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PHYLOGENETIC RELATIONSHIPS OF ORYZOMINE RODENTS (MUROIDEA: SIGMODONTINAE): SEPARATE AND COMBINED ANALYSES OF MORPHOLOGICAL AND MOLECULAR DATA

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ABSTRACT

In this study I provide a phylogenetic hypothesis for the tribe Oryzomyini that can be used to understand the diversification and evolution of this group of rodents and to revise the current generic-level classification. Morphological and molecular data were used for these purposes in combined and separate analyses. Molecular data consisted of partial sequences (1266 bp) from the first exon of the nuclear gene encoding the interphotoreceptor retinoid binding protein (IRBP); the morphological matrix comprised 99 characters, including 16 integumental characters, 32 skull characters, 29 dental characters, 7 postcranial characters, and 10 characters from the phallus and soft-anatomy systems. I present anatomical descriptions for each character, including delineation of different states observed among oryzomyines. Results of the combined analysis were congruent with the IRBP-only dataset for oryzomyine higher-level relationships. Morphological analyses, although showing discrepancies from the combined or IRBP consensus cladograms and with low nodal support values, recovered several clades similar to the combined and IRBP analyses. Systematics of the tribe and the evolution of a few pivotal characters are discussed in light of the proposed phylogeny. Different taxonomic arrangements for species currently included in the genus *Oryzomys* are suggested. Finally, I evaluate evolutionary and biogeographic hypotheses that are compatible with our current knowledge on oryzomyine relationships.

INTRODUCTION

Sigmodontine rodents—the monophyletic group that includes almost all South American muroids and excludes North American neotomines and tylomyines (Reig, 1980; Smith and Patton, 1999; Jansa and Weksler, 2004)—have challenged students of mammalian systematics for the past two centuries. After an explosive radiation following an ancestral invasion of South America at the end of the Tertiary (Pardiñas et al., 2002; Steppan et al., 2004), sigmodontines became the most diverse family-level mammalian clade in the Neotropical region: with about 70 genera and 320 recognized species (Musser and Carleton, 1993), this group now accounts for roughly 29% of all Neotropical mammals. The sheer number of sigmodontine species, coupled with pervasive homoplasy in classically studied character systems such as the skull and dentition, has made rigorous testing of phylogenetic hypotheses difficult. Systematic research during the last several decades, however, has improved our understanding of sigmodontine relationships at all taxonomic levels (e.g., Voss, 1988, 1991, 1993; Smith and Patton, 1993; Voss and Carleton, 1993; Steppan, 1995; Bonvicino and Weksler, 1998; Musser et al., 1998; Smith and Patton, 1999; Bonvicino and Moreira, 2001; Geise et al., 2001; Pardiñas et al., 2002; D'Elía, 2003; D'Elía et al., 2003; Pacheco, 2003; Weksler, 2003).

Despite such progress, many significant problems remain, especially among the 16 extant genera and approximately 115 species currently assigned to the sigmodontine tribe Oryzomyini. Oryzomyines are ubiquitous in the Neotropics, ranging from Tierra del Fuego to the southern United States. Oryzomyines occupy forests, savannas, swamps, scrublands, and semi-arid environments, and they are often among the most abundant small mammals in many of these habitats (Eisenberg, 1999). Most oryzomyines are ordinary-looking rodents that somewhat resemble common house rats and mice. Nevertheless, other oryzomyines display a range of morphological diversity hardly surpassed by other muroid groups of equivalent taxonomic rank. Varying in size from small (ca. 10 g) to large (ca. 300 g), most oryzomyines are predominantly cursorial, but some species display marked specializations for arboreal or semiaquatic (amphibious) life.

Long considered a basal group in the radiation of Neotropical muroids (e.g., by Hershkovitz, 1962; Gardner and Patton, 1976; Reig, 1986), oryzomyines are now thought to be nested among other derived sigmodontine clades (Steppan, 1995; Engel et al., 1998; Smith and Patton, 1999; D'Elía, 2003; Pacheco, 2003; Weksler, 2003). Although the taxonomic composition of the Oryzomyini as originally defined and diagnosed by Voss and Carleton (1993) has

been corroborated by subsequent phylogenetic studies (Steppan, 1995; Weksler, 2003), relationships among members of the tribe are still unclear. Below, I provide a synopsis of oryzomyine taxonomic history and summarize previous hypotheses of intratribal relationships.

Oryzomyine Composition and Taxonomic History

Neotropical muroid rodents were originally divided into two groups based on the presence/absence of the mesoloph (id) on upper and lower molars (Winge, 1887). Thomas (1906, 1917) further divided the pentalophodont genera (i.e., taxa with the mesoloph) into an *Oryzomys* group including *Oryzomys*, *Oligoryzomys*, *Rhagomys*, and *Oecomys*, and a *Thomasomys-Rhipidomys* group, including *Thomasomys*, *Delomys*, *Phaenomys*, and *Rhipidomys*, based on the morphology of the hard palate and (to a lesser degree) the number of mammae. However, ''oryzomyines'' were first explicitly diagnosed as such by Hershkovitz (1944: 12–13), who included nine genera or subgenera (*Melanomys*, *Microryzomys*, *Neacomys*, *Nectomys*, *Nesoryzomys*, *Oligoryzomys*, *Oryzomys*, *Scolomys*, *Sigmodontomys*) on the basis of the following traits:

> Eyes normal; ears usually small but well developed, more or less haired both inside and out, never naked; tail terete [cylindrical and slightly tapering], thinly haired, the scales plainly visible; pollex with a nail, never a claw; sole of hind foot with five or six tubercles, naked except sometimes at heel; the three middle digits of hind foot partly, but not always conspicuously, webbed; mammae eight (four pectoral and four inguinal). Proximal parts of nasals somewhat concave mesially with the concavity frequently continued back on the frontals; supraorbital margins of frontal square, beaded, ridged, or produced as a shelf; antorbital foramen open both forward and upward, subcylindrical above, slitlike in front; upper anterior border of zygomatic plate rounded or slightly pointed, but not produced as conspicuous spine; palate produced posteriorly beyond plane of last molars; a rather well-developed fossa on the posterolateral border of each palatine bone marked with a distinct pit or a reticulation of two or more pits; posterior border of palate square or concave, never V-shaped, and sometimes provided with a short median spine which is never produced onward as median palatal ridge; parapterygoid fossa, as viewed from the ventral surface, relatively shallow with the lateral wall flattened, the anterior corner not undercut. Incisors more or less recurved, their face smooth, not grooved; anterior and posterior cingula present; mesostyle (id) and mesoloph (id) united, always present and well developed.... The structure of the palate and the presence in each molar of a fused mesostyle (id) and mesoloph (id) are characters which together are sufficient to distinguish the oryzomyine rodents from any others with which comparison need [sic] to made.

Other authors, however, have not regarded the differences in palatal morphology as a sufficient character for separating oryzomyines from thomasomyines, and they included both in the same group (e.g., Tate, 1932d; Vorontsov, 1959; Reig, 1980, 1984, 1986). In particular, Vorontsov's (1959) classification of ''hamster-like'' muroids (including sigmodontines, cricetines, neotomines, and tylomyines), which provided the formal nomenclatural ranks for the tribes currently used in sigmodontine classification, included several thomasomyines (sensu Hershkovitz, 1962: *Rhipidomys*, *Thomasomys*, *Phaenomys*, *Chilomys*, and *Rhagomys*) as well as tylomyines (*Tylomys*, *Ototylomys*, *Nyctomys*, and *Otonyctomys*) in his concept of Oryzomyini.

Three genera currently recognized as oryzomyines were placed by Hershkovitz (1955, 1962) in other suprageneric groups because they were tetralophodont (i.e., lacking a mesoloph). *Holochilus*, for example, was referred to the ''sigmodont group'', whereas *Pseudoryzomys* and *Zygodontomys* were considered to be phyllotines. In Hershkovitz's (1962) evolutionary scenario (fig. 1), oryzomyines were direct descendants of thomasomyines, which in turn were close to the original stock of pentalophodont ''sylvan'' muroids that invaded South America in the middle of the Tertiary. This scenario was further elaborated (e.g., Hershkovitz, 1966b) and extended by hypotheses of karyotypic evolution (Gardner and Patton, 1976) and biogeographical history (Reig, 1980, 1984,

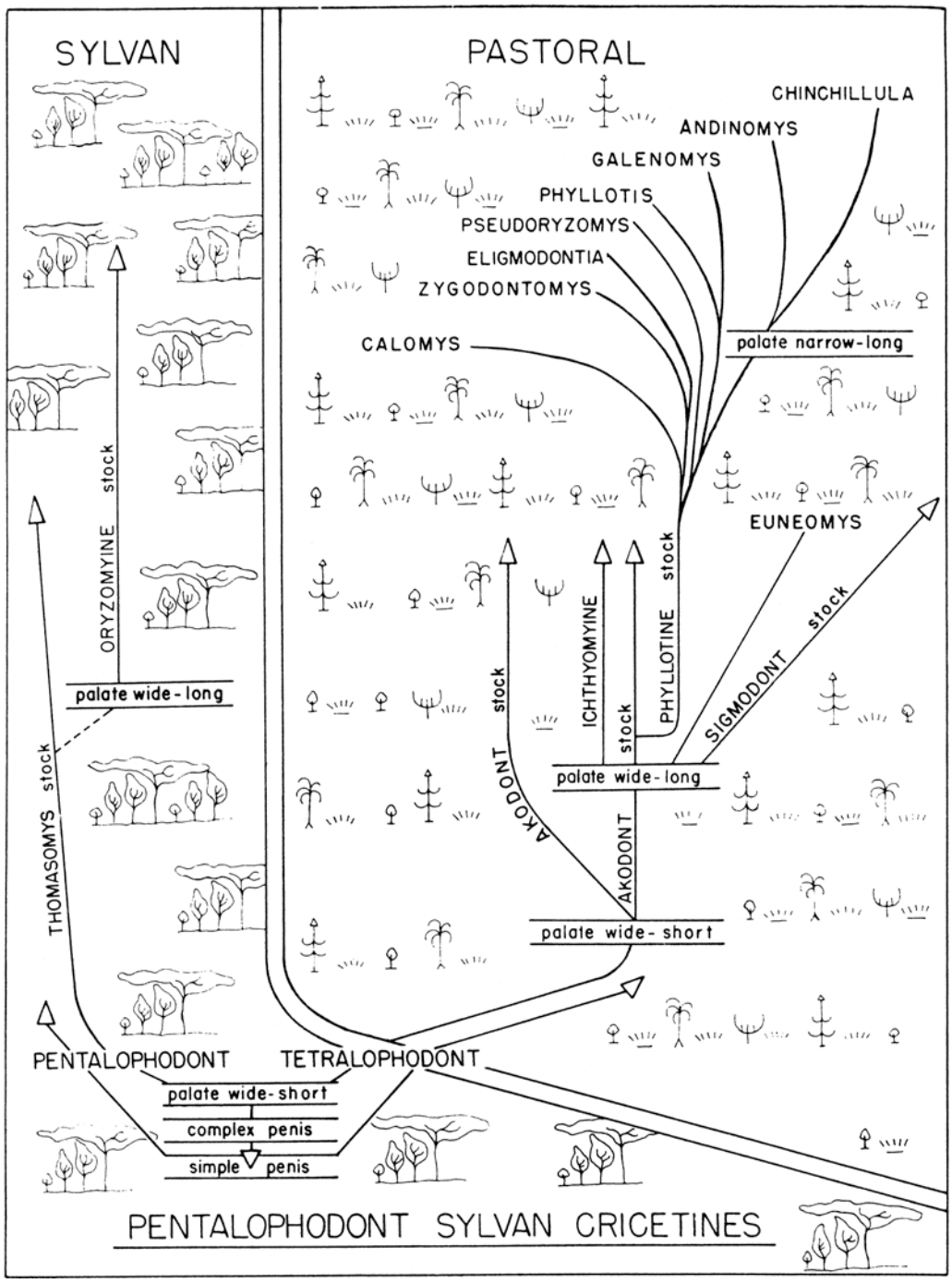


Fig. 1. Evolutionary scenario for the radiation of sigmodontines (Hershkovitz, 1962; reproduced from fig. 2). Note the position of *Zygodontomys* and *Pseudoryzomys* within the phyllotine radiation. *Holochilus* was included by Hershkovitz (1955, 1962) in the "sigmodont" group. The original caption read: "Interrelationship of the phyllotine genera and their morphological and ecological relationship to certain South American cricetines. The progressive pastoral forms with tetralophodont molars evolved from sylvan pentalophodont stock. Cricetines with a simple type of penis probably evolved from a sylvan pentalophodont stock with the complex type of penis."

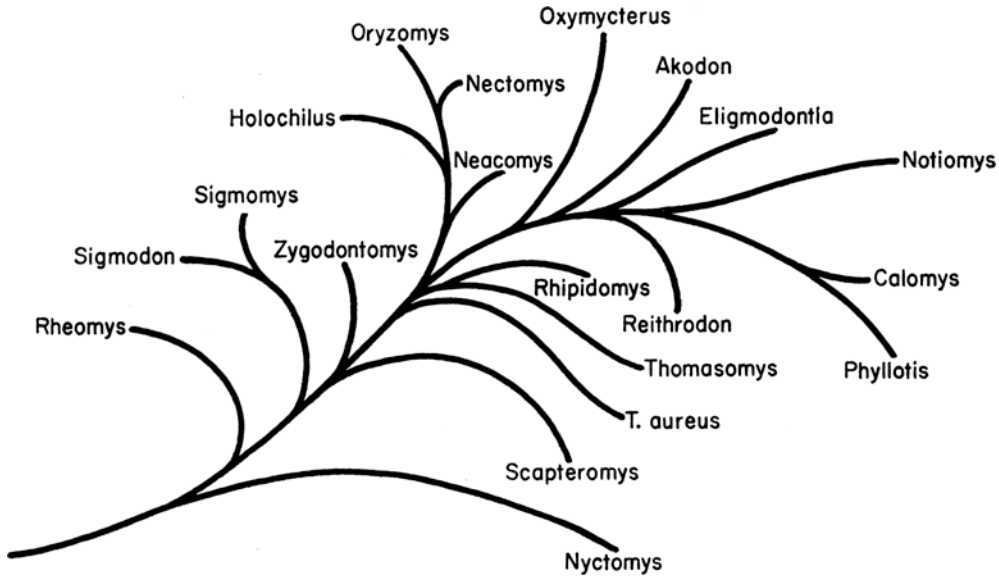


Fig. 2. Relationships among Neotropical muroid rodents based on characters from the glans penis (Hooper and Musser, 1964; reproduced from fig. 8B). Note the inclusion of *Holochilus* in a clade with other oryzomyines. Species of "*Oryzomys*" represented in Hooper and Musser's study included forms now referred to *Oecomys*, *Oligoryzomys*, and *Melanomys*. "*Nectomys*" included *Sigmodontomys*; and *Zygodontomys* included *Bolomys*. The original caption read: "Diagram of possible relationships of ... South American 'cricetines'. Based on information from the glans penis."

1986), which assumed, but did not test, the basal position of oryzomyines.

Hershkovitz's influential classification of Neotropical muroids was first challenged by Hooper and Musser (1964), who described the morphology of the glans penis in representatives of all major sigmodontine groups. Among their results, they observed that the phallus of *Holochilus* (a "sigmodont" according to Hershkovitz) was similar to that of oryzomyines, and they proposed a hypothesis of evolutionary relationships based on penis characters (fig. 2), in which *Holochilus* was placed as the sister group to oryzomyines.

In a series of paper, Voss and co-authors (Voss, 1991, 1992, 1993; Voss and Myers, 1991; Voss and Carleton, 1993) established the currently accepted composition of the tribe Oryzomyini. First, Voss (1991) asserted that oryzomyines sensu Hershkovitz (1944) share a single putative synapomorphy—presence of a long palate—but observed that this trait is also shared by three tetralophodont genera referred to other groups (*Zygodontomys*, *Pseudoryzomys*, and *Holochilus*). He remarked that an additional putative synapomorphy for oryzomyines—absence of the gall bladder—is also shared by the same set of tetralophodont taxa. Subsequently, Voss and Myers (1991) summarized morphological and karyological evidence that *Pseudoryzomys* is more closely related to oryzomyines than to phyllotines, and Voss (1992) summarized morphological and karyological evidence pointing to the polyphyly of Hershkovitz's (1955) sigmodont group (which included *Holochilus*). Finally, Voss (1993) pointed out that the character uniting Oryzomyini sensu Vorontsov (1959; i.e., oryzomyines + thomasomyines)—presence of the mesoloph—was likely a symplesiomorphy.

