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**PHYLOGENETIC ANALYSES OF THE THOMASOMYINI (MUROIDEA:  
SIGMODONTINAE) BASED ON MORPHOLOGICAL DATA**

**(Parts I and II)**

**by**

**Víctor R. Pacheco**

**A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the  
requirements for the degree of Doctor of Philosophy, The City University of New York.**

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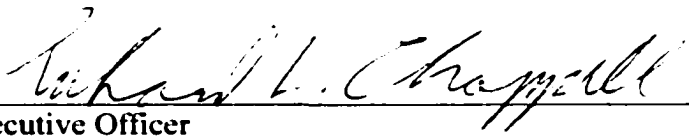
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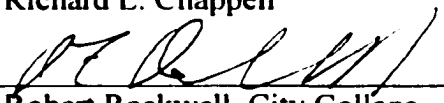
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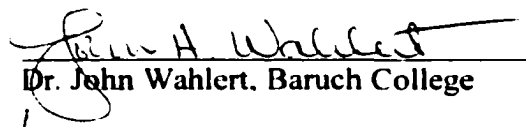
  
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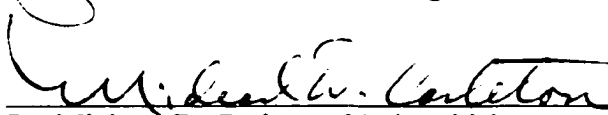
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## Abstract

PHYLOGENETIC ANALYSES OF THE THOMASOMYINI (MUROIDEA:  
SIGMODONTINAE) BASED ON MORPHOLOGICAL DATA

(Parts I and II)

by

Victor R. Pacheco

Adviser: Dr. Robert S. Voss

In part I, the phylogenetic relationships of Thomasomyini were examined based on diverse sets of morphological data (122 characters) for 59 species. Thirty two genera from all the sigmodontine tribes were analyzed as ingroup taxa. Thirteen non-sigmodontine genera were included as outgroups. The monophyly of the thomasomyine group was supported, but with low decay and bootstrap values. The monophyly of Sigmodontinae (sensu Reig, 1980) is moderately supported. The tribal level groups oryzomyines, scapteromyines, and ichthyomyines were also found to be monophyletic; but not the akodontines and phyllotines. Ichthyomyini was placed at the base of the Sigmodontinae. The Oryzomyini and Thomasomyini appear to be sister taxa, sustaining the “pentalophodont” concept of Hershkovitz (1962). The Thomasomyini includes:

Abrawayamys, Aepeomys, Chilomys, Delomys, Juliomys, Phaenomys, Rhagomys, Rhipidomys, Thomasomys (including Erioryzomys, and Inomys), Wiedomys, and Wilfredomys. Delomys and Phaenomys are placed at the base of the tribe. The tribe Wiedomyini Reig, 1980 is synonymized to Thomasomyini. The pairs Wilfredomys + Wiedomys, and Abrawayamys + Rhagomys are found closely related. A monophyletic “Andean” thomasomyine group that includes Aepeomys, Chilomys, Rhipidomys, and Thomasomys is supported. However, the genera Thomasomys and Rhipidomys do not appear to be monophyletic. Aepeomys is nested in a clade of Thomasomys species.

In part II, the monophyly of the Andean thomasomyine group of the Thomasomyini is tested with denser taxon sampling and several suits of morphological characters. The Andean thomasomyine group appears to be monophyletic, and includes Aepeomys, Chilomys, Rhipidomys, and Thomasomys s.l. The monophyly of Chilomys and Rhipidomys is supported. However, Thomasomys as currently understood is clearly polyphyletic; whereas most species of Thomasomys together with Aepeomys lugens and A. reigi cluster with T. cinereus (the type species of Thomasomys), a group of seven species show closer affinities with Rhipidomys. Several generic-level monophyletic groups are recognized and diagnosed to maintain a phylogenetic taxonomy. In addition to Thomasomys s.s. (36 species), these generic-level groups include the aureus group (11 species), the macrotis group (1 species), the oreas group (4 species), the notatus group (1 species), and the bazops group (2 species). Aepeomys, Inomys, and Erioryzomys are synonymized with Thomasomys.

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## Part I



## INTRODUCTION

The subfamily Sigmodontinae (sensu Reig, 1980) which includes the predominantly South American muroid rodents, is an impressive array of no less than 74 genera and 368 species (M.D. Carleton and G.M. Musser, pers. comm.), which are divided among at least seven-tribal level groups depending on the authorities (Carleton and Musser, 1984; Musser and Carleton, 1993; McKenna and Bell, 1997). Topics like the monophyly of the subfamily, monophyly of each of the tribes, and their membership are all highly discussed subjects (Carleton, 1980; Reig, 1980, 1984; Engel et al., 1998; Smith and Patton, 1999). The Sigmodontinae is supported by recent molecular analyses (Engel et al., 1998; Smith and Patton, 1999), but compelling evidence of monophyly based on morphology is lacking (Carleton, 1980; Stepan, 1995). The absence of morphological-based revisions for many sigmodontine groups has limited our understanding of the nature and contents of each of the tribals, as well as the evolution of morphological characters.

Among sigmodontines, the tribe Thomasomyini is a poorly defined group, and one of the least known. This stage of imprecision at higher taxonomic level is unfortunately common among sigmodontine tribes (Smith and Patton, 1999), except for the Ichthyomyini (Voss, 1988). The thomasomyine group includes from seven to nine genera according to recent classifications of mammals (Musser and Carleton, 1993; McKenna and Bell, 1997 respectively). Conversely, other authorities have not recognized the tribe. Reig (1980) included the members of the thomasomyine group with the members of the oryzomyine group in a single tribe, the Oryzomyini. However, support for any of the available classifications based on phylogenetic analyses is absent.

Recent contributions based on morphology and molecular data have questioned thomasomyine monophyly. Voss (1993) suggested that the thomasomyine group as defined by Hershkovitz (1962, 1966) may not be a natural group because the included genera are joined by shared plesiomorphic characters. He suggested that they could be designated as a "plesion" (sensu Wiley, 1981) in formal classifications, or simply called "plesiomorphic Neotropical muroids." This hypothesis was reinforced by results of phylogenetic analyses of sigmodontine rodents based on morphology (Steppan, 1995), and by phylogenetic analyses of sigmodontine rodents based on cytochrome *b* sequencing (Smith and Patton, 1999). However, the latter contribution did support the monophyly of a more restricted thomasomyine group consisting of Thomasomys, Rhipidomys, Chilomys and possibly Aepeomys, which Smith and Patton called the Thomasomyini. In the following pages, I will refer to the tribe Thomasomyini in the traditional sense recognized by Musser and Carleton (1993) and criticized by Voss (1993) as Thomasomyini sensu lato, and I will refer to Smith and Patton's restricted concept as Thomasomyini sensu stricto.

In previous analyses, thomasomyines sensu lato have been allied with sigmodontine and non-sigmodontine rodents. These hypotheses include relationships with oryzomyines (Reig, 1980), akodontines (Smith and Patton, 1993), the peromyscine genus Scotinomys (Steppan, 1995: 56), ichthyomyines (Steppan, 1995: 58), and tylomyines (Hershkovitz, 1962, 1966). Consequently, a reliable and well supported sister group for thomasomyines is ambiguous. Voss (1993: 25) stated that members of his "plesion" "cannot be assigned to any demonstrably monophyletic taxon less inclusive than the Neotropical muroid (= Sigmodontinae)." For this reason, I chose to develop a

phylogenetic analysis of thomasomyines sensu lato in the context of a phylogenetic analysis using the subfamily Sigmodontinae (sensu Reig, 1980) as ingroup, using morphological characters of the integument, pelage, skull, dentition, postcranium, mandible and hyoid apparatus, digestive tract, and urogenital tract.

The present study was designed with the following three purposes: (1) To test the monophyly of thomasomyines sensu lato, a group that includes the following genera: Abrawayaomys, Aepeomys, Chilomys, Delomys, Juliomys, Phaenomys, Rhagomys, Rhipidomys, Thomasomys (including Erioryzomys, and Inomys) and Wilfredomys. This array of taxa is identical in contents to the tribe Thomasomyini of McKenna and Bell (1997) except for the inclusion of Rhagomys, and the exclusion of †Megaoryzomys; and is identical in contents to the “plesion” group of Voss (1993). (2) To find the closer sister taxa for the thomasomyine group sensu lato, if thomasomyine monophyly can be demonstrated. (3) To provide a provisional hypothesis of phylogenetic relationships within the group. Addressing these goals, I intend to provide a testable phylogeny that can serve as a framework for ongoing revisionary studies of thomasomyine genera.

## **HISTORICAL BACKGROUND**

### **The Sigmodontinae**

A detailed history of the systematic position and uncertainties of New World muroid rodents has been presented elsewhere (Rinker, 1954; Steppan, 1995; Tribe, 1996; D'Elia, 2000) and readers are referred to them for lengthy accounts. The following paragraphs provide a short summary and incorporate recent contributions, especially those pertinent to the questions of sigmodontine and thomomysine monophyly.

Hooper and Musser (1964) presented an extensive and pioneering study of the glans penis morphology of Neotropical muroid rodents. These authors concluded that New world muroid rodents can be separated into two distinct geographic groups: one with a "simple" penis type broadly distributed among North American taxa, and the other with a "complex" penis found in a predominantly South American taxa. Later, Hershkovitz (1966, 1969, 1972) employed the tribal names Peromyscini and Sigmodontini, respectively for these groups which he placed within the subfamily Cricetinae of the family Muridae. Reig (1980) was also convinced by this apparent dichotomy and formally recognized the subfamilies Neotominae (including the tylomyine group) and Sigmodontinae for taxa with simple and complex phalli respectively. Later, Reig (1984) also named the subfamily Tylomyinae for the genera (*Tylomys*, etc.) formerly referred to the Neotominae, and this subfamilial trichotomy has been followed by most subsequent authors.

In contrast to previous researchers, Carleton (1980) was first to include information from several morphological character sets in a series of phenetic and

phylogenetic analyses. He found no clear-cut support for the apparent dichotomy based on the morphology of the glans penis, and favored a hypothesis of a simple phallus as ancestral for muroid rodents. He also concluded that the “neotomine-peromyscine” group appears to represent at least four groups of tribal level (neotomines, baiomyines, peromyscines, and tylomyines), and that the predominantly South American muroid group does not constitute a monophyletic clade. However, Carleton (1980: fig. 41) presented a Wagner tree that did support the sigmodontine monophyly.

Similarly, Voss and Linzey (1981) found no support for a dichotomy in New World cricetines based on a comparative morphological study of male accessory glands.

Jacobs and Lindsay (1984) advocated that phyllotines were the primitive group for sigmodontines based on the assumption that molar and mandibular features of Bensonomys represent the plesiomorphic condition for sigmodontines. Previously, Baskin (1978) synonymized the Pliocene fossil Bensonomys of North America with the phyllotine Calomys.

Sarich (1985) presented an albumin immunological dendrogram that depicted a polytomy with three branches: one for Tylomys and Ototylomys, the second for Peromyscus and Neotoma, and the third for a group that corresponds to the subfamily Sigmodontinae.

A DNA hybridization study by Catzefflis et al. (1993) provided additional support for the monophyly of Sigmodontinae and the Neotominae, both of which were included in a clade that included cricetines, arvicolids, and possibly Mystromys.

Musser and Carleton (1993) adopted a conservative approach and expanded the concept of “sigmodontine” to embrace both the “neotomine-peromyscine” and South

American muroid rodents following Carleton (1980) and contra Reig (1980, 1984).

Voss (1993:12) and Voss and Carleton (1993:22) however, assumed the monophyly of a predominantly Neotropical group of sigmodontine genera in which the entepicondylar foramen of the humerus is absent, the entoglossal process of the basihyal is absent, the tuberculum of the first rib articulates with the transverse processes of the seventh cervical and first thoracic vertebrae, and the glans penis is complex. This group corresponds to the "South American cricetines" of Hooper and Musser (1964) excluding Nyctomys (a Central American tylomyine with affinities to Tylomys; see Carleton, 1980). They also assumed that the sigmodontine sister group is to be found among the North and Central American tylomyines, neotomines, peromyscines, and other genera with simple phalli. However, they remarked that no morphological research results justified that assumption, which was based on geographic proximity and biochemical comparisons (Sarich, 1985).

Steppan (1995) also elaborated a phylogenetic analysis of sigmodontines based on morphological data to uncover potential sister groups for his phyllotine analyses, but his results did not constitute a test of sigmodontine monophyly because they were grouped by employing a dummy variable. Sigmodontinae was not monophyletic in his analyses when no dummy variables were included. Monophyly of the subfamily remains to be proved under a cladistic approach, testing whether or not the morphological characters assumed by Voss (1993) and Voss and Carleton (1993) really constitute synapomorphies for the group. Steppan (1995, 1996) also correctly confronted Jacobs and Lindsay (1984)'s arguments and suggested that Bensonomys cannot be a synonym of Calomys or even a phyllotine.

Engel et al. (1998) provided additional support for monophyly of the Sigmodontinae based on their analyses of the mitochondrial genes ND3, ND4L, arginine tRNA, and ND4 genes, and found that the Old World cricetines are the closer sister taxa for the subfamily. However, their sigmodontine exemplars were very limited lacking any scapteromyine, thomasomyine, and ichthyomyine representatives in their analyses.

Similarly, Smith and Patton (1999) examined the phylogenetic relationships of the subfamily Sigmodontinae, based on the complete sequence for the mitochondrial cytochrome *b* (1140 base pairs) from 66 species, and 759 - 1140 base pairs for an additional 19 species. Their samples included representatives of all tribal-level groups of sigmodontines except ichthyomyines. They found relatively strong support for the monophyly of the Sigmodontinae and their data also suggested that Neotominae is the closest sister taxon to Sigmodontinae.

Michaux and Catzefflis (2000) corroborated the relationships of the Sigmodontinae (represented by Akodon) with Neotominae (represented by Neotoma and Peromyscus) based on sequences of the nuclear protein-coding genes Lecithin Cholesterol Acyl Transferase (LCAT).

Michaux et al. (2001) analyzed sequences from the nuclear protein-coding genes Lecithin Cholesterol Acyl Transferase (LCAT) and von Willebrand Factor (vWF), and found Mystromys in a clade with nesomyines, cricetomyines, and dendromurines, and Calomyscus as basal taxon of a clade that included arvicolines, Old World cricetines, sigmodontines (sensu Carleton, 1980), gerbillines, and murines.

Based primarily on this information, I follow the concept of the subfamily Sigmodontinae sensu Reig (1980) and of the subfamilies Neotominae and Tylomyinae

sensu Reig (1980, 1984). However, the monophyly of each of those groups and/or their position among the New World muroids has not been effectively tested in any cladistic analysis of morphological characters.

### **The “Thomasomyine” group**

The nomenclatural history of thomasomyine rodents was first reviewed by Tate (1932a, 1932b), and later by Voss (1993) and Tribe (1996). This section expands and updates the history of the group. Accounts for genera or species are not detailed but included in the text when I consider it is relevant for the understanding of the group.

Thomas (1906) perceived the differentiation of pentalophodont South American rodents when he distinguished a number of species belonging to groups allied to Thomasomys versus Oryzomys. He stated (Thomas, 1906: 443): “ In *Thomasomys*, the mesopterygoid fossa extends further forward (to between the last molars), is, as a rule, rather more squarely open in front than in *Oryzomys* and there are no lateral pits.” In addition, he remarked that most Thomasomys-like taxa were characterized by the possession of 6 mammae, the only exceptions being two Brazilian species of (Thomasomys ferrugineus and T. dorsalis) that exhibit 8 mammae. He also mentioned that the genus Rhipidomys exhibits the same palatal and mammary attributes as Thomasomys, but is distinguished by a long heavily tufted tail, broad climbing feet, and well-marked divergent supraorbital ridges. He also removed Oecomys from Rhipidomys and allied it with Oryzomys, in a group characterized by the presence of 8 mammae and long pitted palates.

Thomas (1917) expanded his former conclusions and remarked on the



differentiation of a Oryzomys-Oecomys group on the one hand, and a Thomasomys-Rhipidomys group on the other. In the latter group he diagnosed and included five genera: Rhipidomys, Thomasomys, and three newly proposed genera (Phaenomys for Oryzomys ferrugineus, Delomys for Hesperomys dorsalis, and Inomys for Oryzomys incanus). In this way, Thomas presented the core of what is currently known as the thomomyine group. With this arrangement, Thomas restricted the definition of Thomasomys and its distribution to the Andean region. He wrote (Thomas, 1917: 194): “the removal of the species ferrugineus, dorsalis, and sublineatus from Thomasomys simplifies the definition and reduces the range of that genus, as these three were outlying Brazilian forms with a different mammary formula, as compared with the true Thomasomys, which inhabits the northern part of the Andean area, with extension eastwards to British Guiana.”

Inomys, one of the newly proposed genera, was diagnosed and distinguished (Thomas, 1917: 197) by “its broad low brain-case, long narrow snout, rounded interorbital region, and small incisors.” Earlier, Thomas (1896) had described Oryzomys lugens and suggested that this species is closely related to O. incanus. Later, Thomas (1898) erected the genus Aepeomys for O. lugens, but, inexplicably, he did not comment on Aepeomys in his description of Inomys.

Thomas (1928) described Thomasomys oenax from Rio Grande do Sul, Brazil, contradicting his own geographic concepts of Thomasomys and Delomys, the former taxon restricted previously by him to the northern part of the Andean region with extension eastward to British Guiana (Thomas, 1917:194).

Tate (1932b) recognized the genera Chilomys, Delomys, Phaenomys, Rhagomys.

Rhipidomys, Thomasomys, Inomys, Aepeomys, all within an oryzomyine group and not supporting Thomas' concept of a separate pentalophodont group allied to Thomasomys.

Osgood (1933a) wrote that neither he nor H.E. Anthony had found any character of "generic importance" to distinguish Aepeomys from Thomasomys. Therefore, he considered Aepeomys as a junior synonym of the latter taxon. Similarly, after reviewing the type of O. incanus, he concluded that Inomys is inseparable from Thomasomys and considered it a junior synonym of Thomasomys as well.

Osgood (1933b) reported Thomasomys pictipes from Misiones, Argentina, and judged that it could be related to T. oenax of Rio Grande do Sul. He argued that the inclusion of oenax in Thomasomys by Thomas (1928) weakened the definition of Thomasomys because of its occurrence outside the Andean region. Osgood then interpreted Thomasomys in a more inclusive sense, and considered Delomys a subgenus of Thomasomys.

Ellerman (1941) maintained Delomys, Inomys and Aepeomys within Thomasomys following Osgood (1933b). For him, Thomasomys was chiefly distinguished by molars of "Oryzomys" type, "narrow" zygomatic plates, unridged interorbital regions, short palates, and six mammae (except in the "dorsalis group"). Osgood's and Ellerman's broad sense of Thomasomys encompasses much of what is now known as the thomasomyine group.

Herskovitz (1944, 1955, 1960) listed the thomasomyine genera with Peromyscus and other North and Central American muroids.

In describing a new genus Wilfredomys for the species previously known as Thomasomys oenax, Avila Pires (1960) considered Phaenomys and Delomys to be good

genera, in contrast to Osgood (1933b) and Ellerman (1941), thus again restricting Thomasomys to the northern Andes.

Cabrera (1961) endorsed Ellerman's (1941) concept of Thomasomys, and also recognized Rhagomys, Rhipidomys, Phaenomys, Chilomys, and Wiedomys as valid genera. However, he listed all South American muroids in the family Cricetidae, proposing no relationships among the genera.

Vorontsov (1959) formalized the tribe "oryzomine" following the list of Tate (1932a, 1932b), without separating the thomasomyines from the oryzomyines.

Hershkovitz (1962: 21, 84) further altered the concept of a thomasomyine group by excluding peromyscines, but including the two Central American muroids Nyctomys and Otonyctomys, the Atlantic Brazilian genus Phaenomys, the widespread neotropical genus Rhipidomys, and Thomasomys (sensu Osgood, 1933a,b ). He apparently overlooked the earlier comment of Thomas (1906: 445) who distinguished Nyctomys from Rhipidomys by the almost obsolete anteromedian cusp of M1. Thomas went on to suggest that: "Nyctomys is ... an offshoot of the Peromyscus stock, with no close relationship to Rhipidomys at all."

Hershkovitz, in his evolutionary concept of the origin and radiation of South American cricetines (1962: fig. 2), envisioned thomasomyines as a sylvan pentalophodont grade at the base of the sigmodontine radiation, from which one lineage gave rise to the oryzomyines and another to the pastoral tetralophodont rodents (akodonts, phyllotines, etc.).

Hooper and Musser (1964) described the glans penis morphology of the thomasomyines Rhipidomys, Thomasomys, and Nyctomys among numerous other

Neotropical muroid rodents. Nyctomys was so distinct from the other thomasomyines that they recommended it be excluded from the group and placed elsewhere. They also stated that phallic data may support the grouping of T. cinereus, T. laniger and R. mastacalis, with the exclusion of T. aureus. Hooper and Musser (1964: 20) remarked that phallic features shared by Thomasomys and Rhipidomys are: "a crenate crater rim bordered by an erect narrow band of non-spinous tissue, and a long baculum (longer than glans), the base of which is shallowly concave ventrally and roughly triangular in ventral view (an apex of the triangle directed proximad)." They recognized the thomasomyine group, along with other four groups of South American cricetines (Oryzomyine, Akodont, Phyllotine, and Sigmodont), but they did not specifically postulate any relationship among them.

Hershkovitz (1966: 125) conceived a thomasomyine group as one of the most coherent among the clustered South American genera that he recognized. He described the group as: "forest dwelling, broad footed, long tailed, 6-mammate, brachyodont-pentalophodont mice with wide-short palate and weakly projecting zygomatic plate. They compose one of the more coherent of the multigeneric groups of South America rodents. Some of the characters shared by the members of the group may be phenetic rather than phyletic but this has yet to be determined."

Gardner and Patton (1976: 32) postulated that thomasomyine karyotypes are characterized by a diploid number of 42 or 44, with predominance of acrocentric autosomal complement.

Pine (1980) judged that the diversity of forms found in Thomasomys did not justify the separation of T. oenax in a different genus and included Wilfredomys oenax

within the genus. However, he considered that the resemblance of Wiedomys pyrrhorhinos with T. oenax in size and coloration, especially the striking reddish patches on the nose and rump, as due to convergence.

Reig (1980) considered that the apparent dichotomy among pentalophodont rodents was not justified and grouped the thomasomyines and oryzomyines in his formally diagnosed tribe Oryzomyini. The oryzomyines subsequently listed by Reig (1984, 1986) suggest that he did not retain the thomasomyines even as a subgroup within his concept of Oryzomyini.

Voss and Linzey (1981) analyzed the male accessory glands of 52 Neotropical muroids, including representatives of thomasomyines (Nyctomys sumichrasti, Thomasomys aureus, T. baeops, T. laniger, and T. rhoadsi) and Chilomys (provisionally considered an oryzomyine). They concluded that Nyctomys departs from South American cricetine group and may not be related to any of them. They also found a unique preputial feature in T. aureus.

Steadman and Ray (1982: 15) provided a formal diagnosis for the tribe Thomasomyini, as a group with a unique combination of characters: "(1) short palate, (2) molars pentalophodont (fide Hershkovitz 1962, 1967), (3) molars medium-sized to large relative to size of the skull." Based on these characters, they included †Megaoryzomys curioi the large extinct recent genus from Galápagos Island, Ecuador, with Thomasomys and Rhipidomys within the thomasomyine group (see table 1).

Cerqueira (1982) conceived the thomasomyine group to include Thomasomys, Rhipidomys, Phaenomys and Delomys, following Avila-Pires (1960).

Eisenberg (1989) also recognized a thomasomyine group. His assemblage included

Aepeomys, Rhipidomys, Thomasomys, and Chilomys (table 1). He distinguished these genera from oryzomyine rodents by a long tail that exceeds head and body length, and by large ears compared to oryzomyines. †Megaoryzomys was explicitly removed from the thomasomyines, and allocated with the oryzomyines (Eisenberg, 1989:347). He also hypothesized that Oryzomyini is phylogenetically closest to Thomasomyini. Reasons or characters were not provided. Redford and Eisenberg (1992: 259) later employed the formal tribal name Thomasomyini, and include the Brazilian species dorsalis, oenax and pictipes in Thomasomys. Subsequently, Eisenberg and Redford (1999) included Delomys and Wilfredomys as valid genera within Thomasomyini, acknowledged that the relationships of Megaoryzomys, Abrawayaomys, Phaenomys, and Rhagomys is problematic, and retained Wiedomys in its own tribe Wiedomyini.

Hutterer and Oromí (1993) reported on additional specimens of †Megaoryzomys curioi from Santa Cruz Island, Galapagos, Ecuador. They reasoned that †Megaoryzomys has cranial and dental characteristics not shared with any Thomasomys, questioning Steadman and Ray (1982)'s argument that Thomasomys was the ancestor of †Megaoryzomys, but concurring with them in that †Megaoryzomys lacks close relationships with Nesoryzomys or Oryzomys. They proposed that †Megaoryzomys is a highly differentiated genus with unknown origins.

Gardner and Romo R. (1993) described Thomasomys macrotis noting that although some dental features are shared with †Megaoryzomys, overall cranial and dental characteristics ally T. macrotis to other Thomasomys rather than to †Megaoryzomys. Leo L. and Gardner (1993) also stated that dental characteristics of †Megaoryzomys serve to place it well apart from other large thomasomyines, although they did not

precisely outline their definition of a thomasomyine group.

Musser and Carleton (1993) recognized Aepeomys, Delomys, Phaenomys, Rhagomys, Rhipidomys, Thomasomys, and Wilfredomys as valid genera of thomasomyines. On the other hand, they retained the tribe Wiedomyini, with Wiedomys and †Cholomys, and regarded Abrawayaomys, and Chilomys as Sigmodontinae incertae sedis.

Voss (1993) provided a detailed morphological revision of Delomys and compared that genus with the type species of Oryzomys and Thomasomys. He found that Thomasomys exhibits the primitive state in a set of analyzed characters whose polarity can plausibly be assessed. He also challenged the validity of the thomasomyines as a natural group, because only plesiomorphic characters have been used to diagnose it. Instead, he proposed the term "plesiomorphic Neotropical muroids" to emphasize its status as an informal group clustered by shared primitive characters. In this group he included: Abrawayaomys, Aepeomys, Chilomys, Delomys, Phaenomys, Rhagomys, Rhipidomys, Thomasomys (including Erioryzomys and Inomys), and Wilfredomys; no comments were provided on †Megaoryzomys and Wiedomys (see table 1). His conclusions were followed, unfortunately often as an axiom, in subsequent researches. However, Voss (1993: 24) was cautious about his conclusions regarding thomasomyines: "This result, of course, depends, on the stated assumptions concerning ingroup [sigmodontine] monophyly and outgroup relationships, and some hypotheses of polarity cannot be defended with much confidence even if those assumptions are granted."

Steppan (1995) included Thomasomys rhoadsi, T. aureus, T. baeops, Rhipidomys latimanus, Chilomys instans, and Wiedomys pyrrhorhinos in his sigmodontine analyses.

He found that neither Thomasomys nor the thomasomyine group is monophyletic but found closer relationships between Rhipidomys latimanus and Thomasomys aureus. He also suggested that W. pyrrhorhinos might belong to the informal "thomasomyine" group as well.

Tribe (1996) provided a comprehensive revision of the thomasomyine genus Rhipidomys. Although no phylogenetic analysis was provided, he suggested that the genus is monophyletic and divided it in three parts: R. leucodactylus group, R. macconnelli group, and R. fulviventer group. He also suggested that †Megaoryzomys should probably be included in Voss's (1993) plesiomorphic group since it was considered to be a thomasomyine by Steadman and Ray (1982). In addition, based on Voss's (1993) character comparisons among Delomys, Thomasomys and Oryzomys, he concluded that derived states occur in only four characters of Rhipidomys: convergent interorbit, reduced stapedial circulation, twelve ribs, and absence of gall bladder. He remarked that the distribution of these states among other sigmodontine genera provides little evidence for the common ancestry of Rhipidomys with Oryzomys, Delomys or Thomasomys to the exclusion of the others, explicitly supporting Voss's arguments, and against the monophyletic nature of the thomasomyine group.

Emmons and Feer (1990, 1997) provided some diagnostic features and notes of natural history for Abrawayaomys, Delomys, Phaenomys, Rhagomys, and Rhipidomys. They listed Abrawayaomys as an oryzomyine, and the other genera as incertae sedis.

McKenna and Bell (1997: 145-146) maintained the thomasomyine group, and expanded its contents to include: †Megaoryzomys, Chilomys, Abrawayaomys, Delomys, Thomasomys, Wilfredomys, Aepeomys, Phaenomys and Rhipidomys, endorsing



Steadman and Ray (1982). They also retained the Tribe Wiedomyini as proposed earlier by Reig (1980) with Wiedomys and †Cholomys, and placed Rhagomys as incertae sedis, all in the subfamily Sigmodontinae (sensu Musser and Carleton, 1993)(table 1).

Engel et al., (1998) claimed that “thomasomyines” are at the base of the South American sigmodontine group. However, they employed Nyctomys as their thomasomyine representative. According to all recent classifications, Nyctomys is placed in the tribe or subfamily Tylomyini(-nae) and is not a thomasomyine nor a sigmodontine (see Carleton, 1980; Voss and Linzey, 1981).

Bonvicino and Otazu (1999) described the karyotype of Wilfredomys pictipes (2N= 36, FN 34) and suggested its karyotype is more similar to those of Rhipidomys than to those of Delomys or species of the tribe Oryzomyini.

Smith and Patton (1999) presented analyses based on cytochrome *b* sequences of an extensive array of sigmodontine species. They found support for a thomasomyine group that included Thomasomys, Chilomys, and Rhipidomys; and suggested that Aepeomys also belongs in the group, concurring with the concept of Eisenberg (1989). They also concluded that neither Delomys, Wiedomys, or Wilfredomys is closely related to the thomasomyines. Two species of Wilfredomys in their analyses, W. pictipes and an undescribed Brazilian species, formed a strongly supported clade. Unfortunately, their analyses did not include Abrawayaomys, Aepeomys, Phaenomys, Rhagomys, or Wilfredomys oenax because tissues were unavailable.

González (2000) recently described Juliomys based on “Wilfredomys” pictipes, rendering Wilfredomys monotypic. Based on the morphological, karyological, and molecular data available, he suggested that Juliomys should be placed as Sigmodontinae

incertae sedis, rather than endorsing a close relationship of Juliomys with Wilfredomys.

Bonvicino et al. (2001) reported additional morphological and cytogenetic information for Phaenomys, comparing it with Juliomys, Delomys, Wilfredomys, Rhipidomys and Thomasomys. They noted that Phaenomys shares important morphological features with other endemic Atlantic Forest genera in support of Smith and Patton's (1999) hypothesis of an endemic Atlantic Forest thomasomyine clade. On the other hand, they found that this group is highly heterogeneous in chromosomal complements, and based nonetheless on diploid number, they remarked that Phaenomys is more similar to Delomys and far from Thomasomys and Rhipidomys.

Voss et al. (2002) erected Handleyomys for the taxon Aepeomys fuscatus Allen, presenting the hypothesis that Handleyomys is member of the oryzomyine clade.

Oliveira and Bonvicino (2002) described Juliomys rimofrons, and place Delomys, Juliomys, Phaenomys, and Wilfredomys in a group informally called the "Atlantic thomasomyines."

## MATERIAL AND METHODS

**Ingroup taxonomic sampling:** I consider the subfamily Sigmodontinae (sensu Reig, 1980) as my ingroup taxon. Monophyly of the Sigmodontinae is supported by Engel et al. (1998) and Smith and Patton (1999) using molecular data. The monophyly of the Sigmodontinae has not been adequately demonstrated by morphological data; however, it is assumed as a working hypothesis by Voss (1993) and Voss and Carleton (1993). Within the Sigmodontinae, I included 46 species in 32 genera, representing all currently recognized tribes: Oryzomyini, Akodontini, Ichthyomyini, Scapteromyini, Sigmodontini, Phyllotini, Wiedomyini, and Thomasomyini following the classification of McKenna and Bell (1997) presented in table 2 as a current hypothesis of tribal limits. All species analyzed are listed in Appendix 1.

The oryzomyines are represented by six genera of 16 known, the phyllotines by five genera of 15 known, the akodontines by four genera of 14 known; the ichthyomyines by three genera of five known, and the scapteromyines by two of three known. The monotypic tribe Sigmodontini is represented by two species of Sigmodon, and the monotypic tribe Wiedomyini by the single extant species Wiedomys pyrrhorhinos. To develop my goals, the tribe Thomasomyini is represented here by exemplars from all the genera currently considered to be members of the tribe, which is equivalent to the plesion of Voss (1993)(table 1). This strategy tests the position of each member of the thomasomyine group in relation to exemplars from other tribes.

Most thomasomyines are well represented by voucher specimens (especially skin and skulls) and their data are relatively complete (ca. 90--100%) in the character matrix

(table 3). However, missing data are unfortunately common for some genera (e.g., Rhagomys, Phaenomys, and Abrawayaomys) that are known from only a few specimens. In the case of Rhagomys and Phaenomys the available skulls are badly fragmented. Wiedomys and Wilfredomys are apparently more common in the wild, but are still poorly represented in museum collections. I chose three species of Rhipidomys to represent the leucodactylus, fulviventer, and macconnelli species groups recognized by Tribe (1996). My examples of Thomasomys (including Erioryzomys and Inomys) include species that represent several informally recognized species groups within the genus. The genus Aepeomys is represented by the type species A. lugens. Chilomys is thought to be monotypic (sensu Musser and Carleton, 1993). For all thomasomyines, I included exemplars that represent currently recognized subspecies.

**Outgroup selection:** Although only one outgroup is needed to root a phylogenetic tree, I follow Nixon and Carpenter (1993) suggestion that phylogenetic results are likely to maintain stability in future studies when more outgroups are used. At least two outgroups are necessary to test ingroup monophyly and to confidently establish character polarities (Maddison et al., 1984). Ideally, outgroups should include the nearest sister-taxa to the ingroup because homoplasy is likely to increase with time (Wiley, 1981; Wiley et al., 1991). In the case of the Sigmodontinae, whose monophyly has not been adequately documented, the choice of outgroups or a specific sister group for sigmodontines have not been firmly proposed. D'Elía (2000) synthesized the current competing hypotheses of muroid subfamilial relationships in a tree in which cricetines, sigmodontines, neotomine-peromyscines, tylomyines and arvicolines form an unresolved polytomy. Moreover, the monophyly of these potential sister groups has not been

adequately sustained. Simmons (1993) explained that monophyly of the outgroups is of potential concern when monophyly of the ingroup has not been adequately supported. Therefore, my choice of outgroups is based on species and not higher-level taxa (i.e., tribes, subfamilies). I included thirteen non-sigmodontine species and genera as outgroups. This number of outgroups was justified by separate analyses of adding and subtracting outgroups. I found that the degree of resolution among the ingroup (Sigmodontinae) was affected by the number of outgroup taxa included, but these results converged as more outgroup taxa were added.

Among my outgroups I included Nelsonia and Neotoma, two of four known genera of neotomines; Nyctomys and Tylomys, two of four known genera of tylomyines; and Baiomys, Ochrotomys, Peromyscus, Reithrodontomys, and Scotinomys, five of twelve known genera of peromyscines.

Sarich (1985) and Catzefflis et al. (1993) found that Microtinae (=Arvicolinae), New World and Old World Cricetidae, and the South African genus Mystromys form an unresolved clade well apart from Murinae. Therefore the inclusion of the arvicoline Microtus, and the cricetines Cricetulus migratorius and Mesocricetus auratus is justified. The South African rat Mystromys was also included as an outgroup in the sigmodontine analysis by Steppan (1995). His results of unconstrained analysis placed this genus within the sigmodontines, an unusual position which he interpreted as the result of convergence. In addition, Engel et al. (1998) found that Mystromys is closer to gerbillines and murines than to sigmodontines; and recently Michaux et al. (2001), based on sequences of nuclear protein-coding genes Lecithin Cholesterol Acyl Transferase (LCAT) and von Willebrand Factor (vWF), found Mystromys to belong in a clade with

nesomyines, cricetomyines, and dendromurines, a group that is basal to calomyscines, arvicolines, Old World cricetines, sigmodontines sensu lato, gerbillines, and murines. I concur with these authors that Mystromys is not closely related to the sigmodontines, and judged it not to be relevant for my analyses.

I included the calomyscine genus Calomyscus as an outgroup because some authors have hypothesized a close relationships of this taxon with some Nearctic muroids of the neotomine-peromyscine group. For example, Osgood (1947) viewed Calomyscus and Peromyscus as remarkably similar and speculated that the former genus represented a late Pleistocene invasion of Eurasia from North America. Later, Pavlinov (1980) considered the auditory ossicles of Calomyscus and sigmodontines as identical. By contrast, Hooper and Musser (1964) did not consider that Calomyscus is closely related to any of the neotomine-peromyscine rodents. The constrained sigmodontine analysis by Steppan (1995: fig. 19) supported this conclusion and placed Calomyscus outside the Sigmodontinae. Recently, Michaux et al. (2001) considered Calomyscus to be a lineage outside of neotomines, peromyscines, arvicolines and the Old World cricetines. Following Hooper and Musser (1964) and Michaux et al. (2001), I rooted my phylogenetic analyses with Calomyscus baluchi on the assumption that it is the most distantly related of the outgroups included in my study.

**Characters:** My data matrix includes 59 taxa scored for 122 morphological characters. Among the characters I analyzed are 17 characters of the integument, 43 characters of the skull, one character of the hyoid, six characters describing the middle ear bones, 21 dental characters, five characters of the mandible, 12 characters of the postcranial skeleton, 12 characters of the glans penis and accessory reproductive glands.

and six characters of the digestive system (Appendix 2). The data matrix was constructed using the program MacClade, version 3.0 (Maddison and Maddison, 1992). In total, 76 characters were binary and 46 multistate; the latter group included 40 characters with three states, five with four states and one with five states.

The matrix includes characters previously reported in the literature and others that I am reporting for the first time. Most of the characters were observed and scored by myself throughout all taxa. However for a few characters (i.e., stomach morphology, glans penis) and for a few species, I relied on the literature. External characters were observed under a stereo microscope from dry and/or fluid-preserved specimens. For the evaluation of skulls, teeth, and mandibles, I examined at least ten specimens for each species when available. For some characters, the organs (stomach, preputial glands, glans penis and gall bladder) were dissected from alcoholic specimens, without any special preparation or staining. Although, modern postcranial skeletal preparations are usually complete, in many older specimens the hands and feet had not been removed from the prepared dry skins. For some species, I removed one hand and foot from the skins, which were then carefully cleaned by dermestid beetles or by hand. With experience, I found that several foot characters can also be evaluated from fluid specimens with minimal dissection.

Missing data were registered in the matrix as "?" or "-". The first symbol was used for data cells that were not evaluated and the latter for inapplicable characters. However, algorithms are not able to differentiate these two coding conventions in the analyses. Two kinds of polymorphism were recognized: taxonomic polymorphism, when more than one state is found in a terminal taxon; and within-species polymorphism, when

a terminal taxon unequivocally recognized as a single species exhibit variability in a character (Simmons, 1993). Additional states were employed to represent cases of within-species polymorphism. This method retains more information than when scoring a polymorphism as missing data (Simmons, 1993). Multistate characters were coded hierarchically except when the results are uninformative characters as explained by Simmons (1993). This method preserves homology information without requiring ordering of the character states.

Completeness of a taxon is defined as the percentage of characters for which it can be scored in a given analysis (Simmons, 1993; Simmons and Geisler, 1998). Data completeness of the entire character matrix was 92%, with a taxonomic range from 62.3% in Rhagomys rufescens to 100% in Akodon boliviensis and Chilomys instans. Several thomomysines from southeastern Brazil accounted for the lowest values in data completeness, such as Phaenomys ferrugineus (64.8%), Abrawayaomys ruschii (71.3%), and Juliomys sp. (79.5%) in addition to the minimally complete Rhagomys rufescens (Table 3). Although some authors exclude taxa with missing data because they may reduce phylogenetic accuracy, recent works suggest that including taxa with incomplete data may have more positive effects on the analyses that outweigh the negative effects (Novacek, 1992; Simmons, 1993; Simmons and Geisler, 1998). Wiens (1998) also supported the practice of including additional taxa rather than avoiding relatively incomplete taxa to have hypothesis useful at a more comprehensive taxonomic scope.

**Phylogenetic analysis:** All analyses were carried out using a beta version of the program PAUP 4.0b10 (Swofford, 1998). The heuristic search option was employed because a large matrix, such as the one analyzed here, is beyond the power of exhaustive



or branch-and-bound methods. I used 1000 repetitions of the heuristic search algorithm with a random taxon addition sequence. Analyses were performed with all characters weighted equally, multistate taxa interpreted as polymorphism, TBR (tree-bisection-reconnection) branch-swapping, multrees and collapse branches options in effect (Swofford and Begle, 1993). Ingroup and outgroup composition was not constrained to allow for a test of ingroup (Sigmodontinae) monophyly (Nixon and Carpenter, 1993). A first set of analyses (Analysis 1) employed all multistate characters unordered.

Recent phylogenetic analysis of muroids were produced with multistate characters ordered (Carleton, 1980; Voss and Carleton, 1993; Steppan, 1995). These works have employed what Wilkinson (1995) termed "composite" character coding, where apparently dependent features are combined in single multistate characters (e.g., glans penis morphology, palatal morphology). Instead, I utilized "reductive" character coding: where characters are broken into apparently independent features (e.g., palatal length, posteropalatal pits). This option reduces the number of composite characters and may obviate the necessity of ordering schemes (Wilkinson, 1995). Wilkinson (1992, 1995) proposed that characters can be ordered by what he termed the "method of intermediates." If one character state is intermediate in form, size, or number between two other character states then it is hypothesized to represent a phylogenetic intermediate between the other states (e.g. small, medium, and large tail; 12, 13 or 14 thoracic vertebrae). In a multistate character with character states 0 -1 -2 -3, only one step is needed for character state "0" to change to a character state "3" when the states are unordered; however, the same change requires three steps assuming that changes occur through intermediate states. Therefore, I performed a second set of analyses (Analysis 2)

in which 50 characters were ordered. Multistate characters where polymorphic states were present within a single taxon were kept unordered. The ordered characters (numbers in parentheses) for Analysis 2 were: claws on manus (1), plantar surface of pes (5), number of mammae (12, 13, 14, and 15), posterior extension of nasals (19), posterodorsal extension of premaxillae (20), anterodorsal margin of zygomatic plate (21, 22), masseteric tubercle (25, 26), infraorbital foramen (27), interorbital region (28), postorbital ridge (29), jugal length (30, 31), alisphenoid strut (33), carotid circulation (34), suprasquamosal foramen (35), ethmoid foramen (43), ethmoturbinals and sphenopalatine foramen formation (44), dorsal aperture of ectotympanic ring (46), incisive foramina (48), palatal length (50), sphenopalatine vacuities (55), mesopterygoid fossa breadth (56), mesopterygoid fossa shape (57), upper incisor orientation (67), M1 position (68), anterocone development (69, 70), mesoloph development (72), labial cingulum of upper molars (74), molar roots, height and occlusal topography (76), cusp arrangement on m1 (78), occlusal complexity of m3 (82), masseteric crest position (89), mental foramen position (90), number of thoracic and lumbar vertebrae (96), number of caudal vertebrae (97), chevron bones (98, 99), peroneal process of fifth metatarsal (101), relative size of hallux [dI of pes] (103), relative size of fifth digit [dV of pes] (104), preputial glands (114, 115), distribution of gastric epithelium (118), and incisura angularis (120).

Strict consensus methods were employed to summarize the common structure of equally most-parsimonious trees using PAUP. Decay analysis and bootstrap analysis were employed to quantify nodal support. The decay analysis was performed following the method of Bremer (1988) as implemented by the program Treerot (Sorenson, 1996). I used both accelerated transformation (ACCTRAN) and delayed transformation

(DELTRAN) algorithms to optimize characters on trees. Accelerated transformations favors reversal over parallel evolution, while delayed transformations favor parallelisms. Additional details on these methods can be found in Simmons (1993) and Simmons and Geisler (1998). A bootstrap analysis was also performed (Felsenstein, 1985) with 1000 replicates, and each with ten random-addition iterations, following the same search options in PAUP that were used for the heuristic search described above.

Although my discussion is based on the results of the strict consensus trees, alternative hypotheses were evaluated by searching for most parsimonious trees with a specified topology enforced. For example, under the hypothesis of a monophyletic Rhipidomys, the species R. leucodactylus, R. fulviventer, and R. macconnelli were forced to constitute a clade, and all the other taxa were left unresolved. The length of the trees produced with monophyly of Rhipidomys enforced was then compared with the most parsimonious unconstrained cladogram, and the differences in length recorded. These hypotheses were evaluated with the same heuristic strategies outlined above, except that 100 random-addition replications were considered sufficient.

## MORPHOLOGICAL CHARACTER SETS

### EXTERNAL MORPHOLOGY

**1. Claws on manus:** *Claws small or moderate in size, not keeled (0); or claws moderately long, keeled for about half the length of each claw (1); or claws very long, subequal to digit or longer, and keeled for more than half the length of each claw (2).*

Most muroids examined have claws that are usually half or less the size of the digits; these small claws can be open or closed at the base, or even slightly keeled, but for this level of analysis I interpreted all these variants as a single state (0). By contrast, a long claw with ventral margins extensively keeled as defined here is seen in scapteromyines and Oxymycterus. The enlarged claws of scapteromyines are said to be associated with fossorial or semi-fossorial habits (Herskovitz, 1966). Abrothrix has claws intermediate in size between scapteromyines and other sigmodontines, with keels that extend about half the length of each claw.

In Analysis 2, transformations of this character were ordered (0↔1↔2) to indicate my assumption that length of claws and extension of the keeled section occur in a progressive fashion.

**2. Manual digits:** *Second digit distinctly longer than fifth (0); or second and fifth digits subequal (1).*

The widespread condition in muroid rodents is that the second digit of the manus (without claws) is distinctly longer than the fifth. In a few species, however, the second and fifth digits are subequal (fig. 1). This condition is seen in Oecomys bicolor, Rhagomys rufescens, Rhipidomys fulviventer, Thomasomys baeops, and Thomasomys

notatus among sigmodontines, and also seen in the tylomyine Nyctomys sumichrasti.

**3. Ungual tuft on pes:** *Present (0); or absent (1).*

The claws of the hindfoot are usually covered by sparse hairs arising from the distal extreme of each digit. These can be developed into a long ungual tuft that conspicuously exceeds the length of the claws. Ungual tufts were previously reported for Microryzomys (Carleton and Musser, 1989: fig. 9), Thomasomys cinereus and Delomys (Voss, 1993), and Sigmodon (Voss and Carleton, 1993). This feature predominates among tylomyines, peromyscines, neotomines and simple-phalli sigmodontines according to Voss (1993), who argued that presence is the primitive condition for Neotropical muroids. By contrast, only scarce and small hairs that do not cover the claws are seen in Oryzomys palustris, Holochilus (Carleton and Musser, 1989; Voss and Carleton, 1993), and ichthyomyines (Voss, 1988); thus, ungual tufts in these taxa are considered to be absent. I also observed the absence of ungual tufts in ichthyomyines, scapteromyines, some oryzomyines, and Rhipidomys leucodactylus. Ungual tufts are present in all other taxa included in my study, including the long-clawed species Abrothrix and Oxymycterus.

**4. Plantar pads of pes:** *Six pads present (0); or hypothenar pad greatly reduced or absent (1).*

The plantar surface of the pes of most rodents is provided with two metatarsal pads, the thenar and the hypothenar, and four interdigital pads, all of them usually distinct and in some genera even swollen. In Oryzomys palustris and a few other sigmodontines only five plantar pads are distinct, with the hypothenar pad absent or greatly reduced (Carleton and Musser, 1989: fig. 9A). Voss (1993) suggested that presence of the lateral metatarsal (hypothenar) pad is the plesiomorphic condition. This

character was first used in phylogenetic analysis by Carleton (1980, character 77), who coded it in conjunction with the position of plantar pads. Although Carleton argued that his scoring scheme reflected integrated changes in foot shape and relative length of digits, I scored the digital proportions separately (see characters 86 and 87 below, which were primarily scored on skeletal material). Among the taxa examined, the hypothenar pad is reduced or absent only in ichthyomyines, Oryzomys, Holochilus, and Scapteromys.

**5. Plantar surface of pes:** *Furred (0); or sparsely haired (1); or naked (2).*

The plantar surface of the muroid pes varies extensively in pilosity of the heel, sole, borders, and interdigits. This complexity limits an attempt to evaluate these features in a wider array of taxa. Carleton (1980) and Steppan (1995) coded the variation of hairiness from the heel to plantar pads as a single character. However, their scoring conventions are not equivalent. For this feature, I scored the hairiness of the plantar surface, only among the plantar pads. A conspicuously furred sole is seen only in Microtus, Cricetulus, and Neotoma. Baiomys, Scotinomys, Ochrotomys, Peromyscus, Punomys, and Phyllotis exhibit sparse hairs among the plantar pads. In contrast, Calomyscus, Reithrodontomys, tylomyines, and all sigmodontines (except Punomys and Phyllotis) present a naked sole.

In Analysis 2, the transformations of this character were ordered (0↔1↔2) to indicate my hypothesis of progressive change of hairiness on the plantar surface.

**6. Plantar squamation of pes:** *Smooth to indistinct squamation (0); or distinctly squamated (1).*

Among muroid rodents, plantar surface of the hindfeet can be either smooth epithelium or distinctly squamated (see Carleton and Musser, 1989: fig 9). To maintain

uniformity of scoring for this trait only the region among the plantar pads was evaluated. Distinct squamation can occur on either naked or hairy plantar surfaces. A distinctly squamated foot is present in Neotoma, peromyscines (except Baiomys), akodontines, oryzomyines (except Oecomys and Handleyomys), ichthyomyines, scapteromyines, phyllotines (except Chinchillula), Sigmodon, Wiedomys, and southeastern Brazilian thomatomyines (except Rhagomys and Juliomys sp.). By contrast, cricetines, Microtus, tylomyines, Baiomys, Chinchillula, Handleyomys, Oecomys, Aepeomys, Chilomys, Rhagomys, Rhipidomys, Thomasomys, and Juliomys sp. have indistinctly squamated plantar surface.

**7. Interdigital webbing on hindfoot: *Absent (0); or present (1).***

Voss (1988) reported that all ichthyomyines exhibit small or well developed interdigital webbing that may extend to the first interphalangeal joint of the middle digits in the hindfoot. Voss and Carleton (1993) employed this character with three states to score a group of oryzomyines and Sigmodon; however, for a broader array of taxa, I employed only two states. Among my samples, distinct interdigital webbing is found only in ichthyomyines, Holochilus, and Oryzomys. Voss and Carleton (1993) noted that some small interdigital membranes may be confused with this feature, which are merely the tissue left between digits.

**8. Genal 1 vibrissae: *Present (0); or absent (1).***

Mystacial, superciliary, subocular, genal, submental and interramal vibrissae are present in most muroids. Brown (1971) and Brown and Yalden (1973) described and illustrated these vibrissae for different mammalian groups, but few comparative analyses are available for muroids. Genal vibrissae occur in one or both of two distinct positions.

here denoted as genal 1 and genal 2 (fig. 2) following Brown (1971: fig. 6). Genal 1 vibrissae (the genal described by most authors) consist of one or more long and stiff hairs located between the posterior canthus of the eye and the anterior margin of the ear on the same side. Wineski (1985) described the musculature, connective, vascular, and nervous tissues associated with these vibrissae in Mesocricetus. Genal 1 vibrissae have been reported for Microryzomys (Carleton and Musser, 1989), Lundomys (Voss and Carleton, 1993), Delomys (Voss, 1993), Sigmodon (Voss, 1992), species of the Akodon boliviensis group (Myers et al., 1990), and Scolomys (Patton and da Silva, 1995). However, genal 1 vibrissae are uniformly absent in ichthyomyines (Voss, 1988). I observed that genal 1 vibrissae are present in cricetines, Calomyscus, Neotoma, peromyscines (except Ochrotomys), tylomyines, akodontines (except Abrothrix), oryzomyines, phyllotines (except Punomys), scapteromyines, and Wiedomys. Genal 1 vibrissae are also present in thomatomyines except Aepeomys lugens and several species of Thomasomys.

**9. Genal 2 vibrissae: *Present (0); or absent (1)*.**

Previously unreported for muroid rodents, genal 2 is a long and stiff vibrissa on the cheek, ventral to genal 1 and close to the lateral line that divides the dorsal from the ventral pelage coloration (fig. 2). The genal 2 vibrissae are shorter and less conspicuous than genal 1 vibrissae but are not confused with ordinary contour hairs. Scoring in recent and well prepared skins or fluid-preserved specimens is ideal since old and badly prepared skins may have lost the vibrissae by rough handling. The genal 2 vibrissae occur in cricetines, Calomyscus, Neotoma, Baiomys, and tylomyines. They are completely absent in most peromyscines, and in all sigmodontines except Oecomys, Kunsia, and



Abrawayamys.

**10. Carpal vibrissae:** *Distinctly longer than metacarpal pads (0); or shorter, inconspicuous or absent (1).*

Brown and Yalden (1973) illustrated and defined the carpal (= ulnar carpal) vibrissae as those found just above the wrist. Carpal vibrissae are usually present in rodents, occurring consistently in both sexes (Beddard, 1902). Most muroids that I examined have a long carpal vibrissa extending from the distal forearm, close to the wrist, to at least the base of the digits. However, in Scapteromys and Kunsia the carpal vibrissa is inconspicuous, appearing absent or very short, even under high magnification. In Oxymycterus paramensis the carpal vibrissa is also inconspicuous, or much shorter than the metacarpal pads (the same condition was observed in O. hispidus, O. hucucha, O. hiska, O. roberti, O. amazonicus, O. rufus, and Bibimys chacoensis; species not included in the analyses). Rhagomys presents a short carpal vibrissa that extends only to the base of the thenar, but only two old specimens were available for examination.

**11. Calcaneal vibrissae:** *Present (0); or absent (1).*

Brown and Yalden (1973) defined calcaneal vibrissae as those found on the inside of the ankle, but no information was provided on the taxonomic distribution of these hairs among mammals. Some muroids have a single long vibrissa located on the medial and ventral side of the heel. Topographic similarity suggests that this corresponds to the calcaneal tract of Brown and Yalden, but calcaneal vibrissae have not previously been documented in rodents. Close comparisons with the previous character indicate that the states of calcaneal vibrissae occurrence are not correlated with those of the carpal vibrissae. Calcaneal vibrissae are present in cricetines, Calomyscus, Neotoma,

tylomyines, and some peromyscines (fig. 3). Calcaneal vibrissae are uniformly absent in all sigmodontine rodents analyzed here. Within species, this character appears to be invariant except for Peromyscus mexicanus, in which calcaneal vibrissae are present in series from Guatemala and Belize, but absent in samples from Oaxaca, Mexico. I scored variation within Peromyscus mexicanus as a taxonomic polymorphism, because it seems likely that more than a single species may be present in this complex (Huckaby, 1980; Carleton, 1989).

**12. Thoracic mammary pair: *Absent (0); or present (1)*.**

I define the thoracic teats as the pair of mammae placed on the sides, posterior to (but not close to) the origin of the forearm (fig. 4). Mammae number has long been recognized of systematic value, and thus used in numerous diagnoses and phylogenetic analyses of muroid rodents (e.g., Carleton, 1980; Voss and Carleton, 1993; Steppan, 1995) where the information derived from the number of mammary loci was combined in a single character. However, I scored each locus independently for the unordered analysis (characters 12, 13, 14, and 15). Voss and Carleton (1993: fig. 8) presented an updated nomenclature for the anatomical loci of mammary pairs, which has been followed by other authors in recent papers. They mentioned that Holochilus brasiliensis has eight mammae in four pairs, one inguinal, one abdominal, one postaxial, and one pectoral, and that some populations of H. sciureus have paired thoracic teats *in addition* to the usual complement implying that thoracic teats are absent in rodents with six or eight pairs of teats. However, I observed that females with five mammary pairs differ from females with four pairs by the addition of the postaxial pair rather than the thoracic, and that both mammary counts exhibit the thoracic pairs. Furthermore, my examination of six-

mammate females supports this observation: their most anterior pair is not close to the forearm and is thoracic in position (rather than postaxial) according to my definition. The mammae loci for a eight-mammate muroid are interpreted here as pairs of inguinal, abdominal, thoracic and pectoral mammae.

All muroids examined herein possess the thoracic teats except for neotomines, tylomyines, and the peromyscines Baiomys, Peromyscus, and Scotinomys. These species only present two pairs of mammae, called either inguinal pairs (Carleton, 1980), or abdominal and inguinal pairs (Voss and Carleton, 1993). Scotinomys teguina presents a case of polymorphism. I observed the absence of the thoracic pair in my samples from Costa Rica, which corresponds to the four-mammate condition reported by Carleton (1980) and Steppan (1995). However, Hooper (1972) reported that only the southernmost populations of this species (from Nicaragua to Panamá) have four mammae, whereas northern populations (from Honduras to Mexico) have six mammae (i.e. thoracic pair present). Hooper used teat number to distinguish four subspecies: S. t. teguina and S. t. rufoniger with three pairs of mammae, and S. t. irazu and S. t. apricus with two pairs. Based on his observations, I interpret the presence or absence of thoracic mammae in Scotinomys as a case of taxonomic polymorphism.

**13. Pectoral I mammary pair: *Absent (0); or present (1).***

I distinguish two kinds of pectoral mammary pairs in the muroids I examined. The pectoral I is always placed anterior and close to the forelimb joint; while the pectoral II is placed posterior to the forelimb joint and closer to the midline and treated in character 14. The condition coded by other authors as eight-mammate in sigmodontines corresponds to the presence of a pectoral I mammary pair (state 1). This pectoral pair is

seen in the akodontines Akodon and Oxymycterus, oryzomyines (except Handleyomys), all phyllotines, scapteromyines, Sigmodon, Wiedomys, and most genera of southeastern Brazilian thomatomyines including Delomys, Juliomys, Wilfredomys, and Phaenomys. Hershkovitz (1959) and Steppan (1995) reported absence of pectoral I in Wiedomys, but I found the pair present in four females (including the holotype). The mammary complement of Abrawayaomys is unknown. The thomatomyine Aepeomys, Chilomys, Rhagomys, Rhipidomys, and Thomasomys examined here uniformly lack pectoral I mammae. Voss (1993) reported presence and absence of pectoral I mammae in Delomys dorsalis. Recent studies of standard karyology (Bonvicino and Geise, 1995) differentiate D. collinus with FN=86 (and pectoral mammae absent) from D. dorsalis with FN=80 (and pectoral pair present); the karyotypes apparently corresponding to the taxa with different teat numbers.

Pectoral I mammary pair is present only in sigmodontine tribes. It is absent among the neotomines, peromyscines and tylomyines examined here and in a larger taxonomic representation of these groups (see Carleton, 1980: table 7), and also absent in Calomyscus, cricetines and Microtus.

**14. Pectoral II mammary pair:** *Absent (0); or present (1).*

Whether pectoral I and pectoral II are homologous is uncertain for my limited number of taxa; however based on the criteria of position, both pairs are considered distinct. The pectoral II pair occurs only in Microtus, Cricetulus, and Mesocricetus (fig. 4).

**15. Postaxial mammae:** *Absent (0); or present (1).*

Sigmodon, Holochilus and Calomys are the only genera known possessing

postaxial mammary pair (Olds, 1988; Voss, 1992; Voss and Carleton, 1993). The postaxial pair is present in Calomys callosus, in agreement with previous reports (Hershkovitz, 1962; Steppan, 1995). However, Olds (1988) reported that number of teats in Calomys varies from 8 to 12; unfortunately no further mention on the nature of the variation was provided.

In Analysis 2, characters 12, 13, 14 and 15 were interpreted as a single character for number of teats, with the states: four (0), six (1), eight (2) and ten (3) mammae. Transformations of this character were ordered ( $0 \leftrightarrow 1 \leftrightarrow 2 \leftrightarrow 3$ ) to reflect my hypothesis that number of mammae pairs are added or reduced in a progressive fashion.

**16. Nose coloration:** *Non-reddish (0); or reddish and sharply contrasting with rest of head (1).*

Among muroids I examined, nose coloration is usually similar to that of the head. However, in Wiedomys, Wilfredomys oenax, and Juliomys pictipes the nose is distinctly reddish, or “pirrorrino” (Avila-Pires, 1960). Osgood (1933b) remarked that pictipes has a “pyrrhorhine” face. This feature was previously reported by Hershkovitz (1959) for Wiedomys and was mentioned also for Wilfredomys oenax (Pine, 1980). Pine (1980) considered the occurrence of pyrrhorhine noses in these apparently unrelated taxa a result of convergence.

**17. Tail pencil:** *Absent(0); or present (1).*

A tail pencil is distinct when a brush of long hairs extends beyond the tail tip at a point usually more than 10 rows of scales. Tribe (1996) considered that a distinct tail pencil is sufficient to recognize Rhipidomys from other sigmodontines. However, I also observed a distinct tail pencil in Thomasomys notatus and Abrawayaomys. In few other

muroids such as Calomyscus, Nyctomys, ichthyomyines, Scapteromys, and Chinchillula the occurrence of a tail pencil is uncertain under my definition. In these taxa the tail is covered with long hairs from base to tip; therefore the “tail pencil” appears to be more a consequence of the densely hairy covering.

## CRANIUM

### **18. Rostral tube:** *Absent (0); or present (1).*

A rostral tube is produced when the premaxillae and nasals extend anteriorly beyond the incisors, thus projecting the nasal cavity anterior to the rest of the snout (Voss, 1993: fig. 5). The extension of the rostral tube is also greater than the depth of the incisors. Voss (1993) described a rostral tube as present in Delomys and absent in Thomasomys cinereus and Oryzomys palustris. He also mentioned that some peromyscines, including Osgoodomys banderanus and Megadontomys thomasi, and the tylomyine Ototylomys phyllotis, exhibit a similar configuration. Most of the muroids I examined lack a conspicuous rostral tube. However, it is seen in Calomyscus, Peromyscus, most akodontines, and some thomasomyines (including Delomys, Aepeomys lugens, T. erro, and T. incanus).

**19. Posterior extension of nasals:** *Very long, extending conspicuously far beyond the maxillary-frontal-lacrimar intersection, thus nose tips are closer to the supraorbital foramina than to the lacrimals (0); or long, extending just posterior to the maxillary-frontal-lacrimar intersection (1); or short, not extending beyond the maxillary-frontal-lacrimar intersection (2).*

This character is defined according to the description and scoring scheme

presented by Steppan (1995: character 9S) in his sigmodontine analysis, except that I include three states (rather than two). Very long nasals are seen only in Mesocricetus, and all ichthyomyines. Long nasals are exhibited in some peromyscines, akodontines, and are common in phyllotines and oryzomyines, in Wiedomys, and in thomasomyines (except Aepeomys, Chilomys and Rhagomys). By contrast, short nasals are seen in tylomyines, neotomines, Sigmodon, and occasionally among other muroid groups. Both states were found in species of Handleyomys, or in different populations of Scotinomys teguina, Thomasomys cinereus, and Thomasomys aureus, and were treated as a taxonomic polymorphism for this feature.

Transformations of this character were ordered (0↔1↔2) in Analysis 2 to reflect the assumption that changes in the relative extension of the nasals occur in progressive fashion.

**20. Posterodorsal extension of premaxillae:** *Premaxillae extending posterior to nasals (0); or terminating level with nasals (1); or terminating anterior to nasals but posterior to the zygomatic notch (2); or terminating anterior to nasals and to the zygomatic notch (3).*

This character corresponds closely to Steppan's (1995) character 10S, except that I include four states (rather than his three states). Long premaxillae extending posterior to the nasals are present in Microtus, cricetines, Calomyscus, Nyctomys, peromyscines (except Baiomys and some Scotinomys), Sigmodon, several thomasomyines (including Chilomys, Juliomys, Rhagomys, Rhipidomys macconnelli, Wilfredomys), and Wiedomys, but rarely in other muroid groups. State (1) is seen only in Baiomys, Scotinomys, and Tylomys; it is the common condition in oryzomyines and phyllotines,

but occurs less commonly in other groups. State (2) apparently occurs only in sigmodontines, where it predominates among ichthyomyines, scapteromyines, and thomasomyines (including Abrawayaomys, Delomys, Phaenomys, and Thomasomys). State (3), corresponding to a very reduced premaxillae, is the common condition in akodontines and some thomasomyines (including Aepeomys lugens, Thomasomys erro, T. incanus, and T. macrotis). Scotinomys and Thomasomys baeops exhibit states (0) and (1) in different populations, variation that I interpret as taxonomic polymorphism.

In Analysis 2 the transformations of this character were ordered (0↔1↔2↔3) to reflect my assumption that changes in the extension of the premaxillae occur in progressive fashion.

**21. Zygomatic notch:** *Absent (0); or present (1).*

The zygomatic notch is defined by a free anterodorsal edge of the zygomatic plate. A zygomatic notch is absent in ichthyomyines (Voss, 1988), and in Mesocricetus and Microtus. All other muroids included in this study exhibit a zygomatic notch that may be shallow or deep.

**22. Anterodorsal margin of zygomatic plate:** *Shallow, depth less than half the width of notch (0); or deep, depth equal to or greater than half the width of notch, spinous process absent (1); or deep with distinct spinous process (2).*

This character can be evaluated only in taxa that have a zygomatic notch (see character 21). My scoring scheme combines definitions presented by Steppan (1995, character 8S) and Voss and Carleton (1993, character 6). Cricetines, Calomyscus, peromyscines, and tylomyines have a shallow zygomatic notch (Carleton, 1980). Among sigmodontines, a shallow zygomatic notch is exhibited in the oryzomyines



Microryzomys and Oecomys, and commonly in thomatomyines, including Aepeomys, Chilomys, Phaenomys, Rhipidomys, Thomasomys and Juliomys sp. A deep zygomatic notch without a spinous process is the widespread condition among sigmodontines, as observed by Stepan (1995). This condition is seen in all akodontines, phyllotines, scapteromyines, in several oryzomyines, Wiedomys, and in most thomatomyines from southeastern Brazil (including Abrawayaomys, Delomys, Juliomys pictipes, Rhagomys, and Wilfredomys). A strong spinous process is seen only in Holochilus and Sigmodon.

In Analysis 2, transformations of this character were ordered (0↔1↔2) to reflect the assumption that changes in the depth of the zygomatic notch and the development of the spinous process occur in a progressive fashion.

**23. Zygomatic plate breadth:** *Narrow (0); or broad (1).*

The zygomatic plate is narrow when the breadth was equal or less than the length of M1; and broad when the breadth of the zygomatic plate is conspicuously larger than M1. Oryzomys palustris, Abrawayaomys ruschi and Rhagomys rufescens exhibit a broad zygomatic plate. All other muroids examined have narrow zygomatic plate.

**24. Zygomatic plate slope:** *Vertical (0); or slanted backward from the base (1).*

The zygomatic plate stands vertical or nearly vertical from the maxillary root in most muroids I examined. By contrast, in Abrothrix longipilis, Microxus mimus, Oxymycterus paramensis, Aepeomys lugens, some populations of Thomasomys aureus and T. cinereus, T. incanus, T. kalinowskii, and T. rhoadsi the zygomatic plate is sloped backwards from the maxillary root.

**25. Masseteric tubercle:** *Absent (0); or present (1).*

The tendon of origin of the superficial masseter attaches to a prominent bony spur

located at the base of the zygomatic plate in all ichthyomyines according to Voss (1988, see fig. 12), who also reported that small masseteric processes are found in the peromyscine Megadontomys and Scotinomys. I also observed small masseteric processes in Baiomys. Only a patch of rugose bone marks the origin of the superficial masseter when a distinct tubercle is absent, which is the typical condition in all other muroid taxa I examined.

**26. Development of masseteric tubercle:** *Small (0); or large (1).*

Masseteric processes are prominent only in ichthyomyines. By contrast, the processes are small in Baiomys and Scotinomys. This feature was not evaluated for those taxa that lack the masseteric tubercle (state "0" of character 25).

In Analysis 2, transformations of character 25 and 26 were ordered in a single character (0↔1↔2) to reflect the progressive change in size of the masseteric tubercle, from absent to large size.

**27. Infraorbital foramen:** *Lumen narrow (0); or lumen moderately open (1); or lumen wide (2).*

Ichthyomyines have an infraorbital foramen with a lumen that is as wide dorsally as ventrally, which contrasts with the ventrally narrowed lumen seen in most muroid rodents (Voss, 1988). However, Aepeomys lugens and Thomasomys erro have an intermediate condition, where the lumen is more open and rectangular in shape than the usual ventrally narrowed foramen. The infraorbital foramen serves as a passage for M. zygomaticomandibularis and the infraorbital nerve, the morphology of which was carefully described and illustrated by Voss (1988: fig. 14).

In Analysis 2, transformations of this character were ordered (0↔1↔2) to reflect

the assumption that changes in the breadth and degree of the aperture of the infraorbital foramen occur in a progressive fashion.

**28. Interorbital region:** *Hourglass-shaped, and supraorbital region smoothly rounded when viewed in cross-section (0); or convergent with supraorbital margins square or weakly beaded when viewed in cross-section(1); or convergent and distinctly beaded when viewed in cross section(2).*

The interorbital region of sigmodontines is highly variable and this variation has been used in previous phylogenetic analyses (Carleton, 1980; Voss, 1993; Steppan, 1995). I interpreted interorbital shape variation as three states. The first state, in which the supraorbital margins of the frontals are smoothly rounded and not convergent anteriorly, is seen in Microtus, cricetines, some peromyscines, all akodontines, all ichthyomyines, and most thomasomyines; this condition also appears occasionally in other groups. A convergent interorbital region with square or weakly beaded margins is less common, and occurs in Calomyscus, several peromyscines, Oligoryzomys, Kunsia, some thomasomyines (including Abrawayaomys, Rhagomys, most Rhipidomys, and Juliomys pictipes), and Wiedomys. Beaded and convergent supraorbital margins are seen in tylomyines, several oryzomyines and phyllotines, Sigmodon, and the thomasomyine Phaenomys.

In Analysis 2, transformations of this character were ordered (0↔1↔2) to reflect my assumption that changes in the development of the interorbital region occur in a progressive fashion.

**29. Postorbital ridge:** *Absent, no conspicuous relief on the posterior orbital wall (0); or distinct ridge on the posterior orbital wall (1); or largely developed (2).*

Voss and Carleton (1993) described a postorbital ridge in Holochilus. A comparable ridge is absent in all muroids I examined, except for Microtus which has a strongly developed postorbital ridge.

In Analysis 2, transformations of this character were ordered (0↔1↔2) to reflect the assumption that changes in the development of the postorbital ridge occur in a progressive fashion.

**30. Jugal:** *Long and massive, anterior margin of each jugal extends forward to at least the anterior margin of the protocone of M1 or beyond. (0); or short, slender or moderately broad, and posterior to protocone of M1 (1).*

A long and massive jugal is seen only in Microtus and Calomyscus. In all other muroids I examined the jugal is shorter, usually slender, and its anterior margin does not extend beyond the anterior margin of M2.

**31. Jugal length:** *Jugal long, widely separating the maxillary and squamosal zygomatic processes by a distance usually twice or more the thickness of the jugal (0); or jugal with maxillary and squamosal processes approximated or overlapping (1); or jugal reduced to a sliver or absent (2).*

The muroid jugal is an elongated bone that usually separates the maxillary and squamosal zygomatic processes approximately in the middle of the zygomatic arch. Long jugals (state 0) are seen in cricetines, Nyctomys, neotomines, peromyscines, Abrothrix, ichthyomyines, and some thomasomyines (including Abrawayaomys, Aepeomys, Chilomys, Juliomys sp., Rhagomys, and a few Thomasomys). Long jugals are also usually slender, and in this context was cited by Carleton (1989: 119) to support his definition of the tribe Peromyscini, stating: "jugal thin but always present and separating

zygomatic extensions of maxillary and squamosal”; a condition that was well illustrated by Klingener (1968: fig. 1). Voss (1988) also observed that jugals are slender in ichthyomyines. The maxillary and squamosal processes are closely approximated or overlapping (state 1) in most other sigmodontines, including phyllotines, scapteromyines, Sigmodon, akodontines (except Abrothrix), most oryzomyines, Wiedomys, and the thomasmomyines Delomys, Phaenomys, Rhipidomys, Thomasomys, and Juliomys pictipes. Voss and Carleton (1993) previously reported this morphology to separate Lundomys from Holochilus by the degree of separation of the zygomatic process of the maxillary and squamosal bones. Carleton and Musser (1989:50) reported a sliver-like jugal for Microryzomys and Oligoryzomys and correctly concluded that jugal reduction is not related to body size (since large rodents like Tylomys also have a sliver-like jugal). Other systematic reports have seldom mentioned jugal morphology.

In Analysis 2, transformations of character 30 and this character were ordered (0↔1↔2↔3) to indicate my assumption that changes in the relative size of the jugals occur in a progressive fashion from a long and massive jugal to a reduced to a sliver condition.

**32. Posterior extension of jugal: Jugal borders glenoid fossa (0); or jugal does not approach the glenoid fossa (1).**

In most muroid taxa examined here, the posterior margin of the jugal extends posteriorly to a point well anterior to the glenoid fossa. However, in Sigmodon the posterior edge of the jugal extends much farther posteriorly, approaching the edge of the glenoid fossa (fig. 5). Among the muroids I examined, a similar condition was scored only in Calomyscus. This feature appears to be rare among New World muroids, but some

nesomyines (e.g., Brachytarsomys) and the mystromyine Mystromys exhibit a jugal morphology like Sigmodon.

**33. Alisphenoid strut:** *Present (0); or incomplete or variable (1); or absent (2).*

A bony alisphenoid strut separates the buccinator-masticatory and the accessory oval foramen in all cricetines, peromyscines, neotomines, tylomyines, ichthyomyines, most akodontines, Sigmodon, and several thomasomyines (Carleton and Musser, 1989; Voss, 1988, 1993). The alisphenoid strut is absent in Calomyscus, most oryzomyines and phyllotines, and in some akodontines, scapteromyines, and thomasomyines.

Chilomys was scored as taxonomic polymorphism: presence or absence of the strut among populations appears to be regional. Voss (1991) reported the absence of an alisphenoid strut in Calomys callosus, whereas Steppan (1995) scored this taxon as polymorphic, but no statement was provided to indicate whether such variation is within or between populations. The samples of C. callosus analyzed here lack the strut. Steppan (1995) defined an intermediate state for the presence of an incomplete strut (represented by a small dorsal process) in Chinchillula and Euneomys, and my samples of Chinchillula agree with his observations. Similarly, Wilfredomys oenax and Juliomys sp. exhibit an incomplete strut (represented mainly by a ventral process), which can occur either unilaterally or bilaterally. Thomasomys erro is also highly variable for this character, with no predominant modal state. I opted to extend the intermediate condition to include these cases of unfixed variation.

In Analysis 2, transformations of this character were ordered (0↔1↔2) to indicate my assumption that a state defined as incomplete, or variable occurrence of a strut, is an intermediate state between fixed states of presence and absence, and that

changes in the occurrence (or absence) of the alisphenoid strut occurs in a sequential fashion.

**34. Carotid Circulation:** *Pattern 1, stapedial foramen, squamosal-alisphenoid groove, and sphenofrontal foramen present(0); or pattern 2, stapedial foramen present, but squamosal-alisphenoid groove and sphenofrontal foramen absent (1); or pattern 3, stapedial foramen small or indistinct, squamosal-alisphenoid groove and sphenofrontal foramen absent (2); or polymorphic, either pattern 1, pattern 2, or pattern 3 (3).*

Nomenclature of the carotid circulation and associated foramina adopted here follows Bugge (1970), Carleton (1980), Wahlert (1985), Voss (1988), and Carleton and Musser (1989), to whose accounts the reader is referred for detailed description and illustrations of this system. I followed Voss's (1988) terminology for my scoring scheme. Pattern 1 is seen in Calomyscus, all cricetines, some peromyscines, all akodontines, all phyllotines, all scapteromyines, in Wiedomys, and several thomasmomyines. Pattern 2 occurs only in Microtus, Neotoma, Anotomys, and Oligoryzomys. Pattern 3 is common only among oryzomyines, but it occurs in several thomasmomyines (including Chilomys, Juliomys pictipes, Rhagomys, and several Thomasomys) and is scattered among a few other groups as well.

The carotid circulation I observed in Nyctomys sumichrasti is somewhat at odds with previous reports. Carleton (1980) reported pattern 3 for this species, whereas Steppan (1995) reported pattern 2 or 3, suggesting regional variation. My sample of 31 Nyctomys sumichrasti from Panajachel, Guatemala (see Appendix 1) exhibited all three carotid variants: pattern 1 (13%), pattern 2 (19%), pattern 3 (52%), and 16% of the sample exhibited alternative states on opposite sides. Reports of all carotid variants co-

occurring in a species is rare, and this sample of Panajachel appears to be unique. Voss (1991) also reported that the carotid circulation system is variable within populations of Zygodontomys brevicauda, although his frequency data show conspicuous geographic trends. Nyctomys might resemble Zygodontomys in this respect, but additional and numerous population samples need to be evaluated. Unpublished examination of other populations of Nyctomys further suggest that there is a geographic trends in the occurrence of the primitive and derived carotid circulation in Nyctomys (M.D. Carleton and G.M. Musser, pers. comm.). I scored my sample of Nyctomys with a unique state (state 3) to represent this case of polymorphism. However, Nyctomys is scored as a case of taxonomic polymorphism with the states 0, 2, and 3.

In Analysis 2 transformations of this character were ordered (0↔1↔2↔3) to indicate my assumption that changes in the morphology of the carotid circulation occur in a progressive fashion. The state 3 of Nyctomys is very unlikely to be an intermediate state from state 0 to state 2 in other muroid species (because no evidence support this unique state in other taxa); therefore, in Analysis 2, I entertain the hypothesis of state 3 as derived from state 2.

**35. Suprasquamosal foramen:** *Present (0); or polymorphic, either present or absent (1); or absent (2).*

I coined the term “suprasquamosal foramen” for the opening that pierces the squamosal bone just dorsal to the root of the squamosal zygomatic process (fig. 6). The distribution of states indicates that the suprasquamosal foramen is not correlated to the transformation states of the carotid circulation (see character 34), since it may be present whether or not the supraorbital branch of the stapedial artery is exhibited. I observed that



the suprasquamosal foramen communicates with an arterial branch that arises from the supraorbital branch of the stapedial artery when the latter is present; however, when the supraorbital branch of the stapedial artery is missing, the suprasquamosal foramen communicates with a vessel leaving the auditory bullae (apparently arising directly from the stapedial artery). This arterial branch apparently corresponds to one of the "meningial rami" arising from the supraorbital branch *en route* to the orbital region (Bugge, 1970; Wible, 1987); the vessel occupies an intrasquamosal groove where it can be easily observed in incompletely cleaned skulls. The suprasquamosal foramen appears to be distinct from the temporal foramen present in other rodents (Wahlert, 1985), and has not been named in previous anatomical studies (e.g., Bugge, 1970; Wible, 1984; Wahlert, 1985; Wible, 1987; Voss, 1988). Hill (1935) reported a "suprasquamosal foramen" in Zapus, but I am not certain whether Hill's usage refers to a temporal foramen or to the suprasquamosal foramen described here.

Although the suprasquamosal foramen can be evaluated easily when present, the complete route of the artery branch needs to be established, especially when the supraorbital branch of the stapedial artery is absent. This foramen is present in Microtus, cricetines, Tylomys, and some peromyscines (including Ochrotomys, Reithrodontomys, and some Baiomys). Among sigmodontines, it is consistently present only in ichthyomyines. Peromyscines that also exhibit this foramen include Podomys floridanus, Isthmomyys pirrensis, Habromys lepturus, Neotomodon alstoni and Onychomys, but the foramen is absent in Megadontomys cryophilus (taxa not included in the analyses). Some species are polymorphic for this character: some specimens exhibit the foramen bilaterally, in others it is unilaterally present, and in others it is

bilaterally absent. Calomyscus, Baiomys, Peromyscus mexicanus and Chinchillula were scored for taxonomic polymorphisms of this kind.

In Analysis 2, the transformations of this character were ordered ( $0 \leftrightarrow 1 \leftrightarrow 2$ ) to accommodate observed polymorphisms which I consider an intermediate state.

**36. Tegmen tympani:** *Overlapping (0); or non-overlapping (1).*

The tegmen tympani is a laminar outgrowth of the periotic that forms the roof of the epitympanic recess in therian mammals and derives from the rostral wall of the vestibular part of the cochlear capsule (Novacek, 1993; van der Klaauw, 1931). In muroids, the tegmen tympani usually overlaps a posterior suspensory process of the squamosal, separating the postglenoid foramen from the middle lacerate foramen, and providing an anterior suspension for the auditory bulla (Voss, 1993). When the tegmen tympani does not overlap the squamosal, a large and semicircular postglenoid foramen is usually continuous with the middle lacerate foramen (Carleton and Musser, 1989). Voss and Carleton (1993) diagnosed the Tribe Oryzomyini based in part on the absence of the posterior suspensory process of the squamosal. My observations agree with previous reports that oryzomyine rodents lack this suspensory process and the resulting overlap with tegmen tympani (Voss and Carleton, 1993; Stepan, 1995). Except for oryzomyines, all of the other muroids examined here exhibit the overlapping condition.

**37. Parietal-supraoccipital contact:** *Contact absent (0); or contact present (1); or polymorphic, either present or absent (2).*

In most muroid rodents, the posterior border of the parietal contacts the supraoccipital and the interparietal does not extend to touch the squamosal, (Stepan, 1995). According to Stepan, parietal-supraoccipital contact is a condition widespread

except in tylomyines, where contact is precluded by a wide interparietal. My observations agree with Steppan's. I also noted that parietal-supraoccipital contact is precluded in most specimens of Microtus pennsylvanicus. In Ochrotomys nuttalli, the interparietal is very broad, with a narrow lateral process that may or may not contact the squamosal on one or both sides of the skull; both conditions are about equally frequent and I coded this condition as within-species polymorphism (state 2).

**38. Parietal-supraoccipital suture breadth:** *Suture narrow (0); or distinctly broad (1).*

The parietal-supraoccipital suture is seen at the caudal end of the parietal bone when the parietal precludes interparietal-squamosal contact (see character 37). The size (width) of the interparietal bone is usually employed for taxonomic purposes and is obviously correlated with the existence of a parietal-supraoccipital suture. However, precise definition has been elusive because of intraspecific variation (Steppan, 1995), and I scored the width of the parietal-supraoccipital suture rather than the width of the interparietal. I define a narrow suture as extending distinctly less than half the width of the caudal margin of the parietal bone, and a broad suture as extending at least half (usually more than half) the width of the caudal margin of each parietal. A broad suture is seen in all ichthyomyines, scapteromyines and akodontines; also in Oryzomys palustris and the thomasomyines Chilomys and Abrawayaomys. This character cannot be evaluated for taxa exhibiting state (0) of character 37.

**39. Length of interparietal:** *Long, greater than one third of parietals when scored along the midsagittal line (0); or short, less than one third of the parietals when scored along the midsagittal line (1).*

This character evaluates length of the interparietal in relation to the parietals along the midsagittal line. The size variation of the interparietal was evaluated by Steppan (1995: character 13S) producing states defined by segment coding. However, I used only two states, which separates the most reduced interparietals. A short interparietal is exhibited only in Scapteromys and the akodontines Abrothrix, Akodon, and Microxus. Rhagomys and Phaenomys were not scored because of incomplete or broken skulls.

**40. Lateral process of parietals:** *Present (0); or absent (1).*

The parietals may present a lateral process that distinctly penetrates the dorsal margin of the squamosal (this is also evidenced by an irregular suture between the squamosal and parietal bones), or the parietals may lack the process. The lateral process is seen in all sigmodontines examined. By contrast, the lateral process was commonly absent in tylomyines, Nelsonia, and the peromyscines Baiomys, Peromyscus mexicanus, and some populations of Scotinomys. I was uncertain about the condition of this feature in Ichthyomys and Neusticomys; therefore they were scored as missing.

**41. Subsquamosal fenestra:** *Present (0); or absent (1).*

The subsquamosal fenestra is a conspicuous excavation of the posterior margin of the squamosal dorsal to the auditory bullae, and separated from the postglenoid foramen by a hamular process of the squamosal. The fenestra transmits no nerves or vessels (Hill, 1935; Voss 1988). It is widespread in muroid rodents (Carleton, 1980), but completely absent in ichthyomyines, tylomyines, Kunsia, and Mesocricetus (Carleton, 1980; Voss, 1988; Steppan, 1995).

**42. Distal expansion of hamular process:** *Expanded (0); or narrower (1); or polymorphic, either expanded or narrow (2).*

The hamular process of the squamosal is a narrow bony strut that separates the postglenoid foramen from the subsquamosal fenestra. In all sigmodontines examined the breadth of the hamular process is more or less uniform from its proximal to distal extremes, producing a subparallel or slightly distally expanded strut. However, in a few other muroid taxa the posterior margin of the hamular process is conspicuously expanded. This condition is seen in Microtus, cricetines, and in the peromyscines Scotinomys and Ochrotomys. Baiomys exhibits the expanded and the unexpanded conditions in the same population sample, which I treated as within-species polymorphism (state 2). Taxa with the subsquamosal fenestra closed (character 41: state 1) cannot be evaluated for this character. However, some young individuals of Nyctomys exhibit a small subsquamosal fissure that appears to trace the margin of a broadly expanded hamular process, suggesting that the closure of the subsquamosal fenestra in this taxon might have resulted from a large development of the hamular process.

**43. Ethmoid foramen:** *Dorsal to M1 (0); or dorsal to M1/M2 contact or to M2 (1); or dorsal to M2/M3 contact, or more posteriorly (2).*

The ethmoid foramen is situated in the frontal bone close to the orbitosphenoid and frontal suture (Wahlert, 1985), but its position in muroid rodents has not previously been evaluated. In most taxa I examined, the ethmoid foramen is dorsal to M2. In Microtus the ethmoid foramen is situated more anteriorly, dorsal to M1. In akodontines, Neusticomys, Scapteromys, and Aepeomys lugens the ethmoid foramen is placed more posteriorly, dorsal to the point of M2/M3 contact or, more frequently, dorsal to M3. In Oxymycterus, the ethmoid foramen is posterior to M3, which is seen also in Geoxus and Lenoxus (genera not included in this study).

In Analysis 2, transformations of this character were ordered (0↔1↔2) to reflect my assumption that changes in the position of the ethmoid foramen occur directionally along the anterior-posterior axis.

**44. Ethmoturbinals and sphenopalatine foramen formation:** *Ethmoturbinals absent or small (0); or distinct, moderate (1); or large and inflated (2).*

Wahlert (1985) described the sphenopalatine foramen as bounded by the maxilla, and usually the frontal and the palatine bones, and observed that occasionally the ethmoturbinals are exposed on the dorsal margin of the foramen. He evaluated Phyllotis magister, but not other sigmodontines. Among the muroids I examined, the ethmoturbinals vary from absent to a distinctly inflated condition (fig. 7). Ethmoturbinals are small or absent in Microtus, cricetines, Calomyscus, Neotoma, tylomyines, some peromyscines, all oryzomyines (except Handleyomys), phyllotines (except Chinchillula), Sigmodon, Ichthyomys, Kunsia, and the thomasomyines Phaenomys and Rhipidomys leucodactylus. By contrast, ethmoturbinals are large, inflated, and exposed on the dorsal margin of the sphenopalatine foramen in all akodontines, Neusticomys, and several thomasomyines (including Abrawayaomys, Aepeomys, Chilomys, Rhipidomys macconnelli, and most species of Thomasomys). I scored an intermediate condition, in which the ethmoturbinals are distinctly present, but neither conspicuously large nor inflated, which is seen in Delomys, Rhipidomys fulviventer, Wilfredomys, Juliomys, and some Thomasomys among the thomasomyines, and rarely among other muroid groups.

In Analysis 2, the transformations of this character were ordered (0↔1↔2) to reflect the logical sequence of transformations from small or absent (0) to a large and inflated ethmoturbinals (2).

**45. Dorsal projection of alisphenoid:** *Well developed (0); or moderate (1); or polymorphic, either well developed or moderate (2).*

The dorsal margin of the alisphenoid bone in muroid rodents (as viewed laterally) contacts the orbitosphenoid, frontal, and the squamosal bones, but never the parietals. In most muroids I examined the dorsal margins of the alisphenoid are low and level with the dorsal margin of the orbitosphenoid; both sphenoid bones are always ventral to the squamosal root of the zygomatic arch. By contrast, Microtus, Mesocricetus, and Calomyscus have a larger and higher alisphenoid bone, which extends dorsally to both the squamosal root of the zygomatic arch and the orbitosphenoid of each side. This character has not been previously reported, however Carleton (1984: fig. 4) illustrated a large alisphenoid in Microtus oeconomus. In Cricetulus, the projection of the alisphenoid is variable, but usually at level of the squamosal root of the zygomatic arch and was scored with a different state (2).

**46. Dorsal aperture of ectotympanic ring:** *Closed (0); or polymorphic, either closed or open (1); or open (2).*

In most muroids I examined, the anterodorsal edge of the ectotympanic extends posteriorly to contact or closely approach the petrosal; as a result the dorsal margin of the auditory meatus appears "closed" by the ectotympanic. By contrast, in some taxa the anterodorsal edge of the ectotympanic is shorter and does not extend far posteriorly, and does not contact the petrosal; as a result, the dorsal margin of the auditory meatus appears "open" and is bordered by a well exposed tegmen tympani (fig. 8). This "open" condition is seen only in Rhipidomys, Chilomys, Aepeomys lugens, and Thomasomys. In T. aureus the ectotympanic ring is "closed" in my series from Pichincha, Ecuador, but

predominantly "open" in my sample from Puno, Peru. I scored this taxon as a taxonomic polymorphism. Thomasomys baeops exhibits the "open" condition in specimens from Napo, Ecuador; but the "open" and "close" conditions occur in specimens from Pichincha, Ecuador. Similarly, T. kalinowskii has populations with the "open" condition, and others that exhibit both conditions. I erected state (1) for these cases of within-species polymorphism.

In Analysis 2, transformations of this character were ordered ( $0 \leftrightarrow 1 \leftrightarrow 2$ ) to accommodate observed variability in this feature and to reflect my assumption that changes in the degree of contact between the ectotympanic and the petrosal occur in a progressive fashion through the intermediate state 1.

**47. Supraoccipital process:** *Long (0); or short (1).*

The supraoccipital produces a dorsolateral process that dorsally surrounds the mastoid bulla on each side. In most muroids I examined, this process is short or only moderately developed, and is dorsal to the hamular process of the squamosal. However, in a few species the process extends more deeply, ventrally and posteriorly to contact the posterior margin of the hamular process. This condition was seen only in Microtus and Sigmodon.

**48. Incisive foramina:** *Short, the posterior margin of the foramina extends in front of M1 anterocone(0); or long, the foramina extending to or between the M1 procingula (1); or deep, the foramina extending between the M1 protocones or more posteriorly (2).*

A short incisive foramen that extends to front of the first upper molars is seen in Microtus, cricetines, Calomyscus, tylomyines, Neotoma, peromyscines (except



Baiomys), ichthyomyines, many oryzomyines, Sigmodon peruanus, and most thomasomyines (including Abrawayaomys, Aepeomys, Chilomys, Delomys, Phaenomys, Rhagomys, Rhipidomys, some Thomasomys, and Juliomys pictipes). Long foramina are present in all phyllotines, scapteromyines, most akodontines, S. hispidus, Wiedomys, and the thomasomyines Juliomys sp., Rhipidomys macconnelli, Wilfredomys and several Thomasomys. The deep foramina were observed only in Akodon and Oxymycterus in my samples. Oxymycterus paramensis, Thomasomys cinereus, and T. notatus exhibit two states in distinct populations. Thomasomys cinereus has a long incisive foramina in the series from Cajamarca, Peru, while in most specimens from Piura, Peru the foramina is short. Similarly, T. notatus from Cuzco, Peru exhibits a long foramina while in the series from Huánuco, Peru is short. These taxa probably constitute more than one species, and therefore were scored as taxonomic polymorphisms.

In Analysis 2, the transformations of this character were ordered (0↔1↔2) to reflect the logical assumption that the size of the incisive foramina changes from short state (0) to deep state (2).

**49. Maxillary septum length:** *Septum short, extending half the length of the incisive foramina or less (0); or long, extending distinctly more than half the length of the foramina (1); or polymorphic, either short or long (2).*

The maxillary septum forms part of the bony bridge that separates the right and left incisive foramina. A long maxillary septum is commonly found in Microtus, Cricetulus, Calomyscus, peromyscines (except Scotinomys), and all akodontines. A short maxillary septum is the common condition in neotomines, tylomyines, and other sigmodontines. Stepan (1995: character 39P) employed this feature for his phyllotine

phylogenetic analyses and he observed that: "... most akodontines have a very short septa ( $<1/2$ ) and most oryzomyines have septa that exceed  $3/4$  the incisive foramina length."

My observations of akodontine and oryzomyine species disagree with his statement, but our state definitions are not equivalent, and some of his taxa were not included by me, which may partially explain this discrepancy. Unfortunately, Steppan did not employ this character for his more inclusive sigmodontine analysis. Among thomasomyines, Chilomys exhibits alternative conditions in different populations, variation that I treat as taxonomic polymorphism. Individuals of Tylomys from apparently a single population exhibit both states 0 and 1, and were scored as within-species polymorphism.

**50. Palatal length:** *Palate short, extending to or between the posterior margins of M3s (0); or palate moderately long, not extending beyond half of M3 tooth-length posterior to M3 (1); or palate long, extending more than half of M3 tooth-length posterior to M3 (2).*

Palatal length is an informative feature that has been used in sigmodontine taxonomy ever since Thomas (1906) distinguished the "short-palate" Thomasomys and Rhipidomys from the "long-palate" Oryzomys and Oecomys. Later, Hershkovitz (1962) interpreted the palatal morphology in two dimensions: length and width. My scoring strategy is intermediate between the classical "short versus long" dichotomy and the four states of palatal length employed by Steppan (1995). All three states are widespread in sigmodontines and except for scapteromyines (all have a moderately long palate), no other tribe can be characterized by a uniform palatal morphology. A short palate, however, is predominant among akodontines and thomasomyines and a long palate is common to ichthyomyines, oryzomyines, and phyllotines. All thomasomyines have a short palate,

except for Chilomys and Rhagomys. Unfortunately, information on palatal length variation within species is often overlooked. My material of Microxus mimus and Abrothrix longipilis is polymorphic for states 0 and 1, whereas Chilomys instans is polymorphic for states 1 and 2. I scored these taxa as taxonomic polymorphisms in recognition of the diverse localities sampled.

In Analysis 2, the transformations of this character were ordered (0↔1↔2) to indicate an assumption that changes in the size of the palate occur in a progressive fashion.

**51. Palatal breadth:** *Palate breadth wide, the distance between the protocones of the first upper molar exceeds the length of first molars (0); or narrow, the distance between protocones is subequal to the length of the first molar or less (1).*

The definition for this character comes from Hershkovitz (1962). A broad palate occurs in most muroid rodents I examined here, and is characteristics of Aepeomys, Chilomys, Delomys, Rhagomys, Rhipidomys, Juliomys, and most species of Thomasomys among thomomysines. By contrast, Phaenomys, Thomasomys aureus, T. macrotis, and Wilfredomys oenax among thomomysines have a distinctly narrow palate.

**52. Posterolateral palatal pits:** *Pits simple, and level with, or posterior to the anterior margin of the mesopterygoid fossa (0); or simple and distinctly anterior to the mesopterygoid fossa (1); or complex (one or more pits are present in a common sulcus), and anterior to the mesopterygoid fossa (2).*

Posterolateral palatal pits are usually interpreted as part of the same complex character as palatal length. Voss and Carleton (1993), for example, proposed that a long palate with prominent posterolateral pits is a synapomorphy that diagnoses the tribe

Oryzomyini. However, in a wider array of taxa these two structures are not necessarily correlated. Stepan (1995) also found no evidence of correlation in his phyllotine analysis, and I decided to score both characters independently. Cricetines, neotomines, akodontines, Sigmodon, and thomomyines (except Rhagomys) have simple pits placed posteriorly to the anterior margin of the mesopterygoid fossa (state 0). By contrast, all peromyscines (except Ochrotomys), ichthyomyines (except Neusticomys) and most phyllotines exhibit state "1". Complex palatal pits are found only in oryzomyines except for Holochilus sciureus (state 0), and Microrhizomys minutus (state 1).

**53. Palatine suture:** *Suture straight (0); or convoluted (1).*

The suture between the right and left palatine bones in the posterior palate is "straight" when the margin between palatines is very close to a straight line. This kind of suture is seen in all neotomines, peromyscines, tyromyines, Calomyscus, Microtus, and Sigmodon. By contrast, the palatine suture is sinuous or irregular in cricetines and in the remaining sigmodontines (fig. 9). This character and the striking taxonomic dichotomy it reflects has not been reported before. My samples of Sigmodon hispidus exhibit both states: the convoluted suture occurs more commonly in specimens from Mexican localities, whereas the straight suture is present in samples from Florida, USA. Sigmodon hispidus has an extraordinarily wide distribution in North and South America, and very likely represents a complex of closely related species (Voss, 1992; Peppers et al. (2002). I therefore interpret this condition as a case of taxonomic polymorphism.

**54. Maxillary palatal pits:** *Absent (0); or present in the maxillary bone (1).*

I coin the term maxillary palatal pits for the small pits in the maxillary bone located on both sides of the palate, at the level of the first molar, and between the incisive

foramina and the posterior palatine foramina. They are distinct from the posterior palatine foramina, which are small perforations that occur in the hard palate usually at or near the maxillary-palatine suture (Voss, 1988). Maxillary palatal pits are present in all thomatomyine genera except Chilomys and Rhagomys. They are practically absent in all other muroids I examined except in Oxymycterus, Ichthyomys, and Sigmodon. In a few species like Thomasomys baeops, some specimens exhibit maxillary palatal pits only on one side, but for this analysis I interpreted this trait as present in such cases. Tribe (1996) apparently observed these pits in Rhipidomys, but interpreted them as supernumerary pits, without providing comparisons with other sigmodontines.

**55. Sphenopalatine vacuities:** *Absent, no perforations on the dorsal roof of the mesopterygoid fossa, or barely as narrow slits on each side of the basisphenoid-presphenoid suture (0); or moderate perforations, usually elongated, that extend at both sides of the basisphenoid-presphenoid suture, largely visible from the mesopterygoid fossa but inconspicuous from the interorbital region (1); or large perforations, usually oval shaped and distinctly visible from the interorbital region (2).*

Sphenopalatine vacuities are perforations in the bony roof of the mesopterygoid fossa and are present in most Myomorpha (Wahlert, 1985). State 0 is seen in tylomyines, ichthyomyines, some akodontines, and most thomatomyines. State 1 occurs in all cricetines, Calomyscus, Microtus, peromyscines, some akodontines, oryzomyines (except Oecomys and Handleyomys), scapteromyines, Punomys, Juliomys, Wiedomys, Wilfredomys, and Thomasomys notatus. By contrast, a large vacuity (state 2) is only exhibited in phyllotines (except Punomys), and Sigmodon, concurring with Steppan's (1995) observations.

In Analysis 2, the transformations of this character were ordered (0↔1↔2) to reflect a logical assumption that changes in the size of the sphenopalatine vacuity occur in a progressive fashion.

**56. Mesopterygoid fossa breadth:** *Broader than adjacent parapterygoid fossae (0); or mesopterygoid and parapterygoid fossae subequal (1); or mesopterygoid fossa distinctly narrower than parapterygoid fossae (2).*

The mesopterygoid fossa is often employed in taxonomic comparisons, but the potential ambiguity of defining states in the absence of consistent landmarks has apparently limited its use in phylogenetic analyses (Steppan, 1995). I follow Steppan's strategy (1995: character 18S) by evaluating the relative width of the mesopterygoid fossa in relation to the parapterygoid fossae at the level of the basisphenoid-presphenoid suture. A broad mesopterygoid fossa is the predominant condition in tylomyines, ichthyomyines, and thomasomyines. Sigmodon, several oryzomyines, and some representatives of other groups have subequal mesopterygoid and parapterygoid fossae. Phyllotines (except for Chinchillula, and Punomys) have a mesopterygoid fossa narrower than the parapterygoid fossae. Steppan (1995) indicated that this condition is a synapomorphy of the tribe Phyllotini, but I observed this feature in Cricetulus, Calomyscus, Baiomys, Reithrodontomys, the akodontines Akodon and Microxus, the oryzomyines Holochilus and Oligoryzomys, Wiedomys, and the thomasomyine Wilfredomys. Thomasomys notatus exhibits a mesopterygoid fossa that is highly variable in width, representing all three states defined above. Because I was unable to understand the source of variation in this taxon, I scored it as missing. By contrast, Chilomys instans exhibits states (0) and (1) in different populations, a clear case of

taxonomic polymorphism.

In Analysis 2, the transformations of this character were ordered (0↔1↔2) to reflect a logical assumption that changes in the breadth of the mesopterygoid fossa occur in a progressive fashion.

**57. Mesopterygoid fossa shape:** *Posteriorly convergent (0); or parallel sided (1); or posteriorly divergent (2).*

This character was employed by Steppan (1995: character 19S). I follow his state definitions to simplify comparisons. Tylomyines, most peromyscines, Sigmodon, and most thomomyines are the only groups in which a posteriorly convergent fossa is predominant. Within my surveyed taxa, all akodontines, ichthyomyines, oryzomyines, scapteromyines, the phyllotine Chinchillula and Punomys, Wiedomys, and some thomomyines (e.g., Abrawayaomys, Aepeomys, Chilomys, Wilfredomys) presented a parallel-sided mesopterygoid fossa. A posteriorly divergent fossa is seen only in the phyllotines Calomys, Graomys, and Phyllotis.

In Analysis 2 the transformations of this character were ordered (0↔1↔2) to reflect the likely progressive nature of the shape of the mesopterygoid fossa from convergency (0) to divergency (2).

