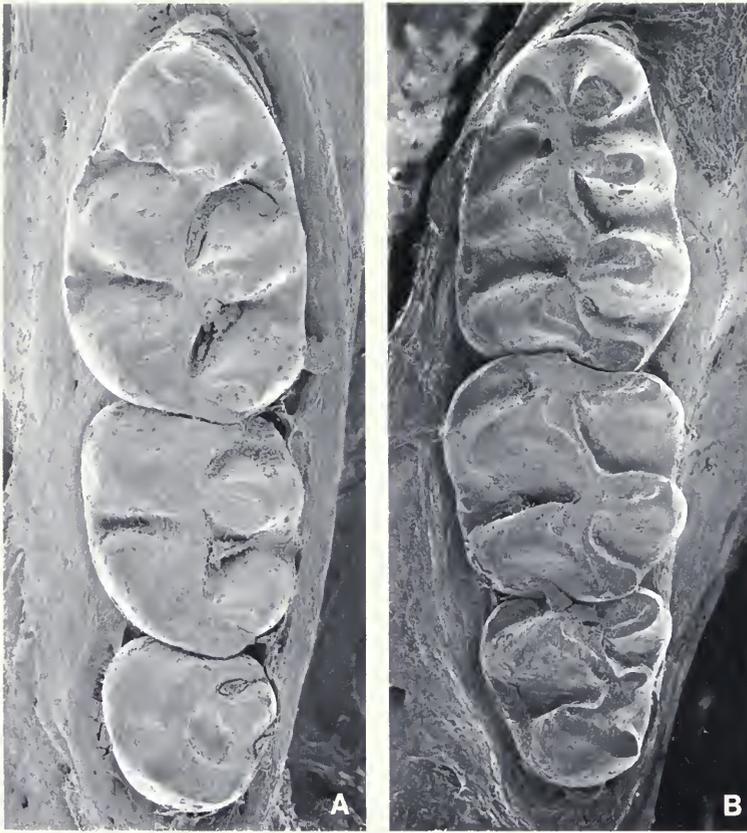


FIG. 26. Upper and lower molars of *Calomys laucha* (FMNH 29246).

gentina, far northern Chile, Paraguay, Uruguay, to southwestern and eastern Brazil. *Calomys hummelincki* has a poorly known distribution in northern Venezuela, eastern Colombia, and several offshore Caribbean islands.

COMMENTS—Phylogenetic relationships within *Calomys* are poorly known. Olds (1988) revised the genus and recognized five species-groups, two of which are monospecific, of unknown interrelationship. Her groupings were based on tail length, diploid number, and multivariate size and shape of skulls. The five groups (with modal mammae counts) are as follows: *callosus* (10), *venustus* (10–14), and *tener* (10); *laucha* (8), *bimaculatus* (10), and *hummelincki* (8); *murillus* (10–12) and *musculus* (12–14); *lepidus* (8); and *sorellus* (8). These groupings bear little resemblance to the three recognized by Vitullo et al. (1990) based on karyotypes. Group I is closely related to the ancestral type hypothesized by Pearson and Patton (1976) and includes *sorellus* (2N = 64, FN = 68), *laucha* (2N = 64, FN = 68), and *hummelincki* (2N = 60,

FN = 64). Group II consists of a Robertsonian series from *venustus* (2N = 54–56, FN = 66) to *fecundus* (2N = 50, FN = 66), and *callidus* (2N = 48, FN = 66). Group III consists of *callosus* (2N = 36, FN = 48), *lepidus* (2N = 36, FN = 68), and *musculus* (2N = 38, FN = 56). Number of ribs is consistent with Olds's scheme, as specimens assigned by her to *callosus*, *venustus*, and *tener* all share the derived condition of 12 ribs and seven lumbar vertebrae. *Calomys laucha* and *lepidus* have the primitive 13 ribs and six lumbar vertebrae. This observation contradicts the statement that "*C. callosus*, *C. laucha*, and *C. lepidus* generally [have] . . . 13 thoracic, with 13 pairs of ribs, 6–7 lumbar" (Olds, 1988, p. 50). Many of the same specimens were examined in both studies. This observation also contradicts the coding by Carleton (1980), who coded *callosus* as having 13 ribs. Nineteen of the 20 skeletons of *callosus* examined in this study clearly had only 12 ribs, and one had a thin, short thirteenth pair that did not articulate with the twelfth thoracic vertebra.

The most-parsimonious trees from the phylogenetic analysis (Figs. 22, 23; Steppan, 1993) indicate that *sorellus* is not a member of a *Calomys* clade but may instead be the sister taxon to all other phyllotines. The analysis above is equivocal, but the hypothesis that *sorellus* shares a more recent ancestor with other phyllotines than it does with *Calomys* is supported by the presence of a ventral pair of preputials (97), more than 25 caudal vertebrae (80), loss of the parastyle/anteroflexus M1 (12), a long interparietal (56), and two roots on m3 (9).

Necomys Ameghino (1889) was synonymized with *C. callosus* by Hershkovitz (1962), but the type specimen was considered a senior synonym of *Bolomys* by Massoia and Pardiñas (1993).

Graomys Group

INCLUDED TAXA—*Eligmodontia* and *Graomys*.

DIAGNOSIS—Members of the tribe Phyllotini descended from a common ancestor with the following traits: no reduction in the mesoflexus of M3 relative to M2 (24), hypoflexus of M3 intact, not pinched to form lake (26), premaxillaries produced well anterior to incisors (37), supraorbital region posteriorly divergent (49), supraorbital edges ridged, overhanging (except *Eligmodontia*) (50), maxillary tooth rows parallel (except *Eligmodontia*) (74), squamosal fenestra present between masticatory-buccinator trough and squamosal-alisphenoid groove (77), alisphenoid strut present (78), and tail dorsum sparsely furred (except *G. pearsoni*) (90).

COMMENTS—This generic group may well include *Phyllotis amicus* and *P. gerbillus*, but as the current analysis cannot confidently resolve the issue, I prefer not to make formal nomenclatural changes. Should further studies confirm the inclusion of *amicus* and *gerbillus*, then they should be included in the *Graomys* group as well.

***Eligmodontia* F. Cuvier**

(Figs. 27, 28)

Eligmodontia F. Cuvier, 1837. Ann. Sci. Nat. (Paris), ser. 2, 7:168.

Eligmodon Wagner, 1841. Arch. Naturg., 1:125.

Heligmodontia Agasiz 1846. Nomencl. Zool. Mamm., Addenda, 5:136, 175.

TYPE SPECIES—*Eligmodontia typus* Cuvier, 1837, by original designation.

INCLUDED SPECIES—At least three species have been demonstrated from karyotypic data: *typus*, *puerulus* Philippi, 1896, and *morgani* Allen, 1901.

DIAGNOSIS—Members of the *Graomys* group descended from a common ancestor with the following traits: hyper-opisthodont upper incisors (2), anterolabial cingulum ml indistinct (14), posterior shift of hypoflexid m3 relative to m2 (30), knob of anterior masseteric ridge exceeds dorsal edge of diastema (35), supraorbital edges angled (50), eustachian tubes do not reach posterior edge of pterygoid processes (63), parapterygoid fossa 1.5–2.5 times mesopterygoid fossa width (64), maxillary tooth rows posteriorly convergent (74), deltoid tuberosity greater than 59% of humerus length from condyle (84), ventral surface of claws forming distinct keel (85), D1 and D5 of pes subequal in length (86), sole of pes furred (88), *hind feet elongated, hypothenar pad absent, *fused plantar pads D2–4, and hair in pectoral region entirely white from base to tip.

DISTRIBUTION—Found throughout southern Argentina, far eastern Chile in the south, along the eastern slopes of the Andes in western and northern Argentina, and in the altiplano of northern Chile, southwestern Bolivia, and extreme southern Peru.

COMMENTS—Three species are now recognized, based mostly on karyotypes: *typus*, *puerulus*, and *morgani*. The specimens examined from Neuquén Province in western Argentina and from southern Chile are tentatively referred to the species *morgani*, the name offered by Kelt et al. (1991) for specimens with a karyotype of 2N = 32–33, FN = 32. Kelt et al. (1991) and Ortells et al. (1989) also recognize two other species of *Eligmodontia*: *puerulus* (2N = 50, FN = 48) from Bolivia, Peru, and northern Chile and *typus* (2N = 43–44, FN = 44) from central and eastern Argentina. Zambelli et al. (1992) found *typus* to be sympatric with *morgani* at two localities in Neuquén Province near where some of the specimens examined in this study were collected. The recent chromosomal studies do not include morphological data that would allow more confident species assignments for the specimens examined in this study.

***Graomys* Thomas**

(Figs. 28, 29)

Graomys Thomas, 1916. Ann. Mag. Nat. Hist., ser. 8, 17:141.

Andalgalomys Williams and Mares, 1978. Ann. Carnegie Mus., 47:197.



FIG. 27. Cranium and mandible of *Eligmodontia morgani* (FMNH 133070).

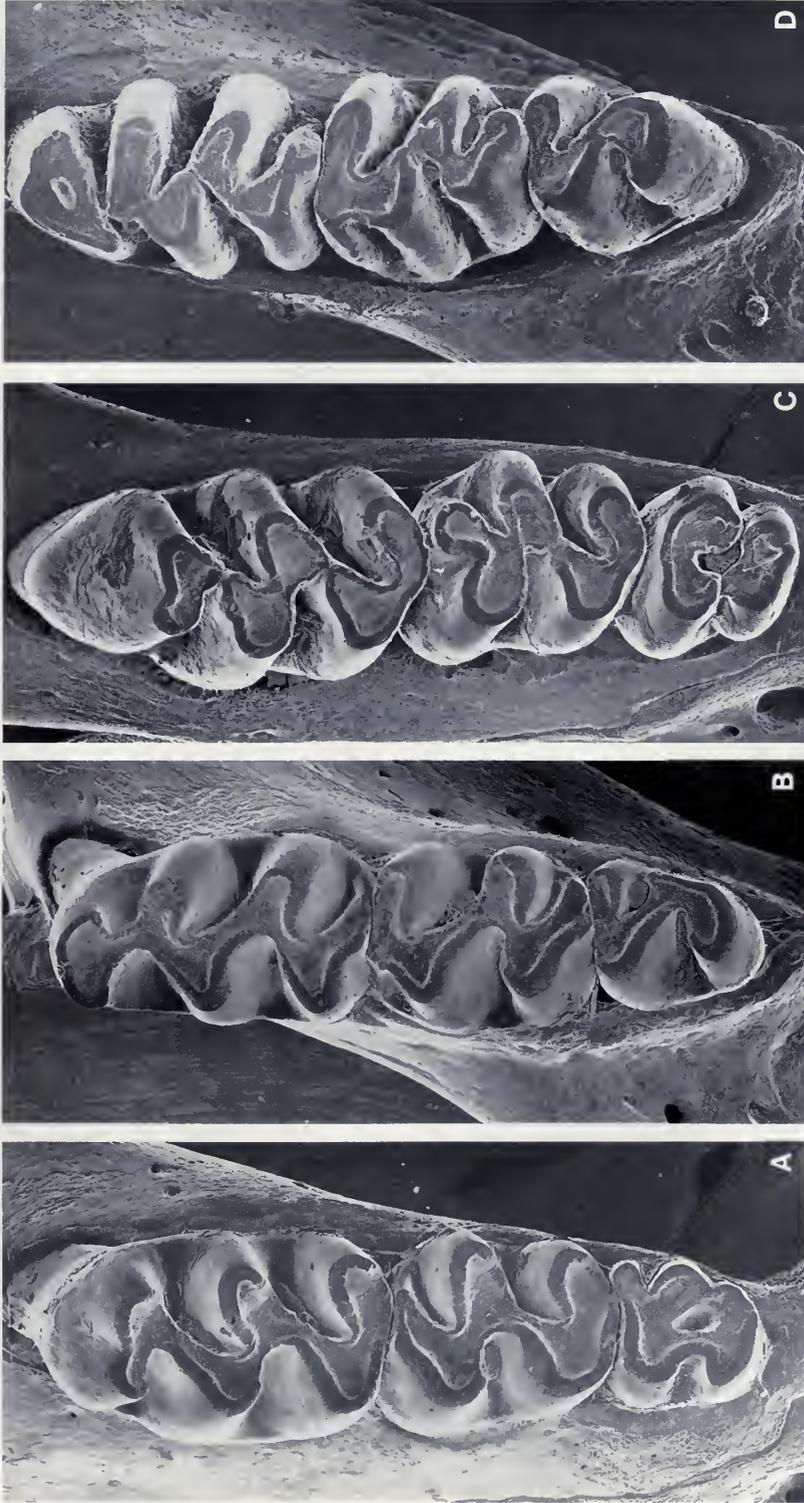


FIG. 28. Upper and lower molars of *Eligmodontia morgani* (FMNH 133070) (A, B) and *Graomys griseoflavus* (FMNH 41290) (C, D).



FIG. 29. Cranium and mandible of *Graomys griseoflavus* (FMNH 28423).

TYPE SPECIES—*Mus (Phyllotis) griseo-flavus* Waterhouse, 1837, by original designation.