Voss and Carleton (1993) consolidated the inference of previous studies and proceeded to delimit and diagnose the tribe Oryzomyini, within which they placed four tetralophodont genera (*Holochilus*, *Pseudoryzomys*, *Zygodontomys*, and *Lundomys*) together with the core oryzomyine group of Hershkovitz (1944). Although exceptions that they interpreted as reversals were noted, most of these taxa possess the diagnostic synapomorphies

of the tribe: (1) a pectoral pair of mammae, (2) a long palate with prominent posterolateral pits, (3) no alisphenoid strut, (4) no suspensory process of the squamosal attached to the tegmen tympani, and (5) no gall bladder. Subsequent phylogenetic analyses of morphological and molecular data have corroborated Voss and Carleton's (1993) hypothesis and simultaneously increased the list of synapomorphies that support oryzomyine monophyly (Steppan, 1995; Weksler, 2003).

Phylogenetic Studies of Oryzomyines

Most early taxonomic work on oryzomyines was focused at the generic or species level and provided few insights about phylogenetic relationships. Several extracts from influential papers by Philip Hershkovitz illustrate the vague notions of clade recognition that characterized this early literature:

> The apparent relationship of *Sigmodontomys* to *Nectomys* however, is probably attributable to an independent development, along parallel lines, of certain characters derived from the common oryzomyine stock rather than to divergence from a necessarily more recent *Nectomys*-like stock. (Hershkovitz, 1944: 71).

> [Except] for the presence of intermediate forms, typical *Oryzomys* and subgenus *Oecomys* might well be treated as generically distinct. (Hershkovitz, 1960: 521).

> The differences between each of the genera and subgenera of oryzomyine rodents are entirely within the framework of the general pattern and usually depend upon the recognition of some one extremely developed character of, presumably, an adaptive nature. Thus, the spiny pelage of both *Neacomys* and *Scolomys* represents their chief, if not sole, claim to generic rank; the short, broad hind foot with recurved claws supplemented by the long, penciled tail, designed for an arboreal habitat, is distinctive of *Oecomys*, though it is not clear where the line between it and the *trinitatis* (= *tectus*) group of *Oryzomys* could be drawn. The long-tailed *Microryzomys* and *Oligoryzomys* represent hardly more than size gradations leading to the larger *Oryzomys*, and *Melanomys* includes only the darkest, shortest-tailed species of the group in question. *Nesoryzomys* is characterized chiefly by its short, stout, markedly hairy feet. The cranial and dental characters which distinguish the oryzomyine categories higher than species are merely combinations or marked modifications of structural details common to the group as a whole, but not peculiar to any one species. (Hershkovitz, 1944: 13).

Explicitly phylogenetic research on oryzomyines started to advance with the accumulation of data from different character systems and the adoption of numerical analytical procedures. Data from four main sources have been used to analyze oryzomyine relationships: (1) chromosomes, (2) morphological data, (3) allozymes, and (4) sequences from mitochondrial and nuclear genes.

Oryzomyines display an exceptional range of karyotypic variability in diploid and fundamental numbers, surpassing any other mammalian group of equivalent taxonomic rank (Gardner and Patton, 1976; Baker et al., 1983). Two attempts to analyze oryzomyine relationships have been based on such chromosomal variation. Gardner and Patton (1976) first described the extensive variation in oryzomyine karyotypes and suggested that certain taxa formerly included as subgenera of *Oryzomys*, such as *Oecomys* and *Nesoryzomys*, should be considered as distinct genera. Gardner and Patton (1976) also provided an evolutionary scenario based on chromosomes for the Neotropical sigmodontine radiation (fig. 3). The exceptional range of variability in diploid and fundamental numbers was postulated to have resulted from a rapid adaptive radiation. Because of their putatively primitive morphology and karyotypes (oryzomyines have higher modal values of diploid and fundamental numbers than do other sigmodontine groups), oryzomyines were considered to be the stem stock from which all other sigmodontine lineages were derived. Baker et al. (1983) reported the results of a parsimony analysis using chromosomal arrangements as characters, and they provided an explicit hypothesis of oryzomyine relationships. Their analysis (fig. 4, left cladogram) recovered a basal *Nectomys* among the analyzed oryzomyine taxa and a polytomy including *Holochilus* and various clades such as *Oryzomys*, *Oligoryzomys*, *Oecomys*, and *Melanomys*. Voss and Carleton (1993), however, recoded and reanalyzed Baker et al.'s (1993) data and

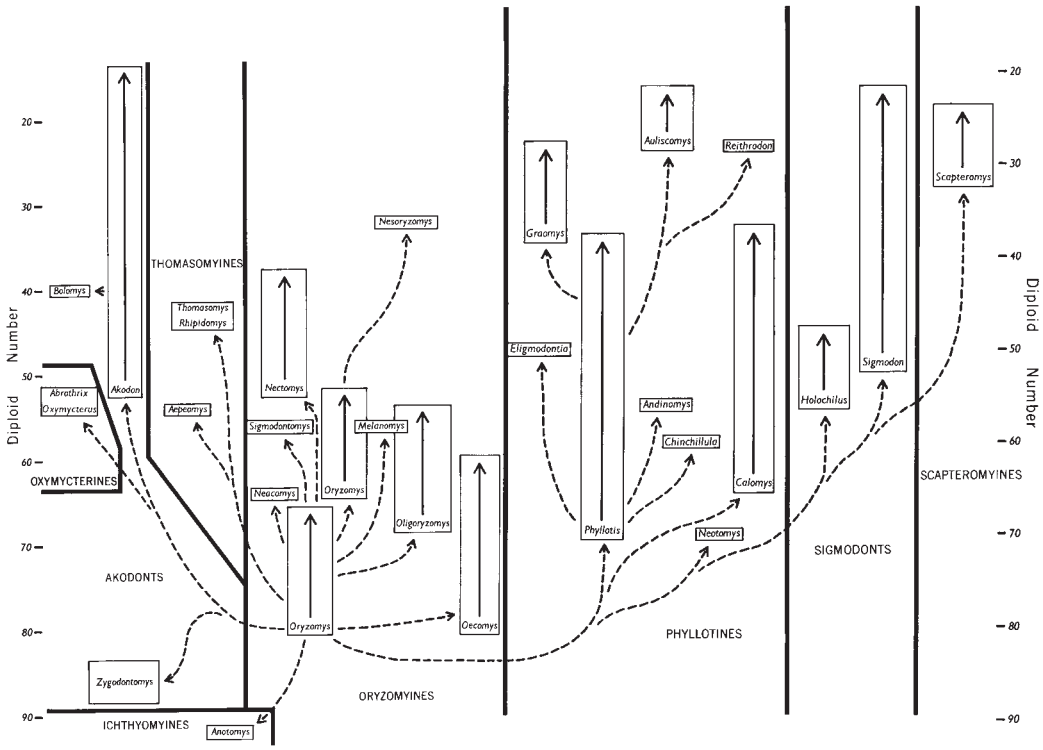


Fig. 3. Interrelationships and evolutionary scenario for the karyotypic evolution of sigmodontines (Gardner and Patton, 1976; reproduced from fig. 10). Oryzomyines were postulated to be the basal group from which other sigmodontine groups originated. Note the exclusion of *Zygodontomys* (which included *Bolomys* in then-current usage) and *Holochilus* from oryzomyines. The original caption read: ''Directional trends and suggested relationships among the Neotropical cricetines based primarily on karyotypic data, but also including an appreciation for cranial, dental, and phallic morphological characters and zoogeographic considerations.''

recovered a far less resolved topology. Their strict consensus of 10,000 shortest trees (fig. 4, right cladogram) shows *Nectomys* as the sister group to a large polytomy including 13 of the 16 analyzed taxa.

Most morphological phylogenetic analyses of oryzomyines have been limited in taxonomic scope and/or character sampling. Such analyses were designed to test restricted hypotheses of relationships within oryzomyines and thus did not provide comprehensive hypotheses of intratribal relationships. Several of these analyses assessed the relationships of the tetralophodont taxa *Holochilus*, *Lundomys*, *Zygodontomys*, and *Pseudoryzomys* (e.g., Voss and Carleton, 1993; Steppan, 1996; Carleton and Olson, 1999). Carleton and Olson (1999) provided the largest analysis of this kind, in which the authors scored 40 morphological characters (16 dental, 19 cranial, and 5 external) for nine oryzomyine taxa. Their results (fig. 5A) recovered the tetralophodont taxa as a monophyletic group. Eighteen synapomorphies (10 of which were nonhomoplasious) supported a clade containing *Holochilus* and †*Noronhomys* (a Brazilian fossil), with *Lundomys*, *Pseudoryzomys*, *Zygodontomys*, *Oryzomys*, and *Microryzomys* as successively more distant sister taxa.

Other phylogenetic analyses based on morphology have focused on higher-level relationships and included few oryzomyine terminals. For example, Carleton (1980) scored 79 morphological characters (15 dental, 19 cranial, 8 skeletal, 3 external, and

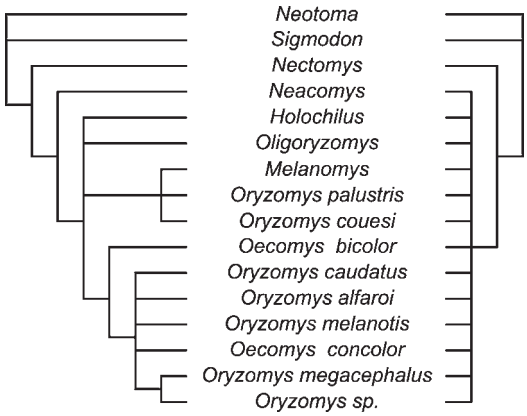


Fig. 4. Hypotheses of relationships among oryzomyine rodents based on G-banded chromosome morphology (Baker et al., 1983), with generic taxonomy updated to reflect current usage. The matrix consisted of 14 oryzomyine taxa, one non-oryzomyine sigmodontine (*Sigmodon hispidus*) and one neotomine (*Neotoma micropus*) used as outgroups scored for 15 characters (only 9 of which were parsimony-informative). The construction of the cladogram was manual, and the characters were treated as additive. The left-hand diagram shows the original tree as presented by Baker et al. (1983; redrawn after their fig. 4); the right-hand diagram is the consensus tree of more than 10,000 fundamental cladograms recovered in a subsequent reanalysis of the chromosomal data performed by Voss and Carleton (1993; redrawn after their fig. 16), in which character-states were analyzed using PAUP* with unordered transformations and *Neotoma micropus* as the designated outgroup. For simplicity, species-level taxonomic sampling is not illustrated in these condensed diagrams, except for genera that were not recovered as monophyletic groups.

34 from soft anatomy) for 75 muroid taxa, including five oryzomyines (*Holochilus brasiliensis*, *Oryzomys palustris*, *Oryzomys megacephalus*, *Oligoryzomys fulvescens*, and *Nectomys squamipes*). The Wagner tree recovered in this analysis (Carleton, 1980: fig. 41) depicted oryzomyines as a paraphyletic group, and analysis of his data using PAUP* (fig. 6) also failed to recover an oryzomyine clade because *Holochilus* is found as the sister group of *Sigmodon*. In another study, Steppan (1995) scored 40 morphological characters (3 dental, 21 cranial, 8 skeletal, 3 external, and 5 from soft anatomy) for 29 sigmodontines, including 8 oryzomyines and 11 outgroup (non-sigmodontine) taxa. In the topology he favored, oryzomyines were recovered as a monophyletic group with *Wiedomys* as their sister taxon (fig. 5B). The tetralophodont taxa *Pseudoryzomys*, *Holochilus,* and *Zygodontomys* formed a clade, but *Oryzomys* was paraphyletic. Pacheco (2003) also analyzed sigmodontine relationships, scoring 122 characters (21 dental, 54 cranial, 12 skeletal, 17 external, and 18 from soft anatomy) for 46 sigmodontines, including 7 oryzomyines and 13 outgroups. He also recovered oryzomyines as a monophyletic group but with thomasomyines (sensu Hershkovitz, 1962) as their closest sister group.

Only a few studies of oryzomyine relationships have been based on allozymes, and most have been centered on small sets of taxa. Patton and Hafner (1983), for example, presented allozymic evidence suggesting that *Oryzomys bauri* is more closely related to *O. xanthaeolus* than to *Nesoryzomys* or to *Oryzomys palustris*. In a more inclusive study, Dickerman and Yates (1995) analyzed allozyme variation at 18 loci among 15 oryzomyine species using distance, maximum likelihood, and several bootstrap parsimony techniques. Among other results (fig. 5C), they recovered *Oligoryzomys* and *Microryzomys* as monophyletic groups, but *Oryzomys* was not monophyletic.

Most molecular analyses of oryzomyine relationships have been based on nucleotide sequences from the mitochondrial gene cytochrome *b* (Myers et al., 1995; Patton and da Silva, 1995; Smith and Patton, 1999; Bonvicino and Moreira, 2001; Andrade and Bonvicino, 2003; Bonvicino et al., 2003; Gómez-Laverde et al., 2004). A few congruent results among these analyses include (fig. 7): (1) the monophyly of several genera, such as *Zygodontomys*, *Oecomys*, *Neacomys*, *Oligoryzomys*, and *Scolomys*; (2) a clade including *Neacomys*, *Microryzomys*, and sometimes *Oligoryzomys*; (3) a clade including *Oecomys* and the *yunganus*, *megacephalus* and *nitidus* species groups of *Oryzomys*; (4) a clade including *Nectomys* and the *subflavus* and *angouya* species groups of *Oryzomys*; and (5) polyphyly of *Oryzomys*. The same studies, however, have produced contradictory results for most higher-level oryzomyine

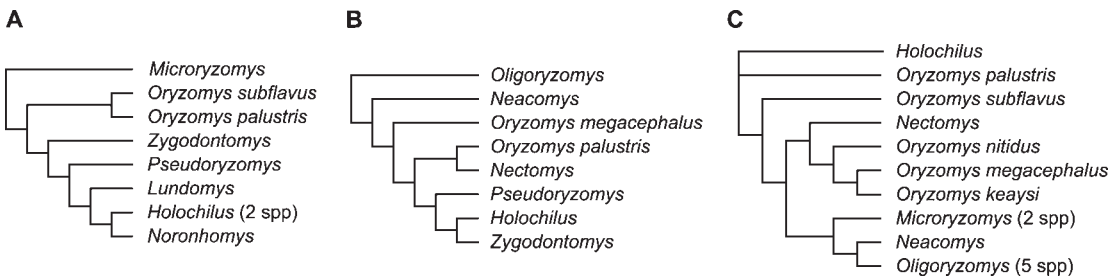


Fig. 5. Hypotheses of relationships among oryzomyine rodents based on morphological characters and allozymic data. For simplicity, species-level taxonomic sampling is not illustrated in these condensed diagrams, except for genera that were not recovered as monophyletic groups. The taxonomy has been updated to reflect current usage. **A,** Cladistic relationships among oryzomyines based on 40 morphological characters (Carleton and Olson, 1993; redrawn after their fig. 25; their tree was rooted with a hypothetical ancestor). **B,** Portion of sigmodontine phylogeny based on 40 morphological characters showing relationships among oryzomyines (Steppan, 1995; redrawn after his fig. 19). The tree on which this diagram was based was recovered in a parsimony analysis using a dummy character included to favor sigmodontine monophyly. Analysis without such a character (Steppan, 1995: fig. 20) recovers a basal polytomy involving *Neacomys*, *Oligoryzomys*, *Oryzomys megacephalus*, and the clade containing remaining oryzomyines, as well as *Chilomys* as sister group of *oryzomyines*. Eleven characters were informative about oryzomyine relationships. **C,** Dickerman and Yates' (1995; redrawn after their fig. 2) favored hypothesis of relationships among oryzomyines based on 22 allozymic loci. The depicted tree is the consensus topology of the bootstrap tree derived from five algorithms (binary parsimony, multistate parsimony, Fitch-Margoliash, frequency parsimony, and maximum likelihood). *Holochilus* was used to root the tree.

relationships (fig. 7), which tend to be poorly supported by bootstrap and other resampling measures with values below 50%.