**58. Shape of parapterygoid fossa:** *Rectangular (0); or triangular (1).*

The shape of parapterygoid fossa can be operationally defined by comparing the breadth of the fossa at the level of the posterior tip of the hamular process of the pterygoids versus its breadth at the basisphenoid-presphenoid suture. By my definition, a ratio of 1.5 or less reflects a parapterygoid fossa with a "rectangular" outline, which is the common condition in most muroid groups I examined. By contrast, a ratio greater

than 1.5 defines a parapterygoid fossa with a "triangular" outline. This condition is seen in Neotoma, Sigmodon hispidus, Wiedomys, and all thomatomyine rodents except Thomasomys erro. Thomasomys notatus exhibits a triangular parapterygoid fossa in populations from Cuzco, Peru, and a rectangular fossa in samples from Huánuco and Pasco, Peru, variation that I treated as taxonomic polymorphism.

**59. Hypoglossal foramen:** *Level with or anterior to the paraoccipital process (0); or posterior to the paraoccipital process (1).*

The hypoglossal foramen is situated between the paraoccipital process and the occipital condyle on each side of the skull, posteromedial to the jugular foramen (Wahlert, 1985). The widespread condition among my surveyed taxa is the hypoglossal foramen positioned level with or slightly anterior to the paraoccipital process. By contrast, the hypoglossal foramen is posterior to the paraoccipital process in Mesocricetus, all ichthyomyines, and Oxymycterus.

**60. Entoglossal process of basihyal:** *Entoglossal process present knob-like or long (0); or entoglossal process absent (1).*

Carleton (1980) described and scored the hyoid morphology among an extensive array of muroid rodents; his scheme is followed here but with an emphasis on the entoglossal process of the basihyal. Carleton interpreted a short, knob-like entoglossal process as primitive for muroid rodents and therefore its absence constitutes a potential synapomorphy for sigmodontine rodents as suggested by Voss and Carleton (1993). All sigmodontines I examined lack the entoglossal process. By contrast, in all other muroids I examined the entoglossal process is present. However, the hyoid morphology of Baiomys is controversial. Sprague (1941) observed that Baiomys taylori lacked an



entoglossal process based on his examination of a single specimen. Packard (1960: fig. 5) also reported that the entoglossal process was much reduced or absent in B. taylori, but present in Baiomys musculus. Later, Carleton (1980) noted that the entoglossal process is present in both species of Baiomys; he questioned Sprague's observation, but provided no comments on Packard's. In the skeletal material of Baiomys musculus that I examined (see Appendix 1), only two specimens (AMNH 177937, 177945) preserved the tiny basihyal element, but in both of these the entoglossal process was clearly absent (resembling the condition in Sigmodon). The observations that the entoglossal process is either present (Packard, 1960; Carleton, 1980) or absent (this work) in Baiomys musculus is difficult to reconcile without examining a larger series of specimens. In the meantime, I scored Baiomys musculus as taxonomic polymorphism on the grounds that reports were based on different populations. The presence or absence of a knob-like entoglossal process in Baiomys deserves further evaluation with an emphasis on evaluating geographic variation in this trait.

**61. Malleus and incus exposure:** *Malleus and incus exposed in lateral view (0); or largely concealed (1).*

Among New World muroid rodents the widespread condition is that the middle ear ossicles, particularly the malleus and incus, are clearly visible in lateral view through the pars flaccida of the tympanic membrane. However, ichthyomyines lack a well-developed pars flaccida, and the ossicles are concealed dorsally by broad anterior and posterior laminae of the ectotympanic (Voss, 1988: 299). Similar condition was observed only among the outgroups Mesocricetus and Microtus.

**62. Orbicular apophysis of malleus:** *Absent (0); or present (1).*

The orbicular apophysis of the malleus is uniformly present among the muroids I examined, but an orbicular apophysis is absent in Microtus and cricetines. Among sigmodontines, the orbicular apophysis of the ichthyomyines I scored here is always small and spur-like, but it is absent in Chibchanomys and in some species of Neusticomys (Voss, 1988).

**63. Manubrium orientation:** *Perpendicular (0); or parallel (1).*

The manubrium is an elongated shaft-like process arising from the ventral margin of the malleus (Cockerell et al., 1914). Two kinds of muroid mallei, "perpendicular" and "parallel" types, have been defined in terms of the orientation of the manubrium in relation to the main longitudinal axis of the skull. In addition, I observed that in the "perpendicular" type, the angle between the manubrium and the head of the malleus is obtuse and closer to 180 degrees; in a "parallel" type the manubrium forms a right angle with the head of the malleus. These morphotypes have often been employed for the diagnosis of higher level groups of rodents. Musser and Carleton (1984) described an intermediate condition for cricetines, while indicating a malleus of the perpendicular type for arvicolines. My scoring strategy departs from Carleton's (1980) definitions of "perpendicular" and "parallel" types of mallei in that I evaluate the orbicular apophysis separately (see character 62) to retain the most information possible. Perpendicular mallei are seen in Microtus and Mesocricetus, and also reported in other arvicolines and cricetines (Cockerell et al., 1914). I also interpret the mallei of the ichthyomyines Ichthyomys and Neusticomys as perpendicular, a feature that is apparently unique among sigmodontines. The parallel type is the widespread condition in all the remaining muroids that I examined.

**64. Processus brevis of incus:** *Processus brevis with base thick, usually short, tip pointed or knob-like, more robust in appearance (0); or base narrow, usually long and tapering to a pointed tip, delicate in appearance (1).*

The processus brevis of incus is a posterior outward extension from the body of the incus according to Cockerell et al. (1914), who described variation in the morphology of the processus brevis among an extensive array of rodents. I have tentatively summarized the existing variation of the processus brevis of incus in two types. A robust processus brevis, in which the base is broad and its posterior extension is usually short, is the widespread condition among all muroid groups except thomasomyines. By contrast, a more delicate processus brevis (with base distinctly narrower, longer and more slender) is seen in Nelsonia, Microxus, Calomys, Wiedomys, and all thomasomyines I examined.

**65. Cephalic process of malleus:** *Cephalic process exhibits a thin but distinct crest that is continuous with the crest of the cephalic peduncle of malleus (0); or cephalic process lacks a crest, but crest present on cephalic peduncle of malleus (1).*

A cephalic process is located on the dorsal margin of the head of the malleus and “frequently bounding above and without a large thin plate or *lamina*” (Cockerell et al., 1914: 348). A large lamina is absent in my surveyed taxa, but a thin and distinct crest is usually present, bounding the dorsal margin of the malleus lamina and continuing posteriorly and downward to the crest on the cephalic peduncle of the malleus (fig. 10). This feature represents the widespread condition in my surveyed taxa. By contrast, the crest of the cephalic process is greatly reduced or absent in Ochrotomys, akodontines (except Oxymycterus), Ichthyomys, scapteromyines, and Sigmodon.

**66. Petromastoid bony tube for the stapedia artery:** *Present (0); or absent*

(1).

The stapedia artery runs along the petromastoid before crossing the stapes, marking or not a groove in all muroids I examined, except for Microtus and Mesocricetus. In Microtus, the stapedia artery is protected by a long bony tube that crosses the stapes. In Mesocricetus, this protection is reduced to a wide bony arch placed just before the stapedia artery crosses the stapes.

## DENTITION

**67. Upper incisor orientation:** *Opisthodont (0); or orthodont (1); or proodont (2).*

My state definitions for this character follow Hershkovitz (1962) and Steppan (1995). Opisthodont incisors are widespread in practically all muroid groups. Among those I examined, all neotomines, peromyscines, tylomyines, oryzomyines, all phyllotines (except Chinchillula), Sigmodon and Wiedomys are opisthodont. Orthodont incisors are less common, but they occur within all major groups of sigmodontines, notably in all scapteromyines. Proodont incisors were found only in Chilomys and Abrawayaomys. Thomasomyines exhibit all three conditions, but most species are opisthodont; the degree of opisthodonty is slight, except in Delomys, which has strongly opisthodont teeth.

In Analysis 2, transformations of this character were ordered (0↔1↔2) to reflect the logical sequence of transformation from opisthodont state (0) to proodont incisors state (2).

**68. M1 position:** *Alveolus of first upper molar anterior to the posterior margin of*

*the zygomatic plate (0); or below the posterior margin of the zygomatic plate (1); or posterior to the zygomatic plate (2).*

I evaluated the position of the first upper molar alveolus in relation to the posterior border of the zygomatic plate as seen from a ventral view on adult skulls. The state (0) is uncommon but occurs among all groups examined, particularly akodontines, ichthyomyines, phyllotines, and in few thomasomyines (e.g., Aepeomys lugens, Thomasomys kalinowskii, and T. macrotis). Similarly, state (1) is seen in several groups including thomasomyines (e.g., Abrawayaomys, Delomys and some Thomasomys). However, state (2) appears to be the most frequent condition, and particularly predominates among oryzomyines, thomasomyines (including Chilomys, Phaenomys, Rhagomys, Rhipidomys, Thomasomys baeops, T. notatus, and Wilfredomys), and Wiedomys. To evaluate this character, age variation must be considered since the molars are usually more anteriorly placed in juveniles than in adults. Chilomys shows variation among populations that was treated as taxonomic polymorphism.

In Analysis 2, the transformations of this character were ordered (0↔1↔2) to reflect the logical assumption that changes of the position of M1 occur sequentially along an anterior-posterior axis from anterior to the zygomatic plate (state 0) to posterior to the zygomatic plate (state 2).

**69. Anteromedian flexus: Present (0); or absent (1).**

The anteromedian flexus is a distinct median indentation on the anterocone of M1 that divides that cusp into labial and lingual conules. It is usually observed in adults, but the unworn teeth of juveniles and subadults are more suitable for scoring in some taxa. A distinct anteromedian flexus is widespread in several taxonomic groups including

cricetines, tylomyines, and all thomasomyines. It is also observed in peromyscines (including Baiomys, Scotinomys and Reithrodontomys), and occurs in some akodontines, some oryzomyines, phyllotines and scapteromyines. The flexus is absent in Microtus, Calomyscus, all neotomines, the peromyscines Ochrotomys and most Peromyscus, the akodontines Abrothrix and Microxus, ichthyomyines, most phyllotines, most oryzomyines, and Sigmodon.

**70. Anterocone:** *Anterolabial and anterolingual conules subequal (0); or anterolingual conule distinctly smaller, about half the size or less of the anterolabial conule (1).*

The anteromedian flexus divides the anterocone into anterolabial and anterolingual conules which are subequal in most muroid taxa examined by me. However, a distinctly reduced anterolingual conule was reported in the original description of Phaenomys (Thomas, 1917). Reig (1980) also observed the unusually small anterolingual conule of Wiedomys, and this feature was cited in his diagnosis of the tribe Wiedomyini. I recorded small anterolingual conules in Nyctomys, in Wiedomys, and all southeastern Brazilian thomasomyines (Abrawayaomys, Juliomys, Phaenomys, Rhagomys, and Wilfredomys) except Delomys. I concur with Voss (1993), who noted that in Delomys, the lingual conule is sometimes smaller than the labial conule, especially in D. sublineatus.

This character cannot be evaluated in taxa lacking anteromedian flexus, the state (1) of the character 69.

In Analysis 2 the transformations of characters 69 and 70 were ordered (0↔1↔2) in a single character to reflect the hypothesis that changes in the development of the anterocone occur in successive steps from absence of the anteromedian flexus to

anterolingual conule distinctly smaller, passing through an anterocone with subequal conules.

**71. Metaloph on M1-M2:** *Absent (0); or present (1).*

Wahlert (1984, fig. 3) observed in Mesocricetus and other cricetine genera that the metaloph forms a strong and high transverse loph between the metacone and the hypocone. This "cricetine" morphology was also seen in Cricetulus, but absent in other muroid taxa examined here.

**72. Mesoloph development:** *Mesoloph absent (0); or mesoloph small, not reaching labial cingulum (1); or mesoloph complete, reaching mesostyle on the labial cingulum (2).*

Presence or absence of a complete mesoloph defines the morphotypes traditionally known as pentalophodonty and tetralophodonty in muroid rodents (Hershkovitz, 1962). A "complete" mesoloph reaches a mesostyle on the labial cingulum (producing a mesoloph-mesostyle; Hershkovitz, 1962), and may be coalesced or not with either a paralophule or a metalophule. A complete mesoloph is seen in several peromyscines, Nyctomys, the akodontines Abrothrix and Microxus, Scapteromys, oryzomyines (except Holochilus; Voss and Carleton, 1993), Wiedomys, and all thomatomyines. A small mesoloph that may stand free or be partially fused to the paracone is seen in a few "tetralophodont" taxa. A mesoloph is absent in Microtus, cricetines, Calomyscus, neotomines, Baiomys, phyllotines (except Punomys), ichthyomyines (except Anotomys), Sigmodon, and Holochilus sciureus. Like Steppan (1995), I score Scotinomys as missing.

I originally included and scored variation in the development of the anteroloph-

parastyle, following Voss and Carleton's (1993) analysis of Lundomys. However, the states of that character were correlated with those of the mesoloph, as previously observed by Hooper (1957) and Carleton (1980). Therefore, I excluded the anteroloph-parastyle from my analyses.

In Analysis 2 the transformations of this character were ordered ( $0 \leftrightarrow 1 \leftrightarrow 2$ ) to reflect my hypothesis that changes in the development of the mesoloph occur in successive steps.

**73. M3 Mesoloph:** *Absent or vestigial (0); or present and usually well developed (1).*

M3 provides an evolutionary scenario different from that of the other upper molars. Hershkovitz (1962) stated that the process of simplification from pentalophodonty to cylindriform molars occurs first in the third molars. Voss and Carleton (1993) also argued that the mesoloph of M3 undergoes evolutionary transformations that appear to be independent of mesoloph modifications on the other molar teeth. My observations support these statements. An M3 mesoloph occurs in Tylomys, the peromyscines Ochrotomys and Reithrodontomys, all oryzomyines, Wiedomys, and all thomatomyines (except Chilomys). Within sigmodontines, an M3 mesoloph is absent in all akodontines, ichthyomyines, phyllotines, scapteromyines, Sigmodon, and Chilomys.

**74. Labial cingulum of upper molars:** *Weak or absent (0); or incomplete, mesoflexus sometimes open (1); or well developed (2).*

In most muroid rodents I examined, the labial flexi (mesoflexus and metaflexus) are open or inconsistently closed by a labial cingulum. According to Tribe (1996),



"Rhipidomys differ from ... Delomys and *most* Thomasomys in that the [labial] cusps and styles are linked by these marginal ridges" (my italics). I agree with his observations with respect to the species of Rhipidomys, Delomys and most Thomasomys included herein. Rhipidomys exhibits a well developed labial cingulum that encloses the mesoflexus, metaflexus, paraflexus, and anteroflexus. A similar feature was also observed in Oecomys. Other thomasomyines either lack this cingulum, or the labial flexi are weakly enclosed by a low ridge. Thomasomys notatus exhibits what may be an "intermediate" condition: specimens have a labial cingulum that is more developed than that seen in other Thomasomys (e.g., T. cinereus), but the mesoflexus is not completely closed off.

In Analysis 2, transformations of this character were ordered ( $0 \leftrightarrow 1 \leftrightarrow 2$ ) to reflect a logical assumption that changes in the degree of development of labial cingulum occur in a progressive fashion.

**75. Protoflexus on M2: Present (0); or faint or absent (1).**

The protoflexus, the most anterior flexus on the lingual side of M2, can be conspicuous, faint, or absent among the surveyed taxa. Because the protoflexus is sometimes obliterated by attrition on the worn molars of adults, subadults and juveniles were also examined to score this character. The protoflexus is uniformly present in Calomyscus, tylomyines, the peromyscines Ochrotomys and Reithrodontomys, Anotomys, Punomys, some oryzomyines and all thomasomyine genera except Delomys and Aepeomys. It is absent from cricetines, Neotoma, several peromyscines, akodontines, all phyllotines (except Punomys), scapteromyines, Sigmodon, and from some oryzomyines and thomasomyines. Both states occur in Wiedomys; even on

unworn teeth; the protoflexus is present in specimens from Bahia and Ceara, Brazil while it is absent in the specimens from Pernambuco, Brazil. Although no subspecific distinction is reported for the species, I favor a hypothesis of taxonomic polymorphism based on these apparently disjunct distributional records.

**76. Molar roots, height and occlusal topography:** *Molars rooted, brachyodont, and bunodont (0); or rooted, moderately high-crowned, and planar (1); or rooted, hypsodont, and planar (2); or rootless and hypsodont (3).*

I follow Carleton (1980: character 4) in describing the evolution of molars from the bunodont/brachyodont state to the hypsodont/planar configuration. The rooted bunodont-brachyodont molars are the widespread condition in the examined muroids. Molars moderately high-crowned and planar are observed only in Holochilus, Chinchillula, Sigmodon, and Kunsia. Neotomines have hypsodont and planar molars, and Microtus have rootless and hypsodont molars.

In Analysis 2, the transformations of this character were ordered (0↔1↔2↔3) to reflect my assumption that changes from the bunodont/brachyodont molar to the hypsodont/planar molar occur in a progressive fashion. This transformation agrees with Carleton's assumption (1980).

**77. Molar occlusal design:** *Labial and lingual folds not interpenetrating (0); or folds with slight to deep interpenetration, as seen mainly between hypoflexus and metaflexus of M1-M2 (1).*

Voss (1993) and Voss and Carleton (1993) employed the degree of fold interpenetration to assess relationships among several Neotropical muroid taxa. They emphasized the correlation between cusp position and folding, because interpenetrating

folds are usually associated with alternating cusps. However, this does not always hold in the context of a wider array of taxa. Therefore, I scored the degree of interpenetration on M1-M2 as a separate character from cusp alternation (see character 78, below). Non-interpenetrating molar lophs are the widespread condition among the taxa I examined. Interpenetrating molar lophs (slight or deep) are represented by a few taxa scattered among several groups, including Tylomys, neotomines, the oryzomyines Holochilus, Oecomys and Handleyomys, Graomys, Sigmodon, Delomys, Rhipidomys fulviventris, Thomasomys kalinowskii, T. macrotis, and T. notatus. Interpenetrating lophs are never seen in cricetines, Calomyscus, peromyscines, akodontines, ichthyomyines, and scapteromyines.

**78. Cusp arrangement on m1: *Alternate (0); or intermediate (1); or opposite (2).***

I follow Carleton (1980: character 3) in selecting the degree of opposition of the primary cusps (protoconid-metaconid and hypoconid-entoconid) as the basis for scoring this character. The primary cusps are considered to be alternate when both of the lingual cusps (metaconid and entoconid) are markedly anterior to their labial counterparts; thus, the metaconid lies across the protoflexid, and the entoconid across the hypoflexid (as seen in Peromyscus). In the opposite arrangement, the main cusps define an almost perfect square. In the intermediate condition, the lingual cusps are only slightly anterior to the labial ones.

This character has been utilized for studies of "neotomine-peromyscine" and phyllotine relationships (Carleton, 1980; Steppan, 1995), but for several of my sampled taxa, there is no congruence with previous reports, apparently due to dissimilar state definitions; in general, my scoring agrees better with Carleton's (1980) than with

Steppan's (1995). The alternate condition is predominant in my non-sigmodontine outgroups. Among sigmodontines this feature is seen in all akodontines, all scapteromyines, most phyllotines, Holochilus sciureus, Sigmodon peruanus, and only the thomasomyine Abrawayaomys. The intermediate condition is seen only in Tylomys, Reithrodontomys, some phyllotines and oryzomyines, Sigmodon hispidus, Wiedomys, and all thomasomyines except Abrawayaomys. The opposite condition is far less common, but characterizes all ichthyomyine rodents (Voss, 1988).

My sample of Reithrodontomys mexicanus from Costa Rica exhibits alternate cusps. However, supposedly conspecific samples from Mexico exhibit the intermediate condition; these are samples identified as the subspecies cherrii and howellii respectively. Therefore, I scored Reithrodontomys mexicanus as a case of taxonomic polymorphism. Alternation of cusps on the upper molars appears to be correlated with cusp arrangements on the lower molars. Taxa with alternate cusps on the lower teeth usually exhibit the intermediate condition on the uppers, and taxa with intermediate cusp arrangement on the lower teeth have more opposite configurations on the upper dentition.

In Analysis 2, transformations of this character were ordered (0↔1↔2) to reflect my assumption that changes in the degree of alternation between cusps occur in a progressive fashion.

**79. Ridge on anterolabial cingulum of m1: *Present (0); or reduced or absent (1).***

Gardner and Romo R. (1993) described a ridge on the anterolabial cingulum of m1 that extends posteriorly from the anterolabial conulid and suggested that this ridge is characteristic of Thomasomys (s.l.). This character was also evaluated by Steppan (1995).

character 14P) for his phyllotine phylogeny. When present (state 0), a well developed ridge reaches the protoconid and encloses the protoflexid, which is shallow or deep depending on the height of the ridge. In the reduced or absent condition (state 1), the protoflexid is more or less open to the labial margin. I observed that a ridge on the anterolabial cingulum of m1 is widespread, and is present in Calomyscus, tylomyines, some peromyscines, most oryzomyines, phyllotines and thomasomyines. By contrast, cricetines, neotomines, akodontines, ichthyomyines, Holochilus, Punomys, scapteromyines, Sigmodon, and the thomasomyines Abrawayaomys and Chilomys all have the state (1).

**80. Metaflexid morphology on m1:** *Metaflexid appressed (0); or metaflexid open (1).*

The metaflexid is located on the lingual side between the anteroconid and the metaconid on m1 (Reig, 1977). The metaconid and anteroconid of m1 are considered antero-posteriorly compressed when both conulids are tightly close producing a thin or sometimes absent metaflexid; otherwise, when the cusps are not close the metaflexid is open and distinct. Partial correlation of this morphology with the alternate arrangements of the main cusps (character 78, state 0) might be suspected since appressed metaflexid are absent in all cases of parallel or intermediate arrangements. I evaluated this morphology only in taxa exhibiting the alternate condition between the primary cusps of m1 (character 78, state 0).

This morphology has apparently not been reported, except by Hooper (1952: 22, fig. 5), who noted in his revision of Reithrodontomys: "... and the first secondary fold in M<sub>1-3</sub> are always short; often they are absent". The first secondary fold corresponds to

the metaflexid (sensu Hershkovitz, 1994). An appressed metaflexid is seen only in Calomyscus, Nyctomys, and all peromyscines. By contrast, an open metaflexid is seen in cricetines and all sigmodontines. This feature readily separates Calomys from peromyscine rodents.

**81. Internal enameled pit of m1 procingulum:** *Internal enamel pit absent (0); or internal enamel pit prominent (1).*

Voss and Carleton (1993) observed the presence of a well developed pit in the procingulum of the first lower molar of Holochilus, Lundomys, Oryzomys subflavus, and Pseudoryzomys, and suggested this pit may be a remnant of an ancestral anteromedian flexid. In addition to Holochilus and Oryzomys, I also observed the internal enameled pit in Handleyomys and Oecomys, but found it absent in the oryzomyines Oligoryzomys and Microryzomys, and all other muroid groups examined here. Recently, Carleton and Olson (1999) reported also the enamel pit in Noronhomys.

**82. Occlusal complexity of m3:** *Lower third molar complex, similar to m2, posteroflexid patent (0); or m3 simple, posteroflexid reduced to a pit (1); or m3 simple, posteroflexid absent (2).*

Carleton (1980, character 5) evaluated the occlusal complexity of m3 focusing on the degree of development of the main cuspids and their arrangement. My definition here focuses on the degree of development of the entoconid, hypoconid and posteroflexid, rather than on their position. The cusp arrangement of m3 appears to follow the arrangement pattern of m1, already evaluated above (character 78). A complex m3, with cuspids and flexids developed to about the same extent as in m2, is seen only in cricetines, Ochrotomys, tylomyines, and the thomasomyines Phaenomys, Rhipidomys, and

Thomasomys notatus. In the intermediate condition (state 1) the entoconid and hypoconid are reduced and are coalesced with the posterior cingulid; in consequence, the posteroflexid is present but reduced to a small internal fossetid. This condition is seen in some peromyscines, oryzomyines except Holochilus, Scapteromys, Wiedomys, and several thomasomyines. In the third condition, the entoconid-hypoconid are indistinct from the reduced posterior cingulid and the posteroflexid is absent; this state is observed in Calomyscus, some peromyscines, all akodontines, all ichthyomyines, all phyllotines, Sigmodon, Kunsia, and Chilomys. This character cannot be scored in taxa with conditions other than brachyodont/bunodont, or incipiently hypsodont/planar molars (see character 76, states 0 and 1).

In Analysis 2, the transformations of this character were ordered (0↔1↔2) to reflect my assumption that changes on the complexity of m3 occur in a progressive fashion.

**83. Mesolophid:** *Present (0); or absent (1).*

The mesoloph-mesostyle morphology on upper molars is usually correlated with the mesolophid-mesostylid complex on lower molars. However, I noted that Wiedomys, Rhagomys, and Abrawayaomys have strongly reduced (or absent) mesolophids even though their mesolophs are yet conspicuous. Reig (1980) noted this condition in Wiedomys. This feature was evaluated only for those taxa with well developed mesoloph (character 72, state 2).

**84. Metacone of M3:** *Tuberculate (0); or shallow (1).*

In the muroids I examined with bunodont/brachyodont molars, M3 has a distinct tuberculated protocone and paracone, and a shallow metacone. However, the M3 of the

tylomyines Nyctomys and Tylomys differs from all others. They exhibit a metacone conspicuously tuberculate (as opposed to shallow), therefore the cusps on M3 resemble the cusps on M2. I evaluated this feature in all muroids examined except for those taxa with planar/hypsodont molars which have shallow metacones. Tuberculated metacones on M3 were also observed in the tylomyines Ototylomys and Otonyctomys (although not included in the analyses).

**85. Accessory labial root of M1: *Absent (0); or present (1)*.**

The upper molars of most muroids examined exhibit three roots in anterior, posterior and lingual position, all externally visible. Voss and Carleton (1993) described the presence of an additional root on the labial side of M1 for Holochilus, Sigmodon, Oryzomys subflavus, and Pseudoryzomys simplex, which is different from other accessory roots that may arise elsewhere on the tooth. This feature has been used in recent phylogenetic analyses of muroid rodents by Carleton (1980), Voss and Carleton (1993) and Steppan (1995). The accessory labial root of M1 is absent in most taxa I examined. Labial accessory roots are present in the oryzomyines Holochilus and Handleyomys, all phyllotines (except Punomys), scapteromyines, Sigmodon, and the thomasomyine genera Aepeomys and several species of Thomasomys.

**86. Lingual roots on M1-M2: *One root (0); or two roots (1)*.**

Carleton (1980: characters 8, 10) scored the lingual roots of M1 and M2 as separate characters, but in my study I observed that additional lingual roots on one tooth are usually mirrored in the other. However, the lingual root in M2 is usually larger (and externally more conspicuous) than in M1. My scoring agrees largely with Carleton's except that I observed accessory lingual roots in M2 of Nyctomys and Tylomys.



Accessory lingual roots were observed in cricetines, Calomyscus, tylomyines, Scotinomys, and the thomasomyines Phaenomys, and Rhagomys. Microtus was my only representative with the rootless condition, which I scored as inapplicable for this character.

**87. Roots on m2:** *Two roots (0); or three roots (1).*

Carleton (1980: characters 14, 15) scored the molar roots of m2 and m3 as separate characters. Likewise, Steppan (1995: characters 8P, 9P) evaluated the molar roots of m2 and m3 separately in his phyllotine analyses. Within my surveyed taxa, the number of roots of these teeth appears to be correlated one to the other (see also Carleton, 1980: table 7). Steppan's data suggest that scores on both teeth are at least partially independent. Unfortunately, Steppan's (1995: 21, table 4) statements about the root conditions on m3 are in some cases contradictory (e.g., he mentioned: "Two roots were found in Andalgalomys, Eligmodontia, Galenomys, and Neotomys"; but scored them as "three roots"). Here, I evaluate only the molar roots of m2, based on data from Carleton (1980), Steppan(1995), and my own observations. Two roots beneath m2 is the widespread condition, observed in all non-sigmodontine outgroups, all akodontines, ichthyomyines, most oryzomyines, Punomys, and all thomasomyines examined. By contrast, three roots are seen in all phyllotines (except Punomys), Holochilus, Handleyomys, Sigmodon, and Scapteromys. Carleton (1980) scored two roots for Oryzomys palustris, but Carleton and Musser (1989, fig. 27) reported that two and three roots may be present in that species. I found that two roots anchoring m2 occurs in most Oryzomys palustris from disjunct localities that I have examined. I score this taxon as state 0.

## MANDIBLE

**88. Mandible:** *Cricetine morphotype (0); or New-World muroid morphotype (1).*

Carleton and Musser (1984: 311) characterized the cricetine mandible as:

"coronoid process strongly developed with deep sigmoid notch", but did not comment on the mandibular design of sigmodontines. Hershkovitz (1962: 221) also differentiated Mystromys from phyllotines based on the mandibular design. The shape of the mandible is highly variable among the muroids I examined here; but overall inspection indicates that previous arguments can be expanded to involve two designs. In the cricetine morphotype, the coronoid process is extremely long (extending posteriorly to a point dorsal to the condylar and angular processes), the sigmoid notch is deep and almost dorsal to an also deep angular notch (fig. 11). By contrast, in the New-World muroid morphotype, the coronoid process is small to moderately long (terminating at a point anterior to the condylar and angular processes), the sigmoid notch is shallow or moderate, and placed anterior to a shallow angular notch (fig. 11). Mesocricetus, Cricetulus, Calomyscus, and the arvicoline Microtus exhibit the cricetine morphology (as does Mystromys, not included in my analyses). All other examined muroids exhibit the New-World muroid morphology. Among them, some sigmodontines (e.g., ichthyomyines, Holochilus) have a long and high coronoid process, but the overall morphology agrees with the New-World muroid plan.

**89. Masseteric crest position:** *Anterior edge of the masseteric crests posterior to the procingulum of m1 (0); or anterior edge of the masseteric crests below the procingulum of m1 (1); or anterior edge of the masseteric crests anterior to the*

*procingulum of m1(2).*

The superior and inferior masseteric crests of the mandible converge anteriorly approaching the mental foramen. This character evaluates the position of the anterior most point of the masseteric crests in relation to the position of the anterior edge of the m1 procingulum. The masseteric crest is posterior to the procingulum of m1 in Tylomys, Scotinomys, akodontines, ichthyomyines, Punomys, and several thomasomyines. Among thomasomyines, Aepeomys lugens, Phaenomys, Rhipidomys macconnelli, and all Thomasomys (except T. baeops and T. notatus) exhibit such a posteriorly placed masseteric crest (state 0). State 1 is predominant in my non-sigmodontine outgroups except Scotinomys and Tylomys, which exhibit the posterior condition. Among thomasomyines, state 1 is seen in Delomys, Chilomys, Juliomys sp., Wilfredomys, some Rhipidomys, and in Thomasomys notatus and T. baeops. The masseteric crest extends anterior to the procingulum of m1 in most oryzomyines and phyllotines, Sigmodon, Kunsia, Wiedomys, and few thomasomyines (especially those from southeastern Brazil, e.g., Abrawayaomys, Rhagomys, and Juliomys pictipes) (fig. 11).

Wiedomys pyrrhorhinus is polymorphic for this character; specimens from Bahia and Ceara, Brazil, exhibit state 1, whereas specimens from Pernambuco, Brazil, exhibit state 2. My sample is too small to assess accurately whether this variation corresponds to a case of within-species or taxonomic polymorphism. Although no subspecific distinction has been reported for the species, I scored this species as a taxonomic polymorphism, which is more in agreement with the distributional records. Rhipidomys fulviventer is also geographically variable in this character; Colombian specimens from Cauca exhibit state 0, while my single Colombian specimen from La Macarena exhibits

state 1. I observed similar variability in population samples from Venezuela. I also scored this species as a case of taxonomic polymorphism.

In Analysis 2, the transformations of this character were ordered (0↔1↔2) to indicate my hypothesis that changes in the position of the anteromost point of the masseteric crest occur along a longitudinal axis in a progressive fashion.

**90. Mental foramen position:** *Low, more than one foraminal diameter ventral to the diastema (0); or high, closer to the diastema (1); or very high, on the dorsal surface of the diastema (2).*

The mental foramen serves as a passage for the inferior labial vein and artery (Greene, 1935), and in all muroids examined is placed in the diastema not far in front of ml. Among the taxa I surveyed, a low mental foramen (state 0) is seen only in Microtus, cricetines, tylomyines, and Ochrotomys. Calomyscus, neotomines, peromyscines (except Ochrotomys), and most sigmodontines exhibit a more dorsally positioned mental foramen (state 1), but only Sigmodon and Juliomys pictipes exhibit a mental foramen positioned directly on the dorsal surface of the diastema (state 2) (fig. 11). This position was reported previously for Sigmodon (e.g., S. allenii) by Martin (1979).

In Analysis 2, the transformations of this character were ordered (0↔1↔2) to reflect my assumption that changes in the position of the mental foramen occur along a dorso-ventral axis in a sequential fashion.

**91. Capsular process of lower incisor alveolus:** *Absent (0); or distinct (1).*

A distinct capsular process contains the posterior terminus of the lower incisor alveolus (Voss, 1993). Voss (1993) reported a distinct capsular process present in Oryzomys palustris, but the incisor alveolus terminates in an indistinct swelling or low

ridge in Thomasomys cinereus and Delomys; he postulated that absence of the capsular process is the primitive condition. He also reported the absence of the capsular process in all his outgroup taxa, including tylomyines, neotomines, and peromyscines (except in Onychomys [Carleton and Eshelman, 1979]). My own evaluations agree with Voss's statements. The capsular process of the lower incisor is commonly absent in my non-sigmodontine outgroup genera. Among sigmodontines, the capsular process is absent in akodontines (except Akodon), ichthyomyines, phyllotines (excluding Calomys and Graomys), Scapteromys, Handleyomys, Wiedomys, and several thomasomyines including Aepeomys, Delomys, Phaenomys, Rhipidomys leucodactylus, all Thomasomys (except T. baeops and T. notatus), and Wilfredomys. By contrast, the capsular process is seen in Akodon boliviensis, all oryzomyines (except Handleyomys), Kunsia, Sigmodon, and the thomasomyines Abrawayaomys, Chilomys, Rhagomys, Rhipidomys (except R. leucodactylus), T. baeops, T. notatus, and Juliomys.

I scored Reithrodontomys mexicanus as a case of taxonomic polymorphism. Specimens from Chiapas, Mexico (referable to R. m. howelli) lack the capsular process, whereas those from Costa Rica (referable to R. m. cherriei) exhibit a small but distinct capsular process.

**92. Retromolar region:** *Shallow, as a groove (0); or present, deep in a fossa (1).*

Rinker (1954: 17) described how most fibers of the superficial (or anterior) temporalis muscle “end in a tendon which attaches along the anterior border of the coronoid process and in the groove between the base of that process and the last molars.” Likewise, Greene (1935:34) used the term groove for the region between the molar teeth and the coronoid process where fibers of the temporalis are attached. Voss (1988: 393,

394) apparently refers to this region as the "retromolar fossa" where fibers that originated from the orbital fossa and the aponeurosis of the coronoid edge of the temporalis are inserted. In most muroids, the retromolar region between the last two molars and the medial side of the coronoid process is shallow, narrow, as a groove, and weakly or not perforated. On the contrary, in Abrawayaomys and Rhagomys this region is broad, deeply excavated as a fossa, and highly perforated, probably reflecting extensive vascularization.

## POST-CRANIAL SKELETON

### **93. Entepicondylar foramen of humerus: *Present (0); or absent (1).***

An entepicondylar foramen of the distal humerus above the medial epicondyle is typically present in "neotomine-peromyscines", and absent among sigmodontines and tylomyines (Carleton, 1980). Carleton favored the hypothesis that presence of the entepicondylar foramen is primitive for "neotomine-peromyscine" rodents. Voss and Carleton (1993) subsequently considered the absence of the entepicondylar foramen a potential synapomorphy for the sigmodontines.

I observed, based on relatively large series of Baiomys, Ochrotomys nuttalli, Oligoryzomys, Thomasomys baetops, and T. cinereus among others, that the entepicondylar foramen is symmetrically expressed, and does not exhibit age or sexual differences. Also, scoring for this character is markedly constant within species. The only exception was observed in Ochrotomys nuttalli, where one of 23 individuals (AMNH 254454) exhibits the entepicondylar foramen, which is absent in all others. Absence of the entepicondylar foramen in this species has been unanimously reported

(Carleton, 1980; Manville, 1961; Rinker, 1960). Therefore, this appears to be the first report of a species polymorphic for this character. However, given the small frequency of specimens exhibiting the foramen (4.3%), I scored the species as lacking the foramen.

The entepicondylar foramen is absent in all sigmodontines examined here, but this condition is not restricted to them. Microtus, Mesocricetus, and the peromyscines Baiomys, Ochrotomys, and Scotinomys also lack the foramen. Carleton (1980) also reported absence of the entepicondylar foramen in Hodomys, Isthmomys, some species of Reithrodontomys, and Xenomys.

**94. Supratrochlear fenestra of humerus:** *Absent (0); or present (1); or within-species polymorphism (2).*

The "olecranon" or "anconeal" fossa of the distal humerus (just above the trochlea and between the medial and lateral epicondyle) receives part of the olecranon process of the ulna. A supratrochlear fenestra is produced when the olecranon fossa is deep and the thin bone is perforated (Flower, 1885; Hill, 1937). Steppan (1995, character 30S) referred to this feature as the "supertrochlear foramen," and indicated that it appears to be highly informative for the sigmodontine group. I adopted the term "supratrochlear" following Flower (1885) and Hill (1937). I observed that the supratrochlear fenestra is usually constant within species, although this perforation can appear closed in older individuals. I considered the foramen to be absent when the olecranon fossa is completely ossified, and to be present when an open vacuity is evident or covered by a thin translucent lamina. Microtus, Neotoma, akodontines (except Abrothrix), oryzomyines (except Oecomys), phyllotines, Scapteromys, Sigmodon, and some thomasomyines have the supratrochlear fenestra. By contrast, cricetines, Calomyscus, tylomyines, most

peromyscines, Abrothrix, ichthyomyines, Oecomys, and several thomasomyines (i.e., Chilomys, Rhipidomys, Thomasomys baeops, T. notatus, and Juliomys pictipes) lack the foramen.

Three species were scored as taxonomic polymorphisms. Steppan (1995) scored the supratrochlear fenestra as present for Scotinomys teguina from Costa Rica (his state definitions are reversed, "0" should mean present, and "1" absent, to agree with his statements and matrix). The specimens of S. teguina I examined agree with Steppan's observation. However, samples of S. teguina from Guatemala lack the foramen. My specimens of Peromyscus mexicanus from Mexico lack the foramen while specimens from Guatemala and Honduras present it. Similarly, most of my Mexican specimens of Oligoryzomys fulvescens lack the foramen, but the foramen is present in the specimens from Venezuela. Steppan (1995) reported the supratrochlear fenestra present in his samples of Neusticomys monticolus (predominantly from Papallacta, Ecuador). However, I found the foramen to be absent in my samples from Pichincha, Ecuador. Although I did not review Steppan's samples of N. monticolus, this may represent an additional case of taxonomic polymorphism. I scored Wiedomys with a different state "2" to indicate a case of within-species polymorphism.

**95. First rib articulation:** *First rib articulates only with first thoracic vertebrae (0); or first rib articulates with both seventh cervical and first thoracic vertebrae (1); or within-species polymorphism (2).*

Carleton (1980) first described this feature. The dual articulation (state 1) occurs when the tuberculum of the first rib articulates with the transverse processes of the seventh cervical and the first thoracic vertebrae; in taxa exhibiting this condition, the



transverse process of C7 is usually provided with a demifacet for articulation with the tuberculum of the rib. Carleton found both states 0 and 1 in "neotomine-peromyscine" rodents, but only state 1 in sigmodontines. Voss and Carleton (1993) cited the dual articulation of the first rib (in combination with other apparently derived character states) to support the monophyly of the sigmodontines. Indeed, all my surveyed species of sigmodontines exhibit the dual rib articulation, but this condition also occurs in Microtus, cricetines, the peromyscines Baiomys, Scotinomys, and Reithrodontomys. Ochrotomys nuttalli was previously scored as possessing the dual rib articulation (Carleton, 1980; Steppan, 1995) but this species appears to be polymorphic. I examined 23 skeletons, 10 of them exhibit the dual articulation, in 11 the articulation was mainly with T1 (the transverse processes of C7 being just touched and lacking distinct demifacets), and in two specimens (one juvenile and one subadult) the articulation was simple. I therefore recognized a within-species polymorphic condition for Ochrotomys (state 2). Similarly, Mesocricetus was also scored as exhibiting the dual articulation based on six skeletons examined by Carleton (1980), or exhibiting the simple articulation based on a single skeleton examined by Steppan (1995). I found the simple articulation in one juvenile specimen, and double articulation in three adult specimens of Mesocricetus. Because age might account for such scoring differences, ontogenetic variability should be properly examined with larger series. In the meantime, I scored Mesocricetus as exhibiting dual articulation, in agreement with Carleton (1980). Similarly, Hershkovitz (1998) reported one specimen of Delomys dorsalis and one specimen of D. sublineatus as exhibiting the simple rib articulation; but my five samples of Delomys collinus (= D. d. collinus) exhibit the dual articulation, in agreement with Voss (1993). My specimens of Cricetulus exhibit

the double rib articulation, concurring with Carleton (1980), but not Steppan (1995).

**96. Number of thoracic and lumbar vertebrae:** *Twenty thoraco-lumbars, usually 14 thoracic and 6 lumbars (0); or 13 thoracic and 6 lumbars (1); or 12 thoracic and 7 lumbars (2).*

The thoracic and lumbar vertebrae are defined based on Howell (1926: 129), Hatt (1932: 683) and Wake (1992). The thoracic or rib-bearing vertebrae are identified by the presence of costal facets for rib articulation. However, in some species the last thoracic is hard to distinguish from the first lumbar, especially in incomplete skeletons that lack ribs. Lumbar vertebrae are also recognized by presence of a diapophysis, which is a transverse process that rises from the vertebral centrum. I found that diapophyses are usually present in the first lumbar and always in the second. According to Steppan (1995) supernumerary ribs "... 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." Like Steppan, I found that supernumerary ribs are short, thin, spur-like elements, with deformed heads; supernumerary ribs may be asymmetrical, and they are uncommon. My scoring strategy closely follows Steppan's (1995), except that my first state highlights the differences between taxa with twenty versus nineteen thoraco-lumbars. Carleton (1980) and Steppan (1995) found that 13 thoracic and 6 lumbar vertebrae is the widespread count among neotomines and sigmodontines, and my data agree with their assessment. Thirteen thoracics and six lumbars are uniformly seen in all non-sigmodontine outgroups (except Tylomys), akodontines, ichthyomyines (except Anotomys), Chinchillula, Phyllotis, Scapteromys, and several thomasomyines including Aepeomys, Chilomys, Delomys, Rhipidomys (except R. leucodactylus), and

Thomasomys. Twelve thoracics and seven lumbar are seen in all oryzomyines, Sigmodon, some phyllotines, Wiedomys, and the thomasomyines Juliomys, Rhipidomys leucodactylus, and Wilfredomys. Steppan (1995, table 5) evaluated this character in a diverse array of muroid taxa. He noted discrepancies of his scores compared to previous reports of Calomys callosus by Carleton (1980) and Olds (1988), and reports of Graomys griseoflavus and Sigmodon hispidus by Carleton (1980); however, it is not clear to what extent this is due to differences in definition. My own examination of those species agree with Steppan's counts. He considered the count of twelve thoracics and seven lumbar as a potential synapomorphy for the oryzomyine group.

In Analysis 2 the transformations of this character were ordered (0↔1↔2) to indicate an assumption that changes in number of vertebrae occur in additive fashion.

**97. Number of caudal vertebrae:** *Less than 24 (0); or 24–29 (1); or 30–35 (2); or 36 or more (3).*

Caudal vertebrae are those posterior to the sacral elements. Most sigmodontines have four sacral vertebrae: the first two attached to the ilea, and the remaining two (sometimes called "pseudo-sacrals") with fused wings are not attached directly to the ilea. In some species, especially in younger specimens, the fourth sacral may be free and "caudiform" and might easily be confused with a caudal vertebra. Caudal vertebrae have usually been undefined by previous authors, which might explain some discrepancies noted here. My scoring strategy largely follows Carleton's (1980) and Steppan's (1995). Steppan presented a matrix where most thomasomyines are characterized by large numbers of caudal vertebrae.

A very short tail with less than 24 caudals (state 0) is seen in Microtus, cricetines,

Baiomys, Calomys, and Punomys. Calomyscus, Neotoma, Scotinomys, akodontines, Holochilus, Chinchillula, Scapteromys, and Sigmodon have the state 1. State 2 is exhibited by Tylomys, Ochrotomys, Peromyscus, ichthyomyines, some oryzomyines, Graomys and Phyllotis. Nyctomys, Reithrodontomys, Oecomys, Microryzomys, Wiedomys and all thomatomyines (except Delomys) exhibit high numbers of caudals (state 3), concurring with Steppan's (1995) data. There are no skeletons of the thomatomyines Phaenomys, Rhagomys, and Abrawayaomys available, but if tail length is correlated with number of caudal vertebrae, they are likely to have more than 35, and almost certainly not less than 30 caudals. Phaenomys has an extremely long tail (TL/HBL= 1.26), similar or even longer than other taxa with state 3; therefore, I felt secure to score Phaenomys as state 3. Rhagomys and Abrawayaomys have moderately long tails (TL/HBL= 1.05 and 1.07 respectively) and their number of caudal vertebrae are likely to correspond either to state 2 or 3; because of the uncertainty I scored them as missing. My specimens of Holochilus brasiliensis were unfortunately very limited; one specimen with at least 28 caudals was my highest count. Steppan (1995) scored a more extensive array of Holochilus from distinct populations, reporting variation in the numbers of caudals that I treat as taxonomic polymorphism.

In Analysis 2 the transformations of this character were ordered (0↔1↔2) to indicate a logical assumption that changes in the number of caudal vertebrae occur in additive fashion.

**98. Chevron bones:** *Absent, left and right elements unfused, not forming a closed arch (0); or present, left and right element fused forming an arch (1); or within-species polymorphism (2).*

Flower (1885: 71), when dealing with caudal vertebrae mentioned: "Chevron bones ... are always situated nearly opposite to an intervertebral space, and are generally articulated both to the vertebra in front and the vertebra behind; but sometimes chiefly or entirely either to one or the other .... They ossify from two centers, one on each side, which usually coalesce in the median line below ...." Stepan (1995: character 28S) refers to these structures as hemal processes, or as a "hemal arch" when a complete bony arch is formed. True hemal arches are ventral extensions of the vertebral centrum and as such are completely absent in mammals, while chevron bones are ossifications of the intercentrum and are common in mammals (Wake, 1992). Intercentral hemal arches would be a precise term, but major anatomical treatises have maintained the term chevron bones for rodents (Howell, 1926; Hatt, 1932; Greene, 1935; Hill, 1937) and other mammalian groups (Flower, *ibid*; Osgood, 1921). Stepan (1995) was the first to note that the morphology of chevron bones varies within sigmodontine lineages, and is a structure that merits further investigation. Separate (unfused) chevron bones are uniformly exhibited in my non-sigmodontine outgroups (except Calomyscus and Reithrodontomys), akodontines, ichthyomyines, phyllotines, and in most thomasomyines. By contrast, state 1 occurs in Calomyscus, Reithrodontomys, all oryzomyines, Sigmodon, Wiedomys, and in the thomasomyines Aepeomys, Rhipidomys leucodactylus, Thomasomys cinereus, and Thomasomys kalinowskii. Thomasomys aureus exhibits variation in distinct populations and is treated as taxonomic polymorphism. My samples of Thomasomys baeops exhibit both conditions in equal proportions in what appears to be a single population, which I interpret as within-species polymorphism and scored as state (2). Stepan (1995) proposed that the chevrons formed as a complete bony arch is a putative synapomorphy

for oryzomyines.

**99. Arched chevron bones:** *With simple posterior border (0); or posterior border bearing a spinous process (1); or within-species polymorphism (2).*

Steppan (1995) also reported that a distinct spinous process extending from the posterior border of the arch is seen predominantly in oryzomyine rodents. Like Steppan, I also found chevron arches with distinct spinous process in some oryzomyines (e.g., Holochilus, Oligoryzomys, and Oryzomys), but also in some populations of Thomasomys aureus. I noted that the expression of this trait appears to be affected by age, since the spinous process is better developed in older individuals. A complete arch without a spinous process is seen in Calomyscus, Reithrodontomys, Microryzomys, Oecomys, Handleyomys, Sigmodon, and all thomasomyines (except Thomasomys aureus, which presents a case of taxonomic polymorphism). Steppan (1995) scored several species as polymorphic but was not clear if such variation represented within-species or taxonomic polymorphism. Most of my specimens of Oligoryzomys fulvescens (ten of eleven) exhibit chevron bones with a spinous process. In Wiedomys, four of six specimens have a bony arch without a spinous process, one specimen exhibits the element bones unfused, and the last has both an arch with and one without a spinous process. I scored Wiedomys as state 0. My samples of Holochilus sciureus exhibit both conditions in equal proportions in what appears to be a single population of the species. I interpret this species as a within-species polymorphism and scored it as state (2). Species scored as 0 for the character 98 were not scored for this character.

In Analysis 2 the transformations of character 98 and this character were ordered (0↔1↔2↔3) to reflect the hypothesis that changes in the development of chevron

bones occur in successive steps from the absent condition (0) to chevron present bearing a spinous process (3), passing through the states of chevron with simple posterior border (1) and within-species polymorphism (2).

**100. Position of the trochlear process of calcaneum:** *Trochlear process level or overlap with the posterior articular facet (0); or distinct gap between proximal edge of the trochlear process and posterior articular facet (1).*

My descriptions and coding for this character largely follow Carleton (1980: character 40), but Carleton's state "2", found in Gerbillinae, is absent in my surveyed taxa and was not included. Also, my evaluation focused strictly on the position of the trochlear process (rather than its shape) (fig. 12). Carleton noted that a trochlear process level with the posterior articular facet is taxonomically widespread, and interpreted this condition as primitive for neotomine-peromyscines. Among the taxa I studied this is also the common condition. It is seen in my non-sigmodontine outgroups (except Microtus, Baiomys, and Scotinomys). Abrothrix, ichthyomyines, phyllotines (except Calomys and Phyllotis), and thomasomyines (except Aepeomys, Delomys, and Thomasomys erro). The derived condition occurs in Microtus, Baiomys, Scotinomys, akodontines (except Abrothrix), Sigmodon, Scapteromys, all oryzomyines (except Handleyomys), Calomys, Phyllotis, and a few thomasomyines including Aepeomys, Delomys, and T. erro.

**101. Peroneal process of fifth metatarsal:** *Long, extending proximally to or beyond the proximal surface of the cuboid (0); or shorter, not quite extending to proximal edge of cuboid (1); or very short, not extending proximally beyond about the middle of the cuboid (2).*

This character is similar to that used by Steppan (1995: character 31S) except that

I employ three states (rather than his two). Steppan found the long peroneal process of metatarsal V only in his outgroups. A very long peroneal process was found in Calomyscus, tylomyines, Neotoma, and Ochrotomys (fig. 13). By contrast, a shorter process (state 1) is exhibited in Microtus, cricetines, peromyscines (except Ochrotomys), akodontines (except Oxymycterus and Abrothrix), Punomys, Wiedomys, and all thomasmomyines. A conspicuously small process (state 2) occurs in Oxymycterus, Abrothrix, ichthyomyines, oryzomyines, all phyllotines (except Punomys), scapteromyines, and Sigmodon. Abrothrix longipilis is variable with respect to this character: specimens from Chile exhibit state 1, whereas samples from Argentina exhibit state 2, a phenomenon I interpret as a taxonomic polymorphism.

In Analysis 2, the transformations of this character were ordered ( $0 \leftrightarrow 1 \leftrightarrow 2$ ) to reflect the assumption that changes in the size of the peroneal process occur in a progressive fashion.

**102. Size and proportions of phalange 1 of pollex (dl of manus):** *Long and slender (0); or short and wide (1).*

The first manual digit, or pollex, bears two phalanges in contrast with the other manual digits which each have three. Based on my examination of skeletons, phalange 1 of the pollex varies in absolute size, which I interpret as representing two different conditions. In most sigmodontines, the first phalange is short, cuboid or disc-shaped, its breadth greater or equal to its length. In contrast, in all non-sigmodontine taxa and all ichthyomyines, Sigmodon, and Delomys among the sigmodontines, the first phalange is conspicuously long relative to its breadth (fig. 14).

The above morphology appears to be correlated with the external morphology of



the pollex as observed from skins and alcoholic specimens. Thus, the pollex of neotomines, tylomyines, and ichthyomyines is a relatively long digit, free from the thenar pad at its base. By contrast, in most sigmodontines the thenar is swollen, coalescing with the base of a conspicuously shorter digit.

The length of phalange 1 of the pollex does not appear to be related to any variation in metacarpal or carpal morphology. In a few taxa examined (e.g., Abrothrix, Nyctomys, Aepeomys, Peromyscus, Wilfredomys, Sigmodon), the general proportions of metacarpal 1, trapezoid, and trapezium appear similar in species exhibiting both conditions of phalange size. In general, carpal morphology in sigmodontines is conservative, resembling the conditions previously described for Peromyscus (Stafford and Thorington, 1998) and Neotoma (Howell, 1926).

**103. Relative size of hallux (dI of pes):** *Short, first phalange (p1) of hallux not extending beyond metatarsal of dII, halluctal claw not extending more than about half the length of p1 of dII (0); or moderately long, p1 of hallux level with or extending slightly distal to adjacent metatarsal, halluctal claw not extending to first interphalangeal joint of dII (1); or long, p1 of hallux extending beyond metatarsal of dII, halluctal claw extending to first interphalangeal joint of dII (2); or very long, halluctal claw extending beyond first interphalangeal joint of dII (3).*

Previous authors have usually interpreted the relative sizes of pedal digits I and V as a single character. However, my examinations indicate that these digits are individually informative and the distribution of their states suggests a considerable degree of independence. I therefore treat each digit as a distinct character (see dV, character 104). My state definitions for dI focus on the position of the first phalange in relation to the

metatarsal and phalanges of the adjacent digit dII, and on the distal extension of the halluctal claw. Previous estimations of relative size of dI have relied only on the distal extension of the claw, but this scheme appears to overestimate the size of the claw among taxa and overlook the contribution of pI of the hallux. Therefore, skeletons were the main source for evaluating this and the next character; and in some cases, well prepared skins that exhibit the shape of the bones. A short hallux (state 0) is seen in Microtus, Baiomys, Scotinomys, all akodontines, Sigmodon, some oryzomyines (i.e., Holochilus, Oryzomys, and Handleyomys), phyllotines (except Chinchillula and Punomys), scapteromyines, and some thomasomyines including Abrawayaomys, Delomys, and Aepeomys. A moderate hallux (state 1) is also seen infrequently in several groups, but more commonly in thomasomyines including Chilomys, Juliomys, Rhagomys, most Thomasomys, and Wilfredomys. States 0 and 1 predominate in oryzomyines and phyllotines. A long hallux (state 2) is observed in Mesocricetus, tylomyines, Neotoma, Reithrodontomys, Neusticomys, and the thomasomyines Phaenomys, Rhipidomys, and some Thomasomys. A very long hallux (state 3) is observed only in the ichthyomyines Anotomys and Ichthyomys.

In Analysis 2, the transformations of this character were ordered (0↔1↔2↔3) to indicate a logical assumption that the relative length of dI of the pes occurs in a progressive fashion from a short to a long digit.

**104. Relative size of fifth digit (dV) of pes:** *Short, phalange 1 (p1) of dV not extending beyond metatarsal of dIV, claw of dV extending to first interphalangeal joint of dIV or usually shorter (0); or moderately long, p1 of dV extending beyond metatarsal of dIV, claw of dV extending to but not beyond first interphalangeal joint of dIV (1); or long,*

*p1 of dV is distinctly longer than metatarsal of dIV, claw of dV extending about half the length of p2 of dIV (2); or very long, p1 of dV extending almost to first interphalangeal joint of dIV, claw of dV extending to the base of claw of dIV, or beyond (3).*

Most groups surveyed are heterogeneous with respect to this character. A short fifth digit (state 0) is seen in only a few taxa (e.g., Oxymycterus, Holochilus, Oryzomys, Handleyomys, Calomys, Sigmodon, scapteromyines, and the thomasomyine Abrawayaomys). A moderate dV (state 1) is observed in Baiomys, Scotinomys, Oligoryzomys, phyllotines (except Calomys and Chinchillula), and the thomasomyines Aepeomys, Delomys, and Thomasomys erro. A long dV (state 2) is seen in Microtus, Peromyscus, akodontines (except Oxymycterus), Neusticomys, Microryzomys, Oecomys, and the thomasomyines Juliomys, Phaenomys, Rhagomys, several Thomasomys and Wilfredomys. A very long dV (state 3) is seen in cricetines, Calomyscus, tylomyines, neotomines, Ochrotomys, Reithrodontomys, ichthyomyines (except Neusticomys), Chinchillula, some thomasomyines (including Chilomys, Rhipidomys, and several Thomasomys), and Wiedomys.

In Analysis 2, the transformations of this character were ordered (0↔1↔2↔3) to indicate a logical assumption that the relative length of dV of pes occur in a progressive fashion from a short to a long digit.

## PHALLUS AND SOFT ANATOMY

Most of the following phallic characters follow Carleton's (1980) definitions and scoring conventions, but some of his characters were not included because they are phylogenetically uninformative in my study. Data were retrieved mainly from Hooper

and Musser (1964) and Carleton (1980), with additional or complementary information derived from Díaz de Pascual and Péfaur (1982), Voss (1988), HersHKovitz (1990), Myers et al. (1990), Spotorno (1992), Langguth and Silva-Neto (1993) and my own dissections.

**105. Grooves on glans penis body:** *Shallow or absent (0); or present (1).*

Hooper and Musser (1964) observed deep grooves on the dorsal and ventral midlines of the body of the glans penis in Rhipidomys mastacalis. I also observed this condition in the three species of Rhipidomys included here. On the contrary, Thomasomys notatus and other taxa I examined lack conspicuous grooves, or have short and shallow grooves.

**106. Length divided by width of glans penis:** *Ratio less than or equal to 3.0 (0); or ratio greater than 3.0 (1).*

This character follows Carleton (1980: character 63), who designed it to distinguish notably long glandes penes from other morphologies. However, I employed only two states (versus Carleton's four), which seem appropriate for my predominantly sigmodontine study. A long and narrow glans penis is found only in Peromyscus and Reithrodontomys.

**107. Lateral bacular mounds:** *Present and well defined (0); or absent (1).*

This character follows Carleton (1980: character 60), except that his state 3, which applies only to Gerbillinae, is not included here. Tylomys, neotomines, peromyscines, Abrothrix, Anotomys, and Punomys do not have lateral bacular mounds, but all other muroids I studied possess them. Like Steppan (1995), I opted for scoring the extremely reduced lateral mounds (or papillas) of Nyctomys and Scapteromys as "missing".

**108. Lateral bacular mound shape:** *Simple, not "triple curved" (0); or complexly curved, "triple-curved" (1).*

Hooper and Musser (1964: 20, fig. 6) described the lateral bacular mound of Rhipidomys mastacalis as "more densely spinous and more complexly curved, ... each of the slightly shorter lateral pair triple-curved--distad, ventrad and (terminally) laterad--the distal face of the laterally projecting part spine-studded ...." I observed a similar morphology in Rhipidomys leucodactylus, R. fulviventer, and Thomasomys notatus. The lateral bacular mounds of R. macconnelli are simple, as in all other remaining muroids I examined. This character cannot be evaluated in taxa lacking lateral bacular mounds (character 107, state 1).

**109. Ventral shield:** *Present (0); or absent (1).*

Hooper and Hart (1962:12) defined the ventral shield as a fan-shaped mass of soft tissue protruding between the urethral process and the wall of the crater. This structure is found only in arvicolines and cricetines (Hooper and Hart, 1962; Hooper and Musser, 1964; Carleton, 1980). This character was employed by Carleton (1980: character 62). A ventral shield is also present in Calomyscus baluchi.

**110. Dorsal crater papilla:** *Present (0); or absent (1).*

This character follows Carleton (1980: character 59). Presence of a dorsal papilla is the widespread condition. The dorsal papilla is absent only in the neotomines, peromyscines, Tylomys, and Punomys. Nyctomys and all sigmodontines thus far examined (except Punomys) have a dorsal papilla. The shape and ornamentation of the dorsal papilla may vary extensively, a feature which was not evaluated in this simplified coding scheme.

**111. Position of urinary meatus:** *Subterminal (0); or terminal (1).*

This character follows Carleton (1980: character 55). Hooper (1959, 1960) and Carleton (1980) reported Baiomys, Scotinomys, and Tylomys as exhibiting a terminal urinary meatus. Although Hooper and Musser (1964) stated that Nyctomys exhibits an elevated meatus like Baiomys and Scotinomys, the meatus of Nyctomys was scored as subterminal by Carleton (1980). As I did not examine samples of Nyctomys I am unable to resolve this discrepancy, and I scored Nyctomys as "missing".

**112. Urethral process:** *Present (0); or absent (1).*

This character follows Carleton (1980: character 58) who scored the presence of a urethral process in cricetines, arvicolines, sigmodontines and several neotomines, and reported the urethral process absent in Nelsonia, Peromyscus, Reithrodontomys, Baiomys, and Scotinomys. In all sigmodontines examined by Hooper and Musser (1964), Carleton (1980), or myself, the urethral process is present.

**113. Lateral crater papillae:** *Absent (0); or present (1).*

Hooper (1962) reported for first time the presence of crater papillae in Sigmodon hispidus and S. alstoni. Later, Hooper and Musser (1964) surveyed a broad array of sigmodontines, confirming the presence of the lateral crater papillae in Sigmodon and reporting these structures also in the ichthyomyine Rheomys. Voss (1988) reported that all ichthyomyines he examined have lateral crater papillae. Additional samples examined here confirm that all sigmodontines other than ichthyomyines and Sigmodon lack these papillae.

**114. Preputial glands:** *Absent (0); or present (1).*

Information on muroid male reproductive glands is limited. However, in recent

years, detailed surveys of selected sigmodontines have become available. My data matrix includes information retrieved from Carleton (1980), Voss and Linzey (1981), Carleton and Musser (1989), Myers et al. (1990), and my own dissections. This character evaluates absence or presence of the preputial. The next character evaluates the number of preputials when present (see character 115). Lack of preputials is seen in cricetines, neotomines, Peromyscus, Reithrodontomys, Oligoryzomys, and some thomasomyines (including Rhipidomys leucodactylus, Thomasomys cinereus, T. notatus, and T. rhoadsi).

**115. Number of preputial glands:** *One pair present (0); or two pairs present (1); or numerous (2).*

One pair of preputial glands is the common condition in sigmodontines and is present in all tribal groups except Sigmodontini (= Sigmodon). One pair of preputials is observed in Microtus, Tylomys, peromyscines (except Peromyscus and Reithrodontomys), Akodon, Microxus, ichthyomyines, oryzomyines (except Oligoryzomys), phyllotines (except Graomys and Phyllotis), Scapteromys, and the thomasomyines Chilomys, Rhipidomys (except R. leucodactylus), and T. baeops. The occurrence of two pairs of preputials is restricted to Nyctomys, Abrothrix, Oxymycterus, Graomys, Phyllotis, and Sigmodon.

Voss and Linzey (1981) reported a distinctive condition in Thomasomys aureus, where numerous small sebaceous glands surround the prepuce border. I examined an additional specimen from the same locality in Napo, Ecuador, finding a similar array of numerous glands. However, a specimen I examined from Bolivia exhibits a single pair of large glands. I scored this variation in T. aureus as a case of taxonomic polymorphism.

In Analysis 2, the transformations of character 114 and 115 were ordered

(0↔1↔2↔3) to reflect the hypothesis that the number of preputials are added (or lost) in a sequential fashion from absent (0) to numerous preputial glands (3).

**116. Lateral ventral prostates:** *Present (0); or absent (1).*

My limited data for this character was taken from Carleton (1980: character 70), Voss and Linzey (1981), Voss (1988), Carleton and Musser (1989), and Myers et al. (1990). Absence of the lateral ventral prostates is restricted to Mesocricetus, Tylomys, neotomines, Baiomys, and Scotinomys. Carleton (1980) recognized that Ochrotomys exhibits poorly defined ventral prostates, which might constitute an intermediate stage.

## DIGESTIVE TRACT

**117. Internal cheek pouches:** *Absent (0); or present (1).*

The scoring scheme and data for this character follow Carleton (1980: character 43). Large and capacious cheek pouches are exhibited only by the cricetines Mesocricetus and Cricetulus among my study taxa.

**118. Distribution of gastric epithelium:** *Stomach hemiglandular, bordering fold extends from the incisura angularis (0); or intermediate I, bordering fold crosses the lesser curvature at a point between the pyloric sphincter and the incisura angularis (1); or intermediate II, bordering fold does not cross lesser curvature, which is completely lined with cornified squamous epithelium (2); or discoglandular (3); or pouched (4).*

My description of taxonomic variation in the gastric glandular epithelium follows Carleton (1973, 1980); my coding scheme is slightly modified from Stepan (1995: 39S, 40S) who evaluated the distribution of gastric epithelium as two characters. Data were retrieved from Carleton (1973, 1980), Stepan (1995), and complemented by my own



dissections. A hemiglandular stomach is the common condition among the muroids examined. Among sigmodontines it is present in all akodontines (except Oxymycterus), all oryzomyines, all phyllotines, Sigmodon, and all thomasomyines (except Aepeomys, Thomasomys erro, and some populations of T. aureus). Carleton (1978, 1980) recorded an intermediate stage for Ochrotomys, in which the cornified epithelium slightly penetrates the antrum, but I scored Ochrotomys as hemiglandular because the bordering fold crosses the incisura angularis. The intermediate I (state 1) is exhibited in Neusticomys, and some populations of T. aureus. Carleton (1973) examined one stomach of Thomasomys aureus from Cuzco, Peru, which showed a markedly reduced and divided glandular zone. Two additional specimens of T. aureus that I examined from Cuzco are similar to his description, except that the glandular zone is not divided. A similar undivided glandular epithelium condition was observed in Thomasomys apeco by Leo L. and Gardner (1993). However, in two specimens of T. aureus from Bolivia and in one from Ecuador, the gastric epithelium of the antrum is only slightly reduced. The stomach morphology of Thomasomys aureus is then variable among populations, which agrees with other characters that suggest this species is composite. I treated this variation as a taxonomic polymorphism.

Carleton (1973) and Voss (1988) highlighted the peculiar stomach of some ichthyomyines, in which the lesser curvature is completely lined with cornified epithelium. This condition (state 2) occurs in Anotomys and Ichthyomys among other ichthyomyines. I also scored Thomasomys erro as intermediate II, because the bordering fold has a distinct intersection on the greater curvature. A discoglandular stomach occurs in Microtus, neotomines, Reithrodontomys, Scapteromys, and Aepeomys. The pouched

condition is observed in Peromyscus and Oxymycterus.

In Analysis 2, the transformations of this character were ordered (0↔1↔2↔3↔4) to indicate an hypothesis that changes in the distribution of glandular and squamous epithelium in the stomach occur in successive steps from hemiglandular (0) to pouched (4) stomach.

**119. Gastric epithelium along the greater curvature:** *Hemiglandular (0); or with reduction in glandular zone along greater curvature (1).*

My scoring scheme follows Steppan (1995: 40S) who distinguished this character from the reduction of the gastric epithelium along the lesser curvature. Carleton (1973: 15, fig. 6) described for Neusticomys and Rheomys that the "cornified epithelium projects along the greater curvature such that the bordering fold crosses on its ascending portion rather than at a point opposite the incisura angularis." This type of reduced glandular zone is exhibited only in ichthyomyines (Carleton, 1973; Voss, 1988).

**120. Incisura angularis:** *Shallow, stomach unilocular (0); or intermediate (1); or deep, stomach bilocular (2).*

My data for this character were taken mostly from Carleton (1973, 1980) and my own dissections. A unilocular stomach characterizes some outgroups (e.g. Calomyscus, Baiomys, Scotinomys, and tylomyines), and all sigmodontines (except Punomys and Thomasomys aureus). The intermediate state is seen in Ochrotomys, Reithrodontomys, Punomys, and Thomasomys aureus. By contrast, a deeply bilocular stomach is seen only in my outgroups (i.e., Microtus, cricetines, neotomines, and Peromyscus).

In Analysis 2, the transformations of this character were ordered (0↔1↔2) to reflect a logical assumption that changes in the penetration of the incisura angularis occur

in a progressive fashion.

**121. Sulcus on greater curvature of stomach:** *Absent (0); or present (1).*

I follow Carleton (1980, character 48) for this character. A deep sulcus on the greater curvature of the stomach is exhibited only by Mesocricetus, and Cricetulus.

**122. Gall bladder:** *Present (0); or absent (1).*

My data for this character were taken from Vorontsov (1979), Carleton (1980), Voss (1991), Voss and Carleton (1993), and my own dissections. This structure is absent in tylomyines, Ochrotomys, Ichthyomys, all oryzomyines, Punomys, and the thomasomyine Rhipidomys. All other thomasomyines here examined have a gall bladder.

## RESULTS

As mentioned under "Material and methods" I conducted two separate phylogenetic analyses to investigate the effects of ordering characters. Results are described below and statistical summaries are provided in table 3.

### ANALYSIS 1: CHARACTERS UNORDERED

In this analysis, 21 equally most-parsimonious trees were produced, each with 759 steps (CI = 0.285, RI = 0.594). A strict consensus of these 21 trees is shown in fig. 15.

The strict consensus topology shows that phylogenetic conflicts and lack of resolution are concentrated in two taxonomic groups. The first in a group of Thomasomys species, and the second in the outgroup among the tylomyines and peromyscines; otherwise the strict consensus topology is well resolved. The subfamily Sigmodontinae, as defined by Reig (1980), is monophyletic and moderately supported by a bootstrap value of 60%, but a low decay value of 1. Within the subfamily, several tribal-level clades were also found to be monophyletic as detailed below.

The Ichthyomyini is a strongly supported clade (bootstrap value: 100; decay value: 15) that is basal to all other sigmodontines. Within ichthyomyines, Ichthyomys and Neusticomys are sister taxa; this relationship is moderately supported (bootstrap value: 61; decay value: 1). Other tribal level groups revealed as monophyletic, but with low support, are the Akodontini (bootstrap value: 44; decay value: 1), Scapteromyini (bootstrap value: 36; decay value: 1), and Oryzomyini (bootstrap value: 33; decay value: 1). Thomasomyini sensu lato becomes monophyletic when Wiedomys is included

(bootstrap value: 32; decay value: 2). Phyllotini was found to be paraphyletic with Sigmodon (Sigmodontini) joined to Graomys.

The sister group to ichthyomyini consists of two large clades united with low support (bootstrap value: 31; decay value: 1). The first is a predominantly pentalophodont clade in which the oryzomyine group is recovered as the sister taxon of the thomasomyines, although this relationship is supported with low nodal values (bootstrap value: 15; decay value: 1). The second large sigmodontine clade is a tetralophodont group consisting of akodontines, scapteromyines, phyllotines, and Sigmodon, but it is also poorly supported (bootstrap value: 6; decay value: 1). Within tetralophodonts, the genus Punomys is the sister taxon of Akodontini with weak support (bootstrap value: 5; decay value: 1), and both are sister to the scapteromyine tribal group that includes Kunsia and Scapteromys. The relationship of Abrothrix + Microxus is moderately well supported (bootstrap value: 67; decay value: 3). Chinchillula is at the base of the group that contains the akodontines + Punomys, and the scapteromyines. Monophyly of the tribe Phyllotini (sensu Olds and Anderson, 1989) was not established because of the placement of Chinchillula and Punomys outside the group, and the weakly supported position of Sigmodon (tribe Sigmodontini) within a group composed of Phyllotis, Graomys, and Calomys.

The predominantly pentalophodont tribe Oryzomyini was recovered as a monophyletic group albeit with low nodal support values (bootstrap: 33; decay: 1). Relationships within oryzomyines are resolved but they are usually weakly supported (see fig. 15 for additional decay and bootstrap values). Oryzomys and Holochilus are sister taxa, followed down the tree by Oligoryzomys, Microrizomys and Oecomys are

closely related and sister to the previous group. Handleyomys is the first lineage to diverge at the base of the other oryzomyines.

The pentalophodont tribe Thomasomyini sensu lato was recovered as a monophyletic group consisting of Delomys, Phaenomys, Juliomys, Wilfredomys, Wiedomys, Rhagomys, Abrawayaomys, Chilomys, Rhipidomys, Thomasomys, and Aepeomys. This group includes five clades: (1) a monophyletic genus Delomys, which is strongly supported (bootstrap value: 95; decay value: 3) and placed at the base of the remaining thomasomyines; (2) a lineage represented just by Phaenomys; (3) a clade that includes Wiedomys, Wilfredomys, and Juliomys, but with low support value (bootstrap value: 32; decay value: 1); (4) the sister taxa Rhagomys and Abrawayaomys, but weakly supported (bootstrap value: 49; decay value: 1); and (5) a large clade composed of Thomasomys, Rhipidomys, Aepeomys, and Chilomys, referred here as the “Andean thomasomyine group” because the first three genera have a predominantly Andean distribution. The last two clades (4 and 5) form a weakly supported clade (bootstrap value: 7; decay value: 1), followed down the tree by the clades 3, 2, and 1. In clade 3, Wiedomys and Wilfredomys are sister taxa (bootstrap value: 41; decay value: 1). Because Juliomys sp. and Juliomys pictipes are successive sister taxa to this group, the genus Juliomys does not appear to be monophyletic.

Monophyly of the Andean thomasomyini group (clade 5) that includes Thomasomys, Rhipidomys, Aepeomys, and Chilomys is weakly supported (bootstrap value: 13; decay value: 1). This group is itself composed of two clades, one of which includes Aepeomys and most species of Thomasomys, and the other of Chilomys + T. baeops and Rhipidomys + T. notatus. Within the first group, the sister taxa T. erro +

Aepeomys, T. cinereus + T. rhoadsi, T. incanus, and T. kalinowskii form a polytomy with low support (bootstrap value: 37; decay value: 1). This group sister to T. aureus + T. macrotis, which grouped together with low support (bootstrap value: 25; decay value: 1). The relationship of T. erro and A. lugens is moderately supported (bootstrap value: 62; decay value: 2), as is the clade formed by T. rhoadsi and T. cinereus (bootstrap value: 68; decay value: 1). Within the second clade, T. notatus and R. fulviventer were recovered as sister taxa with moderately strong support (bootstrap value: 78; decay value: 3). Successive sister taxa to this group are R. leucodactylus and R. macconnelli, and the sister taxa T. baeops and Chilomys (see fig. 15 for additional decay and bootstrap values). Thus, the genus Rhipidomys does not appear to be monophyletic unless the species currently known as Thomasomys notatus is included.

Among the outgroups, monophyly of the subfamily Tylomyinae (represented by Nyctomys and Tylomys) is strongly supported (bootstrap value: 96; decay value: 7). Similarly, the tribe Neotomini (represented by Neotoma and Nelsonia) is moderately well supported (bootstrap value: 80; decay value: 2), as is the clade conformed by Baiomys + Scotinomys (bootstrap value: 85; decay value: 1). However, monophyly of the subfamily Neotominae (including “neotomine-peromyscines” but excluding tylomyines) is not supported. Finally, the clade consisting of Baiomys + Scotinomys appears to be the closest sister taxon of the subfamily Sigmodontinae, but associated nodal support values are low (bootstrap value: 27; decay value: 1). Microtus, Mesocricetus and Cricetulus form a strongly supported clade (bootstrap value: 92; decay value: 3) in this analysis.

## ANALYSIS 2: CHARACTERS ORDERED

In total, 50 characters were ordered in this analysis, and 16 most parsimonious trees were produced, each with 837 steps (CI = 0.264, RI= 0.609). The strict consensus topology recovers all of the main groups found in Analysis 1, but minor differences in relationships and degree of support are highlighted in figure 16.

In this analysis, the monophyly of the subfamily Sigmodontinae is also supported but with moderate nodal values (bootstrap: 60; decay: 2). The Ichthyomyini is strongly supported (bootstrap value: 100; decay value: 21). Some other tribal level groups were also recovered as monophyletic groups, but with low support. These are the scapteromyines (bootstrap value: 48; decay value: 3), the oryzomyines (bootstrap value: 30; decay value: 1), and the Thomasomyini sensu lato which includes Wiedomys (bootstrap value: 27; decay value: 2). The phyllotine and akodontine groups however, were not found to be monophyletic.

Within the subfamily Sigmodontinae, the ichthyomyine group was placed at the base as in Analysis 1. The sister-taxon to ichthyomyines is a large group of sigmodontine genera with Chinchillula at the base followed by a clade constituted by phyllotines + Sigmodon; next by a clade of akodontines, scapteromyines, and Punomys; and then by the oryzomyines + thomasomyines. The tetralophodont clade composed of akodontines, scapteromyines, Sigmodon, and phyllotines found in Analysis 1 was not recovered in this analysis.

The basal position of Chinchillula, unlinked to other phyllotines or to the tetralophodont group, was unexpected. The next clade includes Sigmodon (tribe Sigmodontini), which groups weakly with the phyllotine genera Phyllotis, Graomys, and



Calomys. The monophyly of Sigmodon is strongly supported (bootstrap value: 98; decay value: 7).

Moving up the tree, Punomys is basal to the akodontine and scapteromyine groups rather than at the base of the akodontine as it was in Analysis 1. Within the akodontine group, Abrothrix and Microxus were recovered as sister taxa with moderate support (bootstrap value: 67; decay value: 4). Akodon is the successive sister taxon to this group. The monophyly of the tribe Scapteromyini is supported with moderate decay values (bootstrap value: 48; decay value: 3). Oxymycterus is sister taxon of the scapteromyine group rather than a member of the akodontines as suggested by Analysis 1; this relationship is moderately supported (bootstrap value: 41; decay value: 4).

As in Analysis 1, a pentalophodont clade was recovered, with Oryzomyini as the sister taxon of the Thomasomyini sensu lato; the relationships within the oryzomyine group were identical with those previously described. Among the thomasomyines, a monophyletic Delomys (bootstrap value: 90; decay value: 2) and Phaenomys are the first lineages to diverge. Wilfredomys and Wiedomys were also recovered as sister taxa, but these did not form a clade with Juliomys as in Analysis 1, the latter genus was not recovered as a monophyletic group. As in Analysis 1, the pair Abrawayaomys + Rhagomys is sister to the predominantly Andean thomasomyine group that includes Thomasomys, Aepeomys, Chilomys and Rhipidomys, although with poor support (bootstrap value: 15; decay value: 1). The Andean thomasomyine clade consists of two groups: (1) Aepeomys, Chilomys, and most species of Thomasomys, and (2) Rhipidomys and T. notatus. In contrast to Analysis 1, Chilomys and T. baeops are at the base of the first clade (that contain most species of Thomasomys) rather than with

Rhipidomys. The close relationships of A. lugens and T. erro received moderate support in this analysis (bootstrap value: 78; decay value: 3), as did the clade of T. cinereus + T. rhoadsi (bootstrap value: 69; decay value: 2). The last two pairs of species together with T. incanus, T. kalinowskii, T. aureus and T. macrotis form a polytomy with low support (bootstrap value: 39; decay value: 2). By contrast with Analysis 1, T. aureus and T. macrotis do not appear to be closely related in figure 16. As in Analysis 1, however, the three species of Rhipidomys cluster with T. notatus, a relationship that is moderately well supported (bootstrap value: 70; decay value: 4). Within this group, T. notatus and R. fulviventer are sister taxa; this relationship is moderately supported (bootstrap value: 71; decay value: 2). R. leucodactylus and R. macconnelli are successive sister taxa of this group.

Among the outgroups, the tribe Neotomini (bootstrap value: 82; decay value: 3), the subfamily Tylomyini with (bootstrap value: 94; decay value: 7), and a clade constituted by Baiomys + Scotinomys (bootstrap value: 88; decay value: 3) were recovered as monophyletic and strongly supported as in Analysis 1. Similarly, the subfamily Neotominae (excluding the tylomyines) is not found to be monophyletic. In this analysis, Ochrotomys is the sister taxon of tylomyines, but with low support values (bootstrap value: 37; decay value: 1). The clade consisting of Baiomys + Scotinomys is, as in the Analysis 1, the sister group for the subfamily Sigmodontinae, albeit with low support values (bootstrap value: 36; decay value: 1).

## DISCUSSION

Comparisons of the tree topologies obtained in Analyses 1 and 2 indicate that the ordering of character transformations produced some changes as compared with the topology obtained using unordered transformations. Some differences are more localized at the tip of the branches like the different positions of Chilomys and Thomasomys baeops, or at deeper nodes like the relationships among the akodontines, phyllotines, scapteromyines, and Sigmodon. However, many clades were identical. Levels of nodal support in Analyses 1 and 2 were generally similar although corresponding values were usually as not noticeably different at most nodes, with values usually higher in Analysis 2 than in Analysis 1. As expected whenever character transformations are constrained a priori, the overall length of the shortest tree was increased (by 78 steps) in Analysis 2 as compared to Analysis 1.

Several currently recognized tribal-level groupings received little support (in terms of decay and/or bootstrap value) in either analysis. Such outcomes may be indicative that the morphological characters in my data matrix are homoplastic or that these tribes are not clades, or both. Similarly low support values for traditionally recognized “tribes” were obtained in the phylogeny based on morphological characters by Stepan (1995). Smith and Patton (1999) recently presented a phylogeny, based on cytochrome *b* data, and remarked that no tribal-group was confidently placed basal to the others. Although oryzomyines were usually found near the base of their trees, they suggested that more conservative genes may provide added resolution at the basal nodes. Similarly, there are several morphological suites of characters, potentially more

conservative, that still remain largely unexplored among Neotropical muroids, such as the basicranium, wrist and ankle morphology, muscle and nerve systems, lung morphology, reproductive tract, and others that may add resolution at the basal radiation.

## HIGHER-LEVEL CLASSIFICATION

The results of my two phylogenetic analyses were very similar. Both analyses supported the monophyly of the subfamily Sigmodontinae as defined by Reig (1980), as well as the monophyly of the tribes Oryzomyini (*sensu* Voss and Carleton, 1993), Thomasomyini *sensu lato*, Scapteromyini, and Ichthyomyini. Akodontini is monophyletic only in Analysis 1, but it is monophyletic in both analyses if scapteromyines are included, a relationship recently supported by Smith and Patton (1999). Both analyses rejected the monophyly of the tribe Phyllotini. Although the monophyly of most tribal-level groups were recovered, major discrepancies occur with regard to higher relationships among higher sigmodontine tribes (excluding ichthyomyines), especially among the tetralophodont groups. In both analyses, Oryzomyini is sister taxon of the thomasomyines *sensu lato*, the pentalophodont group recognized by Hershkovitz (1962). Diagnostic character states for each node, based on ACCTRAN and DELTRAN character optimizations, are presented in Appendix 3.

The subfamily Sigmodontinae is diagnosed by several unambiguous synapomorphies in these results such as a long palate that extends distinctly more than half the length of M3 (50), a convoluted palatine suture (53), entoglossal process of basihyal absent (60, unique), and dorsal crater papilla present (110). These results confirm the assumption elaborated by Voss (1993) and Voss and Carleton (1993) that the

absence of the entoglossal process of the basihyal is a synapomorphy of the Sigmodontinae; but the absence of the entepicondylar foramen of the humerus, and the double articulation of the first rib are instead synapomorphies of a larger group that includes the subfamily Sigmodontinae, Baiomys and Scotinomys. Within Sigmodontinae, the long palate is reversed in thomatomyines which have uniformly short palates. The dorsal crater papilla is present in nearly all sigmodontines, only a few of which are missing the structure (e.g., Punomys), which is interpreted here as a reversal. Similarly, my results suggest that the dorsal crater papillae present in Sigmodontinae is not homologous to the similar structure that occurs in Nyctomys and other outgroups. Therefore, my results supports then the concepts of Hershkovitz (1966, 1969, 1972), who differentiated the Sigmodontini and Peromyscini within the murid subfamily Cricetinae as well as Reig (1980, 1984). This result is consistent also with recent molecular analyses of DNA sequence (Engel et al., 1998) and cytochrome *b* sequences (Smith and Patton, 1999).

Ichthyomyini is placed at the base of the Sigmodontinae clade. Monophyly of ichthyomyine rodents was established by Voss (1988), in cladistic analyses by Steppan (1995), and also strongly supported in my analyses with a 100% bootstrap value. However, the position of ichthyomyines within sigmodontines and the sister-group relationship of ichthyomyines have been elusive. According to Voss (1988), the group lacks a reliable hypothesis of sister relationship. Unfortunately, ichthyomyines were not included in any recent molecular analyses; therefore, alternate hypotheses from other data sources are still unavailable. My morphological data place Ichthyomyini at the base of Sigmodontinae in all analyses, and support Hooper and Musser's (1964, 43, fig. 8b)

hypothesis that Rheomys is peripheral to the cluster of South American species that represented other sigmodontines in their analysis. Earlier, Hershkovitz (1962) suggested that ichthyomyines were closely related to phyllotines and sigmodonts because they all have tetralophodont molars and wide-long palates. Voss (1988: 438) convincingly refuted Hershkovitz's arguments, and remarked that no morphological features convincingly relate ichthyomyines to any other New World muroid group. Steppan's (1995: figs. 20, 21) analyses also indicated an equivocal position of the ichthyomyines within the sigmodontine clade; in some of his trees, ichthyomyines sister with oryzomyines or thomatomyines, but neither hypothesis is supported by my data. Although, ichthyomyines and Sigmodon uniquely exhibit a pair of lateral crater papillae recessed in the lateral walls of the crater of the phalli (character 113), which might suggest a close relationship between these two groups, my analyses interpreted these papillae as non-homologous character convergences. Diagnostic synapomorphies for the Ichthyomyini, however, are numerous: the ungual tuft on pes absent (3), plantar pad with hypothenar greatly reduced or absent (4), interdigital webbing on hindfoot (7), genal 1 vibrissae absent (8), nasals extending conspicuously beyond the maxillary-frontal-lacrimal (19), zygomatic notch absent (21), the wide lumen of the infraorbital foramen (27, unique), suprasquamosal foramen present (35), parietal-supraoccipital suture broad (38), subsquamosal fenestra absent (41), hypoglossal foramen placed posterior to the paraoccipital process (59), malleus and incus largely concealed (61), cusp arrangement on m1 opposite (78), ridge on anterolabial cingulum of m1 reduced or absent (79), masseteric crest position posterior to the procingulum of m1 (89), hallux very long (103), lateral crater papillae present (113), bordering fold does not cross the lesser curvature which is

completely lined with squamous epithelium (118), and the reduction in glandular zone along the greater curvature (119, unique). Voss (1988) also suggested for ichthyomyines an ancestral morphotype similar to Neusticomys. This statement is supported by my Analysis 2, but not by Analysis 1 which places Anotomys at the base of the ichthyomyine clade. The position of Neusticomys at the base of Ichthyomyini was also supported by Jenkins and Barnett (1977) who also remarked that current generic classification appears not supported by phylogenetic results.

Reig (1987) recognized the Akodontini as including eleven extant genera (Akodon [plus Abrothrix], Blarinomys, Bolomys, Chelemys, Geoxus, Juscelinomys, Lenoxus, Microxus, Notiomys, Oxymycterus, Podoxymys, and the extinct genus Dankomys), an arrangement followed in subsequent major reviews (Musser and Carleton, 1993; McKenna and Bell, 1997). Recently, using cytochrome *b* data, Smith and Patton (1999) demonstrated the non-monophyly of Akodontini sensu Reig. Instead, they identified an “Andean clade” (Abrothrix, Chroeomys, Chelemys, Notiomys, Geoxus, and Pearsonomys) distinguished from a clade that included not only akodontines such as Akodon (as well as Microxus and Hypsimys), Thaptomys, Bolomys, Oxymycterus, Lenoxus, Blarinomys, Brucepattersonius, Podoxymys, Juscelinomys, and Thalpomys, but also the scapteromyine genera (Scapteromys, Kunsia, and Bibimys). By including scapteromyines, Smith and Patton opted for a more expanded definition of Akodontini. Within this expanded concept (Akodontini sensu Smith and Patton), a monophyletic pair of scapteromyines (Scapteromys + Kunsia) was supported by cytochrome *b* data (Smith and Patton, 1999), and in my morphological analyses, but not by Steppan’s (1995) analyses. Bibimys, the third member of the scapteromyine group has not been included

in any recent phylogenetic analysis.

Abrothrix longipilis is my single representative of the “Andean clade” sensu Smith and Patton (1999), which was found to be sister taxon of Microxus mimus, and not outside the Akodontini. In fact, Hershkovitz (1966) previously considered mimus to be a species of Abrothrix. Later, Reig (1980) gave full generic rank to Microxus remarking that it is somewhat intermediate in cranial and dental characters between Oxymycterus and Akodon s.s., but considered Abrothrix a subgenus of Akodon. My results are then more consistent with previous morphological interpretations concerning those taxa, and are hard to reconcile with the cytochrome *b* evidence (Smith and Patton, 1993, 1999). Akodontines were also found paraphyletic in phylogenetic reconstructions based on mitochondrial DNA genes (Engel et al., 1998). Unfortunately, a taxon-dense phylogenetic analysis of the akodontines based on morphological characters is still unavailable. Smith and Patton (1999) mentioned several lines of evidence for the monophyly of the “Andean clade” including a common geographic distribution in the central and southern Andes in Peru, Bolivia, Chile, and Argentina; a similar  $2N=52$  karyotype; an elongated proximal baculum and reduced distal baculum in Abrothrix and Chroeomys (but not in Notiomys); evidence from protein electrophoretic loci that join some species of Abrothrix with Chroeomys, Chelemys, and Geoxus; and the occurrence of some common ectoparasites on some Abrothrix, Chroeomys, and Chelemys. However, no derived morphological character shared by all of the genera currently referred to the “Andean clade” (Abrothrix, Chroeomys, Chelemys, Notiomys, Geoxus, and Pearsonomys) is apparently available. Voss and Linzey (1981) examined the reproductive tract of Abrothrix and Notiomys, but found no character that could shed light on their affinities.



Engel et al. (1998) provided additional tests in which they constrained the tree so that the akodontines are monophyletic, and Smith and Patton (1999) tested a constrained tree in which the Akodontini is sister taxa of the “Andean clade.” Both results concluded that the constrained trees did not differ significantly from the unconstrained trees. If Akodontini and the “Andean clade” become supported in additional morphological and molecular analyses, the tribal designation Abrotrichini is the appropriate name for the “Andean clade” as suggested by Smith and Patton (1999).

Punomys is an enigmatic taxon, that has been treated as incertae sedis at the tribal level by several authors (e.g., Reig, 1984; Smith and Patton, 1999) or has been referred to the Phyllotini (Olds and Anderson, 1989), or has been recovered as a member of a supratribal clade that includes akodontines, phyllotines, and scapteromyines (Steppan, 1995). My results place Punomys within (Analysis 1) or at the base (Analysis 2) of the Akodontini, concurring with Steppan (1995) who concluded that Punomys is not closely related to phyllotines. Punomys has not been included in any molecular phylogeny to date. The akodontines (including Abrothrix and Punomys) are joined by only two unambiguously derived conditions: a small mesoloph that does not reach the labial cingulum (72), and a ridge on the anterolabial cingulum of m1 reduced or absent (79).

My analyses do not support the monophyly of Phyllotini (sensu Olds and Anderson, 1989) because two of my presumptive phyllotines (Chinchillula, and Punomys) did not group with the others in some or all the analyses. In addition, Sigmodon nested within phyllotines in all analyses. Steppan (1995) found an identical result and argued that placement of Sigmodon within phyllotines may be due to convergence and long-branch attraction. Olds and Anderson (1989) indicated that no

morphological character appears to diagnose the tribe Phyllotini. However, the tribe was weakly supported in a recent cladistic analysis of morphological characters (Steppan, 1995). Smith et al. (1986) and Smith and Patton (1999) suggested that Irenomys may not cluster with other phyllotines based on their cytochrome *b* analyses. Likewise, Engel et al.'s (1998) analyses of the mitochondrial genes ND3, ND4L, arginine tRNA, and ND4 genes supported a phyllotine group, but one that excluded Reithrodon. Steppan (1995) defined the Phyllotini as including the genera Andinomys, Auliscomys, Calomys, Chinchillula, Eligmodontia, Euneomys, Galenomys, Graomys (including Andalgalomys), Irenomys, Neotomys, Phyllotis, Loxodontomys, and Reithrodon. Smith and Patton (1999) also included Salinomys, but removed Irenomys and Reithrodon from the group because each genus appears near the base of the sigmodontine radiation, assigning them to "unique lineages." Engel et al. (1998) and Smith and Patton (1999) both suggested that the tribal designation Reithrodontini, coined by Vorontsov (1959), may be appropriate for Reithrodon.

The position of Sigmodon is unresolved and conflicting among morphological and current molecular data. In my analyses, Sigmodon is allied with phyllotines, a result that was also reported by Steppan (1995). However, these results conflict with those obtained from albumin immunological similarities (Sarich, 1985), electrophoretic similarities (Spotorno, 1986), cladistic analysis of electrophoretic allele data (Steppan, 1995), and DNA-DNA hybridization experiments (Catzeflis et al., 1993), all of which suggest that Sigmodon is basal to the sigmodontine clade. More recently, Engel et al. (1998: figs. 4, 5) in their analyses of NADH genes also found Sigmodon placed at the base of a sigmodontine clade comprising phyllotines, oryzomyines, and akodontines. Similarly,

Smith and Patton (1999) based on cytochrome *b* sequences found that Sigmodon is basal to all other sigmodontines in some analyses (figs. 4a and 5) but not in others (fig. 2 and 4b). Although Voss and Carleton (1993) found Sigmodon closely related to Holochilus within an oryzomyine clade in their most parsimonious trees, they favored the hypothesis of convergence because of the high number of dental characters employed in their study.

My analyses revealed a pentalophodont clade comprised of the sister tribes Oryzomyini and Thomasomyini. This hypothesis of relationships is not new. Summarizing the ideas of earlier authors (e.g., Thomas, Tate) cited in the Historical Synopsis (above), Hershkovitz (1962) proposed that a common sylvan pentalophodont stock gave rise to a thomasomyine grade from which the oryzomyine group evolved. This concept is also consistent with the contents of the Tribe Oryzomyini proposed by Reig (1980, 1984), which included “thomasomyine” taxa together with oryzomyines. However, bootstrap support for this node in my analyses is very low. Available evidence from cytochrome *b* (Smith and Patton, 1999) does not support this group, but analyses based on sequences from other nuclear and mitochondrial genes are still unexplored or in progress. Therefore, I consider it premature to formalize a name for this group until further evidence is provided. The following unambiguous derived character states are synapomorphies for the pentalophodont clade in my analyses: M1 positioned posterior to the zygomatic plate (68), a complete mesoloph that reaches the mesostyle on the labial cingulum (72), M3 mesoloph present and usually well developed (73), cusp arrangement on m1 intermediate (78), and occlusal complexity of m3 simple with the posteroflexid reduced to a pit (82).

Voss and Carleton (1993: 31) diagnosed the Oryzomyini by the following derived character states: (1) pectoral pair of mammae present, totaling 8 or more; (2) long palate with prominent posterolateral pits; (3) alisphenoid strut absent; (4) no posterior suspensory process of the squamosal attached to the tegmen tympani; and 5) no gall bladder. An oryzomyine tribe was also supported by Steppan (1995) in his cladistic analysis. Steppan concurred with Voss and Carleton in their characters 1, 2, 3 and 5, adding the following putative synapomorphies: (6) nasals extending posterior to lacrimals, (7) 12 thoracic vertebrae, (8) fewer than 36 caudal vertebrae, (9) and chevron bones (= hemal arch) present. Based on mitochondrial cytochrome *b* sequences, Patton and da Silva (1995) also found strong support for oryzomyines (sensu Voss and Carleton, 1993) relative to the thomatomyine outgroup, and in a larger sigmodontine representation Smith and Patton (1999) arrived at a similar conclusion. However, Patton and da Silva noted that Scolomys differed from other oryzomyines in molecular and morphological characters and Smith and Patton (1999) concluded that Scolomys represented a unique lineage. Bonvicino and Moreira (2001) also presented analyses using mitochondrial cytochrome *b* with a predominance of oryzomyine taxa. They found a monophyletic Oryzomyini only in the neighbor-joining distance analysis but not with a parsimony nor maximum likelihood methods.

The Oryzomyini is clustered in my analyses by the following unambiguous derived character states (Appendix 3): tegmen tympani not overlapping a posterior suspensory process of the squamosal (36, unique); posterolateral palatal pits complex, with one or more pits present in a common sulcus (reversed in Holochilus sciureus and Microroryzomys; 52); mesopterygoid fossa breadth subequal to parapterygoid fossa (56);

distinct capsular process of lower incisor alveolus (91); 12 thoracic and 7 lumbar vertebrae (96); left and right elements of the chevron bones forming an arch (98); and gall bladder absent (122). In the context of my data the following features proposed as putative synapomorphies by Voss and Carleton (1993) and Steppan (1995) are not unambiguously derived character states for the Oryzomyini: a pectoral pair of mammae, long bony palate with posterolateral palatal pits, alisphenoid strut absent, nasals extending posterior to lacrimals, and fewer than 36 caudal vertebrae. Instead, pectoral mammae, and absence of the alisphenoid strut are synapomorphies of the sigmodontine clade (except ichthyomyines). The lack of pectoral mammae in a few oryzomyines such as Handleyomys (Voss et al., 2002) and Scolomys (Patton and da Silva, 1995) are apparently due to convergence.

I recognize the tribe Thomasomyini as the clade that includes Abrawayaomys, Aepeomys, Chilomys, Delomys, Juliomys, Phaenomys, Rhagomys, Rhipidomys, Thomasomys, Wilfredomys, and Wiedomys. The tribe Wiedomyini Reig (1980) is a junior synonym.

My results are incongruent with respect to thomasomyine relationships produced by Smith and Patton (1999) based on cytochrome *b* sequences. They found that Delomys, Wiedomys, and Juliomys (their Wilfredomys) are evolutionarily distinct lineages without any apparent close relatives within the Sigmodontinae. However, because of tissue availability, several generic representatives were not included in their analyses (Aepeomys, Abrawayaomys, Phaenomys, Rhagomys, and Wilfredomys). Possibly, their results could reflect in some degree the lack of critical representatives, and should be interpreted cautiously especially if cytochrome *b* DNA sequences do not

provide sufficient information to assess relationships among those genera (Oliveira and Bonvicino, 2002). In their classification, Smith and Patton (1999) retained Abrawayamys, Phaenomys, and Rhagomys as incertae sedis at the tribal level, without apparent justification except similarity in geographic distribution with other genera that they considered to be evolutionarily distinct lineages. They nonetheless retained Wiedomys in its own tribe, Wiedomyini. Additional information from other sources are needed to evaluate these discordant hypotheses. Smith and Patton (1999) tested the possibility of a monophyletic clade that included Delomys, Wilfredomys, Rhipidomys, Thomasomys and Chilomys. The likelihood of this tree did not differ significantly from the best unconstrained tree, in which Delomys and Wilfredomys were independent lineages.

My results also differ from current hypothesis based on morphological grounds. Voss (1993) suggested that thomasomyines might not constitute a natural group because the included genera are joined by shared plesiomorphic characters. He suggested that they could be designated as a plesion in formal classifications, or simply be called "plesiomorphic Neotropical muroids." However, his assessment was based on a small set of characters and was not based on a formal cladistic analysis. By contrast, my results suggest that the tribe Thomasomyini (including all of the members of his "plesiomorphic Neotropical group" plus Wiedomys) can be diagnosed by the following unambiguously derived states (Appendix 3): premaxillae extending anterior to nasals but posterior to the zygomatic notch (20); palate short not extending beyond the posterior margins of M3s (50); maxillary palatal pits present (54); mesopterygoid fossa posteriorly convergent (57); parapterygoid fossae triangular (58); processus brevis of incus usually long and

tapering to a pointed tip, delicate in appearance (64); anteromedian flexus on M1 present (69); peroneal process of fifth metatarsal short (101). None of these characters is unique, and obviously extensive amount of homoplasy abound among sigmodontines and within the thomasomyine group. Based on parsimony, I consider my hypothesis as the best outcome given current morphological knowledge. Several other characters need to be explored, however, especially among several rare thomasomyines from the Atlantic rainforest biome of the southeastern Brazil.

Voss (1993) wrote: “There is currently no morphological evidence that Delomys is closely related to any other Neotropical muroid genus.” Zanchin et al. (1992) noted more similarity between diploid numbers of Delomys with some oryzomyines than those of Thomasomys. However, standard karyotypes provide no useful information to establish phylogenetic relationship due of the uncertain homologies among autosomal chromosomes. Smith and Patton’s (1999) trees placed Delomys in diverse positions, but as the sister taxon of the Thomasomyini in their fig. 4b.

Bonvicino et al. (2001) recently reported on morphological and cytogenetic information of Phaenomys. A chromosome complement of  $2n = 78$  was reported, and the authors suggested a possible affinity with Delomys, an inference that is consistent with my analysis. However, in some morphological features Phaenomys more closely resembles Wilfredomys. Additional information is therefore needed to refine the affinities of Phaenomys within the Thomasomyini. See Appendix 3 for a list of diagnostic derived character states.

The position of Wiedomys within the Sigmodontinae is controversial. Reig (1980) constructed the tribe Wiedomyini to include the monotypic genus Wiedomys, and the

fossil taxon Cholomys pearsoni based on a set of mandibular and dental characters. Subsequent research has failed to provide a consistent hypothesis of relationships between Wiedomys and other sigmodontines. Maia and Langguth (1987), for example, provided information on standard karyotype, nucleolar organizer regions, and the G and C banding patterns of Wiedomys; they suggested that the genus represents a primitive lineage different from Oryzomyini (sensu Reig, 1980). Langguth and Silva Neto (1993) subsequently described the morphology of the glans penis and the baculum of Wiedomys, and concluded that these structures are similar to those of some phyllotines, but not to those of oryzomyines (comparisons were not provided with thomasomyines). Steppan's (1995) analysis of morphological characters found Wiedomys to be placed at the base of the oryzomyines or near the base of the sigmodontines. On the other hand, Wiedomys was recovered as a lineage closely related to phyllotines or to the Andean group in various analyses based on cytochrome *b* sequences (Smith and Patton, 1999). My analyses, however, consistently recovered Wiedomys and Wilfredomys as sister taxa that are cladistically far removed from any oryzomyine or phyllotine lineage. Two and 14 additional steps, respectively, are required in my constrained trees to place Wiedomys with the Oryzomyini or with the Phyllotini (excluding Sigmodon). Although no probabilistic tests were employed, a placement of Wiedomys outside the thomasomyines appears unlikely from my data.