INCLUDED SPECIES—Includes *griseo-flavus* (Waterhouse, 1837), *domorum* (Thomas, 1902), *olrogi* (Williams & Mares, 1978), and *pearsoni* Myers, 1977. The status of the geographically restricted *edithae* Thomas, 1919, is less clear, and specimens were not examined.

DIAGNOSIS—Members of the *Graomys* group descended from a common ancestor with the following traits: distinct and large anterolabial cingulum m1 (14, 15), no shift of mesoflexid m3 (29), moderately developed zygomatic spine, anterior border of zygomatic plate concave (43), supraorbital sharply ridged, overhanging (50), *laterally apressed stapedial spine (59), *orbital wings of the presphenoid posterior from maximum constriction (69), maxillary tooth rows parallel (74), 12 thoracic and seven lumbar vertebrae (79), and moderately sized distal baculum (93).

DISTRIBUTION—Found at moderate to low elevations in southern Bolivia, western Paraguay, and northern and central Argentina, and reported from southwestern Brazil.

COMMENTS—Synonymy of *Andalgalomys* is required by the strong support for *G. (Andalgalomys) pearsoni* and *G. griseo-flavus* sharing a common ancestor more recently than either does with *G. domorum*.

***Phyllotis* Waterhouse** (Figs. 30, 31)

Phyllotis Waterhouse, 1837. Proc. Zool. Soc. Lond., 1837:27.

Paralomys Thomas, 1926. Ann. Mag. Nat. Hist., ser. 9, 17:315.

TYPE SPECIES: *Mus darwini* (Waterhouse), 1837, by subsequent designation (Thomas, 1884, p. 449).

INCLUDED SPECIES: Minimally, *Phyllotis sensu stricto* includes *caprinus* Pearson, 1958, *chilensis* Mann, 1945, *definitus* Osgood, 1915, *darwini* (Waterhouse, 1837), *haggardi* Thomas, 1898, *magister* Thomas, 1912, *osgoodi* Mann, 1945, *osilae* J. A. Allen, 1901, and *xanthopygus* (Waterhouse, 1837). Additional species included pending further revisionary studies (see Comments): *andium* Thomas, 1912, *wolffsohni* Thomas, 1902, *amicus* Thomas, 1900, and *gerbillus* Thomas, 1900. Musser and Carleton (1993) also recognized *bonariensis* Crespo, 1964, which along with *osgoodi* was not examined for the cladistic analyses.

DIAGNOSIS—See discussion under Comments.

DISTRIBUTION—As currently defined, the genus is distributed throughout nonforest habitats in the Andes from Ecuador to the Straits of Magellan, from near sea level along the Pacific coast, to the altiplano.

COMMENTS—Woodman (1993) has recently recommended that species names for all genera ending in the feminine *-otis* and derived from the Greek *οτος*, for ear, should be feminized. Four species of *Phyllotis* would be affected by this nomenclatural change: *amica* from *amicus*, *caprina* from *caprinus*, *definita* from *definitus*, and *xanthopyga* from *xanthopygus*. However, Pritchard (1994) argued that mammalian generic names ending in *-otis* are actually Latin derivations of the Greek, and Latin words ending in *-is* are of the 3rd declension and may be masculine, feminine, or neuter, depending on priority of usage when grouped with specific names. The first usage of *Phyllotis* with a specific epithet requiring gender agreement was with the masculine *xanthopygus* (Waterhouse, 1837). At issue is whether the *-otis* ending was a proper feminine form of *οτος* or was a latinization of the Greek. The Greek *otis* (*οτις*) means bustard and, while feminine, refers to a bird that lacks external pinnae, and thus may not have originally been derived from “feminine-eared creature,” a literal translation. It certainly serves as a poor reference for names relating to modifications of ears. I retain the historical usage for *Phyllotis* species names, but proper resolution may await further investigation of the etymology of the original Greek forms.

My analysis of morphological characters strongly indicates that *Phyllotis* is either polyphyletic or paraphyletic, but no single alternative hypothesis exists with which to confidently revise existing taxonomy. Therefore, the genus is left unrevised and undiagnosed. It seems likely that *amicus* and *gerbillus* should be removed; the name *Paralomys* Thomas, 1926, is available for a genus including *gerbillus*. In fact, Braun (1993) recently placed them in *Paralomys*, although her analysis indicates that it is paraphyletic. Should *amicus* and *gerbillus* not form a monophyletic group, then *Paralomys* would apply only to *gerbillus*. *Phyllotis andium* falls outside the main *Phyllotis* clade and may well be a basal member that requires generic status in order to maintain a strictly monophyletic *Phyllotis*. The more highly derived *wolffsohni* seems to be a basal member of the clade including *Auliscomys*, *Andinomys*, and *Reithrodon*. After excluding these four species, nine remain to form a monophyletic



FIG. 30. Cranium (FMNH 22325) and mandible (FMNH 22328) of *Phyllotis darwini*.



FIG. 31. Upper and lower molars of *Phyllotis darwini* (FMNH 22326) (A, B) and *Loxodontomys micropus* (FMNH 124393) (C, D).

group in the most-parsimonious tree: *caprinus*, *chilensis*, *darwini*, *definitus*, *haggardi*, *magister*, *osgoodi*, *osilae*, and *xanthopygus*. Though not included in the cladistic analysis, *chilensis* and *osgoodi* are clearly members of *Phyllotis sensu stricto*, virtually identical to *xanthopygus rupestris* for the characters used in the cladistic analysis.

This study follows the recommendation of Walker et al. (1984) to restrict the specific name *darwini* to coastal Chilean populations and to include the north Andean subspecies (e.g., *rupestris*) within *xanthopygus*. Musser and Carleton (1993) cited Walker et al. (1984) in aligning the north Andean subspecies under *darwini* and restricted *xanthopygus* to the south Andean subspecies (e.g., *vaccarum*), but Walker et al. (1984) were quite clear about the restriction of *darwini* to coastal Chilean populations. The specimens referred to *darwini* in Braun (1993) were instead *xanthopygus*.

My recognition of *chilensis* as a distinct species differs from all recent treatments (Hershkovitz, 1962; Mann, 1978; Pearson, 1958). Unpublished morphometric, anatomical, and molecular data collected by me indicate the specific separation of *chilensis* from *P. x. rupestris* in southern Peru. The two taxa form clearly bimodal clusters in principal component space with little overlap. Where good series exist along transects, the transition between the taxa is sharp, identifiable to within a kilometer. Morphological intermediates (outliers) are not associated with proximity to the transition zone. *Phyllotis chilensis* is autapomorphic in being the only phyllotine examined with three pairs of preputial glands. Additionally, Peruvian *rupestris* possesses the narrowest upper incisors in relation to incisor depth of any *Phyllotis*. Spotorno and Walker (1983) also found that *chilensis* was electrophoretically more closely related to *darwini* than to populations of true *xanthopygus*. It is not entirely clear whether *chilensis* or *rupestris* shows evidence of introgression with the other subspecies of *xanthopygus*, but current DNA sequence and revisionary studies should resolve the question.

***Loxodontomys* Osgood**

(Figs. 31, 32)

Loxodontomys Osgood, 1947. J. Mamm., 28:172.

TYPE SPECIES—*Mus micropus* Waterhouse, 1837, by original designation and monotypy.

INCLUDED SPECIES—Includes the single species *micropus*.

DISTRIBUTION—Southern Andes of Chile and Argentina from about 36°S to the Straits of Magellan.

DIAGNOSIS—Members of the tribe Phyllotini and allied to the *Reithrodon* group, descended from a common ancestor with the following traits: ungrooved upper incisors (1), tripartite dentine lake in the upper incisors (3), two labial roots M1 (5), two roots M2 (8), labial root m1 present (7), two roots m2 (8), indistinct parastyle/anteroflexus M1 (12), anterolabial cingulum distinct (14), protoflexid m2 present as groove (22), hypoflexus M3 reduced relative to M2 (23), mesoflexid m3 reduced and shifted anteriorly relative to m2 (28, 29), length of M3 greater than 20% alveolar length of tooth row (32), posterior border of mandibular symphysis sharply angled (36), premaxillaries terminating at or slightly anterior to incisive plane (37), incisive foramina terminating at level of paracone and protocone (38), antorbital bridge $\frac{1}{8}$ – $\frac{1}{4}$ below dorsal surface of rostrum (41), nasals broader than interorbital constriction (48), supra-orbital edges angled for $\frac{1}{2}$ of length (50), supra-orbital ridges and knobs absent (51, 52), internal carotid bounded by both auditory bulla and occipital (62), mesopterygoid fossa distinctly narrower than parapterygoid fossa (64), posterior width of parapterygoid less than 1.5 times anterior width (65), parapterygoid fossa recessed slightly above palate (67), maxillary tooth rows posteriorly divergent (74), sphenopalatine foramen absent or nearly ossified (75), squamosal fenestra present between squamosal groove and masticatory–buccinator trough (77), tail sparsely furred (90), pectoral streaks present (92), and distal baculum less than 63% length of proximal baculum (93).

COMMENTS—Osgood (1947) described *Loxodontomys* as a subgenus of *Phyllotis*, and Braun (1993) elevated it to a genus for *micropus*. Generic status was supported by Steppan (1993). Inclusion within *Auliscomys* is strongly argued against by this study, but karyotypic data would seem to suggest a close association (Walker & Spotorno, 1992). However, the karyotypic analysis assumed rather than tested a monophyletic *Auliscomys sensu lato* by not including outgroups in the analysis. The basal position of *Loxodontomys* relative to the divergence of the *Auliscomys* and *Reithrodon* groups allows the possibility that *Loxodontomys* and *Auliscomys* have retained relatively primitive karyotypes. 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

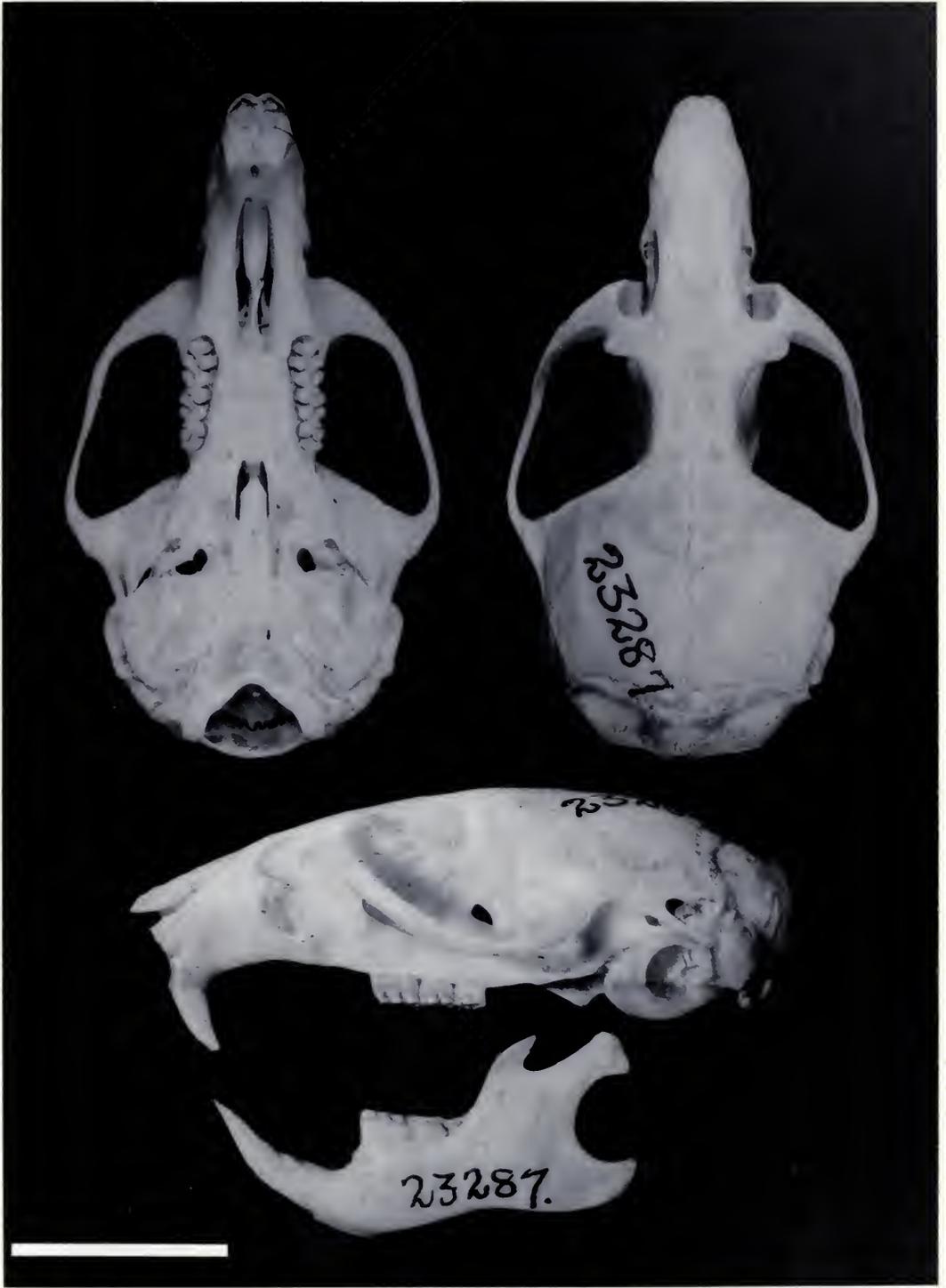


FIG. 32. Cranium and mandible of *Loxodontomys micropus* (FMNH 23287).

are indeed similar, but the 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 that this analysis indicates that it is related to. Their multivariate analysis does not conflict with the results of this study.