Weksler (2003) performed a phylogenetic study of oryzomyines using nuclear gene sequences; parsimony and likelihood analyses were carried out on a dataset composed of 1266 bp of the IRBP gene for 44 oryzomyines, 15 non-oryzomyine sigmodontines, and 12 outgroup taxa. The phylogenetic analyses recovered several well-supported clades, including: (1) a monophyletic Oryzomyini; (2) a clade containing all oryzomyines except *Scolomys* and *Zygodontomys*; (3) a clade containing *Oecomys*, *Handleyomys*, and several species of forest-dwelling *Oryzomys*; and (4) a clade containing the remaining oryzomyine taxa. The last clade was composed of two large subclades, each with lower nodal support, containing the following taxa: (1) *Microryzomys*, *Oligoryzomys*, *Neacomys*, and *Oryzomys balneator*; (2) *Holochilus*, *Lundomys*, *Pseudoryzomys*, *Nectomys*, *Amphinectomys*, *Sigmodontomys*, and several species of open-vegetation or semi-aquatic *Oryzomys*.

The *Oryzomys* Problem

The central remaining problem in oryzomyine phylogenetics concerns *Oryzomys*, the most speciose and geographically widespread genus of the tribe. Compelling justification for the generic recognition of several taxa formerly included as subgenera of *Oryzomys* (e.g., *Microryzomys*, *Oligoryzomys*, *Sigmodontomys*, *Melanomys*, *Oecomys*, and *Nesoryzomys*; table 1) was provided in previous studies (Gardner and Patton, 1976; Patton and Hafner, 1983; Dickerman and Yates, 1995; Myers et al., 1995; Patton and da Silva, 1995; Weksler, 2003). Nonetheless, even in its strict modern sense (Musser and Carleton, 1993), *Oryzomys* is not demonstrably monophyletic (Voss and Carleton, 1993; Dickerman and Yates, 1995; Myers et al., 1995; Patton and da Silva, 1995; Steppan, 1995; Weksler, 1996, 2003; Percequillo, 1998; Bonvicino and Moreira, 2001; Andrade and Bonvicino, 2003; Bonvicino et al., 2003).

Eleven species groups have been recognized within *Oryzomys*, primarily on the basis of morphological similarity (table 2).

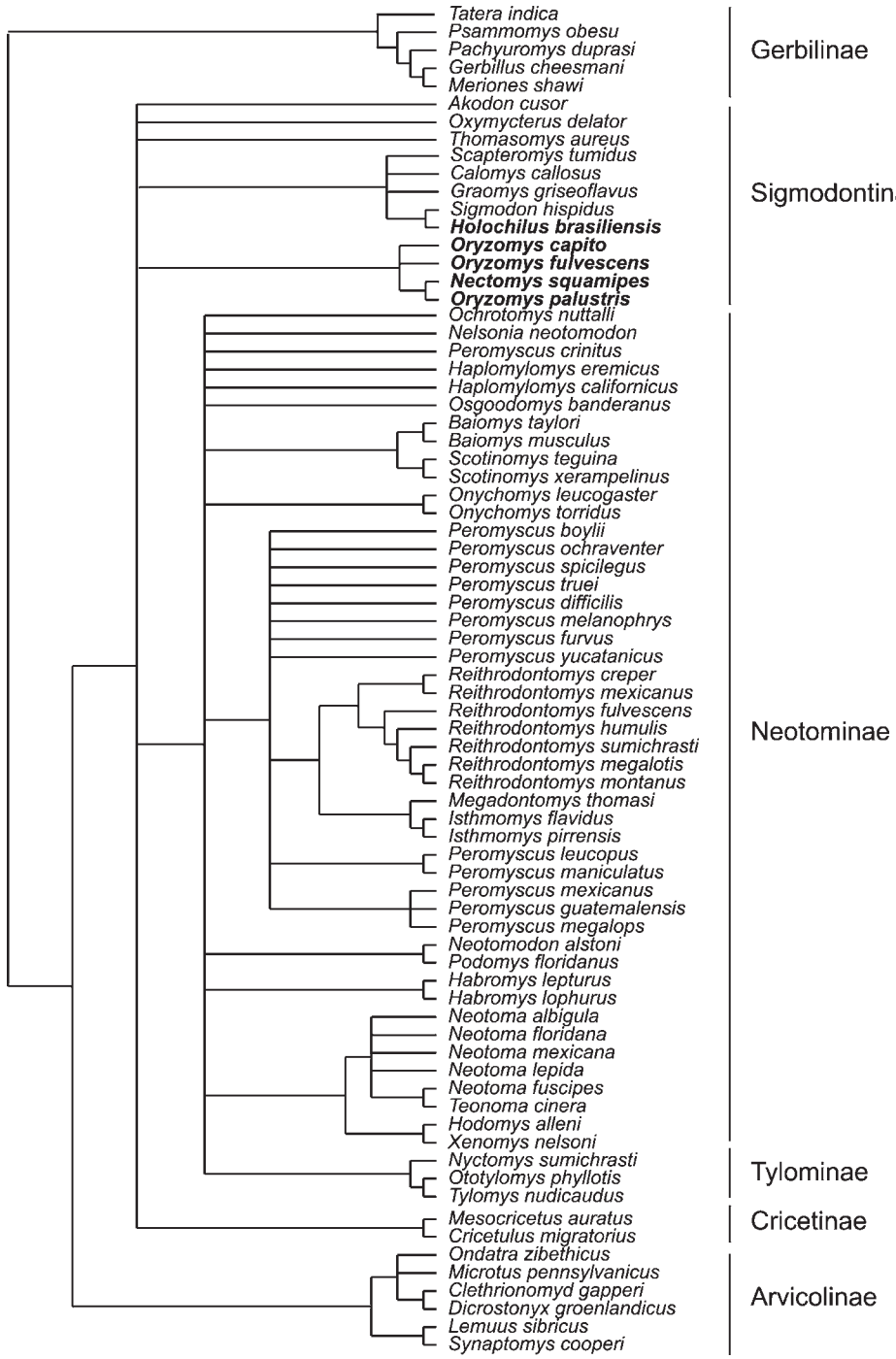


Fig. 6. Result of a parsimony reanalysis of Carleton's (1980) morphological matrix. The original analysis did not employ modern algorithms for parsimony search. Character transformation patterns (Carleton, 1980: table 8) were reproduced using cost matrices. The consensus tree of 15,372 fundamental cladograms (each with 610 steps, CI = 0.277, RI = 0.7529) displays a wide polytomy, which includes several clades of sigmodontines. Oryzomyine taxa are shown in boldface type.

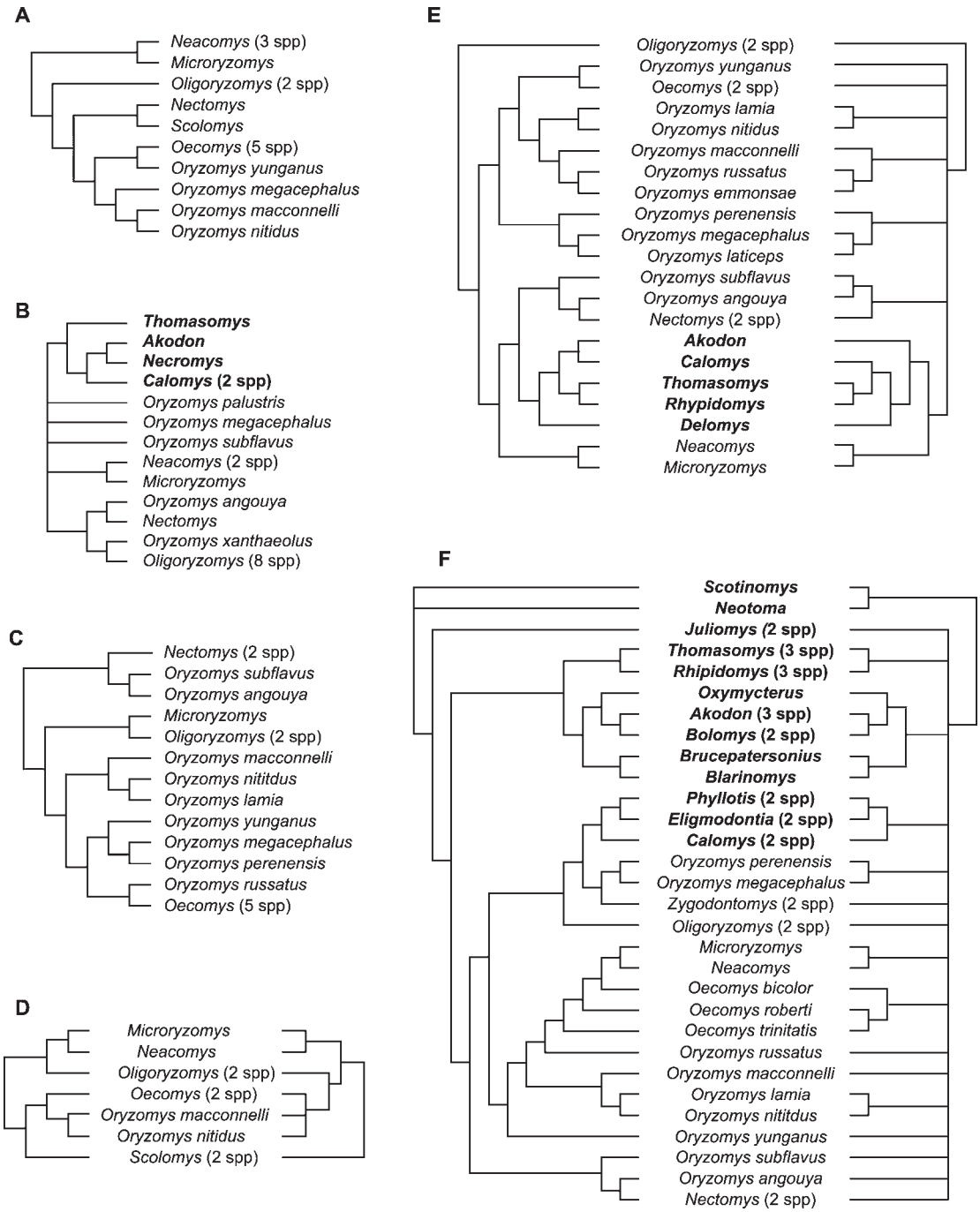


Fig. 7. Hypotheses of relationships among oryzomyine rodents based on the mitochondrial gene cytochrome *b*. For simplicity, species-level taxonomic sampling is not illustrated in these condensed diagrams, except for genera that were not recovered as monophyletic groups. The taxonomy in all of these trees has been updated to reflect current usage. Non-oryzomyine taxa are in boldface type. **A,** Analysis based on 801 bp (Patton and da Silva, 1995; redrawn after their fig. 9B). The depicted cladogram is the result of parsimony analysis of all nucleotide substitutions except third-position transitions. The tree is

TABLE 1
Taxonomic Categories of Six Oryzomyine Genera in Key Taxonomic Checklists

Source	*Melanomys* Thomas, 1902	*Microryzomys* Thomas, 1917	*Nesoryzomys* Heller, 1904	*Oecomys* Thomas, 1906	*Oligoryzomys* Bangs, 1900	*Sigmodontomys* J.A. Allen, 1897
Trouessart (1898)	species within *Oryzomys*	species within *Oryzomys*	no species yet described	species within *Oryzomys*	species within *Oryzomys*	genus
Tate (1932a, 1932b, 1932c, 1932d)	subgenus of *Oryzomys*	synonym of *Oryzomys*	genus	genus (but some species included in *Oryzomys*)	subgenus of *Oryzomys*	synonym of *Nectomys*
Gyldenstolpe (1932)	genus	synonym of *Oryzomys*	genus	genus (but some species included in *Oryzomys*)	genus (but some species included in *Oryzomys*)	synonym of *Nectomys*
Ellerman (1941)	subgenus of *Oryzomys*	subgenus of *Oryzomys*	subgenus of *Oryzomys*	subgenus of *Oryzomys*	subgenus of *Oryzomys*	subgenus of *Nectomys*
Cabrera (1961)	subgenus of *Oryzomys*	subgenus of *Oryzomys*	subgenus of *Oryzomys*	subgenus of *Oryzomys*	synonym of *Oryzomys*	subgenus of *Nectomys*
Honacki et al. (1982)	subgenus of *Oryzomys*	subgenus of *Oryzomys*	genus	subgenus of *Oryzomys*	subgenus of *Oryzomys*	subgenus of *Oryzomys*
Musser and Carleton (1993)	genus	genus	genus	genus	genus	genus

←

rooted with two thomasomyines (*Thomasomys aureus* and *Rhipidomys leucodactylus*) as designated outgroups (not shown). **B,** Analysis based on 401 bp (Myers et al., 1995; redrawn after their fig. 9B). The depicted cladogram is the consensus of two most parsimonious trees obtained by unweighted parsimony analysis of all nucleotide substitutions. The tree is rooted with one murine (*Mus musculus*) as the designated outgroup (not shown). **C,** Analysis based on 801 bp (Andrade and Bonvicino, 2003; redrawn after their fig. 4B). The depicted diagram is the maximum likelihood tree obtained with a 5 : 1 transition:transversion ratio. The tree is rooted with two neotomines (*Neotoma albigula* and *Scotinomys teguina*) as designated outgroups, and also included three non-oryzomyine genera (*Delomys*, *Thomasomys*, and *Rhipidomys*) that form a sister clade to the oryzomyines (not shown). **D,** Analyses based on 801 bp (Gómez-Laverde et al., 2004; redrawn after their figs. 4B and 5). The diagram at the left is the tree recovered by maximum likelihood analysis under the HKY + γ model. The diagram at the right is the strict consensus of two most parsimonious trees obtained by analysis of all nucleotide substitutions except third-position transitions. The trees are rooted with two neotomines (*Neotoma albigula* and *Peromyscus truei*) as designated outgroups, and also include two non-oryzomyine genera (*Thomasomys* and *Rhipidomys*) that form a sister clade to the oryzomyines (not shown). **E,** Trees recovered by Bonvicino and Moreira (2001). The diagram at the left is the maximum likelihood tree obtained with a 5 : 1 transition:transversion ratio. The diagram at the right is the strict consensus of six most parsimonious trees obtained by unweighted parsimony analysis of all nucleotide substitutions. The trees are rooted with two murines (*Mus musculus* and *Rattus norvegicus*) as designated outgroups (not shown). Note that oryzomyines were not recovered as monophyletic groups in either the parsimony or in the likelihood analysis results; however, a neighbor-joining tree (not shown) based on Kimura two-parameter distances recovered a monophyletic Oryzomyini. **F,** Results of Bonvicino et al. (1999) based on DNA sequence data. The diagram at the left is the maximum likelihood tree obtained with a 2 : 1 transition:transversion ratio. The diagram at the right is the bootstrap tree obtained by weighted parsimony analysis with a 5 : 1 transition:transversion ratio. The trees were rooted with two neotomines (*Neotoma albigula* and *Scotinomys teguina*) as designated outgroups (not shown).

TABLE 2
Species Groups Within the Genus *Oryzomys*
Asterisks (*) indicate species in the present analysis.

Group	Species
albigularis[a, b, c, d, e, f, g]	*albigularis*, auriventer, devius, keaysi, levipes*, meridiensis, caracolus*
megacephalus[a, g, h, m, n]	*megacephalus,* oniscus, perenensis, seuanezi*
chapmani[a]	*chapmani*, saturatior*
yunganus[g, h]	*tatei, yunganus**
nitidus[a, b, g, h, i, j]	*emmonsae, lamia*, legatus, macconnelli*, nitidus, russatus**
subflavus[g, o, p, q]	*maracajuensis, marinhus, subflavus*, scotti, andersoni*
melanotis[a, k]	*melanotis, rostratus**
talamancae[g, h]	*boliviaris, talamancae**
Palustris[a, g, k, l]	*couesi,* dimidiatus, gorgasi, nelsoni, palustris**
xanthaeolus[a, g, r, s]	*bauri, galapagoensis, xanthaeolus**
alfaroi[a, g, k]	*alfaroi*, rhabdops*
species without known relationships[a]	*angouya*, balneator*, hammondi*, polius**

Sources are noted with superscript letters: **a**, Musser and Carleton (1993); **b**, Gardner and Patton (1976); **c**, Gardner (1983); **d**, Patton et al. (1990); **e**, Aguilera et al. (1995); **f**, Márquez et al. (2000); **g**, Percequillo (2003); **h**, Musser et al. (1998); **i**, Bonvicino et al., (1998); **j**, Silva et al. (2000); **k**, Goldman (1918); **l**, Sanchez-H. et al. (2001); **m**, Weksler et al. (1999); **n**, Patton et al. (2000); **o**, Langguth and Bonvicino (2002); **p**, Bonvicino (2003); **q**, Brooks et al. (2004); **r**, Patton and Hafner (1983); **s**, Dowler et al. (2000).