Although Smith and Patton (1999) did not include the type species of the genus Wilfredomys (W. oenax) in their analyses, they did include "Wilfredomys" pictipes and "Wilfredomys" sp., which they found to be sister taxa. In some of their analyses these taxa were placed at the base of the sigmodontines or among various well defined tribal



level clades, from which they concluded that Wilfredomys is an independent lineage with no clear affinities to other sigmodontines. González (2000) subsequently proposed the new genus Juliomys for “Wilfredomys” pictipes describing differences in size, craneodental, karyotypic, and integumental characters between it and Wilfredomys oenax; however, no conclusive affinity of Juliomys was proposed. Recently, Oliveira and Bonvicino (2002) described Juliomys rimofrons based on morphology, karyotypes, and cytochrome b substitutions that differentiated it from J. pictipes and from the haplotype that Smith and Patton (1999) called “Wilfredomys” sp. Although, cytochrome b supports the monophyly of Juliomys sensu Oliveira and Bonvicino (2002), Juliomys was not found to be monophyletic in my analyses.

My analyses suggest that Wiedomys and Wilfredomys are closely related, contra Pine’s (1980) argument that several similar external and cranial characteristics of are due to convergence. A cluster of Wiedomys, Wilfredomys and Juliomys is supported by the following traits: nose reddish (16, unique), sphenopalatine vacuities with moderate perforations (55), mesopterygoid fossa and parapterygoid fossa subequal in breadth (56), and 12 thoracic and 7 lumbar vertebrae (96). The option of maintaining Wiedomys in a separate tribe (Wiedomyini), appears to be unjustified. That arrangement would require unnecessary tribal level ranks for Wilfredomys, Juliomys, and other thomasomyines, and would obscure the putative relationships among these taxa. In case the clade consisting of Wiedomys, Wilfredomys and Juliomys is supported from additional sources, the tribal name Wiedomyini is available.

Rhagomys and Abrawayaomys are bizarre rodents, with notable differences in integumental, cranial, and dental features that suggest no clearcut affinities to other

sigmodontines. These genera have been placed as incertae sedis by most authors (Reig, 1980, 1984; Musser and Carleton, 1993; McKenna and Bell, 1997; Smith and Patton, 1999). However, my analyses suggest a close relationships between them. Reig's (1980: 264) suggested that Rhagomys might belong to a tribe of its own. However, such recognition is premature until more information, based on complete specimens and larger series, becomes available (both genera were among those with the lowest percent-completeness; table 3). Neither genus has been sequenced and incorporated in molecular analyses. Rhagomys and Abrawayaomys are joined by a broad zygomatic plate (23), interorbital region convergent with supraorbital margins square or weakly beaded (28), jugal long (31), mesolophids absent (83), masseteric crest anterior to procingulum of m1 (89), and retromolar region of mandible deeply excavated (92, unique).

A clade composed of Aepeomys, Chilomys, Thomasomys, and Rhipidomys is recovered in my analysis. The first three genera exclusively inhabit montane forests in the Central and Northern Andes. Rhipidomys, however, is much more widely distributed in montane and lowland neotropical forests (Tribe, 1996). Although a tribal level designation may be justified for these "Andean" thomasomyines, an analysis with more representatives (in progress) is desirable. This group is consistent with those previously recognized by Hooper and Musser (1964), Eisenberg (1989), and Smith and Patton (1999). Although sequence data were not available for Aepeomys, Smith and Patton (1999) included the genus in their thomasomyine group based on its geographical distribution in the Andes. Aguilera et al. (2000), based on karyological comparisons, supported a strong relationship of Aepeomys with Thomasomys. The following are putative synapomorphies of the Andean thomasomyine group: anterodorsal margin of

zygomatic plate shallow (22), dorsal aperture of ectotympanic ring open (46, unique), and M1 anterocone with labial and lingual conules subequal (70).

The Thomasomyini was formally proposed and diagnosed by Steadman and Ray (1982: 15) for a group that included Thomasomys, Rhipidomys, and †Megaoryzomys, a subfossil taxon from the Galapagos Islands, Ecuador. Leo L. and Gardner (1993), however, described some dental features that place †Megaoryzomys well apart from other large thomasomyines, and Hutterer and Oromí (1993) also refuted a close relationship of †Megaoryzomys with Thomasomys. The latter authors mentioned that short rostrum, hypsodont and planar molars, small and rounded M3, and convergent interorbit with beaded margins of †Megaoryzomys are not present in Thomasomys and remarked that the origins of the former are unknown.

I believe that there is currently enough evidence to conclude that †Megaoryzomys is not a member of the Andean thomasomyine clade or of the Thomasomyini. I arrived at this conclusion based on my own examination of some samples and of photos and illustrations in Lenglet and Coppo (1979), and Hutterer and Oromí (1993). Among other contrasts, the anterodorsal margin of zygomatic plate is deep in †Megaoryzomys, whereas it is shallow in all Andean thomasomyines. Furthermore, a thomasomyine relationship is not supported because †Megaoryzomys has premaxillae extending to the most posterior edge of nasals (rather than anterior to it as in thomasomyines), the maxillary palatal pits are absent (versus present), and the parapterygoid fossa has a subparallel shape (rather than triangular). By contrast, †Megaoryzomys shares several diagnostic features of oryzomyines such as multiple and complex postero lateral palatal pits, and it lacks a posterior suspensory projection of the squamosal. Although, the short

palate exhibited by †Megaoryzomys is a derived condition shared by thomasomyines, a short palate can also be seen in some oryzomyines such as Noronhomys (see Carleton and Olson, 1999). In addition, †Megaoryzomys has a convergent interorbital region with beaded margins, lacks an alisphenoid strut, and has weakly hypsodont and planar molars, all characteristics present (although not exclusively) in several oryzomyine genera. Lastly, the occurrence of other endemic insular oryzomyines such as Nesoryzomys (in the Galapagos), Megalomys (in the Lesser Antilles), and Noronhomys (on Fernando de Noronha) suggest a greater tendency for oryzomyines to colonize and evolve distinctive forms on offshore islands.

Within the Andean thomasomyine group two clades are apparent: one clade that includes Aepeomys and seven species of Thomasomys, and another that contains Rhipidomys and T. notatus. The position of Chilomys and T. baeops is unresolved; in Analysis 1 these taxa cluster with the Rhipidomys clade, but in Analysis 2 they cluster with the Thomasomys clade. I do not name these groups pending the results of an ongoing analysis with denser taxon sampling. However, it seems likely that Aepeomys should be synonymized with Thomasomys based on its close relationship to Thomasomys erro, and its position nested within a larger group of species that includes T. cinereus (the type species of Thomasomys). A valid alternative may be to retain Aepeomys (for lugens, erro, and the recently described species A. reigi (Ochoa et al., 2001)). The latter option, however, would require elevating several Thomasomys lineages to generic rank in order to maintain a monophyletic classification. The genus-group name Inomys Thomas, 1917, is already available for T. incanus, and Thomasomys sensu stricto would include cinereus, rhoadsi, and many related forms, but most other lineages would

require new generic designations. The distinctiveness of T. aureus has been documented for several morphological suites of characters (Hooper and Musser, 1964; Carleton, 1973; Voss and Linzey, 1981) and a group of apparently similar taxa may merit generic recognition as previously suggested by others (Gardner and Romo R., 1993; Leo L. and Gardner, 1993). My analyses are apparently the first to suggest that T. bacops and T. notatus do not group with the main cluster of Thomasomys.

Thus, Thomasomys as currently understood is polyphyletic and seems to be composed of several lineages that probably deserve generic recognition. Trees in which Thomasomys is constrained to be monophyletic are 15 steps longer than the most parsimonious unconstrained tree. Rhipidomys also seems to be paraphyletic, and it should be considered whether T. notatus is a member of the genus to preserve monophyly. Tribe (1996) presented a morphological revision of Rhipidomys and tentatively recognized its monophyly. He noted that T. notatus resembles some species of Rhipidomys but did not suggest a likely relationship. On the other hand, Smith and Patton (1999) supported a monophyletic Rhipidomys based on cytochrome *b* data. Therefore, I consider it premature to reallocate T. notatus pending additional information and recognize Rhipidomys following Tribe (1996). Trees in which Rhipidomys is constrained to be monophyletic are only 3 steps longer than unconstrained trees. In the most parsimonious constrained trees, T. notatus was placed at the base of Rhipidomys. Because these results could be influenced by the few representatives included in these analyses, and given that Thomasomys and Rhipidomys are highly diverse genera, a further taxon-dense analysis is in progress.

## OTHER RELATIONSHIPS AMONG OUTGROUPS

Engel et al. (1998) supported the monophyly of the Neotominae (sensu Reig, 1984) and Sigmodontinae (sensu Reig, 1980), but indicated that both subfamilies may not be sister taxa. They also suggested the Old World cricetines as sister taxon of the sigmodontines. On the other hand, Smith and Patton (1999, fig. 3) suggested that Neotominae (sensu Reig, 1984) is the closest outgroup to Sigmodontinae. Michaux and Catzeflis (2000) also found that the sigmodontine Akodon grouped with the neotomines Peromyscus and Neotoma. My data also identifies several neotomine lineages as successive sister taxa of the sigmodontines, results more consistent with those of Smith and Patton (1999) and Michaux and Catzeflis (2000). Among neotomines, the pair Baiomys + Scotinomys is placed as the sister taxon of the Sigmodontinae. This is not a new discovery. Carleton (1980, fig. 41) previously found Baiomys + Scotinomys placed at the base of a branch leading to sigmodontines, although he interpreted such phylogenetic relationship as ambiguous (Carleton 1980: 139). Putative synapomorphic character states that group Baiomys + Scotinomys with the Sigmodontinae are: calcaneal vibrissae absent (11); posterior extension of nasals long, extending just posterior to the maxillary-frontal-lacrimal intersection (19); posterodorsal extension of premaxillae terminating level with nasals (20); entepicondylar foramen of humerus absent (93); first rib articulates with both seventh cervical and first thoracic vertebrae (95); and preputial glands present (114).

My results did not support a monophyletic Neotominae (sensu Reig, 1984) concurring with Carleton (1980), but only 3 additional steps longer than the most parsimonious trees is needed to obtain a monophyletic Neotominae. My results also

support Carleton's (1980) finding that the neotomines are divided in three groups: the neotomines, peromyscines, and baiomyines.

Recognition of tylomyines as an independent clade has found increasing support since Hooper and Musser (1964) reported the peculiar phallus morphology of the genus Nyctomys, that distinguish it from phallus of other South American cricetines. Carleton (1980) recognized a natural group that included Nyctomys, Tylomys, and Ototylomys, and pointed out the distinction of tylomyines. Steppan (1995) supported the monophyly of tylomyines in his cladistic analysis of morphological traits, and is also supported in my analyses. However, the relationships of tylomyines to other groups are still unresolved.

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## APPENDIX 1: SPECIMENS EXAMINED

I examined specimens from the following museums: American Museum of Natural History, New York, New York, USA (AMNH); British Museum (Natural History), London, England (BMNH); Museo de la Escuela Politécnica Nacional, Quito, Ecuador (EPN); The Field Museum of Natural History, Chicago, Illinois, USA (FMNH); University of Kansas Museum of Natural History, Lawrence, Kansas, USA (KU); Los Angeles County Museum, Los Angeles, California, USA (LACM); Louisiana State University, Museum of Zoology, Baton Rouge, Louisiana, USA (LSUMZ); Museo de Biología, Universidad Central de Venezuela, Caracas, Venezuela (MBUCV); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ); Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, USA (MSB); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM); Museum of Vertebrate Zoology, University of California, Berkeley, California, USA (MVZ); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); United States National Museum, Smithsonian Institution, Washington, D. C., USA (USNM); University of Michigan, Museum of Zoology, Ann Arbor, Michigan, USA (UMMZ); Universitets Zoologisk Museum, Copenhagen, Denmark (UZM).

**Subfamily Arvicolinae****Microtus pennsylvanicus:**

Skin and skull.- **United States:** *Massachusetts*, Nantucket Co., Polpis (AMNH 265059--265062); *New Jersey*, Bergen Co. (AMNH 235286, 139839); *New York*, Orange Co. (AMNH 238114, 238115); Spectacle Pond, Franklin Co. (AMNH 95255); Long Island (AMNH 91048); no locality information (AMNH 238315). Total, 11.

Skeleton.- **United States:** *New Jersey*, Bergen Co. (AMNH 235286, 139839); *New York*, Orange Co. (AMNH 238114, 238115); Spectacle Pond, Franklin Co. (AMNH 95255); Long Island (AMNH 91048); no locality information (AMNH 238315). Total, 7.

**Subfamily Cricetinae****Cricetulus migratorius:**

Skin and skull.- **Iran:** *Luristan*, Khorramabad, Bakhitiari (AMNH 171190, 171191, 171195, 171196, 171198, 171201, 171202, 171204); Karaj (AMNH 171216--171220). Total, 13.

Skeleton.- **West Pakistan:** Gilgit Ag. Naltar (USNM 353286, 353287). Total, 2.

**Mesocricetus auratus:**

Skin and skull.- Lab specimen (AMNH 143858, 143859, 144957, 144767, 144769--144771, 144956, 150013, 150014, 185293, 185294, 185317). Total, 13.

Skeleton.- Lab specimen (AMNH 144766, 144767, 144957, 185317, 235290). Total, 5.

**Subfamily Calomyscinae**



Calomyscus baluchi:

Skin and skull.- **West Pakistan:** Quetta Div.; Quetta-Pishin Dist. (AMNH 212076--212081, 212083--212085). Total, 9.

Skeleton.- **West Pakistan:** Quetta Div.; Quetta-Pishin Dist. (AMNH 212076--212081, 212083--212085). Total, 9.

Gland penis.- **West Pakistan:** Quetta Div.; Quetta-Pishin Dist. (AMNH 212080). Total, 1.

**Subfamily Neotominae****Tribe Neotomini:**

Nelsonia neotomodon: **Mexico:** *Zacatecas*, Plateado (AMNH 13096/11418). Total, 1.

Neotoma floridana:

Skin and skull.- **United States:** *Kansas*, Douglas Co. (AMNH 204637, 204638); *Georgia*, St. Marys (AMNH 23053, 23057); *Florida* (AMNH 1127--1129, 3870, 3871, 4361, 131239). Total, 11.

Skins.- **United States:** *Texas*, Turtle Creek (USNM 96902--96911); Kerville (USNM 97089); Ingram (USNM 117548--117550). Total, 14.

Skeleton.- **United States:** *Florida*, Polk Co. (AMNH 143104); *Pennsylvania*, Huntingdon Co. (AMNH 166910, 166911); *New Jersey* (AMNH 182072); *New York*, Orange Co., West Point (AMNH 98066); *Tennessee*, Marion Co., Nickajack Cave (AMNH 166909). Total, 6.

**Tribe Peromyscini:**Baiomys musculus:

Skin and skull.- **Mexico:** *Oaxaca*, San Gabriel (AMNH 190368--190373); Tapanatepec (AMNH 177244--177255). Total, 18.

Skeleton.- **Mexico:** *Oaxaca*, Tapanatepec (AMNH 177933--177941, 177945). Total, 10.

Ochrotomys nuttalli:

Skin and skull.- **United States:** *Florida*, Highlands Co., Archbold Biological Station (AMNH 215371, 217940, 217942, 217943, 217946, 219373, 219376, 234944, 240689), Leon County, Tallahassee (AMNH 131443), Gadsden Co. Chattahoochee (AMNH 131447, 131449). Total, 12.

Skeleton.- **United States:** *Florida*, Highlands Co., Lake Placid (AMNH 217946, 217949, 217951, 218373, 219372--219376, 240316, 240317, 240689, 242635, 243043--243048, 243279, 250168, 254454); laboratory specimen (AMNH 243049). Total, 23.

Peromyscus mexicanus:

Skin and skull.- **Belize:** Toledo (AMNH 256835, 256836, 256838). **Guatemala:** Esquipulas (USNM 565277--565289). **Mexico:** *Oaxaca*, 2 mi E San Gabriel Mistepec (AMNH 190332--190339); Tehuantepec, Arroyo San Juan (AMNH 147660, 147661). Total, 26.

Skeleton.- **Guatemala:** Mataquescuintla, Jalapa (USNM 275569). **Honduras,** Lempira, Gracias Mejiaca (USNM 565484, 565485). **Mexico:** Oaxaca, 2 mi. E San Gabriel, Mistepec (AMNH 190333--190335, 190339); locality undetermined (AMNH 268733). Total, 8.

Reithrodontomys mexicanus:

Skin and skull.- **Costa Rica:** Tibas (AMNH 141878--141884). **Mexico:** Chiapas, Pueblo Nuevo, Solistahucan (AMNH 177984, 177985); Solis (AMNH 177410). Total, 10.

Skeleton.- **Costa Rica:** Cartago, Villa Mills (USNM 566463). **Mexico:** Chiapas, Pueblo Nuevo, Solistahucan (AMNH 177984, 177985); **Panama:** Bocas del Toro, San Felix, Chiriquí (USNM 541236--541238). Total, 6.

Scotinomys teguina:

Skin and skull.- **Costa Rica:** Alajuela, Lajas (AMNH 139731, 139732, 139734, 139801--139803, 140357--140362). Total, 12.

Skeleton.- **Guatemala:** Cotzal, Quiché (USNM 275607); Alta Vera Paz, Tamahú (USNM 275608, 275609). **Costa Rica:** Alajuela, Lajas (AMNH 140358, 140360); Puntarenas, Finca Helechales (USNM 547990, 547992). Total, 7.

**Tribe Tylomyini:**

Nyctomys sumichrasti:

Skin and skull.- **Belize:** Toledo District (AMNH 256834). **Guatemala:** Panajachel (AMNH 74201--74207, 74209--74241). Total, 40.

Skeleton.- **Belize:** Toledo District (AMNH 256834). **Costa Rica:** Prov. Monteverde, Puntarenas (USNM 559055, 566461). **Honduras:** (USNM 498991). **Panamá:** Bocas del Toro, Cayo Aqua (USNM 323880); Chiriquí, Cerro Punta (USNM 323881); Canal Zone (USNM 396407); Darién, La Laguna (USNM 338266), El Aguacate (USNM 503722); Panamá, Cerro Azul (USNM 306974). NZP (USNM 258856, 260068). Total, 12.

Tylomys nudicaudus:

Skin and skull.- **Guatemala:** La Primavera (AMNH 79301); Ohimoxan (AMNH 79308); Santa Rosa, 2 km NE Chiquenulilla (AMNH 243829). Total, 3.

Skeleton.- National Zoological Park (USNM 398072, 398073, 520882, 520883). Total, 4.

**Subfamily Sigmodontinae**

**Tribe Akodontini:**

Abrothrix longipilis:

Skin and skull.- **Chile:** Cayhaique, Campo Bandera (AMNH 91621, 91622); West of Angel, Araucaria Forest (AMNH 91659); Araucaria Forest W of Lonquemori (AMNH 91610, 91611, 91616); Nahuel buta, Araucaria Forest (AMNH 91604--91606); Valparaíso (AMNH 18963, 18974, 18975), Quilpue (AMNH 33268, 33271). Total, 14.

Skeleton.- **Argentina:** Patagonia, Upper Rio Chico (USNM 49518--49520). **Chile:** Cayhaique, Campo Bandera (AMNH 91621). Total, 5.

Akodon boliviensis:

Skin and skull.- **Bolivia:** *Chquisaca* (AMNH 263632--263635, 263637--263642); *Tarija*, Iscayachi, R. Tomayapo (AMNH 262688, 262689, 262695). **Peru:** *Puno*, Puno (AMNH 213576); *Sorapa* (AMNH 91554--91559). Total, 20.

Skeleton.- **Bolivia:** *La Paz*, Laguna Viscachani (AMNH 268767--268769); *Cochabamba* (AMNH 264334, 268764); *Tarija*, Iscayachi (AMNH 262689, 262693). Total, 7.

Microxus mimus:

Skin and skull.- **Bolivia:** *Cochabamba*, Corani (AMNH 268821, 268822); road of Comarapa (AMNH 260585--260587, 260593, 260595, 260597--260599, 260601); *La Paz*, 0.5 km E Saynani (AMNH 268823--268826), Saynani, R. Zongo (AMNH 268827--268831), R. Unduavi (AMNH 264804), Pongo (AMNH 73094). Total, 22.

Skeleton.- **Bolivia:** *Cochabamba*, Corani (AMNH 268821, 268822); road of Comarapa (AMNH 260593, 260596, 260598, 260599); *La Paz*, 0.5 km E Saynani (AMNH 268825, 268826); Saynani, R. Zongo (AMNH 268828). Total, 9.

Fluid.- **Bolivia:** *Cochabamba*, W of Comarapa (AMNH 261201, 261202, 261204, 261206, 261193, 261197, 261199). Total, 7.

Oxymycterus paramensis:

Skin and skull.- **Bolivia:** *Cochabamba*, Tinkusiri (AMNH 264210); *La Paz*, Río Aceramarca (AMNH 264858--264863); *Tarija*, 3 km WNW Carapari (AMNH 264204); *Tarija* (AMNH 264201, 264203, 264206). Total, 11.

Skeleton.- **Bolivia:** *La Paz*, Río Aceramarca (AMNH 264858--264863); *Tarija*, 3 km WNW Carapari (AMNH 264204); *Tarija* (AMNH 264201, 264203, 264206). Total, 10.

Fluid.- **Bolivia:** *La Paz*, Caracato (AMNH 249007).

**Tribe Ichthyomyini:**Anotomys leander:

Skin and skull.- **Ecuador:** *Napo*, Papallacta (AMNH 155598, 155599, 244605--244607; UMMZ 126296). Total, 6.

Skeleton.- **Ecuador:** *Napo*, Papallacta (AMNH 244607). **Venezuela:** *Táchira*, Buena Vista, 2400 m (USNM 442606). Total, 2.

Glans penis.- RSV 099, 106.

Ichthyomys hydrobates:

Skin and skull.- **Colombia:** *Cauca*, Cerro Munchiquito (USNM 294985). **Ecuador:** *Pichincha*, Río Machángara, Guápulo (AMNH 39593, 39594, 46729--46732); *Zamora-Chinchipe*, 4 km E Sabanilla (USNM 513625). **Venezuela:** *Mérida* (USNM 115315); near Mérida (USNM 123323); Mérida (AMNH 24355; USNM 151288, 172941). Total, 13.

Skeleton.- **Ecuador:** *Pichincha*, Guápulo (AMNH 64624). **Venezuela:** *Mérida* (USNM 123323, 172941). Total, 3.

Neusticomys monticolus:

Skin and skull.- **Ecuador:** *Napo*, 8.2 km W Papallacta (AMNH 244608, 244609; UMMZ 155604--155606); *Pichincha*, R. San Rafael (AMNH 64627); San Ignacio (AMNH 64626); Cañón Río Pita (AMNH 63376, 64628). Total, 9.

Skeleton.- **Ecuador:** *Pichincha*, R. San Rafael (AMNH 64627), San Ignacio (AMNH 64626), Cañón Rio Pita (AMNH 63376, 64628). Total, 4.  
Glans penis.- RSV 117.

### Tribe Oryzomyini:

#### Handleyomys intectus:

Skin and skull.- **Colombia:** *Quindío*, El Roble (AMNH 32928, 32933, 32937), Salento (AMNH 32939). Total, 4.

#### Holochilus brasiliensis:

Skin and skull.- **Uruguay:** *Lavalleja* (AMNH 206367); *Soriano*, 3 km E. Cardona (AMNH 206369, 206371, 206372, 206374--206379, 206382, 206384, 206390); *Tacuarembó* (AMNH 206391). Total, 14.

Skeleton.- **Uruguay:** *Soriano*, 3 km E. Cardona (AMNH 206369, 206371, 206374--206377, 206382, 206384). Total, 8.

Fluid.- **Uruguay:** *Soriano*, 3 km E. Cardona (AMNH 206386). Total, 1.

#### Holochilus sciureus:

Skin and skull.- **Bolivia:** *Beni*, Rio Itenez (AMNH 210290, 210292--210296). Total, 6.

Skeleton.- **Bolivia:** *Beni*, Rio Itenez (AMNH 210288, 210290, 210292--210296); R. Tijamuchi (AMNH 261984, 261985); *Santa Cruz* (AMNH 261982, 261983). Total, 11.

Fluid.- **Bolivia:** *Beni*, Rio Baures (AMNH 210260). Total, 1.

#### Microryzomys minutus:

Skin and skull.- **Bolivia:** *Santa Cruz*, Cochabamba, 31 km by road W of Comarapa (AMNH 260419). **Ecuador:** *Napo*, Papallacta, (UMMZ 127126, 155797, 155678, 155679); *Pichincha*, NW Corazón (AMNH 66534, 66535, 66537, 66538); San Rafael (AMNH 66530). **Peru:** Cajamarca, 4 km W El Chaupe (AMNH 268114, MUSM 10676). Total, 12.

Skeleton.- **Bolivia:** *Santa Cruz*, Cochabamba, 31 km by road W of Comarapa (AMNH 260419). **Venezuela:** *Mérida*, La Coromoto (USNM 374373, 374380, 374443); *Sucre*, Turumiquire (AMNH 69894, 69896). Total, 6.

Fluid.- **Peru**, *Pasco*, P.N. Yanachaga-Chemillen (MUSM 14924). Total, 1.

#### Oecomys bicolor:

Skin and skull.- **Peru:** *Madre de Dios*, Reserva Cuzco Amazónico (MUSM 6287, 6289, 6291--6293, 6295, 6299, 6303, 6309, 6312, 6317). Total, 11.

Skeleton.- MUSM 6299--6301, 6304, 6309, 6314. Total, 6.

Fluid.- MUSM 6298, 6308, 6316. Total, 3.

#### Oligoryzomys fulvescens:

Skin and Skull.- **Costa Rica:** *Puntarenas*, Boruca (AMNH 9580/7921, 9577/7918, 9575/7916, 9574/7915, 9572, 9573/7914); *Cañas Gordas* (AMNH 142440--142451, 142453). **Colombia:** *La Guajira*, San Miguel (AMNH 38920--38924). Total, 24.

Skeleton.- **Costa Rica:** *Puntarenas*, Finca Helechales (USNM 547947--547949). **Ecuador:** *Los Ríos*, Vinces (USNM 534359). **Guatemala:** Escuintla, Finca Los Arcos (USNM 275363). **Mexico:** Hidalgo (AMNH 254711); San Luis de Potosí (AMNH 254712); Oaxaca (AMNH 190328). **Panama:** *Canal Zone*, Buena Vista Peninsula

(USNM 503718); *Chiriquí*, San Felix (USNM 541162); *Panamá*, Cerro Azul (USNM 305677--305679, 305683). **Venezuela:** *Aragua*, Maracay (USNM 517581); *Sucre*, Finca Vuelta (AMNH 257262--257266), Apure (AMNH 257338). Total, 21.

**Oryzomys palustris:**

Skin and skull.- **United States:** *Florida*, Collier Co. (AMNH 252717), Highland Co. (AMNH 250167, 252716, 252718--252721, 253212--253214, 254453), Monroe Co. (AMNH 256405, 256407, 256408); *Virginia*, Lake Drummond (AMNH 13849, 93212). Total, 16.

Skeleton.- **United States:** *Florida*, Collier Co. (AMNH 252717), Highland Co. (AMNH 250167, 252716, 252718--252721, 253212--253214, 254453), Monroe Co. (AMNH 256405--256407), *Virginia*, Lake Drummond (AMNH 208194). Total, 15.

**Tribe Phyllotini:**

**Calomys callosus:**

Skin and skull.- **Bolivia:** *Santa Cruz*, 6 km N Buen Retiro (AMNH 260627, 260628), 3 km SW Las Cruces (AMNH 263709--263718), Ayacucho (AMNH 263314, 263315, 263317, 263318, 263320, 263321), San Jose de Chiquitos (AMNH 260684). Total, 19.

Skeleton.- **Bolivia:** *Chquisaca* (AMNH 261966, 263707), *Santa Cruz*, 3 km SW Las Cruces (AMNH 263709--263718). Total, 12.

**Chinchillula sahamae:**

Skin and skull.- **Bolivia:** *La Paz*, 7 km E. Ulla Ulla (AMNH 247885, 247886, 249020). Total, 3.

Fluid.- **Bolivia:** *La Paz*, 7 km E. Ulla Ulla (AMNH 249018, 249019). Total, 2.

**Graomys griseoflavus:**

Skin and skull.- **Bolivia:** *Santa Cruz* (AMNH 260748, 260750--260752, 260754); *Tarija* (AMNH 246760, 246762, 246763, 246765). Total, 9.

Skeleton.- **Bolivia:** *Tarija*, Padcaya (AMNH 268942--268944). Total, 3.

**Phyllotis darwini:**

Skin and skull.- **Chile:** *Malleco*, Angol (AMNH 93277--93293). Total, 17.

Skeleton.- **Chile:** *Malleco*, Angol (AMNH 93283, 93289). Total, 2.

**Punomys kofordi:**

Skin and skull.- **Peru:** *Cuzco*, Cordillera Carabaya (MUSM, 2 uncatalogued); *Puno*, 8 m. SSW Limbani (AMNH 256780, 256781). Total, 4.

**Tribe Scapteromyini:**

**Kunsia tomentosus:**

Skin and skull.- **Bolivia:** *Beni*, San Joaquín (USNM 364760); *Santa Cruz*, Serranía Huachaca (LHE 1405). Total, 2.

**Scapteromys tumidus:**

Skin and skull.- **Uruguay:** *Soriano*, km E. Cardona (AMNH 206298--206302); *Treinta y Tres*, 16 km SSW Boca del Rio Tacuari (AMNH 206313--206318). **Brazil:** *Rio Grande do Sul*, Quinta (AMNH 235431). Total, 12.

Skeleton.- **Uruguay:** *Soriano*, 3 km E Cardona (AMNH 206299, 206300,

206302, 206309--206312). Total, 7.

### Tribe Sigmodontini:

#### Sigmodon hispidus:

Skin and skull.- **Colombia:** Minca (AMNH 15489, 15270). **Mexico:** *Hidalgo*, Orizatlan (AMNH 254785--254787); *Nayarit* (AMNH 254788); *Puebla*, Rancho el Ajengibre (AMNH 254789); *San Luis Potosi*, Rancho Nuevo (AMNH 254791--254794, 254797, 254798); *Tamaulipas*, Ciudad Monte (AMNH 254799--254803). **United States:** *Florida*, Nassau Co., Amelia Island (AMNH 240314, 240315). Total, 20.

Skeleton.- **Mexico:** *San Luis Potosi*, Ciudad Valles (AMNH 254791--251794, 254796--254798); *Tamaulipas*, Ciudad Monte (AMNH 254800). **United States:** *Kansas*, Douglas Co. (AMNH 213823, 213835, 213836, 213847, 213859, 213871). Total, 14.

#### Sigmodon peruanus:

Skin and skull.- **Ecuador:** *Chimborazo*, Puente de Chimbo (AMNH 62190--62197, 63027--63030); *Guayas*, Puna Island (USNM 120236--120238); *Loja*, Pindal (USNM 461650); *Manabí* (AMNH 34287--34289, 34291--34294, 34296, 34297). **Peru:** *Lambayeque*, Eten (AMNH 16570--16572). Total, 28.

Skeleton.- **Ecuador:** *Chimborazo*, Puente de Chimbo (AMNH 63029); *Guayas*, El Refugio, 5 km E. Manglar Alto (USNM 534376); *Los Ríos*, Hda. Santa Teresita, Abras de Mantequilla (USNM 534374, 534375). Total, 4.

### Tribe Thomasomyini:

#### Abrawayaomys ruschii:

Skin and skull.- **Brazil:** *Minas Gerais*, 6 km SW Viçosa, Mata de Prefeitura, Station G-63 (USNM 552416). Total, 1.

#### Aepeomys lugens:

Skin and skull.- **Venezuela:** *Mérida*, Sierra de Mérida (AMNH 143670), Río Mucujón (AMNH 143669; BMNH 29.3.17.68, 25.7.8.1), La Loma del Morro (BMNH 96.11.1.5, holotype of *lugens*), West Merida (BMNH 99.12.1.31--99.12.1.33), Mérida (BMNH 5.2.5.15), Páramo de los Conejos (AMNH 96169, holotype of *Thomasomys ottleyi*). Total, 10.

Skeleton.- **Venezuela:** *Mérida*, Middle Refugio, 2600 m (USNM 387955). Total, 1.

Fluid.- **Venezuela:** *Mérida*, vicinity of La Mucuy (MBUCV I-2793, I-2794); Trujillo (USNM 495642). Total, 3.

#### Chilomys instans:

Skin and skull.- **Colombia:** *Antioquia*, Urrao (FMNH 71610--71617), Sonson (FMNH 70343--70345), *Caldas*, Manizales (FMNH 71500, 71618--71620); *Cundinamarca*, Bogotá (BMNH 95.10.14.1-holotype, FMNH 71622--71629, 71631--71635); *Huila*, San Agustín (FMNH 71490, 71492, 71496--71498, 71606, 71608); *Norte de Santander* (FMNH 18689). **Ecuador:** *Napo*, Papallacta (UMMZ 155619, 155620, 155795); *Pichincha* (EPN 411, 434). Total, 42.

Skeleton.- **Ecuador:** *Cañar*, Chical (AMNH 62922). **Venezuela:** *Mérida*, near

Middle Refugio (USNM 387964). Total, 2.

Fluid.- **Ecuador:** *Pichincha*, San Ignacio (AMNH 64640), San Rafael (AMNH 64648), R. Pita (AMNH 63370); locality undetermined (AMNH 214897, 214898).

**Venezuela:** *Táchira*, Buena Vista (USNM 495646). Total, 6.

Glans penis.- **Ecuador:** *Pichincha*, R. Pita (AMNH 63372), San Ignacio (AMNH 64640, 64642), San Rafael (AMNH 64645). Total, 4.

**Delomys collinus:**

Skin and skull.- **Brazil:** *Rio de Janeiro*, Terezopolis (USNM 304574, 304575), Itatiaya (BMNH 14.2.23.12, holotype); *São Paulo*, Casa Grande (USNM 461062--461064, 484218--484221). Total, 10.

Skull and skeleton: **Brazil:** *São Paulo*, Município de Salesópolis, Estação Biológica de Boracéia (MVZ 182786, 182788, 183064, 183065). Total, 4.

**Delomys sublineatus:**

Skin and skull: **Brazil:** *Paraná*, Salto Grande (USNM 141451, 141452); *São Paulo* (USNM 460534--460537), Casa Grande (USNM 462075, 484222--484226); *Espírito Santo*, Engenheiro Reeve (BMNH 3.9.4.58, holotype), Nova Lombardia (LACM 62910), Santa Teresa (LACM 62911). Total, 15.

**Juliomys pictipes:**

Skin and skull.- **Brazil:** *São Paulo*, Fazenda Intervales, Capão Bonito (MVZ 182079). Total, 1.

Skeleton.- **Brazil:** *São Paulo*, Fazenda Intervales, Capão Bonito (MVZ 182079). Total, 1.

**Juliomys sp.:**

Skin and skull.- **Brazil:** *São Paulo*, Município de Cotia (MVZ or MZUSP-MAM 139, 141). Total, 2.

Skeleton.- **Brazil:** *São Paulo*, Município de Cotia (MVZ or MZUSP-MAM 139, 141). Total, 2.

**Phaenomys ferrugineus:**

Skin and skull.- **Brazil:** locality undetermined (BMNH 48.5.28.1, 27.11.19.43); *Bahia* (BMNH 63.11.16.2); *Rio de Janeiro* (BMNH 76.12.8.3, holotype). Total, 4.

**Rhagomys rufescens:**

Skin and skull.- **Brazil:** *Rio de Janeiro* (BMNH 86.2.8.5, holotype), locality undetermined (BMNH 48.5.6.13). Total, 2.

**Rhipidomys fulviventris:**

Skin and skull.- **Colombia:** *Cauca*, Cocal (AMNH 32459, 32461, 32462, 32541, 32542); Munchique, 2400 m (AMNH 181475); *Meta*, Macarena Mt. (AMNH 142140). **Venezuela:** *Monagas*, San Agustín (USNM 409926, 409930--409934); *Sucre*, Carapas (AMNH 69902, 69904, 69905), El Latal (AMNH 69901); *Táchira*, Buena Vista (USNM 456339, 456341, 456342). Total, 20.

Skeleton.- **Venezuela:** *Mérida*, 4 km. S and 6.5 km E Tabay (USNM 374541); 7 km SE Tabay, La Coromoto (USNM 387908); 5.5 km. E and 2 km S Tabay (USNM 387911); Carapas (AMNH 69902). Total, 4.

Fluid.- **Venezuela:** (UMMZ 156377). Total, 1.

**Rhipidomys leucodactylus:**

Skin and skull.- **Ecuador:** *Napo*, Limoncocha (USNM 528359). **Peru:** *Ayacucho*, Huanhuachayo (AMNH 241643); *Junín*, Utcuyacu (AMNH 63858); *Loreto*, Boca Río

Curaray (AMNH 71907); *Piura*, Sullana, Cerro Cortezo (USNM 304560). Total, 5.

Skeleton.- **Peru:** *Madre de Dios*, Reserva Cuzco Amazónico (MUSM 7152, 7153, 8303, 8305, 8306). Total, 5.

Fluid.- **Peru:** *Ayacucho*, Huanhuanchayo (AMNH 241643). Total, 1.

**Rhipidomys macconnelli:**

Skin and skull.- **Venezuela:** *Amazonas*, Mt. Duida (AMNH 77161); *Bolívar*, 85 km SSE El Dorado (USNM 387919, 387929, 387931, 387934--387937, 387939, 387941, 387943, 387944, 387947), Auyantepui-Plateau (AMNH 130488, 130490, 130491, 130493--130500, 130924, 130925, 130988--130992), Churi Tepui (AMNH 176306, 176321), Ptari Tepui (AMNH 176300). Total, 34.

Skeleton.- **Venezuela:** *Amazonas*, Cerro Neblina, Camp V (USNM 560656); Camp VII (USNM 560692, 560693, 560695, 560696); *Bolívar*, 132 km SE Rio Cuyuni by road (MVZ 160083), Auyantepui-Plateau (AMNH 130949). Total, 7.

Fluid.- **Venezuela:** *Bolívar*, Mt. Roraima (AMNH 75840); Mt. Duida (AMNH 77658, 77659). Total, 3.

**Thomasomys aureus:**

Skin and skull.- **Ecuador:** *Bolívar*, R. Tatahuazo (MSB 70707); *Pichincha*, near Quito (AMNH 46583, 46587, 46588, 46590--46594, 46596, 46605, 46658); *Tungurahua* (AMNH 67395--67397). **Peru:** *Puno*, Ollaachea (MVZ 172591--172594), Limbani (MVZ 116647, 171499), Yanahuaya (MVZ 172596, 172597). Total, 23.

Skeleton.- **Bolivia:** *Cochabamba*, Comarapa (AMNH 260422); *La Paz*, Saynani, (AMNH 268735, MSB 70446), Río Aceramarca (UMMZ 155942). **Ecuador:** *Bolívar*, R. Tatahuazo (MSB 70707). Total, 5.

Fluid.- **Bolivia:** *La Paz*, Zongo, Cuticucho (UMMZ 156170); *Santa Cruz*, Comarapa (UMMZ 156309). **Ecuador:** *Napo*, Papallacta (AMNH 248281, 248498). **Peru:** *Cuzco*, Acjanaco (MUSM 6726, 9358). Total, 6.

**Thomasomys baeps:**

Skin and skull.- **Ecuador:** *Azuay*, Molleturo (AMNH 61925); *Bolívar*, Río Tatahuazo (MSB 70704); *Napo*, Papallacta (UMMZ 127117, 127118, 155627--155632, 155708, 155767; KU 109495); *Pichincha* (KU 124025; EPN 954421), Cañón of Río Pita (AMNH 65006, 65008, 65009), R. Pita, above Valley of Chillo (BMNH 96.8.1.7, holotype). Total, 19.

Skeleton.- Total, **Ecuador:** *Azuay*, Bestión (AMNH 47677), Molleturo (AMNH 61925), Cinincay (AMNH 61953); *El Oro*, Taraguacocha (AMNH 47699); *Loja* (AMNH 61363). Total, 5.

Fluid.- **Ecuador:** *Napo*, Papallacta (KU 109495), *Tungurahua*, San Francisco (AMNH 63380, 63382). Total, 3.

**Thomasomys cinereus:**

Skin and skull.- **Peru:** *Cajamarca*, Cutervo (BMNH 81.9.7.29, holotype), Paramo de Cajamarca (BMNH 0.3.15.4, 0.3.15.5), Taulis (AMNH 73136, 73147; MVZ 137937--137939); *La Libertad*, South of Huamachuco (BMNH 0.6.6.12); *Lambayeque*, Seques (AMNH 73127, 73129); *Piura*, Cruz Blanca (LSUMZ 27045--27059). Total, 26.

Skeleton.- **Peru:** *Piura*, Cruz Blanca (LSUMZ 27045--27059). Total, 15.

Fluid.- **Peru:** *Cajamarca*, Monteseco (VPT 1629, 1650); *Piura*, Cruz Blanca (LSUMZ 27132, 27138, 27140, 27145, 27146). Total, 7.

**Thomasomys erro:**



Skin and skull.- **Ecuador:** *Napo*, near Papallacta (AMNH 248283; UMMZ 127133, 155633--155642, 155712, 155713); Volcan Sumaco (AMNH 68195, holotype). Total, 15.

Fluid.- **Ecuador:** *Napo*, near Papallacta (AMNH 248283; UMMZ 155633--155642). Total, 11.

**Thomasomys incanus:**

Skin and skull.- **Peru:** *Junín*, Maraynioc, 45 mi NE Tarma (MCZ 38537, 38540). Vitoc Valley (BMNH 94.10.1.4, holotype); *Pasco*, San Alberto (MUSM uncatalogued, EV 513). Total, 4.

Fluid.- **Peru:** *Junín*, Vitoc Valley (BMNH 94.10.1.4, holotype); *Pasco*, San Alberto (MUSM uncatalogued, EV 513). Total, 2.

**Thomasomys kalinowskii:**

Skin and skull.- **Peru:** *Junín*, Maraynioc, 45 mi NE Tarma (FMNH 54202; MCZ 38529--38535, 38538, 38539); Vitoc Valley (BMNH 94.10.1.2-holotype, 94.10.1.3). Total, 12.

Skeleton.- **Peru:** *Ayacucho*, Río Ccarapa (LSUMZ 16742). Total, 1.

Fluid.- **Peru:** *Junín*, Vitoc Valley (BMNH 94.10.1.2-holotype, 94.10.1.3). Total, 2.

**Thomasomys macrotis:**

Skin and skull.- **Peru:** *San Martín*, Pampa del Cuy (USNM 567243), Puerta del Monte (LSUMZ 27285, 27287). Total, 3.

Skeleton.- **Peru:** *San Martín*, Puerta del Monte (LSUMZ 27285, 27287). Total, 2.

Fluid.- **Peru:** *San Martín*, Pampa del Cuy (USNM 567243). Total, 1.

**Thomasomys notatus:**

Skin and skull.- **Peru:** *Cuzco*, Amaybamba (MVZ 173968--173973), Paucartambo (MVZ 171503, 171504, 166706), Torontoy (USNM 194548-holotype, 194894, 194895, 194897), Matchu Picchu (USNM 194898); *Huánuco*, Carpish (LSUMZ 14367, 14368); *Junín*, Utcuyacu (UMMZ 155912). Total, 17.

Skeleton.- **Peru:** *Pasco*, (MUSM 10579, 10580). Total, 2.

Fluid.- **Peru:** *Junín*, Utcuyacu (UMMZ 158028, 158029); *Huánuco*, Carpish (LSUMZ 14367). Total, 3.

**Thomasomys rhoadsi:**

Skin and skull.- **Ecuador:** *Pichincha*, 15 m S. Quito (AMNH 213548), Pichincha (EPN 1277; MVZ 137610), San Ignacio (AMNH 66252--66264). *Tungurahua*, San Francisco, E. of Ambato (AMNH 67532, 67535). Total, 18.

Skeleton.- **Ecuador:** *Pichincha*, 15 m S. Quito (AMNH 213548). Total, 1.

Fluid.- **Ecuador:** *Pichincha*, Río Pita (AMNH 63361). Total, 1.

**Wilfredomys oenax:**

Skin and skull.- **Brazil:** *Rio Grande do Sul*, San Lorenzo (BMNH 27.11.19.44, holotype; ZM 490). **Uruguay:** *Tacuarembó* (AMNH 206018--206021). Total, 6.

Skeleton.- **Uruguay:** *Tacuarembó* (AMNH 206018--206021). Total, 4.

Fluid.- **Brazil:** *Rio Grande do Sul*, San Lorenzo (BMNH 27.11.19.44-holotype, 88.11.30.10; ZM 490). **Uruguay:** *Tacuarembó* (AMNH 206021). Total, 4.

**Tribe Wiedomyini:**

Wiedomys pyrrhorhinos:

Skin and Skull.- **Brazil:** *Bahia*, Caatingas along Riacho de Ressaca (AMNH 574-holotype, skin only), Lamarao (B.M. 3.9.5.63); *Ceará*, Ladeira Grande (BMNH 13.12.18.4); *Pernambuco* (USNM 555760, 555761), Bodoco (USNM 304584). National Zoological Park (USNM 538306, 538314, 538382, 538388). Total, 10.

Skeleton.- NZP (USNM 538306, 538314, 538382, 538386--538388). Total, 6.

## APPENDIX 2: TAXON-CHARACTER MATRIX.

Taxonomic polymorphisms are abbreviated in the matrix for simplicity: a= (0/1); b= (1/2); c= (0/2); d= (0/2/3).

**Microtus pennsylvanicus**

00000 0?110 11010 00020 0-??0 -0020 -1?10 00-00 00000 00010 ?-001 ???00  
100?? 0101- 000?? 3-0?- ?---? -?010 00111 100-1 1002? 00?00 00010 00302  
00

**Cricetulus migratorius**

00000 00000 01010 00020 10000 -0001 01000 01000 00102 01010 0?101 21000  
00100 10200 10?01 00011 00-?0 10010 00001 100-0 1013? 00?00 0000- 01002  
11

**Mesocricetus auratus**

0000? 00000 01010 ?0000 0-000 -0001 01000 01000 1-100 01001 ?0101 11010  
100?? 01100 10?01 00011 00-?0 10010 00101 100-0 1023? 00?00 0000- 11002  
10

**Calomyscus baluchi**

00002 10000 01000 ??120 10000 -0100 -0201 ?1000 01100 01011 00001 21000  
011?0 1021- 00000 00000 ?2-10 10011 00000 11100 00130 00000 000?? ?0000  
0?

**Nyctomys sumichrasti**

01002 00000 00000 0?020 10000 -0201 010d2 00-01 1-101 01000 00000 00000  
01100 10201 02?00 00000 00000 10110 00000 130-0 00230 0?-10 ?0011 00000  
01

**Tylomys nudicaudus**

00002 00000 00000 00021 10000 -0201 21020 00-01 1-101 01020 11000 00000  
01100 10100 01100 0110- ?0-00 10100 00000 020-0 0023? 01-11 10010 10000  
01

**Nelsonia neotomodon**

0000? ??110 00000 ??020 10000 -00?? ?1002 010?1 01121 01100 00001 10000  
01110 1001- ?0001 2101? ??-0 00111 000?0 1??0 ?013? 01-11 01?0- 10302  
00

**Neotoma floridana**

00000 10000 00000 00020 11000 -0101 01012 01000 01101 01000 10001 00100  
01100 1011- 00001 2101- ?---0 00111 00010 110-0 0023? 01-11 0000- 10302  
00

**Baiomys musculus**

00001 00000 10000 00011 10001 00001 01021 01001 02101 01111 01001 2100a  
01100 10100 00001 00000 ?2-10 00111 00101 100-1 1001? 01-11 11010 10000  
00

**Ochrotomys nuttalli**

00001 101?0 11000 ?0020 10000 -0001 01000 02000 00101 01010 00001 00000  
01101 1021- 021?0 00000 00010 00110 00102 120-0 0013? 01-11 00010 00001  
01

**Peromyscus mexicanus**

00001 10010 a0000 00120 10000 -0101 01001 01001 01111 01010 01001 01000  
01100 1021- 020?1 00000 ?1010 00111 000a0 120-0 1012? 11-11 0100- 00402  
00

**Reithrodontomys mexicanus**

00002 1?010 01000 ?0020 10?00 -01?1 01000 010?0 01101 01011 0100? 20000  
01100 10200 021?0 00a00 ?1010 00111 a0001 13100 1023? 11-11 0100- 00301  
00

**Scotinomys teguina**

00001 1?010 1a000 000ba 10001 001?1 01022 010?a 00121 01000 01001 10000  
01100 10000 ????1 000?0 ?2?10 10101 001a1 110-1 10010 01-11 11010 10000  
00

**Abrothrix longipilis**

10002 10110 11000 00113 11010 -0001 01202 01110 01221 0111a 00101 1100?  
01101 1111- 020?1 00011 ?2010 00101 00101 110-0 b102? 01-?? 00?11 0?000  
00

**Akodon boliviensis**

00002 10010 11100 00022 11000 -0001 11002 01110 01221 01210 00101 21001  
01101 10100 01001 00011 02-10 00101 10111 110-1 11020 00010 00010 00000  
00

**Microxus mimus**

00002 10010 11000 00113 11010 -0001 11002 01110 01221 0111a 00100 21001  
01111 1101- 02001 00011 02010 00101 00111 110-1 11020 00010 00010 ?0000  
00

**Oxymycterus paramensis**

20002 10011 11100 ?0123 11010 -0001 11002 01100 01221 01b1a 00110 01011  
01100 10000 01001 00011 02-10 00101 00111 110-1 2100? 00010 00011 ?0400  
00

**Anotomys leander**

00112 11110 11000 0?001 0-001 12001 01010 01100 1-111 ?1001 01100 01011  
111?? 1001- 01000 0021- 02-10 00101 00101 020-0 20330 01-10 00110 ?0210  
00

**Ichthyomys hydrobates**

00112 11110 11000 0?002 0-001 12001 01020 0110? 1-101 01002 01110 01011  
11001 1121- 00001 0021- ?2-10 00101 00101 120-0 ?0330 00010 00110 0?210  
01

**Neusticomys monticolus**

00112 11110 11000 0?002 0-001 12001 0?000 0110? 1-221 01002 00100 11011  
110?? 1001- 00001 0021- 02-10 00101 00101 120-0 20220 00?10 00110 00110  
00

**Handleyomys intectus**

00002 00010 11000 00012 11000 -0001 11202 11000 01111 01002 02100 1100?  
01100 1021- 021?1 0110- 11011 01111 001?1 210-? ??00? ????? ????? ?0000  
01

**Holochilus brasiliensis**

00112 11010 11100 00020 12000 -0211 11022 11000 01101 01001 12101 21001  
01100 1021- 011?1 1111- 12-11 01121 10111 2b111 ?100? 00010 00010 00000

01

**Holochilus sciureus**

00112 11010 11101 00011 12000 -0211 11022 11000 01101 01001 00101 11001  
 01100 1021- 001?1 11011 12-11 01121 10111 21121 2100? ?0??? ????10 ????00

01

**Microryzomys minutus**

00002 10010 11100 00011 10000 -0001 21202 11000 01101 01002 01101 11001  
 01100 10200 02100 0020- 01010 00111 10111 23101 21120 00010 00010 0?000

01

**Oecomys bicolor**

01102 00000 11100 00021 10000 -02?1 11?02 11000 01101 01002 02100 0100?  
 01100 1021- 02120 0110- 11010 0?111 10101 23101 21120 00010 00010 ????00

01

**Oligoryzomys fulvescens**

00002 10010 11100 00011 11000 -0101 21212 11000 01101 01002 02101 21001  
 01100 10200 02101 0010- 01010 00121 101a1 22111 2111? 00?10 0000- 00000

01

**Oryzomys palustris**

00112 11010 11100 00011 11100 -0201 11222 11100 01101 01102 02101 11001  
 01100 1021- 021?0 0010- 11010 00121 10111 22111 21000 00010 00010 00000

01

**Calomys callosus**

00002 10010 11101 00011 11000 -0201 11202 01000 01101 01102 01102 22001  
 01110 10200 00001 00001 02-11 01121 10111 200-1 2100? 00010 00010 00000

00

**Chinchillula sahamae**

00002 00010 11100 0?011 11000 -0001 11101 01000 01111 01101 1?102 11001  
 01100 1101- 00001 1010- -2-11 01111 00111 110-0 2113? 000?0 0??10 ????00

00

**Graomys griseoflavus**

00002 10010 11100 0?021 11000 -0201 11002 01000 01101 01102 01102 22001  
 01100 1011- 00001 01001 02-11 01121 10111 220-0 2101? 00010 00011 0?000

00

**Phyllotis darwini**

00001 100?0 11100 00012 11000 -0001 11202 01000 01101 01102 01102 22001  
 01100 1011- 000?1 00001 02-11 01121 00111 120-1 2?01? 00?10 00011 0?000

00

**Punomys kofordi**

00001 10110 11100 00021 11000 -0001 11202 01000 01101 01101 10101 01001  
 01100 10000 01000 0011- 02-10 00101 001?? ?0??0 11110 01-11 00010 ????01

01

**Kunsia tomentosus**

20102 10001 11100 00022 11?00 -0101 11002 01100 1-10? 01101 10101 0100?  
 01101 1111- 010?1 1001- 02-11 0?121 10??? ????? ????0? ?0??? ????? ?????

?0

**Scapteromys tumidus**

20112 10011 11100 0?012 110?0 -0001 11202 01110 01211 01101 11101 1100?  
01101 11000 02001 00011 01011 01111 00111 110-1 21000 0?-10 00010 00300  
00

**Sigmodon hispidus**

00002 10010 11101 00020 12000 -0201 10022 01000 01101 00101 00a12 10101  
01101 1011- 000?1 1111- 02-11 01122 10111 21101 20000 00010 00111 00000  
00

**Sigmodon peruanus**

00002 10010 11101 00020 12000 -0201 10002 01000 01101 00000 10012 1000?  
01101 1011- 000?1 11011 02-11 01112 10111 21101 2000? ???? ???? ????  
??

**Abrawayaomys ruschii**

00002 10000 1???? 01012 11100 -0101 01002 01100 01121 01000 00110 0110?  
0111? 12101 02100 00011 01110 0?121 11??? ???? ???? ???? ????  
??

**Aepeomys lugens**

00002 00110 11000 00123 10010 -1001 01202 01000 01221 21000 00110 0110?  
01110 11000 021?1 0010- 01011 0?101 00111 13101 1101? 00??? ???? ??300  
00

**Chilomys instans**

00002 00010 11000 00020 10000 -0001 01c22 01100 01121 210ab 00100 a1101  
01110 12b00 02000 0011- 02010 00111 10101 130-0 11130 00010 00010 00000  
00

**Delomys collinus**

00002 10010 11000 00122 11000 -0001 11202 01000 01111 01000 00110 00101  
01110 10100 02101 0110- 01010 00111 00111 120-1 1001? ???? ???? ??000  
?0

**Delomys sublineatus**

00002 1?010 11100 00112 11000 -0001 11202 01000 01111 01000 00110 00101  
01110 10100 02101 0110- 01010 00111 001?1 12??? ??01? ???? ???? ??000  
??

**Juliomys pictipes**

00002 1?010 11100 10020 11000 -01?1 11022 01000 01111 01000 00111 1010?  
01110 10201 02100 0010- 01010 00122 10101 230-0 1112? ???? ???? ????  
??

**Juliomys sp.**

00002 0?010 11100 ?0010 10000 -00?1 01102 01000 0111? 01100 00111 1010?  
01110 10201 02100 0010- 01?10 00111 10111 ?30-0 1112? ???? ???? ????  
??

**Phaenomys ferrugineus**

00002 1?010 11100 00012 10000 -02?1 1120? 010?0 0110? ???? 10110 00???  
???? 10201 02100 0010- 00010 1?101 00??? ?3??? ?22? ???? ???? ????  
??

**Rhagomys rufescens**

01002 00011 11000 00020 11100 -01?1 0?02? 010?0 0??? 0?002 0110? ????  
011?0 11201 02?00 0010- ?1110 1?121 11??? ???? ?112? ???? ???? ????  
??

??

**Rhipidomys fulviventor**

01002 00010 11000 01011 10000 -0001 11002 01000 01111 21000 00110 0110?  
 01110 10200 02121 0110- 00010 001a1 10101 130-0 11231 00110 00010 ?0000  
 01

**Rhipidomys leucodactylus**

00102 00010 11000 01021 10?00 -0101 11022 01000 01101 21000 00110 00101  
 01110 10200 02120 0010- 00010 00111 00101 23100 11231 00110 0000- ??000  
 01

**Rhipidomys macconnelli**

00002 00010 11000 01020 10000 -0101 11022 01000 01121 21100 00100 0010?  
 01110 10200 02120 0010- 00010 00101 10101 130-0 11231 00010 00010 ?0000  
 01

**Thomasomys aureus**

00002 00010 11000 000b2 100a0 -0001 11022 01000 01111 c1100 10110 00101  
 01110 10100 02100 0010- 01011 00101 001?1 13aa0 11230 00010 0001c 00a01  
 00

**Thomasomys baeops**

01002 00010 11000 0002a 10000 -0001 11022 01000 01121 b1100 00110 01101  
 01110 10200 02100 0010- 01011 00111 10101 13200 11130 00010 00010 0?000  
 00

**Thomasomys cinereus**

00002 00110 11000 000b2 100a0 -0001 11002 01000 01121 21a00 00100 0010?  
 01110 11100 02101 0010- 01010 00101 00111 13100 11220 00010 ?000- ?0000  
 00

**Thomasomys erro**

00002 00110 11000 0011? 10000 -1001 01102 0100? 01121 21000 00100 00001  
 01110 11100 02101 0010- 01011 0?101 00??? ?3??1 1?110 00010 ?00?? ??200  
 00

**Thomasomys incanus**

00002 00110 11000 00123 10010 -0001 01022 01000 01121 21000 00110 0010?  
 01110 11100 02101 0010- 01011 00101 00??? ????0 1?12? ?0??? ???? ?0000  
 00

**Thomasomys kalinowskii**

00002 00110 11000 00012 10010 -0001 01222 01000 01121 b1100 00110 00101  
 01110 10000 02101 0110- 01011 0?101 00111 13100 1112? ?0??? ???? ????  
 ?0

**Thomasomys macrotis**

00002 00110 1???? 00023 10000 -0001 11022 01000 01111 21100 10110 0110?  
 01110 11000 02100 0110- 01011 0?101 00111 130-0 1112? ???? ???? ?0000  
 00

**Thomasomys notatus**

01002 00010 11000 01011 10000 -0001 11002 01000 01111 21a00 00111 ?0a01  
 01110 10200 02110 0110- 00010 0?111 10101 130-0 1?230 00110 ?000- ?0000  
 00

**Thomasomys rhoadsi**

00002 00110 11000 00012 10010 -0001 11002 01000 01121 21000 00100 00101  
 01110 11100 02101 0010- 01010 00101 00111 1?0-0 11120 00010 0000- 0?000  
 ?0

**Wilfredomys oenax**

00002 10010 11100 10010 11000 -0001 11102 01000 01111 01100 10111 21101  
 01110 10201 02100 0010- 01010 00111 00111 230-0 11120 00010 ?00?? ??000  
 0?

**Wiedomys pyrrhorhinos**

00002 1?010 11100 10010 11000 -01?1 1120? 01000 011?1 0?100 00101 2110?  
 01110 10201 0210a 0010- 01110 0?1b1 00121 23100 1113? 000?0 ?0??? ??????  
 ??



### APPENDIX 3. CLASSIFICATION AND DERIVED STATES OF SIGMODONTINE CLADES.

The following diagnoses apply to monophyletic groups obtained in Analysis 1, which are described in the text. Both ACCTRAN and DELTRAN optimizations are provided for each node. Diagnoses are formatted as follows: character name, state number ==> state number (character number; consistency index). For example, “dorsal crater papilla, 1 ==> 0 (110; 0.250)” indicates that change from state 1 to 0 in character 110. Unambiguous transformations are indicated by “==>”, while ambiguous transformations (occurring in only some reconstructions) are indicated by “-->”. Unique synapomorphies (not occurring in other nodes) are identified by the CI=1.000.

**SIGMODONTINAE:** ACCTRAN: Thoracic mammary pair, 0 --> 1 (12; 0.400); anterodorsal margin of zygomatic plate, 0 --> 1 (22; 0.222); development of masseteric tubercle, 0 --> 1 (26; 1.000); palate length, 0 ==> 2 (50; 0.333); palatine suture, 0 ==> 1 (53; 0.400); sphenopalatine vacuities, 1 --> 0 (55; 0.182); entoglossal process of basihyal, 0 ==> 1 (60; 1.000); metaflexid morphology on m1, 0 --> 1 (80; 0.500); number of caudal vertebrae, 1 --> 2 (97; 0.294); peroneal process of fifth metatarsal, 1 --> 2 (101; 0.333); lateral bacular mounds, 1 --> 0 (107; 0.200); dorsal crater papilla, 1 ==> 0 (110; 0.250); lateral ventral prostates, 1 --> 0 (116; 0.250). DELTRAN: palate length, 0 ==> 2 (50; 0.333); palatine suture, 0 ==> 1 (53; 0.400); mesopterygoid fossa shape, 0 --> 1 (57; 0.154); entoglossal process of basihyal, 0 ==> 1 (60; 1.000); peroneal process of fifth metatarsal, 0 --> 2 (101; 0.333); dorsal crater papilla, 1 ==> 0 (110; 0.250).

node\_103 --> node\_100 ACCTRAN: Pectoral I mammary pair, 0 ==> 1 (13; 0.200); masseteric tubercle, 1 --> 0 (25; 0.500); jugal length, 0 ==> 1 (31; 0.200); alisphenoid strut, 0 ==> 2 (33; 0.200); posterolateral palatal pits, 1 --> 0 (52; 0.154); supratrochlear fenestra of humerus, 0 ==> 1 (94; 0.455); size and proportions of phalange 1 of pollex (dI of manus), 0 ==> 1 (102; 0.333); relative size of fifth digit (dV) of pes, 3 --> 0 (104; 0.150). DELTRAN: Pectoral I mammary pair, 0 ==> 1 (13; 0.200); anterodorsal margin of zygomatic plate, 0 --> 1 (22; 0.222); jugal length, 0 ==> 1 (31; 0.200); alisphenoid strut, 0 ==> 2 (33; 0.200); metaflexid morphology on m1, 0 --> 1 (80; 0.500); supratrochlear fenestra of humerus, 0 ==> 1 (94; 0.455); position of the trochlear process of calcaneum, 0 --> 1 (100; 0.100); size and proportions of phalange 1 of pollex (dI of manus), 0 ==> 1 (102; 0.333); lateral bacular mounds, 1 --> 0 (107; 0.200).

node\_100 --> node\_74 ACCTRAN: incisive foramina, 0 ==> 1 (48; 0.357); sphenopalatine vacuities, 0 --> 2 (55; 0.182); Accessory labial root of M1, 0 ==> 1 (85; 0.143); roots on m2, 0 ==> 1 (87; 0.250). DELTRAN: incisive foramina, 0 ==> 1 (48; 0.357); Accessory labial root of M1, 0 ==> 1 (85; 0.143); roots on m2, 0 ==> 1 (87; 0.250).

node\_74 --> node\_69 ACCTRAN: palate length, 2 ==> 1 (50; 0.333); palatal breadth, 0 ==> 1 (51; 0.111); upper incisor orientation, 0 --> 1 (67; 0.182); number of caudal vertebrae, 2 ==> 1 (97; 0.294). DELTRAN: palate length, 2 ==> 1 (50; 0.333); palatal breadth, 0 ==> 1 (51; 0.111); number of caudal vertebrae, 2 ==> 1 (97; 0.294).

**Akodontini:** ACCTRAN: posterior extension of nasals, 1 --> 2 (19; 0.250); parietal-supraoccipital suture breadth, 0 --> 1 (38; 0.167); sphenopalatine vacuities, 2 --> 1 (55; 0.182); anteromedian flexus, 1 --> 0 (69; 0.083); mesoloph development, 0 ==> 1

(72; 0.200); ridge on anterolabial cingulum of m1, 0 ==> 1 (79; 0.125). DELTRAN: mesoloph development, 0 ==> 1 (72; 0.200); ridge on anterolabial cingulum of m1, 0 ==> 1 (79; 0.125); relative size of fifth digit (dV) of pes, 3 --> 0 (104; 0.150).

node\_68 --> node\_66 ACCTRAN: upper incisor orientation, 1 --> 0 (67; 0.182); Accessory labial root of M1, 1 ==> 0 (85; 0.143); roots on m2, 1 ==> 0 (87; 0.250); Masseteric crest position, 1 ==> 0 (89; 0.250); peroneal process of fifth metatarsal, 2 --> 1 (101; 0.333). DELTRAN: posterior extension of nasals, 1 --> 2 (19; 0.250); anteromedian flexus, 1 --> 0 (69; 0.083); Accessory labial root of M1, 1 ==> 0 (85; 0.143); roots on m2, 1 ==> 0 (87; 0.250); Masseteric crest position, 1 ==> 0 (89; 0.250).

node\_66 --> node\_65 ACCTRAN: rostral tube, 0 --> 1 (18; 0.167); posterodorsal extension of premaxillae, 1 ==> 3 (20; 0.263); zygomatic plate slope, 0 --> 1 (24; 0.500); alisphenoid strut, 2 ==> 0 (33; 0.200); ethmoid foramen, 1 ==> 2 (43; 0.400); ethmoturbinals, 0 ==> 2 (44; 0.133); maxillary septum, 0 ==> 1 (49; 0.429); palate length, 1 --> 0 (50; 0.333); palatal breadth, 1 ==> 0 (51; 0.111). DELTRAN: posterodorsal extension of premaxillae, 1 ==> 3 (20; 0.263); alisphenoid strut, 2 ==> 0 (33; 0.200); parietal-supraoccipital suture breadth, 0 --> 1 (38; 0.167); ethmoid foramen, 1 ==> 2 (43; 0.400); ethmoturbinals, 0 ==> 2 (44; 0.133); maxillary septum, 0 ==> 1 (49; 0.429); palatal breadth, 1 ==> 0 (51; 0.111); relative size of hallux, 1 --> 0 (103; 0.150).

node\_65 --> node\_64 ACCTRAN: length of interparietal, 0 ==> 1 (39; 0.500); mesopterygoid fossa breadth, 0 ==> 2 (56; 0.150); cephalic process of malleus, 0 ==> 1 (65; 0.200); M1 position, 0 --> 1 (68; 0.150); relative size of fifth digit (dV) of pes, 0 ==> 2 (104; 0.150). DELTRAN: length of interparietal, 0 ==> 1 (39; 0.500); mesopterygoid fossa breadth, 0 ==> 2 (56; 0.150); cephalic process of malleus, 0 ==> 1 (65; 0.200); peroneal process of fifth metatarsal, 2 --> 1 (101; 0.333); relative size of fifth digit (dV) of pes, 0 ==> 2 (104; 0.150).

node\_64 --> node\_63 ACCTRAN: Pectoral I mammary pair, 1 ==> 0 (13; 0.200); posterior extension of nasals, 2 ==> 1 (19; 0.250); upper incisor orientation, 0 ==> 1 (67; 0.182); anteromedian flexus, 0 ==> 1 (69; 0.083); mesoloph development, 1 ==> 2 (72; 0.200). DELTRAN: Pectoral I mammary pair, 1 ==> 0 (13; 0.200); rostral tube, 0 --> 1 (18; 0.167); posterior extension of nasals, 2 ==> 1 (19; 0.250); zygomatic plate slope, 0 --> 1 (24; 0.500); upper incisor orientation, 0 ==> 1 (67; 0.182); anteromedian flexus, 0 ==> 1 (69; 0.083); mesoloph development, 1 ==> 2 (72; 0.200).

node\_63 --> *Abrothrix longipilis* ACCTRAN: claws on manus, 0 ==> 1 (1; 0.667); genal 1 vibrissae, 0 ==> 1 (8; 0.125); jugal length, 1 ==> 0 (31; 0.200); alisphenoid strut, 0 ==> 2 (33; 0.200); mesopterygoid fossa breadth, 2 ==> 1 (56; 0.150); supratrochlear fenestra of humerus, 1 ==> 0 (94; 0.455); position of the trochlear process of calcaneum, 1 ==> 0 (100; 0.100); lateral bacular mounds, 0 ==> 1 (107; 0.200); number of preputial glands, 0 ==> 1 (115; 0.333). DELTRAN: claws on manus, 0 ==> 1 (1; 0.667); genal 1 vibrissae, 0 ==> 1 (8; 0.125); jugal length, 1 ==> 0 (31; 0.200); alisphenoid strut, 0 ==> 2 (33; 0.200); mesopterygoid fossa breadth, 2 ==> 1 (56; 0.150); M1 position, 0 --> 1 (68; 0.150); supratrochlear fenestra of humerus, 1 ==> 0 (94; 0.455); position of the trochlear process of calcaneum, 1 ==> 0 (100; 0.100); lateral bacular mounds, 0 ==> 1 (107; 0.200); number of preputial glands, 0 ==> 1 (115; 0.333).

node\_63 --> *Microxus mimus* ACCTRAN: sphenopalatine vacuities, 1 ==> 0 (55; 0.182); processus brevis of incus, 0 ==> 1 (64; 0.250); M1 position, 1 --> 0 (68; 0.150). DELTRAN: sphenopalatine vacuities, 1 ==> 0 (55; 0.182); processus brevis of incus, 0

=> 1 (64; 0.250).

node\_64 --> Akodon boliviensis ACCTTRAN: rostral tube, 1 --> 0 (18; 0.167); posterodorsal extension of premaxillae, 3 ==> 2 (20; 0.263); zygomatic plate slope, 1 --> 0 (24; 0.500); incisive foramina, 1 ==> 2 (48; 0.357); capsular process of lower incisor alveolus, 0 ==> 1 (91; 0.200). DELTRAN: posterodorsal extension of premaxillae, 3 ==> 2 (20; 0.263); incisive foramina, 1 ==> 2 (48; 0.357); palate length, 1 --> 0 (50; 0.333); M1 position, 0 --> 1 (68; 0.150); capsular process of lower incisor alveolus, 0 ==> 1 (91; 0.200).

node\_65 --> Oxymycterus paramensis ACCTTRAN: claws on manus, 0 ==> 2 (1; 0.667); carpal vibrissae, 0 ==> 1 (10; 0.333); maxillary palatal pits, 0 ==> 1 (54; 0.100); sphenopalatine vacuities, 1 ==> 0 (55; 0.182); hypoglossal foramen, 0 ==> 1 (59; 0.333); peroneal process of fifth metatarsal, 1 --> 2 (101; 0.333); number of preputial glands, 0 ==> 1 (115; 0.333); distribution of gastric epithelium, 0 ==> 4 (118; 0.455). DELTRAN: claws on manus, 0 ==> 2 (1; 0.667); carpal vibrissae, 0 ==> 1 (10; 0.333); rostral tube, 0 --> 1 (18; 0.167); zygomatic plate slope, 0 --> 1 (24; 0.500); maxillary palatal pits, 0 ==> 1 (54; 0.100); sphenopalatine vacuities, 1 ==> 0 (55; 0.182); hypoglossal foramen, 0 ==> 1 (59; 0.333); number of preputial glands, 0 ==> 1 (115; 0.333); distribution of gastric epithelium, 0 ==> 4 (118; 0.455).

node\_66 --> Punomys kofordi ACCTTRAN: plantar surface of pes, 2 ==> 1 (5; 0.286); genal 1 vibrissae, 0 ==> 1 (8; 0.125); parietal-supraoccipital suture breadth, 1 --> 0 (38; 0.167); protoflexus M2, 1 ==> 0 (75; 0.167); cusp arrangement on m1, 0 ==> 1 (78; 0.300); number of caudal vertebrae, 1 ==> 0 (97; 0.294); position of the trochlear process of calcaneum, 1 ==> 0 (100; 0.100); relative size of hallux, 0 --> 1 (103; 0.150); relative size of fifth digit (dV) of pes digit (dV) of pes, 0 ==> 1 (104; 0.150); lateral bacular mounds, 0 ==> 1 (107; 0.200); Dorsal crater papilla, 0 ==> 1 (110; 0.250); incisura angularis, 0 ==> 1 (120; 0.286); gall bladder, 0 ==> 1 (122; 0.125). DELTRAN: plantar surface of pes, 2 ==> 1 (5; 0.286); genal 1 vibrissae, 0 ==> 1 (8; 0.125); protoflexus M2, 1 ==> 0 (75; 0.167); cusp arrangement on m1, 0 ==> 1 (78; 0.300); number of caudal vertebrae, 1 ==> 0 (97; 0.294); position of the trochlear process of calcaneum, 1 ==> 0 (100; 0.100); peroneal process of fifth metatarsal, 2 --> 1 (101; 0.333); relative size of fifth digit (dV) of pes, 0 ==> 1 (104; 0.150); lateral bacular mounds, 0 ==> 1 (107; 0.200); Dorsal crater papilla, 0 ==> 1 (110; 0.250); incisura angularis, 0 ==> 1 (120; 0.286); gall bladder, 0 ==> 1 (122; 0.125).

node\_68 --> node\_67 ACCTTRAN: claws on manus, 0 ==> 2 (1; 0.667); ungual tuft on pes, 0 ==> 1 (3; 0.200); carpal vibrissae, 0 ==> 1 (10; 0.333); posterodorsal extension of premaxillae, 1 ==> 2 (20; 0.263); cephalic process of malleus, 0 ==> 1 (65; 0.200); distribution of gastric epithelium, 0 --> 3 (118; 0.455). DELTRAN: claws on manus, 0 ==> 2 (1; 0.667); ungual tuft on pes, 0 ==> 1 (3; 0.200); carpal vibrissae, 0 ==> 1 (10; 0.333); posterodorsal extension of premaxillae, 1 ==> 2 (20; 0.263); parietal-supraoccipital suture breadth, 0 --> 1 (38; 0.167); cephalic process of malleus, 0 ==> 1 (65; 0.200); upper incisor orientation, 0 --> 1 (67; 0.182); relative size of hallux, 1 --> 0 (103; 0.150).

node\_67 --> Kunsia tomentosus ACCTTRAN: genal 2 vibrissae, 1 ==> 0 (9; 0.125); interorbital region, 0 ==> 1 (28; 0.118); alisphenoid strut, 2 ==> 0 (33; 0.200); subsquamosal fenestra, 0 ==> 1 (41; 0.250); M1 position, 0 ==> 1 (68; 0.150); anteromedian flexus, 0 --> 1 (69; 0.083); molar roots, height and occlusal topography, 0

==> 1 (76; 0.500); Masseteric crest position, 1 ==> 2 (89; 0.250); capsular process of lower incisor alveolus, 0 ==> 1 (91; 0.200). DELTRAN: genal 2 vibrissae, 1 ==> 0 (9; 0.125); posterior extension of nasals, 1 --> 2 (19; 0.250); interorbital region, 0 ==> 1 (28; 0.118); alisphenoid strut, 2 ==> 0 (33; 0.200); subsquamosal fenestra, 0 ==> 1 (41; 0.250); M1 position, 0 ==> 1 (68; 0.150); molar roots, height and occlusal topography, 0 ==> 1 (76; 0.500); Masseteric crest position, 1 ==> 2 (89; 0.250); capsular process of lower incisor alveolus, 0 ==> 1 (91; 0.200).

node\_67 --> Scapteromys tumidus ACCTTRAN: plantar pad of pes, 0 ==> 1 (4; 0.333); posterior extension of nasals, 2 --> 1 (19; 0.250); length of interparietal, 0 ==> 1 (39; 0.500); ethmoid foramen, 1 ==> 2 (43; 0.400); ethmoturbinals, 0 ==> 1 (44; 0.133); posterolateral palatal pits, 0 --> 1 (52; 0.154); mesopterygoid fossa breadth, 0 ==> 1 (56; 0.150); mesoloph development, 1 ==> 2 (72; 0.200); occlusal complexity of m33, 2 ==> 1 (82; 0.200). DELTRAN: plantar pad of pes, 0 ==> 1 (4; 0.333); length of interparietal, 0 ==> 1 (39; 0.500); ethmoid foramen, 1 ==> 2 (43; 0.400); ethmoturbinals, 0 ==> 1 (44; 0.133); posterolateral palatal pits, 0 --> 1 (52; 0.154); mesopterygoid fossa breadth, 0 ==> 1 (56; 0.150); anteromedian flexus, 1 --> 0 (69; 0.083); mesoloph development, 1 ==> 2 (72; 0.200); occlusal complexity of m3, 2 ==> 1 (82; 0.200); distribution of gastric epithelium, 0 --> 3 (118; 0.455).

node\_69 --> Chinchillula sahamae ACCTTRAN: plantar squamation of pes, 1 ==> 0 (6; 0.111); alisphenoid strut, 2 ==> 1 (33; 0.200); suprasquamosal foramen, 2 ==> 1 (35; 0.286); ethmoturbinals, 0 ==> 1 (44; 0.133); mesopterygoid fossa breadth, 0 ==> 1 (56; 0.150); molar roots, height and occlusal topography, 0 ==> 1 (76; 0.500); cusp arrangement on m1, 0 ==> 1 (78; 0.300); position of the trochlear process of calcaneum, 1 ==> 0 (100; 0.100); relative size of hallux, 0 --> 1 (103; 0.150); relative size of fifth digit (dV) of pes, 0 --> 3 (104; 0.150). DELTRAN: plantar squamation of pes, 1 ==> 0 (6; 0.111); alisphenoid strut, 2 ==> 1 (33; 0.200); suprasquamosal foramen, 2 ==> 1 (35; 0.286); ethmoturbinals, 0 ==> 1 (44; 0.133); sphenopalatine vacuities, 1 --> 2 (55; 0.182); mesopterygoid fossa breadth, 0 ==> 1 (56; 0.150); upper incisor orientation, 0 --> 1 (67; 0.182); molar roots, height and occlusal topography, 0 ==> 1 (76; 0.500); cusp arrangement on m1, 0 ==> 1 (78; 0.300); position of the trochlear process of calcaneum, 1 ==> 0 (100; 0.100).

node\_74 --> node\_73 ACCTTRAN: posterolateral palatal pits, 0 --> 1 (52; 0.154); mesopterygoid fossa breadth, 0 ==> 2 (56; 0.150); mesopterygoid fossa shape, 1 ==> 2 (57; 0.154); M1 position, 0 ==> 1 (68; 0.150); Masseteric crest position, 1 ==> 2 (89; 0.250); number of preputial glands, 0 --> 1 (115; 0.333). DELTRAN: posterolateral palatal pits, 0 --> 1 (52; 0.154); sphenopalatine vacuities, 1 --> 2 (55; 0.182); mesopterygoid fossa breadth, 0 ==> 2 (56; 0.150); mesopterygoid fossa shape, 1 ==> 2 (57; 0.154); M1 position, 0 ==> 1 (68; 0.150); Masseteric crest position, 1 ==> 2 (89; 0.250); relative size of hallux, 1 --> 0 (103; 0.150).

node\_73 --> node\_72 ACCTTRAN: Postaxial mammae, 0 --> 1 (15; 0.333); interorbital region, 0 ==> 2 (28; 0.118); capsular process of lower incisor alveolus, 0 ==> 1 (91; 0.200); number of thoracic and lumbar vertebrae, 1 ==> 2 (96; 0.333). DELTRAN: interorbital region, 0 ==> 2 (28; 0.118); capsular process of lower incisor alveolus, 0 ==> 1 (91; 0.200); number of thoracic and lumbar vertebrae, 1 ==> 2 (96; 0.333); relative size of fifth digit (dV) of pes, 3 --> 0 (104; 0.150).

node\_72 --> Calomys callosus ACCTTRAN: processus brevis of incus, 0 ==> 1

(64; 0.250); M1 position, 1 ==> 2 (68; 0.150); anteromedian flexus, 1 ==> 0 (69; 0.083); number of caudal vertebrae, 2 ==> 0 (97; 0.294); number of preputial glands, 1 --> 0 (115; 0.333). DELTRAN: Postaxial mammae, 0 --> 1 (15; 0.333); processus brevis of incus, 0 ==> 1 (64; 0.250); M1 position, 1 ==> 2 (68; 0.150); anteromedian flexus, 1 ==> 0 (69; 0.083); number of caudal vertebrae, 2 ==> 0 (97; 0.294).

node\_72 --> node\_71 ACCTTRAN: posterior extension of nasals, 1 ==> 2 (19; 0.250); alisphenoid strut, 2 ==> 0 (33; 0.200); molar occlusal design, 0 ==> 1 (77; 0.100). DELTRAN: posterior extension of nasals, 1 ==> 2 (19; 0.250); alisphenoid strut, 2 ==> 0 (33; 0.200); molar occlusal design, 0 ==> 1 (77; 0.100); number of preputial glands, 0 --> 1 (115; 0.333).

node\_71 --> Graomys griseoflavus ACCTTRAN: Postaxial mammae, 1 --> 0 (15; 0.333); position of the trochlear process of calcaneum, 1 ==> 0 (100; 0.100); relative size of fifth digit (dV) of pes, 0 --> 1 (104; 0.150). DELTRAN: position of the trochlear process of calcaneum, 1 ==> 0 (100; 0.100); relative size of fifth digit (dV) of pes, 0 --> 1 (104; 0.150).

node\_71 --> node\_70 ACCTTRAN: posterodorsal extension of premaxillae, 1 ==> 0 (20; 0.263); anterodorsal margin of zygomatic plate, 1 ==> 2 (22; 0.222); posterior extension of jugal, 1 ==> 0 (32; 0.500); supraoccipital process, 1 ==> 0 (47; 0.500); palate length, 2 --> 0 (50; 0.333); posterolateral palatal pits, 1 ==> 0 (52; 0.154); palatine suture, 1 --> 0 (53; 0.400); maxillary palatal pits, 0 ==> 1 (54; 0.100); mesopterygoid fossa breadth, 2 ==> 1 (56; 0.150); mesopterygoid fossa shape, 2 ==> 0 (57; 0.154); cephalic process of malleus, 0 ==> 1 (65; 0.200); molar roots, height and occlusal topography, 0 ==> 1 (76; 0.500); ridge on anterolabial cingulum of m1, 0 ==> 1 (79; 0.125); mental foramen position, 1 ==> 2 (90; 0.400); number of caudal vertebrae, 2 ==> 1 (97; 0.294); chevron bones, 0 ==> 1 (98; 0.364); size and proportions of phalange 1 of pollex (dI of manus), 1 ==> 0 (102; 0.333); lateral crater papillae, 0 --> 1 (113; 0.500). DELTRAN: Postaxial mammae, 0 --> 1 (15; 0.333); posterodorsal extension of premaxillae, 1 ==> 0 (20; 0.263); anterodorsal margin of zygomatic plate, 1 ==> 2 (22; 0.222); posterior extension of jugal, 1 ==> 0 (32; 0.500); supraoccipital process, 1 ==> 0 (47; 0.500); posterolateral palatal pits, 1 ==> 0 (52; 0.154); maxillary palatal pits, 0 ==> 1 (54; 0.100); mesopterygoid fossa breadth, 2 ==> 1 (56; 0.150); mesopterygoid fossa shape, 2 ==> 0 (57; 0.154); cephalic process of malleus, 0 ==> 1 (65; 0.200); molar roots, height and occlusal topography, 0 ==> 1 (76; 0.500); ridge on anterolabial cingulum of m1, 0 ==> 1 (79; 0.125); mental foramen position, 1 ==> 2 (90; 0.400); number of caudal vertebrae, 2 ==> 1 (97; 0.294); chevron bones, 0 ==> 1 (98; 0.364); size and proportions of phalange 1 of pollex (dI of manus), 1 ==> 0 (102; 0.333).

node\_70 --> Sigmodon hispidus ACCTTRAN: carotid circulation, 0 ==> 2 (34; 0.133); palate length, 0 --> 1 (50; 0.333); shape of parapterygoid fossa, 0 ==> 1 (58; 0.400); cusp arrangement on m1, 0 ==> 1 (78; 0.300). DELTRAN: carotid circulation, 0 ==> 2 (34; 0.133); palate length, 2 --> 1 (50; 0.333); shape of parapterygoid fossa, 0 ==> 1 (58; 0.400); cusp arrangement on m1, 0 ==> 1 (78; 0.300); lateral crater papillae, 0 --> 1 (113; 0.500).

node\_70 --> Sigmodon peruanus ACCTTRAN: incisive foramina, 1 ==> 0 (48; 0.357); palatal breadth, 0 ==> 1 (51; 0.111); Masseteric crest position, 2 ==> 1 (89; 0.250). DELTRAN: incisive foramina, 1 ==> 0 (48; 0.357); palate length, 2 --> 0 (50; 0.333); palatal breadth, 0 ==> 1 (51; 0.111); palatine suture, 1 --> 0 (53; 0.400);

Masseteric crest position, 2 ==> 1 (89; 0.250).

node\_73 --> Phyllotis darwini ACCTTRAN: plantar surface of pes, 2 ==> 1 (5; 0.286); posterodorsal extension of premaxillae, 1 ==> 2 (20; 0.263); relative size of fifth digit (dV) of pes, 0 --> 1 (104; 0.150). DELTRAN: plantar surface of pes, 2 ==> 1 (5; 0.286); posterodorsal extension of premaxillae, 1 ==> 2 (20; 0.263); relative size of fifth digit (dV) of pes, 3 --> 1 (104; 0.150); number of preputial glands, 0 --> 1 (115; 0.333).

**Pentalophodont clade:** ACCTTRAN: M1 position, 0 ==> 2 (68; 0.150); mesoloph development, 0 ==> 2 (72; 0.200); M3 mesoloph, 0 ==> 1 (73; 0.200); cusp arrangement on m1, 0 ==> 1 (78; 0.300); occlusal complexity of m3, 2 ==> 1 (82; 0.200); relative size of hallux, 0 --> 1 (103; 0.150); DELTRAN: M1 position, 0 ==> 2 (68; 0.150); mesoloph development, 0 ==> 2 (72; 0.200); M3 mesoloph, 0 ==> 1 (73; 0.200); cusp arrangement on m1, 0 ==> 1 (78; 0.300); occlusal complexity of m3, 2 ==> 1 (82; 0.200); relative size of fifth digit (dV) of pes, 3 --> 2 (104; 0.150); relative size of fifth digit (dV) of pes, 0 --> 2 (104; 0.150).

**Oryzomyini:** ACCTTRAN: tegmen tympani, 0 ==> 1 (36; 1.000); posterolateral palatal pits, 0 --> 2 (52; 0.154); sphenopalatine vacuities, 0 --> 1 (55; 0.182); mesopterygoid fossa breadth, 0 ==> 1 (56; 0.150); internal enameled pit of m1 procingulum, 0 --> 1 (81; 0.333); capsular process of lower incisor alveolus, 0 ==> 1 (91; 0.200); number of thoracic and lumbar vertebrae, 1 ==> 2 (96; 0.333); chevron bones, 0 ==> 1 (98; 0.364); gall bladder, 0 ==> 1 (122; 0.125). DELTRAN: tegmen tympani, 0 ==> 1 (36; 1.000); posterolateral palatal pits, 0 --> 2 (52; 0.154); mesopterygoid fossa breadth, 0 ==> 1 (56; 0.150); capsular process of lower incisor alveolus, 0 ==> 1 (91; 0.200); number of thoracic and lumbar vertebrae, 1 ==> 2 (96; 0.333); chevron bones, 0 ==> 1 (98; 0.364); gall bladder, 0 ==> 1 (122; 0.125).

node\_77 --> Handleyomys intectus ACCTTRAN: plantar squamation of pes, 1 ==> 0 (6; 0.111); Pectoral I mammary pair, 1 ==> 0 (13; 0.200); posterodorsal extension of premaxillae, 1 ==> 2 (20; 0.263); ethmoturbinals, 0 ==> 1 (44; 0.133); sphenopalatine vacuities, 1 --> 0 (55; 0.182); molar occlusal design, 0 ==> 1 (77; 0.100); Accessory labial root of M1, 0 ==> 1 (85; 0.143); roots on m2, 0 ==> 1 (87; 0.250); capsular process of lower incisor alveolus, 1 ==> 0 (91; 0.200); position of the trochlear process of calcaneum, 1 ==> 0 (100; 0.100); relative size of hallux, 1 --> 0 (103; 0.150); relative size of fifth digit (dV) of pes, 2 --> 0 (104; 0.150). DELTRAN: plantar squamation of pes, 1 ==> 0 (6; 0.111); Pectoral I mammary pair, 1 ==> 0 (13; 0.200); posterodorsal extension of premaxillae, 1 ==> 2 (20; 0.263); ethmoturbinals, 0 ==> 1 (44; 0.133); sphenopalatine vacuities, 1 --> 0 (55; 0.182); molar occlusal design, 0 ==> 1 (77; 0.100); internal enameled pit of m1 procingulum, 0 --> 1 (81; 0.333); Accessory labial root of M1, 0 ==> 1 (85; 0.143); roots on m2, 0 ==> 1 (87; 0.250); capsular process of lower incisor alveolus, 1 ==> 0 (91; 0.200); position of the trochlear process of calcaneum, 1 ==> 0 (100; 0.100); relative size of hallux, 1 --> 0 (103; 0.150); relative size of fifth digit (dV) of pes, 2 --> 0 (104; 0.150).

node\_77 --> node\_76 ACCTTRAN: ungual tuft on pes, 0 ==> 1 (3; 0.200); plantar pad of pes, 0 ==> 1 (4; 0.333); interdigital webbing on hindfoot, 0 ==> 1 (7; 0.500); interorbital region, 0 ==> 2 (28; 0.118); carotid circulation, 0 ==> 2 (34; 0.133); Masseteric crest position, 1 ==> 2 (89; 0.250); arched chevron bones, 0 ==> 1 (99; 0.750); relative size of hallux, 1 --> 0 (103; 0.150); relative size of fifth digit (dV) of pes, 2 --> 0 (104; 0.150). DELTRAN: ungual tuft on pes, 0 ==> 1 (3; 0.200); plantar pad of

pes, 0 ==> 1 (4; 0.333); interdigital webbing on hindfoot, 0 ==> 1 (7; 0.500); interorbital region, 0 ==> 2 (28; 0.118); carotid circulation, 0 ==> 2 (34; 0.133); internal enameled pit of m1 procingulum, 0 --> 1 (81; 0.333); Masseteric crest position, 1 ==> 2 (89; 0.250); arched chevron bones, 0 ==> 1 (99; 0.750); relative size of hallux, 1 --> 0 (103; 0.150); relative size of fifth digit (dV) of pes, 2 --> 0 (104; 0.150).

node\_76 --> node\_75 ACCTRAN: anterodorsal margin of zygomatic plate, 1 ==> 2 (22; 0.222); postorbital ridge, 0 ==> 1 (29; 1.000); alisphenoid strut, 2 ==> 0 (33; 0.200); palate length, 2 ==> 1 (50; 0.333); mesoloph development, 2 --> 0 (72; 0.200); molar roots, height and occlusal topography, 0 ==> 1 (76; 0.500); molar occlusal design, 0 ==> 1 (77; 0.100); ridge on anterolabial cingulum of m1, 0 ==> 1 (79; 0.125); occlusal complexity of m3, 1 ==> 2 (82; 0.200); Accessory labial root of M1, 0 ==> 1 (85; 0.143); roots on m2, 0 ==> 1 (87; 0.250); number of caudal vertebrae, 2 --> 1 (97; 0.294).

DELTRAN: anterodorsal margin of zygomatic plate, 1 ==> 2 (22; 0.222); postorbital ridge, 0 ==> 1 (29; 1.000); alisphenoid strut, 2 ==> 0 (33; 0.200); palate length, 2 ==> 1 (50; 0.333); molar roots, height and occlusal topography, 0 ==> 1 (76; 0.500); molar occlusal design, 0 ==> 1 (77; 0.100); ridge on anterolabial cingulum of m1, 0 ==> 1 (79; 0.125); occlusal complexity of m3, 1 ==> 2 (82; 0.200); Accessory labial root of M1, 0 ==> 1 (85; 0.143); roots on m2, 0 ==> 1 (87; 0.250).

node\_75 --> Holochilus brasiliensis ACCTRAN: posterior extension of nasals, 1 ==> 2 (19; 0.250); posterodorsal extension of premaxillae, 1 ==> 0 (20; 0.263); palatal breadth, 0 ==> 1 (51; 0.111); mesopterygoid fossa breadth, 1 ==> 2 (56; 0.150); mesoloph development, 0 --> 1 (72; 0.200). DELTRAN: posterior extension of nasals, 1 ==> 2 (19; 0.250); posterodorsal extension of premaxillae, 1 ==> 0 (20; 0.263); palatal breadth, 0 ==> 1 (51; 0.111); mesopterygoid fossa breadth, 1 ==> 2 (56; 0.150); mesoloph development, 2 --> 1 (72; 0.200).

node\_75 --> Holochilus sciureus ACCTRAN: Postaxial mammae, 0 ==> 1 (15; 0.333); posterolateral palatal pits, 2 ==> 0 (52; 0.154); cusp arrangement on m1, 1 ==> 0 (78; 0.300); arched chevron bones, 1 ==> 2 (99; 0.750). DELTRAN: Postaxial mammae, 0 ==> 1 (15; 0.333); posterolateral palatal pits, 2 ==> 0 (52; 0.154); mesoloph development, 2 --> 0 (72; 0.200); cusp arrangement on m1, 1 ==> 0 (78; 0.300); number of caudal vertebrae, 2 --> 1 (97; 0.294); arched chevron bones, 1 ==> 2 (99; 0.750).

node\_76 --> Oryzomys palustris ACCTRAN: zygomatic plate breadth, 0 ==> 1 (23; 0.500); parietal-supraoccipital suture breadth, 0 ==> 1 (38; 0.167); incisive foramina, 0 ==> 1 (48; 0.357); protoflexus M2, 1 ==> 0 (75; 0.167). DELTRAN: zygomatic plate breadth, 0 ==> 1 (23; 0.500); parietal-supraoccipital suture breadth, 0 ==> 1 (38; 0.167); incisive foramina, 0 ==> 1 (48; 0.357); protoflexus M2, 1 ==> 0 (75; 0.167).

node\_77 --> Microryzomys minutus ACCTRAN: anterodorsal margin of zygomatic plate, 1 ==> 0 (22; 0.222); jugal length, 1 ==> 2 (31; 0.200); posterolateral palatal pits, 2 ==> 1 (52; 0.154); anteromedian flexus, 1 ==> 0 (69; 0.083); protoflexus M2, 1 ==> 0 (75; 0.167); cusp arrangement on m1, 1 ==> 2 (78; 0.300); internal enameled pit of m1 procingulum, 1 --> 0 (81; 0.333); number of caudal vertebrae, 2 ==> 3 (97; 0.294). DELTRAN: anterodorsal margin of zygomatic plate, 1 ==> 0 (22; 0.222); jugal length, 1 ==> 2 (31; 0.200); posterolateral palatal pits, 2 ==> 1 (52; 0.154); anteromedian flexus, 1 ==> 0 (69; 0.083); protoflexus M2, 1 ==> 0 (75; 0.167); cusp arrangement on m1, 1 ==> 2 (78; 0.300); number of caudal vertebrae, 2 ==> 3 (97; 0.294).

node\_77 --> Oecomys bicolor ACCTRAN: manual digits dII-dV, 0 ==> 1 (2;

0.200); ungual tuft on pes, 0 ==> 1 (3; 0.200); plantar squamation of pes, 1 ==> 0 (6; 0.111); genal 2 vibrissae, 1 ==> 0 (9; 0.125); posterior extension of nasals, 1 ==> 2 (19; 0.250); anterodorsal margin of zygomatic plate, 1 ==> 0 (22; 0.222); interorbital region, 0 ==> 2 (28; 0.118); sphenopalatine vacuities, 1 --> 0 (55; 0.182); mesopterygoid fossa breadth, 1 ==> 0 (56; 0.150); labial cingulum of upper molars, 0 ==> 2 (74; 0.667); protoflexus M2, 1 ==> 0 (75; 0.167); molar occlusal design, 0 ==> 1 (77; 0.100); supratrochlear fenestra of humerus, 1 ==> 0 (94; 0.455); number of caudal vertebrae, 2 ==> 3 (97; 0.294). DELTRAN: manual digits dII-dV, 0 ==> 1 (2; 0.200); ungual tuft on pes, 0 ==> 1 (3; 0.200); plantar squamation of pes, 1 ==> 0 (6; 0.111); genal 2 vibrissae, 1 ==> 0 (9; 0.125); posterior extension of nasals, 1 ==> 2 (19; 0.250); anterodorsal margin of zygomatic plate, 1 ==> 0 (22; 0.222); interorbital region, 0 ==> 2 (28; 0.118); sphenopalatine vacuities, 1 --> 0 (55; 0.182); mesopterygoid fossa breadth, 1 ==> 0 (56; 0.150); labial cingulum of upper molars, 0 ==> 2 (74; 0.667); protoflexus M2, 1 ==> 0 (75; 0.167); molar occlusal design, 0 ==> 1 (77; 0.100); internal enameled pit of m1 procingulum, 0 --> 1 (81; 0.333); supratrochlear fenestra of humerus, 1 ==> 0 (94; 0.455); number of caudal vertebrae, 2 ==> 3 (97; 0.294).

node\_77 --> *Oligoryzomys fulvescens* ACCTRAN: interorbital region, 0 ==> 1 (28; 0.118); jugal length, 1 ==> 2 (31; 0.200); carotid circulation, 0 ==> 1 (34; 0.133); mesopterygoid fossa breadth, 1 ==> 2 (56; 0.150); anteromedian flexus, 1 ==> 0 (69; 0.083); internal enameled pit of m1 procingulum, 1 --> 0 (81; 0.333); Masseteric crest position, 1 ==> 2 (89; 0.250); arched chevron bones, 0 ==> 1 (99; 0.750); relative size of fifth digit (dV) of pes, 2 ==> 1 (104; 0.150); preputial glands, 1 ==> 0 (114; 0.125). DELTRAN: interorbital region, 0 ==> 1 (28; 0.118); jugal length, 1 ==> 2 (31; 0.200); carotid circulation, 0 ==> 1 (34; 0.133); mesopterygoid fossa breadth, 1 ==> 2 (56; 0.150); anteromedian flexus, 1 ==> 0 (69; 0.083); Masseteric crest position, 1 ==> 2 (89; 0.250); arched chevron bones, 0 ==> 1 (99; 0.750); relative size of fifth digit (dV) of pes, 2 ==> 1 (104; 0.150); preputial glands, 1 ==> 0 (114; 0.125).

**Thomasomyini:** ACCTRAN: posterodorsal extension of premaxillae, 1 ==> 2 (20; 0.263); ethmoturbinals, 0 --> 1 (44; 0.133); palate length, 2 ==> 0 (50; 0.333); maxillary palatal pits, 0 ==> 1 (54; 0.100); mesopterygoid fossa shape, 1 ==> 0 (57; 0.154); shape of parapterygoid fossa, 0 ==> 1 (58; 0.400); processus brevis of incus, 0 ==> 1 (64; 0.250); anteromedian flexus, 1 ==> 0 (69; 0.083); peroneal process of fifth metatarsal, 2 ==> 1 (101; 0.333). DELTRAN: posterodorsal extension of premaxillae, 1 ==> 2 (20; 0.263); palate length, 2 ==> 0 (50; 0.333); maxillary palatal pits, 0 ==> 1 (54; 0.100); sphenopalatine vacuities, 1 --> 0 (55; 0.182); mesopterygoid fossa shape, 1 ==> 0 (57; 0.154); shape of parapterygoid fossa, 0 ==> 1 (58; 0.400); processus brevis of incus, 0 ==> 1 (64; 0.250); anteromedian flexus, 1 ==> 0 (69; 0.083); peroneal process of fifth metatarsal, 2 ==> 1 (101; 0.333).

node\_98 --> node\_96 ACCTRAN: anterocone, 0 ==> 1 (70; 0.333); protoflexus M2, 1 ==> 0 (75; 0.167); number of caudal vertebrae, 2 ==> 3 (97; 0.294); position of the trochlear process of calcaneum, 1 --> 0 (100; 0.100). DELTRAN: anterocone, 0 ==> 1 (70; 0.333); protoflexus M2, 1 ==> 0 (75; 0.167); number of caudal vertebrae, 2 ==> 3 (97; 0.294).

node\_96 --> node\_95 ACCTRAN: posterior extension of nasals, 1 --> 2 (19; 0.250); posterodorsal extension of premaxillae, 2 --> 0 (20; 0.263); alisphenoid strut, 2 ==> 0 (33; 0.200); carotid circulation, 0 --> 2 (34; 0.133); capsular process of lower



incisor alveolus, 0 ==> 1 (91; 0.200). DELTRAN: alisphenoid strut, 2 ==> 0 (33; 0.200); capsular process of lower incisor alveolus, 0 ==> 1 (91; 0.200); position of the trochlear process of calcaneum, 1 --> 0 (100; 0.100).

node\_95 --> node\_91: ACCTTRAN: plantar squamation of pes, 1 --> 0 (6; 0.111); Pectoral I mammary pair, 1 ==> 0 (13; 0.200); Ethmoturbinals, 1 --> 2 (44; 0.133); upper incisor orientation, 0 --> 1 (67; 0.182). DELTRAN: Pectoral I mammary pair, 1 ==> 0 (13; 0.200); Ethmoturbinals, 0 --> 2 (44; 0.133).