Osgood (1943) had included *micropus* in *Auliscomys*, a subgenus of *Phyllotis*, but only supported this alignment by the development of the parastyle M2 (which he described as variable among groups allied to *Phyllotis*) and the "somewhat more oblique pattern" (Osgood, 1943, p. 213) of the molar lophs. Otherwise, he found *micropus* "somewhat anomalous" in association with *Auliscomys*.

Pine et al. (1979) proposed that *Loxodontomys* Osgood was technically a *nomen nudum* because in Osgood's description, "it" referred to *micropus* rather than to *Loxodontomys*. However, in defining *Loxodontomys* as a monotypic taxon, "it" referred to both the species and subgenus, and "it" was compared to other genus-level taxa, not to individual species.

***Auliscomys* Group**

INCLUDED TAXA—*Auliscomys* and *Galenomys*.

DIAGNOSIS—Members of the tribe Phyllotini allied to *Chinchillula*, *Loxodontomys*, and the *Andinomys* and *Reithrodon* groups, descended from a common ancestor with the following traits: curved dentine lake in the upper incisors (3), length of M3 greater than 20% alveolar length of tooth row (32), capsular projection of mandible indistinct or absent (33), medioventral process of mandibular ramus absent, the ramus not sharply angled (36), premaxillaries terminating behind the incisive plane (37), *zygomatic spine absent, zygomatic plate convex and receding dorsally (43), zygomatic plate inclined less than 20° (44), posterior terminus of premaxillaries anterior to nasals (47), nasals broader than interorbital constriction (48), mesopterygoid fossa distinctly narrower than parapterygoid fossa (64), and tails usually densely furred (90) and short to very short, always less than head and body length.

***Auliscomys* Osgood** (Figs 33, 34)

Auliscomys Osgood, 1915. Field Mus. Nat. Hist. Publ., Zool. Ser., 10:190.
Maresomys Braun, 1993:40.

TYPE SPECIES—*Reithrodon pictus* Thomas, 1884, by original designation.

INCLUDED SPECIES—*pictus* (Thomas, 1884), *boliviensis* (Waterhouse, 1846), and *sublimis* (Thomas, 1900).

DIAGNOSIS—Members of the *Auliscomys* group descended from a common ancestor with the following traits: upper incisors with shallow grooves or striae in most specimens (1), incisors orthodont (2), small labial root of M1, set medially (4), posterolophid m1 distinct at all ages (19), procingulum M2 moderately to well developed (21), highly reduced mesoflexid on m3 (28), posterior shift of hypoflexid on m3 (30), supraorbital region anteriorly divergent, narrowest point posterior (except *pictus*) (49), interparietal/parietal length between 0.33 and 0.45 (56), internal carotid canal bounded by both auditory bulla and occipital (62), and maxillary tooth rows parallel (74).

DISTRIBUTION—Altiplano from central Peru to southwestern Bolivia and far northern Argentina and Chile.

COMMENTS—Braun (1993) erected *Maresomys* to contain *boliviensis* primarily because it was less similar to *sublimis* and *pictus* than they were to each other and because her cladistic analysis placed it as the sister-species to *Galenomys garleppi*. No putative synapomorphies for this topology or estimates of confidence were reported. My study does not support sister taxon status between *boliviensis* and *Galenomys* but, instead, strongly supports a monophyletic *Auliscomys* (84% of bootstrap replicates, hypothesized synapomorphies in diagnosis). Phenetic analyses in Braun (1993) and Spotorno (1986) indicate that dissimilarities among *boliviensis*, *sublimis*, and *pictus* are comparable to that seen within *Calomys* and *Phyllotis*. The current taxonomy in regard to *boliviensis*, *sublimis*, and *pictus* appears to fully satisfy the objectives of both cladistic and phenetic concepts of systematics.

The species *micropus* is removed to *Loxodontomys* (see Comments therein).

***Galenomys* Thomas** (Figs. 34, 35)

Galenomys Thomas, 1916. Ann. Mag. Nat. Hist., ser. 8, 17:143.

TYPE SPECIES—*Phyllotis garleppi* Thomas, 1898, by original designation.

INCLUDED SPECIES—Includes the single species *garleppi* (Thomas, 1916).

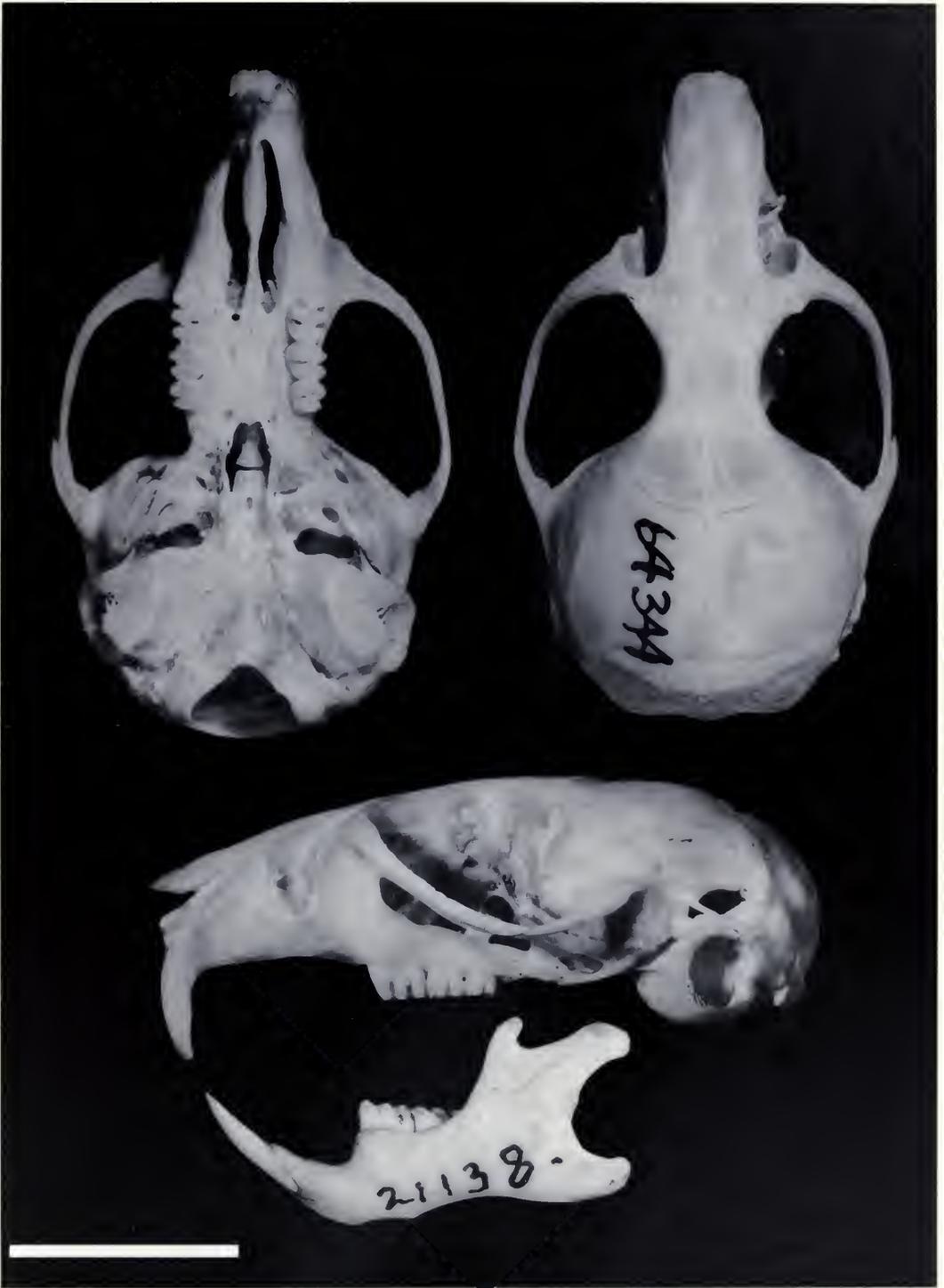


FIG. 33. Cranium and mandible of *Auliscomys pictus* (FMNH 64344).

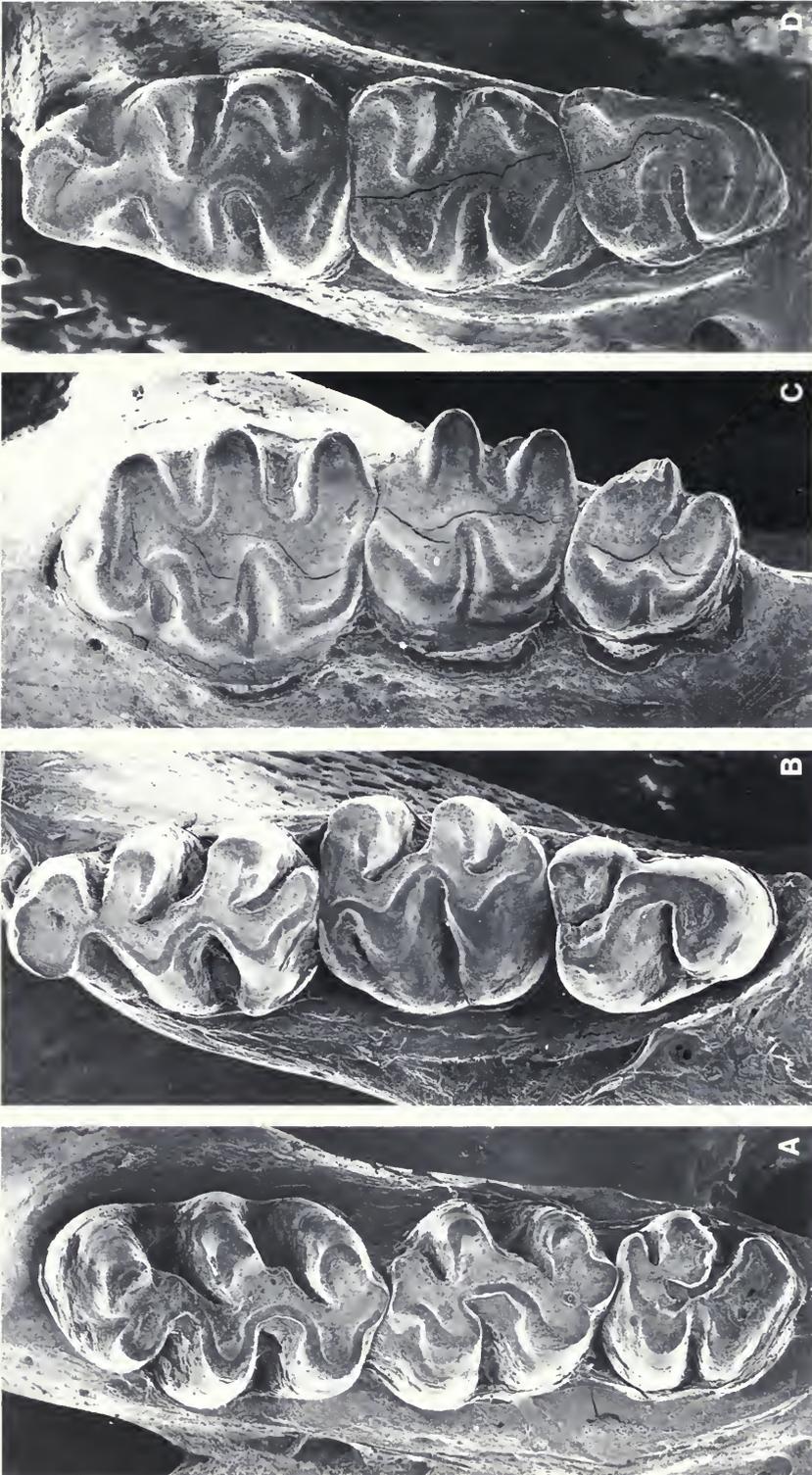


FIG. 34. Upper and lower molars of *Ateliscornys pictus* (FMNH 54734) (A, B) and *Galenomys garleppi* (FMNH 53845) (C, D).



FIG. 35. Cranium (AMNH 246947) and mandible (FMNH 53845) of *Galenomys garleppi*.

DIAGNOSIS—Member of the *Auliscomys* group descended from a common ancestor with the following traits: incisors orthodont (2); lower incisors highly procumbent; three roots on m3 (9); distinct anteromedian flexus on M1 (10); reduced hypoflexus on M3 (24); highly reduced mesoflexid on m3 (28); knob of anterior masseteric ridge reaches dorsal edge of mandible (35); *skull strongly arched upward in region of supraorbital to rostrum, rostrum flexed downward; internal carotid canal bounded by both auditory bulla and occipital (62); maxillary tooth rows posteriorly convergent (74), *outwardly bowed; no fenestra where masticatory–buccinator nerve passes over squamosal–alisphenoid groove (77); deltoid tuberosity greater than 59% along humerus from the condyle (84); soles of hindfeet furred (88); tail densely furred (90); and *tail very short, less than 40% head and body length.