In addition, four other species (*O. balneator*, *O. hammondi*, *O. polius*, and *O. angouya*) have not been assigned by authors to any group. In the past, attempts to develop a comprehensive phylogeny for the genus were hindered by the rudimentary alpha-taxonomy and vague delimitation of these species groups, making taxonomic sampling of *Oryzomys* little better than guesswork. Recently, however, substantial progress in revisionary studies (e.g., Patton and Hafner, 1983; Musser and Carleton, 1993; Musser et al., 1998; Weksler et al., 1999; Patton et al., 2000; Bonvicino and Moreira, 2001; Sanchez-H. et al., 2001; Langguth and Bonvicino, 2002; Andrade and Bonvicino, 2003; Bonvicino, 2003; Percequillo, 1998, 2003; Weksler, 2003) have made it possible to rationally select phylogenetic exemplars among the morass of congeneric forms.

The objective of this study is to provide a phylogenetic hypothesis for the tribe Oryzomyini that can be used to understand the diversification and evolution of this group of rodents and to revise the current generic-level classification. Morphological and molecular data are employed for these purposes in combined and separate analyses. The molecular dataset was obtained from my previous study (Weksler, 2003), but the morphological data are newly assembled herein. To do so, a thorough and strict evaluation was performed on previously described characters, and a few new characters were discovered from comparisons of integumental, cranial, dental, external, and visceral morphology. Below, I provide anatomical descriptions of each suitable character, with definitions of the different states observed among oryzomyines and outgroup taxa. The systematics of the tribe and the evolution of a few pivotal characters are subsequently discussed in light of the proposed phylogeny. Different taxonomic arrangements for species currently included in the genus *Oryzomys* are suggested. Finally, I evaluate evolutionary and biogeographic hypotheses that are compatible with current knowledge of oryzomyine relationships.

MATERIALS AND METHODS

Taxonomic Sampling and Morphological Character Scoring

The designated ingroup for all phylogenetic analyses that follow is restricted to the tribe Oryzomyini as defined by Voss and Carleton (1993), including all extant oryzomyine genera described thereafter. Ingroup terminals were chosen to maximize morphological diversity within speciose genera, thereby providing the most rigorous tests of generic

TABLE 3
Taxonomic Diversity of Extant Oryzomyine Genera and Number of Included Species per Taxon
Species groups are listed for *Oryzomys*.

Genera	No. species	No. included species
Amphinectomys	1	1
Handleyomys	2	1
Holochilus	4	2
Lundomys	1	1
Melanomys	3	1
Microryzomys	2	1
Neacomys	8	3
Nectomys	8	2
Nesoryzomys	4	2
Oecomys	15	5
Oligoryzomys	16	5
Oryzomys	43	19
albigularis	7	2
alfaroi	2	1
chapmani	2	1
megacephalus	4	1
melanotis	2	1
nitidus	6	3
palustris	5	2
subflavus	5	1
talamancae	2	1
xanthaeolus	3	1
yunganus	2	1
unknown position	4	4
Pseudoryzomys	1	1
Scolomys	2	1
Sigmodontomys	2	2
Zygodontomys	3	2
Total	116	49

monophyly. Sampling was densest in *Oryzomys*, *Oligoryzomys*, and *Oecomys,* and a special effort was made to sample all traditionally recognized species groups within *Oryzomys*. In all, I included representatives of all 16 extant oryzomyine genera, consisting of 49 of the 116 currently recognized oryzomyine species (table 3). Type species from all but three genera (*Handleyomys*, *Holochilus*, and *Scolomys*) were included in order to confidently associate analytic results with appropriate clade names.

The outgroups for the analyses consist of five genera: *Peromyscus*, *Nyctomys*, *Thomasomys*, *Wiedomys*, and *Delomys*. The first two are non-sigmodontine cricetids (sensu Jansa and Weksler, 2004; Steppan et al., 2004) and were used to root the tree. The last three are pentalophodont sigmodontines previously regarded as closely related to oryzomyines (Hershkovitz, 1962; Steppan, 1995; Pacheco, 2003) or that exhibit putatively plesiomorphic character-states within sigmodontines (Voss, 1993). All analyses were run with unconstrained ingroup and outgroup designations (Nixon and Carpenter, 1993), and trees were subsequently rooted on the assumption of sigmodontine monophyly.

I scored craniodental characters from cleaned skeletons and skulls and examined external characters using both dried skins and fluid-preserved specimens (when available). Whenever possible, I examined at least 10 specimens per taxon. In several cases, however, available samples were smaller than this, particularly for skeletal and visceral characters. Several characters were examined in restricted semaphoronts: skull characters were usually scored from adult individuals, whereas dental characters were evaluated in younger specimens with newly erupted molars. All examined specimens are listed in appendix 1.

My scoring of male accessory gland traits (characters 90–97) was based entirely on the descriptions of Voss and Linzey (1981) with a few exceptions (the conditions in *Nesoryzomys* and *O. xanthaeolus* were taken from Patton and Hafner, 1983); I did not examine any specimens for this morphological system. Previous studies were also used for scoring characters of the vertebral column (characters 78 and 79; Steppan, 1995), glans penis (85–89; Hooper and Musser, 1964; Carleton, 1980), and digestive tract (98 and 99; Carleton, 1973; Voss, 1991). Nevertheless, direct examination of specimens for these characters were made whenever exemplars were available. Scoring of *Amphinectomys savamis* was based entirely on the original description of the genus (Malygin et al., 1994).

Character Sampling and Description

Because characters were primarily selected to resolve oryzomyine relationships, the dataset does not include autapomorphic characters for outgroup taxa; it does, however, include autapomorphies for ingroup taxa that might serve as synapomorphies for

clades represented by a single species in this analysis. I initially surveyed all morphological characters reported in previous phylogenetic analyses of sigmodontine relationships (Carleton, 1980; Patton and Hafner, 1983; Voss, 1988, 1991; Carleton and Musser, 1989; Braun, 1993; Steppan, 1993, 1995; Voss and Carleton, 1993; Steppan and Pardiñas, 1998; Carleton and Olson, 1999; Luna, 2002; Pacheco, 2003), but other potentially informative features described in the comparative morphological literature (Hooper and Musser, 1964; Carleton, 1973; Voss and Linzey, 1981) and in taxonomic studies (e.g., Goldman, 1918; Hershkovitz, 1962; Steadman and Ray, 1982; Musser and Williams, 1985; Olds and Anderson, 1989; Voss, 1993; Musser et al., 1998; Voss et al., 2002; Voss, 2003) were also evaluated. In total, I surveyed 350 previously described characters, including 136 from the skull, 88 from the dentition, 52 from the external morphology, 16 from the postcranial skeleton, and 57 from the viscera.

Many previously described characters were unsuitable for the present analysis for a variety of reasons. Lengths, ratios, and other quantitative traits were not included because no proper method is currently available for coding continuous characters in a parsimony-analytic context (but see Goloboff et al., 2004). Characters describing relative position, distance, shape, or color were included only if distinct (noncontinuous) differences between states could be established. Several of these characters previously used in studies with few oryzomyine taxa were impossible to score unambiguously in the present study due to continuous variation introduced by anatomically intermediate forms. Numerous characters in the literature were difficult to interpret due to ambiguous state descriptions that could not be associated meaningfully with conditions observed in the present material. Thus, only features with explicitly defined and distinctly different character-states were employed. In a few cases, these criteria were relaxed when a few taxa with intermediate morphologies could not be placed in states that were otherwise distinct in most examined species. Features displaying high intraspecific variation in many taxa were not included. However, characters displaying polymorphism for just a few taxa were included if they were parsimony-informative among the remaining (nonpolymorphic) taxa. An annotated list of all analyzed characters, including rejected characters, is provided in appendix 2.

Multistate characters were treated as ordered if anatomical intermediates could be recognized among the set of alternative conditions. This follows the framework of recognizing internal levels of similarity within characters (Wilkinson, 1992). For simplicity, the conditions observed in the most distant outgroup taxa (*Nyctomys* and *Peromyscus*) were placed as the putatively plesiomorphic state (i.e., "0") on the character descriptions. Proper polarity of characters was determined after rooting the trees.

Polymorphisms were analyzed in two ways, as composites or as ordered transformation series (Campbell and Frost, 1993; Mabee and Humphries, 1993; Wiens, 1995, 2000; Simmons and Geisler, 2002). In the first case, the polymorphic entry is coded as a composite character-state encompassing the observed range of variation (e.g., "{01}" for a taxon with states 0 and 1 observed among its exemplars; "polymorphic" coding of Wiens, 2000). In the second case, the polymorphic condition is considered as a new character-state intermediate to the fixed conditions, and the transformation series is treated as ordered ("scaled" coding of Wiens, 2000). Missing data were scored as "?" if they resulted from lack of specimens with appropriate material or as "–" if they resulted from inapplicable comparisons.

Data Analysis

Cladistic parsimony analyses were performed on three different datasets: (1) IRBP-only, (2) morphology-only, and (3) combined morphology and IRBP matrices. The last two matrices were analyzed with the two different codings for polymorphic entries: composite and transformation series (hereafter referred to as *CO* and *TS* analyses, respectively). The contribution of each data partition for the resolution of the combined topology was inferred by comparing clades recovered in the combined tree with trees recovered from the separate analyses and

evaluating associated measures of nodal support. Such inspection also served to reveal patterns of agreement or incongruence between datasets.

The heuristic search algorithm implemented by PAUP* 4.0b10 (Swofford, 2001) was used in all parsimony analyses. Each heuristic search employed 1000 replicates of random-taxon addition with TBR branch swapping. Only clades with at least one unambiguous synapomorphy (i.e., present in both ACCTRAN and DELTRAN character reconstructions; Wilkinson, 1995) were retained (commands PSET COLLAPSE = MIN; FILTER BEST in PAUP*). This option avoids some of the undesirable analytical artifacts of missing data reported by Platnick et al. (1991), and it reduces the number of fundamental trees to a minimal conservative set.[1]

Characters were equally weighted in all analyses. IRBP sequence characters were always treated as unordered, but some multistate morphological characters were ordered as described above. Most additive multistate characters followed a simple linear sequence (e.g., $0 \leftrightarrow 1 \leftrightarrow 2$), but cost matrices were applied to two multistate characters (Sankoff and Rousseau, 1975; Sankoff et al., 1976) in order to accommodate more complex hypotheses of state transformations (command USERTYPE XX (STEPMATRIX) = XX in PAUP*; fig. 8A). Step matrices were also used to accommodate polymorphism as transformation series entries (fig. 8B) following the approach of Mabee and Humphries (1993). Braces were used for coding polymorphisms as composite entries following PAUP* convention.

Characters were optimized on fundamental cladograms with both accelerated (ACCTRAN) and delayed (DELTRAN) transformation options. Throughout the text, only unambiguous synapomorphies (recovered by both ACCTRAN and DELTRAN optimizations) are reported. However, all ACCTRAN and DELTRAN synapomorphies are listed in appendices 4 and 5 for the morphology-only and combined analyses, respectively. To calculate Bremer support values (or decay index, DI; Bremer, 1988, 1994), heuristic searches (with 10 random-addition replicates and TBR branch swapping) were performed with a constraint placed for each node found in the consensus tree and with the ENFORCE REVERSE options on the heuristic search command in PAUP*. Jackknife values (JK; Farris et al., 1996) were calculated from analyzed 1000 pseudoreplicated datasets using heuristic searches with 10 random-addition replicates and TBR branch swapping; a maximum of 200 trees were retained in each random-addition replicate (for a total of 2000 trees per pseudoreplicate). In each jackknife pseudoreplicate, 36.79% of characters were removed (Farris et al., 1996). Bootstrap resampling (Felsenstein, 1985) provided similar results, but it was omitted for simplicity.

Five ingroup taxa lack IRBP sequences, resulting in many missing entries in the combined data matrix (table 4). To evaluate the potential effects of missing data entries (e.g., spurious phylogenetic relationships [Platnick et al., 1991], lack of resolution [Nixon and Wheeler, 1992], and decreased nodal support), I performed an additional sixth analysis of a reduced supermatrix comprised of molecular and morphological characters but omitting the five taxa without IRBP sequences (hereafter referred to as *reduced* analysis). This analysis was performed with polymorphisms scored as composite entries.

RESULTS

Character Descriptions

External Morphology

Character 1: *Four mammae present in inguinal and abdominal pairs (0); or six mammae in inguinal, abdominal, and postaxial pairs (1); or eight mammae in inguinal, abdominal, postaxial, and pectoral pairs (2).* Almost all oryzomyines have eight mammary glands, and the presence of pectoral mammae was considered one of the synapomorphies for the tribe (Voss and Carleton, 1993; Steppan, 1995). However, specimens of *Scolomys* and *Handleyomys* lack the pectoral

[1] The consensus trees derived from all PAUP*'s collapsing options (MAX, MIN, AMB) have the same topology.

TABLE 4
Summary of Taxon–Character Matrix

Character systems from which information is missing are: DE, dentition; PS, postcranial skeleton; PE, glans penis; GL, male accessory reproductive glands; DS, digestive system.

Taxon	Missing	Inapplicable	% complete	Systems not analyzed
Nyctomys sumichrasti	0	3	97	
Peromyscus maniculatus	4	6	90	
Delomys sublineatus	13	0	87	PE, GL
Thomasomys baeops	3	0	97	
Wiedomys pyrrhorhinos	12	0	88	GL, DS
Amphinectomys savamis	67	0	32	DE, PS, PE, GL, DS
Handleyomys intectus	16	0	84	PE, GL
Holochilus brasiliensis	0	1	99	
Holochilus chacarius	21	1	78	PS, PE, GL
Lundomys molitor	8	1	91	GL
Melanomys caliginosus	1	0	99	
Microryzomys minutus	3	0	97	
Neacomys minutus	22	0	78	PS, PE, GL, DS
Neacomys musseri	16	0	84	PS, GL
Neacomys spinosus	1	0	99	
Nectomys apicalis[a]	15	0	85	PE, GL
Nectomys squamipes	5	0	95	
Nesoryzomys narboroughi	5	0	95	
Nesoryzomys swarthi	37	0	63	DE, PE, GL, DS
Oecomys bicolor	8	0	92	GL
Oecomys catherinae	23	0	77	PS, PE, GL, DS
Oecomys concolor	1	0	99	
Oecomys mamorae	10	0	90	GL
Oecomys trinitatis	12	0	88	GL
Oligoryzomys flavescens	11	0	89	GL
Oligoryzomys fornesi	21	0	79	PE, GL, DS
Oligoryzomys fulvescens	0	1	99	
Oligoryzomys nigripes	8	0	92	
Oligoryzomys stramineus	23	0	77	PS, PE, GL, DS
Oryzomys albigularis	9	0	91	GL
Oryzomys alfaroi	7	0	93	PS
Oryzomys angouya	2	0	98	
Oryzomys balneator	16	0	84	PS, GL
Oryzomys chapmani[a]	10	0	90	GL
Oryzomys couesi	10	0	90	GL
Oryzomys hammondi[a]	23	0	77	PS, PE, GL
Oryzomys lamia	22	0	78	PS, PE, GL
Oryzomys levipes[a]	10	0	90	GL
Oryzomys macconnelli	8	0	92	GL
Oryzomys megacephalus	0	0	100	
Oryzomys rostratus[b]	1	0	99	
Oryzomys palustris	0	0	100	
Oryzomys polius	22	0	78	PS, PE, GL, DS
Oryzomys russatus	14	0	86	PE, GL
Oryzomys subflavus	8	0	92	GL
Oryzomys talamancae	1	0	99	
Oryzomys xanthaeolus	9	0	91	GL
Oryzomys yunganus	11	0	89	GL
Pseudoryzomys simplex	8	1	91	GL
Scolomys ucayalensis	9	0	91	GL

TABLE 4
(*Continued*)

Sigmodontomys alfari	2	0	98	
Sigmodontomys aphrastus[a]	22	0	78	PS, PE, GL
Zygodontomys brevicauda	0	1	99	
Zygodontomys cherriei	0	1	99	

[a] IRBP is missing for this taxon.