**Rhagomys + Abrawayaomys:** ACCTTRAN: zygomatic plate breadth, 0 ==> 1 (23; 0.500); interorbital region, 0 ==> 1 (28; 0.118); jugal length, 1 ==> 0 (31; 0.200); mesopterygoid fossa shape, 0 --> 1 (57; 0.154); mesolophid, 0 ==> 1 (83; 0.500); Masseteric crest position, 1 ==> 2 (89; 0.250); Retromolar region, 0 ==> 1 (92; 1.000). DELTRAN: zygomatic plate breadth, 0 ==> 1 (23; 0.500); interorbital region, 0 ==> 1 (28; 0.118); jugal length, 1 ==> 0 (31; 0.200); mesolophid, 0 ==> 1 (83; 0.500); Masseteric crest position, 1 ==> 2 (89; 0.250); retromolar region, 0 ==> 1 (92; 1.000).

**Abrawayaomys ruschii:** ACCTTRAN: plantar squamation of pes, 0 --> 1 (6; 0.111); genal 2 vibrissae, 1 ==> 0 (9; 0.125); tail pencil, 0 ==> 1 (17; 0.500); posterior extension of nasals, 2 --> 1 (19; 0.250); posterodorsal extension of premaxillae, 0 --> 2 (20; 0.263); carotid circulation, 2 --> 0 (34; 0.133); parietal-supraoccipital suture breadth, 0 ==> 1 (38; 0.167); upper incisor orientation, 1 --> 2 (67; 0.182); M1 position, 2 ==> 1 (68; 0.150); cusp arrangement on m1, 1 ==> 0 (78; 0.300); ridge on anterolabial cingulum of m1, 0 ==> 1 (79; 0.125); relative size of hallux, 1 ==> 0 (103; 0.150); relative size of fifth digit (dV) of pes, 2 ==> 0 (104; 0.150). DELTRAN: genal 2 vibrissae, 1 ==> 0 (9; 0.125); tail pencil, 0 ==> 1 (17; 0.500); parietal-supraoccipital suture breadth, 0 ==> 1 (38; 0.167); mesopterygoid fossa shape, 0 --> 1 (57; 0.154); upper incisor orientation, 0 --> 2 (67; 0.182); M1 position, 2 ==> 1 (68; 0.150); cusp arrangement on m1, 1 ==> 0 (78; 0.300); ridge on anterolabial cingulum of m1, 0 ==> 1 (79; 0.125); relative size of hallux, 1 ==> 0 (103; 0.150); relative size of fifth digit (dV) of pes, 2 ==> 0 (104; 0.150).

**Rhagomys rufescens:** ACCTTRAN: manual digits dII-dV, 0 ==> 1 (2; 0.200); carpal vibrissae, 0 ==> 1 (10; 0.333); palate length, 0 ==> 2 (50; 0.333); posterolateral palatal pits, 0 ==> 1 (52; 0.154); maxillary palatal pits, 1 ==> 0 (54; 0.100); lingual roots on M1-M2, 0 ==> 1 (86; 0.200). DELTRAN: manual digits dII-dV, 0 ==> 1 (2; 0.200); plantar squamation of pes, 1 --> 0 (6; 0.111); carpal vibrissae, 0 ==> 1 (10; 0.333); posterior extension of nasals, 1 --> 2 (19; 0.250); posterodorsal extension of premaxillae, 2 --> 0 (20; 0.263); carotid circulation, 0 --> 2 (34; 0.133); palate length, 0 ==> 2 (50; 0.333); posterolateral palatal pits, 0 ==> 1 (52; 0.154); maxillary palatal pits, 1 ==> 0 (54; 0.100); upper incisor orientation, 0 --> 1 (67; 0.182); lingual roots on M1-M2, 0 ==> 1 (86; 0.200).

**Andean thomatomyine clade:** ACCTTRAN: anterodorsal margin of zygomatic plate, 1 ==> 0 (22; 0.222); dorsal aperture of ectotympanic ring, 0 ==> 2 (46; 1.000); anterocone, 1 ==> 0 (70; 0.333). DELTRAN: plantar squamation of pes, 1 --> 0 (6; 0.111); anterodorsal margin of zygomatic plate, 1 ==> 0 (22; 0.222); carotid circulation, 0 --> 2 (34; 0.133); dorsal aperture of ectotympanic ring, 0 ==> 2 (46; 1.000); anterocone, 1 ==> 0 (70; 0.333).

node\_90 --> node\_84. ACCTTRAN: genal 1 vibrissae, 0 --> 1 (8; 0.125); posterodorsal extension of premaxillae, 0 --> 2 (20; 0.263); M1 position, 2 ==> 1 (68; 0.150); Accessory labial root of M1, 0 ==> 1 (85; 0.143); Masseteric crest position, 1

=> 0 (89; 0.250); capsular process of lower incisor alveolus, 1 ==> 0 (91; 0.200).  
 DELTRAN: M1 position, 2 ==> 1 (68; 0.150); Accessory labial root of M1, 0 ==> 1 (85; 0.143); Masseteric crest position, 1 ==> 0 (89; 0.250); capsular process of lower incisor alveolus, 1 ==> 0 (91; 0.200).

node\_84 --> node\_82 ACCTTRAN: posterior extension of nasals, 2 --> 1 (19; 0.250); zygomatic plate slope, 0 ==> 1 (24; 0.500); jugal length, 1 --> 0 (31; 0.200); protoflexus M2, 0 ==> 1 (75; 0.167); chevron bones, 0 ==> 1 (98; 0.364); preputial glands, 1 --> 0 (114; 0.125). DELTRAN: genal 1 vibrissae, 0 --> 1 (8; 0.125); zygomatic plate slope, 0 ==> 1 (24; 0.500); protoflexus M2, 0 ==> 1 (75; 0.167); chevron bones, 0 ==> 1 (98; 0.364).

node\_82 --> node\_80 ACCTTRAN: rostral tube, 0 ==> 1 (18; 0.167); posterior extension of nasals, 1 --> 2 (19; 0.250); posterodorsal extension of premaxillae, 2 ==> 3 (20; 0.263). DELTRAN: rostral tube, 0 ==> 1 (18; 0.167); posterodorsal extension of premaxillae, 2 ==> 3 (20; 0.263); jugal length, 1 --> 0 (31; 0.200); upper incisor orientation, 0 --> 1 (67; 0.182).

Aepeomys: ACCTTRAN: infraorbital foramen, 0 ==> 1 (27; 1.000); alisphenoid strut, 0 --> 1 (33; 0.200); carotid circulation, 2 ==> 0 (34; 0.133); position of the trochlear process of calcaneum, 0 ==> 1 (100; 0.100); relative size of fifth digit (dV) of pes, 2 ==> 1 (104; 0.150); distribution of gastric epithelium, 0 --> 2 (118; 0.455). DELTRAN: infraorbital foramen, 0 ==> 1 (27; 1.000); carotid circulation, 2 ==> 0 (34; 0.133); position of the trochlear process of calcaneum, 0 ==> 1 (100; 0.100); relative size of fifth digit (dV) of pes, 2 ==> 1 (104; 0.150).

Aepeomys lugens: ACCTTRAN: alisphenoid strut, 1 --> 2 (33; 0.200); ethmoid foramen, 1 ==> 2 (43; 0.400); mesopterygoid fossa shape, 0 ==> 1 (57; 0.154); M1 position, 1 ==> 0 (68; 0.150); relative size of hallux, 1 ==> 0 (103; 0.150); distribution of gastric epithelium, 2 --> 3 (118; 0.455). DELTRAN: posterior extension of nasals, 1 --> 2 (19; 0.250); alisphenoid strut, 0 --> 2 (33; 0.200); ethmoid foramen, 1 ==> 2 (43; 0.400); mesopterygoid fossa shape, 0 ==> 1 (57; 0.154); M1 position, 1 ==> 0 (68; 0.150); relative size of hallux, 1 ==> 0 (103; 0.150); distribution of gastric epithelium, 0 --> 3 (118; 0.455).

Aepeomys erro: ACCTTRAN: posterior extension of nasals, 2 --> 1 (19; 0.250); zygomatic plate slope, 1 ==> 0 (24; 0.500); maxillary palatal pits, 1 ==> 0 (54; 0.100); shape of parapterygoid fossa, 1 ==> 0 (58; 0.400). DELTRAN: zygomatic plate slope, 1 ==> 0 (24; 0.500); alisphenoid strut, 0 --> 1 (33; 0.200); maxillary palatal pits, 1 ==> 0 (54; 0.100); shape of parapterygoid fossa, 1 ==> 0 (58; 0.400); distribution of gastric epithelium, 0 --> 2 (118; 0.455).

Thomasomys incanus: DELTRAN: posterior extension of nasals, 1 --> 2 (19; 0.250).

Thomasomys s.s. ACCTTRAN: jugal length, 0 --> 1 (31; 0.200); carotid circulation, 2 ==> 0 (34; 0.133); maxillary palatal pits, 1 ==> 0 (54; 0.100); Accessory labial root of M1, 1 ==> 0 (85; 0.143). DELTRAN: carotid circulation, 2 ==> 0 (34; 0.133); maxillary palatal pits, 1 ==> 0 (54; 0.100); upper incisor orientation, 0 --> 1 (67; 0.182); Accessory labial root of M1, 1 ==> 0 (85; 0.143); preputial glands, 1 --> 0 (114; 0.125).

Thomasomys cinereus ACCTTRAN: relative size of hallux, 1 ==> 2 (103; 0.150). DELTRAN: relative size of hallux, 1 ==> 2 (103; 0.150).

Thomasomys rhoadsi ACCTTRAN: chevron bones, 1 ==> 0 (98; 0.364).

DELTRAN: chevron bones, 1 ==> 0 (98; 0.364).

Thomasomys kalinowskii ACCTTRAN: alisphenoid strut, 0 ==> 2 (33; 0.200); incisive foramina, 0 ==> 1 (48; 0.357); upper incisor orientation, 1 --> 0 (67; 0.182); M1 position, 1 ==> 0 (68; 0.150); molar occlusal design, 0 ==> 1 (77; 0.100). DELTRAN: jugal length, 1 --> 0 (31; 0.200); alisphenoid strut, 0 ==> 2 (33; 0.200); incisive foramina, 0 ==> 1 (48; 0.357); M1 position, 1 ==> 0 (68; 0.150); molar occlusal design, 0 ==> 1 (77; 0.100).

node\_84 --> node\_83: ACCTTRAN: ethmoturbinals, 2 ==> 1 (44; 0.133); incisive foramina, 0 ==> 1 (48; 0.357); palatal breadth, 0 ==> 1 (51; 0.111). DELTRAN: ethmoturbinals, 2 ==> 1 (44; 0.133); incisive foramina, 0 ==> 1 (48; 0.357); palatal breadth, 0 ==> 1 (51; 0.111).

Thomasomys aureus: ACCTTRAN: genal 1 vibrissae, 1 --> 0 (8; 0.125); upper incisor orientation, 1 --> 0 (67; 0.182); relative size of hallux, 1 ==> 2 (103; 0.150); relative size of fifth digit (dV) of pes, 2 ==> 3 (104; 0.150); incisura angularis, 0 ==> 1 (120; 0.286). DELTRAN: relative size of hallux, 1 ==> 2 (103; 0.150); relative size of fifth digit (dV) of pes, 2 ==> 3 (104; 0.150); incisura angularis, 0 ==> 1 (120; 0.286).

Thomasomys macrotis: ACCTTRAN: posterodorsal extension of premaxillae, 2 ==> 3 (20; 0.263); mesopterygoid fossa shape, 0 ==> 1 (57; 0.154); M1 position, 1 ==> 0 (68; 0.150); molar occlusal design, 0 ==> 1 (77; 0.100). DELTRAN: genal 1 vibrissae, 0 --> 1 (8; 0.125); posterior extension of nasals, 1 --> 2 (19; 0.250); posterodorsal extension of premaxillae, 2 ==> 3 (20; 0.263); mesopterygoid fossa shape, 0 ==> 1 (57; 0.154); upper incisor orientation, 0 --> 1 (67; 0.182); M1 position, 1 ==> 0 (68; 0.150); molar occlusal design, 0 ==> 1 (77; 0.100).

node\_90 --> node\_89: ACCTTRAN: upper incisor orientation, 1 --> 0 (67; 0.182); supratrochlear fenestra of humerus, 1 ==> 0 (94; 0.455); relative size of fifth digit (dV) of pes, 2 ==> 3 (104; 0.150). DELTRAN: posterior extension of nasals, 1 --> 2 (19; 0.250); posterodorsal extension of premaxillae, 2 --> 0 (20; 0.263); supratrochlear fenestra of humerus, 1 ==> 0 (94; 0.455); relative size of fifth digit (dV) of pes, 2 ==> 3 (104; 0.150).

node\_89 --> node\_85: ACCTTRAN: mesopterygoid fossa shape, 0 ==> 1 (57; 0.154). DELTRAN: mesopterygoid fossa shape, 0 ==> 1 (57; 0.154).

node\_85 --> Chilomys instans ACCTTRAN: jugal length, 1 ==> 0 (31; 0.200); parietal-supraoccipital suture breadth, 0 ==> 1 (38; 0.167); palate length, 0 ==> 1 (50; 0.333); maxillary palatal pits, 1 ==> 0 (54; 0.100); upper incisor orientation, 0 ==> 2 (67; 0.182); M3 mesoloph, 1 ==> 0 (73; 0.200); ridge on anterolabial cingulum of m1, 0 ==> 1 (79; 0.125); occlusal complexity of m3, 1 ==> 2 (82; 0.200). DELTRAN: jugal length, 1 ==> 0 (31; 0.200); parietal-supraoccipital suture breadth, 0 ==> 1 (38; 0.167); palate length, 0 ==> 1 (50; 0.333); maxillary palatal pits, 1 ==> 0 (54; 0.100); upper incisor orientation, 0 ==> 2 (67; 0.182); M3 mesoloph, 1 ==> 0 (73; 0.200); ridge on anterolabial cingulum of m1, 0 ==> 1 (79; 0.125); occlusal complexity of m3, 1 ==> 2 (82; 0.200).

node\_85 --> Thomasomys baeops ACCTTRAN: manual digits dII-dV, 0 ==> 1 (2; 0.200); incisive foramina, 0 ==> 1 (48; 0.357); Accessory labial root of M1, 0 ==> 1 (85; 0.143); chevron bones, 0 ==> 2 (98; 0.364). DELTRAN: manual digits dII-dV, 0 ==> 1 (2; 0.200); incisive foramina, 0 ==> 1 (48; 0.357); Accessory labial root of M1, 0 ==> 1 (85; 0.143); chevron bones, 0 ==> 2 (98; 0.364).

node\_89 --> node\_88: ACCTTRAN: tail pencil, 0 ==> 1 (17; 0.500); interorbital

region, 0 --> 1 (28; 0.118); labial cingulum of upper molars, 0 ==> 2 (74; 0.667); occlusal complexity of m3, 1 ==> 0 (82; 0.200); relative size of hallux, 1 ==> 2 (103; 0.150); grooves on glans penis, 0 ==> 1 (105; 0.500); gall bladder, 0 ==> 1 (122; 0.125).

DELTRAN: tail pencil, 0 ==> 1 (17; 0.500); labial cingulum of upper molars, 0 ==> 2 (74; 0.667); occlusal complexity of m3, 1 ==> 0 (82; 0.200); relative size of hallux, 1 ==> 2 (103; 0.150); grooves on glans penis, 0 ==> 1 (105; 0.500); gall bladder, 0 ==> 1 (122; 0.125).

node\_88 --> node\_87. ACCTRAN: posterodorsal extension of premaxillae, 0 ==> 1 (20; 0.263); ethmoturbinals, 2 --> 0 (44; 0.133); lateral bacular mound shape, 0 ==> 1 (108; 1.000); preputial glands, 1 --> 0 (114; 0.125). DELTRAN: posterodorsal extension of premaxillae, 0 ==> 1 (20; 0.263); lateral bacular mound shape, 0 ==> 1 (108; 1.000).

node\_87 --> node\_86. ACCTRAN: manual digits dII-dV, 0 ==> 1 (2; 0.200); posterior extension of nasals, 2 ==> 1 (19; 0.250); interorbital region, 1 --> 0 (28; 0.118); carotid circulation, 2 ==> 0 (34; 0.133); ethmoturbinals, 0 --> 1 (44; 0.133); molar occlusal design, 0 ==> 1 (77; 0.100). DELTRAN: manual digits dII-dV, 0 ==> 1 (2; 0.200); posterior extension of nasals, 2 ==> 1 (19; 0.250); carotid circulation, 2 ==> 0 (34; 0.133); ethmoturbinals, 2 --> 1 (44; 0.133); molar occlusal design, 0 ==> 1 (77; 0.100).

Rhipidomys fulviventer ACCTRAN: mesopterygoid fossa shape, 0 ==> 1 (57; 0.154); protoflexus M2, 0 ==> 1 (75; 0.167); preputial glands, 0 --> 1 (114; 0.125). DELTRAN: mesopterygoid fossa shape, 0 ==> 1 (57; 0.154); protoflexus M2, 0 ==> 1 (75; 0.167).

Thomasomys notatus ACCTRAN: sphenopalatine vacuities, 0 ==> 1 (55; 0.182); labial cingulum of upper molars, 2 ==> 1 (74; 0.667); grooves on glans penis, 1 ==> 0 (105; 0.500); gall bladder, 1 ==> 0 (122; 0.125). DELTRAN: sphenopalatine vacuities, 0 ==> 1 (55; 0.182); labial cingulum of upper molars, 2 ==> 1 (74; 0.667); grooves on glans penis, 1 ==> 0 (105; 0.500); preputial glands, 1 --> 0 (114; 0.125); gall bladder, 1 ==> 0 (122; 0.125).

Rhipidomys leucodactylus ACCTRAN: ungual tuft on pes, 0 ==> 1 (3; 0.200); capsular process of lower incisor alveolus, 1 ==> 0 (91; 0.200); number of thoracic and lumbar vertebrae, 1 ==> 2 (96; 0.333); chevron bones, 0 ==> 1 (98; 0.364). DELTRAN: ungual tuft on pes, 0 ==> 1 (3; 0.200); interorbital region, 0 --> 1 (28; 0.118); ethmoturbinals, 2 --> 0 (44; 0.133); capsular process of lower incisor alveolus, 1 ==> 0 (91; 0.200); number of thoracic and lumbar vertebrae, 1 ==> 2 (96; 0.333); chevron bones, 0 ==> 1 (98; 0.364); preputial glands, 1 --> 0 (114; 0.125).

Rhipidomys macconnelli ACCTRAN: incisive foramina, 0 ==> 1 (48; 0.357); maxillary palatal pits, 1 ==> 0 (54; 0.100); Masseteric crest position, 1 ==> 0 (89; 0.250). DELTRAN: interorbital region, 0 --> 1 (28; 0.118); incisive foramina, 0 ==> 1 (48; 0.357); maxillary palatal pits, 1 ==> 0 (54; 0.100); Masseteric crest position, 1 ==> 0 (89; 0.250).

Wiedomys + Wilfredomys + Juliomys: ACCTRAN: nose coloration, 0 ==> 1 (16; 1.000); sphenopalatine vacuities, 0 ==> 1 (55; 0.182); mesopterygoid fossa breadth, 0 ==> 1 (56; 0.150); number of thoracic and lumbar vertebrae, 1 ==> 2 (96; 0.333). DELTRAN: nose coloration, 0 ==> 1 (16; 1.000); posterodorsal extension of premaxillae, 2 --> 0 (20; 0.263); ethmoturbinals, 0 --> 1 (44; 0.133); sphenopalatine vacuities, 0 ==> 1 (55; 0.182); mesopterygoid fossa breadth, 0 ==> 1 (56; 0.150); number

of thoracic and lumbar vertebrae, 1 ==> 2 (96; 0.333).

Juliomys pictipes ACCTAN: interorbital region, 0 ==> 1 (28; 0.118); Masseteric crest position, 1 ==> 2 (89; 0.250); mental foramen position, 1 ==> 2 (90; 0.400); supratrochlear fenestra of humerus, 1 ==> 0 (94; 0.455). DELTRAN: posterior extension of nasals, 1 --> 2 (19; 0.250); interorbital region, 0 ==> 1 (28; 0.118); carotid circulation, 0 --> 2 (34; 0.133); Masseteric crest position, 1 ==> 2 (89; 0.250); mental foramen position, 1 ==> 2 (90; 0.400); supratrochlear fenestra of humerus, 1 ==> 0 (94; 0.455).

node\_94 --> node\_93 ACCTAN: posterior extension of nasals, 2 --> 1 (19; 0.250); alisphenoid strut, 0 ==> 1 (33; 0.200); carotid circulation, 2 --> 0 (34; 0.133); incisive foramina, 0 ==> 1 (48; 0.357). DELTRAN: alisphenoid strut, 0 ==> 1 (33; 0.200); incisive foramina, 0 ==> 1 (48; 0.357).

Juliomys sp. ACCTAN: plantar squamation of pes, 1 ==> 0 (6; 0.111); anterodorsal margin of zygomatic plate, 1 ==> 0 (22; 0.222); jugal length, 1 ==> 0 (31; 0.200). DELTRAN: plantar squamation of pes, 1 ==> 0 (6; 0.111); anterodorsal margin of zygomatic plate, 1 ==> 0 (22; 0.222); jugal length, 1 ==> 0 (31; 0.200).

node\_93 --> node\_92: ACCTAN: mesopterygoid fossa breadth, 1 ==> 2 (56; 0.150); mesopterygoid fossa shape, 0 ==> 1 (57; 0.154); capsular process of lower incisor alveolus, 1 ==> 0 (91; 0.200). DELTRAN: mesopterygoid fossa breadth, 1 ==> 2 (56; 0.150); mesopterygoid fossa shape, 0 ==> 1 (57; 0.154); capsular process of lower incisor alveolus, 1 ==> 0 (91; 0.200).

Wilfredomys oenax ACCTAN: palatal breadth, 0 ==> 1 (51; 0.111). DELTRAN: palatal breadth, 0 ==> 1 (51; 0.111).

Wiedomys pyrrhorhinos ACCTAN: interorbital region, 0 ==> 1 (28; 0.118); alisphenoid strut, 1 ==> 2 (33; 0.200); maxillary palatal pits, 1 ==> 0 (54; 0.100); mesolophid, 0 ==> 1 (83; 0.500); supratrochlear fenestra of humerus, 1 ==> 2 (94; 0.455); chevron bones, 0 ==> 1 (98; 0.364); relative size of fifth digit (dV) of pes, 2 ==> 3 (104; 0.150). DELTRAN: interorbital region, 0 ==> 1 (28; 0.118); alisphenoid strut, 1 ==> 2 (33; 0.200); maxillary palatal pits, 1 ==> 0 (54; 0.100); mesolophid, 0 ==> 1 (83; 0.500); supratrochlear fenestra of humerus, 1 ==> 2 (94; 0.455); chevron bones, 0 ==> 1 (98; 0.364); relative size of fifth digit (dV) of pes, 2 ==> 3 (104; 0.150).

Phaenomys ferrugineus : ACCTAN: anterodorsal margin of zygomatic plate, 1 ==> 0 (22; 0.222); interorbital region, 0 ==> 2 (28; 0.118); ethmoturbinals, 1 --> 0 (44; 0.133); palatal breadth, 0 ==> 1 (51; 0.111); occlusal complexity of m3, 1 ==> 0 (82; 0.200); lingual roots on M1-M2, 0 ==> 1 (86; 0.200); Masseteric crest position, 1 ==> 0 (89; 0.250); relative size of hallux, 1 --> 2 (103; 0.150). DELTRAN: anterodorsal margin of zygomatic plate, 1 ==> 0 (22; 0.222); interorbital region, 0 ==> 2 (28; 0.118); palatal breadth, 0 ==> 1 (51; 0.111); occlusal complexity of m3, 1 ==> 0 (82; 0.200); lingual roots on M1-M2, 0 ==> 1 (86; 0.200); Masseteric crest position, 1 ==> 0 (89; 0.250); relative size of hallux, 1 --> 2 (103; 0.150).

Delomys: ACCTAN: rostral tube, 0 ==> 1 (18; 0.167); M1 position, 2 ==> 1 (68; 0.150); molar occlusal design, 0 ==> 1 (77; 0.100); size and proportions of phalange 1 of pollex (dI of manus), 1 --> 0 (102; 0.333); relative size of hallux, 1 --> 0 (103; 0.150); relative size of fifth digit (dV) of pes, 2 --> 1 (104; 0.150). DELTRAN: rostral tube, 0 ==> 1 (18; 0.167); ethmoturbinals, 0 --> 1 (44; 0.133); M1 position, 2 ==> 1 (68; 0.150); molar occlusal design, 0 ==> 1 (77; 0.100); relative size of hallux, 1 --> 0 (103; 0.150);

relative size of fifth digit (dV) of pes, 2 --> 1 (104; 0.150).

Delomys collinus: ACCTTRAN: Pectoral I mammary pair, 1 ==> 0 (13; 0.200); posterior extension of nasals, 1 ==> 2 (19; 0.250). DELTRAN: Pectoral I mammary pair, 1 ==> 0 (13; 0.200); posterior extension of nasals, 1 ==> 2 (19; 0.250); size and proportions of phalange 1 of pollex (dI of manus), 1 --> 0 (102; 0.333).

Ichthyomys: ACCTTRAN: ungual tuft on pes, 0 ==> 1 (3; 0.200); plantar pad of pes, 0 ==> 1 (4; 0.333); interdigital webbing on hindfoot, 0 ==> 1 (7; 0.500); genal 1 vibrissae, 0 ==> 1 (8; 0.125); posterior extension of nasals, 1 ==> 0 (19; 0.250); zygomatic notch, 1 ==> 0 (21; 0.500); infraorbital foramen, 0 ==> 2 (27; 1.000); suprasquamosal foramen, 2 ==> 0 (35; 0.286); parietal-supraoccipital suture breadth, 0 ==> 1 (38; 0.167); subsquamosal fenestra, 0 ==> 1 (41; 0.250); hypoglossal foramen, 0 ==> 1 (59; 0.333); malleus and incus exposure, 0 ==> 1 (61; 0.500); cephalic process of malleus, 0 --> 1 (65; 0.200); cusp arrangement on m1, 0 ==> 2 (78; 0.300); ridge on anterolabial cingulum of m1, 0 ==> 1 (79; 0.125); Masseteric crest position, 1 ==> 0 (89; 0.250); position of the trochlear process of calcaneum, 1 --> 0 (100; 0.100); relative size of hallux, 0 ==> 3 (103; 0.150); lateral crater papillae, 0 ==> 1 (113; 0.500); distribution of gastric epithelium, 0 ==> 2 (118; 0.455); gastric epithelium along the greater curvature, 0 ==> 1 (119; 1.000). DELTRAN: ungual tuft on pes, 0 ==> 1 (3; 0.200); plantar pad of pes, 0 ==> 1 (4; 0.333); interdigital webbing on hindfoot, 0 ==> 1 (7; 0.500); genal 1 vibrissae, 0 ==> 1 (8; 0.125); posterior extension of nasals, 1 ==> 0 (19; 0.250); zygomatic notch, 1 ==> 0 (21; 0.500); masseteric tubercle, 0 --> 1 (25; 0.500); development of masseteric tubercle, 0 --> 1 (26; 1.000); infraorbital foramen, 0 ==> 2 (27; 1.000); suprasquamosal foramen, 2 ==> 0 (35; 0.286); parietal-supraoccipital suture breadth, 0 ==> 1 (38; 0.167); subsquamosal fenestra, 0 ==> 1 (41; 0.250); sphenopalatine vacuities, 1 --> 0 (55; 0.182); hypoglossal foramen, 0 ==> 1 (59; 0.333); malleus and incus exposure, 0 ==> 1 (61; 0.500); cusp arrangement on m1, 0 ==> 2 (78; 0.300); ridge on anterolabial cingulum of m1, 0 ==> 1 (79; 0.125); Masseteric crest position, 1 ==> 0 (89; 0.250); relative size of hallux, 1 ==> 3 (103; 0.150); lateral crater papillae, 0 ==> 1 (113; 0.500); distribution of gastric epithelium, 0 ==> 2 (118; 0.455); gastric epithelium along the greater curvature, 0 ==> 1 (119; 1.000).

node\_102 --> Anotomys leander ACCTTRAN: carotid circulation, 0 ==> 1 (34; 0.133); ethmoturbinals, 0 ==> 1 (44; 0.133); palate length, 2 ==> 1 (50; 0.333); mesoloph development, 0 ==> 1 (72; 0.200); protoflexus M2, 1 ==> 0 (75; 0.167); number of thoracic and lumbar vertebrae, 1 ==> 0 (96; 0.333); lateral bacular mounds, 0 --> 1 (107; 0.200). DELTRAN: carotid circulation, 0 ==> 1 (34; 0.133); ethmoturbinals, 0 ==> 1 (44; 0.133); palate length, 2 ==> 1 (50; 0.333); posterolateral palatal pits, 0 --> 1 (52; 0.154); mesoloph development, 0 ==> 1 (72; 0.200); protoflexus M2, 1 ==> 0 (75; 0.167); number of thoracic and lumbar vertebrae, 1 ==> 0 (96; 0.333).

node\_102 --> node\_101 ACCTTRAN: posterodorsal extension of premaxillae, 1 ==> 2 (20; 0.263); manubrium orientation, 1 ==> 0 (63; 0.500). DELTRAN: posterodorsal extension of premaxillae, 1 ==> 2 (20; 0.263); manubrium orientation, 1 ==> 0 (63; 0.500); lateral bacular mounds, 1 --> 0 (107; 0.200).

node\_101 --> Ichthyomys hydrobates ACCTTRAN: carotid circulation, 0 ==> 2 (34; 0.133); maxillary palatal pits, 0 ==> 1 (54; 0.100); upper incisor orientation, 0 ==> 1 (67; 0.182); M1 position, 0 ==> 2 (68; 0.150); gall bladder, 0 ==> 1 (122; 0.125). DELTRAN: carotid circulation, 0 ==> 2 (34; 0.133); posterolateral palatal pits, 0 --> 1

(52; 0.154); maxillary palatal pits, 0 ==> 1 (54; 0.100); cephalic process of malleus, 0 --> 1 (65; 0.200); upper incisor orientation, 0 ==> 1 (67; 0.182); M1 position, 0 ==> 2 (68; 0.150); gall bladder, 0 ==> 1 (122; 0.125).

node\_101 --> Neusticomys monticolus ACCTRAN: ethmoid foramen, 1 ==> 2 (43; 0.400); ethmoturbinals, 0 ==> 2 (44; 0.133); posterolateral palatal pits, 1 --> 0 (52; 0.154); mesopterygoid fossa breadth, 0 ==> 1 (56; 0.150); relative size of hallux, 3 ==> 2 (103; 0.150); relative size of fifth digit (dV) of pes, 3 ==> 2 (104; 0.150); distribution of gastric epithelium, 2 ==> 1 (118; 0.455). DELTRAN: ethmoid foramen, 1 ==> 2 (43; 0.400); ethmoturbinals, 0 ==> 2 (44; 0.133); mesopterygoid fossa breadth, 0 ==> 1 (56; 0.150); relative size of hallux, 3 ==> 2 (103; 0.150); relative size of fifth digit (dV) of pes, 3 ==> 2 (104; 0.150); distribution of gastric epithelium, 2 ==> 1 (118; 0.455).

## OTHER MUROID CLADES

**Sigmodontinae + sister taxon:** ACCTRAN: calcaneal vibrissae, 0 ==> 1 (11; 0.500); posterior extension of nasals, 2 ==> 1 (19; 0.250); posterodorsal extension of premaxillae, 0 ==> 1 (20; 0.263); masseteric tubercle, 0 --> 1 (25; 0.500); mesopterygoid fossa shape, 0 --> 1 (57; 0.154); entepicondylar foramen of humerus, 0 ==> 1 (93; 0.333); first rib articulation, 0 ==> 1 (95; 0.500); position of the trochlear process of calcaneum, 0 --> 1 (100; 0.100); peroneal process of fifth metatarsal, 0 --> 1 (101; 0.333); relative size of hallux, 1 --> 0 (103; 0.150); preputial glands, 0 ==> 1 (114; 0.125). DELTRAN: calcaneal vibrissae, 0 ==> 1 (11; 0.500); posterior extension of nasals, 2 ==> 1 (19; 0.250); posterodorsal extension of premaxillae, 0 ==> 1 (20; 0.263); occlusal complexity of m3, 0 --> 2 (82; 0.200); entepicondylar foramen of humerus, 0 ==> 1 (93; 0.333); first rib articulation, 0 ==> 1 (95; 0.500); preputial glands, 0 ==> 1 (114; 0.125).

node\_104 --> node\_62: ACCTRAN: plantar surface of pes, 2 ==> 1 (5; 0.286); carotid circulation, 0 ==> 2 (34; 0.133); lateral process of parietals, 0 --> 1 (40; 0.400); distal expansion of hamular process, 1 --> 0 (42; 0.500); mesopterygoid fossa breadth, 0 --> 1 (56; 0.150); anteromedian flexus, 1 ==> 0 (69; 0.083); relative size of fifth digit (dV) of pes, 3 ==> 1 (104; 0.150); position of urinary meatus, 0 ==> 1 (111; 0.500); urethral process, 0 ==> 1 (112; 0.250). DELTRAN: plantar surface of pes, 2 ==> 1 (5; 0.286); masseteric tubercle, 0 --> 1 (25; 0.500); carotid circulation, 0 ==> 2 (34; 0.133); posterolateral palatal pits, 0 --> 1 (52; 0.154); anteromedian flexus, 1 ==> 0 (69; 0.083); position of the trochlear process of calcaneum, 0 --> 1 (100; 0.100); peroneal process of fifth metatarsal, 0 --> 1 (101; 0.333); relative size of hallux, 1 --> 0 (103; 0.150); relative size of fifth digit (dV) of pes, 3 ==> 1 (104; 0.150); position of urinary meatus, 0 ==> 1 (111; 0.500); urethral process, 0 ==> 1 (112; 0.250); lateral ventral prostates, 0 --> 1 (116;

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**Part II**

## INTRODUCTION

A recent phylogenetic analysis based on morphological data (Pacheco, Part I) supported the monophyly of the muroid rodent tribe Thomasomyini, a group that includes the taxa traditionally recognized as: Abrawayamys, Aepeomys, Chilomys, Delomys, Juliomys, Phaenomys, Rhagomys, Rhipidomys, Thomasomys, Wiedomys, and Wilfredomys. The same analysis also indicated that the Oryzomyini is the sister taxon of the Thomasomyini. Recent molecular analyses based on cytochrome *b* (Smith and Patton, 1999) are not consistent with these results, however, additional evidence from either morphological, karyological or molecular sources are needed to refute or support the monophyly of the Thomasomyini in the sense defined above. Nonetheless, Smith and Patton (1999) and Pacheco (Part I) both recovered a monophyletic group that included Thomasomys, Aepeomys, Chilomys, and Rhipidomys. Smith and Patton (1999) labeled this group "Thomasomyini sensu stricto", while Pacheco (Part I) informally referred to it as the "Andean thomasomyine group" because the first three genera have a predominantly Andean distribution.

Within the Andean thomasomyines, the genus Aepeomys was partially revised by Ochoa et al. (2001), and its contents were delimited by Voss et al. (2002) and by Pacheco (Part I). Chilomys is currently considered to be monotypic, but a formal taxonomic revision is lacking (Musser and Carleton, 1993). Rhipidomys was revised by Tribe (1996) based on morphological characters, and a phylogenetic analysis by Smith and Patton (1999) supports the monophyly of the genus. Similarly, the genus Thomasomys was included in recent phylogenetic analyses (Steppan, 1995; Smith and Patton, 1999;

Pacheco, Part I), but a complete taxonomic revision is still awaited.

The Andean thomasomyines are a highly diverse group that constitutes one of the main components of mammalian diversity in montane forests habitats and paramos in Bolivia, Peru, Ecuador, Colombia and Venezuela. Although Musser and Carleton (1993) listed 42 species in this complex (two of Aepeomys, one of Chilomys, fourteen of Rhipidomys, and twenty five of Thomasomys), additional species have been described in the last decade. One species of Aepeomys, one species of Rhipidomys, and three species of Thomasomys have been recently named, with several other available names resurrected to species (Leo L. and Gardner, 1993; Gardner and Romo, 1993; Patton et al., 2000; Ochoa et al., 2001; Luna and Pacheco, 2002). Despite such progress, a proper understanding of the biogeographic patterns of this group along the Andes is still impeded by a lack of comprehensive taxonomic revision in a phylogenetic context. The aim of the present work is to analyze the phylogenetic relationships of the species that belongs to the Andean thomasomyine group, especially those traditionally referred to the genus Thomasomys. I intend to: 1) to provide an hypothesis of relationships among the Andean thomasomyine genera, 2) to uncover the presence of natural groups within the genus Thomasomys, and 3) to provide generic classifications for new monophyletic groups. Given the extent and phylogenetic emphasis of the present work, in-depth taxonomic revision of Thomasomys (or its members) is not presented here but will be treated in subsequent contributions.

## TAXONOMIC HISTORY

The taxonomic history of the tribe Thomasomyini was reviewed by Voss (1993), Tribe (1996), and Pacheco (Part I). An updated summary of the taxonomic history of the Andean thomasomyines is presented here.

The history of the group began with the description of Rhipidomys by Tschudi (1845). According to Tribe (1996), Rhipidomys Tschudi, 1844, is not available because the name was not accompanied by a definition or description, nor by an available species-group name.

Coues (1884) next described Thomasomys based on H[esperomys]. Rhipidomys cinereus (Thomas, 1882).

Thomas (1897) described Chilomys based on Oryzomys instans (Thomas, 1895).

Bangs (1890) reported Erioryzomys as a subgenus of Oryzomys, based on Oryzomys monochromos, but this new name was synonymized with Thomasomys by Thomas (1906), decision that has been accepted until the present time.

Thomas (1898) described Aepeomys based on Oryzomys lugens (Thomas, 1896), but this genus was considered to be a synonym of Thomasomys by Osgood (1933a) who stated that neither he nor H.E. Anthony had found morphological difference of “generic importance” between Aepeomys and Thomasomys. Osgood’s decision was followed by Ellerman (1941), Cabrera (1961), and Handley (1976). More recently, most authors have agreed in considering Aepeomys to be a valid genus (e.g. Musser and Carleton, 1993; Aguilera et al. 1994, 2000; Soriano and Ochoa, 1997; Ochoa et al., 2001; Voss et al., 2002), but see Pacheco (Part I).

Osgood (1912) described Thomasomys hylophilus and noted its similarity to T. laniger and T. monochromos.

Thomas (1917) described Inomys, the last name of generic rank in the Andean thomasomyine group based on Oryzomys incanus (Thomas, 1894).

Thomas (1920: 234) pointed out the difficulty of properly placing T. notatus in Thomasomys or Rhipidomys: "...this well marked species presents a problem of considerable difficulty; for with the general skull shape of the less typical species of genus Thomasomys, it has comparatively broad feet, showing that it is a climbing animal; and it is just the broad feet which are supposed to characterize the members of Rhipidomys, while those of Thomasomys, ... have long narrow feet."

Thomas (1921) included Thomasomys aureus, T. nicefori, T. princeps, and T. popayanus as members of an informal aureus group of Thomasomys.

Tate (1932) recognized Chilomys, Rhipidomys, Thomasomys, Inomys, and Aepeomys as valid genera.

Osgood (1933a) synonymized Inomys to Thomasomys, a decision that has been accepted until the present time.

Cabrera (1961) recognized Chilomys and Rhipidomys as valid genera, but included Aepeomys, Delomys, Erioryzomys, Inomys, and Wilfredomys within Thomasomys; all these genera were listed in the family Cricetidae.

Hooper and Musser (1964) described the morphology of the glans penis in some species of Rhipidomys and Thomasomys. They stated that phallic data appeared to support the grouping of T. cinereus, T. laniger, and R. mastacalis, to the exclusion of T. aureus. Hooper and Musser (1964: 20) remarked that phallic features shared by



Thomasomys and Rhipidomys are: "a crenate crater rim bordered by an erect narrow band of non-spinous tissue, and a long baculum (longer than glans), the base of which is shallowly concave ventrally and roughly triangular in ventral view (an apex of the triangle directed proximad)."

Carleton (1973) analyzed the stomach morphology of several thomasomyines including Chilomys instans; Rhipidomys latimanus, R. leucodactylus, R. mastacalis, and R. macconnelli; and several species of Thomasomys (aureus, baeops, cinereus, hylophilus, ischyrus, paramorum, and rhoadsi). He observed that the stomach of T. aureus departed notably from those of other Thomasomys and other thomasomyines, suggesting that aureus would be better removed from Thomasomys if additional evidence were to confirm the differences observed in the morphology of the stomach and glans penis.

Gardner and Patton (1976) described the karyotypes of Aepeomys fuscatus, Rhipidomys latimanus, and six species of Thomasomys (aureus, kalinowskii, monochromos, notatus, taczanowskii, and one unidentified species). They concluded that Aepeomys falls chromosomally within the oryzomyines. Gardner and Patton (1976: 32) postulated that thomasomyine karyotypes are characterized by a diploid number of 42 or 44, with predominance of acrocentric autosomal complement, and that non-Robertsonian arrangements characterized the Thomasomys-Rhipidomys group.

Vorontsov (1979) discussed the comparative morphology of Thomasomys.

Pine (1980) provided morphological data on new specimens of Wiedomys, Wilfredomys oenax, Juliomys pictipes, and Thomasomys pyrrhonotus.

Voss and Linzey (1981) analyzed the male accessory reproductive glands of

Chilomys instans, Thomasomys aureus, T. baeops, T. laniger, and T. rhoadsi. They found great variability in the reproductive morphology of Thomasomys, reporting the absence of preputial glans in T. laniger, one pair in T. baeops, and numerous pairs in T. aureus. They also found that species of Thomasomys exhibit differences in the relative length of the lateral and medial ventral prostate glands.

Díaz de Pascual and Péfaur (1982) described the bacular morphology of Rhipidomys venezuelae, and Aepeomys lugens from Venezuela, but provided no comments about their phylogenetic relationships.

Patton (1986) analyzed the phylogenetic relationships among Peruvian species of Thomasomys based on electrophoretic characters (24 loci). He found that T. gracilis and T. oreas are sister taxa, and this pair is close to T. notatus; and that T. daphne and T. australis are also sister taxa, and this pair close to T. aureus. He treated T. australis as a valid species.

Voss (1988: 432) listed six sympatric species of Thomasomys from Papallacta, Provincia Napo, Ecuador. He recognized T. cinnameus (previously synonymized with T. gracilis) and T. erro (previously synonymized with T. cinereiventer) as valid species.

Eisenberg (1989) included Aepeomys, Chilomys, Rhipidomys, and Thomasomys in the thomomyine group.

Patton et al. (1990) remarked that Thomasomys notatus exhibits considerable similarities in cranial structure and body proportions to T. oreas, but the electrophoretic characters he analyzed did not support a close relationships between them.

Voss (1991) reported the presence of a gall bladder in Aepeomys lugens, Chilomys instans, and eight species of Thomasomys (aureus, baeops, daphne,

hylophilus, laniger, paramorum, rhoadsi, and silvestris; but noted its absence in five species of Rhipidomys (couesi, fulviventer, leucodactylus, macconnelli, and mastacalis).

Musser and Carleton (1993) recognized 25 valid species in the genus Thomasomys: aureus (including altorum, nicefori, popayanus, praetor, and princeps as synonyms), baeops, bombycinus, cinereiventer (including contradictus, dispar, and erro as synonyms), cinereus (including caudivarius as synonym), daphne (including australis as synonym), eleusis, gracilis (including cinnameus and hudsoni as synonyms), hylophilus, incanus (including fraternus as synonym), ischyrus, kalinowskii, ladewi, laniger (including emeritus as synonym), monochromos, niveipes, notatus, oreas, paramorum, pyrrhonotus (including auricularis as synonym), rhoadsi (including fumeus as synonym) rosalinda, silvestris, taczanowskii, and vestitus.

Leo L. and Gardner (1993) described Thomasomys apeco, the largest known thomatomyine. They recognized Thomasomys princeps (Thomas, 1900) as a valid species, and member of the Thomasomys aureus complex.

Gardner and Romo R. (1993) described Thomasomys macrotis and suggested that it resembles T. ischyrus and T. incanus. Based on dental and cranial morphology, they hypothesized that T. macrotis is closely relationship to T. ischyrus. They also referred to Thomasomys aureus as comprising a complex of three or more morphologically similar species.

Smith and Patton (1993) analyzed the phylogenetic relationships of 8 genera and 28 species of akodontines, based on cytochrome b sequences. They included exemplars of the tribes Oryzomyini, Phyllotini, and Thomatomyini as outgroups. Their results suggested that Rhipidomys leucodactylus and Thomasomys aureus (the only

thomasomyines included in this study) are sister taxa.

Voss (1993) reviewed the genus Delomys and provided updated information on the morphology of Thomasomys cinereus, the type species of the genus Thomasomys.

Aguilera et al. (1994) described the karyotype of an unidentified species of Aepeomys. The reported karyotype ( $2n = 44$ ) is similar to those previously reported for Thomasomys by Gardner and Patton (1976).

Steppan (1995) analyzed the phylogenetic relationships of the sigmodontine rodents and concluded that the tribe Thomasomyini and the genus Thomasomys are paraphyletic. His analytical terminals included only five thomasomyines (Thomasomys aureus, T. baeops, T. rhoadsi, Rhipidomys latimanus, and Chilomys instans). He concluded that the monophyly of the genus Thomasomys is not supported because T. rhoadsi was consistently placed either with ichthyomyines or at the base of a clade comprising the remaining non-thomasomyine rodents in his analysis. He also found that Rhipidomys latimanus might be the sister taxon of a clade comprising T. aureus and T. baeops.

Tribe (1996) doubted the sister relationship of Rhipidomys and Thomasomys aureus previously suggested by Smith and Patton (1993) and Steppan (1995). He explicitly excluded Thomasomys notatus from the genus Rhipidomys, but recognized that the definition and membership of Rhipidomys are to some extent provisional pending a revision of the genus Thomasomys.

Gómez-Laverde et al. (1997) provided detailed morphological comparisons to distinguish Thomasomys niveipes from T. laniger. They also described the chromosomes of T. niveipes ( $2n = 24$ ,  $FN = 42$ ), the first thomasomyine with a karyotype different

from the standard formula of  $2n = 42, 44$  reported for the genus Thomasomys by Gardner and Patton (1976).

Bonvicino and Otazu (1999) found that karyotype of Wilfredomys pictipes is more similar to those of Rhipidomys than to those of Delomys or any species of the tribe Oryzomyini.

Smith and Patton (1999) presented a phylogeny of the Sigmodontinae based on sequences of the mitochondrial cytochrome *b* gene. They recognized the Thomasomyini as a monophyletic group that includes Aepeomys, Chilomys, Rhipidomys, and Thomasomys. Aepeomys was not included in their analysis, but membership within the Thomasomyini was suggested based on its Andean distribution. Their cladograms depicted a close relationship between Chilomys and Thomasomys, followed by Rhipidomys.

Tirira (1999) listed Thomasomys auricularis, T. caudivarius, and T. erro as valid species citing Pacheco (pers. comm.).

Aguilera et al. (2000) described the karyotypes of Aepeomys lugens, Aepeomys sp., Thomasomys laniger and T. vestitus from Venezuela, and concluded that Thomasomys and Aepeomys are closely related taxa.

Patton et al. (2000: 162) described Rhipidomys gardneri from Departamento de Madre de Dios, Peru, and Acre, Brazil; and provided morphological and karyotype comparisons with R. leucodactylus.

Ochoa et al. (2001) described Aepeomys reigi from the Andean region of Venezuela (Lara and Trujillo states), and provided morphological and karyotypic comparisons with A. lugens and several species of Thomasomys. They presented a case

in which two morphological similar taxa differ extensively in karyotypic characters ( $2N=28$ ,  $FN=48$  in A. lugens versus the  $2N=44$ ,  $FN=46$  in A. reigi). They postulated that the karyological differences between the two species could be largely explained by Robertsonian changes, and hypothesized that the karyotype of A. lugens is more derived than that of A. reigi.

Voss et al. (2001: 125) reviewed the taxonomic status of Rhipidomys nitela, and noted that the material previously identified as R. nitela from eastern Bolivia (Anderson, 1997) is referable to the genus Thomasomys.

Luna and Pacheco (2002) described Thomasomys onkiro from southeastern Peru, noting its close resemblance to T. silvestris from western Ecuador. They advocated recognizing T. caudivarius as a valid species.

Voss et al. (2002) erected the new genus Handleyomys for the taxon originally described as Aepeomys fuscatus Allen (1912) and Oryzomys intectus Thomas, 1921. They restricted the content of Aepeomys to lugens and reigi, referring vulcani Thomas (1898) to Thomasomys. Among the taxonomic comparisons they discussed salient external, cranial, dental and visceral characters of Aepeomys were tabulated.

Pacheco (Part I) analyzed the phylogenetic relationships of thomatomyines based on morphological characters concluding that the tribe Thomasomyini is monophyletic. According to him, the Thomasomyini includes: Abrawayaomys, Aepeomys, Chilomys, Delomys, Juliomys, Phaenomys, Rhagomys, Rhipidomys, Thomasomys (including Erioryzomys, and Inomys), Wiedomys, and Wilfredomys. He synonymized the tribe Wiedomyini Reig, 1980 with Thomasomyini. Within this group, the Andean thomatomyines comprised a natural group that include Aepeomys, Chilomys,

Rhipidomys, and Thomasomys. In addition, he concluded that Aepeomys and T. erro form a monophyletic group, and both nested within a clade of Thomasomys. The monophyly of Thomasomys and Rhipidomys were not supported.

## SYNOPSIS

### Aepeomys Thomas, 1898

The genus Aepeomys is here interpreted as consisting two species: A. lugens and A. reigi following Ochoa et al. (2001), and Voss et al. (2002). A. reigi is known from the Venezuelan states of Lara and Trujillo, at elevations from 1600-3230 m. It is a relatively uncommon species, and has been collected in densely forested sites or in open areas close to the páramo-forest ecotone. Remains of coleoptera were found in the stomach of one specimen, but others were fed in captivity with Orthoptera, domestic fruits and seeds (Ochoa et al., 2001). The second species, A. lugens is known from the Venezuelan states of Mérida and Táchira from 1990 to 3200 m. Voss et al. (2002) indicated that records from Colombia previously reported by Cuervo Díaz et al. (1986) and Alberico et al. (2000) are likely based on misidentified specimens. Most recent authors have considered Aepeomys a valid genus, including Musser and Carleton (1993), Aguilera et al. (1994), Soriano and Ochoa (1997), Ochoa et al. (2001) and Voss et al. (2002). However, Pacheco (Part I) found that Aepeomys lugens appears to be closely related to T. erro, and suggested that Aepeomys and Thomasomys might not be reciprocally monophyletic groups.

### Chilomys Thomas, 1897

The genus Chilomys is currently regarded monotypic with C. instans as the single

valid species (Musser and Carleton, 1993). They included fumeus as a synonym of instans. However, I consider C. fumeus a valid species following Osgood (1912), and morphological evidence presented in this paper. Chilomys has an extensive distribution from the Venezuelan states of Mérida and Táchira (Handley, 1976) to central Ecuador, and from 1120 to 3399 m (Musser et al., 1998: 108).

#### Rhipidomys Tschudi, 1845

This genus was recently revised by Tribe (1996) but generic monophyly has yet to be demonstrated. Tribe recognized three main divisions or sections in the genus. The R. fulviventer section (with fulviventer, wetzeli, caucensis and ochrogaster), the R. macconnelli section (macconnelli), and the R. leucodactylus section (couesi, leucodactylus, modicus, austrinus, latimanus [including venezuelae], nitela, emiliae, macrurus, mastacalis, and four unnamed taxa). Rhipidomys has a very broad distribution from eastern Panamá throughout Amazonia to southeastern Brazil and northern Argentina. Whereas Tribe's first two sections have predominantly montane distributions, his leucodactylus section occurs mainly at lower elevations. Rhipidomys gardneri remains to be explicitly assigned to one of Tribe's sections.

#### Thomasomys Coues, 1884

Based on the literature summarized above, the following taxa are recognized as valid species of Thomasomys: apeco, aureus (including altorum, nicefori, popayanus, praetor, and princeps as synonyms), auricularis, australis, baeops, bombycinus, caudivarius, cinereiventer (including contradictus and dispar as synonyms), cinereus, daphne, eleusis, erro, gracilis (including hudsoni as synonym), hylophilus, incanus (including fraternus as synonym), ischyrus, kalinowskii, ladewi, laniger (including



emeritus as synonym), macrotis, monochromos, niveipes, notatus, onkiro, oreas, paramorum, pyrrhonotus, rhoadi (including fumeus as synonym) rosalinda, silvestris, taczanowskii, and vestitus based on Voss (1988), Gardner and Romo R. (1993), Leo L. and Gardner (1993), Musser and Carleton (1993), Tirira S. (1999), and Luna and Pacheco (2002). The genus is distributed from Venezuela to southeastern Bolivia along the Andes, from about 1000 m to above 4000 m. It is restricted to premontane, cloud and elfin forest on the eastern and western Andean Cordillera, and contributes a major percentage of the diversity and endemism of montane forest mammal fauna (Pacheco, 2002). Fossil material of Thomasomys cf. aureus, and Thomasomys cf. baeops has been reported from the late Pleistocene-Holocene of northern Ecuador (Fejfar et al., 1993).

## MATERIALS AND METHODS

**Ingroup taxonomic sampling:** I consider the Andean thomasomyine group of the tribe Thomasomyini (sensu Pacheco, Part I) as my ingroup, which consists of species currently assigned to the genera of Aepeomys, Chilomys, Rhipidomys and Thomasomys. The monophyly of this cluster is consistent with the karyological data (Gardner and Patton, 1976; Aguilera et al., 2000; Ochoa et al., 2001), cytochrome *b* sequence analyses (Smith and Patton, 1999), and morphological data analysed by (Pacheco, Part I).

The ingroup terminals included in my analysis include all the species of Thomasomys currently recognized as valid (see synopsis, above) together with eleven unnamed forms and other taxa that are currently treated as synonyms or subspecies: contradictus, dispar, emeritus, fumeus, hudsoni, nicefori, popayanus, praetor and princeps. From the genus Aepeomys, the species A. lugens and A. reigi are included. From the genus Chilomys I include not only C. instans but also fumeus Osgood, 1912 (currently regarded as a synonym or subspecies). From the genus Rhipidomys, I include exemplars of Tribe's fulviventer group (R. caucensis, R. fulviventer), macconnelli group (R. macconnelli), and leucodactylus group (R. latimanus, R. leucodactylus, R. ochrogaster), together with the unclassified species R. gardneri. In total, 64 ingroup taxa are analyzed herein ( see Appendix 1).

**Outgroup selection:** Based on the phylogenetic results presented by Pacheco (Part I) other thomasomyine genera (those from southeastern Brazil) are employed as outgroups. These include Abrawayaomys ruschii, Delomys collinus and D. sublineatus, Juliomys pictipes and Juliomys sp., Phaenomys ferrugineus, Rhagomys rufescens and R.

longilingua, Wilfredomys oenax, and Wiedomys pyrrhorhinus. In addition, six oryzomyine species are included as more distant outgroups (Handleymys fuscatus, Holochilus brasiliensis, Microryzomys minutus, Oecomys bicolor, Oligoryzomys fulvescens, and Oryzomys palustris), based on the hypothesis that Oryzomyini is the sister group of the Thomasomyini (Pacheco, Part I). All outgroup species analyzed are listed in Appendix 1.

**Characters:** A data matrix of 80 taxa (64 ingroup and 16 outgroup terminals) and 145 morphological characters was constructed. This included 27 characters of the integument, 51 characters of the skull, 3 characters of the middle ear bones, 33 dental characters, 8 characters of the mandible, 6 characters of the postcranial skeleton, 4 characters of the digestive system, and 13 characters of the glans penis and male accessory reproductive glands (Appendix 2). The data matrix was constructed using the program MacClade, version 4.0 (Maddison and Maddison, 1992). In total, 86 characters were binary and 59 multistate. The multistate characters include 43 characters with three states, 15 with four states and 1 with five states.

Multistate characters were treated as ordered (unless noted) based on Wilkinson's (1992, 1995) method of intermediates. If one character state is intermediate in form, size, or number between two other character states then it is hypothesized to represent a phylogenetic intermediate between the other states (e.g. small, medium, and large tail; 12, 13 or 14 thoracic vertebrae). In one multistate character (with character states 0 -1 -2 -3), only one step is needed for character state "0" to change to a character state "3" when the states are unordered; however, the same change requires three steps assuming that changes occur through the intermediate states. Recent phylogenetic analysis of muroids were

produced with multistate characters ordered (Carleton, 1980; Steppan, 1995; Voss and Carleton, 1993; and Pacheco [Part I]) assuming this strategy retains most of the information and homology. Pacheco [Part I] found few differences between separate analyses of unordered and ordered multistate characters. In this work, the multistate characters were ordered because a large suite of characters are binary.

Most of the characters were observed and scored by myself throughout all taxa. However, I relied on the literature for some characters or species as cited below. External characters were observed under a stereo microscope from fluid specimens when available, or skins otherwise. For the evaluation of skulls, teeth, and mandibles, at least ten specimens for each species were examined when available. For some characters, the organs (stomach, reproductive tracts, glans penis, and gall bladder) were dissected from alcoholic specimens without any special preparation or staining.

Missing data were registered in the matrix as "?" or "-". The first symbol was used for data cells that were not evaluated due to lack of suitable material, and the latter for inapplicable characters. Two kinds of polymorphism were employed: taxonomic polymorphism, when a terminal taxon has more than one state and is likely representing a complex of taxa; and, within-species polymorphism, when a terminal taxon unequivocally recognized as a single species exhibit variability in a character (Simmons, 1993).

Alphabetic ambiguity codes are used to identify taxonomic polymorphisms in the data matrix (Appendix 2), but additional states are employed to represent cases of within-species polymorphism; this method retains more information than scoring a polymorphism as missing data (Simmons, 1993). I assume all within-species polymorphism were treated as intermediate to the fixed states. Several "species" of

Thomasomys probably include two or more morphological similar taxa. These cases of polymorphism are explained in the character accounts that follow.

**Phylogenetic analysis:** All analyses were produced with a beta version of PAUP 4.0b10 (Swofford, 1998) using routines identical to those employed by Pacheco (Part I). Briefly, the heuristic search option was employed and all characters were ordered and weighted equally, with the algorithm TBR (tree-bisection-reconnection) for branch-swapping, multrees and collapse tree options in effect; simple-addition sequence and random-addition sequence with 1000 repetitions. The most parsimonious trees found were subjected to strict consensus methods to summarize all information of unequivocal relationships. Non-parametric bootstrap analysis (1000 replications, each with ten random-addition iterations, and the same search strategies employed for the heuristic search) was employed to assess evidential support (Felsenstein, 1985). In addition, decay values were obtained following the method outlined by Bremer (1988).

In addition, alternative hypotheses were evaluated by searching for the most parsimonious trees consistent with a specified constraint. The most-parsimonious constraint trees produced were combined in a strict consensus cladogram and the length tree was compared with the most parsimonious cladogram. These hypotheses were evaluated searching with the same strategies outlined above except that 100 replications were considered sufficient.

## MORPHOLOGICAL CHARACTER SETS

### EXTERNAL MORPHOLOGY

#### 1. Ungual tufts on manual claws: *Present (0); or absent (1).*

In most thomasomyines, the claws of the manus are covered dorsally by a basal tuft of long silvery hairs. In some species, however, only a few short hairs are present, which do not cover the claws. Ungual tufts are absent in Aepeomys, a few Thomasomys (e.g., Thomasomys erro, T. fumeus, T. incanus, T. notatus, T. rhoadsi), Rhipidomys (except R. fulviventer, and R. macconnelli), and some outgroup taxa (Holochilus, Oryzomys and Wiedomys). This feature appears to be independent from the ungual tufts that occur at the base of pedal claws (present in all thomasomyines).

**2. Ventral base of claws on manus:** *Base of claws open (0); or margins of claws closed at base (1); or medially keeled (2).*

Steppan (1995: character 85P) scored this morphological trait in his analysis of phyllotines. The claws are open in Rhipidomys (except R. caucensis and R. latimanus), Thomasomys notatus, and T. taczanowskii; and also in Holochilus, Juliomys, Oecomys, and Wilfredomys. Claws are closed basally in Chilomys, Rhipidomys caucensis, R. latimanus, several species of Thomasomys, and some outgroup taxa (Abrawayaomys ruschii, Handleyomys fuscatus, Microryzomys minutus, and Wiedomys pyrrhorhinos). Claws are medially keeled in Aepeomys, T. cinnameus, T. eleusis, T. erro, T. fumeus, T. incanus, T. ischyryrus, T. kalinowskii, T. ladewi, T. macrotis, T. niveipes, T. rhoadsi, Thomasomys sp. 6, Thomasomys sp. 7, and Thomasomys sp. 10.

#### 3. Manual digit proportions: *Second digit distinctly longer than fifth (0); or*

*second and fifth digits subequal (1).*

The widespread condition in muroid rodents is that the second digit of the manus (without claws) is distinctly longer than the fifth. In a few species, however, the second and fifth digits are subequal (Pacheco, Part I: fig. 1). This condition (state 1) is seen in Rhipidomys caucensis, R. fulviventer, R. latimanus, Thomasomys baeops, T. gracilis, T. notatus, T. oreas, T. taczanowskii, Thomasomys sp. 8, Thomasomys sp. 9, and some outgroup taxa (Oecomys bicolor, Rhagomys rufescens and R. longilingua).

**4. Ungual tuft on pes:** *Present on all digits (0); or present on all digits except in dl (1); or absent in all digits (2).*

As described by Pacheco (Part I: character 3), the pedal claws are usually covered by a basal tuft of long silvery hairs that conspicuously exceeds the length of claws on all digits. The first digit or hallux (dl) lacks a distinct tuft in some Andean thomomyines, including Aepeomys lugens, Thomasomys fumeus, T. rhoadsi, Thomasomys sp. 6, Thomasomys sp. 7, and Thomasomys sp. 10. Ungual tufts are absent on all pedal digits in some outgroup taxa (oryzomyines) and Rhipidomys leucodactylus.

**5. Dark metatarsal patches:** *Absent (0); or present (1).*

Dark patches of densely melanized hairs on the dorsal metatarsus, where they contrast with the paler coloration of the ankle, digits and lateral margins of the pes. Dorsal metatarsal patches occur in Thomasomys aureus, T. baeops, T. gracilis, T. notatus, T. oreas, T. princeps, Thomasomys sp. 1, Thomasomys sp. 2, Thomasomys sp. 8, Thomasomys sp. 9, and in all examined species of Rhipidomys.

**6. Plantar squamation of pes:** *Sole of hind foot smooth to indistinctly squamated (0); or distinctly squamated (1).*

As described by Pacheco (Part I: character 6), the plantar surface of the muroid hindfoot can be either smooth or distinctly squamated (Carleton and Musser, 1989: fig 9). To facilitate taxonomic comparisons, only the central plantar region (between the plantar pads) was evaluated. A distinctly squamated pes is present in oryzomyines (except Handleyomys) and southeastern Brazilian thomatomyines (except Juliomys sp., Rhagomys rufescens, and R. longilingua). All other taxa examined for this analysis have smooth or indistinctly squamated hindfeet.

**7. Hypothenar pad of pes:** *Present and well developed (0); or greatly reduced or absent (1).*

The plantar surface of the pes of most rodents is provided with two metatarsal (thenar and hypothenar) pads, and four interdigital pads, all of them usually distinct (and in some genera even swollen). However, the hypothenar (lateral metatarsal) pad is absent or greatly reduced in Holochilus brasiliensis and Oryzomys palustris (see Carleton and Musser, 1989: fig. 9A).

**8. Position of hypothenar pad in relation to thenar (pes):** *Gap between hypothenar and thenar pads (0); or polymorphic, with or without gap (1); or gap absent, the hypothenar and thenar pads level or overlap (2).*

The thenar and hypothenar pads are conspicuous epidermal protuberances on the plantar surface of the metatarsus, of which the thenar is placed proximal and medial and the hypothenar is distal and lateral (fig. 1). A gap occurs between these pads in Aepeomys, Chilomys, Rhipidomys macconnelli, Thomasomys australis, T. bombycinus, T. caudivarius, T. cinnameus, T. contradictus, T. dispar, T. eleusis, T. emeritus, T. erro, T. fumeus, T. hudsoni, T. hylophilus, T. incanus, T. ischyryus, T. kalinowskii, T. ladewi,



T. laniger, T. macrotis, T. monochromos, T. paramorum, T. praetor, T. pyrrhonotus, T. rhoadsi, T. silvestris, Thomasomys sp. 2, Thomasomys sp. 4, Thomasomys sp. 5, Thomasomys sp. 6, Thomasomys sp. 7, Thomasomys sp. 10, and in some outgroup taxa (Handleyomys fuscatus, Microryzomys minutus, Oligoryzomys fulvescens, Delomys sublineatus, Phaenomys ferrugineus, Wiedomys pyrrhorhinos, and Wilfredomys oenax). State 2 (no gap) is observed in all Rhipidomys (except R. macconnelli), and several species of Thomasomys (e.g., T. apeco, T. aureus, T. auricularis, T. australis, T. baeops, T. cinereiventer, T. cinnameus, T. daphne, T. gracilis, T. hylophilus, T. incanus, T. nicefori, T. notatus, T. onkiro, T. oreas, T. paramorum, T. popayanus, T. praetor, T. princeps, T. pyrrhonotus, T. rosalinga, T. taczanowskii, and T. vestitus), and the outgroups (Oecomys bicolor, Abrawayaomys ruschii, Delomys collinus, Juliomys, Rhagomys rufescens, and R. longilingua). Within-species polymorphism is exhibited by Thomasomys baeops, T. bombycinus, T. cinereus, T. niveipes, and Thomasomys sp. 1.

**9. Position of hypothenar pad in relation to interdigital pad 4 (pes):** *Gap present between hypothenar and interdigital pad 4 (0); or gap absent, the hypothenar pad level with the interdigital pad 4 or both overlap (1).*

The hypothenar pad is placed in the distal metatarsal region between the thenar and the interdigital pads. A distinct gap between the hypothenar pad and the fourth interdigital pad is the common condition (fig. 1c); however, state 1 is exhibited by all examined species of Rhipidomys (fig. 1a).

**10. Position of hypothenar pad in relation to interdigital pad 1 (pes):** *Gap present between hypothenar and interdigital pad 1 (0); or gap absent, the hypothenar pad level with or overlapping interdigital pad 1 (1).*

This character was first described by Stepan (1995: character 87P) in his analysis of phyllotine relationships. Most ingroup exhibit state 1, but thomatomyines from southeastern Brazil (except Delomys and Wiedomys) exhibit a distinct gap between both pads (state 0).

**11. Interdigital webbing on hindfoot:** *Absent (0); or present (1).*

As defined by Voss (1988), Voss and Carleton (1993), and Pacheco (Part I), the interdigital webbing is completely absent in thomatomyines. As noted by Voss and Carleton (1993), some small interdigital membranes that are merely the tissue left between digits may be confused with this feature. Well developed interdigital webbing is only present in some oryzomyines (Holochilus brasiliensis and Oryzomys palustris).

**12. Nail on hallux:** *absent (0); or present (1).*

The hallux of sigmodontine rodents typically bears a sharp. By contrast, Rhagomys rufescens and R. longilingua exhibit a halluctal nail as described by Luna and Patterson (2003).

**13. Relative size of hallux (dl of pes):** *Short, first phalange (p1) of hallux not extending beyond metatarsal of dII, halluctal claw not extending more than about half the length of p1 of dII (0); or moderately long, halluctal claw not extending to first interphalangeal joint of dII (1); or long, halluctal claw extending to first interphalangeal joint of dII or beyond (2).*

This character was described by Pacheco (Part I: character 103). A short hallux (state 0) is seen in several groups, but is uniformly present in Aepeomys, some species of Thomasomys (e.g., T. bombycinus, T. cinereiventer, T. contradictor, T. dispar, T. erro, and T. fumeus), and the outgroups Abrawayaomys, Delomys, Handleyomys, Holochilus,

and Oryzomys. A long hallux (state 2) is seen in Rhipidomys, a few species of Thomasomys such as T. apoco, T. aureus, T. auricularis, T. baops, T. cinereus, T. gracilis, T. nicefori, T. notatus, T. oreas, T. popayanus, T. praetor, T. princeps, T. pyrrhonotus, T. rosalinda, T. taczanowskii, Thomasomys sp. 1, Thomasomys sp. 2, Thomasomys sp. 8 and Thomasomys sp. 9; and in the outgroups Phaenomys and Rhagomys longilingua. A moderately long hallux (state 1) is present in Chilomys, the remaining species of Thomasomys, and in the outgroups Juliomys, Rhagomys rufescens, Wiedomys, and Wilfredomys.

**14. Relative size of fifth digit (dV) of pes:** *Short, claw of dV not extending to first interphalangeal joint of dIV (0); or moderately long, claw of dV extending to but not beyond first interphalangeal joint of dIV (1); or long, claw of dV extending about half the length of p2 of dIV (2); or very long, claw of dV extending to the base of claw of dIV, or beyond (3).*

As described in Pacheco (Part I: character 104) the muroid fifth digit exhibits considerable variation in length relative to the adjacent fourth digit. The state 1 is only exhibited in Aepeomys, Thomasomys dispar, T. erro, and Thomasomys sp. 4; while, the states 2 and 3 are the most common conditions among Andean thomasomyines. State 2 is exhibited in several species of Thomasomys (e.g., T. caudivarius, T. cinereiventer, T. cinereus, T. incanus, T. laniger, T. macrotis) and the outgroups Microryzomys, Oecomys, Juliomys sp., Phaenomys, Rhagomys, and Wilfredomys. The state 3 is seen in all species of Rhipidomys and some species of Thomasomys (e.g., T. aureus, T. baops, T. cinnameus, T. gracilis, T. notatus). The state 0 is exhibited only in a few outgroups (e.g., Sigmodon, Handleyomys, Holochilus, Oryzomys, and Abrawayaomys). Taxonomic

polymorphism (states 2 and 3) is observed only in Chilomys.

**15. Genal 1 vibrissae:** *Absent (0); or polymorphism, either present or absent (1); or present(2).*

As first reported by Pacheco (Part I: character 8), both of the two kinds of genal vibrissae (Brown, 1971; Brown and Yalden, 1973) are present in Neotropical muroids. Genal 1 vibrissae are present (state 2) in all species in the outgroup, Chilomys, Rhipidomys (except R. ochrogaster), T. gracilis, T. notatus, T. oreas, T. taczanowskii, and the aureus group of Thomasomys (see Appendix 2). The within-species polymorphism (state 1) is present in Rhipidomys ochrogaster and some populations of Thomasomys baeops and T. cinereus. Taxonomic polymorphism is exhibited in T. baeops, T. cinereus, and T. cinnamomeus. All remaining species of Thomasomys (e.g., T. caudivarius, T. erro, T. incanus, T. laniger, T. paramorum, T. rhoadsi) uniformly lack the genal 1 vibrissae.

**16. Genal 2 vibrissae:** *Present (0); or absent (1).*

Genal 2 vibrissae, consisting of a long and stiff hair on each cheek ventral to genal 1 and close to the lateral line that divides the dorsal from the ventral pelage coloration, was first reported to occur in muroids by Pacheco (Part I: character 9). Genal 2 vibrissae are completely absent in the ingroup, and in most species of the outgroup, with the exception of Oecomys, Abrawayaomys and Phaenomys.

**17. Length of mystacial vibrissae:** *Mystacials short, not extending to the posterior margin of the pinna (0); or moderately long, extending slightly beyond the posterior margin of pinnae to a point less half the length of pinna (1); or very long, extending well beyond the posterior margin of pinnae to a point greater than the length of*

*one pinna (2).*

Short mystacials (state 0) are exhibited only in Aepeomys and the outgroup Holochilus. The genus Chilomys and most species of Thomasomys (e.g., T. cinereus, T. erro, T. incanus, T. rhoadsi) present moderately long mystacials (state 1). Rhipidomys species (except R. gardneri) and some species of Thomasomys (e.g., T. aureus, T. baeops, T. laniger, T. oreas) exhibit very long vibrissae (state 2). All outgroup species exhibit the state 1, with the exception of Juliomys and Phaenomys that have the state 2, and Holochilus that exhibit the state 0.

**18. Antitragus and pinnae structure:** *Broad (0); or narrow to moderate size (1).*

The antitragus is an internal eminence of the pinnae that extends from the intertragal notch posteriorly and medially (Brown, 1971). Broad antitragus (state 0) is exhibited in some species of Thomasomys (e.g., T. aureus, T. daphne, T. gracilis, T. laniger, T. paramorum), and all outgroup taxa with the exception of Oecomys, Abrawayaomys, and Juliomys pictipes. In the ingroup, the genera Aepeomys, Chilomys, Rhipidomys and several species of Thomasomys (e.g., T. caudivarius, T. cinereus, T. erro, T. incanus, T. ladewi, T. rhoadsi, T. silvestris, T. vestitus) exhibit the state 1.

**19. Rostral fur coloration:** *Rostral fur brownish or grayish, not contrasting with color of cheeks and crown (0); or rostral fur reddish, sharply contrasting with color of cheeks and crown (1).*

This feature was previously described by Osgood (1933b), Hershkovitz (1959), and (Pine, 1980); and used by Pacheco (Part I: character 16) in his thomatomyine phylogeny. The rostral fur coloration is similar to that of the cheeks and crown in most

muroids. However, in Wiedomys, Wilfredomys, and Juliomys, the rostral fur (immediately surrounding the rhinarium) is distinctly reddish, a resemblance that Pine (1980) attributed to convergence. This contrasting coloration was called “pirrorrino” by Avila-Pires (1960), or “pyrrhorhine” by Osgood (1933b).

**20. Body pelage pattern:** *Indistinctly or not countershaded (0); or moderately countershaded (1); or distinctly countershaded (2).*

This character follows the scoring scheme developed by Steppan (1995: character 91P) in his phyllotine analysis except that I have added an intermediate state. The pelage pattern of most thomasomyines is monocolored, in which the ventral pelage is uniformly dull and only slightly paler than the dorsal fur, as seen in Aepeomys, Chilomys, some species of Thomasomys (e.g. T. daphne, T. erro, T. hylophilus, T. silvestris), and the outgroups Microryzomys and Rhagomys rufescens. A moderately countershaded condition in which the ventral pelage is paler than dorsal but not sharply demarcated (state 1) is seen in Rhipidomys leucodactylus, R. macconnelli, R. ochrogaster, and several species of Thomasomys (e.g., T. aureus, T. baeops, T. cinereus). By contrast, a conspicuous line of demarcation that sharply distinguish the dorsal from the ventral pelage (state 2) is exhibited by Rhipidomys caucensis, R. fulviventer, R. latimanus, R. gardneri, Thomasomys notatus, T. pyrrhonotus, Holochilus, Oecomys, Oryzomys, and most southeastern Brazilian thomasomyines with the exception of Rhagomys rufescens (with state 0) and Abrawayaomys (with state 1).

**21. Pelage texture:** *Pelage soft, without spines (0); or pelage spiny (1).*

The widespread condition among thomasomyines is a soft, spineless pelage, but Abrawayaomys that has spiny fur. Luna and Patterson (2003) recently reported a spiny

fur in Rhagomys longilingua.

**22. Pectoral markings:** *Absent (0); or present (1).*

Pectoral markings are absent in outgroup taxa and most thomasomyines.

However, a colourful (reddish, buffy, grayish-brown, etc. depending on the species) streak of hairs that contrast with the ventral pelage is seen in Thomasomys apeco, T. auricularis, T. ladewi, T. praetor, T. pyrrhonotus, and T. rosalinda.

**23. Pectoral mammary pair:** *Absent (0); or present (1).*

Described by Pacheco (Part I: character 13) as the Pectoral I mammae. These teats are here described simply as “pectoral” because other pectoral types are absent in all sigmodontine rodents. Pacheco (Part I) showed that besides the inguinal, abdominal and thoracic mammary pairs (present in all sigmodontine rodents), several oryzomyines and most Brazilian thomasomyines have pectoral mammae (except Delomys collinus, and Rhagomys rufescens). As documented herein, pectoral mammae pair are absent in all ingroup taxa (Aepeomys, Chilomys, Rhipidomys, and Thomasomys). The pectoral mammae are also absent in Rhagomys longilingua (see Luna and Patterson, 2003).

**24. Protuberant anus:** *Anus a simple orifice flush with the inguinal surface, not protuberant (0); or anus slightly protuberant, usually half the size of the male or female prepuce (1); or anus conspicuously protuberant, usually approaching the size of the prepuce or larger (2).*

The anal orifice of most Andean thomasomyines is contained in a moderate to large fleshy protuberance at the base of the tail (fig. 2). This feature was first observed and described by S. N. Rhoads in his field description of Thomasomys rhoadsi: “... all of them, or possible only the males, were supplied with a remarkable prolongation of the

anus, that organ being extended, or rather extensible, beyond the thighs for half an inch or more, ... This prolongation was not an internal extension, but external, being hairy throughout.” (Stone, 1914: 13). When present, a protuberant anus is exhibited by adult males and females alike (without apparent sexual dimorphism), although it may be less apparent in mature males with distended testes. For obvious reasons, this feature is better scored from alcoholic specimens than from dried skins. A large protuberant anus is present in Aepeomys and most species of Thomasomys. State 1 is observed in Chilomys, Rhipidomys, Thomasomys baeops, T. notatus, T. oreas, and T. taczanowskii. By contrast, all outgroup taxa (oryzomyines and Atlantic thomasomyines) lack a protuberant anus (state 0).

**25. Countershading of tail:** *Tail monocolored or indistinctly bicolored (0); or distinctly bicolor (1).*

This feature was employed by Stepan (1995: character 89P) for his phyllotine phylogenetic analyses. Most species of the Andean thomasomyine group are characterized by a monocolored or indistinctly bicolored tail (state 0). By contrast, a distinctly bicolored tail, in which a dark dorsal surface sharply contrast with a pale ventral surface (state 1) is seen only in Rhipidomys latimanus, R. macconnelli, Thomasomys sp. 4; and several species of the outgroup (e.g., Oecomys, Oligoryzomys, Oryzomys, Delomys, Juliomys, and Wilfredomys).

**26. Uniform pattern coloration of tail:** *Uniform coloration from the base to the tip of the tail (0); or polymorphic, either uniform or with the tip white (1) or tip of tail consistently white (2); or more than 1/3 of the tail white (3).*

Most muroid tails are uniformly colored from base to tip (state 0), but some



species (e.g., Rhipidomys latimanus and Thomasomys baeops) are polymorphically marked with white tail tips (state 1). Other ingroup species (e.g., Chilomys, T. caudivarius, T. daphne, T. hylophilus) and also the outgroup Abrawayaomys have consistently white-tipped tails (state 2). Thomasomys apeco and T. macrotis, two of the largest species in the subfamily Sigmodontinae, have a long white distal tail marking (state 3). Taxonomic polymorphism is present in Thomasomys erro, T. hudsoni, and T. paramorum.

**27. Tail pencil:** *Absent or short (0); or present when a small tuft of long hairs, extends beyond the tail tip at a point more than 10 row of scales (1).*

My scoring for this character follows the state definition of Pacheco (Part I: character 17). Tribe (1996) considered that a distinct tail tuft or pencil of long hairs is sufficient to recognize Rhipidomys from other sigmodontines. However, a lack of distinct pencil of long hairs was reported in R. gardneri (Patton et al., 2000) and in R. venezuelae (Voss, 2002). No other thomomyines, except Thomasomys erro, T. notatus, and Abrawayaomys exhibit a distinct tail pencil. Although, the tail pencil of these thomomyines are less developed than in most Rhipidomys, it falls with my definition of a distinct tail pencil.

## SKULL

**28. Rostral tube:** *Absent (0); or moderately developed (1); or present and distinct (2).*

Voss (1993) described a rostral tube (formed by an extended suture between the premaxillae and nasal bones anterodorsal to the incisors) as present in Delomys but

absent in Thomasomys cinereus and Oryzomys palustris. Later, Pacheco (Part I: character 18) defined a rostral tube as when the premaxillae extend anteriorly to a point beyond the depth of the upper incisors. A distinct rostral tube (state 2) is present in Aepeomys, some species of Thomasomys (e.g. T. dispar, T. erro, T. hudsoni, T. incanus, T. ischyrys), and also in Delomys. In the context of this analysis, an intermediate state is raised (state 1) is used to describe the condition where the premaxillae extend anteriorly beyond the incisors by not more than the depth of the incisors; this condition is seen in Thomasomys bombycinus, T. caudivarius, T. cinereiventer, T. contradictor, T. eleusis, T. gracilis, T. niveipes, T. paramorum, and T. silvestris. A rostral tube is absent in Chilomys, Rhipidomys, most Thomasomys; and most outgroups (oryzomyines and southeastern Brazilian thomasomyines, except Delomys).

**29. Posterior extension of nasals:** *Nasals long, extending posteriorly to the maxillary-frontal-lacrimal intersection (0); or polymorphic, either long or short (1); or short, not extending to the maxillary-frontal-lacrimal intersection (2).*

Following Steppan (1995, character 9S) and Pacheco (Part I: character 19), nasal length can be defined in relation to the intersection of the maxillary, frontal, and lacrimal sutures on the dorsal surface of rostrum. Long nasals (state 0) is exhibited in Rhipidomys fulviventer, R. ochrogaster, a few of Thomasomys (e.g., T. auricularis, T. niveipes); and also in the outgroups (except in Holochilus, Oecomys, Delomys, and Rhagomys). Some species exhibit within-species polymorphism (e.g., T. cinereiventer, T. emeritus, T. laniger, T. silvestris). The Andean thomasomyines Aepeomys, Chilomys, Rhipidomys (except R. fulviventer and R. ochrogaster) and some Thomasomys (e.g., T. aureus, T. baeops, T. caudivarius, and T. incanus) have short nasals (state 2). Taxonomic

polymorphism in this trait is found in Thomasomys cinereus, T. monochromos, T. pyrrhonotus, Thomasomys sp. 6, and the outgroup taxon Juliomys pictipes.

**30. Posterodorsal extension of premaxillae:** *Premaxillae long, extending posterior to nasals (0); or moderately long, terminating level with nasals (1); or short, terminating anterior to nasals but posterior to the zygomatic notch (2); or very short, terminating anterior to nasals and the zygomatic notch (3).*

Described by Pacheco (Part I: character 20), this character corresponds closely to Stepan's (1995) character 10S, except that I include four states (rather than his three states). Long premaxillae that extend posterior to the nasals (state 0) are present in several Andean thomasomyines (e.g., Chilomys, Rhipidomys caucensis, R. macconnelli, Thomasomys baeops, T. monochromos, T. pyrrhonotus and T. taczanowskii) as well as several outgroup genera (e.g., Holochilus, Juliomys, Rhagomys, Wiedomys and Wilfredomys). Moderately long premaxillae (state 1) is seen in the genera Rhipidomys (except R. caucensis, R. macconnelli and R. ochrogaster), Thomasomys (e.g., T. apęco, T. australis, T. baeops, T. caudivarius, T. cinnameus, T. daphne, T. emeritus, T. ladewi, T. monochromos, T. notatus, and T. rosalinda), and also in oryzomyines (except Handleyomys and Holochilus). Short premaxillae (state 2) occurs in the Andean thomasomyines Rhipidomys ochrogaster, several Thomasomys (e.g., T. aureus, T. cinereus, T. gracilis, T. kalinowskii and T. laniger), and also in certain outgroups (Abrawayaomys, Delomys, Handleyomys, and Phaenomys). Very short premaxillae (state 3) are seen in a few thomasomyines including Aepeomys, Thomasomys erro, T. incanus, T. ischyrys and T. macrotis. Certain species (Thomasomys baeops, T. monochromos, T. cinnameus, T. notatus, and T. pyrrhonotus) exhibit two states in

different geographic populations, variation that I interpret as taxonomic polymorphism (see Appendix 2).

**31. Anterodorsal margin of zygomatic plate:** *Zygomatic plate shallow, its depth less than half the width of notch (0); or deep, its depth equal to or greater than half the width of notch (1).*

This character was evaluated by Pacheco (Part I: character 21, 22) based on scoring criteria described by Stepan (1995: character 8S) and Voss and Carleton (1993: character 6). Andean thomomysines exhibit state 0 (except T. niveipes and Thomasomys sp. 2) whereas state 1 is present in most outgroup taxa.

**32. Zygomatic plate breadth:** *Broad, breadth of zygomatic plate greater than M1 length (0); or moderately broad, subequal to M1 length (1); or narrow, shorter than M1 length (2).*

This character was defined by Pacheco (Part I: character 23) to have two states (narrow versus broad) but an intermediate condition is here recognized to allow additional distinctions. A broad zygomatic plate (state 0) is exhibited only in Thomasomys sp. 4 among the Andean thomomysines, and in several outgroup taxa (e.g., Abrawayaomys, Oryzomys and Rhagomys). Moderately broad zygomatic plate (state 1) is present in most Andean thomomysines with the exception of Aepeomys, Chilomys fumeus, Thomasomys cinnameus, T. dispar, T. erro, T. fumeus, T. gracilis, T. silvestris, and Thomasomys sp. 5. which have narrow zygomatic plates (state 2).

**33. Zygomatic plate slope:** *Anterior margin of zygomatic plate vertical (0); or polymorphic, either vertical or sloped (1); or sloping backward from its base (2).*

This character was described by Pacheco (Part I: character 24). Vertical zygomatic

plate (state 0) is exhibited by Chilomys, Rhipidomys, several species of Thomasomys (e.g., T. aureus, T. baeops, T. erro, and T. oreas), and all outgroup genera. A few species have the polymorphic condition (e.g., Thomasomys cinereus, T. dispar and T. silvestris). Sloping zygomatic plates (state 2) is observed in Aepeomys, and several species of Thomasomys (e.g., T. bombycinus, T. incanus, T. ladewi, T. laniger and T. rhoadsi). Taxonomic polymorphism is present in Thomasomys cinereus, T. contradictor, T. paramorum, and Thomasomys sp. 3.

**34. Masseteric tubercle:** *Absent (0); or present (1).*

Masseteric tubercles (a bony spur located at the base of the zygomatic plate) are prominent only in ichthyomyines (Voss, 1988). However, the masseteric tubercle of Aepeomys and Thomasomys sp. 5 is relatively large in comparisons to other muroids examined.

**35. Premaxilla-maxilla suture:** *Suture straight or nearly straight (0); or suture moderately angled in middle of rostrum (1).*

In most thomasomyines, the premaxillary-maxillary suture is more-or-less straight, vertically oriented, and perpendicular to the diastema, or it is smoothly sloped. However, in Aepeomys lugens and some species of Thomasomys (e.g., T. eleusis, T. erro, T. hudsoni, T. incanus, T. ischyrys, and T. kalinowskii) the premaxillary-maxillary suture pronouncely bends backward at level of the middle rostrum, or just below it, and continues either vertical or inclined (but not approaching horizontal) at ventral end (fig. 3). This feature is not similar to that reported by Olds and Anderson (1989) and Stepan (1995, character 45P) in phyllotines of the Reithrodon group, where the premaxillary-maxillary suture makes a sharp bend (equal or greater than 90°) in the middle of the

rostrum and is almost horizontal when it passes around to the ventral side.

**36. Infraorbital foramen:** *Lumen of foramen laterally compressed (0); or lumen of foramen moderately open (1).*

The lumen of the infraorbital foramen is broadly expanded only in ichthyomyines (Voss, 1988). Pacheco (Part I: character 27) scored all thomasomyines as having a narrow foraminal lumen (state 0), but a few (e.g., Aepeomys and Thomasomys erro) exhibit state 1.

**37. Notch between maxillary zygomatic process and lacrimal bone:** *Absent (0); or present (1).*

Leo L. and Gardner (1993) described the presence of a notch between the lacrimal bone and the adjacent maxillary zygomatic process in Thomasomys apeco. This notch is also present in the thomasomyines Aepeomys reigi, Rhipidomys gardneri, T. australis, T. caudivarius, T. cinnameus, T. daphne, T. gracilis, T. ladewi, T. oreas. The notch is absent in all examined outgroup taxa.

**38. Lacrimal posterior projection:** *Without posterior projection (0); or with posterior projection (1).*

Gardner and Romo R. (1993) described a postero dorsal projection of the lacrimals in Thomasomys macrotis. This morphology is also exhibited by Thomasomys apeco, T. bombycinus, T. cinereiventer, T. eleusis, and Thomasomys sp. 2. The remaining thomasomyine and outgroup taxa lack this projection.

**39. Position of antorbital bridge:** *High, antorbital bridge placed below dorsal surface of rostrum but less than 1/4 of the rostrum height (0); or low, antorbital bridge below 1/4 of the rostrum height (1).*

This character was described by Steppan (1995: character 5S, 41P) as the structure connecting the dorsal surface of the zygomatic plate with the rostrum. Low antorbital bridge (state 1) is exhibited in several Andean thomomyines (e.g., Aepeomys, Thomasomys contradictor, T. dispar, T. emeritus, T. erro, T. fumeus, T. incanus, T. ischyrys, T. macrotis, and T. rhoadsi) and also in the outgroup genera Delomys, Juliomys pictipes, Microrhynchomys, Oligoryzomys, Oryzomys, and Wilfredomys.

**40. Divergence of squamosal roots of zygomatic arch:** *Squamosal roots of zygomatic arch not expanding laterally, joining the braincase at oblique angle (0); or squamosal roots of zygomatic arch laterally expanded, joining the braincase more perpendicularly (1).*

This morphology was previously described in Wiedomys as a species with non expanded zygomatic arches (Reig, 1980). Tribe (1996) described the squamosal roots of zygomatic arches of Rhipidomys, Phaenomys and Oecomys as non expanded, but expanded in Delomys, Wilfredomys oenax and Thomasomys. The state 0 is exhibited in Rhipidomys and a few species of Thomasomys (e.g., T. baeops, T. gracilis, T. notatus, T. oreas, and T. taczanowskii). In contrast, the state 1 is seen in Aepeomys, Chilomys, and all remaining species of Thomasomys. All thomomyines in the outgroup (except Delomys) and the oryzomyine Oecomys exhibit the state 0, whereas the outgroup taxa (e.g., Handleyomys, Holochilus, Oligoryzomys, and Oryzomys) have the state 1.

**41. Shape of zygomatic arches:** *Zygomatic arches convergent anteriorly producing a triangular outline (0); or arches project anteriorly producing a more parallel outline (1).*

Most Andean thomomyines exhibit zygomatic arches that converge anteriorly

producing a triangular outline (state 0), as seen in Aepeomys, Chilomys instans and most species of Thomasomys (e.g., T. aureus, T. cinereus, and T. laniger). By contrast, parallel zygomatic arches are exhibited in Rhipidomys, some species of Thomasomys (e.g., T. baeops, T. gracilis, T. hudsoni, T. notatus, and T. oreas), and all outgroup taxa except Abrawayaomys and Delomys.

**42. Zygomatic arch dip:** *Low, the ventral margin of zygomatic arches reach the orbital floor or lower (0); high, the ventral margin of the zygomatic arch dip to a point slightly above the orbital floor (1); or very high, the ventral margin of the zygomatic arch placed above the orbital floor by half the orbital region (2).*

Low zygomatic arches (state 0) are seen in oryzomyines (except Handleyomys and Holochilus), Wiedomys, Wilfredomys, Rhipidomys leucodactylus, and R. ochrogaster). High zygomatic arch (state 1) is the widespread condition among thomasomyines as seen in Aepeomys, Delomys, Rhipidomys (except leucodactylus and ochrogaster), Thomasomys, and the outgroup taxa, Delomys, Handleyomys, Phaenomys and Rhagomys longilingua. The state 2 is exhibited only in a few thomasomyines (e.g., Abrawayaomys, Chilomys, and Rhagomys rufescens), and the oryzomyine Holochilus.

**43. Interorbital region:** *Hourglass-shaped, and supraorbital region smoothly rounded when viewed in cross-section (0); or incipiently squared or edged (1); or convergent with supraorbital margins without or weakly beaded when viewed in cross-section(2); or convergent and distinctly beaded when viewed in cross section(3).*

This character was described by Pacheco (Part I: character 28). Among thomasomyines the interorbital region varies from an hourglass to a convergent and distinctly beaded states. The state 0 is present in Aepeomys, Chilomys, several



Thomasomys (e.g., T. cinereus, T. erro, T. hylophilus, T. macrotis, and T. paramorum) and in the outgroup taxa Delomys, Juliomys sp., Handleymys, and Microryzomys. The state 1 is observed in Thomasomys baeops, T. cinereiventer, T. daphne, T. eleusis, T. gracilis, T. ladewi, T. notatus, T. popayanus, T. taczanowskii, and two undescribed species. The state 2 is present in Rhipidomys caucensis, R. fulviventer, and a few species of Thomasomys (e.g., T. apeco, T. aureus, T. praetor, T. princeps, T. pyrrhonotus, and T. rosalinda). Distinctly beaded interorbital region (state 3) is exhibited in Rhipidomys (except R. caucensis, R. fulviventer) and the outgroup thomomyines Phaenomys, Wiedomys, and Rhagomys longilingua.

**44. Interorbital region breadth:** *Narrow (0); or intermediate (1); or broad (2).*

Narrow interorbital region (state 0) can be recognized by the large exposure of the maxillary bridge of the molar rows and the base of the zygomatic plate when the skull is seen from a dorsal view. The state (0) is exhibited in the genus Thomasomys (e.g., T. aureus, T. baeops, T. gracilis, T. niveipes, and T. notatus), and the thomomyines Phaenomys and Wilfredomys. An intermediate condition (state 1) is defined when the interorbital region (seen from a dorsal view) obscures most of the base of the zygomatic plate, but large extension of the maxillary bridge is yet visible. State 1 is exhibited by Rhipidomys (except R. latimanus and R. gardneri) and several species of Thomasomys (e.g., T. caudivarius, T. daphne, T. hylophilus, T. paramorum, and T. rhoadsi). By contrast, a broad interorbital region (state 2) obscures most of the maxillary bridge and base of zygomatic plate when the interorbital region is seen from a dorsal view (fig. 4). This last condition is observed in Aepeomys, Chilomys, Rhipidomys latimanus, R. gardneri, Thomasomys erro, T. incanus, T. ischyrys, Thomasomys sp. 4, Thomasomys

sp. 5 and Thomasomys sp. 6; and also in the outgroups Abrawayaomys, Oecomys, Oryzomys, and Rhagomys.

**45. Interfrontal fontanella:** *Absent (0); or polymorphic, either absent or present (1); or present (2).*

The occurrence of interfrontal fontanelles in sigmodontine rodents were recently summarized by Gardner and Anderson (2001). However, they did not survey or find these structures in thomasomyine rodents. Interfrontal fontanelles are exhibited in several species of Thomasomys (e.g., T. niveipes, T. notatus, T. oreas, and T. pyrrhonotus), but they are absent (state 0) in Aepeomys, Rhipidomys, all remaining species of Thomasomys and outgroup taxa. Thomasomys baeops is polymorphic.

**46. Postorbital ridge:** *Absent, no conspicuous relief on the posterior orbital wall (0); or distinct ridge on the posterior orbital wall (1).*

Voss and Carleton (1993) described the presence of a postorbital ridge in Holochilus brasiliensis. This consists of a rugosae prominence on the squamosal, that runs nearly parallel to the fronto-squamosal suture. A postorbital ridge behind the suture of frontal and squamosal bones is seen in the T. aureus group (e.g., T. apeco, T. aureus, T. praetor, and T. pyrrhonotus), T. ladewi, and T. macrotis.

**47. Jugal length:** *Jugal long, widely separating the maxillary and squamosal zygomatic processes by a distance usually twice or more the thickness of the jugal (0); or jugal short, with maxillary and squamosal processes approximated or overlapping (1); or jugal reduced to a sliver, or absent (2).*

This character was previously described by Musser and Carleton (1989) and used by Pacheco (Part I: character 31) in his phylogeny of Thomasomyines. Jugal is an

elongated bone that bridges the maxillary and squamosal bones at the zygomatic arches. A long jugal (state 0) is observed in Aepeomys, Chilomys, a few species of Thomasomys (e.g., T. apeco, T. daphne, T. erro, T. incanus, and T. kalinowskii), and the outgroups Abrawayaomys, Juliomys sp., and Rhagomys. The state (1) is exhibited in Rhipidomys, many species of Thomasomys (e.g., T. aureus, T. baeops, T. cinereus, T. gracilis, T. macrotis, and T. notatus) and also in the outgroups Delomys, Juliomys pictipes, Phaenomys, Wiedomys, Wilfredomys, and Rhagomys longilingua. State 2 is present only in the outgroups Oligoryzomys and Microryzomys.

**48. Ethmoid foramen:** *Foramen placed dorsal to M2 (0); or dorsal or posterodorsal to M2/M3 contact, (1).*

This character was first described by Pacheco (Part I: character 43). In all muroid taxa examined here the ethmoid foramen is placed dorsal to M2. However, in Aepeomys the ethmoid foramen is placed more posteriorly, frequently dorsal to M3.

**49. Ethmoturbinals and sphenopalatine foramen formation:** *Ethmoturbinals absent or small (0); or polymorphism, either absent, small or moderate (1); or moderately large (2); or large and inflated (3).*

This character was first described by Pacheco (Part I: character 44). Wahlert (1985) described the sphenopalatine foramen as bounded by the maxilla, and usually the frontal and the palatine bones, and interpreted this conformation as the primitive condition, observing that occasionally the ethmoturbinals is exposed on the dorsal margin of the foramen. In addition, I observed that ethmoturbinals may be from absent to inflated and largely exposed. Small or absent ethmoturbinals (state 0) is seen in outgroup oryzomyines, and the thomasomyines Phaenomys and Rhipidomys leucodactylus. An

intermediate stage in which the ethmoturbinals are distinctly present, but neither conspicuously large nor inflated (state 2) is seen in Delomys, Juliomys, all Rhipidomys (except R. leucodactylus, and R. macconnelli, some Thomasomys (e.g., T. aureus, T. gracilis, T. hylophilus, T. niveipes, T. oreas ), and Wilfredomys among the thomasomyines. Wiedomys was scored as polymorphic (state 1) because specimens exhibit either the state 0 or 2. Large and inflated ethmoturbinals and exposed on the dorsal margin of the sphenopalatine foramen (state 3) is exhibited in Abrawayaomys, Aepeomys, Chilomys, Rhipidomys macconnelli, and many species of Thomasomys (e.g., T. baeops, T. cinereus, T. erro, T. incanus, and T. rhoadsi).

**50. Optic foramen:** *Moderate or large optic foramen, placed dorsal to at least half the length of M3 (0); or small, the foramen is placed posterodorsal to M3 (1).*

Moderate or large optic foramen (state 0) is observed in Rhipidomys, and most species of Thomasomys. By contrast, a small optic foramen (state 1) is seen in Aepeomys, Chilomys, a few species of Thomasomys (e.g., T. dispar, T. eleusis, T. erro, T. fumeus, T. incanus, T. ischyurus, and T. rhoadsi), and the outgroups Abrawayaomys and Delomys.

**51. Alisphenoid strut:** *Present (0); or incomplete or variable (1); or absent (2).*

Pacheco (Part I: character 33) recorded that the alisphenoid strut is absent in most oryzomyines, and few thomasomyines. The alisphenoid strut is present (state 0) in most Andean thomasomyines, but absent (state 2) in Aepeomys, Chilomys, and Thomasomys kalinowskii. Chilomys instans was scored as taxonomic polymorphism; since presence or absence of the strut among populations appears to be regional. The state 1 includes cases where the strut is incomplete, represented mainly by a ventral process in one or both

sides (e.g., Wilfredomys oenax and Juliomys sp.), and cases where the strut is either present or absent within a species (e.g., Thomasomys auricularis, T. eleusis, T. erro, T. ischyurus, and T. niveipes).

**52. Carotid Circulation:** *Pattern 1, stapedial foramen, squamosal-alisphenoid groove, and sphenofrontal foramen present (0); or pattern 2, stapedial foramen present, but squamosal-alisphenoid groove and sphenofrontal foramen absent (1); or pattern 3, stapedial foramen small or indistinct, squamosal-alisphenoid groove and sphenofrontal foramen absent (2).*

The nomenclature of the carotid circulation system and associated foramina follows Bugge (1970), Carleton (1980), Carleton and Musser (1989), Voss (1988), and Wahlert (1985) to whom the reader is referred for detailed description of the system. I followed Voss's (1988) terminology for my scoring scheme. This character was previously used by Pacheco (Part I: character 34) for his thomatomyine phylogeny. State 0 is present in Aepeomys, Rhipidomys fulviventer, R. ochrogaster, many species of Thomasomys (e.g., T. caudivarius, T. cinereus, T. emeritus, T. erro, T. gracilis, T. monochromos, T. niveipes, and T. notatus), and in the outgroups Abrawayaomys, Delomys, Juliomys sp., Phaenomys, Wiedomys, and Wilfredomys. By contrast, the state (2) that describes the pattern 3 is exhibited in Chilomys, Rhipidomys (except fulviventer and ochrogaster) and several species of Thomasomys (e.g., T. aureus, T. baeops, T. daphne, T. incanus, and T. macrotis). The pattern 2 (state 1) is not observed in any thomatomyine, but is present in Oligoryzomys (Carleton and Musser, 1989).

**53. Exposure of internal carotid artery:** *Non-exposed (0); or exposed (1).*

Voss (1988: 298) explained that for the pattern 3 of carotid circulation, the

“ophthalmic and internal maxillary circulations are, instead, both supplied by a different vessel that departs from the internal carotid artery inside the braincase, passes obliquely over the roof of the parapterygoid fossa and enters the orbit through the anterior alar fissure.” However, in a few species of thomasomyines the orbital branch of the internal carotid artery pierces the parapterygoid fossa and therefore is exposed ventrally (state 1). This condition is exhibited only in Chilomys instans, T. incanus, and Thomasomys sp. 4 (fig. 5).

**54. Tegmen tympani:** *Overlapping (0); or non-overlapping (1).*

Tegmen tympani overlapping a posterior process of the squamosal is exhibit in all thomasomyines examined. By contrast, the tegmen tympani does not (usually) contact or overlap the posterior process of the squamosal in oryzomyines (Voss, 1993).

**55. Sinus groove on tegmen tympani:** *Present (0); or absent (1).*

Voss (1993) observed that the tegmen tympani in Thomasomys cinereus and Delomys is prominently grooved by the postglenoid vein, as opposed to Oryzomys palustris that lack such groove, and apparently associated with the non-overlapping tegmen tympani (see character 54). However, the scores of this character suggest that the variation of the postglenoid vein groove is in some extent independent of the suspension of the tegmen tympani. A distinct groove is exhibited in all thomasomyines, except in Wilfredomys and Rhagomys longilingua.