DISTRIBUTION—Restricted distribution in the provinces or departments of Puno in Peru, La Paz and Oruro in Bolivia, and Tarapacá in Chile.

COMMENTS—Braun (1993) erected *Maresomys* for *boliviensis* based on its sister-group status with *Galenomys*, creating an otherwise paraphyletic *Auliscomys*. The strength of a *Galenomys*/*Maresomys* clade relative to other topologies cannot be evaluated because no synapomorphies are reported. This study indicates robust support for a monophyletic *Auliscomys*, to which *Galenomys* is the sister-group.

***Chinchillula* Thomas** (Figs. 36, 37)

Chinchillula Thomas, 1898. Ann. Mag. Nat. Hist., ser. 7, 1:280.

TYPE SPECIES—*Chinchillula sahamae* Thomas, 1898, by original designation.

INCLUDED SPECIES—Includes the single species *sahamae*.

DIAGNOSIS—Member of the tribe Phyllotini and allied to the *Auliscomys* and *Andinomys* generic groups, descended from a common ancestor with the following traits: characterized by *very large body size; curved fissures in upper incisors (3); one root on M3 (6); *lingual root of M2 absent; three roots on m2 (8); small mesostyles present (11); opposing flexi on M1 do not overlap (13); posterolophid m1 absent (19); procingulum M2 absent (21); length of M3 less than 0.205 times the

length of the molar tooth row (32); zygomatic plate rounded, spine absent (43); anterior root of zygomatic inserting near dorsal surface of rostrum (41); supraorbital ridges raised dorsally (51); frontoparietal suture straight, forming a right or acute angle (54, 55); postglenoid foramen anterior to subsquamosal foramen (61); internal carotid not bounded by basioccipital (62); anterior border of mesopterygoid fossa lying between 0 and 0.33 tooth-length behind M3s (70); ventral surface of claws on manus fused, forming distinct keel (85); highly distinctive coloration, with white hip patches contrasting with dark brown to black side patches, tawny over dark gray back, and white postauricular patches.

DISTRIBUTION—Altiplano of southern Peru, far western Bolivia, and far northern Chile.

COMMENTS—I regard *Chinchillula* as *Phyllotini sedis mutabilis* to reflect the uncertainty as to the two near equally parsimonious positions it can occupy: the basal member of the *Auliscomys* group or the basal member of the *Andinomys* group. Neither topology is strongly supported, but *Chinchillula*'s basal position near the divergence of these two groups seems highly likely.

***Andinomys* Group**

INCLUDED TAXA—*Andinomys* and *Irenomys*.

DIAGNOSIS—Members of the tribe Phyllotini and allied to the *Auliscomys* and *Reithrodon* generic groups, descended from a common ancestor with the following traits: fissure of upper incisor curved or tripartite (3); labial root M1 small or absent (4); two roots m2 (8); well-developed procingulum m2 (22); no reduction hypoflexus M3 (23); length of M3 greater than 25% alveolar length of tooth row (32); anterior masseteric ridge well ventral and posterior to dip in diastema (35); posterior border of mandibular ramus sharply angled (36); premaxillaries at or slightly anterior to incisive plane (37); separation of anterior apices of incisive foramina greater than 80% that of posterior apices (40); nasals broader than interorbital constriction (48); incomplete fusion or vascularization of frontals (53); frontoparietal sutures straight, forming acute or right angle (54, 55); internal carotid not bounded by basioccipital (62); mesopterygoid fossa and parapterygoid fossa subequally broad (64); mesopterygoid fossa reaching M3s (70); posterior palatal pits located subequal or posterior to anterior border of mesopterygoid fossa (73); and maxillary tooth rows posteriorly divergent (74).



FIG. 36. Cranium (FMNH 52479) and mandible (FMNH 52478) of *Chinchillula sahamae*.

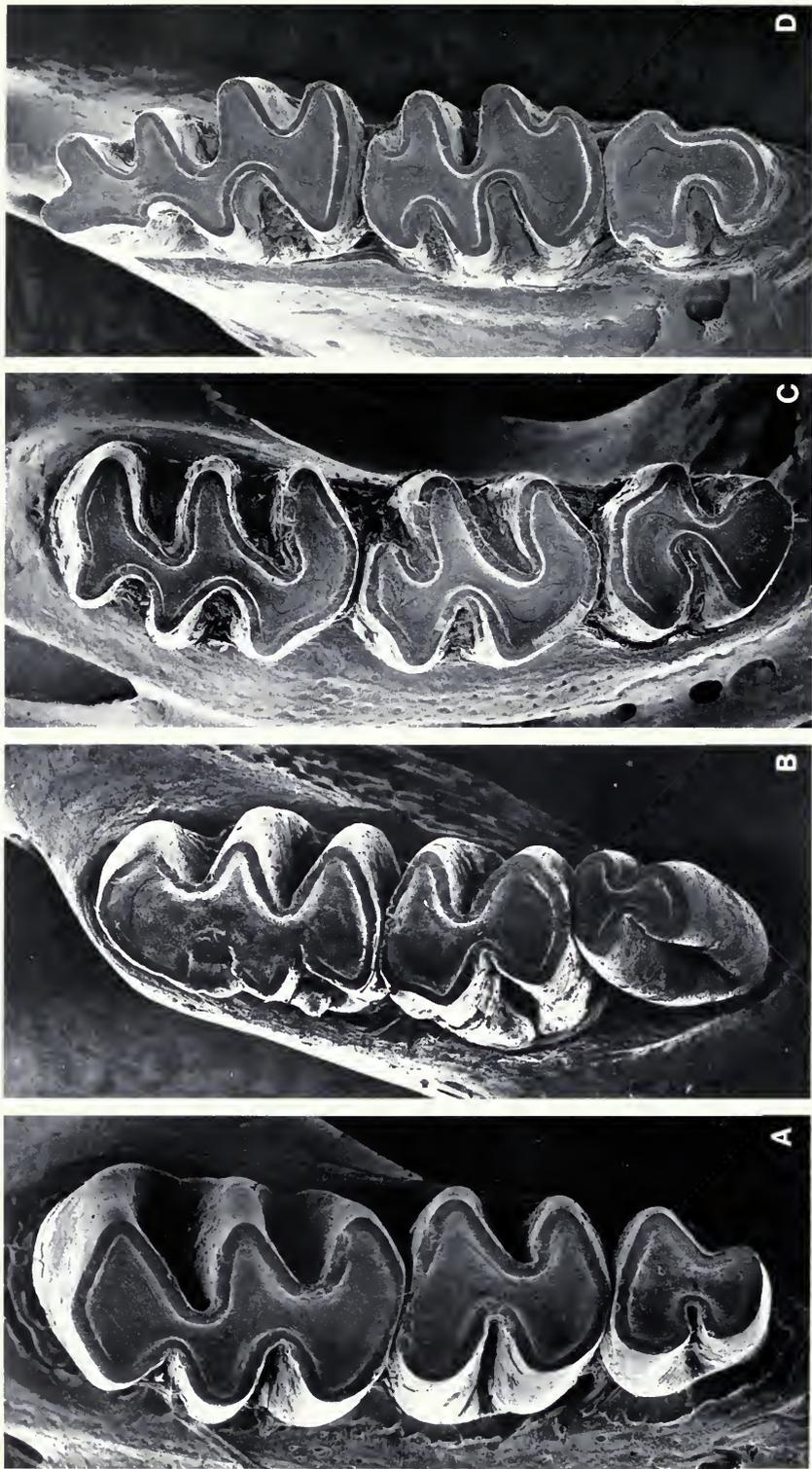


FIG. 37. Upper and lower molars of *Chinchillula sahamae* (FMNH 52478) (A, B) and *Andinomys edax* (FMNH 74869) (C, D).

***Andinomys* Thomas**
(Figs. 37, 38)

Andinomys Thomas, 1902. Proc. Zool. Soc. Lond., 1902(1):116.

TYPE SPECIES—*Andinomys edax* Thomas, 1902, by original designation.

INCLUDED SPECIES—Includes the single species *edax*.

DIAGNOSIS—Members of the *Andinomys* group descended from a common ancestor with the following traits: molars opisthodont (2); labial root of M1 present, small, set medially (4); primary cusps alternate (16); lophs sharply angled; anteromedian flexid m1 prominent (17); mesoflexid m3 highly reduced (28); moderate zygomatic spine, anterior border of zygomatic plate weakly concave (43); supraorbital region anteriorly divergent (49); supraorbital swellings present (52); *fontanelle formed by incomplete fusion of frontals (53); postglenoid foramen anterior to subsquamosal foramen (61); eustachian tubes extend anteriorly to base of pterygoid processes (63); parapterygoid recessed slightly above level of bony palate (67); second cervical neural spine enlarged into “plow”-shaped, distinct keel (82); hypothenar pad intermediate to first interdigital and thenar pads (87); and tail bicolored and densely furred (89, 90).

DISTRIBUTION—Found in the highlands of southern Peru, far northern Chile, southwestern Bolivia, and northern Argentina.

COMMENTS—Previously, I had treated northern and southern populations of *A. edax edax* as separate OTUs for the cladistic analysis (Steppan, 1993) because of geographic differentiation for qualitative characters. Subsequent examination of additional material has indicated that, although the variation is significant, it is also complex, and the recognition of separate taxa would be premature until a thorough generic revision has been conducted.

***Irenomys* Thomas**
(Figs. 39, 40)

Irenomys Thomas, 1919. Ann. Mag. Nat. Hist., ser. 9, 3:201.

TYPE SPECIES—*Reithrodon longicaudatus* Philippi, 1900, by original designation.

INCLUDED SPECIES—*Irenomys tarsalis* (Philippi, 1900).

DIAGNOSIS—Members of the *Andinomys* group descended from a common ancestor with the following traits: incisors deeply grooved (1); labial root M1 absent (4); three roots on M3 (6); labial root of m1 absent (7); *opposing flexi/flexids of all molars meet at midline, nearly severing mures/murids (13); cusps opposite (16); posterolophid of m1 absent (19); procingulum of M2 absent (21); height of the coronoid process subequal with mandibular condyle (34); incisive foramina extending to protocone (38); hamular process of the squamosal reduced in thickness along entire length (60); medial process of the posterior palate absent (71); alisphenoid strut present as a consistent dorsal process that does not cross the foramen ovale (78); more than 30 caudal vertebrae (80); deltoid tuberosity greater than 59% of the length of the humerus measured from the condyle (84); heels of the pes only sparsely furred (88); and tail monocolored (89).

DISTRIBUTION—Low to moderate elevations from Ñuble Province in south central Chile to the Straits of Magellan; Chiloé Island and Guaitecas Islands.

COMMENTS—Characters, distribution, and ecology reviewed by Kelt (1993).

***Reithrodon* Group**

INCLUDED TAXA—Includes the highly differentiated genera *Euneomys*, *Neotomys*, and *Reithrodon*. This group was first formally identified by Olds and Anderson (1989).

DIAGNOSIS—Members of the tribe Phyllotini allied to *Loxodontomys* and the *Auliscomys* and *Andinomys* groups, descended from a common ancestor with the following traits: distinct grooves on the upper incisors (1); tripartite dentine lake in the upper incisors (3); *sigmoidal molars; three roots on M3 (6); no labial root on m1 (7); indistinct or weakly developed anterolabial cingulum m1 (14); procingulum on m2 absent (22); no reduction or shift of m3 mesoflexid (28, 29); length of M3 greater than 20% alveolar length of tooth row (32); height of the coronoid process subequal with the mandibular condyle (34); posterior border of mandibular symphysis sharply angled or with distinct process (36); strong zygomatic plate; anterior root of zygomata inserting near or on dorsal surface of rostrum (41); *premaxillo-maxillary suture with acutely angled bend, so that it lies nearly horizontal as it passes under ventral surface of rostrum (45); interorbital region narrow; supraorbital



FIG. 38. Cranium (FMNH 29157) and mandible (FMNH 23435) of *Andinomys edax*.



FIG. 39. Cranium and mandible of *Irenomys tarsalis* (FMNH 133164).



FIG. 40. Upper and lower molars of *Irenomys tarsalis* (FMNH 124057) (A, B) and *Euneomys chinchilloides* (FMNH 50600) (C, D).

ridges raised dorsally (51); supraorbital swellings present (52); temporal vacuities positioned anterodorsally (61); mesopterygoid fossa distinctly narrower than parapterygoid fossa (64); posterior width parapterygoid less than 1.5 times anterior width (65); medium to deep parapterygoid fossa (67); maxillary tooth rows posteriorly divergent (74); and fewer than 25 caudal vertebrae (80).

Euneomys Coues

(Figs. 40, 41)

Euneomys Coues, 1874. Proc. Acad. Nat. Sci. Philadelphia, 26:185.

?*Bothriomys* Ameghino, 1889. Act. Acad. Nat. Cienc. Rep. Argentina, 6:118.

Chelemyscus Thomas, 1925. Ann. Mag. Nat. Hist., ser. 9, 15:584–585.

TYPE SPECIES—*Reithrodon chinchilloides* Waterhouse, 1839, by original designation.