[b] Weksler (2003) incorrectly reported *Oryzomys melanotis* from El Salvador. In reality, it is *Oryzomys rostratus*, the same taxon used here. *O. rostratus* and *O. melanotis* are the only two members of the *melanotis* species group. Hooper (1953) considered them as subspecies of *O. melanotis*, but Goldman (1918) and Engstrom (1984; fide Musser and Carleton, 1993) retained them as separated species.

pair.[2] Among non-oryzomyine taxa, *Nyctomys* has only four mammae, *Peromyscus* and *Thomasomys* have six, and *Delomys* and *Wiedomys* have eight. Lacking suitable female material, I could not determine the number of mammae in *Amphinectomys*, *Holochilus chacarius*, *Nesoryzomys narboroughi*, and *N. swarthi*.[3]

My scoring of several taxa is at odds with some observations in the literature. Steppan (1995: table 6; also Gyldenstolpe, 1932), for example, stated that *Neacomys* has only six mammae (lacking the pectoral pair); however, all exemplars of the three included species of *Neacomys* that I analyzed have eight mammae, including the pectoral pair (see also Voss et al., 2001). The same is true for *Wiedomys*, which Steppan (1995) reported as having six mammae, whereas I observed eight (see also Pacheco, 2003). More problematic is the positional identification of the "axillarie" pair (Arvy, 1974) of *Scolomys*. Patton and da Silva (1995), using the positional chart of muroid mammary loci of Voss and Carleton (1993), described *Scolomys* as having a thoracic pair of mammae rather than a postaxial pair. Indeed, the anteriormost pair of mammae in *Scolomys* is situated more posteriorly than are the postaxial mammae of most oryzomyines. Because there seems to be a continuous variation in the position of this pair among other oryzomyines, however, it is impossible to falsify the hypothesis that the thoracic mammae of *Scolomys* and the postaxial mammae of other oryzomyines are homologous using topographical criteria. Lacking other (e.g., ontogenetic) information, it seems more parsimonious to recognize thoracic mammae only when postaxial mammae are also present. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).[4]

Character 2: *Claws of manus small, not extending much beyond digital pads, not keeled (0); or claws long, extending conspicuously beyond digit pads and ventrally, keeled for about half their length (1).* Although claw size is a continuous trait, the two described states can be unambiguously differentiated by the presence or absence of keels on the ventral surface of the unguis. Long keeled claws were observed only in *Lundomys*. The remaining ingroup and outgroup taxa have small claws that are ventrally open, or keeled only in proximity of contact with the digit. No information is currently available about the morphology of the claws in *Amphinectomys* (scored as missing, "?", in table 5).

Character 3: *Ungual tufts at base of manual claws present and long (0); or reduced or absent (1).* Ungual tufts, consisting of hairs rooted at the base of claws, have been extensively cited in sigmodontine phylogenetic studies (see character 7), but the presence or absence of the tufts on the manus has only been recently used (Pacheco, 2003).

[2] Some populations of *Holochilus sciureus* (taxon not included in the analysis) have individuals with 10 mammae (thoracic pair present; Carleton and Voss, 1993), constituting the only other known oryzomyine without 8 mammae.

[3] Available specimens of congenerics *Nesoryzomys darwini* and *N. indefessus* displayed 8 mammae.

[4] Analyses with the condition of each mammae loci treated as a separated binary character arrived at the same phylogenetic results.

TABLE 5
Data Matrix
Polymorphic entries are coded as: {01} = A; {02} = B; {12} = C; {23} = D.

Taxon	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890
Nyctomys sumichrasti	0000000001	0001000000	0400000000	1001030001	0000100000
Peromyscus maniculatus	1000010000	2000001001	0000010000	0000000000	1010100000
Delomys sublineatus	2000110001	1100001001	0000010110	0001010100	1011000100
Thomasomys baeops	1000001001	01001100A2	0000110011	0001122000	1010200111
Wiedomys pyrrhorhinos	2000010001	00001000A2	0300010100	0101100100	2010000?11
Amphinectomys savamis	???????121	?100000002	14?0020110	1203?1???1	???01?0???
Handleyomys intectus	1000101001	0100100012	1000A20111	1202020100	011010011C
Holochilus brasiliensis	2011213121	0100100001	1211110201	111D202000	2110211112
Holochilus chacarius	?011213121	0100100001	1211110201	1212202000	2100211?12
Lundomys molitor	2111213121	0100100011	0100110211	0212212100	1110100102
Melanomys caliginosus	2000112002	010020001C	1401120111	1102122101	1100110?12
Microryzomys minutus	2000111001	1100200011	0000011002	1102110100	0110200100
Neacomys minutus	2000111001	0111000012	0400010101	1202110100	0110200?00
Neacomys musseri	2000111001	0111000012	0400010101	1202111100	0110100?00
Neacomys spinosus	2000111001	0111000012	0400010101	1202110100	01A0200?10
Nectomys apicalis	2011213121	0100100112	0401120111	1103122101	1100210112
Nectomys squamipes	2001212121	0100100112	1401110111	11031C2101	1100110112
Nesoryzomys narboroughi	?000111000	2000110001	1100110111	0203102101	2100211112
Nesoryzomys swarthi	?000111000	1000110001	1100110110	0103102100	2100211112
Oecomys bicolor	2000001001	0101000001	1400110001	1202120A00	A1A0200?10
Oecomys catherinae	2000001001	0100000001	0400110011	1202120100	1101100?10
Oecomys concolor	2000001001	0101100001	0400110001	1202122A00	A110100?10
Oecomys mamorae	2000011001	0101100001	040011000C	1202122100	1110100?10
Oecomys trinitatis	2000001001	0100000001	1400110001	1202120A00	A1A0200?11
Oligoryzomys flavescens	2000111001	1100100011	0000010102	1202001100	0111201?00
Oligoryzomys fornesi	2000111001	1100100011	0000010102	1202001100	0111201?00
Oligoryzomys fulvescens	2000111001	1100100011	0000010102	1202001100	0111201100
Oligoryzomys nigripes	2000111001	11000000A1	0000010102	1202001100	0111201100
Oligoryzomys stramineus	2000111001	1100000011	0000010102	1202001100	0111201?00
Oryzomys albigularis	2000101001	1100010001	0000A10112	1103110A00	11A0100101
Oryzomys alfaroi	2000101001	210000000C	0300A10111	120D100100	1110100?12
Oryzomys angouya	2000110001	11000000A1	A1001C0111	0103102100	1110200?11
Oryzomys balneator	2000111001	0101000012	0000010002	1102110100	0111200?01
Oryzomys chapmani	2000101001	0100000001	0300A101A1	1203102100	111A200?12
Oryzomys couesi	2001212001	1100100001	1400120101	0203122100	1110200?12
Oryzomys hammondi	200010200?	0100100001	0301110010	1101120101	0100000?00
Oryzomys lamia	2000101001	2100000012	0300010112	1202120A00	1100200?01
Oryzomys levipes	2000101001	1100000001	1100AC0111	1003110000	1110100?01
Oryzomys macconnelli	2000101001	2100000001	0300AC0111	1202120100	1100000101
Oryzomys megacephalus	2000101001	1100000001	1100010111	120D1C1100	1110000100
Oryzomys palustris	2011212011	2100000011	1400120101	0203102100	111010011C
Oryzomys polius	2000110000	2100100001	0400120111	0103202000	1110010100
Oryzomys rostratus	2000111001	1100000001	0300010101	1203100100	A110100?12
Oryzomys russatus	2000101001	2100000001	0300010111	1102120A00	1100200101
Oryzomys subflavus	2000111001	1100000001	04001C010C	0103102101	11A1200112
Oryzomys talamancae	2000101001	1100000001	0300A10111	120D110100	11A0100?00
Oryzomys xanthaeolus	2000111001	11000000AC	14001C01A1	0203102101	11A0110112
Oryzomys yunganus	200A101001	2100000001	0300010111	1202121100	1110000?00
Pseudoryzomys simplex	2001212011	2100000011	1300110201	0202102A00	1110200112
Scolomys ucayalensis	1001111001	0110100112	1300020000	1202122110	1100100100
Sigmodontomys alfari	2001212012	01000000AC	140111010C	1102112101	11002A0112
Sigmodontomys aphrastus	2001203002	0100200112	1401110000	1101112101	1100A00?12
Zygodontomys brevicauda	2000111001	11001000A1	040002011C	02021B2100	1101101100
Zygodontomys cherriei	2000101001	11001000A1	0400020111	0202100101	1101211100

TABLE 5
(*Continued*)

Taxon	5555555556 1234567890	6666666667 1234567890	7777777778 1234567890	8888888889 1234567890	999999999 123456789
Nyctomys sumichrasti	0000000000	0000100001	0100000000	00000--000	112000-10
Peromyscus maniculatus	0000000000	00100-0110	1010002000	00000----2	000????0-
Delomys sublineatus	0000002000	0000000001	1100000010	0111??????	???????00
Thomasomys baeops	0000000000	0000000002	1100000011	A1001??101	00001?000
Wiedomys pyrrhorhinos	0000000000	0001000002	1000000111	111110?00?	?????????
Amphinectomys savamis	?1?0??????	??????????	??????????	??????????	?????????
Handleyomys intectus	1100002200	0000010111	11000?011?	111???????	???????10
Holochilus brasiliensis	1011112230	01110-0001	1020002110	2111101011	000011011
Holochilus chacarius	1011112230	02110-0001	1020002l??	??????????	???????11
Lundomys molitor	A000111010	01000-1001	1010002110	2111100000	???????10
Melanomys caliginosus	0100000220	1001000011	1000000111	2111110001	000011010
Microryzomys minutus	0000000000	1000000102	1000000111	11111??0?1	000011011
Neacomys minutus	0000000000	1000000111	1000000???	??????0???	?????????
Neacomys musseri	0000000000	1000000111	100001O???	????10000?	???????11
Neacomys spinosus	0000000200	1000000111	1000000111	1111100001	000111010
Nectomys apicalis	0000001220	0001000011	100001011?	21?1??????	???????11
Nectomys squamipes	0000001220	0001000001	100000011?	21?110???1	000011011
Nesoryzomys narboroughi	0000000000	1001000001	1000000110	011111??01	111?11?10
Nesoryzomys swarthi	?000000???	??????????	???????110	2111??????	?????????
Oecomys bicolor	0000001200	0000100011	1100000111	1101101001	???????10
Oecomys catherinae	0000001200	0000100001	1100000???	??????????	?????????
Oecomys concolor	0000001000	0000100001	1100000110	1101101001	000011010
Oecomys mamorae	0000001200	0000100001	1100000111	111?10100?	???????10
Oecomys trinitatis	0000001200	0000100001	1100000111	111110????	???????10
Oligoryzomys flavescens	0000000000	1000000011	1000000111	?11?100101	????????1?
Oligoryzomys fornesi	0000000000	1000000011	100000012?	?????????1	?????????
Oligoryzomys fulvescens	0000000000	1000000001	1000000111	2111100102	000-11010
Oligoryzomys nigripes	0000000000	1000000001	1000000111	211?100102	???????10
Oligoryzomys stramineus	0000000000	1000000011	1000000???	??????????	?????????
Oryzomys albigularis	0000002000	0000000011	1100000011?	1111101002	???????10
Oryzomys alfaroi	1000000200	1000010111	110000012?	????110001	000011110
Oryzomys angouya	0000000001	1000010001	1100000110	2101101001	00001101?
Oryzomys balneator	0000000000	1000000102	1000000???	????10000?	???????11
Oryzomys chapmani	1000000200	1000010111	1000000111	111?11000?	???????10
Oryzomys couesi	?000000200	1000010001	1000100111	2111100112	???????10
Oryzomys hammondi	?100002200	1001000001	110001O???	??????????	???????10
Oryzomys lamia	0000001200	0000000101	0000000???	??????????	????????1?
Oryzomys levipes	0000002000	0000000011	1100000110	1111101002	????????1?
Oryzomys macconnelli	0000001200	1000010101	1100000110	1111101002	???????10
Oryzomys megacephalus	0000000200	0000000101	1100000111	1111101001	000010110
Oryzomys palustris	A000000100	1000010001	1000100111	2111101111	000011110
Oryzomys polius	?000000000	0000000011	100010012?	??????????	?????????
Oryzomys rostratus	1000000200	A000010111	1000000111	1111110001	000011210
Oryzomys russatus	0000001200	0000010101	1000000110	1111??????	????????1?
Oryzomys subflavus	0000000100	A0000100A1	1000000110	2111110002	???????10
Oryzomys talamancae	0000002200	0000000111	1100000110	1111101001	000010110
Oryzomys xanthaeolus	1000000020	1001000011	1000000110	211?11000?	???????10
Oryzomys yunganus	0000001200	0000010111	110000011?	111?10100?	???????10
Pseudoryzomys simplex	1000000130	11000-1001	0020001111	211111?001	???????11
Scolomys ucayalensis	0100000220	1001001111	1000000111	01111?100?	???????10
Sigmodontomys alfari	1000001220	0001000011	1001010110	2111110001	000?2101?
Sigmodontomys aphrastus	?100002220	0001000011	1000110???	??????????	???????11
Zygodontomys brevicauda	1000000230	22010-1001	1020002111	?111101001	000011010
Zygodontomys cherriei	1000000230	22010-1101	1020002111	?111101001	000011010

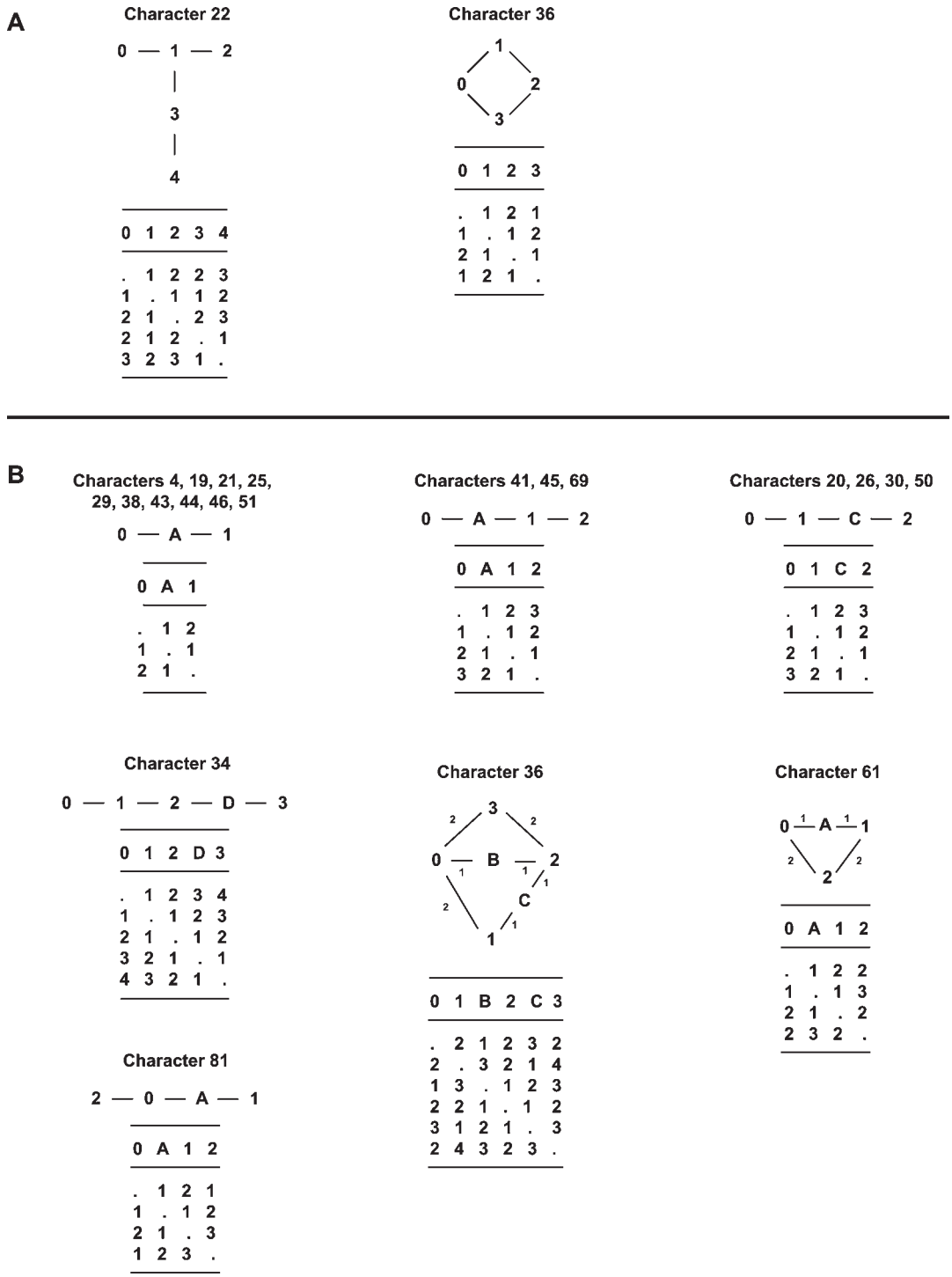


Fig. 8. Transformation series and step matrices for characters with complex change patterns (**A**) and for characters with polymorphic data entries in the analysis of polymorphism as transformations series (**B**).