**56. Hamular process and development of the postglenoid foramen:** *Very short postglenoid foramen, almost indistinct, with short hamular process (0); short postglenoid foramen, distinct but shorter than tegmen tympani (1); or polymorphism, either short or large (2); or large, anterior edge level with the tegmen tympani or forward*

(3).

The length of the postglenoid foramen is assessed in relation to the anterior margin of the tegmen tympani. Very short postglenoid foramen (state 0) is exhibited in all Aepeomys and Rhipidomys. The state 1 is present in Chilomys and most species of Thomasomys (e.g., T. baeops, T. cinereus, T. erro, T. gracilis, T. incanus, and T. macrotis) and also in the outgroups Abrawayaomys, Juliomys, Wiedomys, and Wilfredomys. By contrast, the postglenoid foramen is long and narrow extending to the anterior margin of the tegmen tympani or beyond (state 3) in several species of Thomasomys (e.g., T. apeco, T. aureus, T. auricularis, T. ladewi, T. nicefori, T. niveipes, T. notatus, T. popayanus, T. praetor, T. princeps, T. pyrrhonotus, and T. rosalinda), and the outgroups Delomys and Phaenomys. The polymorphic condition (state 2) is observed only in a few species of Thomasomys (e.g., T. bombycinus, T. cinereiventer, T. cinnamomeus, T. emeritus, T. laniger, and T. taczanowskii). Taxonomic polymorphism is reported for T. monochromos and Thomasomys sp. 6.

**57. Height of subsquamosal fenestra:** *Subsquamosal fenestra highly placed, level with squamosal root of zygomatic arch (0); or low, subsquamosal fenestra placed distinctly below the squamosal root of zygomatic arch (1).*

The hamular process of the squamosal separates the postglenoid foramen from the squamosal fenestra, and extends from the supraoccipital to the base of the squamosal root of the zygomatic arch. In most rodents examined the hamular process is long, marking a squamosal fenestra that approaches the squamosal root of the zygomatic arch and therefore excavating deeply the squamosal. However, in Rhipidomys, Phaenomys, and Rhagomys longilingua the hamular process is distinctly short, producing a subsquamosal

fenestra far from the base of the squamosal root of the zygomatic arch, and thus the squamosal bone is greatly exposed.

**58. Parietal-supraoccipital suture breadth:** *Suture narrow, length of suture is less than one fourth of the posterior margin of parietal (0); or polymorphic, either narrow or intermediate (1); or intermediate, suture is about one third the posterior margin of parietal (2); or distinctly broad, suture is at least half the posterior margin of parietal (3).*

This character was described by Pacheco (Part I: character 38) in two states. The parietal-supraoccipital suture is produced when the parietals precludes the interparietal to contact the squamosal. A narrow suture (state 0), extending distinctly less than a quarter of the caudal end of parietal bone, is seen in most oryzomyines and thomasomyines. An intermediate suture (state 2) is present in several andean thomasomyines (e.g., Aepeomys, Rhipidomys ochrogaster, T. hudsoni, T. incanus, and T. silvestris). By contrast, a broad suture (state 3) is exhibited in Chilomys, Abrawayaomys, and Oryzomys. The polymorphic condition (state 1) is recorded only in Thomasomys sp. 4.

**59. Lambdoid ridge development:** *Absent to weak (0); or present (1).*

The lambdoid ridge is absent (state 0) in most muroids examined, but present (state 1) in a few thomasomyines (e.g., Rhipidomys fulviventor, Thomasomys apeco, T. aureus, T. auricularis, T. macrotis, T. nicefori, T. praetor, T. princeps, and T. pyrrhonotus) and the outgroups Oryzomys and Abrawayaomys. Taxonomic polymorphism is exhibited in Rhipidomys fulviventor and Thomasomys sp. 1.

**60. Dorsal aperture of ectotympanic ring:** *Closed, anterodorsal edge of the ectotympanic extends backward to contact or approach closer to the petrosal (0); or*



*polymorphic, either closed or open (1); or open, anterodorsal lamina of the ectotympanic do not contact the petrosal producing a gap (2).*

I follow Pacheco (Part I: character 46) for the description of this character. In most muroids I examined, the anterodorsal edge of the ectotympanic extends posteriorly to contact or closely approach the petrosal, as result the dorsal margin of the auditory meatus appears to be "closed" by the ectotympanic (state 0). By contrast, the "open" condition (state 2), hypothesized to represent a derived condition (Pacheco, Part I), is exhibited by the Andean thomomyines Chilomys, Aepeomys, Rhipidomys (except R. latimanus, and R. gardneri), and Thomasomys (except T. apeco, T. auricularis, T. ischyus, T. kalinowskii, T. pyrrhonotus, and T. taczanowskii). Some species are polymorphic presenting either the state 0 or the state 2 (including T. apeco, T. auricularis, T. ischyus, T. kalinowskii, T. pyrrhonotus, and T. taczanowskii). Taxonomic polymorphism is present in T. aureus and Thomasomys baeops.

**61. Ectotympanic dorsal expansion:** *Not expanded laterally (0); or distinctly expanded laterally (1).*

In all muroids examined the ectotympanic does not expand laterally (state 0). By contrast, the ectotympanic is conspicuously expanded laterally in Wiedomys and Wilfredomys. This feature is better examined from dorsal view.

**62. Incisive foramina:** *Short, the posterior margin of the incisive foramina extends to a point in front of M1 by a distance about the length of the anterocone of M1 or greater(0); or moderately long, the posterior margin of the foramina extends to level M1 or just in front (1); or long, the foramina extending between the M1 procingula (2).*

Definition is based on Pacheco (Part I: character 48). Short incisive foramina (state

0) are seen in Aepeomys reigi, Chilomys, T. contradictor, T. dispar, T. vestitus, Thomasomys sp. 11, and the outgroups Handleyomys and Rhagomys. By contrast, moderately long incisive foramina (state 1) is the widespread condition among thomatomyines and is exhibited in Aepeomys lugens, some species of Rhipidomys (e.g., R. caucensis, R. gardneri, and R. leucodactylus), several species of Thomasomys (e.g., T. baeops, T. caudivarius, T. erro, T. hylophilus, and T. rhoadsi) and also in the outgroups Abrawayaomys, Delomys, Juliomys pictipes, and Phaenomys. Long incisive foramina (state 2) are exhibited in Rhipidomys fulviventer, R. latimanus, R. macconnelli, R. ochrogaster, some species of Thomasomys (e.g., T. aureus, T. eleusis, T. gracilis, T. oreas, and T. paramorum) and also the outgroups Juliomys sp., Wiedomys, and Wilfredomys. Taxonomic polymorphism is recorded for Rhipidomys fulviventer, Thomasomys cinereus, T. cinnamomeus, T. nicefori, T. notatus, T. princeps, and Thomasomys sp. 6.

**63. Maxillary septum length:** *Short, less than half the length of the incisive foramina (0); or long, approximately half the length of the incisive foramina or larger (1).*

This character was described by Pacheco (Part I: character 49). All muroids examined here exhibit a short septum (state 0), except Chilomys fumeus, Rhipidomys caucensis, R. fulviventer, R. macconnelli, some Thomasomys (e.g., T. auricularis, T. baeops, T. eleusis, T. hudsoni, T. incanus, T. ischyryus, T. kalinowskii, T. notatus, T. oreas, T. princeps, T. taczanowskii), Juliomys, and Phaenomys which exhibit a maxillary septum that extends to half the length of the incisive foramina (state 1). Taxonomic polymorphism is seen in Chilomys instans.

**64. Palatal length:** *Palate short, extending to or between the posterior margins of*

*M3s (0); or polymorphic, either short or moderately long (1); or palate moderately long, not extending beyond half of M3 tooth-length posterior to M3 (2); or palate long, extending more than half of M3 tooth-length posterior to M3 (3).*

Described in Pacheco (Part I: character 50). Palate length is a taxonomically informative feature used since Thomas (1906) employed it to distinguish the short-palate rodents (e.g., Thomasomys, Rhipidomys) from the long palate rodents (e.g., Oecomys and Oryzomys). All thomatomyines exhibit short palates (state 0) with the exception of Chilomys and Rhagomys (which have the state 3), and Aepeomys reigi and Chilomys instans that have moderately long palate (state 2). Taxonomic polymorphism is seen in Chilomys instans.

**65. Palatal breadth:** *Palate wide, the distance between the protocones of the first upper molar exceeds the length of first molars (0); or narrow, the distance between protocones is subequal to the length of the first molar or less (1).*

This character was described by Hershkovitz (1962), and used in phylogenetic analyses by Stepan (1995) and Pacheco (Part I: character 51). A wide palate is defined when the distance between the protocones of the first upper molar exceeds the length of first molars; and narrow palate when the distance is equal to the length of the first molar or less (fig. 6).

A broad palate is exhibited by most thomatomyines including Aepeomys, Chilomys, Rhipidomys, and most species of Thomasomys. By contrast, a distinctly narrow palate (state 1) is seen in several ingroup taxa (e.g., T. apeco, T. aureus, T. auricularis, T. macrotis, T. popayanus, T. praetor, T. princeps, T. pyrrhonotus, T. rosalinda, and Thomasomys sp. 1), and the outgroups Phaenomys and Wilfredomys.

**66. Medial process of posterior margin of palate bridge:** *Absent (0); or polymorphic, either absent or present (1); or present (2).*

Absence of the medial process of the palate (state 0) is the widespread condition. It is seen in Aepeomys reigi, Chilomys, Rhipidomys caucensis, R. fulviventris, R. latimanus, R. leucodactylus, most species of Thomasomys, and all the outgroups. By contrast, a medial process (state 2) is exhibited in Aepeomys lugens, some Rhipidomys (e.g., R. gardneri, R. macconnelli, and R. ochrogaster), and some species of Thomasomys (e.g., T. apeco, T. cinereiventris, T. daphne, T. dispar, T. paramorum, and T. vestitus). Taxonomic polymorphism is seen in Rhipidomys leucodactylus, T. bombycinus, T. cinereus, and T. hylophilus.

**67. Posterolateral palatal pits:** *Pits simple, and level with, or posterior to the anterior margin of the mesopterygoid fossa (0); or simple and distinctly anterior to the mesopterygoid fossa (1); or incipiently complex, pits of moderate size, subequal to half M3, with accessory pits, not situated in a fossa (2); or complex, one or more pits present in a common fossa, and anterior to the mesopterygoid fossa (3).*

This character was described by Pacheco (Part I: character 52). All Andean thomasomyine taxa, and the outgroups Abrawayaomys, Delomys, Juliomys and Phaenomys exhibit posterolateral palatal pits simple (state 0). State 1 is observed in Microryzomys and Rhagomys rufescens. The incipiently complex pit (state 2) is exhibited only in Wiedomys and Wilfredomys, whereas the state 3 is seen in all oryzomyines (except Microryzomys) and Rhagomys longilingua.

**68. Maxillary palatal pits:** *Absent (0); or present (1).*

This character was first described by Pacheco (Part I: character 54). The maxillary

palatal pits are small pits of the maxillary bone situated at both sides of the palate, at level of first molar, and between the incisive foramina and the posterior palatine pit.

Aepeomys, Rhipidomys (except R. macconnelli), and many Thomasomys (e.g., T. aureus, T. baeops, T. incanus, T. macrotis, T. notatus) exhibit the maxillary palatal pits. The pits are also predominant among outgroups, and are seen in Abrawayaomys, Delomys, Juliomys, Phaenomys, and Wilfredomys.

**69. Depth and shape of the molar-bearing portion of the maxillae:** *Low and rectangular shape (0); or deep with conspicuous triangular shape (1).*

The maxillary portion that holds the roots of the upper molars varies in depth and shape in thomasomyines. The maxilla is nearly rectangular especially on the last two molars (state 0) as seen in Rhipidomys, and several species of Thomasomys (e.g., T. aureus, T. gracilis, T. laniger, and T. vestitus). By contrast, the molar-bearing portion of the maxilla looks triangular when progressively become thinner from M1 to M3 (state 1) as is exhibited in Aepeomys, Chilomys, and many Thomasomys (e.g., T. baeops, T. cinereus, T. erro, T. incanus, and T. macrotis). Leo L. and Gardner (1993) and Gardner and Romo R. (1993) described and illustrated this feature.

**70. Maxillary at posterior base of M3:** *Normal (0); or swollen (1).*

This character describes the palatal side of the maxillary bone that encloses the alveolus of M3. The maxillary bone just behind M3 is nearly horizontal and levels with the palate region in all muroids examined, except in Thomasomys apeco, T. bombycinus, T. cinereiventer, T. incanus, T. rhoadsi, and Thomasomys sp. 6 in which the region is swollen.

**71. Sphenopalatine vacuities:** *Absent, no perforations on the dorsal roof of the*

*mesopterygoid fossa, or barely as narrow slits on each side of the basisphenoid-presphenoid suture (0); or moderately large perforations, usually elongated, that extend at both sides of the basisphenoid-presphenoid suture, largely visible from the mesopterygoid fossa and inconspicuous from the interorbital region (1); or large perforations, usually oval shaped, and distinctly visible from the interorbital region(2).*

This character was described by Pacheco (Part I: character 55). All Andean thomomysines lack sphenopalatine vacuities or exhibited only as narrow slits on each side of the basisphenoid-presphenoid suture (state 0), except in Thomasomys emeritus, T. gracilis, T. niveipes, T. oreas, T. praetor, T. pyrrhonotus, T. rosalinda, and three undescribed species which present moderately large perforations (state 1). Thomasomys incanus and T. paramorum are polymorphic, presenting states 0 and 1 in apparently disjunct populations. Among outgroups, the state 0 is exhibited in Handleyomys, Oecomys, Abrawayaomys, Delomys, Phaenomys, and Rhagomys longilingua. Moderately large perforations (state 1) is seen only in Juliomys, whereas large perforations (state 2) are seen in Holochilus brasiliensis, Microryzomys minutus, Oligoryzomys fulvescens, Oryzomys palustris, Wiedomys pyrrhorhinos, and Wilfredomys oenax.

**72. Shape of parapterygoid fossa: Rectangular (0); or triangular (1).**

This character was first described by Pacheco (Part I: character 58). The lateral divergence of the parapterygoid fossa is evaluated by comparisons of the breadth of the parapterygoid fossa, at level of the basisphenoid-parasphenoid suture, versus the breadth of the parapterygoid fossa at the posterior edge of hamular process. A ratio of 1.5 or less reflects a more-or-less rectangular parapterygoid fossa (state 0), and is the common

condition in oryzomyines. However, a ratio greater than 1.5 highlight a parapterygoid fossa with a sharp "triangular" outline (state 1), which is seen in all thomasomyine species except Aepeomys lugens, T. caudivarius, T. erro, Thomasomys sp. 6, and Thomasomys sp. 8. T. notatus is polymorphic presenting both states.

**73. Parapterygoid vacuity:** *Absent or faint (0); or distinct (1).*

The parapterygoid vacuity is absent or present just as an elongated slit (state 0), in most Andean thomasomyines. However, a conspicuous perforation between the palatine and alisphenoid bones in the parapterygoid fossa (state 1) is observed in Rhipidomys macconelli, a few species of Thomasomys (e.g., T. australis, T. cinnamomeus, T. daphne, T. emeritus, T. gracilis, T. hudsoni, T. niveipes, T. pyrrhonotus, and T. vestitus), and Rhagomys longilingua. Tribe (1996) indicated that parapterygoid vacuities are usual in several species of Rhipidomys, however my samples consistently lacked the parapterygoid vacuities except R. macconnelli. Taxonomic polymorphism is common and observed in Chilomys instans, Rhipidomys fulviventer, T. monochromos, T. notatus, T. paramorum, Thomasomys sp. 3, and Thomasomys sp. 6.

**74. Mesopterygoid fossa breadth:** *Broader than adjacent parapterygoid fossae (0); or mesopterygoid and parapterygoid fossae subequal (1); or mesopterygoid fossa distinctly narrower than parapterygoid fossae (2).*

This character was first described by Steppan (1995) and used also by Pacheco (Part I: character 56). Most thomasomyine species have the mesopterygoid fossa broader than the adjacent parapterygoid fossae (state 0). In a few taxa (e.g., Chilomys instans, Thomasomys baeops, T. niveipes, and T. taczanowskii) the mesopterygoid and parapterygoid fossae are subequal (state 1), and only Wiedomys pyrrhorhinos and

Wilfredomys oenax exhibit a narrow mesopterygoid fossa (state 2). Taxonomic polymorphism is recorded in T. daphne and T. pyrrhonotus.

**75. Mesopterygoid fossa shape:** *Posteriorly convergent (0); or parallel sided (1).*

This character was described by Stepan (1995, character 19S), and used also by Pacheco (Part I, character: 57). Posteriorly convergent mesopterygoid fossa is exhibited in Rhipidomys (except R. gardneri and R. ochrogaster) and several species of Thomasomys (e.g., T. cinereiventer, T. gracilis, T. laniger, T. oreas, and T. rhoadsi). By contrast, parallel mesopterygoid fossa (state 1) is present in Aepeomys, Chilomys, many species of Thomasomys (e.g., T. aureus, T. baeops, T. daphne, T. hylophilus, and T. paramorum), and all outgroups (except for Delomys, Juliomys sp., and Phaenomys). Taxonomic polymorphism is reported in T. cinereus, T. incanus, and T. notatus.

**76. Alisphenoid squamosal posterior margin:** *Notch absent (0); or notch present (1).*

The posterior margin of the alisphenoid and squamosal bones that border the middle lacerate foramen is smooth and uniform in all muroids examined, but these bones (especially the squamosal) are slightly excavated producing a notch (state 1) in Chilomys instans, and some Thomasomys (e.g., Thomasomys eleusis, T. incanus, T. ischyurus, and T. taczanowskii) (fig. 7). Myers et al. (1990) described a similar morphology for Akodon boliviensis group.

**77. Bullae inflation:** *Not inflated (0); or moderately inflated, Eustachian tube small (1); or inflated, Eustachian tube indistinct (2).*

Definition is based on Leo L. and Gardner (1993) who described the inflation of the auditory bullae of Thomasomys apeco in relation to the pterygoid processes. Bullae



are considered inflated (state 2) when their ventral margins extend distinctly ventral to the hamular process of the pterygoids when the skull is viewed on a horizontal plane (fig. 8). In thomasomyines, the degree of bulla inflation is apparently associated with the size of Eustachian tube, and the breadth of the basioccipital bone; thus, inflated bulla appears associated with a reduced (or absent) Eustachian tube and a narrow basioccipital bone. In contrast, a small non-inflated bullae is associated with a distinct Eustachian tube and broad basioccipital bone. Non-inflated bullae (state 0) is exhibited by Aepeomys, Chilomys, Rhipidomys, several species of Thomasomys (e.g., T. aureus, T. baecops, T. cinereus), Delomys collinus, Juliomys pictipes, Rhagomys longilingua and oryzomyines. Moderately inflated bulla (state 1) is exhibited by many Thomasomys (e.g., T. australis, T. cinnameus, T. contradictus, T. daphne, T. erro, T. hylophilus, T. incanus, T. ischyrys, T. kalinowskii, T. monochromos, T. nicefori, T. praetor, and T. rosalinda), and the outgroups Delomys sublineatus, Juliomys sp., and Rhagomys rufescens. Inflated bullae (state 2) is exhibited by some species of Thomasomys (e.g., T. auricularis, T. emeritus, T. gracilis, T. hudsoni, T. laniger, T. niveipes, T. oreas, T. paramorum, T. pyrrhonotus) and the outgroups Abrawayaomys ruschii, Wiedomys pyrrhorhinos, and Wilfredomys oenax.

**78. Anterior process of the ectotympanic:** *Small (0); or robust, long (1).*

Steppan (1995, character 59P) described and used this morphology in his phyllotine analysis, but with emphasis on the degree of compression of the "stapedial spine" against the bullae. My definition here focus strictly on the degree of development of the spine. In taxa with a large process, the process conspicuously fills the space of the middle lacerate foramen. Most of the Andean thomasomyines exhibit a small anterior process of the ectotympanic (state 0), but this is long and robust (state 1) in Chilomys,

all Rhipidomys (except R. ochrogaster), Thomasomys apeco, T. aureus, T. macrotis, T. niveipes, T. notatus, T. popayanus, T. praetor, Thomasomys sp. 1, Thomasomys sp. 2, the oryzomyines (except Handleyomys and Microrizomys), and the thomasomyines Abrawayaomys, Delomys, Juliomys, and Wilfredomys. Chilomys instans exhibits the states 0 and 1 in distinct populations.

**79. Malleus lamina:** *Broad, square-like (0); or narrow, rectangular shape (1).*

A broad and square-like malleus lamina (state 0) is the common condition in the ingroup taxa. However, Chilomys, Rhipidomys, Thomasomys sp. 4, and Thomasomys sp. 8 exhibit a malleus lamina that is distinctly short along the antero-posterior axes suggesting a rectangular shape. The state 1 is also seen in the outgroup taxa with the exception of Abrawayaomys ruschii, Juliomys sp., Wiedomys pyrrhorhinos, and Wilfredomys oenax. Juliomys pictipes is polymorphic.

**80. Ventral margin of malleus lamina:** *Shallow (0); or with a distinct deep ridge and fossa (1).*

In all species examined the ventral margin of the malleus lamina smoothly follows with the orbicular apophysis. In contrast, in Thomasomys pyrrhonotus and T. auricularis, the ventral margin of the malleus lamina has a strong shelf near the joins with the orbicular apophysis.

**81. Processus brevis of incus:** *Base thick, usually short, tip pointed or knob-like, more robust in appearance (0); or base narrow, usually long and tapering to a pointed tip, delicate in appearance (1).*

This character was first described by Pacheco (Part I: character 64). Robust processus brevis, with a broad base and a short posterior extension (state 0), is the

widespread condition among oryzomyines. By contrast, a more delicate processus brevis with a narrow base, longer and slender (state 1), is seen in all thomasomyines I have examined except in Thomasomys praetor. Juliomys pictipes is polymorphic for this morphology.

## DENTITION

**82. Upper incisor orientation:** *Opisthodont (0); or polymorphic, either opisthodont or orthodont (1); or orthodont (2); or proodont (3).*

My definitions follow HersHKovitz (1962), Steppan (1995), and Pacheco (Part I: character 67). The incisors orientation is described based on the position of the cutting edge of the incisor in relation to the vertical-incisive plane. Opisthodont incisors (state 0) occur when the cutting edge is placed distinctly posterior to the vertical-incisive plane; orthodont incisors (state 2) if both planes coincide close in a single plane; and proodont incisors (state 3) when the cutting edge of incisors lies anterior to the vertical-incisive plane. In the ingroup, orthodont incisors is the common condition. In contrast, Rhipidomys and some Thomasomys (e.g., T. aureus, T. baeops, T. emeritus, T. gracilis, T. niveipes, and T. notatus) have opisthodont incisors. Proodont incisors are exhibited in Chilomys and a few Thomasomys (e.g., T. australis, T. daphne, and Thomasomys sp. 11). Within-taxon polymorphism (state 1) was observed in Thomasomys cinereiventer, whereas taxonomic polymorphism was recorded in T. cinnamomeus, T. contradictus, and T. paramorum. In the outgroup, all taxa exhibit opisthodont incisors except for Rhagomys and Abrawayaomys ruschii which upper have orthodont and proodont incisors respectively.

**83. Upper incisor wear pattern:** *Wear surface of incisors more-or-less flat, facing backward (0); or wear surface of incisors oriented medially (1).*

The wear surface of upper incisors is produced in two shapes (fig. 9). The worn surface of each upper incisor faces completely backward (state 0) in Chilomys, Rhipidomys, a few species of Thomasomys (e.g., T. baeops, T. gracilis, T. notatus, T. oreas, and T. taczanowskii) and all outgroup taxa. By contrast, the worn surfaces of each upper incisor are faced medially (state 1) in Aepeomys and remaining species of Thomasomys.

**84. M1 position:** *Alveolus of first upper molar anterior to the posterior margin of the zygomatic plate (0); or polymorphic, either anterior or below (1); or below the posterior margin of the zygomatic plate (2); or posterior to the zygomatic plate (3).*

This character describes the position of first upper molar alveolus in relation to the posterior border of the zygomatic plate as seen from ventral view (see Pacheco, Part I: character 68). An M1 alveolus placed anterior to zygomatic plate (state 0) is uncommon and seen in Aepeomys, and some species of Thomasomys (e.g., T. bombycinus, T. cinereiventer, T. contradictus, T. dispar, T. eleusis, T. incanus, T. ischyrys, T. kalinowskii, T. ladewi, T. macrotis, T. princeps, and T. vestitus). Polymorphic condition (state 1) is seen only in Thomasomys silvestris. An M1 alveolus just below the posterior margin of the zygomatic plate (state 2) is seen in the thomatomyines Abrawayaomys, Delomys, and some Thomasomys (e.g., T. aureus, T. cinereus, T. daphne, T. hylophilus, and T. niveipes). However, the placement of M1 posterior to zygomatic plate (state 3) is the most common condition and is exhibited in Chilomys fumeus, Rhipidomys, several species of Thomasomys (e.g., T. baeops, T. caudivarius, T. cinnamomeus, T. gracilis, T.

hudsoni, T. laniger, T. notatus, T. oreas, and T. taczanowskii) and the outgroup taxa Juliomys, Phaenomys, Rhagomys, Wiedomys, Wilfredomys, and oryzomyines. To evaluate this character age variation must properly be considered since juveniles usually have the molar teeth more anteriorly placed. Chilomys instans shows variation among populations, and was treated as taxonomic polymorphism.

**85. Molar height topography:** *Molars brachyodont (0); or, moderately high-crowned hypsodont(1).*

Based on Pacheco (Part I: character 76). Most Andean thomasomyine species have teeth that are conspicuously brachyodont. By contrast, moderately hypsodont molars are exhibited in Aepeomys, Thomasomys apeco, T. aureus, T. bombycinus, T. cinereiventer, T. contradictus, T. erro, T. fumeus, T. macrotis, T. praetor, T. pyrrhonotus, T. rhoadsi, T. vestitus, and the outgroup Holochilus brasiliensis.

**86. Molar occlusal design:** *Labial and lingual folds not interpenetrating (0); or folds with slight to deep interpenetration, as seen mainly between hypoflexus and metaflexus of M1-M2 (1).*

Voss (1993: 20) and Voss and Carleton (1993) were first to use the degree of fold interpenetration to assess phylogenetic relationships among sigmodontines, and subsequently applied also by Pacheco (Part I: character 77) in his thomasomyine phylogeny. Among surveyed thomasomyine, only some species present interpenetrating molar design (e.g., Delomys, Rhipidomys caucensis, Thomasomys bombycinus, T. cinereiventer, T. kalinowskii, T. ladewi, T. notatus, T. oreas, T. princeps, and T. rosalinda), and T. aureus is polymorphic for this character. Among oryzomyines, Microryzomys minutus, Oligoryzomys fulvescens and Oryzomys palustris have a non-

interpenetrating molar design (state 0), whereas Handleyomys fuscatus, Holochilus brasiliensis, and Oecomys bicolor exhibit the state 1.

**87. Anteromedian flexus:** *Present (0); or absent (1).*

Based on Pacheco (Part I: character 69). A deep anteromedian flexus divides the M1 anterocone in roughly two cones. The anteromedian flexus on M1 is present in all thomomyines except for Chilomys fumeus, C. instans (which is polymorphic), T. silvestris, T. vestitus, and Thomasomys sp. 10. In oryzomyines, the anteromedian flexus is present only in Microryzomys minutus and Oligoryzomys fulvescens.

**88. Anterocone:** *Anterolabial and anterolingual conules subequal (0); or anterolingual conule distinctly reduced, about half the size or less of the anterolabial conule (1).*

This character follows Pacheco (Part I: character 70). The anterolabial and anterolingual conules on M1 are subequal (state 0) in most muroid taxa examined here. However very small anterolingual conules, about half size or less of the anterolabial conules, was reported in the description of Phaenomys (Thomas, 1917). Reig (1980) observed also the unusually small anterolingual conules in Wiedomys, and used this characteristic in his diagnosis of the Tribe Wiedomyini. In addition, small anterolingual conules are exhibited in Chilomys instans, Rhipidomys ochrogaster, Thomasomys notatus, all thomomyines from the Atlantic Forest region, and in Rhagomys longilingua.

**89. Procingulum anterior edge of M1:** *Without additional edge (0); or with additional edge accompanied by an accessory lophule (1).*

Thomasomys apeco, T. auricularis, T. rosalinda, and the outgroups Phaenomys ferrugineus, and Rhagomys longilingua exhibit an additional anterior edge on the

procingulum of M1 (state 1), which is absent in the remaining sigmodontines examined.

**90. Anteroflexus M1:** *Distinct (0); or small to indistinct (1).*

This character was scored only in taxa with a distinct anteroloph (see character 91). The anteroflexus M1 is small to indistinct (state 1) in Aepeomys, a few species of Thomasomys (e.g., T. bombycinus, T. caudivarius, T. cinereiventer, T. dispar, T. eleusis, T. emeritus, T. erro, T. fumeus, and T. hylophilus), and the outgroups Delomys, and Rhagomys rufescens.

**91. Anteroloph:** *Distinct (0); or indistinct (1).*

Most muroids examined exhibit a distinct anteroloph on M1 (not coalesced with the anterolabial conule) that reaches the labial margin of the molar. However, an indistinct anteroloph produced by a quick coalescence with the anterolabial conule (state 1) is exhibited in a few thomasomyine species (e.g., Abrawayaomys, Juliomys, Thomasomys cinnameus, T. incanus, T. ladewi, T. laniger, T. monochromos, T. paramorum, T. rhoadsi, and T. silvestris).

**92. Anteroloph orientation:** *Anteroloph perpendicular (0); anteroloph oriented backward (1).*

This character was scored only in taxa with a distinct anteroloph (see character 91). Most muroids examined exhibit an anteroloph perpendicular to the mure that reaches the labial cingulum (state 0). In contrast, the anteroloph exhibit a backward orientation toward the paracone (state 1) in a few species of Thomasomys (e.g., T. apeco, T. aureus, T. auricularis, T. nicefori, T. popayanus, T. praetor, T. princeps, T. pyrrhonotus, and T. rosalinga) and the outgroup Wiedomys pyrrhorhinos.

**93. Paraloph orientation in M1:** *Oriented perpendicularly to the protocone (0);*

*or oriented to the mure; with or without additional connection to the mesoloph (1); or oriented to the joint between the mure and the mesoloph (2); or oriented backward to the mesoloph (3).*

I scored the paraloph orientation only for M1 because the paraloph orientation in M2 appears to be largely correlated. In thomatomyine rodents the paraloph oriented to the mure (state 1) is the predominant condition. Only Abramomys, Juliomys, Chilomys, and T. hylophilus present the paraloph oriented to the joint between the mure and the mesoloph (state 2). All oryzomyines (except Handleyomys fuscatus and Oecomys bicolor which have the state 1) exhibit a paraloph oriented perpendicularly to the protocone (state 0).

**94. Hypoflexus size of M1:** *Narrow (0), or broad (1).*

The hypoflexus, observed through an antero-posterior axis, is narrow (state 0) in most taxa. By contrast, a broad hypoflexus broad, presenting a rectangular shape rather than angular (state 1), is exhibited in Rhipidomys (except R. caucensis, R. gardneri, and R. macconnelli), several species of Thomasomys (e.g., T. apeco, T. aureus, T. auricularis, T. nicefori, T. popayanus, T. praetor, T. princeps, T. pyrrhonotus, T. rosalinda, and T. vestitus), and all thomatomyine outgroups (except Delomys).

**95. Hypoflexus width of M2:** *Hypoflexus width similar to mesoflexus (0); or distinctly narrower than mesoflexus (1).*

In all muroids examined the hypoflexus and mesoflexus width of M2 are subequal (state 0). By contrast, a distinctly narrow and less deep hypoflexus (state 1) is only seen in Aepeomys lugens, A. reigi and Chilomys fumeus.

**96. Protostyle and enterostyle on M1:** *Absent (0); or polymorphism, either*



*absent or present (1); or present (2).*

The protostyle and enterostyle on M1 are absent (state 0) in most Andean thomatomyines; but they are present (state 2) in Rhipidomys (except R. caucensis and R. fulviventer), some species of Thomasomys (e.g., T. nicefori, T. notatus, T. oreas, and T. princeps) and all thomatomyines from the Atlantic region except for Delomys collinus. Taxonomic polymorphism is reported in T. aureus, T. gracilis and T. hylophilus whereas within-taxon polymorphism is reported in T. eleusis, T. ischyrys, and Thomasomys sp. 5.

**97. Protoflexus on M2:** *Present (0); or faint or absent (1).*

The protoflexus on M2 was evaluated by Pacheco (Part I: character 75) in his thomatomyine phylogeny. The protoflexus on M2 is present in Chilomys, Rhipidomys (except for R. caucensis, R. fulviventer and R. ochrogaster), many species of Thomasomys (e.g., T. daphne, T. gracilis, T. macrotis, T. notatus, and T. vestitus), and all outgroups (except Handleyomys, Holochilus, Oligoryzomys, and Delomys). Several species of Thomasomys lack or have a faint protoflexus (e.g., T. aureus, T. baeops, T. cinereus, T. dispar, T. incanus, T. rhoadsi, and T. silvestris). Thomasomys hylophilus, T. paramorum, Thomasomys sp. 3, and Wiedomys pyrrhorhinus were scored as taxonomic polymorphism.

**98. Hypoflexus of M3:** *Inconspicuous to absent (0); or present (1).*

The hypoflexus on M3 was scored independently from the hypoflexus on the other molars because is indicative of the degree of simplification of M3. The hypoflexus is frequently absent or inconspicuous (state 0) in Andean thomatomyines, but is present (state 1) in Aepeomys, Chilomys, Rhipidomys caucensis, R. fulviventer, several species

of Thomasomys (e.g., T. australis, T. cinereiventer, T. cinereus, T. cinnamomeus, T. contradictus, T. daphne, T. dispar, T. erro, T. hylophilus, T. laniger, T. monochromos, T. paramorum, and T. rhoadsi), and the outgroups Delomys, Rhagomys, and Handleyomys.

**99. Anteromedian flexid of m1:** *Present (0); or faint or absent (1).*

The anteromedian flexid of m1 is present in Rhipidomys (except R. caucensis) and many species of Thomasomys (e.g., T. aureus, T. baeops, T. cinereus, T. erro, and T. macrotis), but is absent in Aepeomys, Chilomys, and several Thomasomys species (e.g., T. gracilis, T. incanus, T. ladewi, T. rhoadsi, and T. silvestris). In the outgroup, the anteromedian flexid (state 0) is exhibited by all thomasomyines (except for Delomys, Juliomys sp., and Rhagomys) and the oryzomyines Microryzomys minutus and Oligoryzomys fulvescens.

**100. Internal enamelled pit of m1 procingulum:** *Internal enamel pit absent (0); or internal enamel pit prominent (1).*

Voss and Carleton (1993) suggested that a developed pit in the procingulum of the first lower molar may be a remnant of an ancestral anteromedian flexid. This character was only evaluated among the species with faint or absent anteromedian flexid and considered inapplicable for taxa with patent anteromedian flexid (see character 99). These pits were observed only in oryzomyine rodents: Handleyomys fuscatus, Holochilus brasiliensis, and Oryzomys palustris.

**101. Ectolophid m1:** *Absent (0); or ectolophid present (1).*

Ectolophids on lower molars were reported for Delomys by Voss (1993). An ectolophid-stylid divides the m1 hypoflexid in a few pentalophodont sigmodontines. It is fully exhibited in the thomasomyines Rhipidomys gardneri, some species of

Thomasomys (e.g., T. emeritus, T. nicefori, T. popayanus, T. princeps, T. pyrrhonotus, and T. rosalinga), and the outgroups Delomys, Juliomys, Phaenomys, Wilfredomys, and Oecomys.

**102. Ridge on anterolabial cingulum of m1:** *Present, a ridge on the anterolabial cingulum of m1 that extends posteriorly to the anterolabial conulid to form the anterior margin of protoflexid (0); or ridge reduced or absent (1).*

Gardner and Romo R. (1993) described the presence of a ridge on the anterolabial cingulum of m1 suggesting it is characteristic of Thomasomys (s.l.). Pacheco (Part I: character 79) employed this morphology in his thomasomyine phylogeny. Here, the anterolabial cingulum of m1 is the widespread feature, being reduced or absent only in Abrawayaomys, Aepeomys reigi, Chilomys fumeus, Thomasomys fumeus, T. hudsoni, T. rhoadsi, and Thomasomys sp. 10.

**103. Orientation of metalophid m1:** *Metalophid anteromedially oriented to the murid (0); or metalophid with double connections, one oriented anteromedially to the murid and the other oriented antero-posteriorly (1); or a metalophid antero-posteriorly oriented that closes the anterolingual cingulum (2).*

Leo L. and Gardner (1993) described the anterior-posterior orientation of the metalophids (and entolophids) in the first two lower molars of Thomasomys apeco and T. aureus. Among thomasomyines, the state 0 is the widespread condition, but the state 2 is exhibited by Aepeomys, the T. aureus group (except T. praetor that has the state 0, and T. nicefori that has the state 1), other species of Thomasomys (e.g., T. caudivarius, T. hylophilus, T. incanus, T. ischyus, T. laniger, and T. niveipes), and the outgroups Juliomys sp. and Wilfredomys. By contrast, the state 1 is seen in a few species of

*Thomasomys* (e.g., *T. eleusis*, *T. gracilis*, *T. kalinowskii*, *T. ladewi*, *T. macrotis*, and *T. nicefori*) and *Phaenomys*. In the outgroup, the state 0 is also exhibited in all thomasomyines.

**104. Entolophids of m1-m2:** *Entolophid perpendicularly oriented to the murid (0); or anteromedially oriented to the mesolophid-murid angle or the base of mesolophid (1); or oriented to the mesolophid (2).*

The orientation of an entolophid varies apparently among groups. *Aepeomys*, *Chilomys*, *Rhipidomys*, and most *Thomasomys* species exhibit the state 0. The entolophid is oriented anteromedially to the mesolophid-murid angle or the base of mesolophid (state 1) in a few species of *Thomasomys* (e.g., *T. apeco*, *T. aureus*, *T. nicefori*, and *T. princeps*) but is perpendicularly oriented to the mesolophid (state 2) in *Thomasomys auricularis*, *T. hudsoni*, and *T. pyrrhonotus*. All outgroup taxa have the state 0 with the exception of *Wilfredomys oenax* that has the state 1, and *Phaenomys ferrugineus* and *Rhagomys longilingua* that have the state 2.

**105. Mesolophids of m1-m2:** *Present, well developed (0); or indistinct, rudimentary, or absent (1).*

Pacheco (Part I: character 83) noted that the occurrence of the mesolophid mirrors those on the upper molars; except in a few thomasomyines in which it appears to follow an independent evolutionary trend. All examined species exhibit well developed mesolophids (state 0) except *Thomasomys praetor* and the outgroups *Abrawayaomys ruschii*, *Wiedomys pyrrhorhinos*, and *Rhagomys rufescens*.

**106. Mesolophid on m3:** *Conspicuous (0); or indistinct (1).*

It appears that the presence or reduction of the mesolophid on the third lower

molars varies independently from the other two lower molars. In thomasomyines, a conspicuous mesolophid on m3 (state 0) is exhibited in Rhipidomys, some species of Thomasomys (e.g., T. apeco, T. notatus, and T. oreas), and the outgroups Delomys, Phaenomys, and Wilfredomys. Indistinct mesolophid on m3 (state 1) is present in Aepeomys, Chilomys, and all other species of Thomasomys.

**107. Anterolabial cingulum of m2-m3:** *Present only in m2 although usually weak (0); or distinct in both molars (1); or large and patent in both molars (2).*

The anterolabial cingulum, present only in m2 (state 0), is exhibited in Aepeomys, Chilomys, and several Thomasomys species (e.g., T. baeops, T. notatus, and T. oreas). The state 1 is recorded in Rhipidomys caucensis, R. fulviventer, R. gardneri, R. ochrogaster, several Thomasomys species (e.g., T. cinereus, T. ischyus, T. kalinowskii, T. taczanowskii), and the outgroups Wiedomys and Wilfredomys. Large and distinct anterolabial cingulum in m2 and m3 (state 2) is exhibited in Rhipidomys latimanus, R. leucodactylus, R. macconnelli, some Thomasomys species (e.g., T. apeco, T. aureus, T. nicefori, and T. rosalinga), and the outgroups Abrawayaomys, Juliomys, Phaenomys, and Rhagomys.

**108. Posteroflexid breadth of m1-m2:** *Narrow and oblique (0); or broad and semicircular (1).*

In all muroids examined the posteroflexids in m1 and m2 are narrower than the adjacent murid, and their shape are usually oblique or smoothly concave (state 0). By contrast, the posteroflexids in m1 and m2 are deep, their breadth are equal or greater than the breadth of the adjacent murid, and have a strong comma shape (state 1) in a few species (e.g., Abrawayaomys, Juliomys pictipes, Phaenomys, Wilfredomys, Rhagomys

longilingua, Thomasomys apeco, T. aureus, T. auricularis, T. nicefori, T. popayanus, T. praetor, T. princeps, T. pyrrhonotus, and T. rosalinda).

**109. Entoconid on m3:** *Absent (0); or present (1).*

Leo L. and Gardner (1993) observed a well developed entoconid on third lower molars of Thomasomys apeco and its absence in T. aureus. Here, I observed a developed entoconid only in Thomasomys apeco and Phaenomys ferrugineus.

**110. Molar flexus (-ids) crenulation:** *No crenulated (0); or crenulated (1).*

Margins of lophs, lophids, flexus and flexids, mures and murids may be wrinkled or crenulated in some thomasomyines (state 1). Gardner and Romo R. (1993) reported and illustrated this feature as "wrinkled" for Thomasomys macrotis. State 1 is exhibited in Rhipidomys caucensis, Thomasomys bombycinus, T. cinereiventer, T. gracilis, T. macrotis, T. notatus, T. oreas, Thomasomys sp. 8, and Thomasomys sp. 9. Rhipidomys latimanus is polymorphic for this character.

**111. Accessory labial root of M1:** *Absent (0); or present (1).*

Based on Pacheco (Part I: character 85). All muroids examined lack accessory labial roots on M1 (state 0), but they are present in Aepeomys lugens, Thomasomys apeco, T. aureus, T. auricularis, T. dispar, T. eleusis, T. erro, T. gracilis, T. incanus, T. ischyrus, T. kalinowskii, T. macrotis, T. monochromos, T. nicefori, T. popayanus, T. praetor, T. princeps, T. pyrrhonotus, T. rosalinda, some undescribed species of Thomasomys, and the oryzomyines Handleyomys fuscatus and Holochilus brasiliensis.

**112. Lingual roots on M1:** *One root (0); or a single bilobed root (1); or two roots (2).*

This character is based on Carleton (1980: characters 8, 10) and Pacheco (Part I:

character 86). A single root on the lingual side of M1 (state 0) is the widespread condition in the sigmodontines examined, but accessory lingual roots (state 2) were observed in the Andean thomomyines Thomasomys macrotis, T. praetor, T. pyrrhonotus, Thomasomys sp. 1; and the outgroup taxa Phaenomys. I consider an intermediate state when the lingual margin of the lingual root and alveolus are deeply divided (state 1) as seen in Aepeomys, some species of Thomasomys (e.g., T. eleusis, T. ischyryus, T. kalinowskii, T. ladewi, T. monochromos, and T. rosalinda), and the outgroups Juliomys pictipes and Rhagomys.

**113. Lingual root on M3:** *One root (0); or a single bilobed root (1); or two roots (2).*

Most taxa exhibit just a single lingual root on M3 (state 0). Thomasomys princeps and Thomasomys sp. 2 have a bilobed root on M3 (state 1), whereas Thomasomys apeco, T. pyrrhonotus, and Thomasomys sp. 1 exhibit two roots on M3 (state 2).

**114. Roots on m2:** *Two roots (0); or three roots (1).*

This character was based on Pacheco (Part I: character 87). All muroids examined exhibit two roots on m2 (state 0), however three roots (state 1) are seen in Aepeomys, Thomasomys apeco, T. auricularis, T. eleusis, T. ischyryus, T. kalinowskii, T. macrotis, T. princeps, T. pyrrhonotus, and the oryzomyines Handleyomys fuscatus and Holochilus brasiliensis.

## LOWER JAW

**115. Masseteric crest position:** *Anterior edge of the masseteric crest posterior to the procingulum of m1 (0); or anterior edge of the masseteric crest below the procingulum*

*of m1 (1); or anterior edge of the masseteric crest anterior to the procingulum of m1 (2).*

This character follows Pacheco (Part I: character 89) who described the most anterior's edge of the masseteric crest in relation to the position of m1. The anterior edge of the masseteric crest is placed distinctly posterior to procingulum of m1 (state 0) in Aepeomys, Phaenomys, Rhipidomys latimanus, R. macconnelli, and all species of Thomasomys (except T. baeops, T. daphne, and T. notatus). The masseteric crest is placed just below the procingulum of m1 (state 1) in Chilomys, Rhipidomys caucensis, R. leucodactylus, R. gardneri, R. ochrogaster, Thomasomys baeops, T. daphne, and the outgroups Delomys, Juliomys sp., Wilfredomys oenax; Handleyomys fuscatus, Microryzomys minutus, and Oecomys bicolor. Masseteric crests placed far anterior to the procingulum of m1 (state 2) is exhibited in the outgroups Holochilus brasiliensis, Oligoryzomys fulvescens, Oryzomys palustris, Abrawayaomys ruschii, Juliomys pictipes, Rhagomys rufescens, R. longilingua, and Wiedomys pyrrhorhinos.

**116. Mental foramen position:** *Low, below the diastema (0); or high, on the dorsal surface of the diastema or very near (1).*

This character was described by Pacheco (Part I: character 90). Among the taxa I surveyed, a low mental foramen (state 0) is seen in most sigmodontines, but only Juliomys pictipes, Wiedomys pyrrhorhinos, and Wilfredomys oenax exhibit a mental foramen positioned directly on the dorsal surface of the diastema (state 1).

**117. Mandibular diastemal shape:** *The m1 alveolus and the diastema form a straight and acute angle (0); or the angle is obtuse, more open (1); or the angle is very obtuse, much close to horizontal (2).*

An obtuse angle between the m1 alveolus and the diastema (state 1) is the



widespread condition among examined taxa. A straight and acute angle (state 0) is exhibited in Thomasomys apeco, T. aureus, T. auricularis, T. nicefori, T. praetor, T. princeps, T. pyrrhonotus, Thomasomys sp. 1, Thomasomys sp. 2, and all outgroup thomomyines (except in Rhagomys longilingua, which has the state 1). A very horizontal angle (state 2) is exhibited only in Chilomys.

**118. Capsular process of lower incisor:** *Absent (0); or distinct (1).*

Voss (1993) reported that capsular process of lower incisors is absent in Thomasomys cinereus and Delomys, and distinctly present in Oryzomys palustris; he postulated that absence of capsular process is the primitive condition. This character was used by Pacheco (Part I: character 91). The capsular process is found absent (state 0) in most surveyed thomomyines. On the contrary, a capsular process (except Handleyomys fuscatus) is exhibited in Chilomys instans, Rhipidomys caucensis, R. latimanus, R. macconnelli, several species of Thomasomys (e.g., T. baeops, T. daphne, T. notatus, T. oreas, and T. taczanowskii), and in the outgroup taxa Abrawayaomys, Juliomys, Rhagomys, and all oryzomyines (except Handleyomys). Chilomys fumeus and Rhipidomys fulviventer are polymorphic.

**119. Relative Length of condylar and angular processes:** *Condylar process level with the angular process (0); or condylar process extending posteriorly beyond the angular process (1).*

The posterior extension of the condylar process is assessed in relation to the posterior extension of the angular process. A condylar process extending backward beyond the angular process (state 1) is observed in Aepeomys, Chilomys, Rhipidomys, many Thomasomys species (e.g., T. baeops, T. caudivarius, T. erro, T. incanus, T.

notatus, and T. oreas), and all the thomasomyines in the outgroup (except for Delomys, Phaenomys, and Wilfredomys). In contrast, the state 0 is exhibited in several Thomasomys species (e.g., T. aureus, T. cinereus, T. ischyus, and T. vestitus).

**120. Coronoid Process:** *Short, extending below the condylar process (0); or long and falciform, equal or higher than the condylar process (1).*

All Andean thomasomyine species (except Rhipidomys fulviventris, R. leucodactylus, R. gardneri, R. ochrogaster and Thomasomys gracilis) exhibit a long and falciform coronoid process, equal or higher than the condylar process (state 1). All outgroup taxa exhibit a short coronoid process (state 0) with the exception of Delomys, Handleyomys fuscatus, Holochilus brasiliensis, and Oryzomys palustris.

**121. Retromolar region:** *Shallow, as a narrow groove (0); or present, deep in a fossa (1).*

This character was described by Rinker (1954), Greene (1935), Voss (1988), Luna and Patterson (2003), and Pacheco (Part I: character 92). The retromolar region between the last two lower molars and the medial side of the coronoid process is a shallow, narrow groove that is weakly or not perforated (state 0). In contrast, in Abrawayaomys, and Rhagomys, this region is broad, deeply excavated in a fossa, and highly perforated.

**122. Ventral margin of mandible:** *slight concavity (0); or conspicuously horizontal (1).*

The ventral margin of the mandible exhibit a weak concavity (state 0) in most sigmodontines. By contrast, the ventral margin of the mandible in Rhagomys is almost horizontal or flat, in part due to the strong development of the inferior masseteric crest.

## POST-CRANIAL SKELETON

**123. Supratrochlear fenestra of humerus:** *Absent (0); or polymorphic, either absent or present (1); or present (2).*

I follow Pacheco (Part I: character 94) for this character. State 0 and 2 are present in similar proportions in thomasomyines, but state 2 is dominant in oryzomyines. Among thomasomyines, the "olecranon" or "anconeal" fossa of the distal humerus has a thin translucent lamina or is usually pierced by a small perforation (state 2) in Aepeomys lugens, some species of Thomasomys (e.g., T. cinereus, T. emeritus, T. hylophilus, T. kalinowskii, T. macrotis, T. paramorum, and T. rhoadsi), and the outgroups Delomys collinus, Juliomys sp., and Wilfredomys. By contrast, the bony lamina is thicker, not translucent and not perforated (state 0) in Chilomys, Rhipidomys, a few species of Thomasomys (e.g., T. baeops, T. notatus, and T. taczanowskii), and the outgroups Juliomys and Rhagomys longilingua.

**124. Number of thoracic vertebrae:** *13 thoracics (0); or 12 thoracics (1).*

I employ only two states following Pacheco (Part I: character 96) who reported that thomasomyines possess only 13 or 12 thoracic vertebrae. Stepan (1995) reported the state (0) for Thomasomys cinereus (which I reidentified as T. caudivarius), T. daphne, T. hylophilus, T. oreas, T. paramorum, and T. pyrrhonotus (which I reidentified as T. auricularis). All thomasomyines exhibit 13 thoracic vertebrae, except Rhipidomys gardneri, Wiedomys, and Wilfredomys. By contrast, all oryzomyines possess 12 thoracic vertebrae. Juliomys pictipes presented both states in apparently distinct populations.

**125. Number of caudal vertebrae:** *24 -- 29 (0); or 30 -- 35 (1); or 36 -- 40 (2); or 41 or more (3).*

This character was employed by Pacheco (Part I: character 97) in his thomasomyine phylogeny. Aepeomys, Chilomys and Rhipidomys, and several Thomasomys (e.g., T. baeops, T. cinereus, T. gracilis, and T. paramorum) have moderately long tail with 36 to 40 vertebrae (state 2). Tails with 41 or more vertebrae (state 3) are predominantly exhibited only in Thomasomys (e.g., T. aureus, T. caudivarius, T. daphne, T. erro, and T. macrotis). The outgroup thomasomyines exhibit the state 2, except Delomys that has the state 1.

**126. Chevron bones:** *Absent, left and right elements unfused, not forming a closed arch (0); or polymorphic, either elements unfused or fused forming an arch (1); or present, left and right element fused forming an arch without a spinous process (2); or arch with a posterior border bearing a spinous process (3).*

This character is based on Stepan (1995: character 28S) and used also by Pacheco (Part I: characters 98, 99) in his thomasomyine phylogeny. State 0 is the most common condition among the muroids examined. State 1 is only exhibited by Thomasomys baeops and T. taczanowskii. The state 2 is relatively common in the Andean thomasomyine group (e.g., Aepeomys lugens, Chilomys fumeus, Rhipidomys gardneri, Thomasomys cinereus, T. daphne, T. hylophilus, and T. kalinowskii). Among the outgroup taxa, the state 0 is present in Delomys collinus, Juliomys, Rhagomys longilingua, Wilfredomys oenax, and the oryzomyine Oecomys bicolor; whereas, the state 2 is exhibited by Wiedomys, Handleyomys fuscatus and Microryzomys minutus and the state 3 in the oryzomyines Holochilus brasiliensis, Oligoryzomys fulvescens and Oryzomys palustris.

**127. Position of the trochlear process of calcaneum:** *Trochlear process level*

*or overlap with the posterior articular facet (0); or distinct gap between proximal edge of the trochlear process and posterior articular facet (1).*

This character follows Pacheco (Part I: character 100). Most thomatomyines exhibit a trochlear process that level or overlaps with the posterior articular facet. however Aepeomys lugens, Chilomys fumeus, Thomasomys erro, and the outgroups Delomys collinus, Rhagomys longilingua, and all oryzomyines examined have a distinct gap between the proximal edge of the trochlear process and posterior articular facet (state 1).

**128. Peroneal process of fifth metatarsal:** *Moderately long, not quite extending to proximal edge of cuboid (0); or polymorphic, either moderately long or short (1); or short, not extending proximally beyond about the middle of the cuboid (2).*

This character was based on Stepan (1995: character 31S) and Pacheco (Part I: character 101). Among the taxa I surveyed, a moderately long peroneal process (state 0) is seen in all thomatomyines. By contrast, a short peroneal process (state 2) is exhibited only in the oryzomyines Handleyomys fuscatus, Holochilus brasiliensis, Oecomys bicolor, and Oryzomys palustris. Microryzomys minutus and Oligoryzomys fulvescens exhibit both states which I interpret as within-species polymorphism (state 1).

## DIGESTIVE TRACT

**129. Transverse palatal ridges:** *Two complete diastemal and five incomplete intermolar ridges (0); or two complete diastemal and six incomplete intermolar ridges (1).*

All sigmodontine rodents examined here present two complete diastemal palatal ridges (=rugae); however, variation is found in the number of intermolar ridges. Five

incomplete intermolar ridges are found in all thomasomyines except in Thomasomys niveipes, T. notatus, and Thomasomys sp. 9 which have six incomplete intermolar ridges.

**130. Distributional gastric epithelium:** *Stomach hemiglandular, bordering fold extends from the incisura angularis (0); or intermediate I, bordering fold crosses the lesser curvature at a point between the pyloric sphincter and the incisura angularis (1); or intermediate I state with an extensive incursion of cornified squamous epithelium (2); or intermediate II, bordering fold does not cross lesser curvature, which is completely lined with cornified squamous epithelium (3); or discoglandular (4).*

Carleton (1973) and Pacheco (Part I: character 118) found that the hemiglandular stomach is the widespread condition among sigmodontines and thomasomyines in particular. However, extensive variation exists in the thomasomyine group. The state 1 is exhibited in Thomasomys eleusis, T. kalinowskii, Thomasomys sp. 4, Thomasomys sp. 5, and Thomasomys sp. 7. A similar state but with extensive incursion of cornified squamous epithelium (state 2) is reported in Thomasomys apeco and Thomasomys sp. 1. A further reduction of the glandular epithelium (state 3) is exhibited only in Thomasomys erro. A distinct discoglandular stomach (state 4) occurs only in Aepeomys lugens (fig. 10).

**131. Incisura angularis:** *Shallow (0); or moderately deep (1).*

Pacheco (Part I: character 120) employed this character following the scoring scheme of Carleton (1980). All muroids examined present a shallow incisura angularis, conforming to the unilocular stomach type, except Thomasomys apeco, T. aureus, T. praetor, Thomasomys sp. 1, Thomasomys sp. 2, and Thomasomys sp. 4 (fig. 10) in which the incisura angularis is moderately deep. These results support Carleton's (1973)

description based on a single specimen of Thomasomys aureus.

**132. Gall bladder:** *Present (0); or absent (1).*

Vorontsov (1979), Carleton (1980), Voss (1991), and Voss and Carleton (1993) have interpreted the absence of gall bladder as derived, and apparently this organ has been lost independently among sigmodontine rodents (Steppan, 1995). Voss (1991) observed a gall bladder in Aepeomys, Chilomys, and several species of Thomasomys, but uniformly absent in Rhipidomys. Luna and Patterson (2003) reported the absence of a gall bladder in Rhagomys longilingua. Pacheco (Part I: character 122) also found the gall bladder in several Thomasomys. My data matrix here documents the gall bladder as present in all species of thomasomyines studied here except in Rhipidomys, Rhagomys longilingua, Thomasomys oreas, and Thomasomys sp. 4. The gall bladder is also absent in oryzomyines.

## GLANS PENIS AND REPRODUCTIVE TRACT

**133. Distribution of spines on glans penis body:** *Spines present throughout body (0); or spines present only in a region reduced (1); or spines absent (2).*

The distribution of spines on the glans penis body in some thomasomyines was observed by Hooper and Musser (1964) and Pacheco (Part I). Presence of spines throughout the whole body (state 0) is the widespread condition. Chilomys instans and Thomasomys baeops present spines in a reduced region (state 1). Absence of spines is reported in Aepeomys reigi and Thomasomys aureus.

**134. Grooves on glans penis body:** *Shallow or absent (0); or distinct but usually extends no more than half the body (1); or deep, and extends beyond half the length of*

*body* (2).

Hooper and Musser (1964) observed in Rhipidomys mastacalis a deep groove on dorsal and ventral midline of the glans penis body. Pacheco (Part I: character 105) further observed such deep grooves in other three species of Rhipidomys, but absent or reduced in other thomatomyines (fig. 11). My expanded matrix confirms that deep grooves (state 2) are exhibited in all Rhipidomys, and in Thomasomys apeco (fig. 11). Mid dorsal and midventral grooves are shallow or absent (state 0) in Aepeomys reigi, Chilomys instans, several species of Thomasomys (T. australis, T. cinereus, T. dispar, T. erro, T. gracilis, T. niveipes, T. notatus, and T. silvestris), and in the oryzomyine Oryzomys palustris. In contrast, state 1 is exhibited in some Thomasomys (e.g., T. aureus, T. baeops, T. bombycinus, T. kalinowskii, T. oreas, and T. rhoadsi), and the outgroups Microrizomys, Oecomys, and Wilfredomys.

**135. Crater rim:** *Rim uniform (0); or rim multiply divided (1).*

A uniform crater rim (state 0) is the widespread condition, however Hooper and Musser (1964) reported a crater rim that is multiply divided (state 1) in some thomatomyines. I observed that this state occurs in Chilomys instans, Rhipidomys leucodactylus, R. gardneri, Thomasomys apeco, T. aureus, T. baeops, T. ladewi, T. laniger, T. nicefori, T. rhoadsi and Thomasomys sp. 1.

**136. Dorsal and ventral margin of crater rim:** *Both dorsal and ventral margins are about the same height (0); or the dorsal margin is distinctly longer than the ventral one (1).*

A glans penis with the dorsal and ventral margins of the crater rim equally developed is the common condition in sigmodontines; however, the dorsal margin of the



crater rim is distinctly longer than the ventral margin (state 1) in a few species such as Aepeomys reigi, Thomasomys apeco, T. kalinowskii, T. ladewi, T. laniger, T. rhoadsi and Thomasomys sp. 1.

**137. Notch on midventral margin:** *Absent (0); or present (1).*

A crater rim relatively uniform in its ventral margin is the common condition in sigmodontines; however, the ventral margin of the rim is deeply incised forming a notch in a few thomasomyines as seen in Aepeomys reigi, Chilomys instans, Thomasomys apeco, T. laniger, T. nicefori, T. praetor, T. silvestris, and Thomasomys sp. 1.

**138. Medial bacular mound length:** *Extending slightly distal to lateral bacular mounds (0); or remarkably long, well beyond the lateral bacular mounds (1).*

All sigmodontines examined present a medial bacular mound of the glans penis that extends slightly distal to the lateral bacular mounds (state 0), except in Thomasomys apeco, T. nicefori, and Thomasomys sp. 1 in which extremely long medial mounds are observed.

**139. Lateral bacular mound shape:** *Simple, not "triple curved" (0); or complexly curved, "triple-curved" (1); or distal portion of the lateral mounds pointed (2).*

Simple lateral bacular mound is the predominant condition among the sigmodontines examined. However, Hooper and Musser (1964: 20, fig. 6) described the triple-curved shape of the lateral bacular mound (state 1) of Rhipidomys mastacalis as: "the lateral mounds are more densely spinous and more complexly curved, ... each of the slightly shorter lateral pair triple-curved--distad, ventrad and (terminally) laterad--the distal face of the laterally projecting part spine-studded...." Pacheco (Part I: character 108) observed the triple-curved lateral mound (state 1) in other species of Rhipidomys.

The state 1 is here observed in all Rhipidomys (except R. macconnelli), Thomasomys notatus, T. oreas, and Thomasomys sp. 9. In contrast, Thomasomys baeops and T. taczanowskii exhibit lateral mounds with the distal border slender and conical that projects slightly ventrad and mediad to the medial bacular mound, distinct from the lateral mounds as seen in Rhipidomys. These states were analysed as unordered transformations.

**140. Lateral mound relative position:** *Lateral mounds not visible, tips placed deep in crater (0); or visible, tips extending to crater rim or just beyond it (1); or large and distinctly visible, tips extending far beyond the crater rim (2).*

The glans penis morphology among thomasomyines is very diverse. Among the oryzomyines and Andean thomasomyines the widespread condition is to have the tips of the lateral mounds extending near the crater rim or just beyond it (state 1). However, the lateral mounds are found deep in the crater (state 0) in Thomasomys laniger, T. nicefori, T. rhoadsi, and Thomasomys sp. 1. Only in a few species the tips of the lateral mounds extend well beyond the crater rim as in Rhipidomys, Thomasomys notatus, T. oreas, and Thomasomys sp. 9.

**141. Spines on the lateral mounds:** *Absent (0); or present (1).*

Absence of spines on the lateral mounds (state 0) is the widespread condition among examined taxa. However, spines are present on the distal margin of the lateral mounds in several thomasomyines. (e.g., Rhipidomys gardneri, R. leucodactylus, R. macconnelli, Thomasomys hylophilus, T. kalinowskii, T. niveipes, T. notatus, and T. oreas).

**142. Spines on the urethral flap of glans penis:** *Absent (0); or polymorphic,*

*either absent or present (1); or present (2).*

Hooper and Musser (1964) evaluated the glans penis of some species of Thomasomys and Rhipidomys. They observed that the urethral flap of the glans penis usually exhibited a spinous region (state 2), with the exception of T. aureus. My observations in the presented data matrix agree with them. Non-spinous urethral flaps (state 0) are exhibited in Aepeomys reigi, Rhipidomys macconnelli, Thomasomys aureus, T. australis, T. bombycinus, T. cinereus, T. daphne, T. gracilis, T. laniger, T. praetor, Wilfredomys, and all oryzomyines. Langguth and Silva Neto (1993) suggested that oryzomyines exhibit non-spinous urethral flaps as opposed to the spinous flaps present in Wiedomys, phyllotines, and akodontines. They also suggested that absence of spinous may be primitive for Sigmodontines.

**143. Spines on dorsal papilla:** *Spines absent (0); or spines present (1).*

The disposition of spines on the dorsal papilla is highly variable and potentially very informative. Spines when present usually cover the dorsal surface of the papilla or might occur as a single large spine on the tip. Size and number of spines are also apparently informative but few data on the intraspecific variability (especially ontogenetic) is available to confidentially include this information in a phylogenetic context. For this reason, I interpret all variations as only spines present. Presence of spines (state 1) is the widespread condition in the sigmodontines examined; however, spines are absent in a few species of thomasomyines (e.g., Aepeomys reigi, Thomasomys aureus, T. cinereus, T. gracilis, T. laniger, T. praetor, and Thomasomys sp. 3), and in the outgroups Microryzomys minutus and Oecomys bicolor.

**144. Preputial glands:** *Absent (0); or one pair (1); or two pairs (2); or*

*numerous (3).*

Information on reproductive glands of sigmodontine rodents is limited. My scheme coding follows Pacheco (Part I: character 115). Preputials are absent in Rhipidomys leucodactylus, R. gardneri, Thomasomys cinereus, T. emeritus, T. kalinowskii, T. ladewi, T. notatus, T. rhoadsi, T. silvestris, Thomasomys sp. 4, Thomasomys sp. 5, and the oryzomyine Oryzomys fulvescens. The unusually numerous preputials (state 3) reported for Thomasomys aureus (Voss and Linzey, 1981) is also exhibited in Thomasomys erro, T. paramorum, T. praetor, Thomasomys sp. 1, Thomasomys sp. 3, Thomasomys sp. 7, and Wilfredomys (fig. 12).

**145. Prostate ventral glands:** *Lateral ventral prostate larger than medial (0) ; or ventral prostates of equal size (1); or medial ventral prostates larger than laterals (2).* Voss and Linzey (1981) described the reproductive tract morphology of Chilomys instans, T. aureus, T. baeops, T. laniger, and T. rhoadsi. They found that in Thomasomys the medial and lateral ventral prostates are of equal size except in T. laniger in which the medial pair is much larger. Among the thomasomyines I examined (fig. 13), ventral prostates of equal size (state 1) are reported for Rhipidomys gardneri, Thomasomys baeops, T. kalinowskii, T. ladewi, T. praetor, T. rhoadsi, T. taczanowskii, Thomasomys sp. 1, Thomasomys sp. 4, and Thomasomys sp. 7. By contrast, lateral ventral prostate larger than the medial ones (state 0) are seen only in Thomasomys cinereus, T. daphne, T. oreas, and T. notatus. Medial ventral prostates larger than the lateral ones (state 2) are reported in Chilomys instans, Thomasomys emeritus, Thomasomys sp. 5, Rhagomys longilingua, and oryzomyines (except Microryzomys minutus which has state 1).

## RESULTS

With all characters weighted equally and multistate transformations ordered, 192 equally most-parsimonious trees were produced, each one with 1512 steps (CI = 0.270, RI = 0.608). A strict consensus of these trees is shown in figure 14. The tree is rooted to the oryzomyine species following the hypothesis of Pacheco (Part I). Results are described below and statistical summaries are provided in tables 1 and 2.

The strict consensus tree shows that the Andean thomasomyine group is monophyletic and includes Aepeomys, Chilomys, Rhipidomys, and Thomasomys, although is weakly supported (bootstrap value: 18; decay value: 1). The group is composed of two large clades: (1) In the first clade, Rhipidomys clusters with several species of Thomasomys (e.g., T. baeops, T. gracilis, T. notatus, T. oreas, T. taczanowskii, Thomasomys sp. 8, and Thomasomys sp. 9), although is supported with low values (bootstrap value: 20; decay value: 1). At the base of the group, Thomasomys baeops + T. taczanowskii comprise a monophyletic group (bootstrap value: 57; decay value: 1), allied to a clade that includes a monophyletic Rhipidomys (bootstrap value: 43; decay value: 2) and a group of small-sized species of Thomasomys (bootstrap value: 57; decay value: 3). In this last group, T. notatus is placed at the base, followed up by T. oreas that is sister to an unresolved group of T. gracilis + Thomasomys sp. 8 + Thomasomys sp. 9 (bootstrap value: 52, decay value: 3). (2) In the second clade, Chilomys is sister taxon of a group that contains Aepeomys and all remaining species of Thomasomys (bootstrap value: 17; decay value: 2). Chilomys is a monophyletic genus supported by large values (bootstrap value: 98; decay value: + 3), whereas the group of

all other species of Thomasomys (including Aepeomys) received low support (bootstrap value: 18; decay value: 2). This last group consists of two smaller clades: the first is a group (bootstrap value: 32; decay value: 2) that includes Thomasomys macrotis as sister species to a largely unresolved group that includes Thomasomys aureus and similar species (e.g., T. pyrrhonotus + T. rosalinda + T. auricularis, T. apeco + Thomasomys sp. 1, T. aureus, T. nicefori, T. popayanus, T. praetor, T. princeps, and Thomasomys sp. 2). This last group is relatively well supported (bootstrap value: 75; decay value: +3).

The second group is a largely unresolved clade that includes ten lineages of Thomasomys that are weakly supported (bootstrap value: 5; decay value: 2). One lineage includes a large group of species: Aepeomys lugens + A. reigi (bootstrap value: 100; decay value: +3) that is sister to Thomasomys erro (bootstrap value: 85; decay value: +3), followed down in the tree by T. incanus + Thomasomys sp. 6, Thomasomys sp. 7, T. ischyrys, Thomasomys sp. 4 + Thomasomys sp. 5, T. eleusis, T. kalinowskii, T. ladewi, and T. contradictus + T. dispar at the base. A second lineage includes a group where Thomasomys hudsoni is sister to T. niveipes + T. paramorum (bootstrap value: 7; decay value: 2). This group clusters with two small groups: one conformed by T. daphne + Thomasomys sp. 3 and T. australis (bootstrap value: 29; decay value: 2), and the second by T. monochromos that is sister to the pair T. cinnameus + Thomasomys sp. 11. In another lineage Thomasomys rhoadsi forms an unresolved clade with Thomasomys sp. 10 and T. fumeus. Other pair-group relationships are: T. bombycinus + T. cinereiventer, T. caudivarius + T. hylophilus, and T. emeritus + T. laniger.

Rhagomys is found sister taxa to the Andean thomasomyine group although with poor support (bootstrap value: 8; decay value: 1). The remaining thomasomyine taxa

from southeastern Brazil are successively basal outliers to Rhagomys and the Andean thomasomyine group. At the base of the Thomasomyini, Delomys is closely related to Phaenomys although with weak support (bootstrap value: 13; decay value: 1). Wiedomys and Wilfredomys form a monophyletic group but with low support (bootstrap value: 46; decay value: 2). Two species of Juliomys are next in the tree, but they did not make a monophyletic genus. Abrawayaomys follows up in the tree. The monophyly of Rhagomys is strongly supported (bootstrap value: 88; decay value: + 3).

## DISCUSSION

The results of my phylogenetic analysis confirm the monophyly of the Andean thomasomyine group, supporting the analyses based on sequences of cytochrome *b* by Smith and Patton (1999) and the previous phylogeny based on morphological characters by Pacheco (Part I). The last author identified the following putative synapomorphies of the Andean thomasomyine group: anterodorsal margin of zygomatic plate shallow, dorsal aperture of ectotympanic ring open, and M1 anterocone with labial and lingual conules subequal. This study confirms the anterodorsal lamina of the ectotympanic not contacting the petrosal (60) as a putative synapomorphy. In addition, the following unambiguously derived conditions (representing putative synapomorphies) are also identified: the hypothenar pad level with or overlapping interdigital pad 1 (10); the interorbital region incipiently squared or edged (43); anterolabial cingulum present only in m2, although usually weak (107); posteroflexid breadth of m1-m2 narrow and oblique (108); anterior edge of the masseteric crest below the procingulum of m1 (115); and the coronoid process long and falciform, equal or higher than the condylar process (120). A formal designation of the Andean thomasomyine clade of the Thomasomyini must await until further studies test the monophyly of the tribe Thomasomyini and the groups included as identified by Pacheco (Part I).

With the much denser taxon sampling of this study, the monophyly of Rhipidomys and Chilomys is confirmed. However, Thomasomys as currently understood (e.g., Musser and Carleton, 1993) is clearly polyphyletic; whereas most species of Thomasomys together with Aepeomys lugens and A. reigi cluster with T.



cinereus (the type species of Thomasomys), a group of seven species show closer affinities with Rhipidomys. My results therefore reject the hypothesis of monophyly advanced by Smith and Patton (1999) based on seven species of Thomasomys. On the other hand, my results are consistent with other phylogenetic studies based on morphology that have rejected a monophyletic Thomasomys. For example, Steppan (1995) recovered T. rhoadsi and T. aureus + T. baeops in different clades, whereas Pacheco (Part I) recovered T. notatus in a clade with species of Rhipidomys.

Smith and Patton (1999: figs. 4, 5) did not advocate an hypothesis of sister taxa for the Andean thomasomyine group. Their analyses clustered the Andean thomasomyines with the Akodontini + Scapteromyini + Phyllotini + Andean Clade in trees produced with a maximum parsimony approach, or with the Andean clade in the maximum likelihood analysis. In contrast, Pacheco (Part I) found that the Andean thomasomyines are successively sister to thomasomyines from southeastern Brazil although the support was very low. In this study, the phylogenetic relationships of the Andean thomasomyines to those from the southeastern Brazil are similarly reiterated. Thomasomyine representatives from southeastern Brazil by Smith and Patton (1999) were very limited, lacking the genera Abrawayaomys, Phaenomys, Rhagomys, and Wilfredomys s.s. Aepeomys s.s. from the northern Andes was not included either. Inclusion of genetic data from other thomasomyine lineages may modify the current molecular hypothesis. It is too early to reconcile discrepancies between the molecular and morphological evidences until taxonomic sampling has been expanded.

Nonetheless, karyotypic data available from other thomasomyines indicates some support to Pacheco's (Part I) hypothesis that links the Andean thomasomyine to those

from southeastern Brazil. For example, Bonvicino and Otazu (1999) reported the karyotype of Juliomys pictipes to be  $2N = 36$ ,  $FN = 34$ , different from reported karyotypes of Delomys and species of Oryzomyini (sensu Voss and Carleton, 1993) based on the low diploid and fundamental numbers. In addition, the karyotype of Juliomys shared at least one homology with the G-band karyotype of Rhipidomys mastacalis ( $2N = 44$ ,  $FN = 74$ ) and Rhipidomys sp. ( $2N = 44$ ,  $FN = 50$ ), a finding which suggests that Juliomys is more closely related to Rhipidomys. Similarly, Bonvicino et al. (2001) reported the karyotype of Phaenomys ferrugineus to be  $2N = 78$ , suggesting an affinity with Delomys, and that karyotypes of Andean thomomyines could be collectively distinguished from endemic thomomyines of southeastern Brazil.

Rhagomys is an enigmatic taxon of traditionally uncertain affinities. Thomas (1917) allied Rhagomys rufescens with Oryzomys-Oecomys, but most authors have considered it as Sigmodontinae incertae sedis (see summaries in Luna and Patterson [2003] and Pacheco [Part I]). Rhagomys longilingua was recently described from southeastern Peru by Luna and Patterson (2003). The authors provided a detailed morphological description of R. longilingua and R. rufescens, concluding that Rhagomys is monophyletic. However, the relationships of Rhagomys to other sigmodontines are still elusive. Luna-Wong (2002) suggested that Rhagomys longilingua may be sister taxa of the oryzomyine Scolomys, whereas Luna and Patterson (2003) listed some character states that might suggest a close relationships of Rhagomys with either oryzomyines or thomomyines. Pacheco (Part I) suggested that Rhagomys (represented by R. rufescens) is closely related to Abrawayaomys or is basal to the Andean thomomyine clade. This study confirms the monophyly of Rhagomys, suggesting also a closer relationship with

the Andean thomatomyines, although the latter relationship lacks substantial support.

The phylogenetic position of Abrawayomys within Sigmodontinae is also uncertain. In this study, with a denser taxon sampling, Rhagomys and Abrawayomys are not found closely related, but both are found successively basal to the Andean thomatomyines. No other cladistic hypothesis is known, except for Luna-Wong's (2002: fig. 20) who suggested a closely relationship of Abrawayomys with Phaenomys.

Delomys + Phaenomys is a novel relationship found at the base of all the Thomatomyini clade. This group is followed up by the clade Wiedomys + Wilfredomys, Juliomys pictipes, and Juliomys sp. My results support Bonvicino et al. (2001), based on diploid number comparisons, who remarked that the karyotype of Phaenomys is most similar to Delomys, than to karyotypes of Thomasomys or Rhipidomys.

Tribe (1996) presented a thorough taxonomic revision of Rhipidomys. He provided morphological comparisons with other genera that show resemblance to Rhipidomys, including several species of Thomasomys, the arboreal genus Oecomys, and the tyromyine Nyctomys. However, Tribe did not provide cladistic evidence for the monophyly of Rhipidomys but noted the need for such a study. Smith and Patton (1999) demonstrated the monophyly of Rhipidomys based on six species. This hypothesis is confirmed in this study based on seven species representing each of the three morphological sections (e.g., R. fulviventer, R. leucodactylus and R. macconnelli) proposed by Tribe (1996). Only the species R. macconnelli is common to both studies. My results also suggest that, except for the relationship between R. caucensis and R. fulviventer, the relationships among other species in the genus are unresolved, not concurring with the three sections identified by Tribe (1996).

Chilomys has been viewed as an enigmatic genus of peculiar morphology with uncertain affinities. This genus was previously considered an oryzomyine (Tate, 1932; Cabrera, 1961; Voss and Linzey, 1981; Reig, 1984), but Musser and Carleton (1993) suggested it might be closely related to thomasmomyines. Voss and Carleton (1993) subsequently defined and delimited the contents of the tribe Oryzomyini omitting Chilomys. Recently, Smith and Patton (1999) confirmed the thomasmomyine affinities of Chilomys suggesting that it may be sister to Thomasomys. Pacheco (Part I) supported the hypothesis that Chilomys is a thomasmomyine, and this study provides further corroboration based on much denser ingroup taxon sampling. In addition, this study suggests Chilomys is sister taxon of the large clade that contains most species of Thomasomys and Aepeomys (fig. 14).

The generic status of Aepeomys is not supported, since A. lugens (the type species of the genus Aepeomys), falls within a clade that includes Thomasomys cinereus (the type species of the genus) and other species of Thomasomys. This finding is not new. Osgood (1933a) earlier concluded that Aepeomys is a synonym of Thomasomys. Aguilera et al. (2000), based on karyological comparisons, supported a strong relationship of Aepeomys with Thomasomys since the diploid number ( $2N= 40, 42$ ) and predominance of acrocentric chromosomes are found in both taxa. However, the same argument may be valid to support the hypothesis that Aepeomys is a synonym of Thomasomys. If the generic status of Aepeomys is maintained as currently accepted (Musser and Carleton, 1993; Aguilera et al., 2000; Ochoa et al., 2001; Voss et al., 2002), then Inomys, Erioryzomys and probably other lineages should be elevated to genus to maintain monophyletic taxa. In the meantime, it seems advisable to retain Aepeomys as a

subgenus within Thomasomys because the moderately large support values obtained.

With a few exceptions, the relationships among the species of the genus Thomasomys are unresolved and weakly supported. Seven species of Thomasomys (e.g., T. baeops, T. gracilis, T. notatus, T. oreas, T. taczanowskii, and two undescribed species) show more affinities with Rhipidomys than with the clade that contains Thomasomys cinereus. To maintain a monophyletic Thomasomys, several generic-level monophyletic groups are recognized and require diagnosis to maintain a phylogenetic taxonomy.

Nine species of Thomasomys (e.g., T. apeco, T. aureus, T. auricularis, T. nicefori, T. popayanus, T. praetor, T. princeps, T. pyrrhonotus, T. rosalinda, and two undescribed species) are recovered in a moderately well supported clade which has been traditionally referred as the Thomasomys aureus group or complex (Thomas, 1921; Leo L. and Gardner, 1993; Gardner and Romo R., 1993). I agree with earlier suggestions that members of the T. aureus group should be removed from the remaining species of Thomasomys (Hooper and Musser, 1964; Carleton, 1973; Voss and Linzey, 1981); accordingly a new generic designation is proposed for this group.

Gardner and Romo R. (1993) suggested that Thomasomys macrotis is more closely related to T. ischyryus than to the Thomasomys aureus complex. However, my results suggest that T. macrotis is sister to the Thomasomys aureus group, although support values are low. T. macrotis is distinguished from the T. aureus group in several other characteristics (see Gardner and Romo R., 1993).

All remaining species of Thomasomys form a large clade which I tentatively consider the Thomasomys sensu stricto since it contains T. cinereus (the type species of

the genus). However, additional work is required to further support (or reject) the monophyly of this clade and to uncover the phylogenetic relationships within its members. Thomasomys s.s. contains 30 valid and six undescribed species (see Appendix 2). Derived character states found for these terminal taxa are presented in Appendix 3.

## CLASSIFICATION AND TAXONOMIC DIAGNOSES OF INGROUP CLADES

Below, I diagnose all currently recognized Andean thomasomyine genera, recovered as monophyletic groups in the analysis reported above, and I also diagnose several groups of species that my results suggest merit a genus status. Synapomorphies for all nodes and terminal taxa are presented in Appendix 3. Unambiguously derived conditions (representing putative synapomorphies) are shown in italic type. Ambiguous transformations (occurring in only some reconstructions) are written in standard type. Unique synapomorphies (not occurring in other nodes) are highlighted in boldface type. Numbers refer to character descriptions in the foregoing text.

### Thomasomys Coues, 1884

Figures 15, 16, 17

Thomasomys Coues, American Naturalist, 1884: 1275.

Aepeomys Thomas, Ann. Mag. Nat. Hist., ser. 7, vol. 1, 1898: 452.

Erioryzomys Bangs, Proc. New England Zool. Club, 1900: 96.

Inomys Thomas, Ann. Mag. Nat. Hist., ser. 8, vol. 20, 1917: 197.

Thamasomys Thomas, 1920: 233 (incorrect subsequent spelling).

TYPE SPECIES: Hesperomys cinereus Thomas, 1882.

GEOGRAPHIC DISTRIBUTION: From the Venezuelan states of Mérida and Lara, southward along the Andes to the Bolivian departments of Cochabamba and Santa Cruz states, mostly above 1500 m of elevation.

INCLUDED SPECIES: australis Anthony, 1925; bombycinus Anthony, 1925;

caudivarius Anthony, 1923; cinereiventer J. A. Allen, 1912; cinereus Thomas, 1882; cinnamomeus Anthony, 1924; contradictus Anthony, 1925; daphne Thomas, 1917; dispar Anthony, 1925; eleusis Thomas, 1926; emeritus Thomas, 1916; erro Anthony, 1926; fumeus Anthony, 1924; hudsoni Anthony, 1923; hylophilus Osgood, 1912; incanus Thomas, 1894 (including fraternus Thomas, 1927); ischyrus Osgood, 1914; kalinowskii Thomas, 1894; ladewi Anthony, 1926; laniger Thomas, 1895; lugens Thomas, 1896 (including ottleyi Anthony, 1932); monochromos Bangs, 1900; niveipes Thomas, 1896; onkiro Luna and Pacheco, 2002; paramorum Thomas, 1898; reigi Ochoa G., Aguilera, Pacheco and Soriano, 2001; rhoadsi Stone, 1914; silvestris Anthony, 1924; vestitus Thomas, 1898; vulcani Thomas, 1898; and several undescribed species ("Thomasomys" sp. 3, "Thomasomys" sp. 4, "Thomasomys" sp. 5, "Thomasomys" sp. 6, "Thomasomys" sp. 7, "Thomasomys" sp. 10, and "Thomasomys" sp. 11 of Appendix 2).

EMENDED DIAGNOSIS: *Carotid circulation pattern 1 (with stapelial foramen, squamosal-alisphenoid groove, and sphenofrontal foramen present: 52); anterior process of ectotympanic small (78); protoflexus on M2 faint or absent (97); crater rim of glans penis multiply divided (135); notch on midventral crater margin absent (137); preputial glands absent (144).* DELTRAN: *genal 1 vibrissae absent (15); maxillary palatal pits absent (68); hypoflexus of M1 narrow (94).*

#### New genus A

Figs. 18, 19, 20, 21, 22

TYPE SPECIES: Hesperomys aureus Tomes, 1860.



**GEOGRAPHIC DISTRIBUTION:** Montane forests mostly above 1500 m elevation from the Venezuelan state of Táchira, southward along the Andes to the Bolivian departments of Cochabamba and Santa Cruz.

**INCLUDED SPECIES:** apeco Leo L. and Gardner, 1993; aureus Tomes, 1860 (including altorum J. A. Allen, 1914); auricularis Anthony, 1923; nicefori Thomas, 1921; popayanus J.A. Allen, 1912; praetor Thomas, 1900; princeps Thomas, 1895; pyrrhonotus Thomas, 1886; rosalinda Thomas and St. Leger, 1926; and two undescribed species ("Thomasomys" sp. 1; and "Thomasomys" sp. 2 of Appendix 2).

**DIAGNOSIS:** *Hypothenar and thenar pad of peds level or overlap (8); halluctal claw extending to first interphalangeal joint of dII or beyond (13); claw of dV very long, extending to the base of claw of dIV, or beyond (14); genal 1 vibrissae present (15); mystacial vibrissae very long, extending well beyond the posterior margin of pinnae to a point greater than the length of one pinna (17); body pelage pattern moderately countershaded (20); interorbital region convergent, not beaded (43); interorbital region narrow (44); postglenoid foramen large, its anterior margin level with the tegmen tympani or forward (56); incisive foramina long extending between the M1 procingula (62); molar-bearing portion of the maxillae rectangular (69); upper incisors opisthodont (82); anteroloph oriented backward (92); M1 paraloph oriented backward to the mesoloph (93); M1 hypoflexus broad (94); m1 metalophid antero-posteriorly oriented to the front (103); entolophids of m1-m2 anteromedially oriented to the mesolophid-murid angle or to the base of mesolophid (104); anterolabial cingulum of both m2-m3 large (107); posteroflexid breadth of m1-m2 broad and semicircular (108); lingual root on M3 bilobed (113); angle formed by the m1 alveolus and the diastema is straight and acute (117);*

*incisura angularis intermediate* (131). In addition DELTRAN optimization found the following characters: crater rim multiple divided (135); notch on midventral margin present (137); and numerous preputial glands (144).

#### New genus B

Figs. 23, 24

TYPE SPECIES: Oryzomys baeops Thomas, 1899

GEOGRAPHIC DISTRIBUTION: Montane forests mostly above 1000 m elevation from the Colombian departments of Antioquia and Caldas, southward along the Andes to the Peruvian departments of Cajamarca and Lambayeque.

INCLUDED SPECIES: baeops Thomas, 1899, and taczanowskii Thomas, 1882.

DIAGNOSIS: *pattern coloration of tail polymorphic either uniform or with the tip white* (26); dorsal aperture of ectotympanic ring polymorphic either close or open (60); *mesopterygoid fossa breadth subequal* (74); *anterior process of the ectotympanic small* (78); *chevron bones polymorphic, left and right elements either unfused or fused forming an arch (but without spines)* (126); distal portion of the lateral mounds pointed (139).  
DELTRAN: manual digits with second and fifth digits subequal (3); maxillary septum long, approximately half the length of the incisive foramina or larger (63); hypoflexus size of M1 narrow or moderate (94); protostyle and enterostyle on M1 absent (96); distal portion of the lateral bacular mounds pointed (139).

#### New genus C

Figs. 25, 26, 27

TYPE SPECIES: Thomasomys gracilis Thomas, 1917

GEOGRAPHIC DISTRIBUTION: Eastern montane forests from the Peruvian department of San Martín to the Bolivian department of Cochabamba, mostly above 2500 m elevation.

INCLUDED SPECIES: gracilis Thomas, 1917; oreas Anthony, 1926; and two undescribed species ("Thomasomys" sp. 8, "Thomasomys" sp. 9 in appendix 2).

DIAGNOSIS: ungual tufts on manual claws well developed (1); margins of the manus claws closed at base (2); tip of tail without pencil (27); *notch between the maxillary zygomatic process and lacrimal bone present* (37); *maxillary palatal pits absent* (68); *sphenopalatine vacuities with moderately large perforations* (71); *bullae inflated*. *Eustachian tube indistinct* (77); *anterior process of the ectotympanic small* (78); *anterior edge of the masseteric crests posterior to the procingulum of m1* (115); left and right elements of chevron bones form an arch without a spinous process (126). DELTRAN: ventral base of claws on manus closed at base (2); premaxillae extended anterior to nasals but posterior to zygomatic notch (30); incisive foramina long, extending between M1 procingula (62); molar-bearing portion of the maxillae rectangular (69).

#### New genus D

TYPE SPECIES: Thomasomys macrotis, Gardner and Romo R., 1993.

GEOGRAPHIC DISTRIBUTION: Peru, San Martín Department, Parque Nacional Río Abiseo, Puerta del Monte, ca 3250 m.

INCLUDED SPECIES: macrotis Gardner and Romo R. (1993).

DIAGNOSIS: *Ventral base of claws on manus medially keeled* (2); *Gap present*

*between hypothenar and interdigital pad 1 (10); more than one third of the tail length white (26); premaxillae terminating anterior to nasals and the zygomatic notch (30); lacrimal with posterior projection (38); antorbital bridge low, below 1/4 of the rostrum height (39); alveolus of first upper molar anterior to the posterior margin of the zygomatic plate (84); molars moderately hypsodont (85); molar flexus (-ids) crenulation present (110); two lingual roots on M1 (112). DELTRAN: gap between the hypothenar and thenar pad of pes (8); genal 1 vibrissae absent (15); hypoflexus of M1 narrow or moderate (94).*

#### New genus E

Figs. 28, 29, 30

TYPE SPECIES: Thomasomys notatus Thomas, 1917

GEOGRAPHIC DISTRIBUTION: Eastern montane forests of Peru, from Amazonas to Cuzco departments, at elevations from ca. 1400 to 3000 m.

INCLUDED SPECIES: notatus Thomas, 1917.

DIAGNOSIS: *Body pelage pattern, distinctly countershaded (20); posterior extension of nasals long (29); postglenoid foramen longer than tegmen tympani (56); molar-bearing portion of the maxillae triangular (69); anterocone with small anterolingual conule (88); preputial glands absent (144). DELTRAN: ungual tufts on manual claws absent (1); tip of tail with a small tuft of long hairs (27); anterolabial cingulum exhibited only on m2 (107); grooves on glans penis body shallow (134).*

#### Chilomys Thomas, 1897

Figs. 31, 32

TYPE SPECIES: Oryzomys instans Thomas, 1895

GEOGRAPHIC DISTRIBUTION: Venezuelan states of Táchira and Mérida, southward along the Andes to Cañar Province in Ecuador, mostly above 1100 m of elevation.

INCLUDED SPECIES: fumeus Osgood, 1912; instans Thomas, 1895.

EMENDED DIAGNOSIS: *tip of tail white* (26); *ventral margin of the zygomatic arch placed above the orbital floor by half the orbital region* (42); *interorbital region broad* (44); *jugal bone long* (47); *optic foramen, posterior to M3* (50); *alisphenoid strut absent* (51); *parietal-supraoccipital suture distinctly broad, suture is at least half the posterior margin of parietal breadth* (58); *incisive foramina small* (62); *palatal length long* (64); *Alisphenoid squamosal posterior margin with notch* (76); *malleus lamina of rectangular shape* (79); *upper incisors proodont* (82); *anteromedian flexus absent* (87); *anterocone small* (88); *hypoflexus of M1 wide* (94); *hypoflexus of M3 indistinct* (98); *anteromedian flexid of m1 absent or weak* (99); *ridge on anterolabial cingulum of m1 short or absent* (102); *shape of the mandibular diastemal flat almost horizontal* (117); *spines on glans penis body partially distributed* (133); *grooves on glans penis body shallow* (134).

DELTRAN: *position of hypothenar pad in relation to thenar (pes) polymorphic* (8); *interorbital region breadth broad* (44); *maxillary palatal pits absent* (68); *anterolabial cingulum only on m2* (107).

Rhipidomys Tschudi, 1845

Figs. 33, 34

TYPE SPECIES: Hesperomys leucodactylus Tschudi, 1845

GEOGRAPHIC DISTRIBUTION: Eastern Panamá throughout Amazonia to southeastern Brazil and northern Argentina from 350 to 3500 m approximately.

INCLUDED SPECIES (after Musser and Carleton, 1993): austrinus Thomas, 1921; caucensis J. A. Allen, 1913; couesi J. A. Allen and Chapman, 1893; fulviventer Thomas, 1896; gardneri Patton, da Silva, and Malcolm, 2000; latimanus Tomes, 1860; leucodactylus Tschudi, 1845; macconnelli De Winton, 1900; mastacalis Lund, 1840; nitela Thomas, 1901; ochrogaster J. A. Allen, 1901; scandens Goldman, 1913; venezuelae Thomas, 1896; venustus Thomas, 1900; and wetzelii Gardner, 1989.

EMENDED DIAGNOSIS: Second digit of manus distinctly longer than fifth (3); ***hypothenar pad level or overlap interdigital pad 4 of pes, then gap absent*** (9); antitragus narrow to moderate (18); *interorbital region convergent and distinctly beaded when viewed in cross section* (43); *postglenoid foramen very short, almost indistinct, with short hamular process* (56); *subsquamosal fenestra low, distinctly placed below the squamosal root of zygomatic arch* (57); maxillary septum short, less than half the length of the incisive foramina (63); medial process of posterior margin of palate bridge present (66); *malleus lamina of rectangular shape* (79); hypoflexus size of M1 broad (94); anterolabial cingulum of m2-m3 distinct in both molars (107); coronoid process short, below the condylar process (120); *gall bladder absent* (132); *groove on glans penis deep extending more than half the length of body* (134). In addition DELTRAN identified the following states with ambiguous optimization: ungual tufts on manual claws absent (1); tail pencil present (27); molar-bearing portion of maxillae low and rectangular (69).

## APPENDIX 1: SPECIMENS EXAMINED

I examined 1085 specimens. Museums housing those specimens are as follows: American Museum of Natural History, New York, New York, USA (AMNH); British Museum (Natural History), London, England (BMNH); Colección Boliviana de Fauna, La Paz, Bolivia (CBF); Colección Venezolana, Universidad Simón Bolívar, Venezuela (CVUSB); Museo de la Escuela Politécnica Nacional, Quito, Ecuador (EPN); The Field Museum of Natural History, Chicago, Illinois, USA (FMNH); University of Kansas Museum of Natural History, Lawrence, Kansas, USA (KU); Los Angeles County Museum, Los Angeles, California, USA (LACM); Louisiana State University, Museum of Zoology, Baton Rouge, Louisiana, USA (LSUMZ); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ); Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, USA (MSB); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM); Museum of Vertebrate Zoology, University of California, Berkeley, California, USA (MVZ); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); National Museum of Natural History, Smithsonian Institution, Washington, D. C., USA (USNM); University of Michigan, Museum of Zoology, Ann Arbor, Michigan, USA (UMMZ); Universitets Zoologisk Museum, Copenhagen, Denmark (UZM).

**Tribe Oryzomyini:**

*Handleyomys fuscatus*: **Colombia**: *Cauca*, Peñas Blancas (USNM 507267--507269), San Antonio (AMNH 32227--32229, 32230-holotype, 32233, 32236--32239). Total, 12.

*Holochilus brasiliensis*: **Uruguay**: *Lavalleja* (AMNH 206367); *Soriano*, 3 km E. Cardona (AMNH 206369, 206371, 206372, 206374--206379, 206382, 206384, 206386, 206390); *Tacuarembó* (AMNH 206391). Total, 15.

*Microryzomys minutus*: **Bolivia**: *Santa Cruz*, Cochabamba, 31 km by road W of Comarapa (AMNH 260419). **Ecuador**: *Napo*, Papallacta (UMMZ 127126, 155678, 155679, 155797); *Pichincha*, NW Corazón (AMNH 66534, 66535, 66537, 66538), San Rafael (AMNH 66530). **Peru**: *Cajamarca*, 4 km W El Chaupe (AMNH 268114; MUSM 10676); *Pasco*, P.N. Yanachaga-Chemillen (MUSM 14924). **Venezuela**: *Mérida*, La Coromoto (USNM 374373, 374380, 374443); *Sucre*, Turumiquire (AMNH 69894, 69896). Total, 18.

*Oecomys bicolor*: **Peru**: *Madre de Dios*, Reserva Cuzco Amazónico (MUSM 6287, 6289, 6291--6293, 6295, 6298--6301, 6303, 6304, 6308, 6309, 6312, 6314, 6316, 6317); Cusco, La Convención, Camisea, Cashiriari, 695 m (MUSM 14194). Total, 19.

*Oligoryzomys fulvescens*: **Colombia**: *La Guajira*, San Miguel (AMNH 38920--38924). **Costa Rica**: *Puntarenas*, Boruca (AMNH 9572, 9573/7914, 9574/7915, 9575/7916, 9577/7918, 9580/7921), Cañas Gordas (AMNH 142440--142451, 142453), Finca Helechales (USNM 547947--547949). **Ecuador**: *Los Ríos*, Vinces (USNM 534359). **Guatemala**: *Escuintla*, Finca Los Arcos (USNM 275363). **Mexico**: *Hidalgo* (AMNH 254711); *Oaxaca* (AMNH 190328); *San Luis de Potosí* (AMNH 254712). **Panama**: *Canal Zone*, Buena Vista Peninsula (USNM 503718); *Chiriquí*, San Felix (USNM 541162); *Panamá*, Cerro Azul (USNM 305677--305679, 305683). **Venezuela**: *Aragua*, Maracay (USNM 517581); *Sucre*, Apure (AMNH 257338), Finca Vuelta

(AMNH 257262--257266). Total, 45.

Oryzomys palustris: **United States**: *Florida*, Collier Co. (AMNH 252717), Highland Co. (AMNH 250167, 252716, 252718--252721, 253212--253214, 254453), Monroe Co. (AMNH 256405, 256407, 256408); *Virginia*, Lake Drummond (AMNH 13849, 93212, 208194). Total, 17.

### **Tribe Thomasomyini**

Abrawayomys ruschii: **Brazil**: *Minas Gerais*, 6 km SW Viçosa, Mata de feitura, Station G-63 (USNM 552416). Total, 1.

Thomasomys erro: **Ecuador**: *Napo*, near Papallacta (AMNH 248283; UMMZ 127133, 155633--155642, 155712, 155713); Volcán Sumaco (AMNH 68195, holotype). Total, 15.

Aepeomys lugens: **Venezuela**: *Mérida*, La Loma del Morro (BMNH 96.11.1.5, holotype), Mérida (BMNH 5.2.5.15), Middle Refugio, 2600 m (USNM 387955), Páramo de los Conejos (AMNH 96169, holotype of Thomasomys otteleyi), Río Mucujon (AMNH 143669; BMNH 29.3.17.68, 25.7.8.1), Sierra de Mérida (AMNH 143670), vicinity of La Mucuy (MBUCV I- 2793, 2794), West Merida (BMNH 99.12.1.31--99.12.1.33). Total, 13.

Aepeomys reigi: **Venezuela**: *Lara*, El Blanquito, Parque Nacional Yacambú, 17 km SE Sanare, 9°40'N, 69°37'W (CVUSB 927, 928-holotype, 1419); *Trujillo*, Hacienda Misisi, 14 km E. Trujillo (USNM 495642). Total, 4.

Chilomys fumeus: **Colombia**: *Norte de Santander*, Paramo de Tama (FMNH 18689). **Venezuela**: *Mérida*, near Middle Refugio (USNM 387964, 442342, 579558), Páramo Tambor (FMNH 22172); *Táchira*, Buena Vista (USNM 495646). Total, 6.

Chilomys instans: **Colombia**: *Antioquia*, Sonsón (FMNH 70343--70345), Urrao (FMNH 71610--71617); *Caldas*, Manizales (FMNH 71500, 71618--71620); *Cundinamarca*, Bogotá (BMNH 95.10.14.1-holotype; FMNH 71622--71629, 71631--71638); *Huila*, Acevedo (FMNH 71621), San Agustín (FMNH 71490--71493, 71495--71499, 71600--71609). **Ecuador**: *Cañar*, Chical (AMNH 62922); *Napo*, Papallacta (UMMZ 155619, 155620, 155795); *Pichincha*, Río Pita (AMNH 63370, 63372), San Ignacio (AMNH 64640, 64642), San Rafael (AMNH 64645, 64648); locality undetermined (AMNH 214897, 214898; EPN 411, 434). Total, 66.

Delomys collinus: **Brazil**: *Rio de Janeiro*, Itatiaya (BMNH 14.2.23.12, holotype), Terezopolis (USNM 304574, 304575); *São Paulo*, Casa Grande (USNM 461062--461064, 484218--484221), Município de Salesópolis, Estação Biológica de Boracéia (MVZ 182786, 182788, 183064, 183065). Total, 14.

Delomys sublineatus: **Brazil**: *Espírito Santo*, Engenheiro Reeve (BMNH 3.9.4.58, holotype), Nova Lombardia (LACM 62910), Santa Teresa (LACM 62911); *Paraná*, Salto Grande (USNM 141451, 141452); *São Paulo* (USNM 460534--460537), Casa Grande (USNM 462075, 484222--484226). Total, 15.

Juliomys pictipes: **Brazil**: *São Paulo*, Fazenda Intervalles, Capão Bonito (MVZ 182079), Rocha (FMNH 94552). Total, 2.

Juliomys sp.: **Brazil**: *São Paulo*, Município de Cotia (MAM 139, 141). Total, 2.

Phaenomys ferrugineus: **Brazil**: *Bahia* (BMNH 63.11.16.2); *Rio de Janeiro* (BMNH 76.12.8.3, holotype); locality undetermined (BMNH 48.5.28.1, 27.11.19.43). Total, 4.



**Rhagomys rufescens**: **Brazil**: *Rio de Janeiro* (BMNH 86.2.8.5, holotype); locality undetermined (BMNH 48.5.6.13). Total, 2.

**Rhipidomys caucensis**: **Colombia**: *Cauca*, Munchique (AMNH 32466, holotype), Cocal (AMNH 32569, 32572). Total, 3.

**Rhipidomys fulviventris**: **Colombia**: *Cauca*, Cocal (AMNH 32459, 32461, 32462, 32541, 32542), Munchique, 2400 m (AMNH 181475); *Meta*, Macarena Mt. (AMNH 142140). **Venezuela**: *Mérida*, 4 km. S and 6.5 km E Tabay (USNM 374541), 7 km SE Tabay, La Coromoto (USNM 387908), 5.5 km. E and 2 km S Tabay (USNM 387911); *Monagas*, San Agustín (USNM 409926, 409930--409934); *Sucre*, Carapas (AMNH 69902, 69904, 69905), El Latal (AMNH 69901); *Táchira*, Buena Vista (USNM 456339, 456341, 456342); no located (UMMZ 156377). Total, 24.