INCLUDED SPECIES—Includes *Euneomys chinchilloides* (Waterhouse, 1839), *E. mordax* Thomas, 1912, and *E. petersoni* J. A. Allen, 1903. Status of the fossil *Bothriomys catenatus* (Ameghino, 1889) is uncertain (see Comments).

DIAGNOSIS—Members of the *Reithrodon* group descended from a common ancestor with the following traits: anterior incisor grooves (1); anterolabial cingulum absent (14); *procingulum separated from anterior murid in m1 by fusion of metaflexid and protoflexid (18); posteroflexid in m3 present as shallow groove in juveniles, absent in adults (20); anteroflexus M2 shallow (21); hypoflexus pinched off to form dentine lake in M3 (26); *dorsal surface of zygomatic plate rising above dorsal surface of rostrum, anterior root of zygomatic inserting at dorsal surface (41); zygomatic plate inclined less than 20° from vertical (44); alisphenoid strut present (78); *highly elongated neural spine of third thoracic vertebra (81); and spine of second cervical vertebra overlaps third cervical vertebra (83).

DISTRIBUTION—Andes from central Chile and Argentina to Tierra del Fuego.

COMMENTS—Hershkovitz (1962) lists *Bothriomys*, the type of which is the Pleistocene mandible designated *catenatus* (Ameghino, 1889), as a synonym of *Euneomys*. While the specimen does share with *Euneomys* the number and depth of the lophids, as well as the diagnostic separation of the procingulum on m1, the angles of the labial lophids and the triangular shape of the procingulum are very different from those found in extant *Euneomys*. The triangular shape of the procingulum is

most similar to that found in *Reithrodon* and to a lesser extent *Neotomys*. Likewise, the obtuse orientation of the opposing lophids resembles *Reithrodon* and *Neotomys* more than the parallel lophids in *Euneomys*. In fact, Pardiñas (in press) reports that the type of *Bothriomys* is an immature individual, and synonymizes it with *Graomys*.

Pearson and Christie (1991) provided compelling morphologic evidence for specific distinction between *chinchilloides* and *mordax*, fully consistent with data from karyotypes and ordination of morphometric data (Reise & Gallardo, 1990). *Chelemyscus* is based on a mismatched skin and skeleton whose associated locality is also suspect (Hershkovitz, 1962; Pearson & Christie, 1991). The skull is the type of *fossor*, but it is unclear at this time to which species of *Euneomys* it belongs (Pearson & Christie, 1991). Musser and Carleton (1993) recognized *petersoni* as a species, in contrast to Hershkovitz (1962), Reise and Gallardo (1990), and Pearson and Christie (1991). However, Reise and Gallardo's (1990) results show *petersoni* to be largely distinct from *chinchilloides* in multivariate analyses, with some minimal overlap. Musser and Carleton (1993) correctly call for a rigorous revision.

Neotomys Thomas

(Figs. 42, 43)

Neotomys Thomas, 1894. Ann. Mag. Nat. Hist., ser. 6, 14:346.

TYPE SPECIES—*Neotomys ebriosus* Thomas, 1894, by original designation.

INCLUDED SPECIES—Includes the single species *ebriosus*.

DIAGNOSIS—Members of the *Reithrodon* group descended from a common ancestor with the following traits: *anterior surface of upper incisors slightly concave; *upper incisor grooves forming distinctly pinched fold on lateral margin (1); lower incisors steeply angled; three roots on lower m2 (8); three roots on m3 (9); primary cusps alternate (16); anteromedian flexid lost (17); reduction of mesoflexid in m3 (28); very large M3s, greater than ¼ tooth row length (32); *mandible very deep and robust; indistinct capsular projection of the mandible (33); coronoid process below level of mandibular condyle (34); *distinct ventromedial process of mandibular ramus (36); premaxillaries protruded well anterior of incisive plane (37); *in-



FIG. 41. Cranium and mandible of *Euneomys chinchilloides* (FMNH 133088).



FIG. 42. Cranium and mandible of *Neotomys ebriosus* (FMNH 107842).

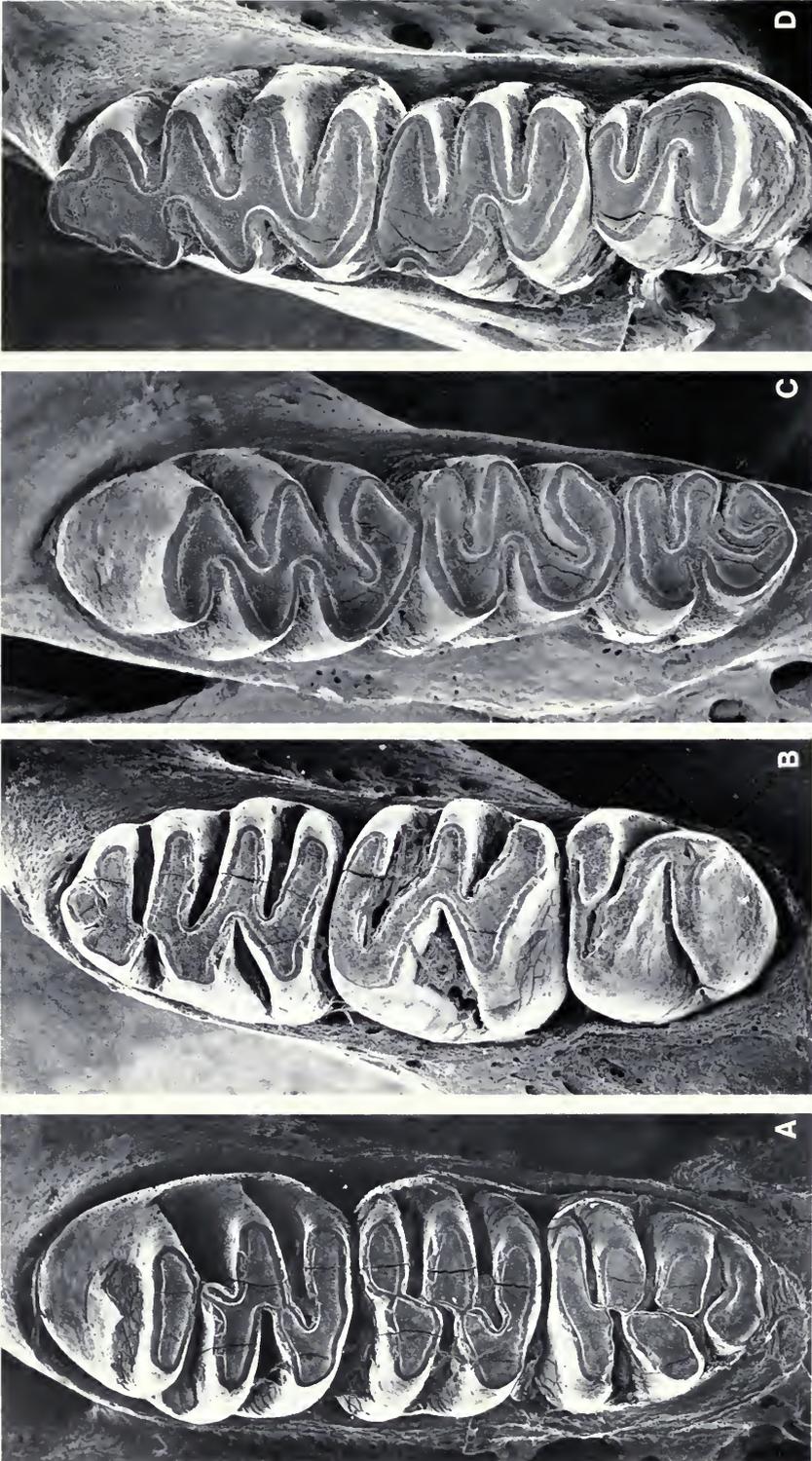


FIG. 43. Upper and lower molars of *Neotomys ebriosus* (FMNH 24777) (A, B) and *Reithrodon auritus* (FMNH 124426) (C, D).



FIG. 44. Cranium and mandible of *Reithrodon auritus* (FMNH 134225).

cisive foramina not reaching anterior conules of M1 (38); anterior apexes of incisive foramina as broadly separated as posterior apexes (40); well-developed zygomatic spine (43); supraorbital ridges weak (51); frontals incompletely fused or vascularized (53); interparietal/parietal length between 0.33 and 0.45 (56); eustachian tubes extend past base of pterygoid processes (63); parapterygoid deeply excavated (67); mesopterygoid fossa reaches M3s (70); distinct posterior palatine ridge (72); stapedia foramen present, sphenofrontal foramen and squamosal-alisphenoid groove absent (76); alisphenoid strut absent (78); neural spine on second cervical vertebra enlarged into "plow"-shaped keel (82); tail bicolored and densely furred (89, 90); and pectoral streak present (92).

DISTRIBUTION—Altiplano and highlands of Peru, southwestern Bolivia, far northern Chile, to highlands of northern Argentina.

***Reithrodon* Waterhouse**

(Figs. 43, 44)

Reithrodon Waterhouse, 1837. Proc. Zool. Soc. Lond., 1837:29.

Ptyssophorus Ameghino, 1889. Act. Acad. Nat. Cienc. Rep. Argentina, Pl. IV.

Tretomys Ameghino, 1889. Act. Acad. Nat. Cienc. Rep. Argentina, Pl. IV.

?*Proreithrodon* Ameghino, 1908. Anal. Mus. Nac. Buenos Aires, 10:424.

TYPE SPECIES—*Reithrodon typicus* Waterhouse, 1837, by original designation.

INCLUDED SPECIES—Includes *auritus* (Fischer, 1814), and *typicus* Waterhouse, 1837.

DIAGNOSIS—Members of the *Reithrodon* group descended from a common ancestor with the following traits: an additional shallow groove at midline of the upper incisors (1); upper incisors hyperopisthodont (2); distinct, laterally positioned, labial root of M1 (4); *two lingual roots on M2; presence of a labial root in m1 (7); three roots on m2 (8); primary cusps alternate (16); protoflexid present on m2 as short groove (22); *incisive foramina extending posterior to hypocone (38); *deeply excised zygomatic plate and long zygomatic spine (43); vaulted cranium; *tegmen tympani does not contact suspensory process of squamosal (58); hamular process of the squamosal reduced along entire length (60); internal carotid canal bounded by both auditory bulla and occipital (62); posterior width of mesopterygoid fossa greater than 2.5 times the anterior width (66); parapterygoids deeply ex-

cavated (67); *optic foramen very large, orbital wings of the presphenoid filamentous (68); distinct posterior palatine ridge (72); *large sphenopalatine foramen (75); *stapedial foramen, sphenofrontal foramen, and squamosal-alisphenoid groove all absent (76); alisphenoid process present (78); 12 thoracic and 7 lumbar vertebrae (79); nuchal ligament sometimes attaches to third thoracic vertebra (81); and first and fifth digits of pes short and subequal in length (86).

DISTRIBUTION—Central and southern Argentina, southern Chile, Uruguay, and southernmost Brazil.

COMMENTS—At least 13 species-group names have been proposed for *Reithrodon*. Its systematics have recently been reviewed by Ortells et al. (1988) in the context of new karyotype data. They recognized two species: *typicus* for the Uruguayan-Brazilian form with $2N = 28$ and *auritus* Fischer, 1814 (= *physodes* Olfers, 1818) for the pampean and central Argentinean form with $2N = 34$. The fossils described as *Reithrodon chapalmalense* Ameghino may not belong to *Reithrodon*. Based on the drawing in Roverto (1914), one anterior cranium lacks two diagnostic characters: the incisive foramina do not extend posterior to the anterior conules, and the premaxillo-maxillary suture does not make an acute-angled bend (diagnostic of the generic group). These two traits cannot be assessed in the Pleistocene fossils attributed to *Ptyssophorus* (left mandible) and *Tretomys* (left upper molars and anterior root of zygomatic), which otherwise appear referable to *Reithrodon*.

Of 16 skeletons examined, one shows a longer neural spine on the third thoracic vertebra than on the second thoracic vertebra; this is the condition otherwise found only in *Euneomys*. Five other skeletons show spines on both T2 and T3 equally elongated, but no alcohol specimens were dissected to verify the insertion of the nuchal ligament, which in ichthyomyines is coincident with the elongated spine (Voss, 1988). The phallus of *Reithrodon* has been characterized by Hooper (1962). Additional taxonomic history can be found in Osgood (1943) and Tate (1932b).

Acknowledgments

Sincere thanks go to Bruce D. Patterson for his contributions in innumerable discussions, his time, and his expertise. Philip Hershkovitz shared many

insights into Neotropical mammals and was always available for discussions. Robert Voss generously examined specimens and added many insights. Thanks go to Sydney Anderson, James L. Patton, and Philip Myers for making specimens available for examination on loan, to Angel Spotorno, Jose Yañez, and Chris Carmichael for access to specimens in their care, and to Bill Stanley, Barbara Stein, Juan Carlos Torres-Mura, and Laura Abraczinskas for assisting with access to specimens. Bruce Patterson and Philip Hershkovitz provided helpful comments on earlier drafts of the manuscript. Michael Carleton, Philip Myers, and three anonymous reviewers provided detailed comments that significantly improved the organization and content of this manuscript. Barry Chernoff, John Flynn, Joel Brown, Jack Fooden, Lawrence Heaney, Oliver Pearson, and Angel Spotorno provided helpful comments in discussions. I thank Betty Strack for her instruction and assistance with the scanning electron microscope. Volunteer Jessica G. Shull drew the illustrations in Figures 6–8, 10–12, 17, and 18. Vincent Ferguson printed the photographs. A. Mayumi Kawamoto assisted with the figure preparation and drew the illustrations in Figures 9 and 15. Financial support was provided principally by the Rowley Graduate Fellowship of the Field Museum of Natural History and the Searle Fellowship of the University of Chicago, as well as by a Collections Study Grant from the American Museum of Natural History, a Grant-in-Aid of Research from the National Academy of Sciences, through Sigma Xi, the Scientific Research Society, a Center for Latin American Studies Travel Grant, and a Grant-in-Aid of Research from the American Society of Mammalogists. The Marshall Field III Fund provided financial support for the acquisition of some of the specimens examined.