Although ungual tufts on the manus and pes are serially homologous, they exhibit distinct patterns of occurrence among oryzomyines. Most examined taxa have ungual tufts on the manual claws, but *Holochilus*, *Lundomys*, *Nectomys apicalis*, and *Oryzomys palustris* lack them. No information is currently available about the occurrence of manual ungual tufts in *Amphinectomys* (coded "?").

Character 4: *Hypothenar pad of pes present (0); or absent or vestigial (1).* Plantar foot pads are epidermal and dermal thickening of discrete areas on the surface of feet, often containing eccrine glands (Brown and Yalden, 1973; Haffner, 1998). In rodents, pads are usually most developed in arboreal taxa, whereas pads of semiaquatic or fossorial rodents are the least developed (Hershkovitz, 1944, 1960; Brown and Yalden, 1973). Most oryzomyines (and sigmodontines in general) have two metatarsal pads on the hindfoot, the thenar and hypothenar pads (fig. 9A, B). In contrast, the hindfoot of *Holochilus*, *Lundomys*, *Nectomys*, *Scolomys*, *Sigmodontomys*, *Pseudoryzomys*, *Oryzomys palustris*, and *O. couesi* have only a conspicuous thenar pad, with the hypothenar pad being absent or vestigial[5] (fig. 9C). *Oryzomys yunganus* is polymorphic for this trait (see Musser et al., 1998: 58). No information is currently available about morphology of pads in *Amphinectomys* (coded "?").

Character 5: *Plantar pads on hindfeet large and fleshy, interdigitals 1–4 set close together, often in contact (0); or pads smaller but still fleshy, interdigitals 1 and 4 displaced proximally relative to 2 and 3 (1); or interdigital pads distributed as in state 1 but extremely small and with low relief (2).* *Oecomys* is the only oryzomyine with highly developed interdigital pads (fig. 9A), sharing this condition with all outgroup taxa except *Delomys*. *Holochilus*, *Lundomys*, *Nectomys*, *Sigmodontomys*, *Pseudoryzomys*, *Oryzomys palustris*, and *O. couesi* have reduced interdigital pads (fig. 9C), and the remaining taxa have fleshy, but not highly developed, interdigital pads (fig. 9B). With the exception of *Scolomys*, the same taxa that lack the hypothenar pad also have reduced interdigitals pads, suggesting a correlation between this and the last character; previous studies have described both features in a single multistate character (e.g., Carleton, 1980: char. 77; Carleton and Musser, 1989: char. 2; Voss and Carleton, 1993: char. 3). Nevertheless, I preferred to recognize the configuration of *Scolomys* as conflictual, rather than intermediary, and kept each trait as separated characters. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$) to reflect the morphoclinal aspect of the development of pads. No information is currently available about pad morphology in *Amphinectomys* (coded "?").

Character 6: *Plantar surface of hindfeet smooth, without well-developed squamae (0); or plantar surface covered with squamae (1).* The sole of the hindfoot of most oryzomyines is continuously covered with small scalelike irregularities that Voss et al. (2002) called "squamae" (fig. 9C). In contrast, the squamae are absent (fig. 9A), or present as inconspicuous irregularities along the margins of the sole or at the proximal region of the digits (but never at the central sole region around the plantar pads; fig. 9B), in *Handleyomys*, all *Oecomys* species except *Oe. mamorae*, several *Oryzomys* species (*O. albigularis*, *O. alfaroi*, *O. chapmani*, *O. hammondi*, *O. lamia*, *O. levipes*, *O. macconnelli*, *O. megacephalus* [contra Voss et al., 2001: fig. 53; see Musser et al., 1998: fig. 17], *O. russatus*, *O. talamancae*, and *O. yunganus*), *Sigmodontomys aphrastus*, and *Zygodontomys cherriei*. Among outgroups, *Nyctomys* and *Thomasomys* lack squamae. No information is currently available about the plantar surface morphology in *Amphinectomys* (coded "?").

Character 7: *Ungual tufts present on all claws of hindfoot as a uniform thick sheath extending to or beyond claw tip (0); or tufts absent on digit I (dI), present on dII–dV as a uniform thick sheath extending to or beyond claw tip (1); or tufts absent on dI, present as sparse cover and with few hairs extending beyond the claw tip on dII–dV (2); or tufts extremely reduced or absent on all claws (3).*

[5] Vestigial structures are usually encompassed with the absent states. In those cases, examples of the same taxon display both absent/vestigial structure, as opposed to taxa displaying always present developed structures.

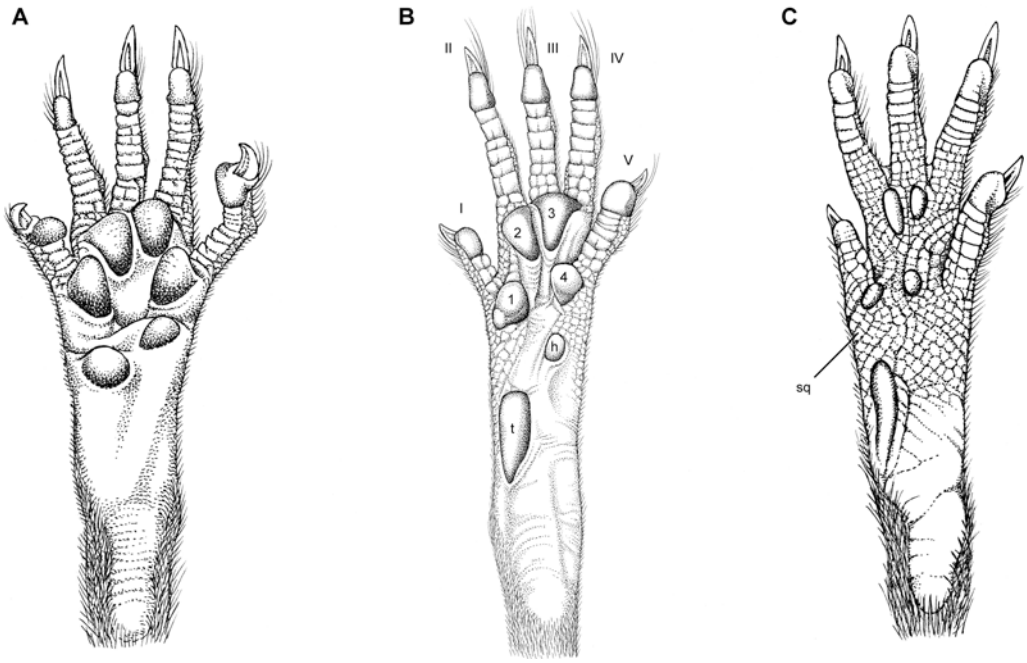


Fig. 9. Plantar views of the left hindfoot illustrating variations in the hypothenar pad (character 4), interdigital pads (character 5), and plantar surface texture (character 6). **A,** *Oecomys auyantepui* (AMNH 267595), showing the hypothenar pad, developed interdigital pads, and smooth plantar surface; **B,** *Handleyomys intectus* (AMNH 16092) showing the hypothenar pad, medium interdigital pads, and smooth plantar surface; and **C,** *Oryzomys palustris* (AMNH 239260), showing the absence of hypothenar pad, small interdigital pads, and squamate plantar surface. Abbreviations are I, hallux; II–V, digits two to five; 1–4, interdigital pads; h, hypothenar pad; t, thenar pad; sq, squamae.

Most oryzomyines have thick ungual tufts on dII–dV of the hindfeet, but lack the tufts on dI (state 1). *Oryzomys angouya* and *O. polius* are the only taxa with thick tufts on all pedal claws (state 0). *Holochilus*, *Lundomys*, *Nectomys apicalis*, and *Sigmodontomys aphrastus* lack, or have extremely reduced, ungual tufts on all pedal digits (state 3), whereas *Pseudoryzomys*, *Melanomys*, *Nectomys squamipes*, *Oryzomys couesi*, *O. hammondi*, *O. palustris*, and *Sigmodontomys alfari* have sparse ungual tufts on dII–dV (state 2). Descriptions of taxonomic variation in the expression of this trait have usually noted only presence or absence of the tufts on dII–dV (e.g., Patton and Hafner, 1983; Carleton and Musser, 1989; Voss, 1993; Voss and Carleton, 1993; Musser et al., 1998; Carleton and Olson, 1999). However, I included the condition of tufts on dI (see also Pacheco, 2003) and introduced an intermediary state of sparse tufts (equivalent to the description of *Oryzomys yunganus* by Musser et al., 1998: 320). Sparse and thick ungual tufts can be distinguished by comparing the proximal and distal portions of the claw, which are uniformly covered in states 0 and 1 (fig. 10A), whereas an unequivocal difference in density between proximal and distal portions exists in state 2, with very few hairs extending onto the terminal portion of the claws and extending beyond it (fig. 10B). The intermediate state avoids ambiguous characterizations, such as the different codings for *Pseudoryzomys* in Voss and Carleton (1993) and Carleton and Olson (1999). All outgroups show state 0, except *Thomasomys*, which exhibits state 1. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2 \leftrightarrow 3$). No information is currently available about ungual tufts in *Amphinectomys* (coded "?").

Character 8: *Natatory fringes on hindfeet absent (0); or present (1).* Natatory fringes are continuous combs of stiff hairs along the

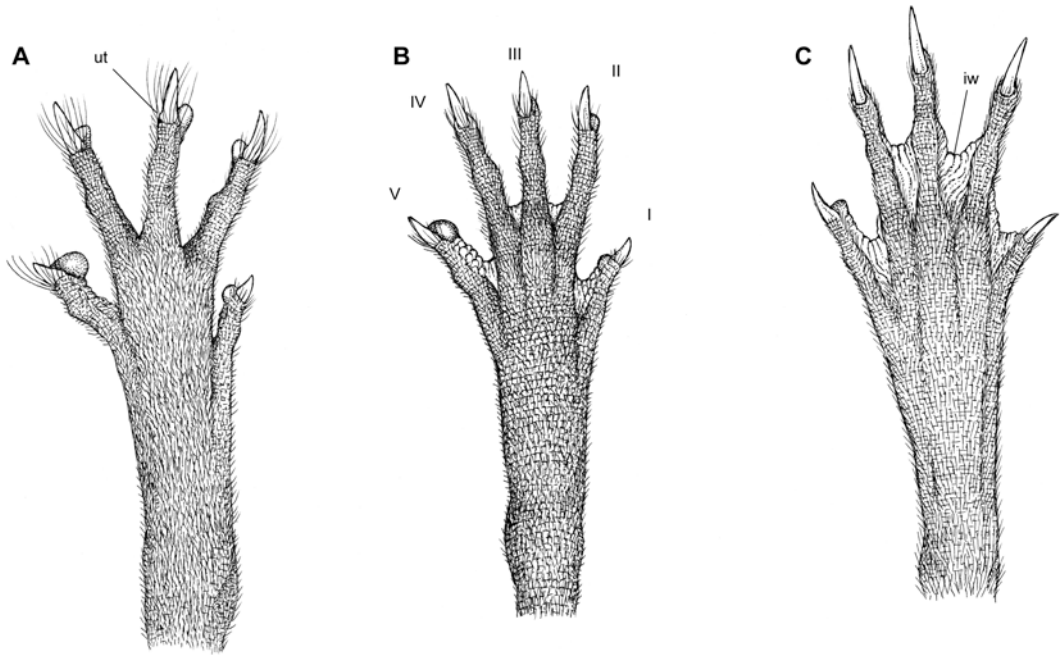


Fig. 10. Dorsal views of left hindfoot illustrating variations in the ungual tufts (character 7) and interdigital web (character 9). **A,** *Oryzomys megacephalus* (AMNH 262085), with developed ungual tufts and without interdigital webbing; **B,** *Oryzomys palustris* (AMNH 239260), with sparse ungual tufts and intermediate webbing; and **C,** *Lundomys molitor* (AMNH 206388), without ungual tufts and with developed interdigital webbing. Abbreviations are I, hallux; II–V, digits two to five; iw, interdigital web; and ut, ungual tufts.

plantar margins and sometimes between the digits of the hindfoot (Voss, 1988: fig. 7). The semiaquatic taxa *Amphinectomys*, *Holochilus*, *Lundomys*, and *Nectomys* are the only oryzomyines to exhibit natatory fringes. Among other sigmodontines, natatory fringes are also present in ichthyomyines, but these were not included in this study.

Character 9: *Interdigital webbing on hindfeet absent (0); or present but small, not extending to first interphalangeal joint of any digit (1); or present and long, extending to or beyond first interphalangeal joints of digits II, III, and IV (2).* Interdigital webbings are present between digits I and IV in *Oryzomys palustris*, *Pseudoryzomys simplex*, and *Sigmodontomys alfari* (small membrane, fig. 10B), and in *Amphinectomys*, *Holochilus*, *Lundomys*, and *Nectomys* (large membrane, fig. 10C). All of the remaining oryzomyines and outgroups lack interdigital webbing (fig. 10A). This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$) to reflect the hypothesis of a morphoclinal change in web development (see Voss and Carleton, 1993).

Character 10: *Dorsal surface of hindfeet densely covered with white hairs, feet appear solid white (0); or dorsal surface sparsely covered with short silvery hairs, feet appear grayish white or pale tan (1); or dorsal surface covered with dark hairs, feet appear brown (2).* The overall color of the dorsal surface of the hindfoot depends on the color and density of the covering hairs. Although white, gray, or brown hindfeet include a range of subtly different tones, they can be unambiguously recognized in side-by-side comparisons. White feet are observed only in *Peromyscus*, *Nesoryzomys*, and *Oryzomys polius*, whereas *Melanomys* and *Sigmodontomys* have brown feet. All of the remaining taxa have grayish dorsal feet surfaces.

Character 11: *Ventral surface of tail covered with dark hairs (0); or covered with hairs with dark basal band and white distal band (1); or covered with white hairs (2).* In

oryzomyines (and muroid rodents in general) the ventral surface of the tail can be paler than the dorsal surface because of the color of the tail scales and the color of the hairs that emerge from them. These two features combine in various ways to create the impression of a bicolored or unicolored tail, with intermediate grayish tones (variously referred to by authors as paler, mottled, or indistinctly bicolored tails). Although caudal scale coloration varies continuously, hair coloration displays clear-cut variation suitable for cladistic character coding. I coded this character from the base (proximal half) of the tail because there is considerable variation in hair color (both within species and among taxa) on the distal half of the tail. The distribution of character-states among ingroup and outgroup taxa is recorded in table 5. In general, but not always, the coding I used is correlated with the bicolored/indistinctly bicolored/distinctly bicolored description of some authors (e.g., Steppan, 1995). This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$). No information is currently available about this character for *Amphinectomys* (coded "?").

Character 12: *Tail densely furred, scales not visible even at higher magnification (0); or tail sparsely furred, scales macroscopically obvious (1).* The tails of muroid rodents always have hair, usually consisting of at least three bristles emerging from the posterior margin of each scale. Short hairs give the tail a naked, scaly appearance, which is the pattern observed in most oryzomyines. In contrast, *Nesoryzomys* and all outgroups except *Delomys* and *Thomasomys* have longer bristles, which provide the tail with a densely furred and scale-free appearance (even when viewed under a stereomicroscope). I could not distinguish an intermediate slightly furred state that has sometimes been recognized in sigmodontine phylogenetics (e.g., Patton and Hafner, 1983; Steppan, 1995).

Character 13: *Dorsal and ventral fur without grooved spines (0); or with grooved spines (1).* *Scolomys* and *Neacomys* have dorsal and ventral guard hairs modified into grooved spines with a broad base, as opposed to the conventional guard hairs with a slender base and soft distal portion present in the remaining taxa. *Scolomys* and *Neacomys*, together with *Rhagomys longilingua* and *Abrawayaomys* (taxa not included in this study), are the only sigmodontines with spiny pelage; however, the presence of dorsal spines is recurrent among other muroid genera (e.g., in *Acomys*, *Echiothrix*, *Maxomys*, *Platacanthomys*, and *Tokudaia*) and among nonmuroid rodents (e.g., Heteromyinae, Echimyidae, Hystricidae, and Erethizontidae).

Character 14: *Ventral fur with plumbeous or dark gray base (0); or ventral fur entirely white, without dark base (1).* The ventral fur of most oryzomyines consists of banded hairs that are dark gray basally and white, cream, or ochraceous distally. In contrast, the ventral fur of some species of *Neacomys*, *Oecomys*, and *Nyctomys* is entirely white.