**Rhipidomys gardneri**: **Peru**: *Cuzco*, La Convención, Camisea (MUSM 14467--14475), Paucartambo, Estación Biológica Bosque Nublado (MUSM 11997); *Madre de Dios*, Candamo (MUSM 17028), Reserva Cuzco Amazónico (MUSM 7152, 7153, 8303, 8305, 8306), Río Manu, Parque Nacional del Manu, Puesto de Vigilancia de Pakitza (MUSM 9344, 9345). Total, 18.

**Rhipidomys latimanus**: **Ecuador**: *Pachihual*, Mindo (AMNH 46661, 46662, 46669, 46735--46741). Total, 10.

**Rhipidomys leucodactylus**: **Colombia**: *Meta*, La Macarena (AMNH 142141). **Ecuador**: *Napo*, Limoncocha (USNM 528359), San José abajo (AMNH 68189). **Peru**: *Ayacucho*, Huanhuachayo (AMNH 241643); *Junín*, Utcuyacu (AMNH 63858); *Loreto*, Boca Río Curaray (AMNH 71906, 71907); *Pasco*, Oxapampa, Pozuzo (MUSM 12152, 12986, 12987); *Piura*, Sullana, Cerro Cortezo (USNM 304560). Total, 11.

**Rhipidomys macconnelli**: **Venezuela**: *Amazonas*, Mt. Duida (AMNH 77161, 77658, 77659), Cerro Neblina, Camp V (USNM 560656), Camp VII (USNM 560692, 560693, 560695, 560696); *Bolívar*, 85 km SSE El Dorado (USNM 387919, 387929, 387931, 387934--387937, 387939, 387941, 387943, 387944, 387947), 132 km SE Río Cuyuni by road (MVZ 160083), Auyantepui-Plateau (AMNH 130488, 130490, 130491, 130493--130500, 130924, 130925, 130988--130992), Churi Tepui (AMNH 176306, 176321), Mt. Roraima (AMNH 75840), Ptari Tepui (AMNH 176300). Total, 43.

**Rhipidomys ochrogaster**: **Perú**: *Puno*, Inca Mines (AMNH 16481- holotype, 16482). Total, 2.

**Thomasomys apeco**: **Perú**: *San Martín*, Valle de los Chochos, ca. 25 km NE Pataz (MUSM 7197, holotype; 7199), Pampa del Cuy (MUSM 7196, 7198, 7201--7204), Puerta del Monte (MUSM 7200). Total, 9.

**Thomasomys aureus**: **Ecuador**: *Bolívar*, R. Tatahuazo (MSB 70707); *Napo*, Papallacta (AMNH 248281, 248498; UMMZ 127114, 155621--155626); *Pichincha*, Guala (AMNH 36279), near Quito (AMNH 36281, 46582--46584, 46587, 46588, 46590--46596, 46605, 46658, 46660), San Ignacio (AMNH 64697, 64698); *Tungurahua* (AMNH 67395--67397); *Morona-Santiago*, Gualaquiza (BMNH 7.1.1.104). Total, 33.

**Thomasomys auricularis**: **Ecuador**: *Cañar*, Chical (AMNH 63326), Piñanque (AMNH 63327), San Antonio (AMNH 63315--63323, 63325); *El Oro*, Taraguacocha (AMNH 47697, holotype). Total, 13.

**Thomasomys australis**: **Bolivia**: *Cochabamba*, Corani (AMNH 268736), Incachaca (AMNH 38550, holotype); *Santa Cruz*, W Comarapa, Siberia (UMMZ 156307). Total, 3.

**Thomasomys baeops:** **Ecuador:** *Azuay*, Bestión (AMNH 47677), Cinincay (AMNH 61953), Molleturo (AMNH 61925); *Bolívar*, Rio Tatahuazo (MSB 70704); *El Oro*, Taraguacocha (AMNH 47699); *Loja* (AMNH 61363); *Napo*, Papallacta (UMMZ 127117, 127118, 155627--155632, 155708, 155767; KU 109495); *Pichincha* (KU 124025; EPN 954421), Cañón of Río Pita (AMNH 65006, 65008, 65009), R. Pita, above Valley of Chillo (BMNH 96.8.1.7, holotype); *Tungurahua*, San Francisco (AMNH 63380, 63382). Total, 25.

**Thomasomys bombycinus:** **Colombia:** *Antioquia*, Paramillo, West Andes (AMNH 37739, 37740-holotype, 37741, 37742), Urrao, Paramo Frontino (FMNH 71320, 71324, 71325, 71328, 71329, 71332, 71334, 71336, 71337, 71339, 71340, 71341, 71344, 71347, 71349), Urrao, Santa Barbara (FMNH 71351, 71353, 71355, 71356, 71359, 71360, 71362). Total, 26.

**Thomasomys caudivarius:** **Ecuador:** *Bolívar*, Rio Tatahuazo, 4 km E. of Cruz de Lizo (MSB 70712, 70714); *El Oro*, Taraguacocha, Cordillera de Chilla (AMNH 47639, 47643, 47655, 47659--47665, 47667, 47668- holotype, 47669; FMNH 53978). **Peru.** *Piura*, Cerro Chinguela (LSUMZ 27082--27093); Huancabamba, Tambo (FMNH 81331), Huancabamba, km 30 on road to San Ignacio (FMNH 81332, 81333, 81337--81340). Total, 35.

**Thomasomys cinereiventer:** **Colombia:** *Cauca*, Páramo 40 mi W of Popayán, (AMNH 32421, 32424, 32428, 32430, 32433--32435, 32436-holotype, 32437--32440). Total, 12.

**Thomasomys cinereus:** **Peru:** *Cajamarca*, Cutervo (BMNH 81.9.7.29, holotype), Monteseco (VPT 1629, 1650), Paramo de Cajamarca (BMNH 0.3.15.4, 0.3.15.5), Taulis (AMNH 73136, 73147; MVZ 137937--137939); *La Libertad*, South of Huamachuco (BMNH 0.6.6.12); *Lambayeque*, Seques (AMNH 73127, 73129); *Piura*, Cruz Blanca (LSUMZ 27045--27059, 27132, 27138, 27140, 27145, 27146). Total, 33.

**Thomasomys cinnamomeus:** **Colombia:** *Antioquia*, Sonson, Páramo, 7 km E (FMNH 70342); *Caldas*, Manizales, Rio Termales (FMNH 71483); *Cauca*, 0.5 km E. Laguna San Raphael, Páramo de Purace (KU 124058); *Huila*, San Agustin, Las Bardas (FMNH 71489). **Ecuador:** *Napo*, 1.6 km W Papallacta (UMMZ 155668--155670), Rio Papallacta valley (UMMZ 155671, 155800), *Tungurahua*, Hacienda San Francisco, east of Ambato (AMNH 67401-holotype). Total, 10.

**Thomasomys contradictus:** **Colombia:** *Antioquia*, Medellin, Las Palmas (FMNH 70339, 70340), Sonson, Las Frias, 10 km E (FMNH 70294), Sonson, Paramo, 7 km E (FMNH 70265, 70266, 70269, 70270, 70275, 70276, 70279, 70280, 70284, 70285, 70286, 70289, 70290, 70293, 70295); *Caldas*, Manizales, Rio Termales (FMNH 71308, 71310, 71313, 71315, 71318, 71319); *Quindío*, Santa Isabel (AMNH 32953, 32954, 32955 holotype, 32956, 32957). Total, 29.

**Thomasomys daphne:** **Peru:** *Cuzco*, Occobamba (BMNH 22.1.1.81; USNM 194902, holotype), Paucartambo, Challabamba, P.V. Acjanaco (MUSM 6729, 9364--9374), 32 km NE [by road] Paucartambo, km 112 (MVZ 166705), 90 km by rd SE Quillabamba (UMMZ 160578--160581). Total, 19.

**Thomasomys dispar:** **Colombia:** *Huila*, Andalucia (AMNH 33760, 33761-holotype, 33762--33767), San Agustin (FMNH 71363, 71366, 71367, 71368, 71370, 71371, 71377, 71378, 71382--71385, 71388, 71390, 71392, 71395, 71397, 71399, 71400, 71401, 71405, 71406, 71407). Total, 31.

Thomasomys eleusis: **Peru**: Amazonas, Chachapoyas, Mountains East of Balsas (AMNH 143673, 143674; FMNH 19808--19810, 19812--19816, 19819--19821, 19823--19829), Tambo Jenés (BMNH 26.4.1.48, holotype). Total, 21.

Thomasomys emeritus: **Venezuela**: Mérida, Montes de Escaguer (BMNH 5.1.1.4, holotype), Paramo Tambor (FMNH 22123, 22124, 22129), R. Mucujun (FMNH 22098), Tabay, 7 km SE Tabay, La Coromoto (USNM 374569, 495630, 495632, 495633, 495638). Total, 10.

Thomasomys fumeus: **Ecuador**: Tungurahua, San Francisco, E. of Ambato (AMNH 67528, 67530--67536, 67537-holotype, 67538--67541). Total, 13.

Thomasomys gracilis: **Perú**: Cuzco, 14 km NE Abra Malaga on Ollantaitambo-Quillabamba Rd. (LSUMZ 19318), 90 km by rd SE Quillabamba (MVZ 166667--166673, 170078, 170079; UMMZ 160582--160584), Cordillera de Vilcabamba (MUSM 13067), Idma road (AMNH 95207), Lucura, Casereni pass (USNM 194813), Lucura, San Miguel road, Corraugwaya, head of San Miguel River (USNM 194810--194812), Matchu Picchu (MCZ 19674, 19675; USNM 194799, 194801, 194816-holotype), Occobamba Valley (USNM 194807, 194808), Torontoy (AMNH 95206; FMNH 43392, 43393; USNM 194785--194787, 194790, 194796). Total, 34.

Thomasomys hudsoni: **Ecuador**: Azuay, Bestión (AMNH 47690, holotype). Total, 1.

Thomasomys hylophilus: **Colombia**: Boyacá, East Andes, E side, Hacienda La Primavera (FMNH 92553, 92554, 92556, 92557, 92560, 92561); Norte de Santander, Paramo de Tama (AMNH 143667, 143668; FMNH 18565, 18575, 18578, 18584, 18586--18588, 18591, 18592). **Venezuela**: Tachira, Buena Vista, 2368 m, 35 km S. and 22 km. N. San Cristobal (USNM 442305), Páramo de Tama (FMNH 18563, 18566, 18597); no localized (UMMZ 156403). Total, 22.

Thomasomys incanus: **Peru**: Huánuco, Mountains 15 mi NE Huánuco (FMNH 23726--23734); Junín, Maraynioc, 45 mi NE Tarma (MCZ 38537, 38540), Vitoc Valley (BMNH 94.10.1.4, holotype of incanus); Pasco, Alcas, 25 mi NE of Cerro (BMNH 27.11.1.169-holotype of fraternus, 27.11.1.170--27.11.1.173), San Alberto (MUSM 11482). Total, 18.

Thomasomys ischyrys: **Perú**: Amazonas, Rodríguez de Mendoza, 10 mi E Molinopampa (AMNH 143671, 143672; FMNH 19794--19796, 19798--19801), Tambo Almirante, near Uchco (FMNH 19804--19806). Total, 12.

Thomasomys kalinowskii: **Peru**: Junín, 16 km NNE (by road) Palca (MVZ 172598, 172599), Maraynioc, 45 mi. NE Tarma (FMNH 54202, MCZ 38529--38535, 38538, 38539), Vitoc Valley (BMNH 94.10.1.2-holotype, 94.10.1.3). Total, 14.

Thomasomys ladewi: **Bolivia**: La Paz, Río Aceramarca (AMNH 72113-holotype, 72114, 264778, 264779, 264780, 264781; MSB 68483, 68484; UMMZ 156294), Tokoaque (CBF 7423). Total, 10.

Thomasomys laniger: **Colombia**: Cundinamarca, Bogotá Region (BMNH 95.8.1.39, holotype), Finca el Soche, 15 km W Soacha (KU 124056, 124057), Fusagasuga (AMNH 76708, 76717), Guasca, Río Balcones (FMNH 71408, 71409, 71414--71417, 71420, 71421, 71424, 71425, 71429, 71430, 71433, 71434, 71436). Total, 20.

Thomasomys macrotis: **Peru**: San Martín, Pampa del Cuy (USNM 567243), Puerta del Monte (LSUMZ 27285, 27287). Total, 3.

Thomasomys monochromos: **Colombia**: Magdalena, Cerros San Lorenzo, San

Lorenzo (USNM 507270--507273), Mamancanaca, nearby (FMNH 69190), Páramo de Macotama, Sierra Nevada de Santa Marta (AMNH 38946). Total, 6.

**Thomasomys nicefori**: **Colombia**: *Antioquia*, Las Palmas [1 mi. NW] (AMNH 149278), Medellín, Las Palmas (FMNH 70326, 70327, 70330), Paramillo (AMNH 37738), Santa Elena (AMNH 37736), San Pedro, Medellín (BMNH 27.7.1.20, holotype), Sonsón, Paramo, 7 km E (FMNH 70307--70311), Urrao, Paramo Frontino (FMNH 71269), Valdivia, Las Ventanas (FMNH 70321, 70322). Total, 15.

**Thomasomys niveipes**: **Colombia**: *Cundinamarca*, Bogotá, (MVZ 113964, 113965), Guasca, Rio Balcones (FMNH 71465), Laguna Verjon (AMNH 62751, 62755--62762, 62766--2768; USNM 239967--239970, 251973, 251977--251979), La Oya del Barro (BMNH 96.11.1.4, holotype), San Cristobal (FMNH 71454, 71462, 71463), San Francisco (FMNH 53981, 71440, 71441, 71444, 71445, 71447--71449, 71455, 71456, 71460). Total, 38.

**Thomasomys notatus**: **Peru**: *Amazonas*, Rio Utcubamba (FMNH 19831), Tambo Jenes (BMNH 26.4.1.52), Uchco (FMNH 19834); *Cuzco*, Amaybamba (MVZ 173968--173973), Matchu Picchu (USNM 194898), Paucartambo (MVZ 166706, 171503, 171504), Torontoy (USNM 194548-holotype, 194894, 194895, 194897); *Huánuco*, Carpish (LSUMZ 14367, 14368); *Junín*, Tarma (AMNH 231084), Utcuyacu (UMMZ 155912, 158027--158030); *Pasco*, Oxapampa, San Alberto (MUSM 10579, 10580, 14994, 14995). Total, 29.

**Thomasomys onkiro**: **Peru**: *Cuzco*, La Convención, Cordillera del Vilcabamba (MUSM 13063, 13064-holotype, 13065; USNM 582123, 582124). Total, 5.

**Thomasomys oreas**: **Bolivia**: *La Paz*, Chuncani (CBF 7427, 7429), Cocopunco, 10,000ft (AMNH 72129, 72130-holotype), Pelechuco (CBF 4041). Total, 5.

**Thomasomys paramorum**: **Ecuador**: *Carchi* (EPN 861696), Montufar (UMMZ 77162, 77215); *Chimborazo*, Paramo, south of Chimborazo (BMNH 97.11.7.82, holotype), Urbina (AMNH 64871--64883); *Napo*, Cuyuco, road to Papallacta (AMNH 46629, 46630, 46641, 46642, 46734), Papallacta (AMNH 248501), Tablon, road to Papallacta (AMNH 46643); *Pichincha*, 10 km NW Quito (MVZ 139527, 139528), 15 mi. S Quito (AMNH 213545--213547), E side Mt. Pichincha (MVZ 137600--137604). Total, 34.

**Thomasomys popayanus**: **Colombia**: *Cauca*, Coast range of Popayán (AMNH 32362, 32366--32370, 32371-holotype, 32372, 32373), Munchique (AMNH 32361). Total, 10.

**Thomasomys praetor**: **Peru**: *Ancash*, Carhuaz, Jangas, Antauran, Cordillera Negra, Qba. Lancash, aprox. 9°24'S: 77°35'W (MUSM 11644); *Cajamarca*, Celendin, Hacienda Limón (FMNH 19256), San Pablo (BMNH 0.3.15.3, holotype); *La Libertad*, 5 mi SW Otuzco (MVZ 137941), Otuzco, Summit between Otuzco and Llagueda (FMNH 19255). Total, 5.

**Thomasomys princeps**: **Colombia**: *Cundinamarca*, Bogotá region (BMNH 95.8.1.37, holotype), Páramo del Verjón (AMNH 62769, 62770), San Francisco (FMNH 71305--71307). Total, 6.

**Thomasomys pyrrhonotus**: **Peru**: *Cajamarca*, 1 km NW Cutervo (LSUMZ 21874, 21875), 4 km W San Andres de Cutervo (MUSM 12, 13, 14), 7 km N. 3 km E Chota (LSUMZ 22317), Bosque Cachil, entre Cascas y Contumaza (MUSM 16), Santa Cruz, entre Monteseco y Udima (MUSM 15), Tambillo, Rio Malleta (BMNH 81.9.7.24,

holotype); *Piura*, Ayabaca, Ayabaca (FMNH 81296), El Tambo (USNM 304538), Faique (FMNH 84439), Huancabamba, Canchaque (FMNH 81295, 84438). Total, 14.

*Thomasomys rhoadsi*: **Ecuador**: *Pichincha*, 15 m S. Quito (AMNH 213548), Pichincha (EPN 1277; MVZ 137610), Río Pita (AMNH 63361), San Ignacio (AMNH 66252--66264), Santa Rosa (AMNH 66265--66277). Total, 30.

*Thomasomys rosalia*: **Perú**: *Amazonas*, Goncha, 8500 ft (BMNH 26.8.6.31, holotype). Total, 1.

*Thomasomys silvestris*: **Ecuador**: *Pichincha*, 11 km W Aloag (KU124032), Antisana, oriente (FMNH 43251), Guala, Ilambo Valley (FMNH 94990, 94991, 94993--94995), Las Maquinas, Santo Domingo trail, W of Corazón (AMNH 66288, holotype), Old Santo Domingo trail (UMMZ 127116, 155754--155759), San Jose, Occidente (FMNH 53243--53247), Santa Rosa, road to Mindo (FMNH 93145, 93147--93152), Upuruni West (FMNH 53407, 53408), Volcan Pichincha, Oriente (FMNH 92000--92003); no localized (EPN 954428). Total, 34.

*Thomasomys taczanowskii*: **Peru**: *Cajamarca*, Taulis (AMNH 73137--73141, 73143, 73146, 73148), 35km WNW Cajamarca (MVZ 137928--137936), Río Zaña (MVZ 181994--182000, 182003), Tambillo (BMNH 81.9.7.22, 81.9.7.23-holotype); *Lambayeque*, Seques (AMNH 73124, 73126, 73128); *Piura*, Cerro Chinguela (LSUMZ 27095--27100), Cruz Blanca (LSUMZ 27101--27104), Huancabamba (AMNH 63713). Total, 41.

*Thomasomys vestitus*: **Venezuela**: *Merida*, Quebrada de la Cienca (USNM 149007), Río Milla (BMNH 98.5.15.3, holotype); *Trujillo*, Hacienda Misisi, 15 km E Trujillo (USNM 374544, 495643). Total, 4.

*Thomasomys* sp. 1: **Bolivia**: *La Paz*, Okara (AMNH 72123), Pelechuco (CBF 4043), Saynani, Río Zongo (AMNH 268735; MSB 70446). **Peru**: *Cuzco*, Amaybamba (MVZ 173964--173967), Challabamba, P.V. Acjanaco (MUSM 6726, 9358); *Pasco*, Oxapampa, San Alberto (MUSM 10557); *Puno*, Ollachea (MVZ 172591--172595), Limbani (MVZ 116071, 116647, 171497--171499), Yanahuaya (MVZ 171500, 172596, 172597). Total, 24.

*Thomasomys* sp. 2: **Bolivia**: *Cochabamba*, W of Comarapa (AMNH 260422); *Santa Cruz*, Comarapa (UMMZ 156309). Total, 2.

*Thomasomys* sp. 3: **Bolivia**: *La Paz*, 18 km by rd. N. Zongo, Cuticucho (UMMZ 156185, 156186), 30 km by rd. N. Zongo, cement mine (UMMZ 156190, 156191), approx. 15 km by rd. NE Unduavi at old RR crossing (UMMZ 155879), approx. 25 km by rd. W Comarapa, Siberia (UMMZ 156244, 156307), Murillo, Cañariri (CBF 4449); Murillo, Cuticucho, 16° 28'S, 68° 06' O (CBF 4450--4452), Murillo, Pok'ollo (CBF 4356), Murillo, valle de Zongo, Cuticucho, 16° 08'S, 68° 06' O (CBF 4413--4416, 4432), Okara (AMNH 72131), Piara (CBF 6791, 6794, 6795), Río Aceramarca (AMNH 72112, 72128), Río Aceramarca, 1 km S Yerbani (UMMZ 155894, 156156, 156194--156196), Río Unduavi (MSB 68482), Saynani (AMNH 268737). **Perú**: *Puno*, 4 mi N Limbani (MVZ 114633), 3 mi N Limbani (MVZ 116054--116059, 139524, 139525), 9 km N Limbani (MVZ 171501, 171502). Total, 41.

*Thomasomys* sp. 4: **Peru**: *Pasco*, Millpo, E Tambo de Vacas on Pozuzo-Chaglla trail (LSUMZ 29166), Santa Cruz, ca. 9 km SSE Oxapampa (LSUMZ 25895, 25897), [many MUSM]. Total, 3.

*Thomasomys* sp. 5: **Peru**: *San Martín*, La Playa, ca 35 km NE Los Alisos

(LSUMZ 27341), Puerta del Monte, Las Papayas (LSUMZ 27300 --27307, 27343, 27351), Puerta del Monte, ca. 30 km NE Los Alisos (LSUMZ 27308 -- 27340, 27342, 27344 -- 27350). Total, 52.

Thomasomys sp. 6: **Peru:** *San Martín*, Puerta del Monte, ca. 30 km NE Los Alisos (LSUMZ 27310, 27311, 27315); *Pasco*, Millpo, E Tambo de Vacas on Pozuzo-Chaglla trail (LSUMZ 29169). Total, 4.

Thomasomys sp. 7: **Perú:** *Huánuco*, 10 km N. Acomayo, Bosque Unchog (LSUMZ 27902, 27904--27906, 27910, 27913--27915, 27928, 27936, 27939, 27943--27947, 27949--27951; MSB 49994, 49995, 49999). Total, 22.

Thomasomys sp. 8: **Peru:** *Ayacucho*, Yuraccyacu, 2600 m (LSUMZ 16735, 16736). Total, 2.

Thomasomys sp. 9: **Peru:** *Cuzco*, 32 km N. Paucartambo (by road, km 112) (MVZ 166702--166704, 166706, 171505, 171506, 172344), below Marcapata (LSU 19319), Occobamba (USNM 194876), Puesto de Vigilancia Acjanaco (MUSM 6727, 9375--9377, 9379), Tres Cruces (MVZ 115645). Total, 15.

Thomasomys sp. 10: **Perú:** *Cajamarca*, Las Ashitas, 4 km. oeste de Pachapiriana, 9200 ft. (MUSM 10708); *Piura*, Cerro Chinguela, ca. 5 km NE Zapalache (LSUMZ 27094). Total, 2.

Thomasomys sp. 11: **Ecuador:** *Napo*, Tablón, road to Papallacta (AMNH 46621, 46622, 46624). Total, 3.

Wiedomys pyrrhorhinos: **Brazil:** *Bahia*, Caatingas along Riacho de Ressaca (AMNH 574, holotype), Lamarao (B.M. 3.9.5.63); *Ceará*, Ladeira Grande (BMNH 13.12.18.4); *Pernambuco* (USNM 555760, 555761), Bodoco (USNM 304584), National Zoological Park (USNM 538306, 538314, 538382, 538386--538388). Total, 12.

Wilfredomys oenax: **Brazil:** *Rio Grande do Sul*, San Lorenzo (BMNH 27.11.19.44, holotype; 88.11.30.10; ZM 490). **Uruguay:** *Tacuarembó* (AMNH 206018 - 206021). Total, 7.

## APPENDIX 2: TAXON-CHARACTER MATRIX

Taxonomic polymorphisms are abbreviated in the matrix for simplicity: a = (0/1); b = (1/2); c = (0/2); d = (2/3); e = (0/1/2); f = (1/3).

**Handleyomys fuscatus**

01000 00000 00002 11?01 000?0 00002 11000 0???1 ?10?0 0102? 20-11 -0200  
00030 0300? 00011 ??01? 00?30 11-00 00100 ?1111 00?00 00000 10?11 01001  
00?1? 202?? ????? ?????

**Holochilus brasiliensis**

10020 11--- 10002 10?02 001?0 00020 1??00 00?01 ?2300 11000 02011 -00?0  
01?2? ?300? 20?21 ??1? 00?31 11-0- ---0? ?1?11 ?1?- -00?0 10012 0?101  
00210 31200 010?? 0?001 00112

**Microryzomys minutus**

01000 10000 00122 1?000 00100 00001 01000 00?10 ?0010 02000 20-11 -0000  
01?30 01010 20?11 000?0 00030 00000 00010 ?000- 00??0 ??000 00?01 01110  
00212 21100 01010 00001 00011

**Oecomys bicolor**

00120 a02?1 00122 01102 00101 00021 01000 0???0 10320 01000 10-1? -0000  
?103? ?3000 00001 ?011? 00030 11-?0 001?0 20?10 10000 02000 000?1 ?1110  
00012 012?? ?1?10 00001 00012

**Oligoryzomys fulvescens**

0?000 10000 00112 1??01 00101 00001 1?00? 0??11 ?02?0 02000 21-1? -00?0  
01030 ?30?? 20?21 ??1?? 00030 000?? ?0?? ?1?0- ?0000 1?000 00?02 01110  
00c11 31100 01??? ?0001 00102

**Oryzomys palustris**

1?020 11--- 10002 1?002 00101 00001 10000 0??11 10320 01000 22011 -0310  
02030 0300? 20011 ?0110 00030 01-00 000?0 20011 00000 01000 00??2 01101  
00211 31200 01?00 00001 0011?

**Abrawayaomys ruschii**

0100? 10200 00002 01101 10??0 21002 10000 00?00 02220 00031 00-00 10310  
01000 00110 01001 0210? 13020 0010- 1-210 2000- 01001 -21?0 00??2 0?110  
10??? ????? ?????

**Delomys collinus**

0?000 10201 00012 11002 0?0?0 00202 11000 00011 01010 01021 20-00 30000  
01000 001?0 01000 00110 10020 10101 00100 01110 10000 00000 00001 00001  
00201 010?0 00??? ?????

**Delomys sublineatus**

0?000 10001 00012 11002 0?1?1 00222 11000 00011 01010 01021 20-00 30000  
01000 001?0 01000 01110 10020 10101 00100 21110 10000 00000 00001 00001  
00?01 ????0 0???? ?????

**Juliomys pictipes**

00000 10200 00132 12112 00101 000c0 11000 00?10 10210 01020 02000 10000  
01000 0010? 11001 001a0 a0030 0010- 1-210 2000- 10000 12100 01002 10110  
000ad 000?? ?????

**Juliomys sp.**

0?000 00200 00122 12012 0?1?1 00000 0100? 0???? ???? ?002? 10-0? 1?0?0  
 ?2100 001?? 11000 ?1?0? 10?30 0010- 1-2?? 20?10 10200 ???? 00001 ??110  
 ?0202 000?? ????? ????? ???? ???? ?

#### **Phaenomys ferrugineus**

0?000 10000 00222 02002 001?0 00002 01000 00?00 11300 01000 20-0? 310??  
 ?1101 00100 01?00 ????? ?0?30 00110 00110 2000- 10120 02110 02??0 00000  
 00??? ????? ????? ???? ???? ?

#### **Rhagomys rufescens**

0?10? 00200 01122 11?00 000?0 00020 10000 00000 ?2220 ?00?? 02?0? ?0?0?  
 ?0030 ?10?? ????? ?1?1? ?2?30 00101 00110 20110 00??1 -2?0? 010?2 0?110  
 11??? ????? ????? ???? ???? ?

#### **Wiedomys pyrrhorhinos**

11000 10001 00132 11012 00100 00000 11000 00000 10310 01010 20-00 10000  
 12010 02000 21021 02000 10030 00100 01110 2a00- 00001 -1000 00002 10010  
 00112 200?? ?0?? ???? 01?? ?

#### **Wilfredomys oenax**

00000 10000 00122 11012 00101 00000 11000 00010 10200 01020 10-01 10000  
 12001 02100 21021 02100 10?30 00100 00110 2000- 10210 01100 00001 10000  
 00212 000?0 0?010 ?0?01 0013?

#### **Rhagomys longilingua**

0?10? 00200 ?1222 1???2 1?0?0 00020 00000 00?00 11320 110?0 02001 01000  
 00030 030?? 01101 ?001? ?2?30 00110 001?0 ?0110 00?20 12100 00??2 01110  
 11002 01?00 01??? ????? ????12

#### **Aepeomys lugens**

12010 00001 00010 10100 00020 00223 02211 10011 01020 00131 20-00 00202  
 01000 20110 00001 0000? 12101 00001 0-301 01110 0?200 1 0000 11?10 01011  
 00202 21004 00??? ????? ???? ?

#### **Aepeomys reigi**

12000 00001 00010 10100 0?0?0 00223 02210 11011 01020 00131 20-00 00202  
 00020 00110 0?001 0000? 12101 00001 0-301 01110 01200 10000 01010 01011  
 00??? ????? ?0200 11?01 000??

#### **Chilomys fumeus**

01000 00001 001d2 11100 0?0?0 20020 0200? 00001 ?202? 00031 22000 10302  
 ?0130 0001? 01?01 ?0110 13030 01-?0 00c11 00110 01000 10000 00001 02a11  
 00002 2100? ????? ????? ???? ?

#### **Chilomys instans**

01000 00001 001d2 11100 00010 20020 01000 00001 02020 00031 c2100 10302  
 00ad0 00010 01a11 10a10 130b0 0a100 00c10 001a0 0a000 10000 00001 02111  
 00002 00000 00101 01001 02112

#### **Rhipidomys caucensis**

11101 00211 00232 12102 000?0 01020 01000 00000 11210 01020 02000 01002  
 01100 0010? 01000 00110 10030 10000 00100 01110 00000 01001 00001 01111  
 00??? ????? ????? ???? ???? ?

#### **Rhipidomys fulviventer**

00a01 00211 00232 12102 00010 01001 01000 00000 ?1210 01020 00-00 010a2  
 0b100 001a? 01a00 00110 10030 00000 00110 0110- ?0000 0100a 0a00a 01a10



00002 00000 01020 00?12 0?11?

**Rhipidomys latimanus**

11101 00211 00232 12102 000?1 11021 01000 00000 1132? 01020 02000 01000  
02000 0010? 0100? 00110 10030 00000 00110 2000- 00000 02000 00000 01111  
00002 0???0 01??? ????? ?????

**Rhipidomys leucodactylus**

10021 00211 00232 12101 00010 01021 01000 00?00 10310 01000 02000 01002  
01000 c0100 01000 00110 10030 00000 00110 2000- 00000 02000 00001 01010  
00??? ?????0 01021 00012 1210?

**Rhipidomys gardneri**

10001 00211 00232 11102 00010 00021 01000 01000 11320 01020 02000 01000  
01000 20100 01001 00110 10030 00000 00100 2000- 10000 01000 00001 01010  
00012 20000 01?21 00012 1?101

**Rhipidomys macconnelli**

00001 00011 00232 12101 00011 01020 01000 00000 11310 01030 02-00 01002  
02100 2000? 01100 00110 10030 00000 00100 2000- 00000 02000 00000 0?111  
0000d 00000 01020 00002 1011?

**Rhipidomys ochrogaster**

10001 00211 00231 12101 000?0 01002 01000 00000 10310 01020 00-00 01202  
02000 2010? 01001 00010 10030 00100 00110 2100- 00000 01000 00001 01010  
00??? ????? ????? ?????

**Thomasomys apeco**

0100? 0020? 00232 12001 010?0 30021 01200 01101 01200 10000 02000 30011  
01001 20101 01001 ?0100 12121 00010 01110 0000- 00210 02110 10210 00001  
00?23 ?00?2 10021 11101 02-??

**Thomasomys aureus**

01001 002?1 00232 12001 00020 00022 01000 00001 01200 1102? 02000 3001c  
02001 0010? 01001 00100 10121 a0000 01310 c100- 00210 12100 10?00 00001  
00?03 ????? 10211 ?0?0? 0003?

**Thomasomys auricularis**

0100? 00201 00232 11001 010?0 00002 0100? 00001 ?1000 11020 12000 30011  
02101 0010? 01001 02001 10120 00010 01310 0000- ?0220 12100 10?10 00001  
00202 0???? ????? ?????

**Thomasomys australis**

01000 00c01 00120 11000 00?00 00021 01000 01?01 01010 0103? 00-00 10002  
01000 0001? 01101 01000 13120 00000 00a00 0010- a0000 11000 00000 01011  
00203 000?? ?0000 ?0001 001??

**Thomasomys baecops**

01101 00b01 0023e 12a01 00010 1002a 01000 00000 11101 01030 02000 1000e  
01100 00110 01011 00000 10030 00000 00100 0100- 00000 10000 00001 01111  
00002 100?0 00111 00021 02111

**Thomasomys bombycinus**

01000 00a01 00020 11100 00020 00102 01200 00101 01010 01030 00-00 20002  
01000 c0001 01000 00000 12101 10001 00100 0100- 00000 10001 00?00 01001  
00??? ?0?0? ?010 ?0?0? 001??

**Thomasomys caudivarius**

01000 00001 00120 11100 000?0 20121 01000 01001 01010 01030 00-00 10002  
 01000 00010 00001 00000 12130 00001 00f00 0100- 00200 11000 00000 ?1011  
 00203 0??0? ????? ????? ?????

#### **Thomasomys cinereiventer**

01000 00201 00020 11101 0?020 00112 01000 001?1 01110 01030 00-00 20002  
 01000 00011 01000 00000 11101 10001 00100 0110- 00000 11001 00000 01001  
 00??? ????? ????? ????? ?????

#### **Thomasomys cinereus**

01000 0010? 0022a 11101 00020 000c2 01a00 00001 010a0 01030 00-00 10002  
 0b000 b0010 0100a 00000 12120 00000 00f00 0110- 00000 11000 00000 01001  
 00202 20000 00000 00001 00000

#### **Thomasomys cinnamomeus**

02000 00c01 0013c 11100 000?0 0002b 02000 01001 01000 01030 00-00 20002  
 0b000 00010 01101 0100? 1c130 0000- 1-?00 01110 00c00 10000 0a000 01011  
 00??? ????? ????? ????? ?????

#### **Thomasomys contradictus**

01000 00001 00020 1?101 00020 00102 01c00 000a1 01010 00030 00-00 10002  
 00000 0000? 01001 01000 1c101 00000 00100 01110 00000 10000 00000 01011  
 00??? ????? ?010 00001 021??

#### **Thomasomys daphne**

01000 00201 00120 11000 00020 20021 01000 01001 01110 00030 02000 10002  
 01000 2001? 011a1 01000 13120 00000 00100 00110 a0000 10000 00001 01111  
 00003 200?0 000?? ?001 00?0

#### **Thomasomys dispar**

01000 00001 00010 1?01 00020 20222 02100 00011 01010 00031 00-00 10002  
 00000 2000? 01001 00000 12100 00001 00100 01110 00000 11000 10000 01001  
 00??? ?00? ?0000 ?0001 021??

#### **Thomasomys eleusis**

02000 00001 00120 11101 00020 00102 01201 00101 01110 00031 12000 10002  
 02100 00110 01001 10000 12100 00001 00100 11010 00100 10000 11010 01001  
 00??? ????1 00??? ????? ?????

#### **Thomasomys emeritus**

01000 00001 00120 12001 000?0 00011 01200 00011 0101? 01030 00-00 20002  
 ?1000 000?? 11100 ?2000 10?20 00001 00100 0100- 10?00 ?1000 00000 ?1011  
 0020? 000?0 00??? ?001 0?02

#### **Thomasomys erro**

12000 00001 00010 11100 00020 ca203 02001 10011 0102? 00031 10-00 10002  
 ?1000 0001? 00000 0100? 121c1 00001 0-300 0110- 00000 11000 10?00 0?011  
 00??3 ?10?3 00000 ?001 0213?

#### **Thomasomys fumeus**

12010 00001 00020 11100 00020 00002 02200 00011 0101? 0?031 00-00 10002  
 ?1000 0001? 01000 00000 12121 00001 00100 01010 01000 10000 00000 01011  
 00??? ????? ????? ?????

#### **Thomasomys gracilis**

01101 00201 00232 11000 000?0 00122 0b000 01000 11100 01020 00-00 10002  
 02000 00000 11100 02000 10030 00000 00100 c001- 00100 a1001 100?0 01010

00?02 ?00?0 0000? 00001 0001?

**Thomasomys hudsoni**

01000 00001 00130 11000 0???0 c0222 01001 00?01 11000 0003? 00-00 10202  
01100 00110 01100 0200? 12130 00000 00000 0100- 01020 10000 000?0 01011  
00??? ????? ????? ????? ?????

**Thomasomys hylophilus**

01000 00c01 00120 11?00 00020 20022 01000 00001 01010 01020 00-00 10002  
01?00 c00?? 01001 01000 12120 00001 00b00 ca10- 00200 ?0000 00000 01011  
00202 200?0 000?0 00001 121??

**Thomasomys incanus**

ab000 00c0a 00120 1110a 00020 00223 01201 00011 01020 00031 02a00 10202  
01100 00111 a100a 11000 12100 0000- 1-100 01010 00200 10000 10000 01011  
00??? ?00?0 00??? ????? ?????

**Thomasomys ischyryus**

02000 00001 00120 11000 00020 00213 01201 00011 0102? 00031 12000 10001  
01100 00110 01000 11000 12100 00000 00100 11010 00200 a1000 11010 01001  
00??? ????? ????? ????? ?????

**Thomasomys kalinowskii**

02000 00000 00120 11100 0?020 00002 01201 00001 01010 00030 22000 10001  
02100 00100 01000 01000 10100 10000 00100 01010 00100 11000 11010 01001  
00202 20001 00010 10001 12101

**Thomasomys ladewi**

02000 00001 00120 11100 01020 20021 01200 01001 01110 10020 02000 30002  
01000 00100 01001 00000 12100 1000- 1-100 01010 00100 11000 01000 01001  
00202 c00?0 00011 10001 02101

**Thomasomys laniger**

01000 00001 00120 12001 000?0 00012 01200 00001 01010 01030 00-00 20002  
01000 0000? 01000 02000 12130 0000- 1-100 0010- 00200 10000 00000 ?1011  
00??? ???0? ??011 11000 000??

**Thomasomys macrotis**

02000 00000 00120 11000 000?0 30023 01000 00111 01010 11020 02-00 10012  
01001 0011? 010?1 00100 12101 00000 00100 0000- 00100 11001 12010 01001  
00203 000?0 00??? ????? ?????

**Thomasomys monochromos**

01000 00001 00120 11000 00020 000ca 01000 00001 ?101? 01030 00-0? f0002  
?1000 0001? 01a01 0100? 12120 00-0- 1-100 01110 00000 11000 11?00 01011  
00??? ????? ????? ????? ?????

**Thomasomys nicefori**

01000 00201 00232 12001 00020 00022 0100? 00001 ?101? 010c0 02000 30012  
?b000 0010? 01001 01000 12120 00000 01110 2?00- 10110 ?2100 1a0?0 00001  
00203 0???? ?011 ?1100 021??

**Thomasomys niveipes**

02000 00101 00120 11001 00020 00102 11000 00001 01002 01020 10-00 30002  
02000 00010 11111 02100 10120 00000 00100 0?00- 00200 10000 00000 ?1011  
00??? ???1? ??000 00001 121??

**Thomasomys notatus**

10101 00201 00232 12002 0?010 0100b 01000 00?00 11102 010c0 00-00 30002  
 0b100 00110 0aa?a 00100 10030 10100 00100 20010 00000 00001 0000b 01111  
 00002 00010 00000 00012 1ca00

#### **Thomasomys onkiro**

01000 00201 00120 11100 000?0 20022 01000 00001 01010 01030 00-00 10002  
 01000 00010 01001 00000 12120 00000 00100 01010 00000 10000 00000 01011  
 00??? ????? ?0?0 ?001 0????

#### **Thomasomys oreas**

01101 00201 00232 12001 00010 00022 01000 01000 11002 01020 00-00 10002  
 02100 00000 11000 02000 10030 10000 00100 20010 00000 00001 00000 01111  
 00??? ????? 01010 00012 12?10

#### **Thomasomys paramorum**

01000 00c01 00120 1?001 0?020 c0122 01c00 00001 01010 01030 00-00 10002  
 02000 20010 ala01 02000 1c120 0000- 1-100 0ala0 00b00 10000 00000 01011  
 00202 0???0 00010 00001 0213?

#### **Thomasomys popayanus**

01000 00201 00232 12000 000?0 000?2 0100? 00001 ?110? 01020 02000 30002  
 ?1001 001?? 01001 0010? ?0120 00000 01310 0100- 102?0 ?21?0 10?00 ?00?  
 ?0??? ????? ????? ????? ?????

#### **Thomasomys praetor**

01000 00c01 00222 11001 01020 20002 01000 00001 01200 11020 02000 30012  
 02001 00110 11001 01100 02121 00000 01310 0100- 00001 12100 120?0 00001  
 00??? ???00 10010 01001 00031

#### **Thomasomys princeps**

01001 00201 00232 12000 0???0 00012 01000 00?01 ?120? 11020 02000 30012  
 ?b101 0010? 01001 0000? 10100 10000 01310 2000- 10210 12100 10110 000?1  
 00??? ????? ????? ????? ?????

#### **Thomasomys pyrrhonotus**

01000 00c01 00222 11002 01020 000cc 01000 00001 01202 11000 02000 30011  
 02001 00100 111a1 02001 101d1 00000 01310 0000- 10220 12100 12210 00001  
 00??? ????? ?0??? ????? ?????

#### **Thomasomys rhoadsi**

12010 00001 00120 11101 00020 00002 01200 00011 01010 01031 00-00 10002  
 01000 00011 01000 00000 12121 0000- 1-100 01110 01000 10000 00000 01011  
 0020? 000?0 00011 1?000 02101

#### **Thomasomys rosalinda**

01000 002?1 00232 11001 01?00 00021 0100? 0???1 0120? 11000 02?0? 30?02  
 ??01 001?? 1?0?1 ?100? ?0?20 10?10 01310 0000- 102?0 121?0 11?00 ?00?  
 ?0??? ????? ????? ????? ?????

#### **Thomasomys silvestris**

01000 00001 00120 1?100 00020 20012 02100 00001 01010 01030 00-00 10202  
 01000 00010 01001 00000 12110 0100- 1-100 01010 00000 11000 00000 01011  
 00??? ???00 00000 01001 0210?

#### **Thomasomys taczanowskii**

00100 00201 00232 12001 00010 20020 01000 00000 01110 01030 02000 20001  
 02100 00110 01011 11000 10030 00000 00100 0000- 00000 11000 00000 01111

00002 1000? ?0010 00021 02111

**Thomasomys vestitus**

0?000 002?a 00120 11100 00?20 00022 01000 00001 01010 01020 00-0? 10002  
00000 2000? 01100 0000? 12101 01000 00110 0000- 00000 10000 000?0 01001  
00??? ????? ?0??? ????? ?????

**Thomasomys sp. 1**

01001 001?1 00232 12000 00020 00021 01200 00001 01200 11020 02000 300a2  
02001 c0100 01001 ?0100 10121 00000 01310 0000- 00?20 12100 122?0 00001  
00003 c0002 10011 11100 02-31

**Thomasomys sp. 2**

01001 00001 00220 1?000 00020 00021 11200 00101 01000 11020 02000 30012  
02100 2001? 01101 01100 12120 0000? 01310 0000- 00220 12100 101?0 00001  
00203 000?0 10??? ????? ?????

**Thomasomys sp. 3**

01000 00201 00120 1?000 000?0 00021 01c00 01001 01010 01030 00-00 10002  
01000 00010 01a01 01000 13120 00000 00f00 0a010 00000 10000 0000a 01111  
00003 20000 00000 00001 0c03?

**Thomasomys sp. 4**

11000 000?1 00110 11100 0?021 00202 00000 10?11 01020 01031 02100 10102  
01000 00100 01000 10010 10101 10000 00100 21110 10000 11000 10000 01001  
002?? 20001 11010 00001 12101

**Thomasomys sp. 5**

1?00? 0?00? 00120 11100 00020 ?0203 02211 10011 01020 00031 12000 20202  
01000 20110 01100 10000 12120 00000 00100 11010 00100 11000 11000 01001  
00202 200?1 00000 00001 12102

**Thomasomys sp. 6**

12010 0000a 00120 11100 00020 002c2 01201 00011 01020 00031 02000 f0c02  
0b100 00a11 10a01 11000 12120 00000 00100 0110- 10200 11000 10000 01011  
00202 000?? ????? ????? ?????

**Thomasomys sp. 7**

02010 00001 00120 11101 00020 00223 01201 00011 01010 00031 12000 10002  
01100 00010 01001 11000 12100 00000 00100 01010 00200 01000 100?0 01001  
00202 20001 ?0?00 ??001 0??31

**Thomasomys sp. 8**

01101 002?1 00232 11001 0?0?0 00002 01000 01000 11102 010?0 00-00 10002  
02100 000?? 10110 12010 10030 10000 00100 2000- 00000 01001 10000 01111  
00??? ????? ????? ?????

**Thomasomys sp. 9**

01101 00201 00232 12001 0?0?0 00022 01000 01000 11102 01020 10-00 10002  
02100 00000 11110 12000 10030 10000 00100 20010 00000 01001 00000 01111  
00002 20010 0000? ?0?12 12?1?

**Thomasomys sp. 10**

12010 00001 00020 11100 00020 00002 0120? 00011 01010 00031 10-00 10202  
01000 0011? 01000 00?00 12120 01-0- 1-100 01110 01000 10000 00000 01011  
0000? 000?? ????? ?????

**Thomasomys sp. 11**

01000 00201 00020 11000 00020 20001 01200 00?01 11000 0103? 00-00 10002  
00000 0001? 01001 01000 ?3130 0000- 1-300 01110 00100 10000 01000 01111  
00??? ????? ????? ?????

### APPENDIX 3. CLASSIFICATION AND DERIVED STATES OF THE "ANDEAN THOMASOMYINE" RODENTS.

The following diagnoses apply to monophyletic groups obtained in the analysis described in the text. Both ACCTRAN and DELTRAN optimizations are provided for each node. Character-state changes are formatted as follows: character name, state number ==> state number (character number). For example, "dorsal crater papilla, 1 ==> 0 (110)" indicates that change from state 1 to 0 in character 110. Unambiguous transformations are indicated by "==">", while ambiguous transformations (occurring in only some reconstructions) are indicated by "-->".

#### **The Andean thomasomyine group**

ACCTRAN: position of hypothenar pad in relation to interdigital pad 1 (pes), 0 ==> 1(10); zygomatic plate breadth, 0 --> 1(32); interorbital region, 2 ==> 1(43); interorbital region breadth, 2 --> 1(44); dorsal aperture of ectotympanic ring, 0 ==> 2(60); maxillary septum length, 0 --> 1(63); anterocone, 1 --> 0(88); hypoflexus size of M1, 1 --> 0(94); protostyle and enterostyle on M1, 2 --> 0(96); anterolabial cingulum of m2-m3, 2 ==> 0(107); posteroflexid breadth of m1-m2, 1 ==> 0(108); masseteric crest position, 2 ==> 1(115); coronoid process, 0 ==> 1(120); retromolar region, 1 --> 0(121); prostate ventral glands, 2 --> 1(145). DELTRAN: position of hypothenar pad in relation to interdigital pad 1 (pes), 0 ==> 1(10); protuberant anus, 0 --> 1(24); anterodorsal margin of zygomatic plate, 2 --> 1(31); interorbital region, 2 ==> 1(43); dorsal aperture of ectotympanic ring, 0 ==> 1(60); anterolabial cingulum of m2-m3, 2 ==> 1(107); posteroflexid breadth of m1-m2, 1 ==> 0(108); masseteric crest position, 2 ==> 1(115); coronoid process, 0 ==> 1(120); gall bladder, 1 --> 0(132); spines on the urethral flap of gland penis, 0 --> 2(142).

#### **Chilomys + (Thomasomys s.s.+ (New genus A + New genus D))**

ACCTRAN: manual digit proportions, 1 --> 0(3); position of hypothenar pad in relation to thenar (pes), 2 ==> 0(8); body pelage pattern, 1 ==> 0(20); divergence of squamosal roots of zygomatic arch, 0 ==> 1(40); shape of zygomatic arches, 1 ==> 0(41); interorbital region, 1 ==> 0(43); M1 position, 3 --> 2(84); crater rim, 0 --> 1(135); notch on midventral margin, 0 --> 1(137). DELTRAN: ventral base of claws on manus, 0 --> 1(2); position of hypothenar pad in relation to thenar (pes), 2 ==> 1(8); body pelage pattern, 1 ==> 0(20); divergence of squamosal roots of zygomatic arch, 0 ==> 1(40); shape of zygomatic arches, 1 ==> 0(41); interorbital region, 1 ==> 0(43); dorsal aperture of ectotympanic ring, 1 --> 2(60); protostyle and enterostyle on M1, 2 --> 0(96).

#### **Thomasomys s.s.+ (New genus A + New genus D)**

ACCTRAN: genal 1 vibrissae, 2 --> 0(15); protuberant anus, 1 ==> 2(24); posterodorsal extension of premaxillae, 0 ==> 2(30); maxillary septum length, 1 --> 0(63); upper incisor wear pattern, 0 ==> 1(83); masseteric crest position, 1 ==> 0(115); capsular process of lower incisor, 1 ==> 0(118); supratrochlear fenestra of humerus, 0 ==> 2(123). DELTRAN: protuberant anus, 1 ==> 2(24); posterodorsal extension of premaxillae, 0 ==> 2(30); upper incisor wear pattern, 0 ==> 1(83); M1 position, 3 --> 2(84); anterocone, 1 --> 0(88); masseteric crest position, 1 ==> 0(115); capsular process of

lower incisor, 1 ==> 0(118); supratrochlear fenestra of humerus, 0 ==> 2(123); prostate ventral glands, 2 --> 1(145).

**Thomasomys sensu stricto**

ACCTTRAN: carotid circulation, 2 ==> 0(52); anterior process of the ectotympanic, 1 ==> 0(78); protoflexus on M2, 0 ==> 1(97); crater rim, 1 --> 0(135); notch on midventral margin, 1 --> 0(137); preputial glands, 1 ==> 0(144). genal 1 vibrissae, 2 --> 0(15); carotid circulation, 2 ==> 0(52); maxillary palatal pits, 1 --> 0(68); anterior process of the ectotympanic, 1 ==> 0(78); hypoflexus size of M1, 1 --> 0(94); protoflexus on M2, 0 ==> 1(97); preputial glands, 1 ==> 0(144). DELTRAN: genal 1 vibrissae, 2 --> 0(15); carotid circulation, 2 ==> 0(52); maxillary palatal pits, 1 --> 0(68); anterior process of the ectotympanic, 1 ==> 0(78); hypoflexus size of M1, 1 --> 0(94); protoflexus on M2, 0 ==> 1(97); preputial glands, 1 ==> 0(144).

node\_110 --> node\_97: ACCTTRAN: zygomatic plate slope, 0 ==> 1(33); jugal length, 1 ==> 0(47); depth and shape of the molar-bearing portion of the maxillae, 1 ==> 0(69); M1 position, 2 ==> 0(84); anteromedian flexid of m1, 0 ==> 1(99); anterolabial cingulum of m2-m3, 0 --> 1(107); relative length of condylar and angular processes, 1 --> 0(119); chevron bones, 0 --> 2(126). DELTRAN: position of hypothenar pad in relation to thenar (pes), 1 --> 0(8); zygomatic plate slope, 0 ==> 1(33); jugal length, 1 ==> 0(47); depth and shape of the molar-bearing portion of the maxillae, 1 ==> 0(69); M1 position, 2 ==> 0(84); anteromedian flexid of m1, 0 ==> 1(99).

node\_97 --> node\_95: ACCTTRAN: ventral base of claws on manus, 1 ==> 2(2); zygomatic plate slope, 1 ==> 2(33); carotid circulation, 0 ==> 2(52); maxillary palatal pits, 0 ==> 1(68); molar occlusal design, 0 --> 1(86); orientation of metalophid m1, 0 ==> 1(103); lingual roots on M1, 0 ==> 1(112); dorsal and ventral margin of crater rim, 0 ==> 1(136). DELTRAN: ventral base of claws on manus, 1 ==> 2(2); zygomatic plate slope, 1 ==> 2(33); carotid circulation, 0 ==> 2(52); maxillary palatal pits, 0 ==> 1(68); orientation of metalophid m1, 0 ==> 1(103); lingual roots on M1, 0 ==> 1(112); relative length of condylar and angular processes, 1 --> 0(119); dorsal and ventral margin of crater rim, 0 ==> 1(136).

node\_95 --> node\_94: ACCTTRAN: posterior extension of nasals, 2 ==> 0(29); premaxilla-maxilla suture, 0 ==> 1(35); alisphenoid strut, 0 ==> 1(51); incisive foramina, 1 --> 2(62); maxillary septum length, 0 ==> 1(63); mesopterygoid fossa shape, 1 --> 0(75); accessory labial root of M1, 0 ==> 1(111); roots on m2, 0 ==> 1(114); distributional gastric epithelium, 0 ==> 1(130); spines on the lateral mounds, 0 --> 1(141). DELTRAN: posterior extension of nasals, 2 ==> 0(29); premaxilla-maxilla suture, 0 ==> 1(35); alisphenoid strut, 0 ==> 1(51); maxillary septum length, 0 ==> 1(63); accessory labial root of M1, 0 ==> 1(111); roots on m2, 0 ==> 1(114); chevron bones, 0 --> 2(126); distributional gastric epithelium, 0 ==> 1(130).

node\_94 --> node\_93: ACCTTRAN: rostral tube, 0 ==> 1(28); optic foramen, 0 ==> 1(50); depth and shape of the molar-bearing portion of the maxillae, 0 ==> 1(69); Alisphenoid squamosal posterior margin, 0 ==> 1(76); molar occlusal design, 1 --> 0(86);



protostyle and enterostyle on M1, 0 ==> 1(96); grooves on glans penis body, 1 --> 0(134). DELTRAN: rostral tube, 0 ==> 1(28); optic foramen, 0 ==> 1(50); depth and shape of the molar-bearing portion of the maxillae, 0 ==> 1(69); Alisphenoid squamosal posterior margin, 0 ==> 1(76); protostyle and enterostyle on M1, 0 ==> 1(96).

node\_93 --> node\_92: ACCTTRAN: rostral tube, 1 ==> 2(28); posterodorsal extension of premaxillae, 2 --> 3(30); position of antorbital bridge, 0 ==> 1(39); interorbital region breadth, 1 ==> 2(44); incisive foramina, 2 --> 1(62). DELTRAN: rostral tube, 1 ==> 2(28); position of antorbital bridge, 0 ==> 1(39); interorbital region breadth, 1 ==> 2(44).

node\_92 --> node\_90: ACCTTRAN: posterior extension of nasals, 0 ==> 1(29); bullae inflation, 0 ==> 1(77); orientation of metalophid m1, 1 ==> 2(103); notch on midventral margin, 0 --> 1(137); spines on the lateral mounds, 1 --> 0(141); preputial glands, 0 --> 3(144). DELTRAN: posterior extension of nasals, 0 ==> 1(29); posterodorsal extension of premaxillae, 2 --> 3(30); bullae inflation, 0 ==> 1(77); orientation of metalophid m1, 1 ==> 2(103).

node\_90 --> node\_89: ACCTTRAN: posterior extension of nasals, 1 ==> 2(29); mesopterygoid fossa shape, 0 --> 1(75); protostyle and enterostyle on M1, 1 ==> 0(96); lingual roots on M1, 1 ==> 0(112). DELTRAN: posterior extension of nasals, 1 ==> 2(29); protostyle and enterostyle on M1, 1 ==> 0(96); lingual roots on M1, 1 ==> 0(112); grooves on glans penis body, 1 --> 0(134); preputial glands, 0 --> 3(144).

node\_89 --> node\_88: ACCTTRAN: ungual tufts on manual claws, 0 ==> 1(1); parietal-supraoccipital suture breadth, 0 --> 2(58); shape of parapterygoid fossa, 1 --> 0(72); hypoflexus of M3, 0 --> 1(98); relative length of condylar and angular processes, 0 ==> 1(119). DELTRAN: ungual tufts on manual claws, 0 ==> 1(1); relative length of condylar and angular processes, 0 ==> 1(119).

### **Thomasomys erro + Aepeomys**

ACCTTRAN: relative size of hallux (dI of pes), 1 ==> 0(13); relative size of fifth digit (dV) of pes, 2 ==> 1(14); zygomatic plate breadth, 1 ==> 2(32); infraorbital foramen, 0 ==> 1(36); carotid circulation, 2 ==> 0(52); maxillary septum length, 1 ==> 0(63); Alisphenoid squamosal posterior margin, 1 ==> 0(76); molar height topography, 0 ==> 1(85); anteroflexus M1, 0 ==> 1(90); paraloph orientation in M1, 1 ==> 3(93); position of the trochlear process of calcaneum, 0 ==> 1(127); distributional gastric epithelium, 1 ==> 3(130). DELTRAN: relative size of hallux (dI of pes), 1 ==> 0(13); relative size of fifth digit (dV) of pes, 2 ==> 1(14); zygomatic plate breadth, 1 ==> 2(32); infraorbital foramen, 0 ==> 1(36); carotid circulation, 2 ==> 0(52); maxillary septum length, 1 ==> 0(63); shape of parapterygoid fossa, 1 --> 0(72); Alisphenoid squamosal posterior margin, 1 ==> 0(76); molar height topography, 0 ==> 1(85); anteroflexus M1, 0 ==> 1(90); paraloph orientation in M1, 1 ==> 3(93); hypoflexus of M3, 0 --> 1(98); position of the trochlear process of calcaneum, 0 ==> 1(127); distributional gastric epithelium, 1 ==> 3(130).

### **Aepeomys**

ACCTTRAN: length of mystacial vibrissae, 1 ==> 0(17); masseteric tubercle, 0 ==> 1(34); ethmoid foramen, 0 ==> 1(48); alisphenoid strut, 1 ==> 2(51); hamular process and development of the postglenoid foramen, 1 ==> 0(56); bullae inflation, 1 ==> 0(77); hypoflexus width of M2, 0 ==> 1(95); ridge on anterolabial cingulum of m1, 0 --> 1(102); anterolabial cingulum of m2-m3, 1 ==> 0(107); lingual roots on M1, 0 ==> 1(112); distributional gastric epithelium, 3 --> 4(130); distribution of spines on glans penis body, 0 --> 2(133); spines on the urethral flap of gland penis, 2 --> 0(142); spines on dorsal papilla, 1 --> 0(143). DELTRAN: length of mystacial vibrissae, 1 ==> 0(17); masseteric tubercle, 0 ==> 1(34); ethmoid foramen, 0 ==> 1(48); alisphenoid strut, 1 ==> 2(51); hamular process and development of the postglenoid foramen, 1 ==> 0(56); parietal-supraoccipital suture breadth, 0 --> 2(58); bullae inflation, 1 ==> 0(77); hypoflexus width of M2, 0 ==> 1(95); anterolabial cingulum of m2-m3, 1 ==> 0(107); lingual roots on M1, 0 ==> 1(112).

node\_85 --> Aepeomys lugens: ACCTTRAN: ungual tuft on pes, 0 ==> 1(4); medial process of posterior margin of palate bridge, 0 ==> 2(66). DELTRAN: ungual tuft on pes, 0 ==> 1(4); medial process of posterior margin of palate bridge, 0 ==> 2(66); distributional gastric epithelium, 3 --> 4(130).

node\_85 --> Aepeomys reigi: ACCTTRAN: premaxilla-maxilla suture, 1 ==> 0(35); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); incisive foramina, 1 ==> 0(62); palatal length, 0 ==> 2(64); accessory labial root of M1, 1 ==> 0(111). DELTRAN: premaxilla-maxilla suture, 1 ==> 0(35); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); incisive foramina, 1 ==> 0(62); palatal length, 0 ==> 2(64); ridge on anterolabial cingulum of m1, 0 --> 1(102); accessory labial root of M1, 1 ==> 0(111); distribution of spines on glans penis body, 0 --> 2(133); notch on midventral margin, 0 --> 1(137); spines on the urethral flap of gland penis, 2 --> 0(142); spines on dorsal papilla, 1 --> 0(143).

node\_86 --> Thomasomys erro: ACCTTRAN: posterior extension of nasals, 2 ==> 0(29); zygomatic plate slope, 2 ==> 0(33); parietal-supraoccipital suture breadth, 2 --> 0(58); maxillary palatal pits, 1 ==> 0(68); mesopterygoid fossa shape, 1 ==> 0(75); anteromedian flexid of m1, 1 ==> 0(99); orientation of metalophid m1, 2 ==> 0(103); number of caudal vertebrae, 2 ==> 3(125). DELTRAN: posterior extension of nasals, 2 ==> 0(29); zygomatic plate slope, 2 ==> 0(33); maxillary palatal pits, 1 ==> 0(68); mesopterygoid fossa shape, 1 ==> 0(75); anteromedian flexid of m1, 1 ==> 0(99); orientation of metalophid m1, 2 ==> 0(103); number of caudal vertebrae, 2 ==> 3(125).

node\_88 --> node\_87: ACCTTRAN: alisphenoid strut, 1 ==> 0(51); maxillary at posterior base of M3, 0 ==> 1(70); sphenopalatine vacuities, 0 --> 1(71); roots on m2, 1 ==> 0(114); chevron bones, 2 --> 0(126); distributional gastric epithelium, 1 --> 0(130). DELTRAN: alisphenoid strut, 1 ==> 0(51); maxillary at posterior base of M3, 0 ==> 1(70); roots on m2, 1 ==> 0(114).

node\_87 --> Thomasomys incanus: ACCTTRAN: shape of parapterygoid fossa, 0 --> 1(72); anteroflexus M1, 0 ==> 1(91); hypoflexus of M3, 1 --> 0(98); anterolabial

cingulum of m2-m3, 1 ==> 0(107). DELTRAN: parietal-supraoccipital suture breadth, 0 --> 2(58); anteroflexus M1, 0 ==> 1(91); anterolabial cingulum of m2-m3, 1 ==> 0(107); distributional gastric epithelium, 1 --> 0(130).

node\_87 --> Thomasomys sp. 6: ACCTTRAN: ungual tuft on pes, 0 ==> 1(4); posterodorsal extension of premaxillae, 3 ==> 2(30); M1 position, 0 ==> 2(84); anteromedian flexid of m1, 1 ==> 0(99); ectolophid m1, 0 ==> 1(101). DELTRAN: ungual tuft on pes, 0 ==> 1(4); posterodorsal extension of premaxillae, 3 ==> 2(30); sphenopalatine vacuities, 0 --> 1(71); shape of parapterygoid fossa, 1 --> 0(72); M1 position, 0 ==> 2(84); hypoflexus of M3, 0 --> 1(98); anteromedian flexid of m1, 1 ==> 0(99); ectolophid m1, 0 ==> 1(101); chevron bones, 2 --> 0(126).

node\_89 --> Thomasomys sp. 7: ACCTTRAN: ungual tuft on pes, 0 ==> 1(4); body pelage pattern, 0 ==> 1(20); interorbital region breadth, 2 ==> 1(44); maxillary palatal pits, 1 ==> 0(68); mesolophid on m3, 1 ==> 0(106). DELTRAN: ungual tuft on pes, 0 ==> 1(4); body pelage pattern, 0 ==> 1(20); interorbital region breadth, 2 ==> 1(44); maxillary palatal pits, 1 ==> 0(68); mesolophid on m3, 1 ==> 0(106).

node\_90 --> Thomasomys ischyryus: ACCTTRAN: antitragus and pinnae structure, 1 ==> 0(18); dorsal aperture of ectotympanic ring, 2 ==> 1(60). DELTRAN: antitragus and pinnae structure, 1 ==> 0(18); dorsal aperture of ectotympanic ring, 2 ==> 1(60); mesopterygoid fossa shape, 1 --> 0(75).

node\_92 --> node\_91: ACCTTRAN: ungual tufts on manual claws, 0 ==> 1(1); ventral base of claws on manus, 2 --> 1(2); infraorbital foramen, 0 ==> 1(36); parietal-supraoccipital suture breadth, 0 ==> 1(58); maxillary septum length, 1 ==> 0(63); roots on m2, 1 ==> 0(114); dorsal and ventral margin of crater rim, 1 ==> 0(136). DELTRAN: ungual tufts on manual claws, 0 ==> 1(1); infraorbital foramen, 0 ==> 1(36); parietal-supraoccipital suture breadth, 0 ==> 1(58); maxillary septum length, 1 ==> 0(63); mesopterygoid fossa shape, 1 --> 0(75); roots on m2, 1 ==> 0(114); dorsal and ventral margin of crater rim, 1 ==> 0(136); spines on the lateral mounds, 0 --> 1(141).

node\_91 --> Thomasomys sp. 4: ACCTTRAN: relative size of fifth digit (dV) of pes, 2 ==> 1(14); countershading of tail, 0 ==> 1(25); posterodorsal extension of premaxillae, 3 --> 2(30); zygomatic plate breadth, 1 ==> 0(32); zygomatic plate slope, 2 ==> 0(33); premaxilla-maxilla suture, 1 ==> 0(35); jugal length, 0 ==> 1(47); alisphenoid strut, 1 ==> 0(51); exposure of internal carotid artery, 0 ==> 1(53); depth and shape of the molar-bearing portion of the maxillae, 1 ==> 0(69); malleus lamina, 0 ==> 1(79); upper incisor orientation, 2 ==> 0(82); molar height topography, 0 ==> 1(85); molar occlusal design, 0 ==> 1(86); protostyle and enterostyle on M1, 1 ==> 2(96); hypoflexus of M3, 0 ==> 1(98); ectolophid m1, 0 ==> 1(101); orientation of metalophid m1, 1 ==> 0(103); lingual roots on M1, 1 ==> 0(112); incisura angularis, 0 ==> 1(131); gall bladder, 0 ==> 1(132); grooves on glans penis body, 0 --> 1(134). DELTRAN: ventral base of claws on manus, 2 --> 1(2); relative size of fifth digit (dV) of pes, 2 ==> 1(14); countershading of tail, 0 ==> 1(25); zygomatic plate breadth, 1 ==> 0(32); zygomatic plate slope, 2 ==> 0(33); premaxilla-maxilla suture, 1 ==> 0(35); jugal length, 0 ==> 1(47); alisphenoid strut, 1 ==>

0(51); exposure of internal carotid artery, 0 ==> 1(53); depth and shape of the molar-bearing portion of the maxillae, 1 ==> 0(69); malleus lamina, 0 ==> 1(79); upper incisor orientation, 2 ==> 0(82); molar height topography, 0 ==> 1(85); molar occlusal design, 0 ==> 1(86); protostyle and enterostyle on M1, 1 ==> 2(96); hypoflexus of M3, 0 ==> 1(98); ectolophid m1, 0 ==> 1(101); orientation of metalophid m1, 1 ==> 0(103); lingual roots on M1, 1 ==> 0(112); incisura angularis, 0 ==> 1(131); gall bladder, 0 ==> 1(132).

node\_91 --> Thomasomys sp. 5: ACCTTRAN: zygomatic plate breadth, 1 ==> 2(32); masseteric tubercle, 0 ==> 1(34); hamular process and development of the postglenoid foramen, 1 ==> 2(56); parietal-supraoccipital suture breadth, 1 ==> 2(58); medial process of posterior margin of palate bridge, 0 ==> 2(66); parapterygoid vacuity, 0 ==> 1(73); M1 position, 0 ==> 2(84); prostate ventral glands, 1 ==> 2(145). DELTRAN: posterodorsal extension of premaxillae, 2 --> 3(30); zygomatic plate breadth, 1 ==> 2(32); masseteric tubercle, 0 ==> 1(34); hamular process and development of the postglenoid foramen, 1 ==> 2(56); parietal-supraoccipital suture breadth, 1 ==> 2(58); medial process of posterior margin of palate bridge, 0 ==> 2(66); parapterygoid vacuity, 0 ==> 1(73); M1 position, 0 ==> 2(84); grooves on glans penis body, 1 --> 0(134); prostate ventral glands, 1 ==> 2(145).

node\_93 --> Thomasomys eleusis: ACCTTRAN: body pelage pattern, 0 ==> 1(20); lacrimal posterior projection, 0 ==> 1(38); interorbital region, 0 ==> 1(43); mesopterygoid fossa shape, 0 --> 1(75); anteroflexus M1, 0 ==> 1(90); anterolabial cingulum of m2-m3, 1 ==> 0(107). DELTRAN: body pelage pattern, 0 ==> 1(20); lacrimal posterior projection, 0 ==> 1(38); interorbital region, 0 ==> 1(43); incisive foramina, 1 --> 2(62); anteroflexus M1, 0 ==> 1(90); anterolabial cingulum of m2-m3, 1 ==> 0(107).

node\_94 --> Thomasomys kalinowskii: ACCTTRAN: position of hypothenar pad in relation to interdigital pad 1 (pes), 1 ==> 0(10); alisphenoid strut, 1 ==> 2(51); dorsal aperture of ectotympanic ring, 2 ==> 1(60); bullae inflation, 0 ==> 1(77); upper incisor orientation, 2 ==> 0(82). DELTRAN: position of hypothenar pad in relation to interdigital pad 1 (pes), 1 ==> 0(10); alisphenoid strut, 1 ==> 2(51); dorsal aperture of ectotympanic ring, 2 ==> 1(60); incisive foramina, 1 --> 2(62); mesopterygoid fossa shape, 1 --> 0(75); bullae inflation, 0 ==> 1(77); upper incisor orientation, 2 ==> 0(82); molar occlusal design, 0 --> 1(86); spines on the lateral mounds, 0 --> 1(141).

node\_95 --> Thomasomys ladewi: ACCTTRAN: pectoral markings, 0 ==> 1(22); uniform pattern coloration of tail, 0 ==> 2(26); posterodorsal extension of premaxillae, 2 ==> 1(30); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); interorbital region, 0 ==> 1(43); postorbital ridge, 0 ==> 1(46); ethmoturbinals and sphenopalatine foramen formation, 3 ==> 2(49); hamular process and development of the postglenoid foramen, 1 ==> 3(56); anteroflexus M1, 0 ==> 1(91); crater rim, 0 ==> 1(135). DELTRAN: pectoral markings, 0 ==> 1(22); uniform pattern coloration of tail, 0 ==> 2(26); posterodorsal extension of premaxillae, 2 ==> 1(30); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); interorbital region, 0 ==> 1(43); postorbital ridge, 0 ==> 1(46); ethmoturbinals and sphenopalatine foramen

formation, 3 ==> 2(49); hamular process and development of the postglenoid foramen, 1 ==> 3(56); molar occlusal design, 0 --> 1(86); anteroflexus M1, 0 ==> 1(91); crater rim, 0 ==> 1(135).

node\_97 --> node\_96: ACCTTRAN: relative size of hallux (dl of pes), 1 ==> 0(13); body pelage pattern, 0 ==> 1(20); rostral tube, 0 ==> 1(28); position of antorbital bridge, 0 --> 1(39); incisive foramina, 1 ==> 0(62); hypoflexus of M3, 0 ==> 1(98). DELTRAN: relative size of hallux (dl of pes), 1 ==> 0(13); body pelage pattern, 0 ==> 1(20); rostral tube, 0 ==> 1(28); incisive foramina, 1 ==> 0(62); hypoflexus of M3, 0 ==> 1(98).

node\_96 --> Thomasomys contradictus: ACCTTRAN: posterior extension of nasals, 2 ==> 0(29); bullae inflation, 0 ==> 1(77); molar height topography, 0 ==> 1(85); anterolabial cingulum of m2-m3, 1 --> 0(107); relative length of condylar and angular processes, 0 --> 1(119). DELTRAN: posterior extension of nasals, 2 ==> 0(29); bullae inflation, 0 ==> 1(77); molar height topography, 0 ==> 1(85); anterolabial cingulum of m2-m3, 1 --> 0(107).

node\_96 --> Thomasomys dispar: ACCTTRAN: relative size of fifth digit (dV) of pes, 2 ==> 1(14); uniform pattern coloration of tail, 0 ==> 2(26); rostral tube, 1 ==> 2(28); zygomatic plate breadth, 1 ==> 2(32); optic foramen, 0 ==> 1(50); medial process of posterior margin of palate bridge, 0 ==> 2(66); anteroflexus M1, 0 ==> 1(90); accessory labial root of M1, 0 ==> 1(111); grooves on glans penis body, 1 ==> 0(134). DELTRAN: relative size of fifth digit (dV) of pes, 2 ==> 1(14); uniform pattern coloration of tail, 0 ==> 2(26); rostral tube, 1 ==> 2(28); zygomatic plate breadth, 1 ==> 2(32); position of antorbital bridge, 0 --> 1(39); optic foramen, 0 ==> 1(50); medial process of posterior margin of palate bridge, 0 ==> 2(66); anteroflexus M1, 0 ==> 1(90); accessory labial root of M1, 0 ==> 1(111); relative length of condylar and angular processes, 1 --> 0(119); grooves on glans penis body, 1 ==> 0(134).

node\_110 --> node\_105: ACCTTRAN: position of hypothenar pad in relation to thenar (pes), 0 --> 1(8); antitragus and pinnae structure, 1 ==> 0(18); parapterygoid vacuity, 0 ==> 1(73); bullae inflation, 0 ==> 1(77); grooves on glans penis body 1 0.154 1 --> 0(134); preputial glands, 0 ==> 3(144); prostate ventral glands, 1 --> 0(145). DELTRAN: antitragus and pinnae structure, 1 ==> 0(18); parapterygoid vacuity, 0 ==> 1(73); bullae inflation, 0 ==> 1(77); preputial glands, 0 ==> 3(144).

node\_105 --> node\_102: ACCTTRAN: position of hypothenar pad in relation to thenar (pes), 1 --> 2(8); posterodorsal extension of premaxillae, 2 ==> 1(30); hypoflexus of M3, 0 ==> 1(98); anteromedian flexid of m1, 0 --> 1(99); number of caudal vertebrae, 2 --> 3(125); spines on the urethral flap of gland penis, 2 --> 0(142). DELTRAN: posterodorsal extension of premaxillae, 2 ==> 1(30); hypoflexus of M3, 0 ==> 1(98).

node\_102 --> node\_99: ACCTTRAN: notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); upper incisor orientation, 2 ==> 3(82); protoflexus on M2, 1 ==> 0(97). DELTRAN: notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); upper incisor orientation, 2 ==> 3(82); protoflexus on M2, 1 ==> 0(97);

number of caudal vertebrae, 2 --> 3(125); grooves on glans penis body, 1 --> 0(134); spines on the urethral flap of gland penis, 2 --> 0(142).

node\_99 --> Thomasomys australis: ACCTTRAN: anteromedian flexid of m1, 1 --> 0(99); anterolabial cingulum of m2-m3, 0 --> 1(107).

node\_99 --> node\_98: ACCTTRAN: masseteric crest position, 0 --> 1(115); capsular process of lower incisor, 0 ==> 1(118); supratrochlear fenestra of humerus, 2 ==> 0(123); chevron bones, 0 ==> 2(126); spines on dorsal papilla, 1 --> 0(143). DELTRAN: position of hypothenar pad in relation to thenar (pes), 1 --> 2(8); anteromedian flexid of m1, 0 --> 1(99); anterolabial cingulum of m2-m3, 1 --> 0(107); capsular process of lower incisor, 0 ==> 1(118); supratrochlear fenestra of humerus, 2 ==> 0(123); chevron bones, 0 ==> 2(126).

node\_98 --> Thomasomys daphne: ACCTTRAN: uniform pattern coloration of tail, 0 ==> 2(26); interorbital region, 0 ==> 1(43); jugal length, 1 ==> 0(47); carotid circulation, 0 ==> 2(52); medial process of posterior margin of palate bridge, 0 ==> 2(66). DELTRAN: uniform pattern coloration of tail, 0 ==> 2(26); interorbital region, 0 ==> 1(43); jugal length, 1 ==> 0(47); carotid circulation, 0 ==> 2(52); medial process of posterior margin of palate bridge, 0 ==> 2(66); masseteric crest position, 0 --> 1(115); prostate ventral glands, 1 --> 0(145).

node\_98 --> Thomasomys sp. 3: ACCTTRAN: hypoflexus of M3, 1 ==> 0(98). DELTRAN: hypoflexus of M3, 1 ==> 0(98); spines on dorsal papilla, 1 --> 0(143).

node\_102 --> node\_101: ACCTTRAN: anteroflexus M1, 0 ==> 1(91); lingual roots on M1, 0 ==> 1(112). DELTRAN: anteroflexus M1, 0 ==> 1(91); anteromedian flexid of m1, 0 --> 1(99); lingual roots on M1, 0 ==> 1(112).

node\_101 --> node\_100: ACCTTRAN: interorbital region breadth, 1 ==> 0(44); M1 position, 2 ==> 3(84); paraloph orientation in M1, 1 --> 3(93); orientation of metalophid m1, 0 --> 1(103). DELTRAN: interorbital region breadth, 1 ==> 0(44); M1 position, 2 ==> 3(84); anterolabial cingulum of m2-m3, 1 --> 0(107).

node\_100 --> Thomasomys cinnameus: ACCTTRAN: ventral base of claws on manus, 1 ==> 2(2); relative size of fifth digit (dV) of pes, 2 ==> 3(14); antitragus and pinnae structure, 0 ==> 1(18); zygomatic plate breadth, 1 ==> 2(32); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); hamular process and development of the postglenoid foramen, 1 ==> 2(56). DELTRAN: ventral base of claws on manus, 1 ==> 2(2); relative size of fifth digit (dV) of pes, 2 ==> 3(14); antitragus and pinnae structure, 0 ==> 1(18); zygomatic plate breadth, 1 ==> 2(32); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); hamular process and development of the postglenoid foramen, 1 ==> 2(56).

node\_100 --> Thomasomys sp. 11 : ACCTTRAN: relative size of hallux (dI of pes), 1 ==> 0(13); uniform pattern coloration of tail, 0 ==> 2(26); posterior extension of nasals, 2

==> 0(29); zygomatic plate slope, 0 ==> 2(33); shape of zygomatic arches, 0 ==> 1(41); incisive foramina, 1 ==> 0(62); parapterygoid vacuity, 1 ==> 0(73); upper incisor orientation, 2 ==> 3(82); capsular process of lower incisor, 0 ==> 1(118). DELTRAN: position of hypothenar pad in relation to thenar (pes), 1 --> 2(8); relative size of hallux (dl of pes), 1 ==> 0(13); uniform pattern coloration of tail, 0 ==> 2(26); posterior extension of nasals, 2 ==> 0(29); zygomatic plate slope, 0 ==> 2(33); shape of zygomatic arches, 0 ==> 1(41); incisive foramina, 1 ==> 0(62); parapterygoid vacuity, 1 ==> 0(73); upper incisor orientation, 2 ==> 3(82); paraloph orientation in M1, 1 --> 3(93); orientation of metalophid m1, 0 --> 1(103); capsular process of lower incisor, 0 ==> 1(118).

node\_101 --> Thomasomys monochromos: ACCTTRAN: position of hypothenar pad in relation to thenar (pes), 2 --> 0(8); anterolabial cingulum of m2-m3, 0 --> 1(107); accessory labial root of M1, 0 ==> 1(111). DELTRAN: position of hypothenar pad in relation to thenar (pes), 1 --> 0(8); accessory labial root of M1, 0 ==> 1(111).

node\_105 --> node\_104: ACCTTRAN: rostral tube, 0 ==> 1(28); interorbital region breadth, 1 --> 0(44); bullae inflation, 1 ==> 2(77); transverse palatal ridges, 0 --> 1(129). DELTRAN: rostral tube, 0 ==> 1(28); bullae inflation, 1 ==> 2(77); anterolabial cingulum of m2-m3, 1 --> 0(107).

node\_104 --> Thomasomys hudsoni: ACCTTRAN: position of hypothenar pad in relation to thenar (pes), 1 --> 0(8); relative size of fifth digit (dV) of pes, 2 ==> 3(14); rostral tube, 1 ==> 2(28); premaxilla-maxilla suture, 0 ==> 1(35); shape of zygomatic arches, 0 ==> 1(41); jugal length, 1 ==> 0(47); parietal-supraoccipital suture breadth, 0 ==> 2(58); maxillary septum length, 0 ==> 1(63); maxillary palatal pits, 0 ==> 1(68); mesopterygoid fossa shape, 1 ==> 0(75); M1 position, 2 ==> 3(84); paraloph orientation in M1, 1 ==> 0(93); ridge on anterolabial cingulum of m1, 0 ==> 1(102); entolophids of m1-m2, 0 ==> 2(104). DELTRAN: position of hypothenar pad in relation to thenar (pes), 1 --> 0(8); relative size of fifth digit (dV) of pes, 2 ==> 3(14); rostral tube, 1 ==> 2(28); premaxilla-maxilla suture, 0 ==> 1(35); shape of zygomatic arches, 0 ==> 1(41); interorbital region breadth, 1 --> 0(44); jugal length, 1 ==> 0(47); parietal-supraoccipital suture breadth, 0 ==> 2(58); maxillary septum length, 0 ==> 1(63); maxillary palatal pits, 0 ==> 1(68); mesopterygoid fossa shape, 1 ==> 0(75); M1 position, 2 ==> 3(84); paraloph orientation in M1, 1 ==> 0(93); ridge on anterolabial cingulum of m1, 0 ==> 1(102); entolophids of m1-m2, 0 ==> 2(104).

node\_104 --> node\_103: ACCTTRAN: body pelage pattern, 0 ==> 1(20); incisive foramina, 1 ==> 2(62); sphenopalatine vacuities, 0 --> 1(71); upper incisor orientation, 2 --> 0(82); orientation of metalophid m1, 0 ==> 2(103). DELTRAN: body pelage pattern, 0 ==> 1(20); incisive foramina, 1 ==> 2(62); orientation of metalophid m1, 0 ==> 1(103).

node\_103 --> Thomasomys niveipes: ACCTTRAN: ventral base of claws on manus, 1 ==> 2(2); posterior extension of nasals, 2 ==> 0(29); anterodorsal margin of zygomatic plate, 0 ==> 1(31); interfrontal fontanella, 0 ==> 2(45); ethmoturbinals and sphenopalatine foramen formation, 3 ==> 2(49); alisphenoid strut, 0 ==> 1(51); hamular

process and development of the postglenoid foramen, 1 ==> 3(56); mesopterygoid fossa breadth, 0 ==> 1(74); anterior process of the ectotympanic, 0 ==> 1(78); spines on the lateral mounds, 0 ==> 1(141). DELTRAN: ventral base of claws on manus, 1 ==> 2(2); posterior extension of nasals, 2 ==> 0(29); anterodorsal margin of zygomatic plate, 0 ==> 1(31); interorbital region breadth, 1 --> 0(44); interfrontal fontanella, 0 ==> 2(45); ethmoturbinals and sphenopalatine foramen formation, 3 ==> 2(49); alisphenoid strut, 0 ==> 1(51); hamular process and development of the postglenoid foramen, 1 ==> 3(56); sphenopalatine vacuities, 0 --> 1(71); mesopterygoid fossa breadth, 0 ==> 1(74); anterior process of the ectotympanic, 0 ==> 1(78); upper incisor orientation, 2 --> 0(82); orientation of metalophid m1, 1 --> 2(103); transverse palatal ridges, 0 --> 1(129); grooves on glans penis body, 1 --> 0(134); spines on the lateral mounds, 0 ==> 1(141).

node\_103 --> Thomasomys paramorum: ACCTTRAN: interorbital region breadth, 0 --> 1(44); medial process of posterior margin of palate bridge, 0 ==> 2(66); anteroflexus M1, 0 ==> 1(91); hypoflexus of M3, 0 ==> 1(98); grooves on glans penis body, 0 --> 1(134). DELTRAN: medial process of posterior margin of palate bridge, 0 ==> 2(66); anteroflexus M1, 0 ==> 1(91); hypoflexus of M3, 0 ==> 1(98).

node\_110 --> node\_106: ACCTTRAN: position of hypothenar pad in relation to thenar (pes), 0 --> 1(8); relative size of hallux (dl of pes), 1 ==> 0(13); rostral tube, 0 ==> 1(28); posterior extension of nasals, 2 ==> 1(29); lacrimal posterior projection, 0 ==> 1(38); hamular process and development of the postglenoid foramen, 1 ==> 2(56); maxillary at posterior base of M3, 0 ==> 1(70); mesopterygoid fossa shape, 1 ==> 0(75); M1 position, 2 ==> 0(84); molar height topography, 0 ==> 1(85); molar occlusal design, 0 ==> 1(86); anteroflexus M1, 0 ==> 1(90); molar flexus (-ids) crenulation, 0 ==> 1(110); relative length of condylar and angular processes, 1 ==> 0(119); spines on the urethral flap of gland penis, 2 --> 0(142). DELTRAN: relative size of hallux (dl of pes), 1 ==> 0(13); rostral tube, 0 ==> 1(28); posterior extension of nasals, 2 ==> 1(29); lacrimal posterior projection, 0 ==> 1(38); hamular process and development of the postglenoid foramen, 1 ==> 2(56); maxillary at posterior base of M3, 0 ==> 1(70); mesopterygoid fossa shape, 1 ==> 0(75); M1 position, 2 ==> 0(84); molar height topography, 0 ==> 1(85); molar occlusal design, 0 ==> 1(86); anteroflexus M1, 0 ==> 1(90); molar flexus (-ids) crenulation, 0 ==> 1(110); relative length of condylar and angular processes, 1 ==> 0(119).

node\_106 --> Thomasomys bombycinus: ACCTTRAN: posterior extension of nasals, 1 ==> 0(29); zygomatic plate slope, 0 ==> 2(33); depth and shape of the molar-bearing portion of the maxillae, 1 ==> 0(69). DELTRAN: posterior extension of nasals, 1 ==> 0(29); zygomatic plate slope, 0 ==> 2(33); depth and shape of the molar-bearing portion of the maxillae, 1 ==> 0(69); anterolabial cingulum of m2-m3, 1 --> 0(107); spines on the urethral flap of gland penis, 2 --> 0(142).

node\_106 --> Thomasomys cinereiventer: ACCTTRAN: position of hypothenar pad in relation to thenar (pes), 1 ==> 2(8); body pelage pattern, 0 ==> 1(20); interorbital region, 0 ==> 1(43); upper incisor orientation, 2 ==> 1(82); hypoflexus of M3, 0 ==> 1(98); anterolabial cingulum of m2-m3, 0 --> 1(107). DELTRAN: position of hypothenar pad in



relation to thenar (pes), 1 ==> 2(8); body pelage pattern, 0 ==> 1(20); interorbital region, 0 ==> 1(43); upper incisor orientation, 2 ==> 1(82); hypoflexus of M3, 0 ==> 1(98);

node\_110 --> node\_107: ACCTTRAN: uniform pattern coloration of tail, 0 ==> 2(26); anteroflexus M1, 0 ==> 1(90); orientation of metalophid m1, 0 ==> 2(103); spines on the lateral mounds, 0 --> 1(141). DELTRAN: uniform pattern coloration of tail, 0 ==> 2(26); anteroflexus M1, 0 ==> 1(90); orientation of metalophid m1, 0 ==> 2(103).

node\_107 --> Thomasomys caudivarius: ACCTTRAN: rostral tube, 0 ==> 1(28); posterodorsal extension of premaxillae, 2 ==> 1(30); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); shape of parapterygoid fossa, 1 ==> 0(72); M1 position, 2 ==> 3(84); anterolabial cingulum of m2-m3, 0 --> 1(107); number of caudal vertebrae, 2 ==> 3(125). DELTRAN: position of hypothenar pad in relation to thenar (pes), 1 --> 0(8); rostral tube, 0 ==> 1(28); posterodorsal extension of premaxillae, 2 ==> 1(30); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); shape of parapterygoid fossa, 1 ==> 0(72); M1 position, 2 ==> 3(84); number of caudal vertebrae, 2 ==> 3(125).

node\_107 --> Thomasomys hylophilus: ACCTTRAN: ethmoturbinals and sphenopalatine foramen formation, 3 ==> 2(49); bullae inflation, 0 ==> 1(77); hypoflexus of M3, 0 ==> 1(98); chevron bones, 0 ==> 2(126). . DELTRAN: ethmoturbinals and sphenopalatine foramen formation, 3 ==> 2(49); bullae inflation, 0 ==> 1(77); hypoflexus of M3, 0 ==> 1(98); anterolabial cingulum of m2-m3, 1 --> 0(107); chevron bones, 0 ==> 2(126); spines on the lateral mounds, 0 --> 1(141).

node\_110 --> Thomasomys cinereus: ACCTTRAN: position of hypothenar pad in relation to thenar (pes), 0 --> 1(8); relative size of hallux (dI of pes), 1 ==> 2(13); body pelage pattern, 0 ==> 1(20); medial process of posterior margin of palate bridge, 0 ==> (12) (66); hypoflexus of M3, 0 ==> 1(98); anterolabial cingulum of m2-m3, 0 --> 1(107); relative length of condylar and angular processes, 1 ==> 0(119); chevron bones, 0 ==> 2(126); grooves on glans penis body, 1 ==> 0(134); spines on the urethral flap of gland penis, 2 ==> 0(142); spines on dorsal papilla, 1 ==> 0(143); prostate ventral glands, 1 ==> 0(145). . DELTRAN: relative size of hallux (dI of pes), 1 ==> 2(13); body pelage pattern, 0 ==> 1(20); medial process of posterior margin of palate bridge, 0 ==> (12) (66); hypoflexus of M3, 0 ==> 1(98); relative length of condylar and angular processes, 1 ==> 0(119); chevron bones, 0 ==> 2(126); grooves on glans penis body, 1 ==> 0(134); spines on the urethral flap of gland penis, 2 ==> 0(142); spines on dorsal papilla, 1 ==> 0(143); prostate ventral glands, 1 ==> 0(145).

node\_110 --> node\_108: ACCTTRAN: length of mystacial vibrissae, 1 ==> 2(17); antitragus and pinnae structure, 1 ==> 0(18); body pelage pattern, 0 ==> 1(20); posterior extension of nasals, 2 ==> 1(29); zygomatic plate slope, 0 ==> 2(33); hamular process and development of the postglenoid foramen, 1 ==> 2(56); depth and shape of the molar-bearing portion of the maxillae, 1 --> 0(69); mesopterygoid fossa shape, 1 ==> 0(75); bullae inflation, 0 ==> 2(77); anteroflexus M1, 0 --> 1(90); orientation of metalophid m1, 0 --> 2(103); crater rim, 0 --> 1(135); dorsal and ventral

margin of crater rim, 0 --> 1(136); notch on midventral margin, 0 --> 1(137); spines on the urethral flap of gland penis, 2 --> 0(142); spines on dorsal papilla, 1 --> 0(143); prostate ventral glands, 1 --> 2(145). DELTRAN: position of hypothenar pad in relation to thenar (pes), 1 --> 0(8); length of mystacial vibrissae, 1 ==> 2(17); antitragus and pinnae structure, 1 ==> 0(18); body pelage pattern, 0 ==> 1(20); posterior extension of nasals, 2 ==> 1(29); zygomatic plate slope, 0 ==> 2(33); hamular process and development of the postglenoid foramen, 1 ==> 2(56); mesopterygoid fossa shape, 1 ==> 0(75); bullae inflation, 0 ==> 2(77).

node\_108 --> Thomasomys emeritus: ACCTTRAN: posterodorsal extension of premaxillae, 2 ==> 1(30); position of antorbital bridge, 0 ==> 1(39); sphenopalatine vacuities, 0 ==> 1(71); parapterygoid vacuity, 0 ==> 1(73); upper incisor orientation, 2 ==> 0(82); ectolophid m1, 0 ==> 1(101); anterolabial cingulum of m2-m3, 0 --> 1(107). DELTRAN: posterodorsal extension of premaxillae, 2 ==> 1(30); position of antorbital bridge, 0 ==> 1(39); sphenopalatine vacuities, 0 ==> 1(71); parapterygoid vacuity, 0 ==> 1(73); upper incisor orientation, 2 ==> 0(82); anteroflexus M1, 0 --> 1(90); ectolophid m1, 0 ==> 1(101); prostate ventral glands, 1 --> 2(145).

node\_108 --> Thomasomys laniger: ACCTTRAN: M1 position, 2 ==> 3(84); anteroflexus M1, 0 ==> 1(91); protoflexus on M2, 1 ==> 0(97); hypoflexus of M3, 0 ==> 1(98); lateral mound relative position, 1 ==> 0(140). DELTRAN: depth and shape of the molar-bearing portion of the maxillae, 1 --> 0(69); M1 position, 2 ==> 3(84); anteroflexus M1, 0 ==> 1(91); protoflexus on M2, 1 ==> 0(97); hypoflexus of M3, 0 ==> 1(98); orientation of metalophid m1, 0 --> 2(103); anterolabial cingulum of m2-m3, 1 --> 0(107); crater rim, 0 --> 1(135); dorsal and ventral margin of crater rim, 0 --> 1(136); notch on midventral margin, 0 --> 1(137); lateral mound relative position, 1 ==> 0(140); spines on the urethral flap of gland penis, 2 --> 0(142); spines on dorsal papilla, 1 --> 0(143);

node\_110 --> node\_109: ACCTTRAN: ungual tufts on manual claws, 0 ==> 1(1); ventral base of claws on manus, 1 ==> 2(2); ungual tuft on pes, 0 ==> 1(4); relative size of hallux (dl of pes), 1 --> 0(13); posterior extension of nasals, 2 ==> 0(29); zygomatic plate slope, 0 ==> 2(33); position of antorbital bridge, 0 ==> 1(39); optic foramen, 0 ==> 1(50); maxillary at posterior base of M3, 0 --> 1(70); mesopterygoid fossa shape, 1 ==> 0(75); molar height topography, 0 --> 1(85); anteroflexus M1, 0 --> 1(90); anteroflexus M1, 0 --> 1(91); hypoflexus of M3, 0 --> 1(98); anteromedian flexid of m1, 0 ==> 1(99); ridge on anterolabial cingulum of m1, 0 ==> 1(102); crater rim, 0 --> 1(135); dorsal and ventral margin of crater rim, 0 --> 1(136); lateral mound relative position, 1 --> 0(140). DELTRAN: ungual tufts on manual claws, 0 ==> 1(1); ventral base of claws on manus, 1 ==> 2(2); ungual tuft on pes, 0 ==> 1(4); position of hypothenar pad in relation to thenar (pes), 1 --> 0(8); posterior extension of nasals, 2 ==> 0(29); zygomatic plate slope, 0 ==> 2(33); position of antorbital bridge, 0 ==> 1(39); optic foramen, 0 ==> 1(50); mesopterygoid fossa shape, 1 ==> 0(75); anteromedian flexid of m1, 0 ==> 1(99); ridge on anterolabial cingulum of m1, 0 ==> 1(102); anterolabial cingulum of m2-m3, 1 --> 0(107).

node\_109 --> Thomasomys fumeus: ACCTTRAN: zygomatic plate breadth, 1 ==> 2(32);

anteroflexus M1, 1 --> 0(91); hypoflexus of M3, 1 --> 0(98). DELTRAN: relative size of hallux (dl of pes), 1 --> 0(13); zygomatic plate breadth, 1 ==> 2(32); molar heighth topography, 0 --> 1(85); anteroflexus M1, 0 --> 1(90).

node\_109 --> Thomasomys rhoadsi: ACCTTRAN: relative size of hallux (dl of pes), 0 --> 1(13); body pelage pattern, 0 ==> 1(20). DELTRAN: body pelage pattern, 0 ==> 1(20); maxillary at posterior base of M3, 0 --> 1(70); molar heighth topography, 0 --> 1(85); anteroflexus M1, 0 --> 1(91); hypoflexus of M3, 0 --> 1(98); crater rim, 0 --> 1(135); dorsal and ventral margin of crater rim, 0 --> 1(136); lateral mound relative position, 1 --> 0(140).

node\_109 --> Thomasomys sp. 1: ACCTTRAN: jugal length, 1 ==> 0(47); alisphenoid strut, 0 ==> 1(51); parietal-supraoccipital suture breadth, 0 ==> 2(58); maxillary palatal pits, 0 ==> 1(68); molar heighth topography, 1 --> 0(85); anteromedian flexus, 0 ==> 1(87); supratrochlear fenestra of humerus, 2 ==> 0(123). DELTRAN: relative size of hallux (dl of pes), 1 --> 0(13); jugal length, 1 ==> 0(47); alisphenoid strut, 0 ==> 1(51); parietal-supraoccipital suture breadth, 0 ==> 2(58); maxillary palatal pits, 0 ==> 1(68); anteromedian flexus, 0 ==> 1(87); anteroflexus M1, 0 --> 1(91); hypoflexus of M3, 0 --> 1(98); supratrochlear fenestra of humerus, 2 ==> 0(123).

node\_110 --> Thomasomys onkiro: ACCTTRAN: position of hypothenar pad in relation to thenar (pes), 0 ==> 2(8); uniform pattern coloration of tail, 0 ==> 2(26); anteromedian flexid of m1, 0 ==> 1(99). DELTRAN: position of hypothenar pad in relation to thenar (pes), 1 ==> 2(8); uniform pattern coloration of tail, 0 ==> 2(26); anteromedian flexid of m1, 0 ==> 1(99); anterolabial cingulum of m2-m3, 1 --> 0(107).

node\_110 --> Thomasomys silvestris: ACCTTRAN: uniform pattern coloration of tail, 0 ==> 2(26); posterior extension of nasals, 2 ==> 1(29); zygomatic plate breadth, 1 ==> 2(32); zygomatic plate slope, 0 ==> 1(33); parietal-supraoccipital suture breadth, 0 ==> 2(58); M1 position, 2 ==> 1(84); anteromedian flexus, 0 ==> 1(87); anteroflexus M1, 0 ==> 1(91); anteromedian flexid of m1, 0 ==> 1(99); anterolabial cingulum of m2-m3, 0 --> 1(107); grooves on glans penis body, 1 ==> 0(134); notch on midventral margin, 0 ==> 1(137). DELTRAN: position of hypothenar pad in relation to thenar (pes), 1 --> 0(8); uniform pattern coloration of tail, 0 ==> 2(26); posterior extension of nasals, 2 ==> 1(29); zygomatic plate breadth, 1 ==> 2(32); zygomatic plate slope, 0 ==> 1(33); parietal-supraoccipital suture breadth, 0 ==> 2(58); M1 position, 2 ==> 1(84); anteromedian flexus, 0 ==> 1(87); anteroflexus M1, 0 ==> 1(91); anteromedian flexid of m1, 0 ==> 1(99); grooves on glans penis body, 1 ==> 0(134); notch on midventral margin, 0 ==> 1(137).

node\_110 --> Thomasomys vestitus: ACCTTRAN: position of hypothenar pad in relation to thenar (pes), 0 ==> 2(8); ethmoturbinals and sphenopalatine foramen formation, 3 ==> 2(49); incisive foramina, 1 ==> 0(62); medial process of posterior margin of palate bridge, 0 ==> 2(66); depth and shape of the molar-bearing portion of the maxillae, 1 ==> 0(69); parapterygoid vacuity, 0 ==> 1(73); mesopterygoid fossa shape, 1 ==> 0(75); M1 position, 2 ==> 0(84); molar heighth topography, 0 ==> 1(85); anteromedian flexus, 0

==> 1(87); hypoflexus size of M1, 0 ==> 1(94); protoflexus on M2, 1 ==> 0(97); relative length of condylar and angular processes, 1 ==> 0(119). DELTRAN: position of hypothenar pad in relation to thenar (pes), 1 ==> 2(8); ethmoturbinals and sphenopalatine foramen formation, 3 ==> 2(49); incisive foramina, 1 ==> 0(62); medial process of posterior margin of palate bridge, 0 ==> 2(66); depth and shape of the molar-bearing portion of the maxillae, 1 ==> 0(69); parapterygoid vacuity, 0 ==> 1(73); mesopterygoid fossa shape, 1 ==> 0(75); M1 position, 2 ==> 0(84); molar height topography, 0 ==> 1(85); anteromedian flexus, 0 ==> 1(87); hypoflexus size of M1, 0 ==> 1(94); protoflexus on M2, 1 ==> 0(97); anterolabial cingulum of m2-m3, 1 --> 0(107); relative length of condylar and angular processes, 1 ==> 0(119).

#### **New genus A + new genus D**

ACCTTRAN: antitragus and pinnae structure, 1 ==> 0(18); postorbital ridge, 0 ==> 1(46); ethmoturbinals and sphenopalatine foramen formation, 3 ==> 2(49); lambdoid ridge development, 0 ==> 1(59); palatal breadth, 0 ==> 1(65); maxillary palatal pits, 0 --> 1(68); orientation of metalophid m1, 0 ==> 1(103); anterolabial cingulum of m2-m3, 0 --> 1(107); accessory labial root of M1, 0 ==> 1(111); roots on m2, 0 ==> 1(114); relative length of condylar and angular processes, 1 ==> 0(119); number of caudal vertebrae, 2 ==> 3(125); medial bacular mound length, 0 --> 1(138); spines on dorsal papilla, 1 --> 0(143); preputial glands, 1 --> 3(144). DELTRAN: antitragus and pinnae structure, 1 ==> 0(18); postorbital ridge, 0 ==> 1(46); ethmoturbinals and sphenopalatine foramen formation, 3 ==> 2(49); lambdoid ridge development, 0 ==> 1(59); palatal breadth, 0 ==> 1(65); orientation of metalophid m1, 0 ==> 1(103); accessory labial root of M1, 0 ==> 1(111); roots on m2, 0 ==> 1(114); relative length of condylar and angular processes, 1 ==> 0(119); number of caudal vertebrae, 2 ==> 3(125).