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Appendix: Specimens Examined

Specimens are from the Field Museum of Natural History unless otherwise designated. The abbreviations skel(s) and phal(s) designate those specimens from which skeletons or phalli were examined.

Tribe Phyllotini

Calomys callosus—ARGENTINA. Catamarca: La Merced (MSU 19235, 19237—skels). Jujuy: Calilegua (22235—skel, 23373; regarded as *venustus* by Olds, 1988). Tucumán: Concepción (30167–30173; regarded as *venustus* by Olds, 1988). BOLIVIA. El Beni: San Juan (118807, 118808); San Joaquín (117123); Yuatre (118296); Yutiolo (118605, 118610, 118294). Santa Cruz: San Miguel Rincon (AMNH 260686–260690—skels). Tarija: Villa Montes (34238—skel). PARAGUAY. Chaco: Fortín Madrejon, WNW (UMMZ 125466, 125468–125477—skels). Presidente Hayes: Juan de Zalazar, 8 km NE (UMMZ 133915–133922—skels). Total: 35.

Calomys hummelincki—COLOMBIA. La Guajira: W Pto. López, E Maicao (USNM 483982). VENEZUELA. Maru lab colony, originally from Monagas: 45 km S Maturín, close to Río Tigre (USNM 460437–460441, 460447). Monagas: 47 km SSE Maturín, Puente Tigre (USNM 388104, 388105, 388107, 388110, 388113). Total: 12.

Calomys laucha—ARGENTINA. Buenos Aires: Dorrego (50939, 50940, 50942–50945; regarded as *murillus* by Olds, 1988); near Henderson (23395); Partida Balcarce (MSU 16815, 16816, 16818, 16819—skels); Urdampilleta (23405; regarded as *murillus* by Olds, 1988). Río Negro: Chimpay (50932, 50937; regarded as *murillus* by

Olds, 1988). BOLIVIA. Tarija: Villa Montes, 10 km E (AMNH 246668, 246674, 246841, 246849, 246867—skels). PARAGUAY. Presidente Hayes: Juan de Zalazar, 8 km NE (UMMZ 133928—skel). Total: 20.

Calomys lepidus—BOLIVIA. La Paz: Ulla-ulla (UMMZ 121081—skel). PERU. Arequipa: Callalli, 15 km S (MVZ 174019—skel); Laguna Salinas (49752—skel). Ayacucho: San Miguel (75419). Cuzco: Machu Picchu (107823—phal). Huancavelica: Santa Inés (75420). Junín: Carhuamayo (54743). Puno: Hac. Collacachi (49555, 49749—skel, 51429). Total: 10.

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

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

Eligmodontia morgani—ARGENTINA. Neuquén: Chos-Malal (29153); Las Lajas (29155). Río Negro: Choele Choel (41293); Pilcaniyeu (29152). Santa Cruz: Piedra Clavada (35351). CHILE. Aisén: Chile Chico (133010, 133018, 133022, 133025—skels; 133027; 133068—skel); Coihaique Alto (133005—skel); Pto. Ibáñez (133070). Magallanes: Lake Sarmiento (50582). Total: 14.

Graomys domorum—BOLIVIA. Cochabamba: Aiquile (50961—50963); Parotani (21525, 21526); Pena Blanca (AMNH 255966—skel); Tin-Tin (50967—50969, 51920, 51921). Santa Cruz: Comapara (AMNH 260750—260754—skels); Florida (72884). Total: 17.

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

Phyllotis amicus—PERU. Arequipa: Caraveli, Atiquipa (107389—phal). La Libertad: Menocucho (19258—19263). Lima: Chos (107347, 107352—phals). Total: 9.

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

Phyllotis caprinus—ARGENTINA. Jujuy: Maimará (85847); Sierra de Zenta, La Laguna (85848, 85849); Sierra de Zenta (41287). Total: 4.

Phyllotis darwini—CHILE. Aconcagua: Papudo (22679—22684); Pte. Los Molles (119507—119509—skels). Coquimbo: Parque Nac. Fray Jorge (133874, 133875, 133879—133881, 133894; 133896—skel); Romero (22325—22329). Santiago: Cerro Manquehue (119491—119497; 119500—skel). Valparaíso: Olmué (22346). Total: 30.

Phyllotis definitus—PERU. Ancash: Mácate (21126—21128—topotypes). Total: 3.

Phyllotis gerbillus—PERU. Lambayeque: Lambayeque, 16 km NW (MVZ 141847); Mórrope (MVZ 138148, 138149—skels). Piura: Piura (21916, 81265—81273). Total: 13.

Phyllotis haggardi—ECUADOR. Azuay: Contrayerbas (AMNH 61856—skel). Chimborazo: Mt. Chimborazo (53306—53308). Pichincha: Mt. Pichincha (44311, 44313, 44317, 53305, 92012); Salya (53309). Total: 10.

Phyllotis magister—PERU. Arequipa: Arequipa (35360, 35361); Cailloma, Chivay (107690, 107691—phals). Moquegua: Ilubaya, 3 km N Torata (107417); Mariscal Nieto (107469—phal). Tacna: Tarata (107561, 107611—107613, 107616, 107620, 107622—phal, 107623, 107625, 107629; MVZ 143749). Total: 17.

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

Phyllotis wolffsohni—BOLIVIA. Chuquisaca: Padilla, 9 km N (AMNH 263693, 263912, 263913—skels); Río Limon (AMNH 263914—skel). Cochabamba: Liriuni (140814); Pocona (46113); Tapacari (MVZ 120180); Taquiña (50957—50960, 51918, 51919). Santa Cruz: Comarapa, 21 km W (AMNH 263914—skel). Total: 14.

Phyllotis xanthopygus rupestris—BOLIVIA. La

Paz: Esperanza, Pacajes (53607, 53612). CHILE. Antofagasta: E of San Pedro (22303, 22304, 22307, 22308, 22311). Coquimbo: Paiguano (22251, 22271–22273, 22277, 22285). Tarapacá: Arica, 72 km E (133830, 133832, 133835, 133836). PERU. Arequipa: Yura (49744, 49763, 49766). Moquegua: Torata (107405, 107407, 107415—phals). Tacna: Tarata (107617, 197642—phals). Total: 26.

Phyllotis xanthopygus xanthopygus—ARGENTINA. Santa Cruz: Río Ecker (124384–124388, 124436–124439). CHILE. Aisén: Chile Chico (133940, 133943, 133944, 133947, 133958, 133973, 133979, 133982). Magallanes: Última Esperanza, Laguna Lazo (50542). Total: 50.

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

Auliscomys boliviensis—BOLIVIA. La Paz: Pacajes Province, Esperanza (53582, 53583, 53586, 53589–53599). CHILE. Tarapacá: Choquelimpie (22690, 22691). PERU. Arequipa: Cailloma (49765, 49768–49771, 49774—skels); Puno: Pasto Grande, 30 mi W Mazo Cruz (mvz 114719); San Antonio de Esquilache (49574–49577, 49579–49581). Total: 30.

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

Auliscomys sublimis—PERU. Arequipa: Cailloma, Chivay (107696, 107711—phals); Laguna Salinas (49542, 49543, 49546, 49547); Sumbay (49536, 49537, 49539, 49540, 49544, 49545). Puno: Yunguyo, 6 km S (51260); Huacullani (52669–52671); Ilave, 35 km S (107873); Laguna de Lorisgota, 5 mi N (mvz 145613—skel); Puno (AMNH 213596, 213597, 213601). Total: 20.

Chinchillula sahamae—PERU. Arequipa: Cailloma (49406, 49407—skel, 49421, 49422); Sumbay (49401, 49417, 49418). Cuzco: Cordillera de

Sicuani (83475). Puno: Asillo, 3 mi W, Hac. Posocani (51254, 51255); Picotani (52478–52482); Pto. Arturo (53156). Total: 16.

Galenomys garleppi—BOLIVIA. La Paz: Pacajes Province, Esperanza (53845). Oruro: Eucaliptus (AMNH 246941–246947—skels). Total: 8.

Andinomys edax—ARGENTINA. Jujuy: W of Yala (23434, 23435); Tilcara (mvz 120222, 120223, 141617). BOLIVIA. Cochabamba: Ayopaca Province, El Choro (74869). Potosí: Potosí, 20 mi S (mvz 120224–120226); Yuruma (29156, 29157). Tarija: Camataqui, 25 mi SSE (mvz 120227–120232). CHILE. Tarapacá: Arica, 72 km E (132647, 132648, 132651—skels). PERU. Puno: Yunguyo, 6 km S (51279–51283). Tacna: Tarata, 1.5 mi N (mvz 139480, 139481). Total: 27.

Irenomys tarsalis—CHILE. Aisén: La Junta (133164). Chiló: Río Inio (22528, 22529, 22531–22535). Llanquihue: Peulla (50558, 50559—skels; 50563, 50588, 58589). Osorno: Osorno, 84 km SE (124056–124058); Osorno, 53 km SSE (133137, 133138, 133142—skels); Osorno, 44 km SSE (133136, 133139, 133140); Osorno, 32 km SSE (133131, 133155—skel); Maicolpue, 65 km W Osorno (133133, 133136, 133139); Rufugio, Valle de la Picada (127732—skel). Total: 28.

Euneomys chinchilloides—ARGENTINA. Tierra del Fuego: Lago Fagnano (50736). CHILE. Aisén: Pto. Ibáñez (133088, 133089—skels; 134027; 134181, 134182—skels; 134183, 134184, 134186, 134233). Magallanes: Pta. Arenas (50600, 50601). Total: 12.

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

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

Reithrodon auritus evae—ARGENTINA. Neuquén: Estancia Alicurá (mvz 151033); Lago Nahuel Huapí, 11 km NNE (mvz 165853, 169013). Río Negro: San Carlos de Bariloche, 18 km SE (mvz 162272); Comallo, 8 km WSW (mvz 164031). Total: 5.

Reithrodon auritus pachycephalus—CHILE.

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

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

Other Specimens Examined for Phylogenetic Analyses

OLD WORLD “CRICETIDS”

Subfamily Calomyscinae

Calomyscus baluchi—AFGHANISTAN. Bamian: 7.5 mi W Shibar Pass (102956, 102957, 102959); S. Atallah (102960–102962, 102964). PAKISTAN. Malakand: Swat, Karakar Pass (140403–140407—skels). Total: 12.

Subfamily Cricetinae

Cricetulus migratorius—IRAN. Azerbaijan: Rezaieyeh (57893, 57900, 96957–96961). Tehran: DoAb (96956). Total: 8.

Mesocricetus auratus—Asia: captive (122237—skel); domesticated (57114—skel). Total 2.

Phodopus sungorus—Asia: zoo specimens (58804, 58983, 58984, 134492—skels); domesticated (MSU 34350, 35465—skels). Total 6.

Subfamily Mystromyinae

Mystromys albicaudatus—SOUTH AFRICA. Transvaal: Johannesburg (38147). Total: 1.

NEW WORLD “CRICETIDS”

Subfamily Tylomyinae

Nyctomys sumichrasti—COSTA RICA. Puntarenas: Monteverde (USNM 559055, 556461); San

Geronimo (35182–35186). GUATEMALA. Esuintla: Finoa St. Christina (73501—skel). HONDURAS (43308—skel). MEXICO. Chiapas: Ocosingo (64186). PANAMA. Canal Zone: Rodman Ammo Depot (USNM 396407). Chiriqui: Cerro Punta Casa Tilly (USNM 323881). Darién: La Laguna (USNM 338266), El Aguacate (USNM 503722), Bocas del Toro (USNM 323880), Cerro Atul (USNM 306974). Total: 16.

Tylomys nudicaudus—GUATEMALA. Chimaltenango: Yerocapa, Finca Recreo (64568—skel, 64569). MEXICO. Chiapas: Palenque (66949). Oaxaca: San Gabriel Mixtapec, 23 mi N (UMMZ 114186, 114187—skels). Veracruz: Cerro Balzapote (127151). MSU lab colony (UMMZ 159340, 159341—skels). Zoo specimens (60029, 60030, 60767, 104815—skels). US National Zoo (USNM 398072, 398073, 520882, 520883). Total: 16.

Subfamily Neotominae

Neotoma floridana—USA. Arkansas: Logan Co., Magazine Mtn. (67699); Scott Co., Fourche La Fave River (67700); Stone Co., Marcella (63994, 63996). Illinois: Union Co., Pine Hills (64333—skel, 64335). Total: 6.