Character 15: *Dorsal and ventral colors sharply delimited, dorsum much darker than pale ventral surface, resulting in conspicuous countershading (0); or dorsal and ventral colors subtly delimited, dorsum slightly darker than ventral surface, resulting in weak countershading (1); or limits of dorsal and ventral colors indistinct, ventral surface dark, countershading absent (2).* Conspicuous countershading is observed in most oryzomyines as the result of contrast between the darker grizzled-brown dorsal fur and the lighter (white or whitish gray) ventral surface. In several taxa, however, the dividing line between dorsal and ventral color zones is less distinct because of gradual fading of the lateral pigments into a creamy or grayish ventral color, creating a weak countershading effect; ingroup taxa that exhibit this condition include *Handleyomys*, *Holochilus*, *Lundomys*, *Nectomys*, *Nesoryzomys*, *Oecomys concolor*, *Oe. mamorae*, *Oligoryzomys flavescens*, *Ol. fornesi*, *Ol. fulvescens*, *Oryzomys couesi*, *O. hammondi*, *O. polius*, *Scolomys*, and *Zygodontomys*. Two outgroup taxa also exhibit weak countershading (*Thomasomys* and *Wiedomys*). In *Melanomys*, *Microryzomys*, and *Sigmodontomys aphrastus*, however, the ventral surface is almost as dark as the dorsum, resulting in the absence of obvious countershading. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).

Character 16: *Subauricular patches absent (0); or present (1).* Subauricular patches, being whitish areas immediately ventral to the base of each pinna, are rare among

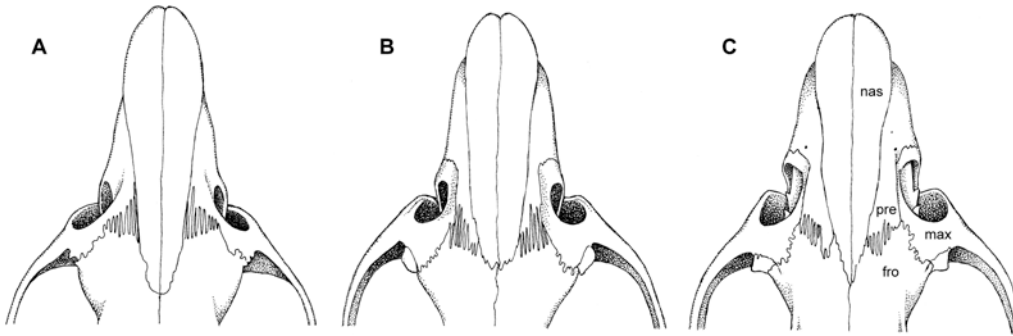


Fig. 11. Dorsal views of rostrum illustrating variations in the posterior morphology of the nasal (characters 18 and 19) and premaxillary (character 20). **A,** *Handleyomys intectus* (ICN 16074), showing the blunt posterior nasal terminus extending beyond the maxillary-frontal suture and the premaxillaries terminating anterior to the nasal; **B,** *Oryzomys megacephalus* (AMNH 209953), showing the blunt posterior nasal terminus and the premaxillaries terminating level with the nasal; **C,** *Nectomys squamipes* (AMNH 61354), showing the pointed posterior nasal terminus extending beyond the maxillary-frontal suture and the premaxillaries terminating anterior to the nasal. Abbreviations are fro, frontal; max, maxillary; nas, nasal; and pre, premaxillary.

oryzomyines, occurring only in exemplars of *Nesoryzomys* and *Oryzomys albigularis*. Among analyzed outgroups, subauricular patches were observed only in specimens of *Thomasomys*. Braun (1993) also reported subauricular patches in both species of *Andalgalomys*, a phyllotine genus not included in the present analysis.

Skull

Character 17: *Rostral tube absent (0); or present (1).* Voss (1993) described the rostral tube in *Delomys* as a substantial anterior projection of the premaxillae and nasals beyond the upper incisive plane, with the bony margins approximated to extend the nasal cavity anteriorly to the rest of the snout. Although there is a continuous variation in the anterior projection of these bones relative to the incisors, the rostral projections of *Peromyscus* and *Delomys* are noticeably longer than in the other species.

Character 18: *Nasals with blunt posterior margin (0); or nasals with acutely pointed terminus, forming a sharp angle (1).* The posterior margins of the nasal bones in oryzomyines are usually bluntly rounded or squared (fig. 11A), although some specimens exhibit small pointed introgressions of the nasal into the frontal (fig. 11B). The lateral nasal borders are slightly convergent (sometimes parallel) throughout most of their length. In contrast, the posterior margins of the nasals of *Nectomys*, *Scolomys*, and *Sigmodontomys aphrastus* always terminate in a sharp angle (fig. 11C), and the lateral nasal borders of these taxa are strongly convergent.

Character 19: *Nasals short, not extending posteriorly beyond the triple-point suture between the maxillary, frontal, and lacrimal (0); or long, extending posteriorly well beyond the maxillary-frontal-lacrimal suture (1).* The posterior extent of the nasals is a continuous trait, but an unambiguous distinction can be made between species with nasals that barely extend beyond the maxillary-frontal suture at its contact with the lacrimal bone (fig. 11B) and species with a substantial penetration of the nasals into the frontals (fig. 11A, C). A small number of taxa, however, could not be placed unequivocally in one or the other state, and they are scored as polymorphic: *Thomasomys*, *Wiedomys*, *Oligoryzomys nigripes*, *Oryzomys angouya*, *O. xanthaeolus*, *Sigmodontomys alfari*, and *Zygodontomys*. The distribution of character-states among the remaining taxa is recorded in table 5. Because of ontogenetic variation in nasal extension, only adult specimens were used in coding this character (see also Steppan, 1995: chars. 9S, 46P).

Character 20: *Premaxillaries long, extending posteriorly beyond the nasals (0); or shorter, extending posteriorly to about the*

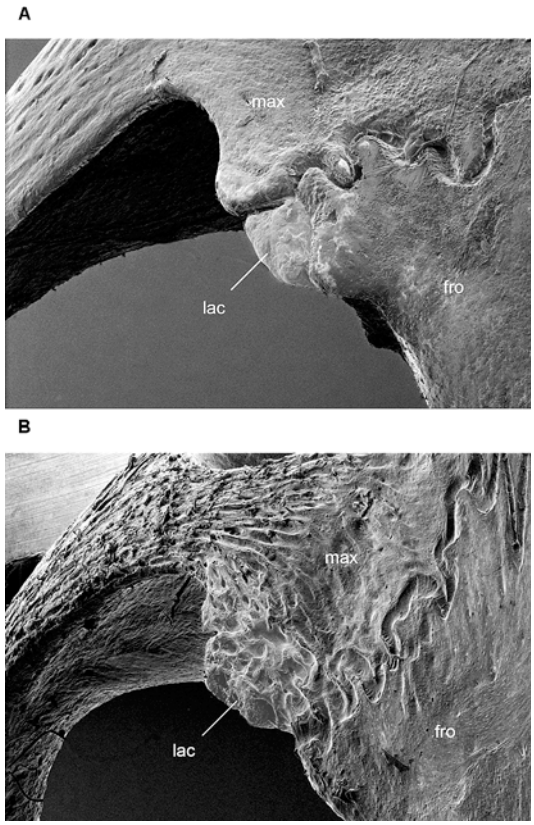


Fig. 12. Dorsal views of lacrimal bone illustrating the variations in its contact with maxillary and frontal (character 21). **A,** *Oryzomys balneator* (AMNH 47593); and **B,** *Oecomys bicolor* (AMNH 272674). Abbreviations are fro, frontal; lac, lacrimal; and max, maxillary.

same level as the nasals (1); or very short, terminating anterior to the nasals (2). As for the previous character, the posterior extension of the premaxillaries varies continuously among taxa, but three states can be unequivocally identified by the relative position of other topographical elements of the cranial dorsum. In state 0, observed only in *Nyctomys*, the nasals are bordered by much longer premaxillaries. In state 2, the premaxillaries terminate anterior to the nasal end (fig. 11A, C). This condition is observed in specimens of *Thomasomys*, *Wiedomys*, *Amphinectomys*, *Handleyomys*, *Neacomys*, *Nectomys*, *Oryzomys balneator*, *O. lamia*, *Scolomys*, and *Sigmodontomys aphrastus*. The remaining taxa have premaxillaries that terminate at about the same level as the nasals (state 1, fig. 11B). A few species that could not be unambiguously placed in a single state were scored as polymorphic (i.e., {12}): *Melanomys caliginosus*, *Oryzomys alfaroi*, *O. xanthaeolus*, and *Sigmodontomys alfari*. Some correlation exists among this and the last two (18 and 19) characters, and it is possible that a single character describing the nasal-premaxillary-frontal contact area might be preferred, especially if it decreases the number of taxa scored as polymorphic. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).

Character 21: *Lacrimal equally contacting maxillary and frontal bones (0); or lacrimal contacting mainly maxillary (1).* In most oryzomyines, and in all outgroups, each lacrimal is wedged between the maxillary and the frontal, and the sutures that the lacrimal shares with these bones have similar lengths (fig. 12A). In several other oryzomyine species, however, the lacrimal is largely enclosed by the maxillary, and its contact suture with the frontal is much reduced (fig. 12B). This condition occurs in *Handleyomys*, *Holochilus*, *Melanomys*, *Nectomys squamipes*, *Nesoryzomys*, *Oecomys bicolor*, *Oe. trinitatis*, *Oryzomys couesi*, *O. levipes*, *O. megacephalus*, *O. palustris*, *O. xanthaeolus*, *Pseudoryzomys*, *Scolomys*, and *Sigmodontomys*. I observed both conditions among specimens of *Oryzomys angouya*, which was scored as polymorphic.

Character 22: *Interorbital region symmetrically constricted (hourglass-shaped or amphoral), with rounded supraorbital margins (0); or interorbital region symmetrically constricted with squared supraorbital margins (1); or interorbital region symmetrically constricted with conspicuously beaded supraorbital margins (2); or interorbital region convergent anteriorly (cuneate) with weakly beaded supraorbital margins (3); or interorbital region convergent anteriorly with well-developed supraorbital crests (4).* Three features of the interorbital region are summarized in this character: the overall shape of the interorbital region, the shape of the supraorbital margins (formed by the dorsal and lateral surfaces of the frontal bone), and the development of supraorbital beads and crests (fig. 13). In the first three states (0, 1, and 2), the interorbital region is symmetrically constricted in the morphology described

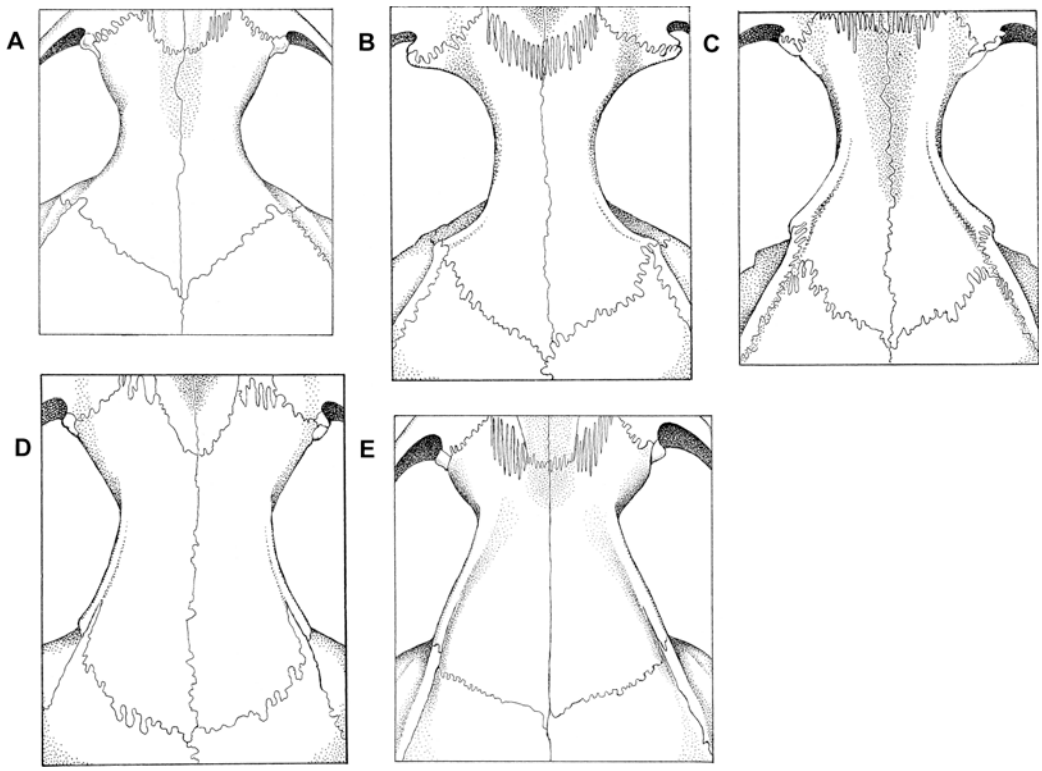


Fig. 13. Dorsal views of interorbital region illustrating the variations in its shape (character 22). **A,** *Handleyomys fuscatus* (ICN 12703); **B,** *Nesoryzomys narboroughi* (ASNHC 8675); **C,** *Holochilus brasiliensis* (AMNH 206372); **D,** *Oryzomys lamia* (AMNH 134763); and **E,** *Oryzomys palustris* (AMNH 242524).

by authors as amphoral or hourglass-shaped, whereas in the latter two states (3 and 4), the interorbital region is convergent anteriorly. The first three states differ in the contact between the lateral and dorsal surfaces of the frontal bone and in the development of supraorbital beads: species with state 0 have smooth, almost rounded supraorbital margins (fig. 13A); species with state 1 have sharp, more-or-less squared supraorbital margins that sometimes develop slight beads in older specimens (fig. 13B); and species with state 2 have supraorbital margins with strongly developed beads (fig. 13C). States 3 and 4 are differentiated by the degree of development of supraorbital ornaments and by the degree of anterior interorbital convergence. In state 3, supraorbital beads are always weakly developed and dorsally oriented (fig. 13D), whereas state 4 is characterized by strongly dorsolaterally expanded supraorbital crests (fig. 13E). Most states of this character are extensively distributed among oryzomyines (see table 5), with the exception of state 2, which is observed only in *Holochilus*. This character is treated as additive, but a step matrix was employed to account for the hypothesized nonlinear transformation between states (fig. 8A).

Converting taxonomic variation of interorbit shape into cladistic characters is difficult, and every analysis to date has presented a new coding scheme (Carleton, 1980: char. 24; Patton and Hafner, 1983: chars. 13, 14; Carleton and Musser, 1989: char. 6; Voss, 1993: char. 6; Voss and Carleton, 1993: char. 7; Steppan, 1995: chars. 11S, 49P, 50P, and 51P); the present study is therefore no exception. Nevertheless, the character-states delineated here are based on those of Carleton and Olson (1999: char. 4), with an additional intermediate condition (state 3) to accommodate *Pseudoryzomys* (scored as state 1 by Carleton and Olson, 1999); another

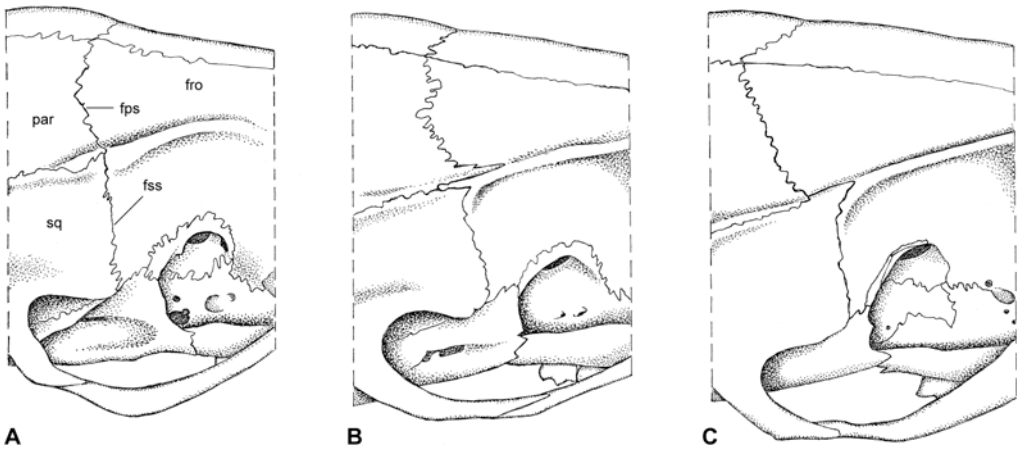


Fig. 14. Lateral views of frontosquamosal and frontoparietal sutures illustrating variations in their contact (character 24). **A,** *Oryzomys alfaroi* (AMNH 142424); **B,** *Oryzomys macconnelli* (AMNH 262033); and **C,** *Melanomys caliginosus* (AMNH 66331). Abbreviations are fro, frontal; fss, frontosquamosal suture; fps, frontoparietal suture; par, parietal; and sq, squamosal.

difference is that the development of temporal ridges (considered here strictly as the ridges at the parietal-squamosal suture) was not taken into account. The rationale for considering interorbital shape and supraorbital ornamentation as a single character, instead of delineating two or more characters, is based on my assumption that anterior interorbital convergence is a morphological consequence of crest development (cf. Carleton, 1980; Carleton and Olson, 1999).