#### **New genus A**

ACCTTRAN: position of hypothenar pad in relation to thenar (pes), 0 ==> 2(8); relative size of hallux (dI of pes), 1 ==> 2(13); relative size of fifth digit (dV) of pes, 2 ==> 3(14); genal 1 vibrissae, 0 --> 2(15); length of mystacial vibrissae, 1 ==> 2(17); body pelage pattern, 0 --> 1(20); interorbital region, 0 ==> 2(43); interorbital region breadth, 1 ==> 0(44); hamular process and development of the postglenoid foramen, 1 ==> 3(56); incisive foramina, 1 ==> 2(62); depth and shape of the molar-bearing portion of the maxillae, 1 ==> 0(69); upper incisor orientation, 2 --> 0(82); anteroloph orientation, 0 ==> 1(92); paraloph orientation in M1, 1 ==> 3(93); hypoflexus size of M1, 0 --> 1(94); orientation of metalophid m1, 1 ==> 2(103); entolophids of m1-m2, 0 ==> 1(104); anterolabial cingulum of m2-m3, 1 ==> 2(107); posteroflexid breadth of m1-m2, 0 ==> 1(108); lingual roots on M3, 0 ==> 1(113); mandibular diastemal shape, 1 ==> 0(117); incisura angularis, 0 ==> 1(131). DELTRAN: position of hypothenar pad in relation to thenar (pes), 1 ==> 2(8); relative size of hallux (dI of pes), 1 ==> 2(13); relative size of fifth digit (dV) of pes, 2 ==> 3(14); length of mystacial vibrissae, 1 ==> 2(17); interorbital region, 0 ==> 1(43); interorbital region breadth, 1 ==> 0(44); hamular process and development of the postglenoid foramen, 1 ==> 3(56); incisive foramina, 1 ==> 2(62); depth and shape of the molar-bearing portion of the maxillae, 1 ==> 0(69); anteroloph orientation, 0 ==> 1(92); paraloph orientation in M1, 1 ==> 3(93); orientation of metalophid m1, 1 ==> 2(103); entolophids of m1-m2, 0 ==> 1(104); anterolabial

cingulum of m2-m3, 1 ==> 2(107); posteroflexid breadth of m1-m2, 0 ==> 1(108); lingual roots on M3, 0 ==> 1(113); mandibular diastemal shape, 1 ==> 0(117); incisura angularis, 0 ==> 1(131); crater rim, 0 --> 1(135); notch on midventral margin, 0 --> 1(137); preputial glands, 1 --> 3(144).

node\_114 --> node\_111: ACCTTRAN: dorsal metatarsal patches, 0 --> 1(5); posterodorsal extension of premaxillae, 2 ==> 1(30); zygomatic plate slope, 0 ==> 2(33); medial process of posterior margin of palate bridge, 0 --> 2(66); molar height topography, 0 ==> 1(85); lingual roots on M3, 1 ==> 2(113); supratrochlear fenestra of humerus, 2 --> 0(123); distributional gastric epithelium, 0 ==> 2(130); dorsal and ventral margin of crater rim, 0 ==> 1(136). DELTRAN: posterodorsal extension of premaxillae, 2 ==> 1(30); zygomatic plate slope, 0 ==> 2(30); interorbital region, 1 --> 2(43); molar height topography, 0 ==> 1(85); lingual roots on M3, 1 ==> 2(113); distributional gastric epithelium, 0 ==> 2(130); dorsal and ventral margin of crater rim, 0 ==> 1(136); medial bacular mound length, 0 --> 1(138).

node\_111 --> Thomasomys apoco: ACCTTRAN: pectoral markings, 0 ==> 1(22); uniform pattern coloration of tail, 0 ==> 3(26); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); lacrimal posterior projection, 0 ==> 1(38); jugal length, 1 ==> 0(47); ethmoturbinals and sphenopalatine foramen formation, 2 ==> 0(49); dorsal aperture of ectotympanic ring, 2 ==> 1(60); incisive foramina, 2 ==> 1(62); maxillary at posterior base of M3, 0 ==> 1(70); upper incisor orientation, 0 --> 2(82); procingulum anterior edge of M1, 0 ==> 1(89); paraloph orientation in M1, 3 ==> 1(93); mesolophid on m3, 1 ==> 0(106); entoconid on m3, 0 ==> 1(109); grooves on glans penis body, 1 ==> 2(134). DELTRAN: body pelage pattern, 0 --> 1(20); pectoral markings, 0 ==> 1(22); uniform pattern coloration of tail, 0 ==> 3(26); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); lacrimal posterior projection, 0 ==> 1(38); jugal length, 1 ==> 0(47); ethmoturbinals and sphenopalatine foramen formation, 2 ==> 0(49); dorsal aperture of ectotympanic ring, 2 ==> 1(60); incisive foramina, 2 ==> 1(62); medial process of posterior margin of palate bridge, 0 --> 2(66); maxillary at posterior base of M3, 0 ==> 1(70); procingulum anterior edge of M1, 0 ==> 1(89); paraloph orientation in M1, 3 ==> 1(93); mesolophid on m3, 1 ==> 0(106); entoconid on m3, 0 ==> 1(109); grooves on glans penis body, 1 ==> 2(134).

node\_111 --> Thomasomys sp. 1: ACCTTRAN: position of hypothenar pad in relation to thenar (pes), 2 ==> 1(8); body pelage pattern, 1 --> 0(20); entolophids of m1-m2, 1 ==> 2(104); lingual roots on M1, 0 ==> 2(112); lateral mound relative position, 1 ==> 0(140). DELTRAN: dorsal metatarsal patches, 0 --> 1(5); position of hypothenar pad in relation to thenar (pes), 2 ==> 1(8); upper incisor orientation, 2 --> 0(82); entolophids of m1-m2, 1 ==> 2(104); lingual roots on M1, 0 ==> 2(112); supratrochlear fenestra of humerus, 2 --> 0(123); lateral mound relative position, 1 ==> 0(140).

node\_114 --> Thomasomys aureus: ACCTTRAN: dorsal metatarsal patches, 0 ==> 1(5); molar height topography, 0 ==> 1(85); protoflexus on M2, 0 ==> 1(97); roots on m2, 1 ==> 0(114); distribution of spines on glans penis body, 0 ==> 2(133); notch on midventral margin, 1 ==> 0(137); spines on the urethral flap of gland penis, 2 ==>

0(142). DELTRAN: dorsal metatarsal patches, 0 ==> 1(5); body pelage pattern, 0 --> 1(20); interorbital region, 1 --> 2(43); upper incisor orientation, 2 --> 0(82); molar height topography, 0 ==> 1(85); protoflexus on M2, 0 ==> 1(97); roots on m2, 1 ==> 0(114); distribution of spines on glans penis body, 0 ==> 2(133); notch on midventral margin, 1 ==> 0(137); spines on the urethral flap of gland penis, 2 ==> 0(142); spines on dorsal papilla, 1 --> 0(143).

node\_114 --> node\_113: ACCTRAN: length of mystacial vibrissae, 2 ==> 1(17); pectoral markings, 0 ==> 1(22); dorsal aperture of ectotympanic ring, 2 --> 1(60); bullae inflation, 0 ==> 2(77); anterior process of the ectotympanic, 1 ==> 0(78); ventral margin of malleus lamina, 0 ==> 1(80); procingulum anterior edge of M1, 0 --> 1(89); ectolophid m1, 0 --> 1(101); entolophids of m1-m2, 1 ==> 2(104); lingual roots on M3, 1 --> 2(113); number of caudal vertebrae, 3 --> 2(125). DELTRAN: length of mystacial vibrissae, 2 ==> 1(17); body pelage pattern, 0 --> 1(20); pectoral markings, 0 ==> 1(22); bullae inflation, 0 ==> 1(77); anterior process of the ectotympanic, 1 ==> 0(78); ventral margin of malleus lamina, 0 ==> 1(80); upper incisor orientation, 2 --> 0(82); entolophids of m1-m2, 1 ==> 2(104).

node\_113 --> Thomasomys auricularis: ACCTRAN: posterior extension of nasals, 2 ==> 0(29); interorbital region, 2 ==> 0(43); alisphenoid strut, 0 ==> 1(51); maxillary septum length, 0 ==> 1(63). DELTRAN: posterior extension of nasals, 2 ==> 0(29); interorbital region, 1 ==> 0(43); alisphenoid strut, 0 ==> 1(51); dorsal aperture of ectotympanic ring, 2 --> 1(60); maxillary septum length, 0 ==> 1(63); bullae inflation, 1 --> 2(77); procingulum anterior edge of M1, 0 --> 1(89); number of caudal vertebrae, 3 --> 2(125).

node\_113 --> node\_112: ACCTRAN: posterodorsal extension of premaxillae, 2 --> 1(30); interfrontal fontanella, 0 --> 2(45); ethmoturbinals and sphenopalatine foramen formation, 2 ==> 0(49); sphenopalatine vacuities, 0 ==> 1(71); lingual roots on M1, 0 ==> 1(112). . DELTRAN: interorbital region, 1 --> 2(43); ethmoturbinals and sphenopalatine foramen formation, 2 ==> 0(49); sphenopalatine vacuities, 0 ==> 1(71); ectolophid m1, 0 --> 1(101); lingual roots on M1, 0 ==> 1(112).

node\_112 --> Thomasomys pyrrhonotus: ACCTRAN: relative size of fifth digit (dV) of pes, 3 ==> 2(14); body pelage pattern, 1 ==> 2(20); parapterygoid vacuity, 0 ==> 1(73); molar height topography, 0 ==> 1(85); procingulum anterior edge of M1, 1 --> 0(89); lingual roots on M1, 1 ==> 2(112). DELTRAN: relative size of fifth digit (dV) of pes, 3 ==> 2(14); body pelage pattern, 1 ==> 2(20); interfrontal fontanella, 0 --> 2(45); dorsal aperture of ectotympanic ring, 2 --> 1(60); parapterygoid vacuity, 0 ==> 1(73); bullae inflation, 1 --> 2(77); molar height topography, 0 ==> 1(85); lingual roots on M1, 1 ==> 2(112); lingual roots on M3, 1 --> 2(113).

node\_112 --> Thomasomys rosalia: ACCTRAN: lambdoid ridge development, 1 ==> 0(59); dorsal aperture of ectotympanic ring, 1 --> 2(60); bullae inflation, 2 --> 1(77); molar occlusal design, 0 ==> 1(86). DELTRAN: posterodorsal extension of premaxillae, 2 --> 1(30); lambdoid ridge development, 1 ==> 0(59); molar occlusal design, 0 ==> 1(86); procingulum anterior edge of M1, 0 --> 1(89).

node\_114 --> Thomasomys nicefori: ACCTTRAN: interorbital region, 2 ==> 0(43); interorbital region breadth, 0 ==> 1(44); postorbital ridge, 1 ==> 0(46); palatal breadth, 1 ==> 0(65); bullae inflation, 0 ==> 1(77); anterior process of the ectotympanic, 1 ==> 0(78); upper incisor orientation, 0 --> 2(82); paraloph orientation in M1, 3 ==> 1(93); protostyle and enterostyle on M1, 0 ==> 2(96); ectolophid m1, 0 ==> 1(101); orientation of metalophid m1, 2 ==> 1(103); lingual roots on M3, 1 ==> 0(113); lateral mound relative position, 1 ==> 0(140); spines on dorsal papilla, 0 --> 1(143). DELTRAN: body pelage pattern, 0 --> 1(20); interorbital region, 1 ==> 0(43); interorbital region breadth, 0 ==> 1(44); postorbital ridge, 1 ==> 0(46); palatal breadth, 1 ==> 0(65); bullae inflation, 0 ==> 1(77); anterior process of the ectotympanic, 1 ==> 0(78); paraloph orientation in M1, 3 ==> 1(93); protostyle and enterostyle on M1, 0 ==> 2(96); ectolophid m1, 0 ==> 1(101); orientation of metalophid m1, 2 ==> 1(103); lingual roots on M3, 1 ==> 0(113); medial bacular mound length, 0 --> 1(138); lateral mound relative position, 1 ==> 0(140).

node\_114 --> Thomasomys popayanus: ACCTTRAN: body pelage pattern, 1 --> 0(20); interorbital region, 2 --> 1(43); postorbital ridge, 1 ==> 0(46); lambdoid ridge development, 1 ==> 0(59); incisive foramina, 2 ==> 1(62); protoflexus on M2, 0 ==> 1(97); ectolophid m1, 0 ==> 1(101). DELTRAN: postorbital ridge, 1 ==> 0(46); lambdoid ridge development, 1 ==> 0(59); incisive foramina, 2 ==> 1(62); upper incisor orientation, 2 --> 0(82); protoflexus on M2, 0 ==> 1(97); ectolophid m1, 0 ==> 1(101).

node\_114 --> Thomasomys praetor: ACCTTRAN: relative size of fifth digit (dV) of pes, 3 ==> 2(14); length of mystacial vibrissae, 2 ==> 1(17); pectoral markings, 0 ==> 1(22); uniform pattern coloration of tail, 0 ==> 2(26); posterior extension of nasals, 2 ==> 0(29); depth and shape of the molar-bearing portion of the maxillae, 0 ==> 1(69); sphenopalatine vacuities, 0 ==> 1(71); bullae inflation, 0 ==> 1(77); processus brevis of incus, 1 ==> 0(81); upper incisor orientation, 0 --> 2(82); molar height topography, 0 ==> 1(85); protoflexus on M2, 0 ==> 1(97); orientation of metalophid m1, 2 ==> 0(103); entolophids of m1-m2, 1 ==> 0(104); mesolophids of m1-m2, 0 ==> 1(105); lingual roots on M1, 0 ==> 2(112); lingual roots on M3, 1 ==> 0(113); crater rim, 1 ==> 0(135); medial bacular mound length, 1 --> 0(138); spines on the urethral flap of gland penis, 2 ==> 0(142). DELTRAN: relative size of fifth digit (dV) of pes, 3 ==> 2(14); length of mystacial vibrissae, 2 ==> 1(17); body pelage pattern, 0 --> 1(20); pectoral markings, 0 ==> 1(22); uniform pattern coloration of tail, 0 ==> 2(26); posterior extension of nasals, 2 ==> 0(29); interorbital region, 1 --> 2(43); depth and shape of the molar-bearing portion of the maxillae, 0 ==> 1(69); sphenopalatine vacuities, 0 ==> 1(71); bullae inflation, 0 ==> 1(77); processus brevis of incus, 1 ==> 0(81); molar height topography, 0 ==> 1(85); protoflexus on M2, 0 ==> 1(97); orientation of metalophid m1, 2 ==> 0(103); entolophids of m1-m2, 1 ==> 0(104); mesolophids of m1-m2, 0 ==> 1(105); lingual roots on M1, 0 ==> 2(112); lingual roots on M3, 1 ==> 0(113); crater rim, 1 ==> 0(135); spines on the urethral flap of gland penis, 2 ==> 0(142); spines on dorsal papilla, 1 --> 0(143).

node\_114 --> Thomasomys princeps: ACCTTRAN: dorsal metatarsal patches, 0 ==>

1(5); body pelage pattern, 1 --> 0(20); posterior extension of nasals, 2 ==> 1(29); maxillary septum length, 0 ==> 1(63); anterior process of the ectotympanic, 1 ==> 0(78); M1 position, 2 ==> 0(84); molar occlusal design, 0 ==> 1(86); protostyle and enterostyle on M1, 0 ==> 2(96); ectolophid m1, 0 ==> 1(101). DELTRAN: dorsal metatarsal patches, 0 ==> 1(5); posterior extension of nasals, 2 ==> 1(29); interorbital region, 1 --> 2(43); maxillary septum length, 0 ==> 1(63); anterior process of the ectotympanic, 1 ==> 0(78); upper incisor orientation, 2 --> 0(82); M1 position, 2 ==> 0(84); molar occlusal design, 0 ==> 1(86); protostyle and enterostyle on M1, 0 ==> 2(96); ectolophid m1, 0 ==> 1(101).

node\_114 --> Thomasomys sp. 2: ACCTTRAN: dorsal metatarsal patches, 0 ==> 1(5); position of hypothenar pad in relation to thenar (pes), 2 ==> 0(8); relative size of fifth digit (dV) of pes, 3 ==> 2(14); genal 1 vibrissae, 2 ==> 0(15); body pelage pattern, 1 --> 0(20); posterodorsal extension of premaxillae, 2 ==> 1(30); anterodorsal margin of zygomatic plate, 0 ==> 1(31); zygomatic plate slope, 0 ==> 2(33); lacrimal posterior projection, 0 ==> 1(38); interorbital region, 2 ==> 0(43); maxillary septum length, 0 ==> 1(63); palatal breadth, 1 ==> 0(65); medial process of posterior margin of palate bridge, 0 ==> 2(66); maxillary palatal pits, 1 ==> 0(68); depth and shape of the molar-bearing portion of the maxillae, 0 ==> 1(69); parapterygoid vacuity, 0 ==> 1(73); bullae inflation, 0 ==> 1(77); upper incisor orientation, 0 --> 2(82); entolophids of m1-m2, 1 ==> 2(104). DELTRAN: dorsal metatarsal patches, 0 ==> 1(5); position of hypothenar pad in relation to thenar (pes), 2 ==> 0(8); relative size of fifth digit (dV) of pes, 3 ==> 2(14); genal 1 vibrissae, 2 ==> 0(15); posterodorsal extension of premaxillae, 2 ==> 1(30); anterodorsal margin of zygomatic plate, 0 ==> 1(31); zygomatic plate slope, 0 ==> 2(33); lacrimal posterior projection, 0 ==> 1(38); interorbital region, 1 ==> 0(43); maxillary septum length, 0 ==> 1(63); palatal breadth, 1 ==> 0(65); medial process of posterior margin of palate bridge, 0 ==> 2(66); maxillary palatal pits, 1 ==> 0(68); depth and shape of the molar-bearing portion of the maxillae, 0 ==> 1(69); parapterygoid vacuity, 0 ==> 1(73); bullae inflation, 0 ==> 1(77); entolophids of m1-m2, 1 ==> 2(104).

### **New genus D**

Thomasomys macrotis: ACCTTRAN: ventral base of claws on manus, 1 ==> 2(2); position of hypothenar pad in relation to interdigital pad 1 (pes), 1 ==> 0(10); uniform pattern coloration of tail, 0 ==> 3(26); posterodorsal extension of premaxillae, 2 ==> 3(30); lacrimal posterior projection, 0 ==> 1(38); position of antorbital bridge, 0 ==> 1(39); M1 position, 2 ==> 0(84); molar height topography, 0 ==> 1(85); molar flexus (-ids) crenulation, 0 ==> 1(110); lingual roots on M1, 0 ==> 2(112). DELTRAN: ventral base of claws on manus, 1 ==> 2(2); position of hypothenar pad in relation to thenar (pes), 1 --> 0(8); position of hypothenar pad in relation to interdigital pad 1 (pes), 1 ==> 0(10); genal 1 vibrissae, 2 --> 0(15); uniform pattern coloration of tail, 0 ==> 3(26); posterodorsal extension of premaxillae, 2 ==> 3(30); lacrimal posterior projection, 0 ==> 1(38); position of antorbital bridge, 0 ==> 1(39); M1 position, 2 ==> 0(84); molar height topography, 0 ==> 1(85); hypoflexus size of M1, 1 --> 0(94); molar flexus (-ids) crenulation, 0 ==> 1(110); lingual roots on M1, 0 ==> 2(112).

### **Chilomys:**



ACCTTRAN: uniform pattern coloration of tail, 0 ==> 2(26); zygomatic arch dip, 1 ==> 2(42); interorbital region breadth, 1 --> 2(44); jugal length, 1 ==> 0(47); optic foramen, 0 ==> 1(50); alisphenoid strut, 0 --> 2(51); parietal-supraoccipital suture breadth, 0 ==> 3(58); incisive foramina, 1 ==> 0(62); palatal length, 0 ==> 3(64); Alisphenoid squamosal posterior margin, 0 --> 1(76); malleus lamina, 0 ==> 1(79); upper incisor orientation, 2 ==> 3(82); anteromedian flexus, 0 --> 1(87); anterocone, 0 --> 1(88); hypoflexus size of M1, 0 --> 1(94); hypoflexus of M3, 0 ==> 1(98); anteromedian flexid of m1, 0 --> 1(99); ridge on anterolabial cingulum of m1, 0 --> 1(102); mandibular diastemal shape, 1 ==> 2(117); distribution of spines on glans penis body, 0 --> 1(133); grooves on glans penis body, 1 --> 0(134). DELTRAN: position of hypothenar pad in relation to thenar (pes), 1 --> 0(8); uniform pattern coloration of tail, 0 ==> 2(26); zygomatic arch dip, 1 ==> 2(42); interorbital region breadth, 1 --> 2(44); jugal length, 1 ==> 0(47); optic foramen, 0 ==> 1(50); parietal-supraoccipital suture breadth, 0 ==> 3(58); incisive foramina, 1 ==> 0(62); palatal length, 0 ==> 2(64); maxillary palatal pits, 1 --> 0(68); malleus lamina, 0 ==> 1(79); upper incisor orientation, 2 ==> 3(82); hypoflexus of M3, 0 ==> 1(98); anterolabial cingulum of m2-m3, 1 --> 0(107); mandibular diastemal shape, 1 ==> 2(117).

node\_117 --> Chilomys fumeus: ACCTTRAN: zygomatic plate breadth, 1 ==> 2(32); M1 position, 2 --> 3(84); hypoflexus width of M2, 0 ==> 1(95); chevron bones, 0 ==> 2(126); position of the trochlear process of calcaneum, 0 ==> 1(127). DELTRAN: zygomatic plate breadth, 1 ==> 2(32); alisphenoid strut, 0 --> 2(51); maxillary septum length, 0 --> 1(63); palatal length, 2 --> 3(64); anteromedian flexus, 0 --> 1(87); hypoflexus width of M2, 0 ==> 1(95); anteromedian flexid of m1, 0 --> 1(99); ridge on anterolabial cingulum of m1, 0 --> 1(102); chevron bones, 0 ==> 2(126); position of the trochlear process of calcaneum, 0 ==> 1(127).

node\_117 --> Chilomys instans: ACCTTRAN: exposure of internal carotid artery, 0 ==> 1(53); mesopterygoid fossa breadth, 0 ==> 1(74). DELTRAN: exposure of internal carotid artery, 0 ==> 1(53); mesopterygoid fossa breadth, 0 ==> 1(74); Alisphenoid squamosal posterior margin, 0 --> 1(76); M1 position, 3 --> (12) (84); distribution of spines on glans penis body, 0 --> 1(133); grooves on glans penis body, 1 --> 0(134); crater rim, 0 --> 1(135); notch on midventral margin, 0 --> 1(137).

#### **New genus B + (Rhipidomys + (new genus C + new genus E))**

ACCTTRAN: ventral base of claws on manus, 1 --> 0(2); dorsal metatarsal patches, 0 --> 1(5); relative size of hallux (dl of pes), 1 ==> 2(13); relative size of fifth digit (dV) of pes, 2 ==> 3(14); length of mystacial vibrissae, 1 ==> 2(17); antitragus and pinnae structure, 1 --> 0(18); incisive foramina, 1 --> 2(62); maxillary palatal pits, 0 --> 1(68); upper incisor orientation, 2 ==> 0(82); lateral bacular mound shape, 0 --> 1(139). DELTRAN: relative size of hallux (dl of pes), 1 ==> 2(13); relative size of fifth digit (dV) of pes, 2 ==> 3(14); length of mystacial vibrissae, 1 ==> 2(17); upper incisor orientation, 2 ==> 0(82); anterocone, 1 --> 0(88); prostate ventral glands, 2 --> 1(145).

#### **Rhipidomys + (new genus C + new genus E)**

ACCTTRAN: ungual tufts on manual claws, 0 --> 1(1); tail pencil, 0 --> 1(27); posterodorsal extension of premaxillae, 0 ==> 1(30); ethmoturbinals and sphenopalatine

foramen formation, 3 ==> 2(49); depth and shape of the molar-bearing portion of the maxillae, 1 --> 0(69); mesopterygoid fossa shape, 1 ==> 0(75); protostyle and enterostyle on M1, 0 --> 2(96); mesolophid on m3, 1 ==> 0(106); lateral mound relative position, 1 ==> 2(140); spines on the lateral mounds, 0 ==> 1(141). DELTRAN: dorsal metatarsal patches, 0 --> 1(5); posterodorsal extension of premaxillae, 0 ==> 1(30); ethmoturbinals and sphenopalatine foramen formation, 3 ==> 2(49); dorsal aperture of ectotympanic ring, 1 --> 2(60); mesopterygoid fossa shape, 1 ==> 0(75); mesolophid on m3, 1 ==> 0(106); lateral bacular mound shape, 0 --> 1(139); lateral mound relative position, 1 ==> 2(140); spines on the lateral mounds, 0 ==> 1(141).

### **Rhipidomys:**

ACCTTRAN: manual digit proportions, 1 --> 0(3); position of hypothenar pad in relation to interdigital pad 4 (pes), 0 ==> 1(9); antitragus and pinnae structure, 0 --> 1(18); interorbital region, 1 ==> 3(43); hamular process and development of the postglenoid foramen, 1 ==> 0(56); height of subsquamosal fenestra, 0 ==> 1(57); maxillary septum length, 1 --> 0(63); medial process of posterior margin of palate bridge, 0 --> 2(66); malleus lamina, 0 ==> 1(79); hypoflexus size of M1, 0 --> 1(94); anterolabial cingulum of m2-m3, 0 --> 1(107); coronoid process, 1 --> 0(120); gall bladder, 0 ==> 1(132); grooves on glans penis body, 1 ==> 2(134). DELTRAN: ungual tufts on manual claws, 0 --> 1(1); position of hypothenar pad in relation to interdigital pad 4 (pes), 0 ==> 1(9); tail pencil, 0 --> 1(27); interorbital region, 1 ==> 3(43); hamular process and development of the postglenoid foramen, 1 ==> 0(56); height of subsquamosal fenestra, 0 ==> 1(57); depth and shape of the molar-bearing portion of the maxillae, 1 --> 0(69); malleus lamina, 0 ==> 1(79); gall bladder, 0 ==> 1(132); grooves on glans penis body, 1 ==> 2(134).

node\_120 --> node\_119: ACCTTRAN: manual digit proportions, 0 --> 1(3); body pelage pattern, 1 ==> 2(20); interorbital region, 3 ==> 2(43); incisive foramina, 2 --> 1(62); maxillary septum length, 0 ==> 1(63); medial process of posterior margin of palate bridge, 2 --> 0(66); protostyle and enterostyle on M1, 2 ==> 0(96); protoflexus on M2, 0 ==> 1(97); hypoflexus of M3, 0 ==> 1(98); molar flexus (-ids) crenulation, 0 --> 1(110); spines on the lateral mounds, 1 --> 0(141). DELTRAN: body pelage pattern, 1 ==> 2(20); interorbital region, 3 ==> 2(43); maxillary septum length, 0 ==> 1(63); protostyle and enterostyle on M1, 2 ==> 0(96); protoflexus on M2, 0 ==> 1(97); hypoflexus of M3, 0 ==> 1(98).

node\_119 --> Rhipidomys caucensis: ACCTTRAN: ventral base of claws on manus, 0 ==> 1(2); posterodorsal extension of premaxillae, 1 ==> 0(30); molar occlusal design, 0 ==> 1(86); hypoflexus size of M1, 1 --> 0(94); anteromedian flexid of m1, 0 ==> 1(99); coronoid process, 0 --> 1(120). DELTRAN: ventral base of claws on manus, 0 ==> 1(2); manual digit proportions, 0 --> 1(3); posterodorsal extension of premaxillae, 1 ==> 0(30); molar occlusal design, 0 ==> 1(86); hypoflexus size of M1, 1 --> 0(94); anteromedian flexid of m1, 0 ==> 1(99); molar flexus (-ids) crenulation, 0 --> 1(110).

node\_119 --> Rhipidomys fulviventer: ACCTTRAN: ungual tufts on manual claws, 1 ==> 0(1); posterior extension of nasals, 2 ==> 0(29); carotid circulation, 2 ==> 0(52). DELTRAN: ungual tufts on manual claws, 1 ==> 0(1); posterior extension of nasals, 2

==> 0(29); carotid circulation, 2 ==> 0(52); coronoid process, 1 --> 0(120); spines on the lateral mounds, 1 --> 0(141).

node\_120 --> Rhipidomys latimanus: ACCTTRAN: ventral base of claws on manus, 0 ==> 1(2); manual digit proportions, 0 ==> 1(3); body pelage pattern, 1 ==> 2(20); countershading of tail, 0 ==> 1(25); uniform pattern coloration of tail, 0 ==> 1(26); interorbital region breadth, 1 ==> 2(44); dorsal aperture of ectotympanic ring, 2 ==> 0(60); medial process of posterior margin of palate bridge, 2 --> 0(66); anterolabial cingulum of m2-m3, 1 ==> 2(107); masseteric crest position, 1 ==> 0(115); coronoid process, 0 --> 1(120). DELTRAN: ventral base of claws on manus, 0 ==> 1(2); manual digit proportions, 0 ==> 1(3); body pelage pattern, 1 ==> 2(20); countershading of tail, 0 ==> 1(25); uniform pattern coloration of tail, 0 ==> 1(26); interorbital region breadth, 1 ==> 2(44); dorsal aperture of ectotympanic ring, 2 ==> 0(60); incisive foramina, 1 --> 2(62); anterolabial cingulum of m2-m3, 1 ==> 2(107); masseteric crest position, 1 ==> 0(115).

node\_120 --> Rhipidomys leucodactylus: ACCTTRAN: ungual tuft on pes, 0 ==> 2(4); zygomatic arch dip, 1 ==> 0(42); ethmoturbinals and sphenopalatine foramen formation, 2 ==> 0(49); incisive foramina, 2 --> 1(62); anterolabial cingulum of m2-m3, 1 ==> 2(107); capsular process of lower incisor, 1 ==> 0(118); crater rim, 0 ==> 1(135); preputial glands, 1 ==> 0(144). DELTRAN: ungual tuft on pes, 0 ==> 2(4); zygomatic arch dip, 1 ==> 0(42); ethmoturbinals and sphenopalatine foramen formation, 2 ==> 0(49); anterolabial cingulum of m2-m3, 1 ==> 2(107); capsular process of lower incisor, 1 ==> 0(118); coronoid process, 1 --> 0(120); crater rim, 0 ==> 1(135); preputial glands, 1 ==> 0(144).

node\_120 --> Rhipidomys gardneri: ACCTTRAN: length of mystacial vibrissae, 2 ==> 1(17); body pelage pattern, 1 ==> 2(20); tail pencil, 1 ==> 0(27); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); interorbital region breadth, 1 ==> 2(44); dorsal aperture of ectotympanic ring, 2 ==> 0(60); incisive foramina, 2 --> 1(62); mesopterygoid fossa shape, 0 ==> 1(75); hypoflexus size of M1, 1 --> 0(94); ectolophid m1, 0 ==> 1(101); capsular process of lower incisor, 1 ==> 0(118); number of thoracic vertebrae, 0 ==> 1(124); chevron bones, 0 ==> 2(126); crater rim, 0 ==> 1(135); preputial glands, 1 ==> 0(144). DELTRAN: length of mystacial vibrissae, 2 ==> 1(17); body pelage pattern, 1 ==> 2(20); tail pencil, 1 ==> 0(27); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); interorbital region breadth, 1 ==> 2(44); dorsal aperture of ectotympanic ring, 2 ==> 0(60); medial process of posterior margin of palate bridge, 0 --> 2(66); mesopterygoid fossa shape, 0 ==> 1(75); hypoflexus size of M1, 1 --> 0(94); ectolophid m1, 0 ==> 1(101); capsular process of lower incisor, 1 ==> 0(118); coronoid process, 1 --> 0(120); number of thoracic vertebrae, 0 ==> 1(124); chevron bones, 0 ==> 2(126); crater rim, 0 ==> 1(135); preputial glands, 1 ==> 0(144).

node\_120 --> Rhipidomys macconnelli: ACCTTRAN: ungual tufts on manual claws, 1 ==> 0(1); position of hypothenar pad in relation to thenar (pes), 2 ==> 0(8); countershading of tail, 0 ==> 1(25); posterodorsal extension of premaxillae, 1 ==> 0(30);

ethmoturbinals and sphenopalatine foramen formation, 2 ==> 3(49); maxillary septum length, 0 ==> 1(63); maxillary palatal pits, 1 ==> 0(68); parapterygoid vacuity, 0 ==> 1(73); hypoflexus size of M1, 1 --> 0(94); anterolabial cingulum of m2-m3, 1 ==> 2(107); masseteric crest position, 1 ==> 0(115); coronoid process, 0 --> 1(120); lateral bacular mound shape, 1 ==> 0(139); spines on the urethral flap of gland penis, 2 ==> 0(142). DELTRAN: ungual tufts on manual claws, 1 ==> 0(1); position of hypothenar pad in relation to thenar (pes), 2 ==> 0(8); countershading of tail, 0 ==> 1(25); posterodorsal extension of premaxillae, 1 ==> 0(30); ethmoturbinals and sphenopalatine foramen formation, 2 ==> 3(49); incisive foramina, 1 --> 2(62); maxillary septum length, 0 ==> 1(63); medial process of posterior margin of palate bridge, 0 --> 2(66); maxillary palatal pits, 1 ==> 0(68); parapterygoid vacuity, 0 ==> 1(73); hypoflexus size of M1, 1 --> 0(94); anterolabial cingulum of m2-m3, 1 ==> 2(107); masseteric crest position, 1 ==> 0(115); lateral bacular mound shape, 1 ==> 0(139); spines on the urethral flap of gland penis, 2 ==> 0(142).

node\_120 --> Rhipidomys ochrogaster: ACCTTRAN: genal 1 vibrissae, 2 ==> 1(15); posterior extension of nasals, 2 ==> 0(29); posterodorsal extension of premaxillae, 1 ==> 2(30); zygomatic arch dip, 1 ==> 0(42); carotid circulation, 2 ==> 0(52); parietal-supraoccipital suture breadth, 0 ==> 2(58); mesopterygoid fossa shape, 0 ==> 1(75); anterior process of the ectotympanic, 1 ==> 0(78); anterocone, 0 ==> 1(88); protoflexus on M2, 0 ==> 1(97); capsular process of lower incisor, 1 ==> 0(118). DELTRAN: genal 1 vibrissae, 2 ==> 1(15); posterior extension of nasals, 2 ==> 0(29); posterodorsal extension of premaxillae, 1 ==> 2(30); zygomatic arch dip, 1 ==> 0(42); carotid circulation, 2 ==> 0(52); parietal-supraoccipital suture breadth, 0 ==> 2(58); incisive foramina, 1 --> 2(62); medial process of posterior margin of palate bridge, 0 --> 2(66); mesopterygoid fossa shape, 0 ==> 1(75); anterior process of the ectotympanic, 1 ==> 0(78); anterocone, 0 ==> 1(88); protoflexus on M2, 0 ==> 1(97); capsular process of lower incisor, 1 ==> 0(118); coronoid process, 1 --> 0(120).

#### **New genus C + new genus E**

ACCTTRAN: posterodorsal extension of premaxillae, 1 --> 2(30); interorbital region breadth, 1 ==> 0(44); interfrontal fontanella, 0 ==> 2(45); carotid circulation, 2 ==> 0(52); molar occlusal design, 0 ==> 1(86); anteromedian flexid of m1, 0 ==> 1(99); molar flexus (-ids) crenulation, 0 ==> 1(110); transverse palatal ridges, 0 ==> 1(129); grooves on glans penis body, 1 --> 0(134); spines on dorsal papilla, 1 --> 0(143); prostate ventral glands, 1 ==> 0(145). DELTRAN: manual digit proportions, 0 --> 1(3); antitragus and pinnae structure, 1 --> 0(18); interorbital region breadth, 1 ==> 0(44); interfrontal fontanella, 0 ==> 2(45); carotid circulation, 2 ==> 0(52); maxillary septum length, 0 --> 1(63); molar occlusal design, 0 ==> 1(86); hypoflexus size of M1, 1 --> 0(94); anteromedian flexid of m1, 0 ==> 1(99); molar flexus (-ids) crenulation, 0 ==> 1(110); transverse palatal ridges, 0 ==> 1(129); prostate ventral glands, 1 ==> 0(145).

#### **New genus C**

ACCTTRAN: ungual tufts on manual claws, 1 --> 0(1); ventral base of claws on manus, 0 --> 1(2); tail pencil, 1 --> 0(27); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); maxillary palatal pits, 1 ==> 0(68); sphenopalatine vacuities, 0

==> 1(71); bullae inflation, 0 ==> 2(77); anterior process of the ectotympanic, 1 ==> 0(78); masseteric crest position, 1 ==> 0(115); chevron bones, 0 --> 2(126). DELTRAN: ventral base of claws on manus, 0 --> 1(2); posterodorsal extension of premaxillae, 1 --> 2(30); notch between the maxillary bone of zygomatic arch and lacrimal, 0 ==> 1(37); incisive foramina, 1 --> 2(62); maxillary palatal pits, 1 ==> 0(68); depth and shape of the molar-bearing portion of the maxillae, 1 --> 0(69); sphenopalatine vacuities, 0 ==> 1(71); bullae inflation, 0 ==> 2(77); anterior process of the ectotympanic, 1 ==> 0(78); masseteric crest position, 1 ==> 0(115).

node\_122 --> node\_121: ACCTTRAN: length of mystacial vibrissae, 2 --> 1(17); parapterygoid vacuity, 0 ==> 1(73); mesopterygoid fossa breadth, 0 --> 1(74); Alisphenoid squamosal posterior margin, 0 --> 1(76); anterolabial cingulum of m2-m3, 0 --> 1(107); accessory labial root of M1, 0 --> 1(111). DELTRAN: parapterygoid vacuity, 0 ==> 1(73); grooves on glans penis body, 1 --> 0(134).

node\_121 --> Thomasomys gracilis: ACCTTRAN: body pelage pattern, 1 ==> 0(20); rostral tube, 0 ==> 1(28); interfrontal fontanella, 2 ==> 0(45); maxillary septum length, 1 ==> 0(63); mesopterygoid fossa breadth, 1 --> 0(74); Alisphenoid squamosal posterior margin, 1 --> 0(76); molar occlusal design, 1 ==> 0(86); orientation of metalophid m1, 0 ==> 1(103); capsular process of lower incisor, 1 ==> 0(118); coronoid process, 1 ==> 0(120); lateral bacular mound shape, 1 ==> 0(139); lateral mound relative position, 2 ==> 1(140); spines on the lateral mounds, 1 ==> 0(141); spines on the urethral flap of gland penis, 2 ==> 0(142). DELTRAN: length of mystacial vibrissae, 2 --> 1(17); body pelage pattern, 1 ==> 0(20); rostral tube, 0 ==> 1(28); interfrontal fontanella, 2 ==> 0(45); maxillary septum length, 1 ==> 0(63); molar occlusal design, 1 ==> 0(86); orientation of metalophid m1, 0 ==> 1(103); accessory labial root of M1, 0 --> 1(111); capsular process of lower incisor, 1 ==> 0(118); coronoid process, 1 ==> 0(120); lateral bacular mound shape, 1 ==> 0(139); lateral mound relative position, 2 ==> 1(140); spines on the lateral mounds, 1 ==> 0(141); spines on the urethral flap of gland penis, 2 ==> 0(142); spines on dorsal papilla, 1 --> 0(143).

node\_121 --> Thomasomys sp. 8: ACCTTRAN: posterior extension of nasals, 2 ==> 0(29); shape of parapterygoid fossa, 1 ==> 0(72); malleus lamina, 0 ==> 1(79); anteromedian flexid of m1, 1 ==> 0(99). DELTRAN: length of mystacial vibrissae, 2 --> 1(17); posterior extension of nasals, 2 ==> 0(29); shape of parapterygoid fossa, 1 ==> 0(72); mesopterygoid fossa breadth, 0 --> 1(74); Alisphenoid squamosal posterior margin, 0 --> 1(76); malleus lamina, 0 ==> 1(79); anteromedian flexid of m1, 1 ==> 0(99); accessory labial root of M1, 0 --> 1(111).

node\_121 --> Thomasomys sp. 9: ACCTTRAN: length of mystacial vibrissae, 1 --> 2(17); alisphenoid strut, 0 ==> 1(51); accessory labial root of M1, 1 --> 0(111). DELTRAN: alisphenoid strut, 0 ==> 1(51); mesopterygoid fossa breadth, 0 --> 1(74); Alisphenoid squamosal posterior margin, 0 --> 1(76); chevron bones, 0 --> 2(126).

node\_122 --> Thomasomys oreas: ACCTTRAN: interorbital region, 1 ==> 0(43); gall bladder, 0 ==> 1(132); grooves on glans penis body, 0 --> 1(134). DELTRAN:

interorbital region, 1 ==> 0(43); anterolabial cingulum of m2-m3, 1 --> 0(107); gall bladder, 0 ==> 1(132). DELTRAN: interorbital region, 1 ==> 0(43); anterolabial cingulum of m2-m3, 1 --> 0(107); gall bladder, 0 ==> 1(132).

### **New genus E**

Thomasomys notatus : ACCTTRAN: body pelage pattern, 1 ==> 2(20); posterior extension of nasals, 2 ==> 0(29); hamular process and development of the postglenoid foramen, 1 ==> 3(56); depth and shape of the molar-bearing portion of the maxillae, 0 --> 1(69); anterocone, 0 ==> 1(88); preputial glands, 1 ==> 0(144). DELTRAN: ungual tufts on manual claws, 0 --> 1(1); body pelage pattern, 1 ==> 2(20); tail pencil, 0 --> 1(27); posterior extension of nasals, 2 ==> 0(29); hamular process and development of the postglenoid foramen, 1 ==> 3(56); anterocone, 0 ==> 1(88); anterolabial cingulum of m2-m3, 1 --> 0(107); grooves on glans penis body, 1 --> 0(134); preputial glands, 1 ==> 0(144).

### **New genus B.**

ACCTTRAN: uniform pattern coloration of tail, 0 ==> 1(26); dorsal aperture of ectotympanic ring, 2 --> 1(60); mesopterygoid fossa breadth, 0 ==> 1(74); anterior process of the ectotympanic, 1 ==> 0(78); chevron bones, 0 ==> 1(126); lateral bacular mound shape, 1 --> 2(139). DELTRAN: manual digit proportions, 0 --> 1(3); uniform pattern coloration of tail, 0 ==> 1(26); maxillary septum length, 0 --> 1(63); mesopterygoid fossa breadth, 0 ==> 1(74); anterior process of the ectotympanic, 1 ==> 0(78); hypoflexus size of M1, 1 --> 0(94); protostyle and enterostyle on M1, 2 --> 0(96); chevron bones, 0 ==> 1(126); lateral bacular mound shape, 0 --> 2(139).

node\_125 --> Thomasomys baeops: ACCTTRAN: ventral base of claws on manus, 0 --> 1(2); interorbital region breadth, 1 ==> 0(44); interfrontal fontanella, 0 ==> 1(45); incisive foramina, 2 --> 1(62); protoflexus on M2, 0 ==> 1(97); distribution of spines on glans penis body, 0 ==> 1(133); crater rim, 0 ==> 1(135). DELTRAN: ventral base of claws on manus, 0 --> 1(2); dorsal metatarsal patches, 0 --> 1(5); interorbital region breadth, 1 ==> 0(44); interfrontal fontanella, 0 ==> 1(45); protoflexus on M2, 0 ==> 1(97); anterolabial cingulum of m2-m3, 1 --> 0(107); distribution of spines on glans penis body, 0 ==> 1(133); crater rim, 0 ==> 1(135).

node\_125 --> Thomasomys taczanowskii: ACCTTRAN: dorsal metatarsal patches, 1 --> 0(5); uniform pattern coloration of tail, 1 ==> 2(26); shape of zygomatic arches, 1 ==> 0(41); hamular process and development of the postglenoid foramen, 1 ==> 2(56); Alisphenoid squamosal posterior margin, 0 ==> 1(76); bullae inflation, 0 ==> 1(77); anterolabial cingulum of m2-m3, 0 --> 1(107); masseteric crest position, 1 ==> 0(115). DELTRAN: antitragus and pinnae structure, 1 --> 0(18); uniform pattern coloration of tail, 1 ==> 2(26); shape of zygomatic arches, 1 ==> 0(41); hamular process and development of the postglenoid foramen, 1 ==> 2(56); incisive foramina, 1 --> 2(62); Alisphenoid squamosal posterior margin, 0 ==> 1(76); bullae inflation, 0 ==> 1(77); masseteric crest position, 1 ==> 0(115).

## OUTGROUP CLADES

node\_130 --> Juliomys pictipes: ACCTRAN: relative size of fifth digit (dV) of pes, 2 ==> 3(14); lingual roots on M1, 0 ==> 1(112). DELTRAN: plantar squamation of pes, 1 ==> 0(6); length of mystacial vibrissae, 1 --> 2(17); countershading of tail, 0 --> 1(25); anterodorsal margin of zygomatic plate, 1 --> 0(31); interorbital region, 2 ==> 0(43); jugal length, 1 ==> 0(47); incisive foramina, 1 --> 2(62); maxillary septum length, 0 ==> 1(63); esopterygoid fossa shape, 1 ==> 0(75); bullae inflation, 0 --> 1(77); anteromedian flexid of m1, 0 ==> 1(99); orientation of metalophid m1, 0 ==> 2(103).

node\_131 --> Juliomys sp.: ACCTRAN: plantar squamation of pes, 1 ==> 0(6); anterodorsal margin of zygomatic plate, 1 --> 0(31); interorbital region, 2 ==> 0(43); jugal length, 1 ==> 0(47); maxillary septum length, 0 ==> 1(63); mesopterygoid fossa shape, 1 ==> 0(75); anteromedian flexid of m1, 0 ==> 1(99); orientation of metalophid m1, 0 ==> 2(103). DELTRAN: relative size of fifth digit (dV) of pes, 2 ==> 3(14); length of mystacial vibrissae, 1 --> 2(17); countershading of tail, 0 --> 1(25); carotid circulation, 0 --> 2(52); lingual roots on M1, 0 ==> 1(112); mental foramen position, 0 --> 1(116).

node\_133 --> node\_132: ACCTRAN: ectotympanic dorsal expansion, 0 ==> 1(61); posterolateral palatal pits, 0 --> 2(67); sphenopalatine vacuities, 1 ==> 2(71); mesopterygoid fossa breadth, 0 ==> 2(74); bullae inflation, 1 ==> 2(77); anterolabial cingulum of m2-m3, 2 --> 1(107); number of thoracic vertebrae, 0 --> 1(124); preputial glands, 1 --> 3(144). DELTRAN: ectotympanic dorsal expansion, 0 ==> 1(61); incisive foramina, 1 --> 2(62); sphenopalatine vacuities, 1 ==> 2(71); mesopterygoid fossa breadth, 0 ==> 2(74); bullae inflation, 0 ==> 2(77); mental foramen position, 0 --> 1(116); capsular process of lower incisor, 1 --> 0(118).

node\_132 --> Wiedomys pyrrhorhinos: ACCTRAN: ungual tufts on manual claws, 0 ==> 1(1); ventral base of claws on manus, 0 --> 1(2); position of hypothenar pad in relation to interdigital pad 1 (pes), 0 ==> 1(10); relative size of fifth digit (dV) of pes, 2 ==> 3(14); countershading of tail, 1 --> 0(25); position of antorbital bridge, 1 ==> 0(39); interorbital region, 2 ==> 3(43); ethmoturbinals and sphenopalatine foramen formation, 2 --> 1(49); alisphenoid strut, 1 --> 2(51); palatal length, 0 ==> 1(64); maxillary palatal pits, 1 ==> 0(68); anterior process of the ectotympanic, 1 ==> 0(78); anteroloph orientation, 0 ==> 1(92); ectolophid m1, 1 ==> 0(101); mesolophids of m1-m2, 0 ==> 1(105); masseteric crest position, 1 ==> 2(115); supratrochlear fenestra of humerus, 2 ==> 1(123); chevron bones, 0 ==> 2(126). DELTRAN: ungual tufts on manual claws, 0 ==> 1(1); ventral base of claws on manus, 0 --> 1(2); position of hypothenar pad in relation to interdigital pad 1 (pes), 0 ==> 1(10); relative size of fifth digit (dV) of pes, 2 ==> 3(14); position of antorbital bridge, 1 ==> 0(39); interorbital region, 2 ==> 3(43); palatal length, 0 ==> 1(64); maxillary palatal pits, 1 ==> 0(68); anterior process of the ectotympanic, 1 ==> 0(78); anteroloph orientation, 0 ==> 1(92); ectolophid m1, 1 ==> 0(101); mesolophids of m1-m2, 0 ==> 1(105); masseteric crest position, 1 ==> 2(115); supratrochlear fenestra of humerus, 2 ==> 1(123); chevron bones, 0 ==> 2(126); spines on the urethral flap of gland penis, 0 --> 1(142).

node\_132 --> Wilfredomys oenax: ACCTRAN: interorbital region breadth, 1 ==> 0(44); sinus groove on tegmen tympani, 0 ==> 1(55); palatal breadth, 0 ==> 1(65); orientation of metalophid m1, 0 ==> 2(103); entolophids of m1-m2, 0 ==> 1(104); posteroflexid breadth of m1-m2, 0 ==> 1(108); relative length of condylar and angular processes, 1 ==> 0(119); spines on the urethral flap of gland penis, 1 --> 0(142). DELTRAN: countershading of tail, 0 --> 1(25); interorbital region breadth, 1 ==> 0(44); ethmoturbinals and sphenopalatine foramen formation, 1 --> 2(49); alisphenoid strut, 2 --> 1(51); sinus groove on tegmen tympani, 0 ==> 1(55); palatal breadth, 0 ==> 1(65); orientation of metalophid m1, 0 ==> 2(103); entolophids of m1-m2, 0 ==> 1(104); posteroflexid breadth of m1-m2, 0 ==> 1(108); relative length of condylar and angular processes, 1 ==> 0(119); preputial glands, 1 --> 3(144).

node\_136 --> node\_135: ACCTRAN: countershading of tail, 1 --> 0(25); posterodorsal extension of premaxillae, 1 ==> 2(30); zygomatic arch dip, 0 ==> 1(42); alisphenoid strut, 1 --> 2(51); hamular process and development of the postglenoid foramen, 1 --> 3(56); mesopterygoid fossa shape 1 ==> 0(75); relative length of condylar and angular processes, 1 ==> 0(119); number of caudal vertebrae, 2 --> 1(125). DELTRAN: posterodorsal extension of premaxillae, 1 ==> 2(30); zygomatic arch dip, 0 ==> 1(42); hamular process and development of the postglenoid foramen, 1 --> 3(56); posterolateral palatal pits, 2 --> 0(67); sphenopalatine vacuities, 1 --> 0(71); mesopterygoid fossa shape, 1 ==> 0(75); capsular process of lower incisor, 1 --> 0(118); relative length of condylar and angular processes, 1 ==> 0(119).

node\_135 --> node\_134: ACCTRAN: position of hypothenar pad in relation to interdigital pad 1 (pes), 0 ==> 1(10); relative size of hallux (dl of pes), 1 ==> 0(13); relative size of fifth digit (dV) of pes, 2 ==> 1(14); rostral tube, 0 ==> 2(28); divergence of squamosal roots of zygomatic arch, 0 ==> 1(40); shape of zygomatic arches, 1 ==> 0(41); interorbital region, 2 ==> 0(43); optic foramen, 0 ==> 1(50); M1 position, 3 ==> 2(84); molar occlusal design, 0 ==> 1(86); anteroflexus M1, 0 ==> 1(90); hypoflexus size of M1, 1 ==> 0(94); protoflexus on M2, 0 ==> 1(97); hypoflexus of M3, 0 ==> 1(98); anteromedian flexid of m1, 0 ==> 1(99); anterolabial cingulum of m2-m3, 2 ==> 0(107); coronoid process, 0 ==> 1(120). DELTRAN: position of hypothenar pad in relation to interdigital pad 1 (pes), 0 ==> 1(10); relative size of hallux (dl of pes), 1 ==> 0(13); relative size of fifth digit (dV) of pes, 2 ==> 1(14); rostral tube, 0 ==> 2(28); divergence of squamosal roots of zygomatic arch, 0 ==> 1(40); shape of zygomatic arches, 1 ==> 0(41); interorbital region, 2 ==> 0(43); ethmoturbinals and sphenopalatine foramen formation, 0 --> 2(49); optic foramen, 0 ==> 1(50); M1 position, 3 ==> 2(84); molar occlusal design, 0 ==> 1(86); anteroflexus M1, 0 ==> 1(90); hypoflexus size of M1, 1 ==> 0(94); protoflexus on M2, 0 ==> 1(97); hypoflexus of M3, 0 ==> 1(98); anteromedian flexid of m1, 0 ==> 1(99); anterolabial cingulum of m2-m3, 1 ==> 0(107); coronoid process, 0 ==> 1(120); number of thoracic vertebrae, 1 --> 0(124); number of caudal vertebrae, 2 --> 1(125).

node\_134 --> Delomys collinus: ACCTRAN: position of hypothenar pad in relation to thenar (pes), 0 ==> 2(8); pectoral mammary pair, 1 ==> 0(23); bullae inflation, 1 --> 0(77); protostyle and enterostyle on M1, 2 ==> 0(96). DELTRAN: position of



hypothenar pad in relation to thenar (pes), 0 ==> 2(8); pectoral mammary pair, 1 ==> 0(23); protostyle and enterostyle on M1, 2 ==> 0(96); gall bladder, 1 --> 0(132). DELTRAN: countershading of tail, 0 --> 1(25); posterior extension of nasals, 0 ==> 2(29); bullae inflation, 0 --> 1(77).

node\_134 --> Delomys sublineatus: ACCTTRAN: countershading of tail, 0 --> 1(25); posterior extension of nasals, 0 ==> 2(29). DELTRAN: countershading of tail, 0 --> 1(25); posterior extension of nasals, 0 ==> 2(29); bullae inflation, 0 --> 1(77).

node\_135 --> Phaenomys ferrugineus: ACCTTRAN: relative size of hallux (dl of pes), 1 ==> 2(13); genal 2 vibrissae, 1 ==> 0(16); length of mystacial vibrissae, 1 ==> 2(17); anterodorsal margin of zygomatic plate, 1 --> 0(31); position of antorbital bridge, 1 ==> 0(39); interorbital region, 2 ==> 3(43); interorbital region breadth, 1 ==> 0(44); ethmoturbinals and sphenopalatine foramen formation, 2 --> 0(49); height of subsquamosal fenestra, 0 ==> 1(57); maxillary septum length, 0 ==> 1(63); palatal breadth, 0 ==> 1(65); procingulum anterior edge of M1, 0 ==> 1(89); orientation of metalophid m1, 0 ==> 1(103); entolophids of m1-m2, 0 ==> 2(104); posteroflexid breadth of m1-m2, 0 ==> 1(108); entoconid on m3, 0 ==> 1(109); lingual roots on M1, 0 ==> 2(112); masseteric crest position, 1 ==> 0(115). . DELTRAN: relative size of hallux (dl of pes), 1 ==> 2(13); genal 2 vibrissae, 1 ==> 0(16); length of mystacial vibrissae, 1 ==> 2(17); anterodorsal margin of zygomatic plate, 1 --> 0(31); position of antorbital bridge, 1 ==> 0(39); interorbital region, 2 ==> 3(43); interorbital region breadth, 1 ==> 0(44); height of subsquamosal fenestra, 0 ==> 1(57); maxillary septum length, 0 ==> 1(63); palatal breadth, 0 ==> 1(65); procingulum anterior edge of M1, 0 ==> 1(89); orientation of metalophid m1, 0 ==> 1(103); entolophids of m1-m2, 0 ==> 2(104); anterolabial cingulum of m2-m3, 1 --> 2(107); posteroflexid breadth of m1-m2, 0 ==> 1(108); entoconid on m3, 0 ==> 1(109); lingual roots on M1, 0 ==> 2(112); masseteric crest position, 1 ==> 0(115).

node\_139 --> Oligoryzomys fulvescens: ACCTTRAN: carotid circulation, 0 --> 1(52); mesopterygoid fossa breadth, 1 ==> 2(74); mesolophid on m3, 0 ==> 1(106); masseteric crest position, 1 --> 2(115); chevron bones, 2 --> 3(126); preputial glands, 1 ==> 0(144). DELTRAN: countershading of tail, 0 --> 1(25); jugal length, 1 --> 2(47); carotid circulation, 0 --> 1(52); mesopterygoid fossa breadth, 1 ==> 2(74); mesolophid on m3, 0 ==> 1(106); masseteric crest position, 1 --> 2(115); chevron bones, 2 --> 3(126); preputial glands, 1 ==> 0(144).

node\_140 --> Handleyomys fuscatus: ACCTTRAN: ventral base of claws on manus, 0 --> 1(2); plantar squamation of pes, 1 ==> 0(6); pectoral mammary pair, 1 ==> 0(23); posterodorsal extension of premaxillae, 1 ==> 2(30); zygomatic arch dip, 0 --> 1(42); interorbital region, 2 ==> 0(43); ethmoturbinals and sphenopalatine foramen formation, 0 ==> 2(49); parietal-supraoccipital suture breadth, 0 --> 2(58); incisive foramina, 1 ==> 0(62); sphenopalatine vacuities, 2 ==> 0(71); anterior process of the ectotympanic, 1 ==> 0(78); molar occlusal design, 0 --> 1(86); paraloph orientation in M1, 0 ==> 1(93); hypoflexus of M3, 0 ==> 1(98); accessory labial root of M1, 0 --> 1(111); capsular process of lower incisor, 1 ==> 0(118); position of the trochlear process of calcaneum, 1

==> 0(127). DELTRAN: ventral base of claws on manus. 0 --> 1(2); plantar squamation of pes. 1 ==> 0(6); pectoral mammary pair. 1 ==> 0(23); posterodorsal extension of premaxillae. 1 ==> 2(30); zygomatic arch dip. 0 --> 1(42); interorbital region. 2 ==> 0(43); ethmoturbinals and sphenopalatine foramen formation 0 ==> 2(49); parietal-supraoccipital suture breadth 0 --> 2(58); incisive foramina. 1 ==> 0(62); sphenopalatine vacuities. 2 ==> 0(71); anterior process of the ectotympanic. 1 ==> 0(78); molar occlusal design. 0 --> 1(86); paraloph orientation in M1. 0 ==> 1(93); hypoflexus of M3. 0 ==> 1(98); accessory labial root of M1. 0 --> 1(111); capsular process of lower incisor. 1 ==> 0(118); position of the trochlear process of calcaneum. 1 ==> 0(127).

node\_140 --> node\_83: ACCTTRAN: ungual tufts on manual claws. 0 ==> 1(1); ungual tuft on pes. 0 ==> 2(4); hypothenar pad of pes. 0 ==> 1(7); interdigital webbing on hindfoot. 0 ==> 1(11); length of mystacial vibrissae. 1 --> 0(17); body pelage pattern. 1 ==> 2(20); zygomatic plate breadth. 1 --> 0(32); interorbital region. 2 ==> 3(43); carotid circulation. 0 ==> 2(52); lambdoid ridge development. 0 --> 1(59); masseteric crest position. 1 --> 2(115); chevron bones. 2 --> 3(126). DELTRAN: ungual tufts on manual claws. 0 ==> 1(1); ungual tuft on pes. 0 ==> 2(4); hypothenar pad of pes. 0 ==> 1(7); interdigital webbing on hindfoot. 0 ==> 1(11); body pelage pattern. 1 ==> 2(20); interorbital region. 2 ==> 3(43); carotid circulation. 0 ==> 2(52); masseteric crest position. 1 --> 2(115); chevron bones. 2 --> 3(126).

node\_83 --> Holochilus brasiliensis: ACCTTRAN: posterior extension of nasals. 0 ==> 2(29); posterodorsal extension of premaxillae. 1 ==> 0(30); position of antorbital bridge. 1 ==> 0(39); zygomatic arch dip. 0 ==> 2(42); interorbital region breadth. 1 ==> 0(44); postorbital ridge. 0 ==> 1(46); alisphenoid strut. 2 ==> 0(51); palatal length. 3 ==> 2(64); mesopterygoid fossa breadth. 1 ==> 2(74); molar height topography. 0 ==> 1(85); molar occlusal design. 0 --> 1(86); ridge on anterolabial cingulum of m1. 0 ==> 1(102); accessory labial root of M1. 0 --> 1(111); number of caudal vertebrae. 1 ==> 0(125). DELTRAN: length of mystacial vibrissae. 1 --> 0(17); posterior extension of nasals. 0 ==> 2(29); posterodorsal extension of premaxillae. 1 ==> 0(30); position of antorbital bridge. 1 ==> 0(39); zygomatic arch dip. 0 ==> 2(42); interorbital region breadth. 1 ==> 0(44); postorbital ridge. 0 ==> 1(46); alisphenoid strut. 2 ==> 0(51); palatal length. 3 ==> 2(64); mesopterygoid fossa breadth. 1 ==> 2(74); molar height topography. 0 ==> 1(85); molar occlusal design. 0 --> 1(86); ridge on anterolabial cingulum of m1. 0 ==> 1(102); accessory labial root of M1. 0 --> 1(111); number of caudal vertebrae. 1 ==> 0(125).

node\_83 --> Oryzomys palustris: ACCTTRAN: countershading of tail. 0 --> 1(25); interorbital region breadth. 1 ==> 2(44); parietal-supraoccipital suture breadth. 0 ==> 3(58); incisive foramina. 1 ==> 2(62); protoflexus on M2. 1 ==> 0(97); anterolabial cingulum of m2-m3. 0 --> 1(107). DELTRAN: countershading of tail. 0 --> 1(25); zygomatic plate breadth. 1 --> 0(32); interorbital region breadth. 1 ==> 2(44); parietal-supraoccipital suture breadth. 0 ==> 3(58); lambdoid ridge development. 0 --> 1(59); incisive foramina. 1 ==> 2(62); protoflexus on M2. 1 ==> 0(97); anterolabial cingulum of m2-m3. 0 --> 1(107).

node\_140 --> node\_139: ACCTTRAN: relative size of hallux (dI of pes), 0 ==> 1(13); relative size of fifth digit (dV) of pes, 0 ==> 1(14); countershading of tail, 0 --> 1(25); jugal length, 1 --> 2(47); anteromedian flexus, 1 ==> 0(87); hypoflexus size of M1, 0 --> 1(94); anteromedian flexid of m1, 1 ==> 0(99); internal enameled pit of m1 procingulum, 1 --> 0(100); anterolabial cingulum of m2-m3, 0 --> 2(107); roots on m2, 1 ==> 0(114); relative length of condylar and angular processes, 0 ==> 1(119); coronoid process, 1 ==> 0(120); peroneal process of fifth metatarsal, 2 ==> 1(128); grooves on glans penis body, 0 --> 1(134). DELTRAN: relative size of hallux (dI of pes), 0 ==> 1(13); relative size of fifth digit (dV) of pes, 0 ==> 1(14); anteromedian flexus, 1 ==> 0(87); anteromedian flexid of m1, 1 ==> 0(99); roots on m2, 1 ==> 0(114); relative length of condylar and angular processes, 0 ==> 1(119); coronoid process, 1 ==> 0(120); peroneal process of fifth metatarsal, 2 ==> 1(128).

node\_139 --> node\_138: ACCTTRAN: relative size of fifth digit (dV) of pes, 1 ==> 2(14); anterodorsal margin of zygomatic plate, 1 --> 0(31); divergence of squamosal roots of zygomatic arch, 1 ==> 0(40); posterolateral palatal pits, 3 --> 1(67); protoflexus on M2, 1 ==> 0(97); number of caudal vertebrae, 1 ==> 2(125); spines on dorsal papilla, 1 --> 0(143). DELTRAN: relative size of fifth digit (dV) of pes, 1 ==> 2(14); divergence of squamosal roots of zygomatic arch, 1 ==> 0(40); hypoflexus size of M1, 0 --> 1(94); protoflexus on M2, 1 ==> 0(97); number of caudal vertebrae, 1 ==> 2(125); grooves on glans penis body, 0 --> 1(134).

node\_138 --> Microrhizomys minutus: ACCTTRAN: ventral base of claws on manus, 0 --> 1(2); body pelage pattern, 1 ==> 0(20); countershading of tail, 1 --> 0(25); interorbital region, 2 ==> 0(43); depth and shape of the molar-bearing portion of the maxillae, 0 ==> 1(69); anterior process of the ectotympanic, 1 ==> 0(78); prostate ventral glands, 2 ==> 1(145). DELTRAN: ventral base of claws on manus, 0 --> 1(2); body pelage pattern, 1 ==> 0(20); anterodorsal margin of zygomatic plate, 1 --> 0(31); interorbital region, 2 ==> 0(43); jugal length, 1 --> 2(47); posterolateral palatal pits, 3 --> 1(67); depth and shape of the molar-bearing portion of the maxillae, 0 ==> 1(69); anterior process of the ectotympanic, 1 ==> 0(78); spines on dorsal papilla, 1 --> 0(143); prostate ventral glands, 2 ==> 1(145).

node\_138 --> node\_137: ACCTTRAN: body pelage pattern, 1 ==> 2(20); jugal length, 2 --> 1(47); alisphenoid strut, 2 --> 1(51); sinus groove on tegmen tympani, 1 --> 0(55); sphenopalatine vacuities, 2 ==> 0(71); mesopterygoid fossa breadth, 1 ==> 0(74); anterocone, 0 --> 1(88); paraloph orientation in M1, 0 ==> 1(93); ectolophid m1, 0 ==> 1(101); chevron bones, 2 ==> 0(126). DELTRAN: body pelage pattern, 1 ==> 2(20); sphenopalatine vacuities, 2 ==> 1(71); mesopterygoid fossa breadth, 1 ==> 0(74); paraloph orientation in M1, 0 ==> 1(93); internal enameled pit of m1 procingulum, 1 --> 0(100); ectolophid m1, 0 ==> 1(101); anterolabial cingulum of m2-m3, 0 --> 1(107); chevron bones, 2 ==> 0(126).

node\_137 --> Oecomys bicolor: ACCTTRAN: manual digit proportions, 0 ==> 1(3); ungual tuft on pes, 0 ==> 2(4); position of hypothenar pad in relation to thenar (pes), 0 ==> 2(8); position of hypothenar pad in relation to interdigital pad 1 (pes), 0 ==> 1(10);

genal 2 vibrissae, 1 ==> 0(16); antitragus and pinnae structure, 0 ==> 1(18); posterior extension of nasals, 0 ==> 2(29); interorbital region, 2 ==> 3(43); interorbital region breadth, 1 ==> 2(44); posterolateral palatal pits, 1 --> 3(67); molar occlusal design, 0 ==> 1(86); anteromedian flexus, 0 ==> 1(87); anteromedian flexid of m1, 0 ==> 1(99); supratrochlear fenestra of humerus, 2 ==> 0(123); peroneal process of fifth metatarsal, 1 ==> 2(128). DELTRAN: manual digit proportions, 0 ==> 1(3); ungual tuft on pes, 0 ==> 2(4); position of hypothenar pad in relation to thenar (pes), 0 ==> 2(8); position of hypothenar pad in relation to interdigital pad 1 (pes), 0 ==> 1(10); genal 2 vibrissae, 1 ==> 0(16); antitragus and pinnae structure, 0 ==> 1(18); countershading of tail, 0 --> 1(25); posterior extension of nasals, 0 ==> 2(29); anterodorsal margin of zygomatic plate, 1 --> 0(31); interorbital region, 2 ==> 3(43); interorbital region breadth, 1 ==> 2(44); alisphenoid strut, 2 --> 1(51); sphenopalatine vacuities, 1 --> 0(71); molar occlusal design, 0 ==> 1(86); anteromedian flexus, 0 ==> 1(87); anteromedian flexid of m1, 0 ==> 1(99); anterolabial cingulum of m2-m3, 1 --> 2(107); supratrochlear fenestra of humerus, 2 ==> 0(123); peroneal process of fifth metatarsal, 1 ==> 2(128); spines on dorsal papilla, 1 --> 0(143).

node\_137 --> node\_136: ACCTTRAN: anterodorsal margin of zygomatic plate, 0 --> 1(31); ethmoturbinals and sphenopalatine foramen formation, 0 --> 2(49); tegmen tympani, 1 ==> 0(54); palatal length, 3 ==> 0(64); posterolateral palatal pits, 1 --> 0(67); maxillary palatal pits, 0 ==> 1(68); shape of parapterygoid fossa, 0 ==> 1(72); bullae inflation, 0 --> 1(77); processus brevis of incus, 0 ==> 1(81); mandibular diastemal shape, 1 ==> 0(117); capsular process of lower incisor, 1 --> 0(118); number of thoracic vertebrae, 1 --> 0(124); peroneal process of fifth metatarsal, 1 ==> 0(128); gall bladder, 1 --> 0(132); spines on the urethral flap of gland penis, 0 --> 1(142); spines on dorsal papilla, 0 --> 1(143). DELTRAN: tegmen tympani, 1 ==> 0(54); sinus groove on tegmen tympani, 1 --> 0(55); palatal length, 3 ==> 0(64); posterolateral palatal pits, 3 --> 2(67); maxillary palatal pits, 0 ==> 1(68); shape of parapterygoid fossa, 0 ==> 1(72); processus brevis of incus, 0 ==> 1(81); anterocone, 0 --> 1(88); mandibular diastemal shape, 1 ==> 0(117); peroneal process of fifth metatarsal, 1 ==> 0(128).

node\_136 --> node\_133: ACCTTRAN: rostral fur coloration, 0 ==> 1(19); posterodorsal extension of premaxillae, 1 ==> 0(30); incisive foramina, 1 --> 2(62); sphenopalatine vacuities, 0 --> 1(71); malleus lamina, 1 ==> 0(79); mental foramen position, 0 --> 1(116); position of the trochlear process of calcaneum, 1 ==> 0(127). DELTRAN: rostral fur coloration, 0 ==> 1(19); posterodorsal extension of premaxillae, 1 ==> 0(30); ethmoturbinals and sphenopalatine foramen formation, 0 --> 1(49); malleus lamina, 1 ==> 0(79); position of the trochlear process of calcaneum, 1 ==> 0(127).

node\_133 --> node\_131: ACCTTRAN: position of hypothenar pad in relation to thenar (pes), 0 ==> 2(8); length of mystacial vibrissae, 1 --> 2(17); anteroflexus M1, 0 ==> 1(91); paraloph orientation in M1, 1 ==> 2(93); mesolophid on m3, 0 --> 1(106); capsular process of lower incisor, 0 --> 1(118); spines on the urethral flap of gland penis, 1 --> 2(142). DELTRAN: position of hypothenar pad in relation to thenar (pes), 0 ==> 2(8); ethmoturbinals and sphenopalatine foramen formation, 1 --> 2(49); alisphenoid strut, 2 --> 1(51); posterolateral palatal pits, 2 --> 0(67); anteroflexus M1, 0 ==> 1(91);

paraloph orientation in M1, 1 ==> 2(93); number of thoracic vertebrae, 1 --> 0(124).

node\_131 --> node\_130: ACCTTRAN: antitragus and pinnae structure, 0 ==> 1(18); alisphenoid strut, 1 ==> 0(51); carotid circulation, 0 --> 2(52); incisive foramina, 2 --> 1(62); bullae inflation, 1 --> 0(77); posteroflexid breadth of m1-m2, 0 ==> 1(108); masseteric crest position, 1 ==> 2(115); supratrochlear fenestra of humerus, 2 ==> 0(123). DELTRAN: antitragus and pinnae structure, 0 ==> 1(18); alisphenoid strut, 1 ==> 0(51); mesolophid on m3, 0 --> 1(106); anterolabial cingulum of m2-m3, 1 --> 2(107); posteroflexid breadth of m1-m2, 0 ==> 1(108); masseteric crest position, 1 ==> 2(115); supratrochlear fenestra of humerus, 2 ==> 0(123).

node\_130 --> node\_129: ACCTTRAN: ventral base of claws on manus, 0 --> 1(2); length of mystacial vibrissae, 2 --> 1(17); rostral fur coloration, 1 ==> 0(19); body pelage pattern, 2 ==> 1(20); pectoral mammary pair, 1 --> 0(23); protuberant anus, 0 --> 1(24); countershading of tail, 1 --> 0(25); zygomatic plate breadth, 1 --> 0(32); position of antorbital bridge, 1 ==> 0(39); zygomatic arch dip, 0 ==> 1(42); interorbital region breadth, 1 --> 2(44); ethmoturbinals and sphenopalatine foramen formation, 2 ==> 3(49); depth and shape of the molar-bearing portion of the maxillae, 0 ==> 1(69); sphenopalatine vacuities, 1 ==> 0(71); upper incisor orientation, 0 ==> 2(82); ectolophid m1, 1 ==> 0(101); mental foramen position, 1 --> 0(116); mandibular diastemal shape, 0 --> 1(117); retromolar region, 0 --> 1(121). DELTRAN: rostral fur coloration, 1 ==> 0(19); body pelage pattern, 2 ==> 1(20); position of antorbital bridge, 1 ==> 0(39); zygomatic arch dip, 0 ==> 1(42); ethmoturbinals and sphenopalatine foramen formation, 2 ==> 3(49); depth and shape of the molar-bearing portion of the maxillae, 0 ==> 1(69); sphenopalatine vacuities, 1 ==> 0(71); upper incisor orientation, 0 ==> 2(82); ectolophid m1, 1 ==> 0(101).

node\_129 --> *Abrawayaomys ruschii*: ACCTTRAN: relative size of hallux (dl of pes), 1 ==> 0(13); relative size of fifth digit (dV) of pes, 2 ==> 0(14); genal 2 vibrissae, 1 ==> 0(16); pelage texture, 0 ==> 1(21); uniform pattern coloration of tail, 0 ==> 2(26); tail pencil, 0 ==> 1(27); posterodorsal extension of premaxillae, 0 ==> 2(30); shape of zygomatic arches, 1 ==> 0(41); zygomatic arch dip, 1 ==> 2(42); jugal length, 1 ==> 0(47); optic foramen, 0 ==> 1(50); carotid circulation, 2 --> 0(52); parietal-supraoccipital suture breadth, 0 ==> 3(58); lambdoid ridge development, 0 ==> 1(59); bullae inflation, 0 ==> 2(77); upper incisor orientation, 2 ==> 3(82); M1 position, 3 ==> 2(84); ridge on anterolabial cingulum of m1, 0 ==> 1(102); mesolophids of m1-m2, 0 ==> 1(105). DELTRAN: ventral base of claws on manus, 0 --> 1(2); relative size of hallux (dl of pes), 1 ==> 0(13); relative size of fifth digit (dV) of pes, 2 ==> 0(14); genal 2 vibrissae, 1 ==> 0(16); pelage texture, 0 ==> 1(21); uniform pattern coloration of tail, 0 ==> 2(26); tail pencil, 0 ==> 1(27); posterodorsal extension of premaxillae, 0 ==> 2(30); zygomatic plate breadth, 1 --> 0(32); shape of zygomatic arches, 1 ==> 0(41); zygomatic arch dip, 1 ==> 2(42); interorbital region breadth, 1 --> 2(44); jugal length, 1 ==> 0(47); optic foramen, 0 ==> 1(50); parietal-supraoccipital suture breadth, 0 ==> 3(58); lambdoid ridge development, 0 ==> 1(59); bullae inflation, 0 ==> 2(77); upper incisor orientation, 2 ==> 3(82); M1 position, 3 ==> 2(84); ridge on anterolabial cingulum of m1, 0 ==> 1(102); mesolophids of m1-m2, 0 ==> 1(105); retromolar region, 0 --> 1(121).

node\_129 --> node\_128: ACCTRAN: manual digit proportions, 0 --> 1(3); plantar squamation of pes, 1 ==> 0(6); posterior extension of nasals, 0 ==> 2(29); anterodorsal margin of zygomatic plate, 1 --> 0(31); maxillary palatal pits, 1 --> 0(68); anteroflexus M1, 1 ==> 0(91); paraloph orientation in M1, 2 ==> 1(93). DELTRAN: plantar squamation of pes, 1 ==> 0(6); pectoral mammary pair, 1 --> 0(23); posterior extension of nasals, 0 ==> 2(29); carotid circulation, 0 --> 2(52); anteroflexus M1, 1 ==> 0(91); paraloph orientation in M1, 2 ==> 1(93); mandibular diastemal shape, 0 --> 1(117).

node\_128 --> node\_84: ACCTRAN: nail on hallux, 0 ==> 1(12); postorbital ridge, 0 --> 1(46); sinus groove on tegmen tympani, 0 --> 1(55); hamular process and development of the postglenoid foramen, 1 --> 0(56); height of subsquamosal fenestra, 0 --> 1(57); incisive foramina, 1 ==> 0(62); palatal length, 0 ==> 3(64); posterolateral palatal pits, 0 ==> 1(67); parapterygoid vacuity, 0 --> 1(73); anterior process of the ectotympanic, 1 --> 0(78); malleus lamina, 0 ==> 1(79); hypoflexus of M3, 0 ==> 1(98); anteromedian flexid of m1, 0 ==> 1(99); entolophids of m1-m2, 0 --> 2(104); ventral margin of mandible, 0 ==> 1(122); position of the trochlear process of calcaneum, 0 --> 1(127); gall bladder, 0 --> 1(132). DELTRAN: manual digit proportions, 0 --> 1(3); nail on hallux, 0 ==> 1(12); zygomatic plate breadth, 1 --> 0(32); interorbital region breadth, 1 --> 2(44); incisive foramina, 1 ==> 0(62); palatal length, 0 ==> 3(64); posterolateral palatal pits, 0 ==> 1(67); maxillary palatal pits, 1 --> 0(68); malleus lamina, 0 ==> 1(79); hypoflexus of M3, 0 ==> 1(98); anteromedian flexid of m1, 0 ==> 1(99); retromolar region, 0 --> 1(121); ventral margin of mandible, 0 ==> 1(122).

node\_84 --> Rhagomys rufescens: ACCTRAN: body pelage pattern, 1 ==> 0(20); anterodorsal margin of zygomatic plate, 0 --> 1(31); zygomatic arch dip, 1 ==> 2(42); jugal length, 1 ==> 0(47); bullae inflation, 0 --> 1(77); anteroflexus M1, 0 ==> 1(90); mesolophids of m1-m2, 0 ==> 1(105); lingual roots on M1, 0 ==> 1(112). DELTRAN: body pelage pattern, 1 ==> 0(20); zygomatic arch dip, 1 ==> 2(42); jugal length, 1 ==> 0(47); bullae inflation, 0 --> 1(77); anteroflexus M1, 0 ==> 1(90); mesolophids of m1-m2, 0 ==> 1(105); lingual roots on M1, 0 ==> 1(112).

node\_84 --> Rhagomys longilingua: ACCTRAN: relative size of hallux (dl of pes), 1 ==> 2(13); body pelage pattern, 1 ==> 2(20); pelage texture, 0 ==> 1(21); interorbital region, 2 ==> 3(43); posterolateral palatal pits, 1 ==> 3(67); procingulum anterior edge of M1, 0 ==> 1(89). DELTRAN: relative size of hallux (dl of pes), 1 ==> 2(13); body pelage pattern, 1 ==> 2(20); pelage texture, 0 ==> 1(21); anterodorsal margin of zygomatic plate, 1 --> 0(31); interorbital region, 2 ==> 3(43); postorbital ridge, 0 --> 1(46); sinus groove on tegmen tympani, 0 --> 1(55); hamular process and development of the postglenoid foramen, 1 --> 0(56); height of subsquamosal fenestra, 0 --> 1(57); posterolateral palatal pits, 1 ==> 3(67); parapterygoid vacuity, 0 --> 1(73); anterior process of the ectotympanic, 1 --> 0(78); procingulum anterior edge of M1, 0 ==> 1(89); entolophids of m1-m2, 0 --> 2(104); position of the trochlear process of calcaneum, 0 --> 1(127).

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## **TABLES**

### **Part I**

TABLE 1.- Alternative arrangement previously proposed for the "thomasomyine" rodents treated here.

| Steadman and Ray<br>(1982) | Musser and Carleton<br>(1993) | Voss (1993)                |
|----------------------------|-------------------------------|----------------------------|
| Thomasomyini               | Thomasomyini                  | "Plesion"                  |
| † <u>Megaoryzomys</u>      | <u>Aepeomys</u>               | <u>Delomys</u>             |
| <u>Rhipidomys</u>          | <u>Delomys</u>                | <u>Abrawayaomys</u>        |
| <u>Thomasomys</u>          | <u>Phaenomys</u>              | <u>Aepeomys</u>            |
|                            | <u>Rhagomys</u>               | <u>Chilomys</u>            |
|                            | <u>Rhipidomys</u>             | <u>Phaenomys</u>           |
|                            | <u>Thomasomys</u>             | <u>Rhagomys</u>            |
|                            | <u>Wilfredomys</u>            | <u>Rhipidomys</u>          |
|                            | Wiedomyini                    | <u>Thomasomys</u>          |
|                            | <u>Wiedomys</u>               | <u>Wilfredomys</u>         |
|                            | Incertae sedis                |                            |
|                            | <u>Abrawayaomys</u>           |                            |
|                            | <u>Chilomys</u>               |                            |
| McKenna and Bell<br>(1997) | Eisenberg (1989)              | Smith and Patton<br>(1999) |
| Thomasomyini               | Thomasomyini                  | Thomasomyini               |
| † <u>Megaoryzomys</u>      | <u>Aepeomys</u>               | <u>Chilomys</u>            |
| <u>Chilomys</u>            | <u>Chilomys</u>               | <u>Rhipidomys</u>          |
| <u>Abrawayaomys</u>        | <u>Rhipidomys</u>             | <u>Thomasomys</u>          |
| <u>Delomys</u>             | <u>Thomasomys</u>             | <u>Aepeomys</u>            |
| <u>Thomasomys</u>          |                               | Wiedomyini                 |
| <u>Wilfredomys</u>         |                               | <u>Wiedomys</u>            |
| <u>Aepeomys</u>            |                               | "Unique lines"             |
| <u>Phaenomys</u>           |                               | <u>Delomys</u>             |
| <u>Rhipidomys</u>          |                               | <u>Wilfredomys</u>         |
| Wiedomyini                 |                               | Incertae sedis             |
| † <u>Cholomys</u>          |                               | <u>Phaenomys</u>           |
| <u>Wiedomys</u>            |                               | <u>Abrawayaomys</u>        |
| Incertae sedis             |                               | <u>Rhagomys</u>            |
| <u>Rhagomys</u>            |                               |                            |

TABLE 2.- Species included in the sigmodontine analyses. Taxonomy follows McKenna and Bell (1997) except as noted.

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OUTGROUP TAXA

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Family Muridae

Subfamily Arvicolinae

Microtus pennsylvanicus

Subfamily Calomyscinae

Calomyscus baluchi

Subfamily Cricetinae

Cricetulus migratorius

Mesocricetus auratus

Subfamily Tylomyinae<sup>1</sup>

Nyctomys sumichrasti

Tylomys nudicaudus

Subfamily Neotominae<sup>2</sup>

Tribe Neotomini

Nelsonia neotomodon

Neotoma floridana

Tribe Peromyscini<sup>3</sup>

Baiomys musculus

Ochrotomys nuttalli

Peromyscus mexicanus

Reithrodontomys mexicanus

Scotinomys teguina

INGROUP TAXA

Subfamily Sigmodontinae

Tribe Akodontini

Abrothrix longipilis

Akodon boliviensis

Microxus mimus

Oxymycterus paramensis

Tribe Ichthyomyini

Anotomys leander

Ichthyomys hydrobates

Neusticomys monticolus

Tribe Oryzomyini

Handleyomys intectus

Holochilus brasiliensis

Holochilus sciureus

Microryzomys minutus

Oecomys bicolor

Oligoryzomys fulvescens

Oryzomys palustris

Tribe Phyllotini

Calomys callosus

Chinchillula sahamae



- Graomys griseoflavus  
Phyllotis darwini  
Punomys kofordi  
 Tribe Scapteromyini  
Kunsia tomentosus  
Scapteromys tumidus  
 Tribe Sigmodontini  
Sigmodon hispidus  
Sigmodon peruanus  
 Tribe Thomasomyini<sup>4</sup>  
Abrawayaomys ruschii<sup>5</sup>  
Aepeomys lugens  
Chilomys instans  
Delomys collinus  
Delomys sublineatus  
Phaenomys ferrugineus  
Rhagomys rufescens  
Rhipidomys fulviventris  
Rhipidomys leucodactylus  
Rhipidomys macconnelli  
Thomasomys aureus  
Thomasomys baeops  
Thomasomys cinereus  
Thomasomys erro  
Thomasomys incanus  
Thomasomys kalinowskii  
Thomasomys macrotis  
Thomasomys notatus  
Thomasomys rhoadsi  
Wilfredomys oenax  
Juliomys pictipes  
Juliomys sp.  
 Tribe Wiedomyini  
Wiedomys pyrrhorhinos

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<sup>1</sup> *Sensu* Reig (1984: 338).

<sup>2</sup> *Sensu* Reig (1980: 260).

<sup>3</sup> Contents of the tribe follows Musser and Carleton (1993). Baiomys and Scotinomys were listed by McKenna and Bell (1997) as Sigmodontinae (*sensu* Musser and Carleton, 1993) incertae sedis.

<sup>4</sup> Position of Rhagomys is uncertain. It was included in the Thomasomyini following Musser and Carleton (1993: 687), but as Sigmodontinae incertae sedis by McKenna and Bell (1997).

<sup>5</sup> Musser and Carleton (1993) indicated that cranaeal characteristics of Abrawayaomys suggest an archaic thomasomyine.

TABLE 3.- Statistics on character codings for Sigmodontine data set

| Terminal taxon                   | Characters scored "0" - "5" <sup>a</sup> |         | Characters scored "-" |         | Characters scored "?" |         | Percent completeness <sup>b</sup> |
|----------------------------------|------------------------------------------|---------|-----------------------|---------|-----------------------|---------|-----------------------------------|
| <u>Microtus pennsylvanicus</u>   | 91                                       | (74.5%) | 13                    | (10.7%) | 18                    | (14.8%) | 85.2%                             |
| <u>Cricetulus migratorius</u>    | 113                                      | (92.6%) | 4                     | (3.3%)  | 5                     | (4.1%)  | 95.9%                             |
| <u>Mesocricetus auratus</u>      | 107                                      | (87.7%) | 6                     | (4.9%)  | 9                     | (7.4%)  | 92.6%                             |
| <u>Calomyscus baluchi</u>        | 109                                      | (89.3%) | 4                     | (3.3%)  | 9                     | (7.4%)  | 92.6%                             |
| <u>Nyctomys sumichrasti</u>      | 112                                      | (91.8%) | 5                     | (4.1%)  | 5                     | (4.1%)  | 95.9%                             |
| <u>Tylomys nudicaudus</u>        | 113                                      | (92.7%) | 7                     | (5.7%)  | 2                     | (1.6%)  | 98.4%                             |
| <u>Nelsonia neotomodon</u>       | 96                                       | (78.7%) | 6                     | (4.9%)  | 20                    | (16.4%) | 83.6%                             |
| <u>Neotoma floridana</u>         | 111                                      | (91%)   | 9                     | (7.4%)  | 2                     | (1.6%)  | 98.4%                             |
| <u>Baiomys musculus</u>          | 117                                      | (95.9%) | 3                     | (2.5%)  | 2                     | (1.6%)  | 98.4%                             |
| <u>Ochrotomys nuttalli</u>       | 114                                      | (93.4%) | 4                     | (3.3%)  | 4                     | (3.3%)  | 96.7%                             |
| <u>Peromyscus mexicanus</u>      | 114                                      | (93.4%) | 5                     | (4.1%)  | 3                     | (2.5%)  | 97.5%                             |
| <u>Reithrodontomys mexicanus</u> | 110                                      | (90.1%) | 3                     | (2.5%)  | 9                     | (7.4%)  | 92.6%                             |
| <u>Scotinomys teguina</u>        | 110                                      | (90.2%) | 2                     | (1.6%)  | 10                    | (8.2%)  | 91.8%                             |
| <u>Abrothrix longipilis</u>      | 110                                      | (90.1%) | 4                     | (3.3%)  | 8                     | (6.6%)  | 93.4%                             |
| <u>Akodon boliviensis</u>        | 119                                      | (97.5%) | 3                     | (2.5%)  | 0                     | 0       | 100%                              |
| <u>Microxus mimus</u>            | 118                                      | (96.7%) | 3                     | (2.5%)  | 1                     | (0.8%)  | 99.2%                             |
| <u>Oxymycterus paramensis</u>    | 116                                      | (95%)   | 3                     | (2.5%)  | 3                     | (2.5%)  | 97.5%                             |
| <u>Anotomys leander</u>          | 110                                      | (90.2%) | 7                     | (5.7%)  | 5                     | (4.1%)  | 95.9%                             |
| <u>Ichthyomys hydrobates</u>     | 111                                      | (91%)   | 6                     | (4.9%)  | 5                     | (4.1%)  | 95.9%                             |
| <u>Neusticomys monticolus</u>    | 110                                      | (90.2%) | 6                     | (4.9%)  | 6                     | (4.9%)  | 95.1%                             |
| <u>Handleyomys intectus</u>      | 99                                       | (81.1%) | 4                     | (3.3%)  | 19                    | (15.6%) | 84.4%                             |
| <u>Holochilus brasiliensis</u>   | 115                                      | (94.2%) | 4                     | (3.3%)  | 3                     | (2.5%)  | 97.5%                             |
| <u>Holochilus sciureus</u>       | 108                                      | (88.5%) | 3                     | (2.5%)  | 11                    | (9%)    | 91%                               |
| <u>Microryzomys minutus</u>      | 119                                      | (97.6%) | 2                     | (1.6%)  | 1                     | (0.8%)  | 99.2%                             |
| <u>Oecomys bicolor</u>           | 113                                      | (92.6%) | 3                     | (2.5%)  | 6                     | (4.9%)  | 95.1%                             |
| <u>Oligoryzomys fulvescens</u>   | 117                                      | (95.9%) | 3                     | (2.5%)  | 2                     | (1.6%)  | 98.4%                             |
| <u>Oryzomys palustris</u>        | 118                                      | (96.7%) | 3                     | (2.5%)  | 1                     | (0.8%)  | 99.2%                             |
| <u>Calomys callosus</u>          | 118                                      | (96.7%) | 3                     | (2.5%)  | 1                     | (0.8%)  | 99.2%                             |
| <u>Chinchillula sahamae</u>      | 109                                      | (89.4%) | 6                     | (4.9%)  | 7                     | (5.7%)  | 94.3%                             |
| <u>Graomys griseoflavus</u>      | 115                                      | (94.2%) | 4                     | (3.3%)  | 3                     | (2.5%)  | 97.5%                             |
| <u>Phyllotis darwini</u>         | 112                                      | (91.8%) | 4                     | (3.3%)  | 6                     | (4.9%)  | 95.1%                             |
| <u>Punomys kofordi</u>           | 111                                      | (91%)   | 4                     | (3.3%)  | 7                     | (5.7%)  | 94.3%                             |
| <u>Kunsia tomentosus</u>         | 86                                       | (70.5%) | 5                     | (4.1%)  | 31                    | (25.4%) | 74.6%                             |
| <u>Scapteromys tumidus</u>       | 115                                      | (94.2%) | 3                     | (2.5%)  | 4                     | (3.3%)  | 96.7%                             |
| <u>Sigmodon hispidus</u>         | 117                                      | (95.9%) | 4                     | (3.3%)  | 1                     | (0.8%)  | 99.2%                             |
| <u>Sigmodon peruanus</u>         | 99                                       | (81.1%) | 3                     | (2.5%)  | 20                    | (16.4%) | 83.6%                             |
| <u>Abrawayaomys ruschii</u>      | 86                                       | (70.5%) | 1                     | (0.8%)  | 35                    | (28.7%) | 71.3%                             |
| <u>Aepeomys lugens</u>           | 106                                      | (86.9%) | 2                     | (1.6%)  | 14                    | (11.5%) | 88.5%                             |
| <u>Chilomys instans</u>          | 119                                      | (97.5%) | 3                     | (2.5%)  | 0                     | 0       | 100%                              |

|                                 |      |         |     |        |     |         |       |
|---------------------------------|------|---------|-----|--------|-----|---------|-------|
| <u>Delomys collinus</u>         | 105  | (86%)   | 3   | (2.5%) | 14  | (11.5%) | 88.5% |
| <u>Delomys sublineatus</u>      | 110  | (90.4%) | 2   | (1.6%) | 10  | (8%)    | 92%   |
| <u>Juliomys pictipes</u>        | 98   | (80.3%) | 3   | (2.5%) | 21  | (17.2%) | 82.8% |
| <u>Juliomys sp.</u>             | 94   | (77%)   | 3   | (2.5%) | 25  | (20.5%) | 79.5% |
| <u>Phaenomys ferrugineus</u>    | 77   | (63.2%) | 2   | (1.6%) | 43  | (35.2%) | 64.8% |
| <u>Rhagomys rufescens</u>       | 74   | (60.7%) | 2   | (1.6%) | 46  | (37.7%) | 62.3% |
| <u>Rhipidomys fulviventris</u>  | 117  | (95.9%) | 3   | (2.5%) | 2   | (1.6%)  | 98.4% |
| <u>Rhipidomys leucodactylus</u> | 116  | (95%)   | 3   | (2.5%) | 3   | (2.5%)  | 97.5% |
| <u>Rhipidomys macconnelli</u>   | 117  | (95.9%) | 3   | (2.5%) | 2   | (1.6%)  | 98.4% |
| <u>Thomasomys aureus</u>        | 119  | (97.6%) | 2   | (1.6%) | 1   | (0.8%)  | 99.2% |
| <u>Thomasomys baeops</u>        | 119  | (97.6%) | 2   | (1.6%) | 1   | (0.8%)  | 99.2% |
| <u>Thomasomys cinereus</u>      | 116  | (95%)   | 3   | (2.5%) | 3   | (2.5%)  | 97.5% |
| <u>Thomasomys erro</u>          | 105  | (86.1%) | 2   | (1.6%) | 15  | (12.3%) | 87.7% |
| <u>Thomasomys incanus</u>       | 99   | (81.2%) | 2   | (1.6%) | 21  | (17.2%) | 82.8% |
| <u>Thomasomys kalinowskii</u>   | 103  | (84.5%) | 2   | (1.6%) | 17  | (13.9%) | 86.1% |
| <u>Thomasomys macrotis</u>      | 100  | (81.9%) | 3   | (2.5%) | 19  | (15.6%) | 84.4% |
| <u>Thomasomys notatus</u>       | 112  | (91.8%) | 4   | (3.3%) | 6   | (4.9%)  | 95.1% |
| <u>Thomasomys rhoadsi</u>       | 115  | (94.2%) | 4   | (3.3%) | 3   | (2.5%)  | 97.5% |
| <u>Wilfredomys oenax</u>        | 113  | (92.6%) | 3   | (2.5%) | 6   | (4.9%)  | 95.1% |
| <u>Wiedomys pyrrhorhinos</u>    | 100  | (82%)   | 2   | (1.6%) | 20  | (16.4%) | 83.6% |
| Total                           | 6402 | (89%)   | 221 | (3.1%) | 576 | (8.0%)  | 92.0% |

<sup>a</sup>Percentage calculated using the total number of characters (122).

<sup>b</sup>Completeness is defined as the percentage of characters scored based on available data. It is calculated by subtracting the percentage of characters scored “?” from 100%.