Ochrotomys nuttalli—USA. Illinois: Alexander Co., Olive Branch (21198—skel). Louisiana: Caldwell Co., Columbia (16486–16488, 16490). North Carolina: Buncombe Co., Weaverville (5265). Total: 6.

Peromyscus leucopus—USA. Illinois: Johnson Co., Ozark (15745–15747, 15752—skel); Pope Co., Golconda (15708, 15709); Union Co., Cobden (139895—skel). Total: 7.

Scotinomys teguina—COSTA RICA. Puntarenas: Monteverde (128560–128563—skels, 128564–128566). Total: 7.

Tribe Akodontini

Akodon albiventer—BOLIVIA. Potosí: Uyumi (mvz 120233—skel). CHILE. Tarapacá: Arica 72 km E (129981–129983—skels, 129986); Putre (129992–129993—skels). PERU. Moquegua: Toquepala (mvz 145543—skel). Puno: Yunguyo (51300). Tacna: Tarata (107578–107581, 107600, 107618, 107621, 107644). Total: 17.

Akodon boliviensis—PERU. Puno: Ilave, 5 km

W (107869, 107882, 107886, 107889, 107892); Santa Rosa, 6 km W (107917, 107928, 107976—skels), 12 km S (mvz 171615, 171617, 171618, 171620, 171621—skels); Yunguyo (51294–51299). Total: 19.

Chroecomys andinus—CHILE. Antofagasta: Pocos (mvz 119554—skel). Tarapacá: Parque Nac. Lauca, Parinacota (130001, 130002—skel, 130004—skel). PERU. Moquegua: Torata (107511, 107516, 107522, 107523, 107525, 107526, 107540, 107541). Total: 12.

Chroecomys jelskii—PERU. Arequipa: Cailloma (49767—skel; mvz 174281, 174283, 174287–174289—skels). Puno: Macusani (mvz 173249, 173251, 173255). Santa Rosa (107919, 107921, 107931, 107932—skels). Total: 13.

Oxymycterus hispidus—ARGENTINA. Misiones: Río Paraná, Caraguaytay (26753–26757; 26841, 26856, 26857—topotypes); Pto. Aguirre (23843). Total: 9.

Tribe Ichthyomyini

Anotomys leander—ECUADOR. Napo: Papallacta, 6.9 km W (UMMZ 126926, 155598–155630—skels). Pichincha: Chinchin Cocha (53367). Total: 8.

Ichthyomys hydrobates—COLOMBIA. Cauca: Chisquío (90293). VENEZUELA. Mérida: La Mucuy (UMMZ 156375—skel). Total: 2.

Neusticomys monticolus—COLOMBIA. Antioquia: Santa Bárbara (71219–71223); Urrao (71218—skel). Huila: San Agustín (71224, 71225). ECUADOR. Napo: Papallacta (UMMZ 155604–155606—skels). Pichincha: Old Santo Domingo Trail (UMMZ 126299, 155789, 155790, 155793—skels). Total: 15.

Tribe Oryzomyini

Holochilus brasiliensis—BOLIVIA. Beni: mouth Río Baures (AMNH 210218–210223—skels). PARAGUAY. Presidente Hayes: Chaco, 15 km NNW (UMMZ 125997–126003, 126005—skels). PERU. Loreto: Río Amazonas (88913–88917); Yarina-cocha (55471, 55476, 62089). Total: 22.

Neacomys spinosus—COLOMBIA. Putumayo: Mecaya (71784—skel). PERU. Cuzco: Paucartambo, 72 km NE (UMMZ 160544—skel). Madre de Dios: Río Alto Madre de Dios (UMMZ 160545—

skel). Pasco: Puerto Victoria (51358—skel). Puno: Bella Pampa (mvz 116665—skel); Sagrario (52495—skel); Río Cayumba, Hac. Exito (24761–24763). Total: 9.

Nectomys squamipes—BOLIVIA. La Paz: Alcoche (117119). BRAZIL. São Paulo: Barra do Rio Juquiá (93046–93048); Ilha do Cardoso (141630–141633, 141636—skels); Primeiro Morro (94393–94379); Ribeirão Fundo (94395); Rocha (94400, 94402—skels); São Sebastião (18200). COLOMBIA. Antioquia: Bellavista (70110, 70111, 70113—skel). Total: 20.

Oligoryzomys fulvescens—COSTA RICA. Puntarenas: Finca Helechales (USNM 547949). GUATEMALA. Chiquimula: Esquipulas (73546–73548—skels). MEXICO. Oaxaca: San Gabriel (AMNH 190328—skel). Puebla: Huachinango (61833, 61834). Veracruz: Achotal (14105–14108, 15882X). PANAMA. Cerro Azul (USNM 305677). Total: 11.

Oryzomys capito—ECUADOR. Napo, San Jose de Payamino (125052, 125058, 125059, 125063—skels). PERU. Cuzco: Quincemil (75222, 75255, 75260, 75270). Madre de Dios: Manu (139864, 139865, 139868, 139869—skels). Total: 12.

Oryzomys palustris—USA. Florida: Highlands Co., Lake Istikpogo (AMNH 242517, 242518), Lake Placid (AMNH 242519, 242521, 242524). Mississippi: Copian Co., Burnell (48450, 48452–48455). New Jersey: Salem Co. (AMNH 232365). Texas: Jefferson Co., Hildebrandt Acres (134427, 134428). Total: 14.

Pseudoryzomys simplex—BOLIVIA. El Beni: San Joaquín (118810). PARAGUAY. Chaco: Ta-caagle (34236). Presidente Hayes: Villa Hayes, 24 km NW (UMMZ 133913). Total: 3.

Zygodontomys brevicauda—COLOMBIA. Bolívar: Socorré, upper Río Sinú (69152—skel). PANAMA. Santa Rita de le Charrero (MSU 20669—skel). SURINAM. Brokopondo: Kwak-oegron (95688, 95784—skels; 95788). TRINIDAD. Cuara (5348). Princetown (5349–5351—topotypes). VENEZUELA. Zulia: Empalado Sabana (18740—skel). Total: 10.

Tribe Scapteromyini

Kunsia tomentosus—BOLIVIA. Beni: San Joaquín (122710, 122711). Total: 2.

Scapteromys tumidus—BRAZIL. Rio Grande do Sul (AMNH 235430–235432—skels). PARA-

GUAY. Cordillera: Tobati (UMMZ 125954, 125956, 137071—skels). URUGUAY. Canelones: Balneario, Salinas (122712, 122713). San Jose: Río Santa Lucía (122714; AMNH 188783, 188784—skels). Taecuarembó: Río Negro (AMNH 188782). Total: 13.

Tribe Sigmodontini

Sigmodon hispidus—BRITISH HONDURAS. Cayo, 12 km S (UMMZ 62985—skel). MEXICO. Chiapas: Bochil (UMMZ 92598—skel). Veracruz: Tenochtitlan (UMMZ 116335, 116336, 116338—skels). USA. Florida: Alachua Co., Gainesville (7955–7963). Georgia: Camoen Co., St. Marys (7953); Lanier Co., Oldfield (135121, 135122—skels); Lowndes Co., I-75 and GA-31 (135123–135125—skels). Louisiana: Hackley (16383–16386, 16388). New Mexico: Otero Co., near Tularosa (125371, 125373—skels). Total: 27.

Tribe Wiedomyini

Wiedomys pyrrhorhinos—BRAZIL. Ceará: Ibiapaba (25249). Pernambuco: Exu (136941); Garanhuns (136942). Locality unknown (USNM 538306, 538314, 538382, 538386–538388). Total: 9.

Thomasomyine Group

Chilomys instans—COLOMBIA. Huila: Las Bardas (71493); San Agustín (71499, 71609). ECUADOR. Cañar: Chical (AMNH 62922—skel). Pichincha: Saloya (53403); Volcan Pichincha (53405). VENEZUELA. Mérida: Páramo Tambor (22172—skel). Total: 7.

Rhipidomys latimanus—COLOMBIA. Antioquia: San Jerónimo (70235, 70237, 70238—skels, 70241, 70242). Huila: Pitalito (71710—skel). ECUADOR. Imbabura NE Penahevvá (UMMZ 77245, 77247—skels). Total: 8.

Thomasomys aureus—BOLIVIA. Cochabamba (AMNH 260422). La Paz: Yerbani (UMMZ 155942—skel). COLOMBIA. Antioquia: SE Medellín (70330—skel); Ventanas (70321—skel). Caldas: Termales (71263, 71264). PERU. Cuzco: Limacpuncu (75228, 75230–75235); Paucartambo, 72 km NE (MVZ 166711—skel; UMMZ 160575—skel). Total: 15.

Thomasomys baeops—COLOMBIA. Huila: San Agustín (71466, 71467, 71472, 71476). ECUADOR. Azuay (AMNH 47677, 61925, 61953); El Oro (AMNH 47699); Loja (AMNH 61363). Total: 9.

Thomasomys rhoadsi—ECUADOR. Pichincha: Cerro Antisana (43246–43250); (AMNH 213548—skel). Total: 6.

Sigmodontinae incertae sedis

Punomys lemminus—PERU. Arequipa: Huaylarco (MVZ 116036). Puno: Abra Aricoma (MVZ 139588, 139589); Limbani, 8 mi. SSW (MVZ 114757, 114758, 116190–116194); San Antonio de Esquilache (49710—holotype). Tacna: Tarata, 20 km NE (MVZ 115948). Total: 12.

Other Specimens Examined for Vertebral Counts (Table 5)

Aepeomys lugens—VENEZUELA. Mérida (USNM 387955). Total: 1.

Akodon (Abrothrix) longipilis—ARGENTINA. Río Negro (MVZ 155725, 155726, 155728, 155729, 163364); Santa Cruz (UMMZ 157154). CHILE. Valparaíso (130905, 130907–130910). Total: 11.

Akodon (Abrothrix) sanborni—CHILE. Chiloé (127565, 127566, 127568, 127569, 127572); Osorno (MVZ 154128, 154130). Total: 7.

Akodon aerosus—PERU. Cuzco (MVZ 166777–166779, 166784); Puno (MVZ 173172, 173174, 173175, 173180). Total: 8.

Akodon azarae—ARGENTINA. Buenos Aires (22233); Corrientes (MVZ 166106—skel); La Pampa (MVZ 173730—skel). Total: 3.

Akodon cursor—BRAZIL. Rio de Janeiro (26626); Pernambuco (123060); São Paulo (141606–141614). Total: 11.

Akodon mollis—PERU. Ancash (129212, 129213, 129215, 129216). Total: 4.

Akodon neocenus—ARGENTINA. La Pampa (MVZ 173726, 173732, 182025). Total: 3.

Akodon olivaceus—ARGENTINA. Neuquén (MVZ 163455, 166063); Río Negro (MVZ 155752–155754). CHILE. Aisén (22230, 22237, 22238); Chiloé (132169–132173, 132275, 132278, 132279); Valdivia (MVZ 154125–154127). Total: 19.

Akodon puer—PERU. Arequipa (mvz 174009, 174100); Puno (mvz 173238, 173240, 173241, 173244, 173245). Total: 7.

Akodon subfuscus—PERU. Ayacucho (mvz 174246–174248); Puno (mvz 173229, 173234–173236). Total: 7.

Akodon urichi—TRINIDAD AND TOBAGO. Tobago (USNM 540711). VENEZUELA. Aragua (USNM 517596, 517599, 517600); Bolivar (USNM 448568). Total: 5.

Akodon torques—PERU. Cuzco (mvz 166744–166751, 166760, 166762). Total: 10.

Akodon xanthorhinus—ARGENTINA. Río Negro (mvz 158401); Tierra del Fuego (USNM 482127, 482129, 482130, 482132–482134). CHILE. Magallanes (127301–127305). Total: 12.

Akodon (Deltamys) kempii—URUGUAY. Rocha (AMNH 206139, 206140, 206142). Total: 3.

Akodon (Microxus) bogotensis—VENEZUELA. Mérida (USNM 374612); Táchira (18678). Total: 2.

Akodon (Microxus) mimus—BOLIVIA. Cochabamba (AMNH 260429, 260586, 260587, 260592, 260593, 260595–260599); La Paz (UMMZ 126779, 155946–155948). PERU. Puno (mvz 171750). Total: 15.

Akodon (Thaptomys) nigrita—PARAGUAY. Itapua (UMMZ 125959–125963, 125968). Total: 6.

Baiomys musculus—MEXICO. Veracruz (56145). Total: 1.

Bolomys amoenus—PERU. Puno (49750; mvz 173191–173193, 173198–173201). Total: 8.

Bolomys lasiurus—PARAGUAY. Paraguari (UMMZ 133947, 137083–137087). Total: 6.

Bolomys obscurus—ARGENTINA. Buenos Aires (MSU 17387). Total: 1.

Brachytarsomys albicauda—MALAGASY (AMNH 100690–100692). Total: 3.

Brachyuromys ramirohitra—MALAGASY (5623). Total: 1.

Calomys musculinus—ARGENTINA. Buenos Aires (MSU 19398); Río Negro (MSU 19186, 19187, 19189). Total: 4.

Cricetulus barabensis—Locality unknown (USNM 521109). Total: 1.