## **Part II**

TABLE 1.- Statistics on character codings for thomasomyine data set.

| Terminal Taxon                  | Characters scored "0" - "5" |         | Characters scored "-" |        | Characters scored "?" |         | Percent completeness |         |
|---------------------------------|-----------------------------|---------|-----------------------|--------|-----------------------|---------|----------------------|---------|
| <u>Handleyomys fuscatus</u>     | 87                          | (60%)   | 2                     | (1.7%) | 56                    | (38.3%) | 89                   | (61.7%) |
| <u>Holochilus brasiliensis</u>  | 89                          | (61.7%) | 9                     | (6.4%) | 46                    | (31.9%) | 99                   | (68.1%) |
| <u>Microryzomys minutus</u>     | 115                         | (79.2%) | 2                     | (1.7%) | 28                    | (19.1%) | 117                  | (80.9%) |
| <u>Oecomys bicolor</u>          | 106                         | (72.8%) | 2                     | (1.7%) | 37                    | (25.5%) | 108                  | (74.5%) |
| <u>Oligoryzomys fulvescens</u>  | 93                          | (63.9%) | 3                     | (2.1%) | 49                    | (34%)   | 96                   | (66%)   |
| <u>Oryzomys palustris</u>       | 115                         | (79.2%) | 4                     | (2.9%) | 26                    | (17.9%) | 119                  | (82.1%) |
| <u>Abrawayaomys ruschii</u>     | 98                          | (67.3%) | 4                     | (2.9%) | 43                    | (29.8%) | 102                  | (70.2%) |
| <u>Delomys collinus</u>         | 117                         | (80.8%) | 2                     | (1.3%) | 26                    | (17.9%) | 119                  | (82.1%) |
| <u>Delomys sublineatus</u>      | 114                         | (78.7%) | 2                     | (1.3%) | 29                    | (20%)   | 116                  | (80%)   |
| <u>Juliomys pictipes</u>        | 117                         | (80.4%) | 2                     | (1.7%) | 26                    | (17.9%) | 119                  | (82.1%) |
| <u>Juliomys sp.</u>             | 78                          | (53.6%) | 2                     | (1.7%) | 65                    | (44.7%) | 80                   | (55.3%) |
| <u>Phaenomys ferrugineus</u>    | 93                          | (64.2%) | 2                     | (1.3%) | 50                    | (34.5%) | 95                   | (65.5%) |
| <u>Rhagomys longilingua</u>     | 82                          | (56.7%) | 1                     | (0.4%) | 62                    | (42.9%) | 83                   | (57.1%) |
| <u>Rhagomys rufescens</u>       | 80                          | (55.4%) | 2                     | (1.7%) | 62                    | (42.9%) | 83                   | (57.1%) |
| <u>Wiedomys pyrrhorhinos</u>    | 124                         | (85.6%) | 3                     | (2.1%) | 18                    | (12.3%) | 127                  | (87.7%) |
| <u>Wilfredomys oenax</u>        | 129                         | (89.3%) | 2                     | (1.3%) | 14                    | (9.4%)  | 131                  | (90.6%) |
| <u>Aepeomys lugens</u>          | 125                         | (86%)   | 2                     | (1.7%) | 18                    | (12.3%) | 127                  | (87.7%) |
| <u>Aepeomys reigi</u>           | 120                         | (82.6%) | 2                     | (1.7%) | 23                    | (15.7%) | 122                  | (84.3%) |
| <u>Chilomys fumeus</u>          | 108                         | (74.8%) | 1                     | (0.9%) | 35                    | (24.3%) | 110                  | (75.7%) |
| <u>Chilomys instans</u>         | 138                         | (95.3%) | 1                     | (0.4%) | 6                     | (4.3%)  | 139                  | (95.7%) |
| <u>Rhipidomys caucensis</u>     | 103                         | (71.1%) | 1                     | (0.4%) | 41                    | (28.5%) | 104                  | (71.5%) |
| <u>Rhipidomys fulviverter</u>   | 123                         | (84.7%) | 2                     | (1.3%) | 20                    | (14%)   | 125                  | (86%)   |
| <u>Rhipidomys latimanus</u>     | 110                         | (75.7%) | 1                     | (0.9%) | 34                    | (23.4%) | 111                  | (76.6%) |
| <u>Rhipidomys leucodactylus</u> | 123                         | (85.1%) | 1                     | (0.9%) | 20                    | (14%)   | 125                  | (86%)   |
| <u>Rhipidomys gardneri</u>      | 98                          | (67.7%) | 1                     | (0.4%) | 46                    | (31.9%) | 99                   | (68.1%) |
| <u>Rhipidomys macconnelli</u>   | 127                         | (87.6%) | 2                     | (1.3%) | 16                    | (11.1%) | 129                  | (88.9%) |
| <u>Rhipidomys ochrogaster</u>   | 102                         | (70.2%) | 2                     | (1.3%) | 41                    | (28.5%) | 104                  | (71.5%) |
| <u>Thomasomys apeco</u>         | 121                         | (83.4%) | 2                     | (1.3%) | 22                    | (15.3%) | 123                  | (84.7%) |
| <u>Thomasomys aureus</u>        | 117                         | (80.8%) | 1                     | (0.9%) | 27                    | (18.3%) | 118                  | (81.7%) |
| <u>Thomasomys auricularis</u>   | 100                         | (68.9%) | 1                     | (0.9%) | 44                    | (30.2%) | 101                  | (69.8%) |
| <u>Thomasomys australis</u>     | 115                         | (79.1%) | 2                     | (1.3%) | 28                    | (19.6%) | 117                  | (80.4%) |
| <u>Thomasomys baeops</u>        | 131                         | (90.2%) | 1                     | (0.9%) | 13                    | (8.9%)  | 132                  | (91.1%) |
| <u>Thomasomys bombycinus</u>    | 118                         | (81.7%) | 2                     | (1.7%) | 24                    | (16.6%) | 121                  | (83.4%) |
| <u>Thomasomys caudivarius</u>   | 117                         | (80.9%) | 2                     | (1.7%) | 25                    | (17.4%) | 120                  | (82.6%) |
| <u>Thomasomys cinereiventer</u> | 117                         | (80.4%) | 2                     | (1.7%) | 26                    | (17.9%) | 119                  | (82.1%) |
| <u>Thomasomys cinereus</u>      | 130                         | (89.8%) | 2                     | (1.7%) | 12                    | (8.5%)  | 133                  | (91.5%) |
| <u>Thomasomys cinnamomeus</u>   | 109                         | (75.4%) | 2                     | (1.7%) | 33                    | (22.9%) | 112                  | (77.1%) |
| <u>Thomasomys contradictus</u>  | 113                         | (78.2%) | 1                     | (0.9%) | 30                    | (20.9%) | 115                  | (79.1%) |
| <u>Thomasomys daphne</u>        | 115                         | (79.6%) | 1                     | (0.4%) | 29                    | (20%)   | 116                  | (80%)   |
| <u>Thomasomys dispar</u>        | 112                         | (77.4%) | 1                     | (0.9%) | 31                    | (21.7%) | 114                  | (78.3%) |

|                                |                     |                   |                     |                     |
|--------------------------------|---------------------|-------------------|---------------------|---------------------|
| <u>Thomasomys eleusis</u>      | 115 (79.1%)         | 1 (0.9%)          | 29 (20%)            | 116 (80%)           |
| <u>Thomasomys emeritus</u>     | 107 (73.6%)         | 2 (1.7%)          | 36 (24.7%)          | 109 (75.3%)         |
| <u>Thomasomys erro</u>         | 125 (86.4%)         | 3 (2.1%)          | 17 (11.5%)          | 128 (88.5%)         |
| <u>Thomasomys fumeus</u>       | 103 (71%)           | 2 (1.3%)          | 40 (27.7%)          | 105 (72.3%)         |
| <u>Thomasomys gracilis</u>     | 126 (86.8%)         | 2 (1.3%)          | 17 (11.9%)          | 128 (88.1%)         |
| <u>Thomasomys hudsoni</u>      | 110 (75.7%)         | 2 (1.7%)          | 33 (22.6%)          | 112 (77.4%)         |
| <u>Thomasomys hylophilus</u>   | 122 (84.3%)         | 2 (1.7%)          | 20 (14%)            | 125 (86%)           |
| <u>Thomasomys incanus</u>      | 121 (83.4%)         | 2 (1.7%)          | 22 (14.9%)          | 123 (85.1%)         |
| <u>Thomasomys ischyrius</u>    | 116 (80%)           | 1 (0.9%)          | 28 (19.1%)          | 117 (80.9%)         |
| <u>Thomasomys kalinowskii</u>  | 137 (94.4%)         | 1 (0.9%)          | 7 (4.7%)            | 138 (95.3%)         |
| <u>Thomasomys ladewi</u>       | 134 (92.4%)         | 2 (1.7%)          | 9 (5.9%)            | 136 (94.1%)         |
| <u>Thomasomys laniger</u>      | 112 (77.4%)         | 4 (2.6%)          | 29 (20%)            | 116 (80%)           |
| <u>Thomasomys macrotis</u>     | 114 (78.7%)         | 2 (1.7%)          | 28 (19.6%)          | 117 (80.4%)         |
| <u>Thomasomys monochromos</u>  | 101 (69.7%)         | 4 (2.6%)          | 40 (27.7%)          | 105 (72.3%)         |
| <u>Thomasomys nicefori</u>     | 113 (77.8%)         | 1 (0.9%)          | 31 (21.3%)          | 114 (78.7%)         |
| <u>Thomasomys niveipes</u>     | 125 (86%)           | 2 (1.7%)          | 18 (12.3%)          | 127 (87.7%)         |
| <u>Thomasomys notatus</u>      | 131 (90.6%)         | 1 (0.9%)          | 12 (8.5%)           | 133 (91.5%)         |
| <u>Thomasomys onkiro</u>       | 102 (70.2%)         | 1 (0.9%)          | 42 (28.9%)          | 103 (71.1%)         |
| <u>Thomasomys oreas</u>        | 127 (87.6%)         | 1 (0.9%)          | 17 (11.5%)          | 128 (88.5%)         |
| <u>Thomasomys paramorum</u>    | 122 (83.9%)         | 3 (2.1%)          | 20 (14%)            | 125 (86%)           |
| <u>Thomasomys popayanus</u>    | 86 (59.1%)          | 1 (0.9%)          | 58 (40%)            | 87 (60%)            |
| <u>Thomasomys praetor</u>      | 120 (82.5%)         | 1 (0.9%)          | 24 (16.6%)          | 121 (83.4%)         |
| <u>Thomasomys princeps</u>     | 97 (66.8%)          | 1 (0.9%)          | 47 (32.3%)          | 98 (67.7%)          |
| <u>Thomasomys pyrrhonotus</u>  | 112 (77%)           | 1 (0.9%)          | 32 (22.1%)          | 113 (77.9%)         |
| <u>Thomasomys rhoadsi</u>      | 121 (83.4%)         | 3 (2.1%)          | 21 (14.5%)          | 124 (85.5%)         |
| <u>Thomasomys rosalia</u>      | 77 (53.2%)          | 1 (0.9%)          | 67 (45.9%)          | 78 (54.1%)          |
| <u>Thomasomys silvestris</u>   | 120 (83%)           | 3 (2.1%)          | 22 (14.9%)          | 123 (85.1%)         |
| <u>Thomasomys taczanowskii</u> | 126 (86.8%)         | 1 (0.9%)          | 18 (12.3%)          | 127 (87.7%)         |
| <u>Thomasomys vestitus</u>     | 99 (68.5%)          | 2 (1.7%)          | 43 (29.8%)          | 102 (70.2%)         |
| <u>Thomasomys sp. 1</u>        | 122 (84.2%)         | 2 (1.3%)          | 21 (14.5%)          | 124 (85.5%)         |
| <u>Thomasomys sp. 2</u>        | 108 (74.4%)         | 1 (0.9%)          | 36 (24.7%)          | 109 (75.3%)         |
| <u>Thomasomys sp. 3</u>        | 117 (80.8%)         | 1 (0.9%)          | 27 (18.3%)          | 118 (81.7%)         |
| <u>Thomasomys sp. 4</u>        | 117 (80.5%)         | 1 (0.4%)          | 28 (19.1%)          | 117 (80.9%)         |
| <u>Thomasomys sp. 5</u>        | 115 (79.2%)         | 1 (0.4%)          | 30 (20.4%)          | 115 (79.6%)         |
| <u>Thomasomys sp. 6</u>        | 107 (74%)           | 1 (0.9%)          | 36 (25.1%)          | 109 (74.9%)         |
| <u>Thomasomys sp. 7</u>        | 115 (79.2%)         | 1 (0.4%)          | 30 (20.4%)          | 115 (79.6%)         |
| <u>Thomasomys sp. 8</u>        | 103 (71%)           | 2 (1.3%)          | 40 (27.7%)          | 105 (72.3%)         |
| <u>Thomasomys sp. 9</u>        | 124 (85.5%)         | 1 (0.9%)          | 20 (13.6%)          | 125 (86.4%)         |
| <u>Thomasomys sp. 10</u>       | 101 (69.7%)         | 4 (2.6%)          | 40 (27.7%)          | 105 (72.3%)         |
| <u>Thomasomys sp. 11</u>       | 91 (63%)            | 2 (1.7%)          | 51 (35.3%)          | 94 (64.7%)          |
| <b>Total</b>                   | <b>8970 (77.3%)</b> | <b>163 (1.4%)</b> | <b>2467 (21.3%)</b> | <b>9133 (78.7%)</b> |

TABLE 2.- Statistics on character diagnostics for Andean thomatomyine data set.

|    |                                                                    | Min<br>steps | Tree<br>steps | Max<br>steps | CI    | RI    | RC    |
|----|--------------------------------------------------------------------|--------------|---------------|--------------|-------|-------|-------|
| 1  | Ungual tufts on manual claws                                       | 2            | 10            | 19           | 0.200 | 0.529 | 0.106 |
| 2  | Ventral base of claws on manus                                     | 3            | 16            | 27           | 0.188 | 0.458 | 0.086 |
| 3  | Manual digit proportions                                           | 2            | 7             | 13           | 0.286 | 0.545 | 0.156 |
| 4  | Ungual tuft on pes                                                 | 2            | 10            | 14           | 0.200 | 0.333 | 0.067 |
| 5  | Dark metatarsal patches                                            | 1            | 6             | 17           | 0.167 | 0.688 | 0.115 |
| 6  | Plantar squamation of pes                                          | 2            | 4             | 12           | 0.500 | 0.800 | 0.400 |
| 7  | Hypothenar pad of pes                                              | 1            | 1             | 2            | 1.000 | 1.000 | 1.000 |
| 8  | Position of hypothenar pad in relation to thenar (pes)             | 18           | 43            | 82           | 0.419 | 0.609 | 0.255 |
| 9  | Position of hypothenar pad in relation to interdigital pad 4 (pes) | 1            | 1             | 7            | 1.000 | 1.000 | 1.000 |
| 10 | Position of hypothenar pad in relation to interdigital pad 1 (pes) | 4            | 9             | 15           | 0.444 | 0.545 | 0.242 |
| 11 | Interdigital webbing on hindfoot                                   | 1            | 1             | 2            | 1.000 | 1.000 | 1.000 |
| 12 | Nail on hallux                                                     | 1            | 1             | 2            | 1.000 | 1.000 | 1.000 |
| 13 | Relative size of hallux (dI of pes)                                | 2            | 14            | 44           | 0.143 | 0.714 | 0.102 |
| 14 | Relative size of fifth digit (dV) of pes                           | 5            | 19            | 44           | 0.263 | 0.641 | 0.169 |
| 15 | Genal 1 vibrissae                                                  | 7            | 12            | 79           | 0.583 | 0.931 | 0.543 |
| 16 | Genal 2 vibrissae                                                  | 1            | 3             | 3            | 0.333 | 0.000 | 0.000 |
| 17 | Length of mystacial vibrissae                                      | 2            | 13            | 25           | 0.154 | 0.522 | 0.080 |
| 18 | Antitragus and pinnae structure                                    | 2            | 10            | 36           | 0.200 | 0.765 | 0.153 |
| 19 | Rostral fur coloration                                             | 1            | 2             | 4            | 0.500 | 0.667 | 0.333 |
| 20 | Body pelage pattern                                                | 3            | 27            | 52           | 0.111 | 0.510 | 0.057 |
| 21 | Pelage texture                                                     | 1            | 2             | 2            | 0.500 | 0.000 | 0.000 |
| 22 | Pectoral markings                                                  | 1            | 4             | 6            | 0.250 | 0.400 | 0.100 |
| 23 | Pectoral mammary pair                                              | 1            | 3             | 11           | 0.333 | 0.800 | 0.267 |
| 24 | Protuberant anus                                                   | 2            | 2             | 23           | 1.000 | 1.000 | 1.000 |
| 25 | Countershading of tail                                             | 1            | 10            | 10           | 0.100 | 0.000 | 0.000 |
| 26 | Uniform pattern coloration of tail                                 | 9            | 35            | 40           | 0.257 | 0.161 | 0.041 |
| 27 | Tail pencil                                                        | 2            | 5             | 9            | 0.400 | 0.571 | 0.229 |
| 28 | Rostral tube                                                       | 2            | 11            | 34           | 0.182 | 0.719 | 0.131 |
| 29 | Posterior extension of nasals                                      | 12           | 49            | 72           | 0.245 | 0.383 | 0.094 |
| 30 | Posterodorsal extension of premaxillae                             | 9            | 30            | 59           | 0.300 | 0.580 | 0.174 |
| 31 | Anterodorsal margin of zygomatic plate                             | 1            | 8             | 13           | 0.125 | 0.417 | 0.052 |
| 32 | Zygomatic plate breadth                                            | 4            | 16            | 20           | 0.250 | 0.250 | 0.062 |
| 33 | Zygomatic plate slope                                              | 9            | 26            | 49           | 0.346 | 0.575 | 0.199 |
| 34 | Masseteric tubercle                                                | 1            | 2             | 3            | 0.500 | 0.500 | 0.250 |
| 35 | Premaxilla-maxilla suture                                          | 1            | 4             | 10           | 0.250 | 0.667 | 0.167 |
| 36 | Infraorbital foramen                                               | 1            | 2             | 5            | 0.500 | 0.750 | 0.375 |
| 37 | Notch between the maxillary bone of zygomatic arch and lacrimal    | 1            | 8             | 13           | 0.125 | 0.417 | 0.052 |
| 38 | Lacrimal posterior projection                                      | 1            | 5             | 6            | 0.200 | 0.200 | 0.040 |
| 39 | Position of antorbital bridge                                      | 2            | 10            | 23           | 0.200 | 0.619 | 0.124 |
| 40 | Divergency of squamosal roots of                                   | 1            | 3             | 23           | 0.333 | 0.909 | 0.303 |

|    |                                                              |    |    |    |       |       |       |
|----|--------------------------------------------------------------|----|----|----|-------|-------|-------|
|    | zygomatic arch                                               |    |    |    |       |       |       |
| 41 | Shape of zygomatic arches                                    | 1  | 6  | 21 | 0.167 | 0.750 | 0.125 |
| 42 | Zygomatic arch dip                                           | 2  | 10 | 14 | 0.200 | 0.333 | 0.067 |
| 43 | Interorbital region                                          | 3  | 32 | 72 | 0.094 | 0.580 | 0.054 |
| 44 | Interorbital region breadth                                  | 3  | 20 | 41 | 0.150 | 0.553 | 0.083 |
| 45 | Interfrontal fontanella                                      | 2  | 9  | 13 | 0.222 | 0.364 | 0.081 |
| 46 | Postorbital ridge                                            | 1  | 6  | 13 | 0.167 | 0.583 | 0.097 |
| 47 | Jugal length                                                 | 2  | 12 | 24 | 0.167 | 0.545 | 0.091 |
| 48 | Ethmoid foramen                                              | 1  | 1  | 2  | 1.000 | 1.000 | 1.000 |
| 49 | Ethmoturbinals and sphenopalatine foramen formation          | 7  | 25 | 63 | 0.280 | 0.679 | 0.190 |
| 50 | Optic foramen                                                | 1  | 6  | 19 | 0.167 | 0.722 | 0.120 |
| 51 | Alisphenoid strut                                            | 4  | 19 | 38 | 0.211 | 0.559 | 0.118 |
| 52 | Carotid circulation                                          | 2  | 21 | 73 | 0.095 | 0.732 | 0.070 |
| 53 | Exposure of internal carotid artery                          | 2  | 3  | 3  | 0.667 | 0.000 | 0.000 |
| 54 | Tegmen tympani                                               | 1  | 1  | 6  | 1.000 | 1.000 | 1.000 |
| 55 | Sinus groove on tegmen tympani                               | 1  | 3  | 6  | 0.333 | 0.600 | 0.200 |
| 56 | Hamular process and development of the postglenoid foramen   | 7  | 22 | 55 | 0.318 | 0.688 | 0.219 |
| 57 | Height of subsquamosal fenestra                              | 1  | 3  | 9  | 0.333 | 0.750 | 0.250 |
| 58 | Parietal supraoccipital suture breadth                       | 5  | 27 | 33 | 0.185 | 0.214 | 0.040 |
| 59 | Lambdoid ridge development                                   | 3  | 7  | 13 | 0.429 | 0.600 | 0.257 |
| 60 | Dorsal aperture of ectotympanic ring                         | 6  | 16 | 44 | 0.375 | 0.737 | 0.276 |
| 61 | Ectotympanic dorsal expansion                                | 1  | 1  | 2  | 1.000 | 1.000 | 1.000 |
| 62 | Incisive foramina                                            | 9  | 28 | 40 | 0.321 | 0.387 | 0.124 |
| 63 | Maxillary septum length                                      | 2  | 16 | 23 | 0.125 | 0.333 | 0.042 |
| 64 | Palatal length                                               | 4  | 14 | 32 | 0.286 | 0.643 | 0.184 |
| 65 | Palatal breadth                                              | 1  | 5  | 12 | 0.200 | 0.636 | 0.127 |
| 66 | Medial process of posterior margin of palate bridge          | 11 | 32 | 32 | 0.344 | 0.000 | 0.000 |
| 67 | Posterolateral palatal pits                                  | 3  | 10 | 24 | 0.300 | 0.667 | 0.200 |
| 68 | Maxillary palatal pits                                       | 2  | 14 | 39 | 0.143 | 0.676 | 0.097 |
| 69 | Depth and shape of the molar-bearing portion of the maxillae | 2  | 14 | 33 | 0.143 | 0.613 | 0.088 |
| 70 | Maxillary at posterior base of M3                            | 1  | 4  | 6  | 0.250 | 0.400 | 0.100 |
| 71 | Sphenopalatine vacuities                                     | 4  | 15 | 26 | 0.267 | 0.500 | 0.133 |
| 72 | Shape of parapterygoid fossa                                 | 2  | 6  | 12 | 0.333 | 0.600 | 0.200 |
| 73 | Parapterygoid vacuity                                        | 8  | 17 | 22 | 0.471 | 0.357 | 0.168 |
| 74 | Mesopterygoid fossa breadth                                  | 4  | 12 | 19 | 0.333 | 0.467 | 0.156 |
| 75 | Mesopterygoid fossa shape                                    | 4  | 17 | 29 | 0.235 | 0.480 | 0.113 |
| 76 | Alisphenoid squamosal posterior margin                       | 1  | 6  | 11 | 0.167 | 0.500 | 0.083 |
| 77 | Bullae inflation                                             | 2  | 25 | 50 | 0.080 | 0.521 | 0.042 |
| 78 | Anterior process of the ectotympanic                         | 2  | 13 | 25 | 0.154 | 0.522 | 0.080 |
| 79 | Malleus lamina                                               | 2  | 7  | 20 | 0.286 | 0.722 | 0.206 |
| 80 | Ventral margin of malleus lamina                             | 1  | 1  | 2  | 1.000 | 1.000 | 1.000 |
| 81 | Processus brevis of incus                                    | 2  | 3  | 8  | 0.667 | 0.833 | 0.556 |
| 82 | Upper incisor orientation                                    | 9  | 33 | 89 | 0.273 | 0.700 | 0.191 |



|     |                                                      |    |    |    |       |       |       |
|-----|------------------------------------------------------|----|----|----|-------|-------|-------|
| 83  | Upper incisor wear pattern                           | 1  | 1  | 25 | 1.000 | 1.000 | 1.000 |
| 84  | M1 position                                          | 7  | 27 | 70 | 0.259 | 0.683 | 0.177 |
| 85  | Molar height topography                              | 1  | 13 | 17 | 0.077 | 0.250 | 0.019 |
| 86  | Molar occlusal design                                | 2  | 14 | 18 | 0.143 | 0.250 | 0.036 |
| 87  | Anteromedian flexus                                  | 2  | 7  | 9  | 0.286 | 0.286 | 0.082 |
| 88  | Anterocone                                           | 1  | 5  | 13 | 0.200 | 0.667 | 0.133 |
| 89  | Procingulum anterior edge of M1                      | 1  | 5  | 5  | 0.200 | 0.000 | 0.000 |
| 90  | Anteroflexus M1                                      | 1  | 9  | 14 | 0.111 | 0.385 | 0.043 |
| 91  | Anteroloph                                           | 1  | 10 | 13 | 0.100 | 0.250 | 0.025 |
| 92  | Anteroloph orientation                               | 1  | 2  | 12 | 0.500 | 0.909 | 0.455 |
| 93  | Paraloph orientation in M1                           | 15 | 27 | 45 | 0.556 | 0.600 | 0.333 |
| 94  | Hypoflexus size of M1                                | 1  | 10 | 25 | 0.100 | 0.625 | 0.062 |
| 95  | Hypoflexus width of M2                               | 1  | 2  | 3  | 0.500 | 0.500 | 0.250 |
| 96  | Protostyle and enterostyle on M1                     | 8  | 21 | 53 | 0.381 | 0.711 | 0.271 |
| 97  | Protoflexus on M2                                    | 5  | 17 | 38 | 0.294 | 0.636 | 0.187 |
| 98  | Hypoflexus of M3                                     | 1  | 18 | 28 | 0.056 | 0.370 | 0.021 |
| 99  | Anteromedian flexid of m1                            | 3  | 19 | 39 | 0.158 | 0.556 | 0.088 |
| 100 | Internal enameled pit of m1<br>procingulum           | 1  | 1  | 3  | 1.000 | 1.000 | 1.000 |
| 101 | Ectolophid m1                                        | 3  | 13 | 18 | 0.231 | 0.333 | 0.077 |
| 102 | Ridge on anterolabial cingulum of<br>m1              | 2  | 7  | 9  | 0.286 | 0.286 | 0.082 |
| 103 | Orientation of metalophid m1                         | 5  | 26 | 53 | 0.192 | 0.562 | 0.108 |
| 104 | Entolophids of m1-m2                                 | 2  | 12 | 19 | 0.167 | 0.412 | 0.069 |
| 105 | Mesolophids of m1-m2                                 | 1  | 4  | 4  | 0.250 | 0.000 | 0.000 |
| 106 | Mesolophid on m3                                     | 3  | 7  | 22 | 0.429 | 0.789 | 0.338 |
| 107 | Anterolabial cingulum of m2 m3                       | 2  | 28 | 49 | 0.071 | 0.447 | 0.032 |
| 108 | Posteroflexid breadth of m1-m2                       | 1  | 5  | 16 | 0.200 | 0.733 | 0.147 |
| 109 | Entoconid on m3                                      | 1  | 2  | 2  | 0.500 | 0.000 | 0.000 |
| 110 | Molar flexus (-ids) crenulation                      | 2  | 5  | 10 | 0.400 | 0.625 | 0.250 |
| 111 | Accessory labial root of M1                          | 1  | 9  | 28 | 0.111 | 0.704 | 0.078 |
| 112 | Lingual roots on M1                                  | 5  | 20 | 25 | 0.250 | 0.250 | 0.062 |
| 113 | Lingual root on M3                                   | 2  | 5  | 8  | 0.400 | 0.500 | 0.200 |
| 114 | Roots on m2                                          | 1  | 6  | 12 | 0.167 | 0.545 | 0.091 |
| 115 | Masseteric crest position                            | 5  | 15 | 35 | 0.333 | 0.667 | 0.222 |
| 116 | Mental foramen position                              | 1  | 2  | 3  | 0.500 | 0.500 | 0.250 |
| 117 | Mandibular diastemal shape                           | 2  | 4  | 17 | 0.500 | 0.867 | 0.433 |
| 118 | Capsular process of lower incisor                    | 3  | 12 | 25 | 0.250 | 0.591 | 0.148 |
| 119 | Relative length of condylar and<br>angular processes | 1  | 10 | 30 | 0.100 | 0.690 | 0.069 |
| 120 | Coronoid process                                     | 1  | 8  | 16 | 0.125 | 0.533 | 0.067 |
| 121 | Retromolar region                                    | 1  | 2  | 3  | 0.500 | 0.500 | 0.250 |
| 122 | Ventral margin of mandible                           | 1  | 1  | 2  | 1.000 | 1.000 | 1.000 |
| 123 | Supratrochlear fenestra of humerus                   | 4  | 15 | 37 | 0.267 | 0.667 | 0.178 |
| 124 | Number of thoracic vertebra                          | 2  | 4  | 10 | 0.500 | 0.750 | 0.375 |
| 125 | Number of caudal vertebrae                           | 5  | 10 | 19 | 0.500 | 0.643 | 0.321 |
| 126 | Chevron bones                                        | 7  | 27 | 45 | 0.259 | 0.474 | 0.123 |
| 127 | Position of the trochlear process of<br>calcaneum    | 1  | 5  | 10 | 0.200 | 0.556 | 0.111 |
| 128 | Peroneal process of fifth metatarsal                 | 2  | 3  | 10 | 0.667 | 0.875 | 0.583 |
| 129 | Transversal palatal ridges                           | 1  | 2  | 3  | 0.500 | 0.500 | 0.250 |

|     |                                            |   |    |    |       |       |       |
|-----|--------------------------------------------|---|----|----|-------|-------|-------|
| 130 | Distributional gastric epithelium          | 4 | 7  | 16 | 0.571 | 0.750 | 0.429 |
| 131 | Incisura angularis                         | 1 | 2  | 6  | 0.500 | 0.800 | 0.400 |
| 132 | Gall bladder                               | 1 | 5  | 13 | 0.200 | 0.667 | 0.133 |
| 133 | Distribution of spines on glans penis body | 2 | 6  | 6  | 0.333 | 0.000 | 0.000 |
| 134 | Grooves on glans penis body                | 2 | 13 | 20 | 0.154 | 0.389 | 0.060 |
| 135 | Crater rim                                 | 1 | 9  | 11 | 0.111 | 0.200 | 0.022 |
| 136 | Dorsal and Ventral margin of crater rim    | 1 | 5  | 7  | 0.200 | 0.333 | 0.067 |
| 137 | Notch on midventral margin                 | 1 | 6  | 8  | 0.167 | 0.286 | 0.048 |
| 138 | Medial bacular mound length                | 1 | 2  | 3  | 0.500 | 0.500 | 0.250 |
| 139 | Lateral bacular mound shape                | 2 | 4  | 8  | 0.500 | 0.667 | 0.333 |
| 140 | Lateral mound relative position            | 2 | 6  | 11 | 0.333 | 0.556 | 0.185 |
| 141 | Spines on the lateral mounds               | 1 | 7  | 11 | 0.143 | 0.400 | 0.057 |
| 142 | Spines on the urethral flap of glans penis | 6 | 25 | 37 | 0.240 | 0.387 | 0.093 |
| 143 | Spines on dorsal papilla                   | 2 | 10 | 10 | 0.200 | 0.000 | 0.000 |
| 144 | Preputial glands                           | 3 | 15 | 28 | 0.200 | 0.520 | 0.104 |
| 145 | Prostate ventral glands                    | 2 | 8  | 11 | 0.250 | 0.333 | 0.083 |

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## ILLUSTRATIONS

### **Part I**

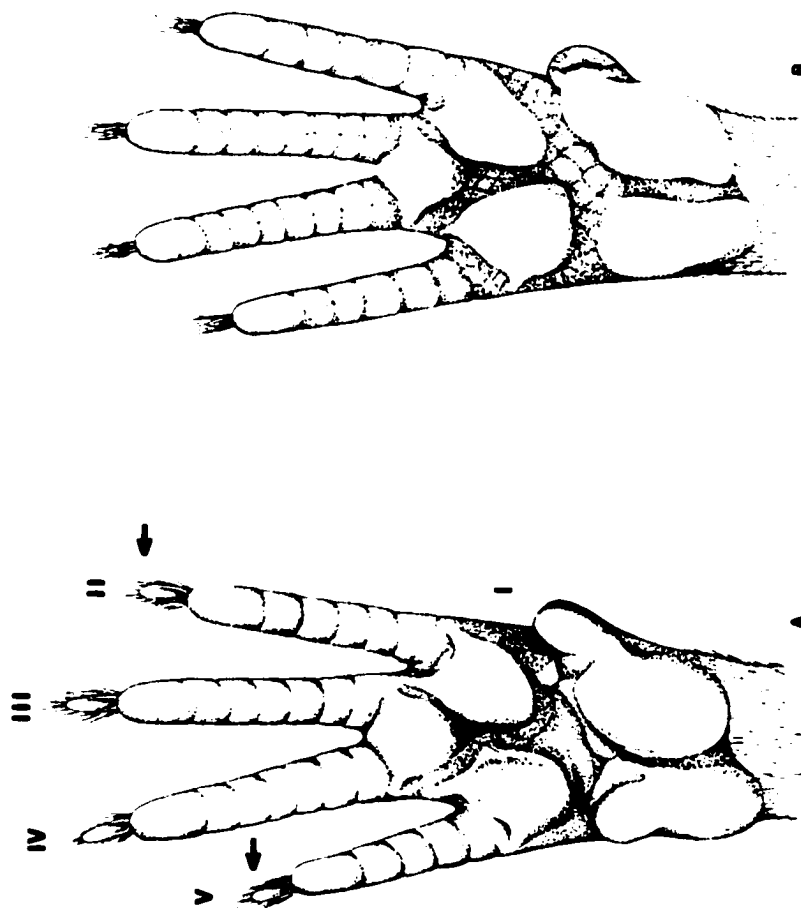


Fig. 1. Plantar view of right manus of alcoholic specimens of Thomasomys aureus (A, UMMZ 156170) and Thomasomys notatus (B, UMMZ 158029). Note the position of d II in relation to d V.

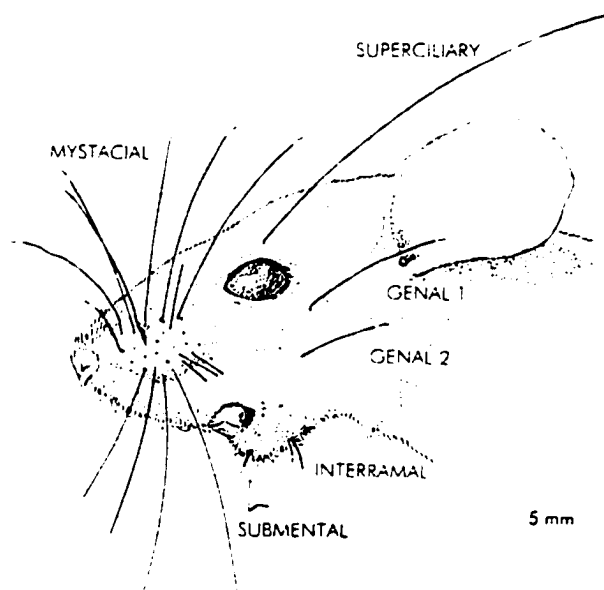


Fig. 2. Facial vibrissae of Nyctomys sumichrasti (AMNH 190330).

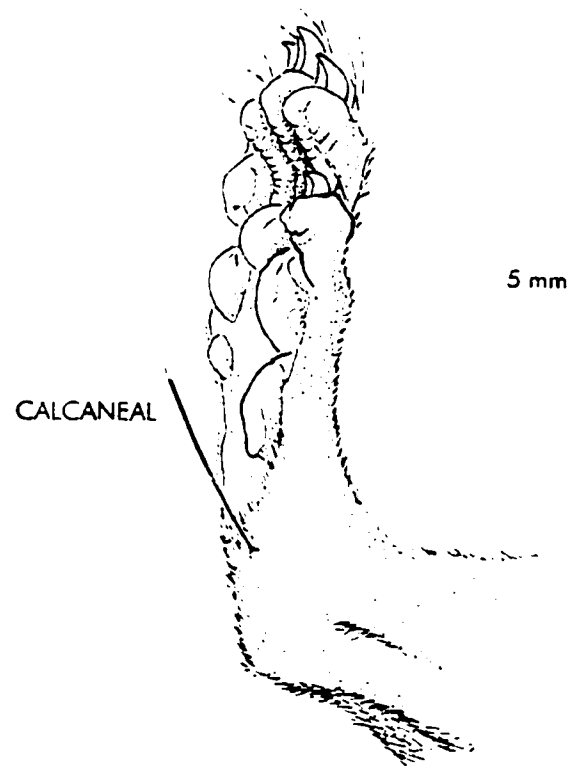


Fig. 3. Calcaneal vibrissae of *Nyctomys sumichrasti* (AMNH 190330).

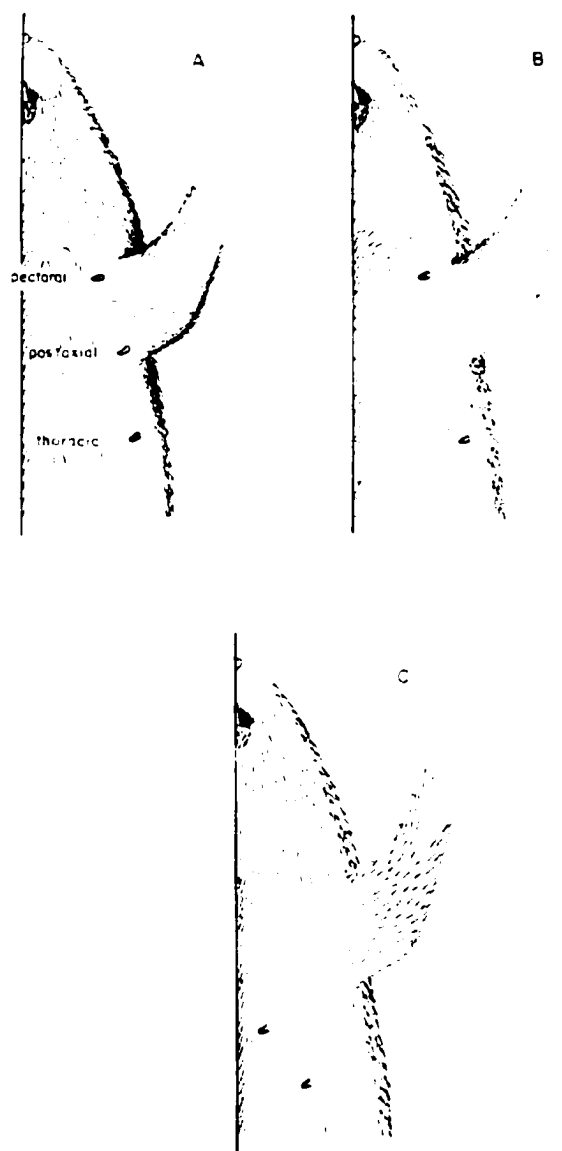


Fig. 4. Anatomical loci of mammary pairs. A. Holochilus brasiliensis (AMNH 206386); B. Holochilus sciureus (AMNH 210260); C. Microtus pennsylvanicus (AMNH 265062).

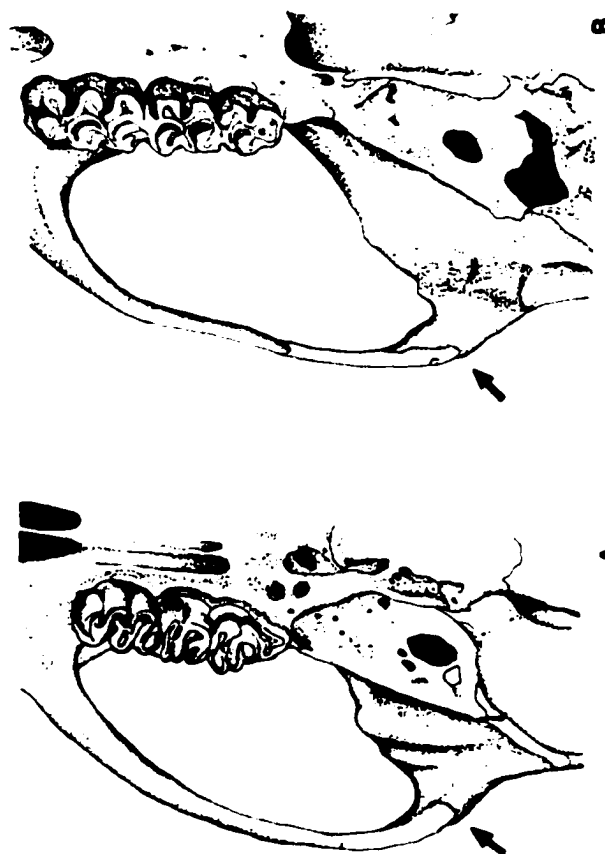


Fig. 5. Position of the posterior ending of the jugal bone and glenoid fossa. A, Sigmodon hispidus (MUSM 2508); B, Thomasomys aureus (MUSM 9353).



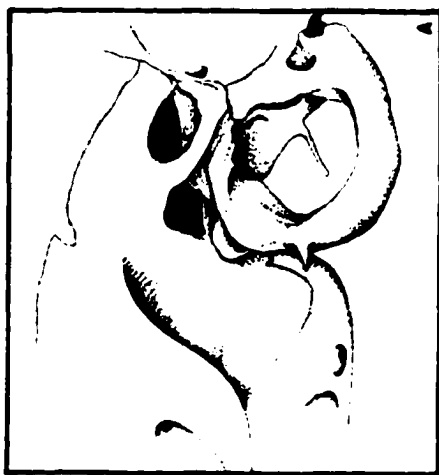
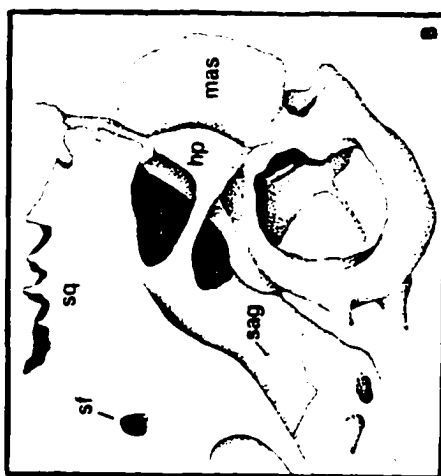


Fig. 6. Lateral view of the skulls of Microxus mimus (A. AMNH 268832) and Ochrotomys nuttalli (B. AMNH 131443). **hp**, hamular process of squamosal; **mas**, mastoid; **sag**, squamosal-alisphenoid groove; **sf**, suprasquamosal foramen; **sq**, squamosal. See character 35.

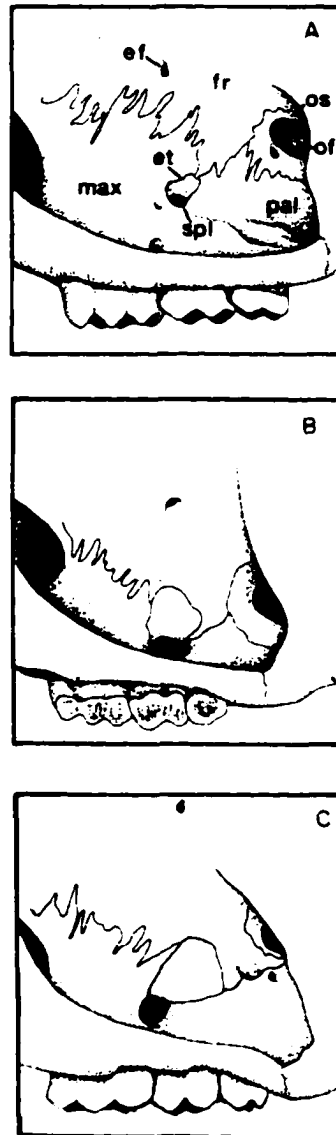


Fig. 7. Lateral view of the left orbital region of A, *Rhipidomys austrinus* (AMNH 264199); B, *Thomasomys notatus* (UMMZ 155912); C, *Chilomys instans* (FMNH 71628). ef, ethmoid foramen; et, ethmoturbinal; f, frontal; max, maxillary; of, optic foramen; os, orbitosphenoid; pal, palatine; spl, sphenopalatine foramen. Note the development of the ethmoturbinal. See character 44.

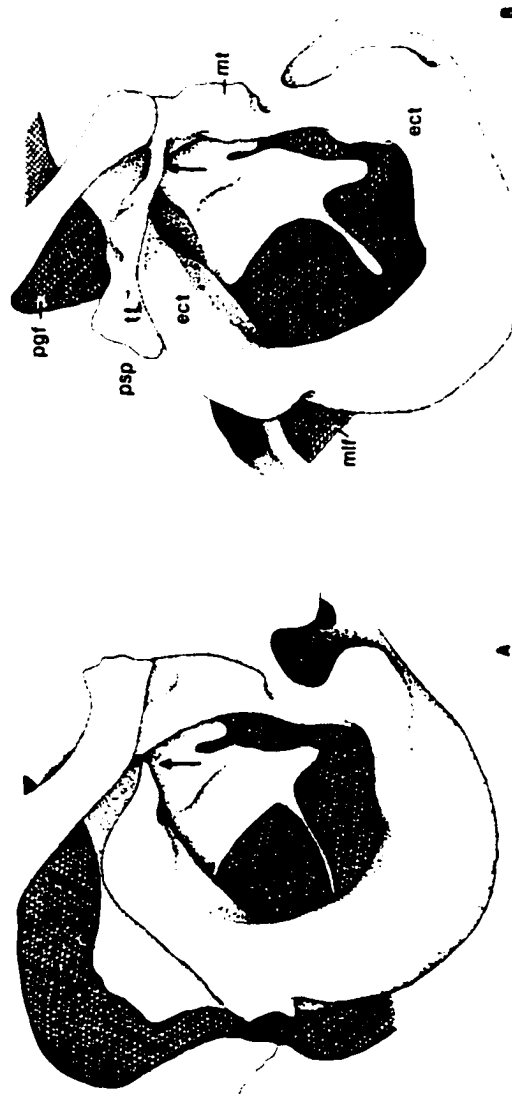


Fig. 8. Lateral view of left auditory bullae of *Oryzomys palustris* (A. AMNH 256707) and *Thomasomys cinereus* (B. MUSM 511). **ect**, ectotympanic; **mlf**, middle lacerate foramen; **mt**, mastoid tubercle; **pgf**, postglenoid foramen; **psp**, posterior suspensory process of squamosal; **tt**, tegmen tympani. The arrows show the ectotympanic closed in *O. palustris*, and open in *T. cinereus*. See character 46.

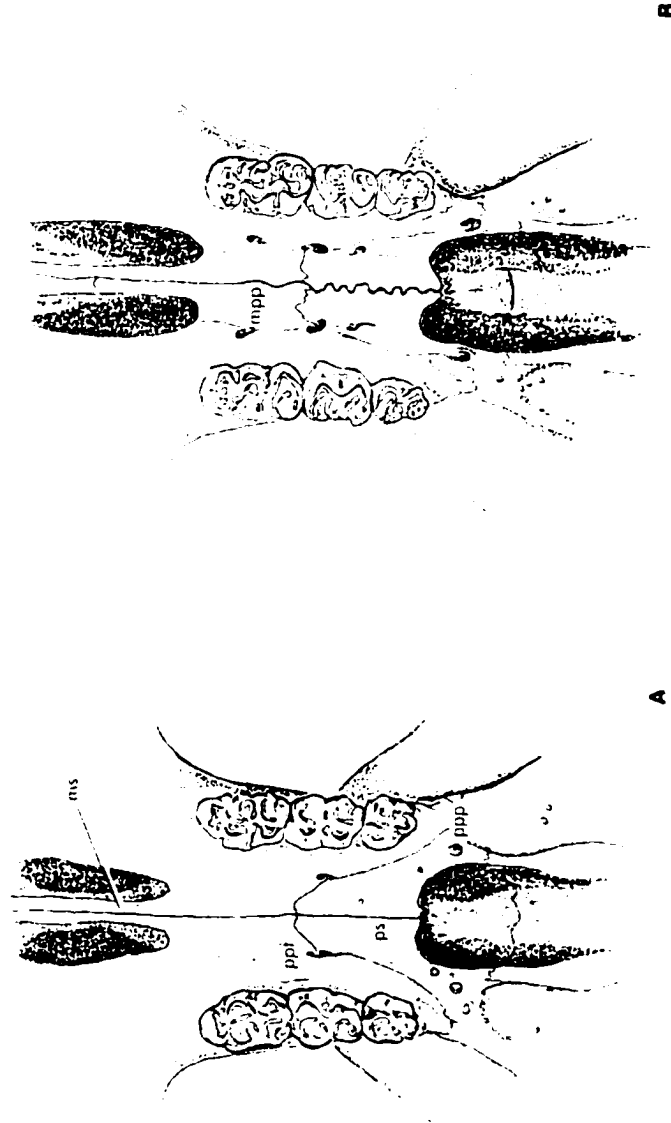


Fig. 9. Ventral view of the palatal region of *Ochrotomys nuttalli* (A, AMNH 131447) and *Rhipidomys leucodactylus* (B, AMNH 71907). **mpp**, maxillary palatal pits; **ms**, maxillary septum of the incisive foramina; **ppf**, posterior palatine foramen; **ppp**, posterolateral palatal pit; **ps**, palatine suture. See character 53.

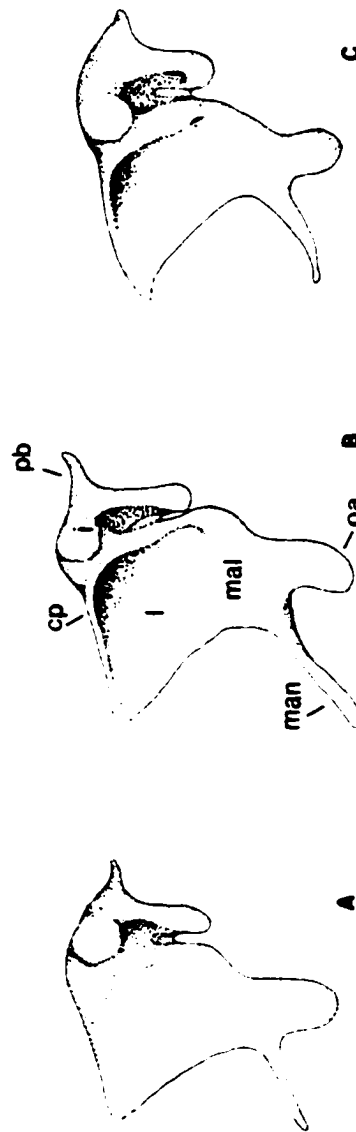


Fig. 10. Lateral view of left auditory ossicles of Microxus mimus (A, AMNH 268832), Thomasomys cinereus (B, MUSM 511), and Oryzomys palustris (C, AMNH 256707). **cp**, cephalic process of malleus; **i**, incus; **l**, lamina of malleus; **mal**, malleus; **man**, manubrium; **oa**, orbicular apophysis; **pb**, processus brevis of incus. See characters 65.



Fig. 11. Lateral view of muroid left mandibles. **A**, *Mesocricetus auratus* (AMNH 144771); **B**, *Thomasomys cinereus* (MUSM 511); **C**, *Oryzomys palustris* (AMNH 256407); **D**, *Microxus mimus* (AMNH 268832); **E**, *Ochrotomys nuttalli* (AMNH 234944); **F**, *Sapteromys tumidus* (AMNH 235431). **ap**, angular process; **con**, condylar process; **cor**, coronoid process; **mc**, masseteric crest; **mf**, mental foramen. See characters 88, 89, and 90.



Fig. 12. Lateral view of left calcaneum of *Nyctomys sumichrasti* (A. AMNH 256834) and *Akodon boliviensis* (B. AMNH 262689). **a**, astragulum; **paf**, posterior articular facet; **tp**, trochlear process of calcaneum (see character 100 for explanation).

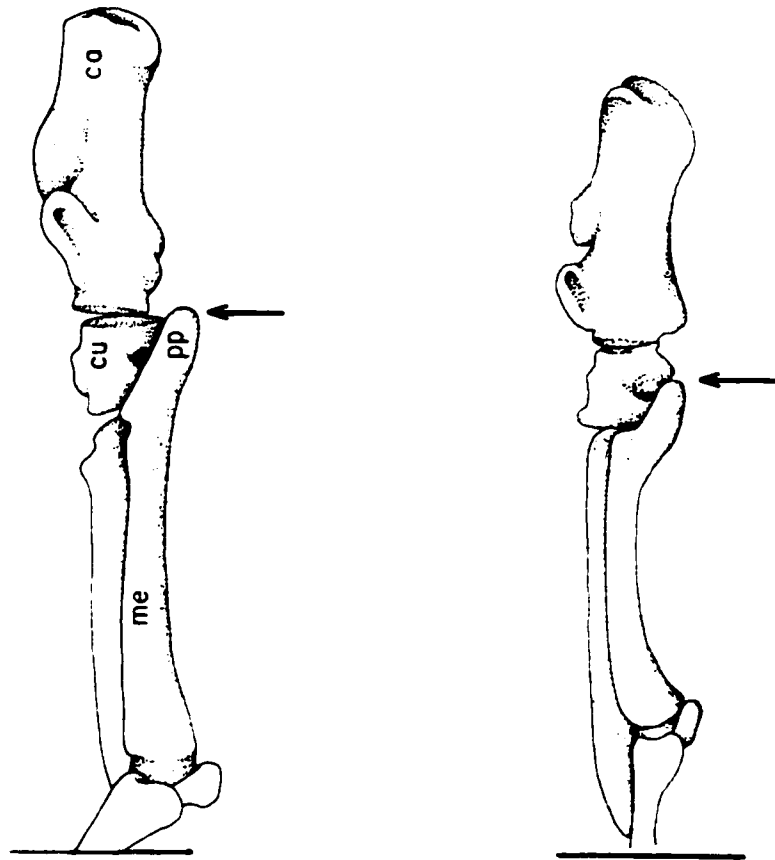


Fig. 13. Lateral view of left foot of *Nyctomys sumichrasti* (top, AMNH 256834) and *Sigmodon peruanus* (bottom, AMNH 63029). **ca.** calcaneum; **cu.** cuboid; **me.** metatarsal; **pp.** peroneal process. Arrows show the extension of the peroneal process of the fifth metatarsal (see character 101 for explanation).



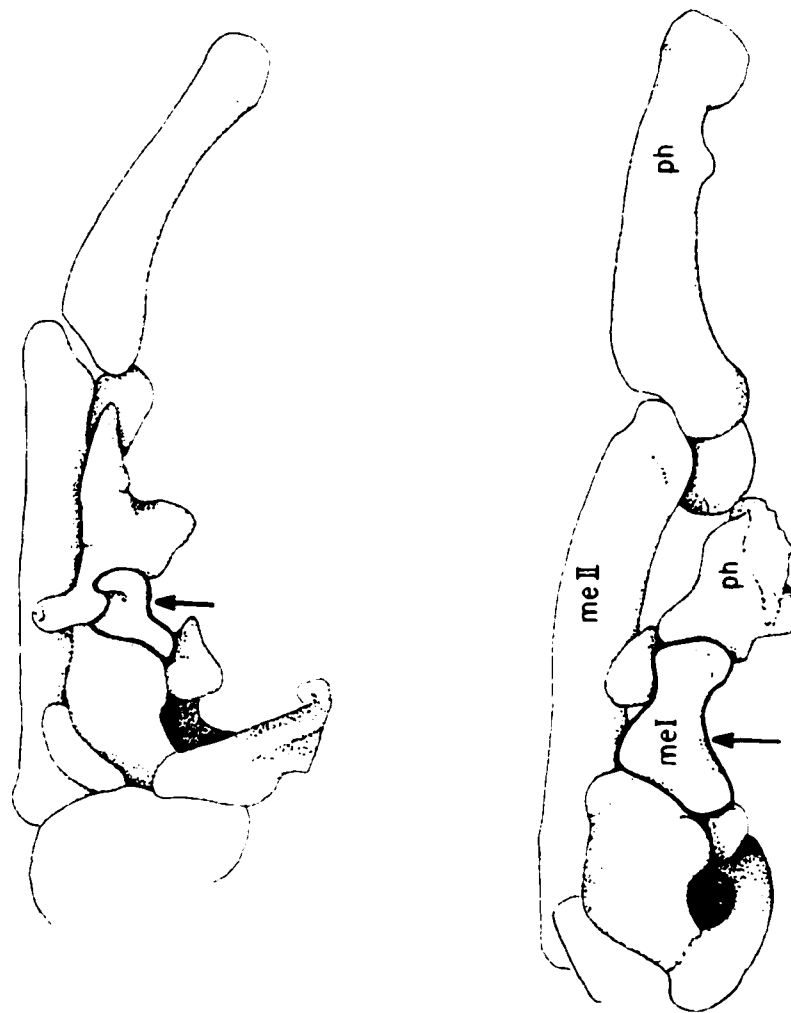


Fig. 14. Medial view of the first digit (pollex) of the left manus of *Akodon boliviensis* (top, AMNH 262689) and *Peromyscus mexicanus* (bottom, AMNH 268733). **me**, metacarpal; **ph**, phalanx. Arrows indicate the metacarpal of the first phalanx (see character 101 for explanation).

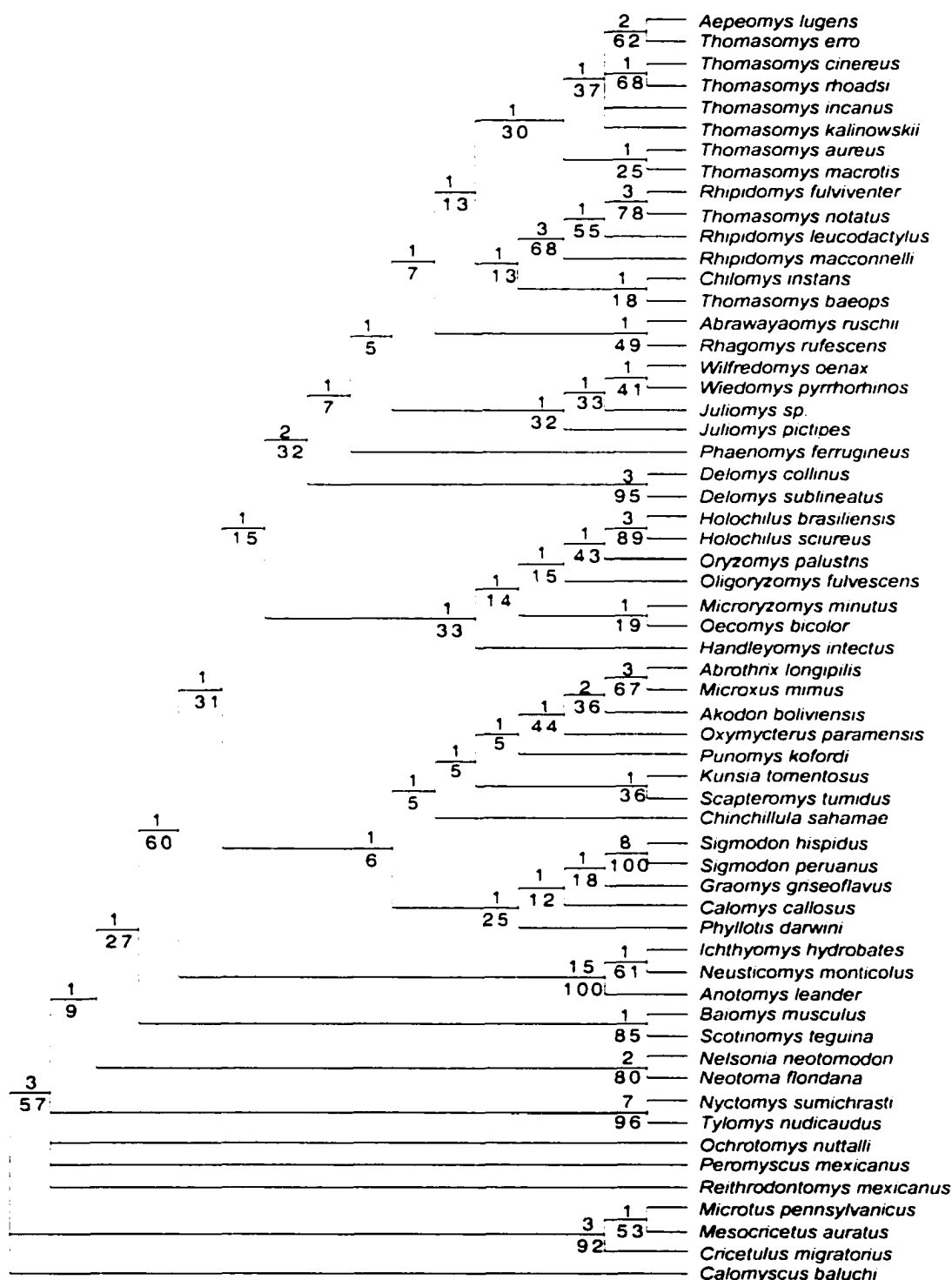


Fig. 15. A strict consensus of 21 equally most-parsimonious trees produced by Analysis 1, using unordered characters and characters equally weighted, each one with 759 steps (CI = 0.285, RI = 0.594). Majority rule bootstrap values are below internal branches. Decay values are above.

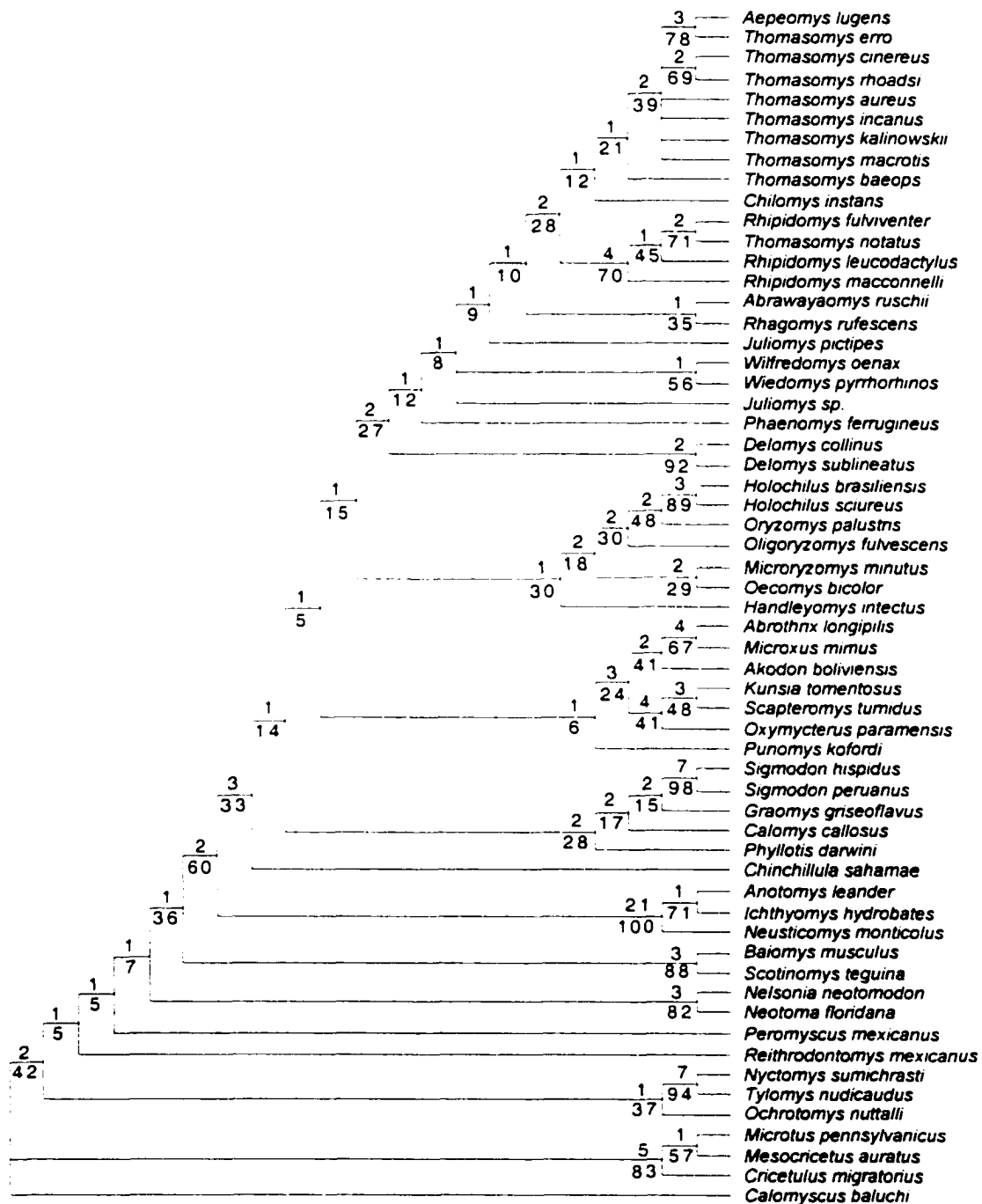


Fig. 16. A strict consensus of 16 equally most parsimonious trees produced in the second analysis of ordered and unweighted characters, each tree with 837 steps (CI = 0.264, RI = 0.609). Majority rule bootstrap values are below internal branches. Decay values are above.

## **Part II**

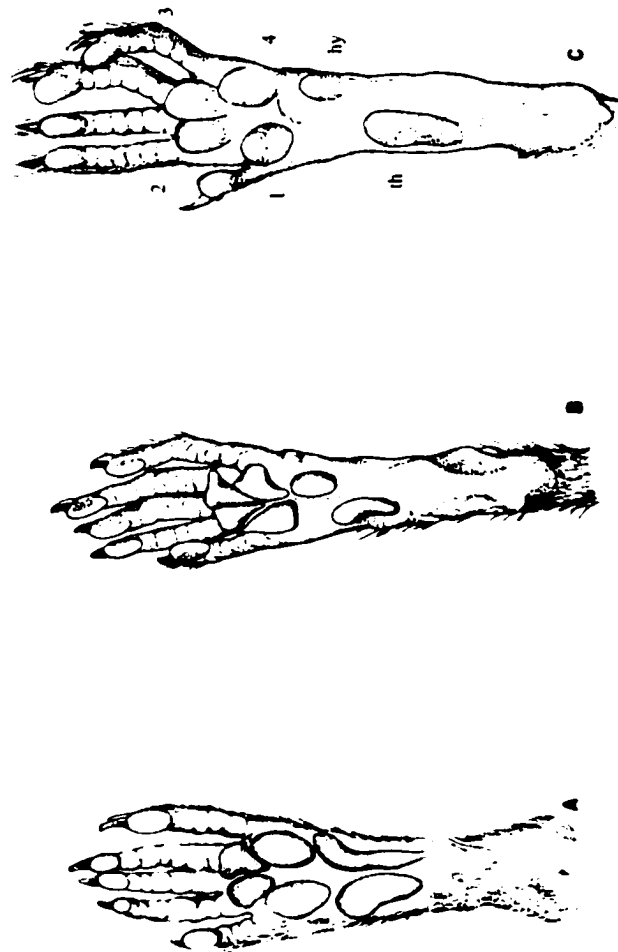


Figure 1. Plantar view of left hind feet of selected thomomyines. A. Rhipidomys leucodactylus (MUSM 12152); B. Thomasomys notatus (MUSM 14995); C. Thomasomys kalinowskii (MCZ 38530). hy, hypothenar pad; th, thenar pad; 1-- 4, first through fourth interdigital pads.



Figure 2. Protuberance of anus in thomomyine species. A, Thomasomys cinereus, VPT 2279, MUSM uncatologued; B, Oecomys bicolor, MUSM 14194.

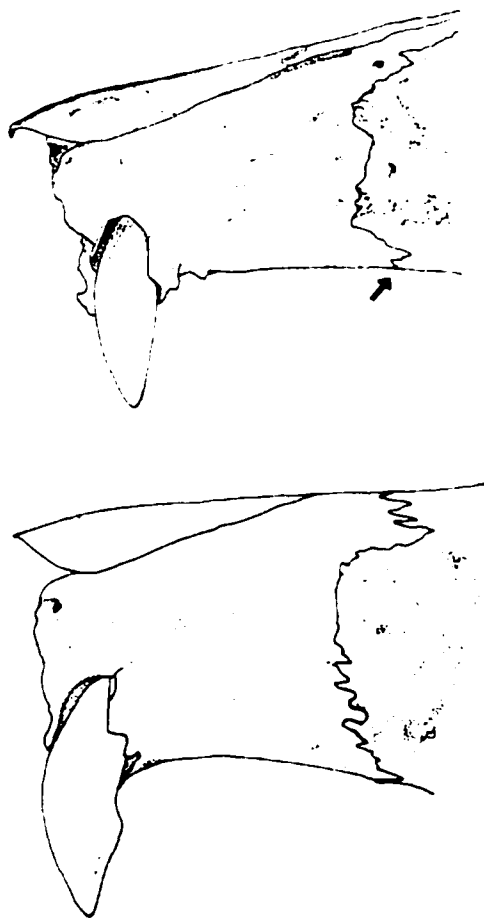


Figura 3. Lateral rostrum of thomomyines; the arrow indicates the premaxilla-maxillary suture. **Above**, Thomasomys incanus (MCZ 38537); **below**, Thomasomys cinereus (MVZ 137939).



Figure 4. Views of a broad, medium, and narrow interorbital region in thomomyines. A, *Chilomys instans* (FMNH 71632); B, *Thomasomys rhoadsi* (AMNH 63361); C, *Thomasomys aureus* (AMNH 9347).



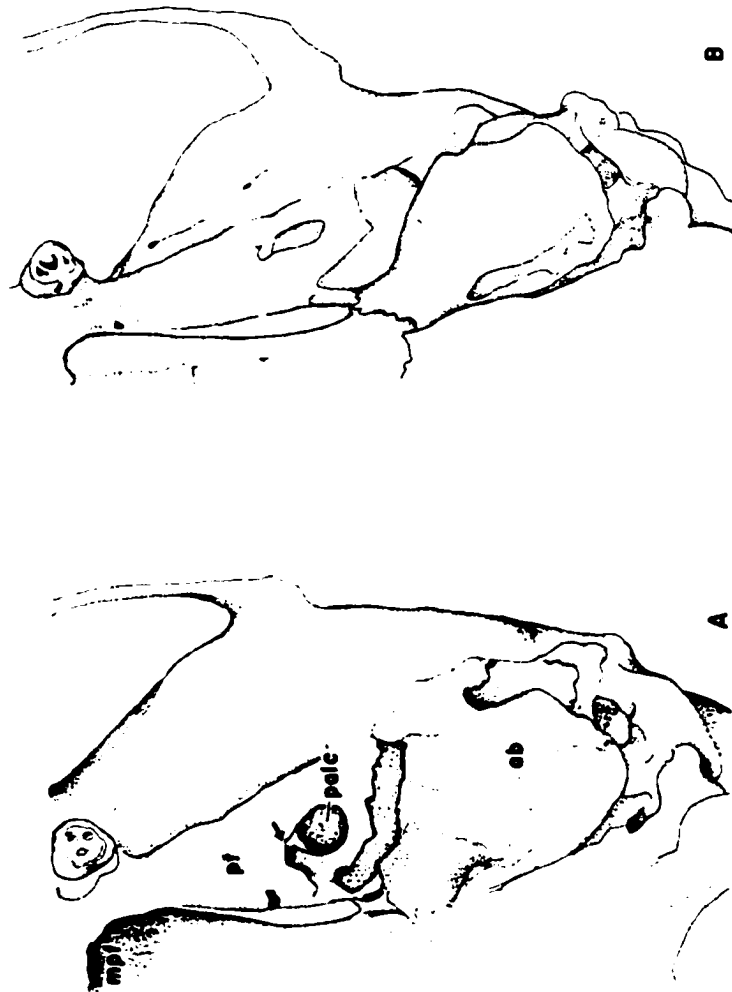


Figure 5. Exposure of internal carotid canal on the parapterygoid fossa. **A**, Thomasomys sp. 4 (MUSM 14962); **B**, Thomasomys cinereus (MVZ 137939). **ab**, auditory bulla (ectotympanic); **mpf**, mesopterygoid fossa; **palc**, posterior opening of the alisphenoid canal; **pf**, parapterygoid fossa.

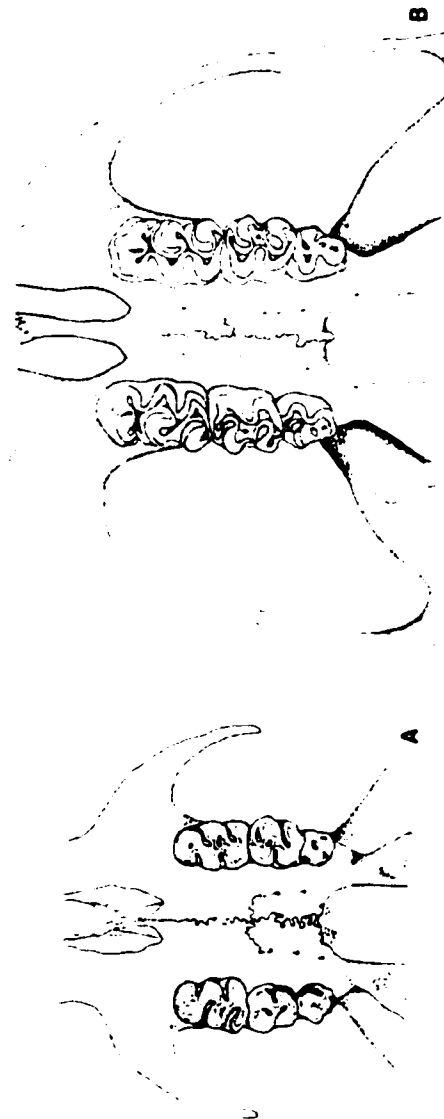


Figure 6. Palatal morphology of thomomyine rodents exhibiting broad and narrow bony palates. A, Thomasomys rhoadsi (AMNH 63361); B, Thomasomys aureus (MUSM 9347).

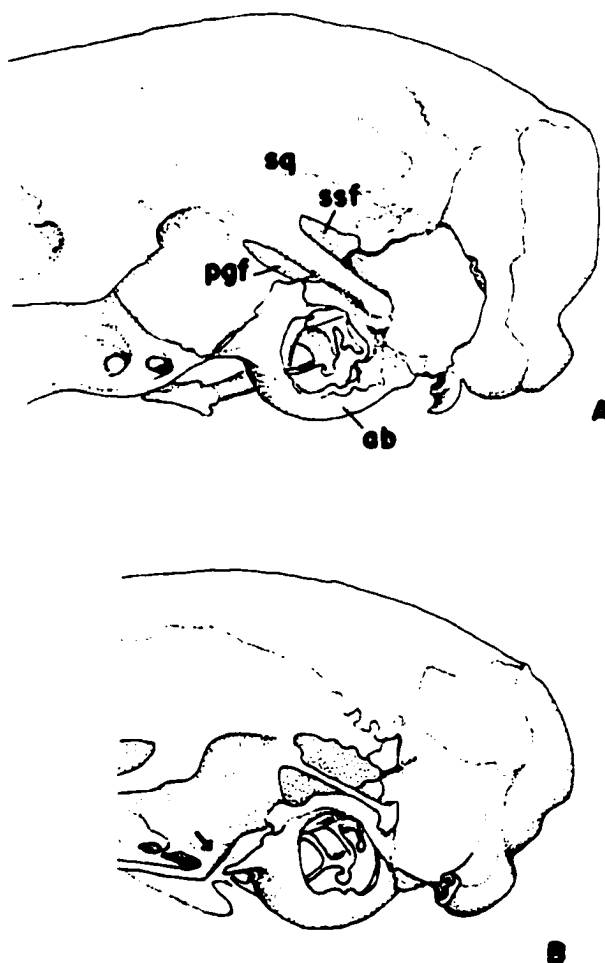


Figure 7. Posterior border of alisphenoid-squamosal suture. **A**, *Thomasomys aureus* (MUSM 6726); **B**, *Thomasomys eleusis* (MUSM 8217). **ab**, auditory bulla (ectotympanic); **pgf**, postglenoid foramen; **ssf**, subsquamosal fenestra; **sq**, squamosal bone.

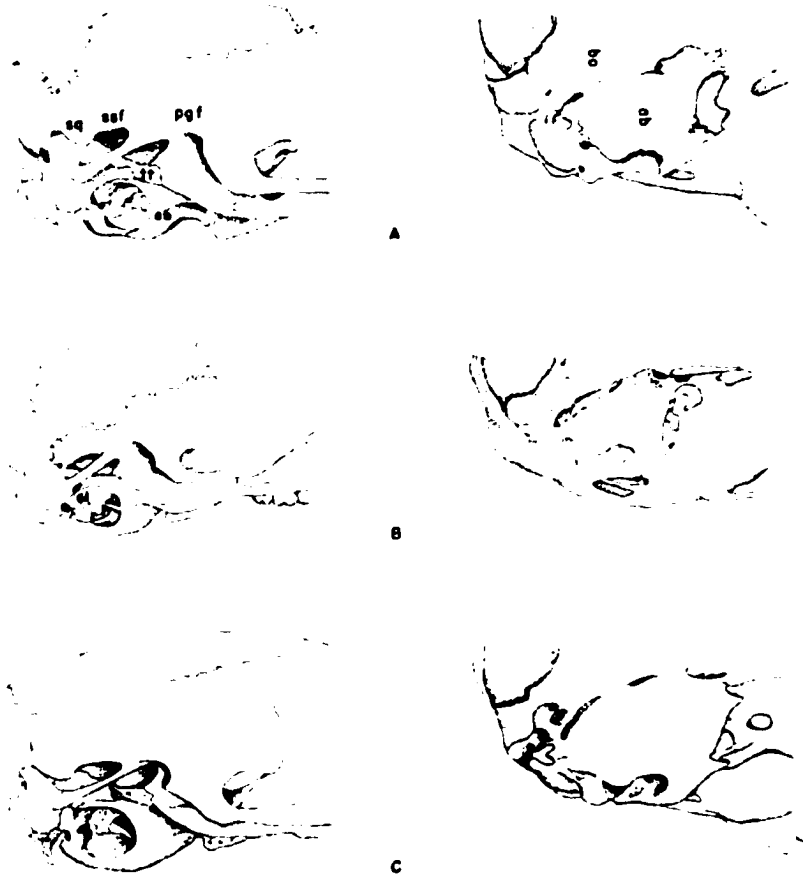


Figura 8. Lateral and ventral view of right auditory bullae of selected thomasomyines. **A.** Thomasomys aureus (AMNH 9347); **B.** Thomasomys incanus (MUSM 11482); **C.** Thomasomys pyrrhonotus (MUSM-VPT 1670). **ab.** auditory bulla (ectotympanic); **bo.** basioccipital bone.

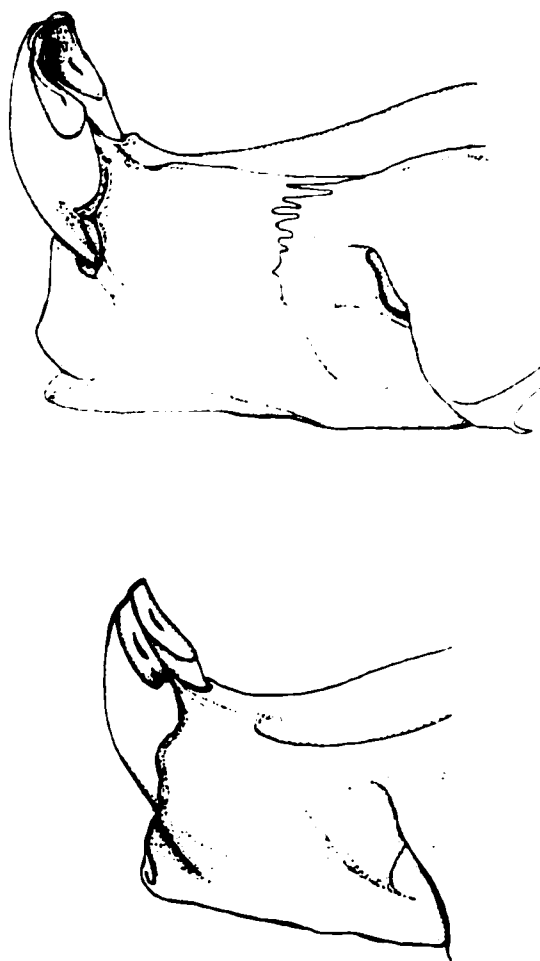


Figure 9. Posterior border of the worn surface of upper incisors. **Above.** Thomasomys kalinowskii (MUSM 14986); **below.** Thomasomys notatus (MUSM 14994).

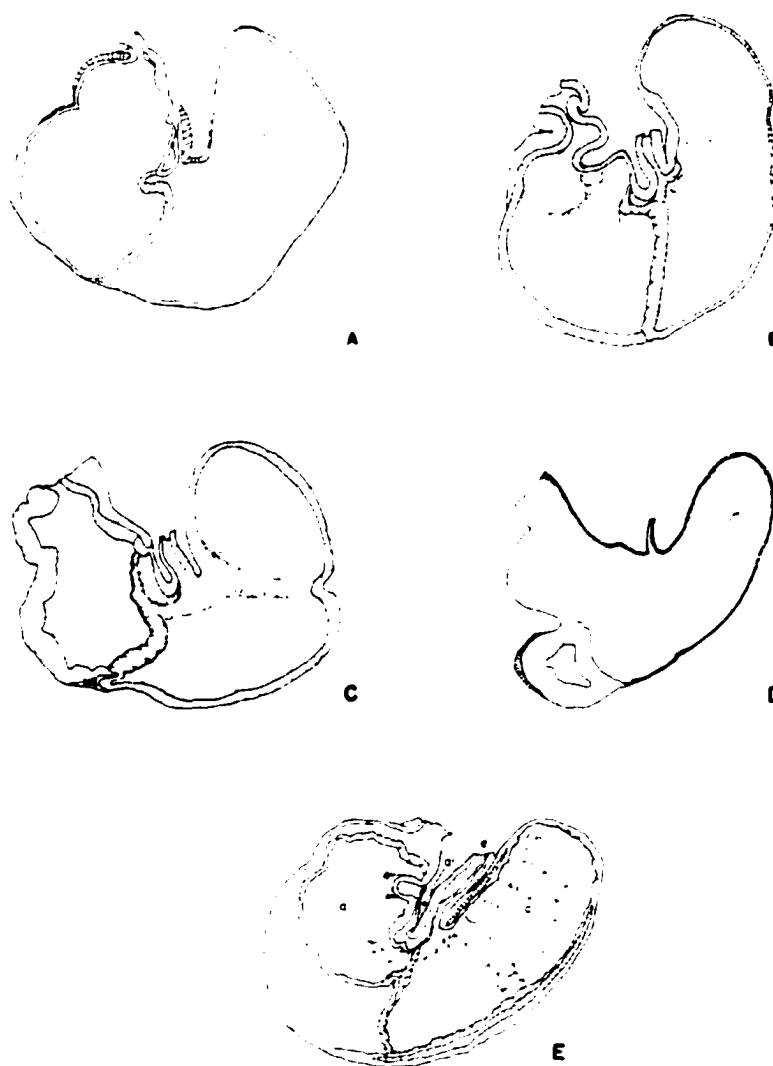


Figure 10. Stomach morphology of thomatomyine rodents. **A**, Thomasomys notatus (UMMZ 158029); **B**, Thomasomys cinereus (MUSM-VPT 2286); **C**, Thomasomys sp. 4 (MUSM 11479); **D**, Aepeomys lugens (MBUCV I- 2793); **E**, Thomasomys aureus (MUSM 9358). **a**, antrum; **c**, corpus; **e**, esophagus; **ia**, incisura angularis.

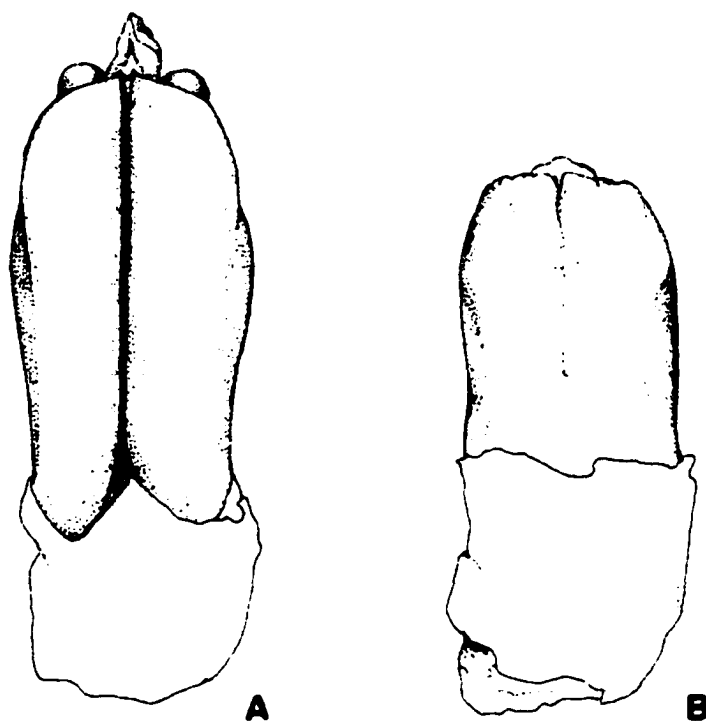


Figure 11. Ventral view of glans penis contrasting a deep versus a shallow ventral groove. A. *Rhipidomys leucodactylus* (AMNH 241643); B. *Thomasomys silvestris* (UMMZ 155759).

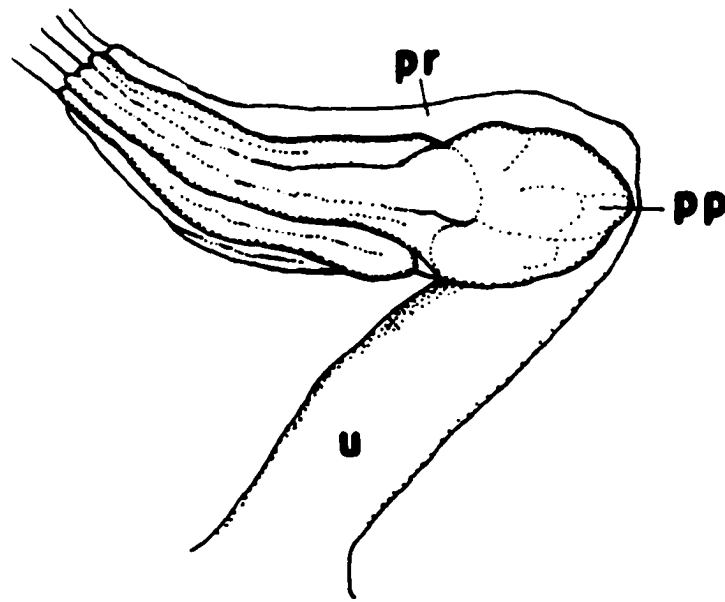


Figure 12. Preputial glands of *Thomasomys praetor* (MUSM VPT 2271). **pp**, preputial gland; **pr**, prepuce; **u**, urethra.



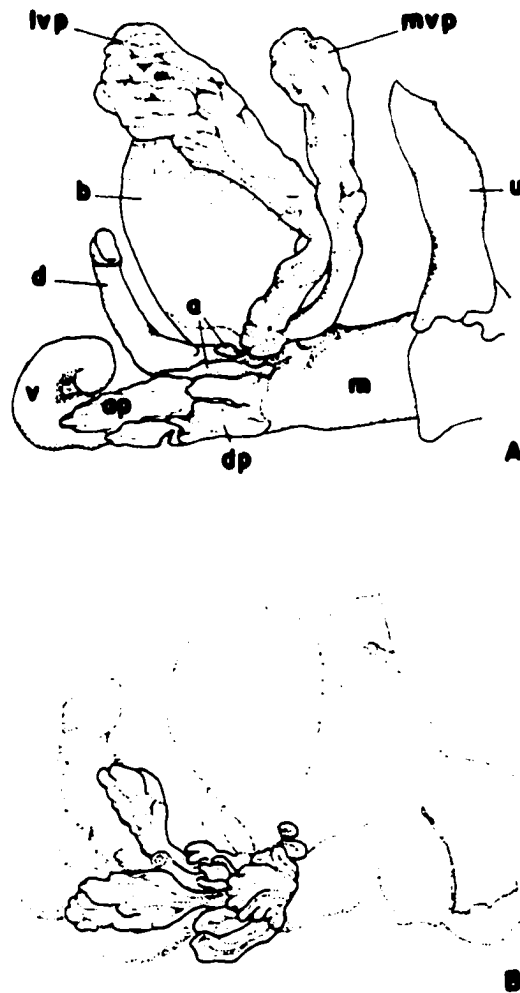


Figure 13. Reproductive tract of A. *Thomasomys praetor* (MUSM VPT 2271), and B. *Thomasomys cinereus* (MUSM-VPT 2274). a, ampullary gland; ap, anterior prostate; b, bladder; d, deferent duct; dp, dorsal prostate; lvp, lateral ventral prostate;.mvp, medial ventral prostate. m, M. compressor urethrae; u, urethra; v, vesicular gland.

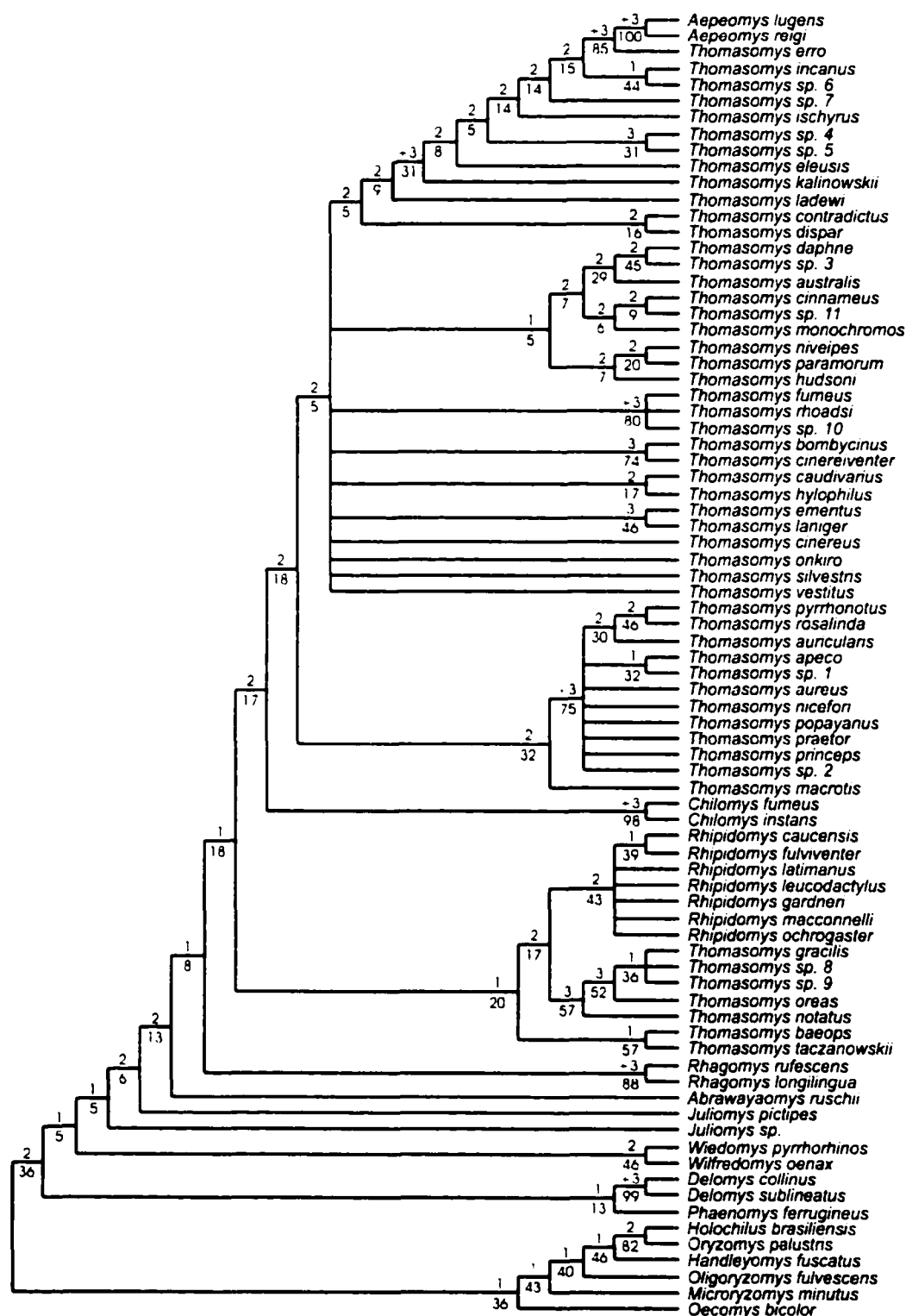


Figure 14. A strict consensus of 192 equally most parsimonious trees produced with ordered and unweighted characters, each tree with 1512 steps (CI = 0.270, RI = 0.608). Majority rule bootstrap values are below internal branches. Decay values are above.



Figure 15. Views of cranium and left dentary of adult Thomasomys cinereus (MVZ 137939).



Figure 16. Views of the upper right and lower right teeth of Thomasomys cinereus (MVZ 137939).

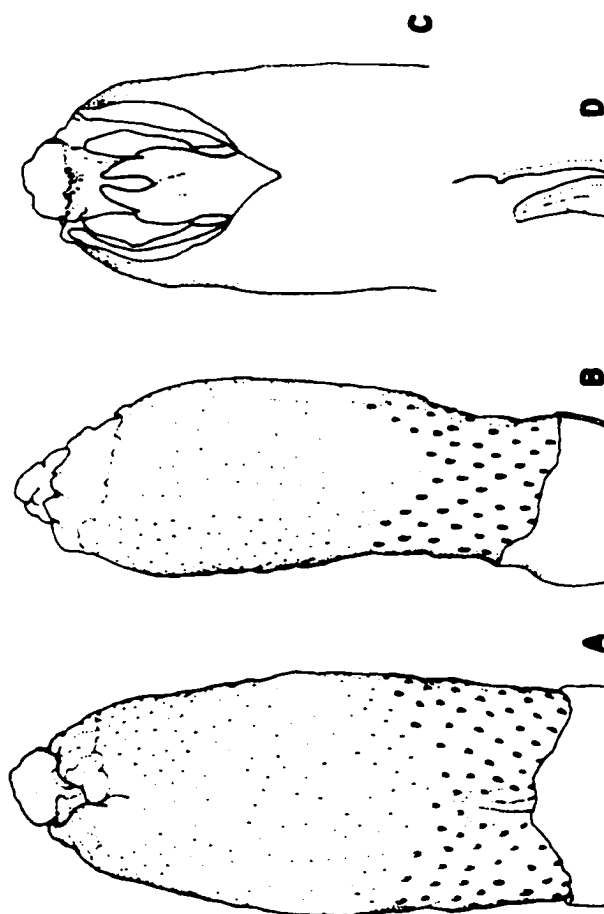


Figure 17. Glans penis of Thomasomys cinereus (MUSM – vpt 2286). ). **A.** Ventral view, **B.** lateral view; **C.** glans incised midventrally; **D.** lateral view of dorsal papilla.



Figure 18. Views of cranium and left dentary of adult Thomasomys aureus (AMNH 46590).



Figure 19. Views of the upper right and lower right teeth of Thomasomys aureus (AMNH 46590).

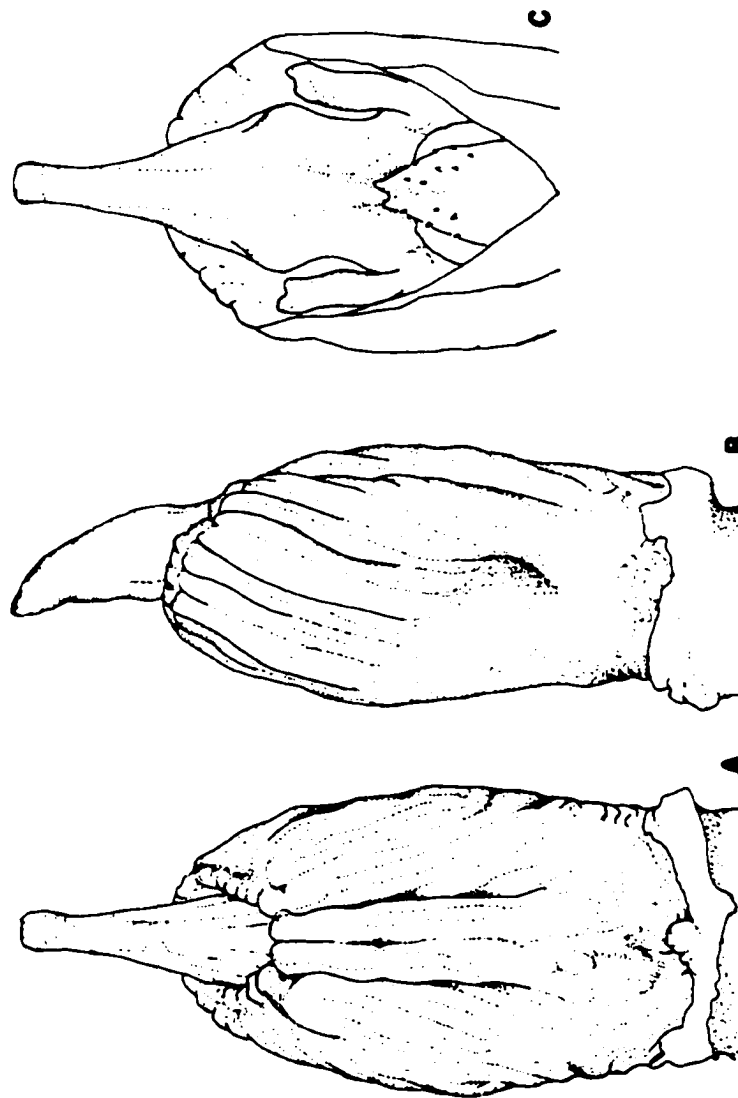


Figure 20. Glans penis of *Thomasomys aureus* (MUSM 12000). A. Ventral view, B. lateral view; C, glans incised midventrally.



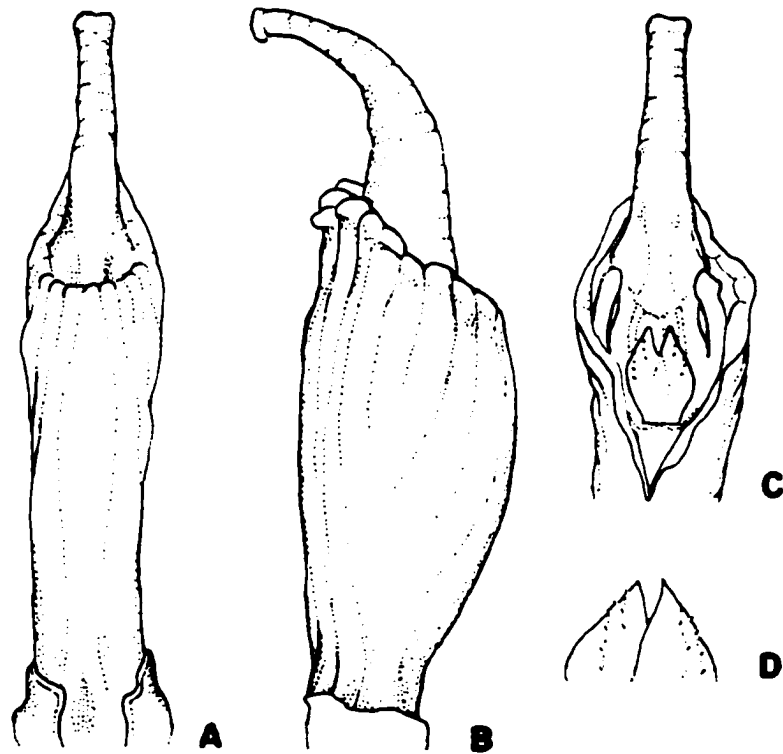


Figure 21. Glans penis of Thomasomys apeco (MUSM 7201). **A.** Ventral view. **B.** lateral view; **C.** glans incised midventrally; **D.** ventral view of urethral flap.

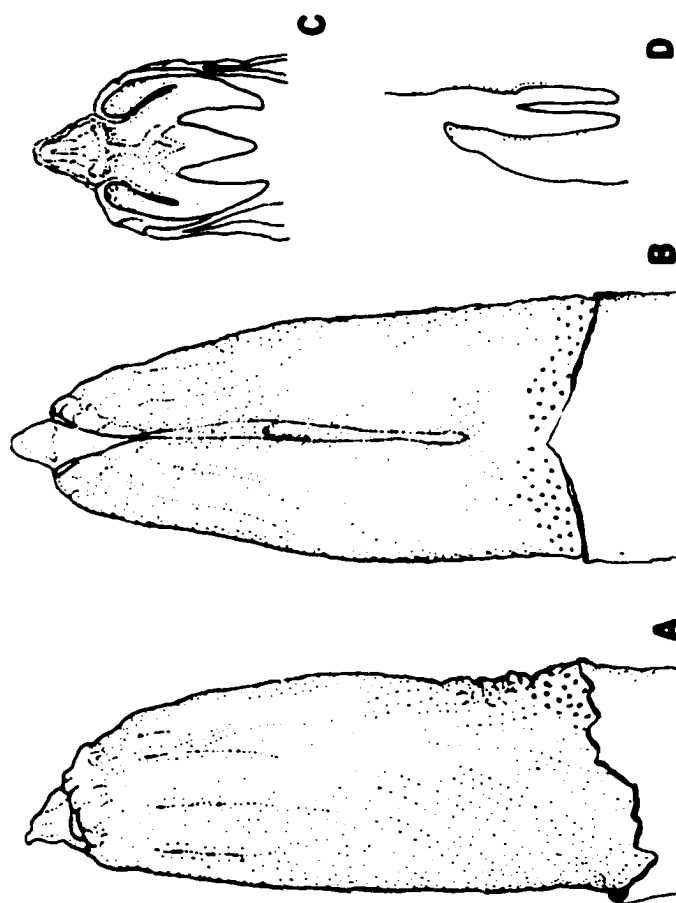


Figure 22. Glans penis of *Thomasomys praetor* (MUSM-VPT 2271). A. Lateral view, B. ventral view; C. glans incised midventrally; D, lateral view of dorsal papilla.



Figure 23. Views of cranium and left dentary of adult Thomasomys baeops (AMNH 65010).



Figure 24. Views of the upper right and lower right teeth of Thomasomys baeops. (AMNH 67477).



Figure 25. Views of cranium and left dentary of adult Thomasomys gracilis (MVZ 166672).



Figure 26. Views of the upper right and lower right teeth of Thomasomys gracilis (MVZ 166672).

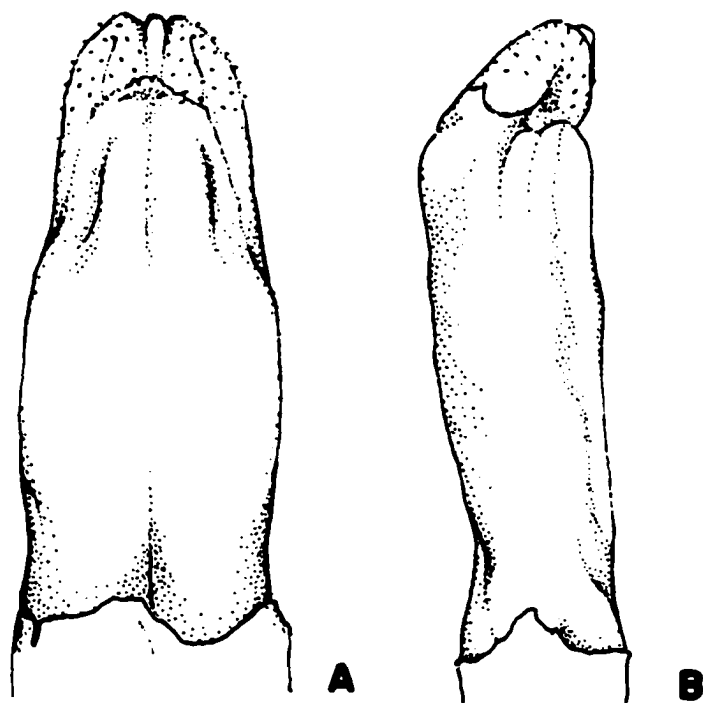


Figure 27. Glans penis of Thomasomys oreas (CBF 7429). **A.** Ventral view, **B.** lateral view.



Figure 28. Views of cranium and left dentary of adult Thomasomys notatus (MVZ 173973).





Figure 29. Views of the upper right and lower right teeth of Thomasomys notatus (MVZ 173973).

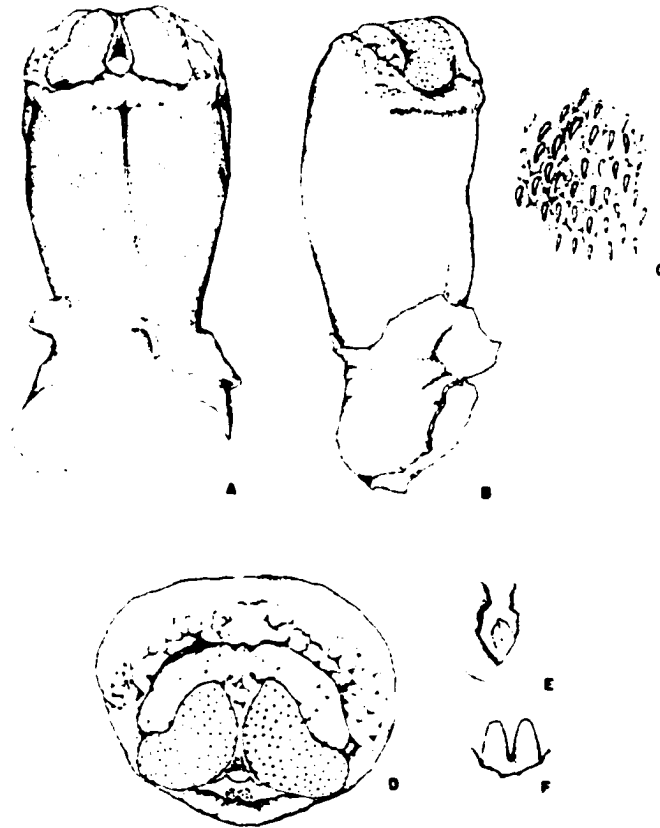


Figure 30. Glans penis morphology of Thomasomys notatus (UMMZ 158029). **A.** Ventral view, **B.** lateral view; **C.** portion of the epidermis surface; **D.** apical view; **E.** lateral view of dorsal papilla; and **F.** ventral view of urethral flap.

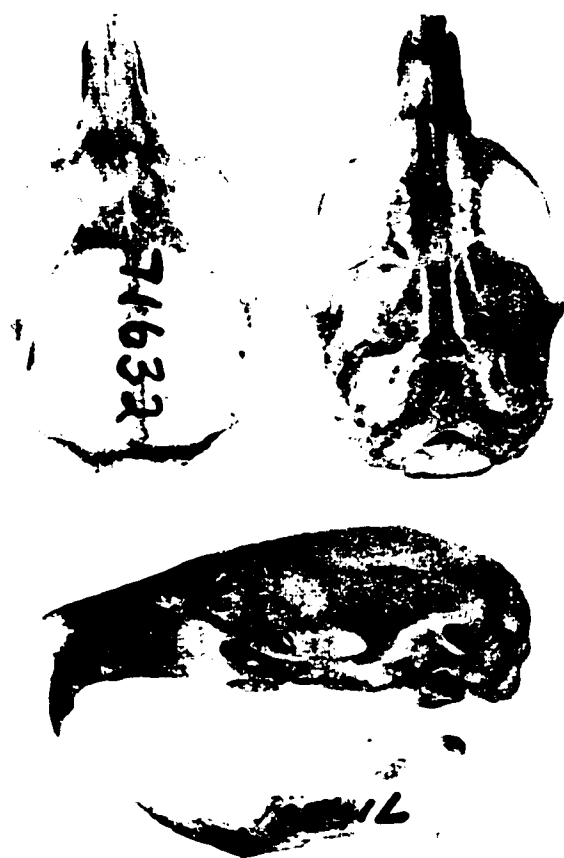


Figure 31. Views of cranium and left dentary of adult Chilomys instans (FMNH 71632).

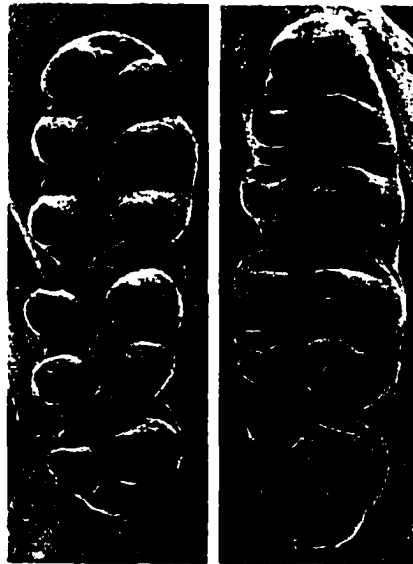


Figure 32. Views of the upper right and lower right teeth of Chilomys instans (FMNH 71632).



Figure 33. Views of cranium and left dentary of adult Rhipidomys leucodactylus (AMNH 71907).



Figure 34. Views of the upper right and lower right teeth of Rhipidomys leucodactylus (AMNH 71907).