Cricetulus longicaudatus—CHINA. Qinghai (USNM 449101, 449115–449118). Total: 5.

Cricetus cricetus—GERMANY. (AMNH 31814). POLAND (USNM 49413). US National Zoo (USNM 294370, 294371). Total: 4.

Chelemys macronyx—ARGENTINA. Río Ne-

gro (mvz 174385–174387). CHILE. Aisén (132957–132959, 132962, 132963); Magallanes (50530). Total: 9.

Delomys dorsalis—BRAZIL. São Paulo (145370, 145371). Total: 2.

Delomys sublineatus—BRAZIL. São Paulo (141628, 141629). Total: 2.

Eliurus myoxinus—MALAGASY. Ampitambe (AMNH 31801). Total: 1.

Geoxus valdivianus—ARGENTINA. Río Negro (mvz 155817, 163382, 172206); Santa Cruz (USNM 49522). CHILE. Osorno (127726, 133090, 133099–133101). Total: 6.

Gymnuromys roberti—MALAGASY (USNM 49670, 49671). Total: 2.

Holochilus brasiliensis vulpinus—ARGENTINA. Entre Rios (UMMZ 166268, 166269, 166399, 166692). URUGUAY. Canelones (AMNH 206362); Sori (AMNH 206372). Total: 6.

Holochilus chacarius—PARAGUAY. Alto Paraguay (UMMZ 166255, 166256, 166259, 166267, 166314, 166438, 166450). Total: 8.

Ichthyomys tweedii—EUCADOR. Pichincha (UMMZ 126300, 155782, 155786, 155787). Total: 4.

Lundomys molitor—URUGUAY. Trienta y Tres (AMNH 206392, 296393). Total: 2.

Macrotarsomys bastardi—MALAGASY. Finarantsoa (USNM 328800, 328806); Toliara (USNM 578716–578718). Total: 5.

Melanomys caliginosus—COLOMBIA. Meta (AMNH 15497). Santa Marta (USNM 280606). COSTA RICA. Heredia (128471, 128472, 128476, 128477, 128484, 128485, 128488, 128489). Total: 10.

Microryzomys altissimus—ECUADOR. Cañar (AMNH 63052); Imbabura (125043); Pichincha (AMNH 213549). Total: 3.

Microryzomys minutus—BOLIVIA. Cochabamba (AMNH 260419). ECUADOR. Tungurahua (47597). VENEZUELA. Mérida (USNM 374373, 374380, 374443); Sucre (AMNH 69894, 69896). Total: 7.

Mystromys albicaudatus—Location unknown (USNM 396240). Total: 1.

Neacomys guianae—BRAZIL. Para (USNM 549553). FRENCH GUYANA. Paracou (AMNH 266555–266558). Total: 5.

Neacomys spinosus—BOLIVIA. Santa Cruz (AMNH 261987, 261989–261991, 263815). ECUADOR. Napo (USNM 534372, 574567). Total: 7.

Neacomys tenuipes—COLOMBIA. Antioquia (USNM 499556, 499557, 499559). VENEZUELA. Aragua (USNM 517585). Total: 4.

Nesomys audeberti—MALAGASY. Finarantsoa (USNM 448946, 449232). Total: 2.

Nesomys rufus—MALAGASY. Finarantsoa (USNM 448954, 448962–448964). Total: 4.

Nesoryzomys narboroughi—ECUADOR. Galapagos (30844; USNM 364938, 364939). Total: 3.

Nesoryzomys indefessus—ECUADOR. Galapagos (30853). Total: 1.

Notiomys edwardsii—ARGENTINA. Río Negro (MVZ 163065). Total: 1.

Oecomys bicolor—BOLIVIA, La Paz (UMMZ 155945); Santa Cruz (AMNH 246808, 262009–262011, 263816). COLOMBIA. Caquetá (72093). ECUADOR. Napo (125044, 125045, 125047). GUYANA. Muzaruni-Potaro (AMNH 64130). PANAMA. San Blas (USNM 335532, 335533). PERU. Madre de Dios (UMMZ 160550). Total: 14.

Oecomys concolor—VENEZUELA. Aragua (USNM 399535, 517572, 517573). Total: 3.

Oecomys mamorae—BOLIVIA. Santa Cruz (AMNH 262013). Total: 1.

Oecomys paricola—GUYANA. Mazaruni-Potaro (AMNH 48142). Total: 1.

Oecomys roberti—BOLIVIA. Pando (AMNH 248996, 262825). BRAZIL. Para (USNM 549537, 549539, 547540). Total: 5.

Oecomys superans—COLOMBIA. Caquetá (125064). PERU. Pasco (AMNH 213540, 232140). Total: 3.

Oecomys trinitatis—PANAMA. Darién (USNM 305708, 310549, 310550). VENEZUELA. Mérida (21823). Total: 4.

Oligoryzomys andinus—BOLIVIA. Oruro (AMNH 260405); Potosí (AMNH 255946). PERU. Ancash (FMNH 129240). Total: 3.

Oligoryzomys chacoensis—BOLIVIA. Chuquisaca (AMNH 262126, 126127, 262129–262131). PARAGUAY. Chaco (UMMZ 125539–125542). Total: 9.

Oligoryzomys delticola—URUGUAY. Durazno (AMNH 205955, 205957, 205959, 205960). Total: 4.

Oligoryzomys destructor—PERU. La Libertad (31702). Total: 1.

Oligoryzomys eliurus—BRAZIL. Mato Grosso (AMNH 134899). Total: 1.

Oligoryzomys flavescens—URUGUAY. Rocha (AMNH 205597–205601). Total: 5.

Oligoryzomys longicaudatus—CHILE. Coquimbo (133215, 133217, 133218; 133596–133599). Total: 7.

Oligoryzomys magellanicus—ARGENTINA. Tierra del Fuego (USNM 482125, 482126). Total: 2.

Oligoryzomys microtis—BOLIVIA. Beni (AMNH 266947–255950, 255952, 255953). Total: 6.

Oligoryzomys microtis fornesi—PARAGUAY. Canendiyu (UMMZ 126013, 126082, 133826, 137018, 137028). Total: 5.

Oligoryzomys nigripes—ECUADOR. El Oro (AMNH 47744, 47745); Pasaje (AMNH 61313). PARAGUAY. Paraguari (UMMZ 133880, 133882, 137041, 137042). Total: 7.

Oryzomys albigularis—COSTA RICA. Heredia (128164, 128462). Puntarenas (128468, 128470, 128573; USNM 559053). ECUADOR. Cañar (AMNH 63330); Pichincha (94979). PANAMA. Darién (USNM 338207). Total: 9.

Oryzomys alfaroi—PANAMA. Darién (USNM 383247, 383256, 383258). GUATEMALA. Esquintla (USNM 275364). Total: 4.

Oryzomys bombycinus—PANAMA. Cerro Azul (USNM 305649, 305653). Total: 2.

Oryzomys buccinatus—PARAGUAY. Canendiyu (UMMZ 133798); Cordillera (UMMZ 126005, 126006). Total: 3.

Oryzomys capito—BOLIVIA. Beni (AMNH 209961, 209968, 210016–210018). Total: 5.

Oryzomys chapmani—MEXICO. Oaxaca (AMNH 254698–254700). Total: 3.

Oryzomys couesi—GUATEMALA. Esquintla (USNM 275365). NICARAGUA. Managua (AMNH 178028, 178030). Total: 3.

Oryzomys intermedius—BRAZIL. São Paulo (94549, 94550, 141637–141641). Total: 7.

Oryzomys keaysi—BOLIVIA. Cochabamba (AMNH 260346–260349, 260351). Total: 5.

Oryzomys melanotis—MEXICO. San Luis Potosí (AMNH 254713–254716). Total: 4.

Oryzomys nitidus—PARAGUAY. Itapua (UMMZ 126008). Total: 1.

Oryzomys polius—PERU. Amazonas (129242, 129243, 129245). Total: 3.

Oryzomys ratticeps—PARAGUAY. Canendiyu (UMMZ 133794); Itapua (UMMZ 136007); Misiones (UMMZ 125458, 125459). Total: 4.

Oryzomys subflavus—BOLIVIA. Beni (AMNH 210024–210027). Total: 4.

Oryzomys talamancae—COLOMBIA. Chocó

(72408). EUCADOR. Loja (AMNH 61335). VENEZUELA. Zulia (USNM 448597, 448605, 448607–448609). Total: 7.

Oryzomys xantheolus—PERU. La Libertad (44433). Total: 1.

Otodylomys phyllotis—BELIZE. Orange Walk District (58546). GUATEMALA. Alta Verapaz (64564, 64565); Peten (UMMZ 63556); San Miguel (UMMZ 110907). MEXICO. Yucatan (AMNH 91222). Total: 6.

Otodylomys phyllotis fumeus—NICARAGUA. Chinandega (UMMZ 115519). Total: 1.

Oxymycterus delator—PARAGUAY. Canendiyu (UMMZ 126079, 126085–126087), (AMNH 248437). Total: 5.

Oxymycterus inca—BOLIVIA. Santa Cruz (AMNH 260604, 260605, 263344–263347, 263349–263353). Total: 11.

Oxymycterus paramensis—ARGENTINA. Jujuy (22234). BOLIVIA. Entre Rios (USNM 271399). PERU. Puno (52476). Total: 3.

Oxymycterus rufus—ARGENTINA. Buenos Aires (USNM 236296). BOLIVIA. La Paz (AMNH 249003–249005); Tarija (AMNH 262968). BRAZIL. Santa Catarina (USNM 236672). URUGUAY. Canelones (AMNH 206168, 206169); Cerro Largo (AMNH 206177). Total: 9.

Rheomys raptor—COSTA RICA. San Jose (UMMZ 111985, 111986, 112300, 112301). Total: 4.

Rheomys thomasi—EL SALVADOR. Chalatenango (MVZ 98811, 98813, 98815); San Miguel (MVZ 98799–98801, 99805, 131998). GUATEMALA. Huehuetenango (UMMZ 118235). Total: 9.

Rheomys underwoodi—COSTA RICA. Alajuela (UMMZ 115389, 115460). Total: 2.

Rhipidomys couesi—BOLIVIA. Chuquisaca (AMNH 263919); La Paz (AMNH 262991, 262992); Tarija (AMNH 246827). BRAZIL. Mata Grosso (AMNH 134522). TRINIDAD AND TOBAGO. Trinidad (AMNH 212140, 212141, 235071). Total: 8.

Rhipidomys fulviventor—COLOMBIA. Antioquia (71720). Total: 1.

Rhipidomys macconnelli—VENEZUELA. Bolivar (mvz 160083). Total: 1.

Rhipidomys mastacalis—BRAZIL. Goyaz (AMNH 134524); Para (USNM 549554). VENEZUELA. Bolivar (USNM 448620, 448621). Total: 3.

Rhipidomys scandens—PANAMA. Darién (USNM 338265). Total: 1.

Rhipidomys venezuelae—VENEZUELA. Aragua (USNM 517589, 517591, 517592). Zulia (USNM 448629). Total: 4.

Rhipidomys venustus—VENEZUELA. Mérida (USNM 387908). Total: 1.

Sigmodon alleni—MEXICO. Guerrero (UMMZ 109664); Michoacan (UMMZ 109660, 119602, 119604). Total: 4.

Sigmodon fulviventor—USA. Arizona (UMMZ 85455, 85456). Total: 2.

Sigmodon leucotis—MEXICO. Oaxaca (UMMZ 96298; 127152). Total: 2.

Sigmodon ochrognathus—USA. Texas (UMMZ 79140, 79153–79155). Total: 4.

Sigmodontomys alfari—COLOMBIA. Palmares del Pacifico (USNM 483981). ECUADOR. Camolima (UMMZ 77241). PANAMA. Tacarcuna (USNM 310588, 310589, 310590). Total: 5.

Thalpomys lasiotis—BRAZIL. Distrito Federal (128327). Total: 1.

Thomasomys cinereus—ECUADOR. El Oro (AMNH 47659–47661, 47667). Total: 4.

Thomasomys daphne—BOLIVIA. La Paz (UMMZ 155894). PERU. Cuzco (UMMZ 160580). Total: 2.

Thomasomys gracilis—PERU. Cuzco (UMMZ 160584). Total: 1.

Thomasomys hylophilus—COLOMBIA. Norte de Santander (18586). VENEZUELA. Tachira (USNM 442305). Total: 2.

Thomasomys oreas—PERU. Cuzco (UMMZ 160587). Total: 1.

Thomasomys paramorum—ECUADOR. Pichincha (AMNH 213545–213547; FMNH 47595, 47596, 125061). Total: 6.

Thomasomys pyrrhonotus—ECUADOR. Cañar (AMNH 63316, 63326). Total: 2.

Tscherskia triton—NORTH KOREA. Kumhwa (USNM 294636). Total: 1.

Tylomys fulviventor—PANAMA. Darién (USNM 310600, 310602–310605). Total: 5.

Tylomys mirae—COLOMBIA. Boyacá (71216); Caldas (71215). Total: 2.

Tylomys panamensis—PANAMA. Canal Zone (USNM 396409); Cerro Azul (USNM 306972); (USNM 503720, 503721). Total: 4.

Tylomys watsoni—COSTA RICA. Cartago (USNM 566460). Total: 1.



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