Character 23: *Postorbital ridge absent, posterior orbital wall without conspicuous relief, frontosquamosal suture exposed (0); or postorbital ridge present and concealing frontosquamosal suture in most old specimens (1).* The postorbital ridge is a vertical bony ridge extending from the anterior contact between the frontal and parietal to above the zygomatic root of the squamosal, following the frontosquamosal suture (Voss and Carleton, 1993). *Holochilus* is the only taxon that displays this feature among the analyzed terminals of this study. No information is currently available about this character for *Amphinectomys* (coded "?" in table 5).

Character 24: *Frontosquamosal suture continuous with the frontoparietal suture, dorsal facet of frontal never in contact with squamosal (0); or frontosquamosal suture anterior to frontoparietal suture, leading to an area of contact between dorsal facet of frontal and squamosal (1).* The sutures of the frontal with the squamosal and parietal are collinear in most oryzomyines (fig. 14A, B). In *Holochilus, Melanomys, Nectomys*, *Oryzomys hammondi*, and *Sigmodontomys*, however, the frontosquamosal suture is situated anterior to the frontoparietal suture, creating an area of contact between the dorsal facet of frontal and the squamosal. (fig. 14C).

Character 25: *Parietals restricted to the dorsal surface of the braincase, or slightly expanded below the lateral edges of the dorsal at about the squamosal root of the zygomatic arch (0); or parietals deeply expanded onto lateral surface of the braincase (1).* The parietals of *Amphinectomys*, *Microryzomys*, *Neacomys*, *Oligoryzomys*, *Oryzomys balneator*, *O. lamia*, *O. megacephalus*, *O. rostratus*, *O. russatus*, *O. yunganus*, *Scolomys*, and *Zygodontomys* are restricted to the dorsal surface of the braincase, or they extend only slightly onto the lateral surface on the squamosal, forming a shallow deflection at the level of the squamosal zygomatic root (fig. 15A). In contrast, the parietals of *Holochilus*, *Lundomys*, *Melanomys*, *Nectomys*, *Nesoryzomys*, *Oecomys*, *Oryzomys angouya*, *O. couesi*, *O. hammondi*, *O. palustris*, *O. polius*, *O. subflavus*, *O. xanthaeolus*, *Pseudoryzomys*, and *Sigmodontomys* have an extensive expansion onto the lateral surface of the braincase (fig. 15B). I observed both

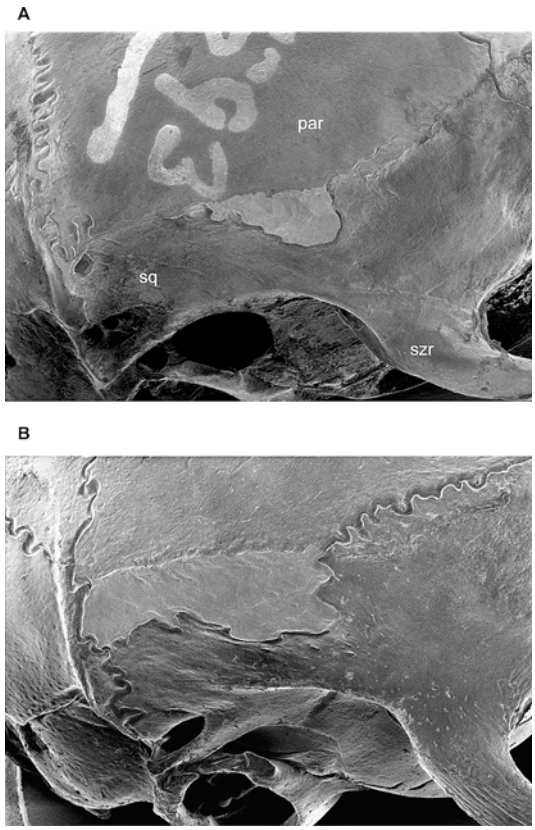


Fig. 15. Lateral views of braincase illustrating variations in the lateral expansion of the parietal (character 25). **A,** *Oryzomys balneator* (AMNH 47593); **B,** *Oecomys bicolor* (AMNH 272674). Abbreviations are par, parietal; sq, squamosal; and szr, squamosal zygomatic root.

conditions among specimens of *Handleyomys* and several *Oryzomys* species (*O. albigularis*, *O. alfaroi*, *O. chapmani*, *O. levipes*, *O. macconnelli*, and *O. talamancae*; see also Musser et al., 1998: fig. 62). *Thomasomys* is the only outgroup with deep lateral expansions of the parietals.

Character 26: *Interparietal wider than posterior border of frontals, in contact with squamosal (0); interparietal strap-shaped, nearly as wide as posterior border of frontals, but not in contact with squamosal (1); or interparietal wedge-shaped, about half as wide as posterior border of frontals, not in contact with squamosal (2).* Taxonomic variation in the relative breadth of the interparietal is continuous, but the three described states can be differentiated by taking into account the overall shape of the interparietal and the contact area between parietal and occipital. Strap-shaped interparietals (state 1) extend laterally, almost in contact with the squamosal, leaving a diminutive area of contact between parietal and occipital (fig. 16A). Most oryzomyine taxa display this pattern. In the wedge-shaped pattern (state 2), the interparietal does not extend laterally, leading to a large parietal-occipital suture line that is visible even without magnification (fig. 16B). *Amphinectomys*, *Handleyomys, Melanomys, Nectomys apicalis, Oryzomys couesi*, *O. palustris*, *O. polius*, *Scolomys*, and *Zygodontomys* display this pattern. State 0 is observed only in Nyctomys, which has an interparietal that contacts the squamosal on either side. Five species of *Oryzomys* display intraspecific variation for this character (*O. angouya*, *O. levipes*, *O. macconnelli*, *O. subflavus*, and *O. xanthaeolus*) and were scored as polymorphic (i.e., {12}). This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).

Character 27: *Basicranial flexion weakly pronounced, foramen magnum oriented mostly caudad (0); or strongly pronounced, foramen magnum oriented mostly posteroventrally (1).* A weakly pronounced posteroventrad basicranial flexion is observed in all taxa except *Microryzomys*, which has a strongly pronounced basicranial flexion. This feature was described by Carleton and Musser (1989) as an apomorphy for *Microryzomys*.

Character 28: *Zygomatic plate narrow and zygomatic notch indistinct; anterior border of plate flat, below or slightly in front of anterior margin of superior maxillary root of zygoma (0); or plate broad with moderate or deep notch; anterodorsal margin smoothly rounded, conspicuously anterior to superior maxillary root of zygoma (1); or plate broad and notch conspicuous; anterodorsal margin produced as a sharp corner or spinous process, conspicuously anterior to superior maxillary root of zygoma (2).* The anterodorsal margin of the zygomatic plate in most oryzomyines is rounded and projects anteriorly to the superior maxillary root of zygoma, forming the zygomatic notch (state 1; fig. 17B). *Pseudoryzomys*, *Lundomys*, and *Holochilus*, however, have deeper zygomatic notches because the anterodorsal margin of the

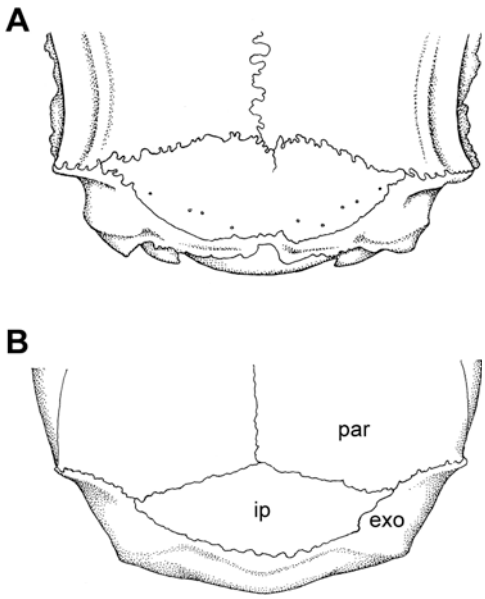


Fig. 16. Dorsal views of occipital region illustrating the variations in interparietal morphology (character 26). **A,** *Nectomys melanius* (MNHN 1981.1296); **B,** *Handleyomys intectus* (ICN 16079). Abbreviations are exo, exoccipital; ip, interparietal; and par, parietal (from Voss et al., 2001: fig. 45; and Voss et al., 2002: fig. 15).

zygomatic plate projects rostrally as a spinous process (state 2; fig. 17C). The zygomatic plate of five oryzomyine taxa (*Microryzomys*, *Oryzomys balneator*, *Oecomys*, *Scolomys*, and *Sigmodontomys aphrastus*) and three non-oryzomyines (*Nyctomys*, *Peromyscus*, and *Thomasomys*) have squared or flat anterodorsal margins situated at the same plane of the anterior margin of the antorbital bridge; consequently, the zygomatic notch, albeit present, is indistinct (state 0; fig. 17A). Because the development of the zygomatic notch is an anatomical consequence of the morphology and position of the anterior border of the zygomatic plate, I treated these two features as a single character (contra Steppan, 1995: chars. 8S, 43P; see also Patton and Hafner, 1983: chars. 11, 12). This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).

Character 29: *Posterior margin of zygomatic plate situated anterior to the alveolus of M1 (0); or approximately even with the alveolus of M1 (1).* Although the position of the posterior margin of the zygomatic plate relative to the alveolus of M1 appears to vary continuously among analyzed taxa, an unequivocal gap was detected between species with posterior margins unambiguously anterior to the M1 alveolus (fig. 18A) and those with the margins at about the same level as the alveolus (fig. 18B). Only two species—*Oryzomys chapmani* and *O. xanthaeolus*—appear to exhibit intermediate conditions, and they were consequently scored as polymorphic for this character. The distribution of character-states among remaining taxa is recorded in table 5. Character definition is taken from Carleton and Olson (1999: char. 2), which is similar to Steppan (1995: chars. 6S, 42P). My scoring for *Zygodontomys brevicauda* and *Oryzomys megacephalus*, however, differed from that assigned by Steppan (1995).

Character 30: *Jugal present and large, maxillary and squamosal processes of the zygoma not overlapping (0); or jugal present and small, maxillary and squamosal processes overlapping, but not in contact (1); or jugal absent, or reduced to slivers of bones, maxillary and squamosal processes in contact (2).* The jugal of most oryzomyine species is small, and the maxillary and squamosal roots of the zygomatic arch are overlapping (in lateral view) but are not in contact (state 1; fig. 19A). In contrast, the jugal of most outgroups (except *Thomasomys*) is robust, and the squamosal and maxillary processes of the zygoma do not overlap in lateral view (state 0). In *Oligoryzomys*, *Microryzomys*, *Oryzomys balneator*, and *O. lamia*, the jugal is usually absent (state 2; fig. 19B); when present, the jugal is reduced to diminutive bony slivers (fig. 19C). This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).

Character 31: *Posterior margins of incisive foramina conspicuously projecting between first molars (0); or terminating anteriorly or at the front of first molar alveoli (1).* The incisive foramina of most oryzomyines are short and do not project between the molar rows (fig. 18B). On the other hand, the foramina of *Lundomys*, *Nesoryzomys*, *Pseudoryzomys*, *Zygodontomys*, and several *Oryzomys* species (*O. angouya*, *O. couesi*, *O. palustris*, *O. polius*, *O. subflavus*, and *O. xanthaeolus*) are much longer and extend posteriorly between the procingula of the left

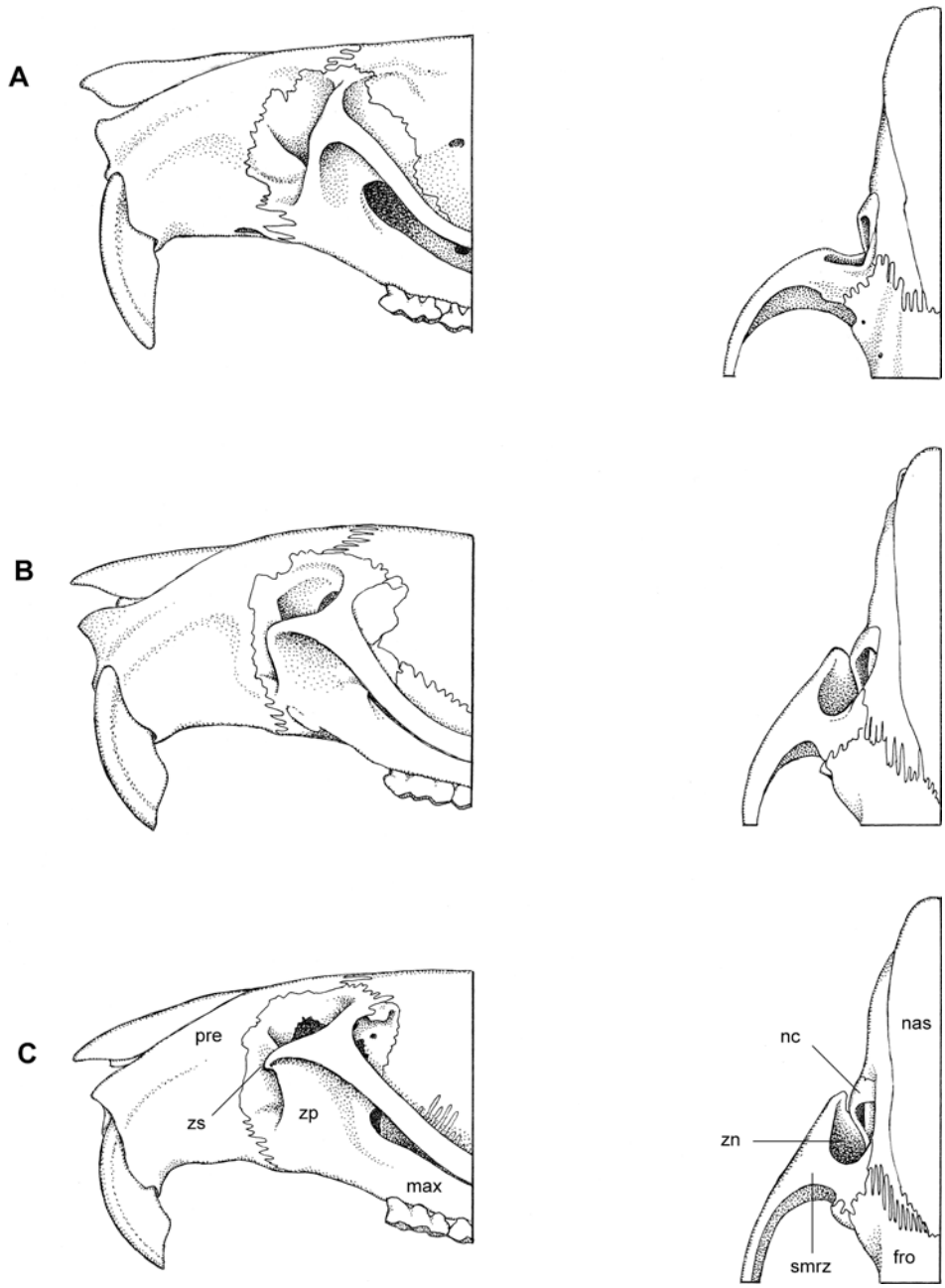


Fig. 17. Lateral views of the rostral and zygomatic regions illustrating the variations in the zygomatic plate and notch (character 28). **A,** *Microryzomys minutus* (AMNH 46808); **B,** *Oryzomys palustris* (AMNH 242523); **C,** *Pseudoryzomys simplex* (AMNH 262048). Abbreviations are fro, frontal; max, maxillary; nc, nasolacrimal capsule; nas, nasal; pre, premaxillary; smrz, superior maxillary root of zygoma; zn, zygomatic notch; zp, zygomatic plate; and zs, zygomatic spine.

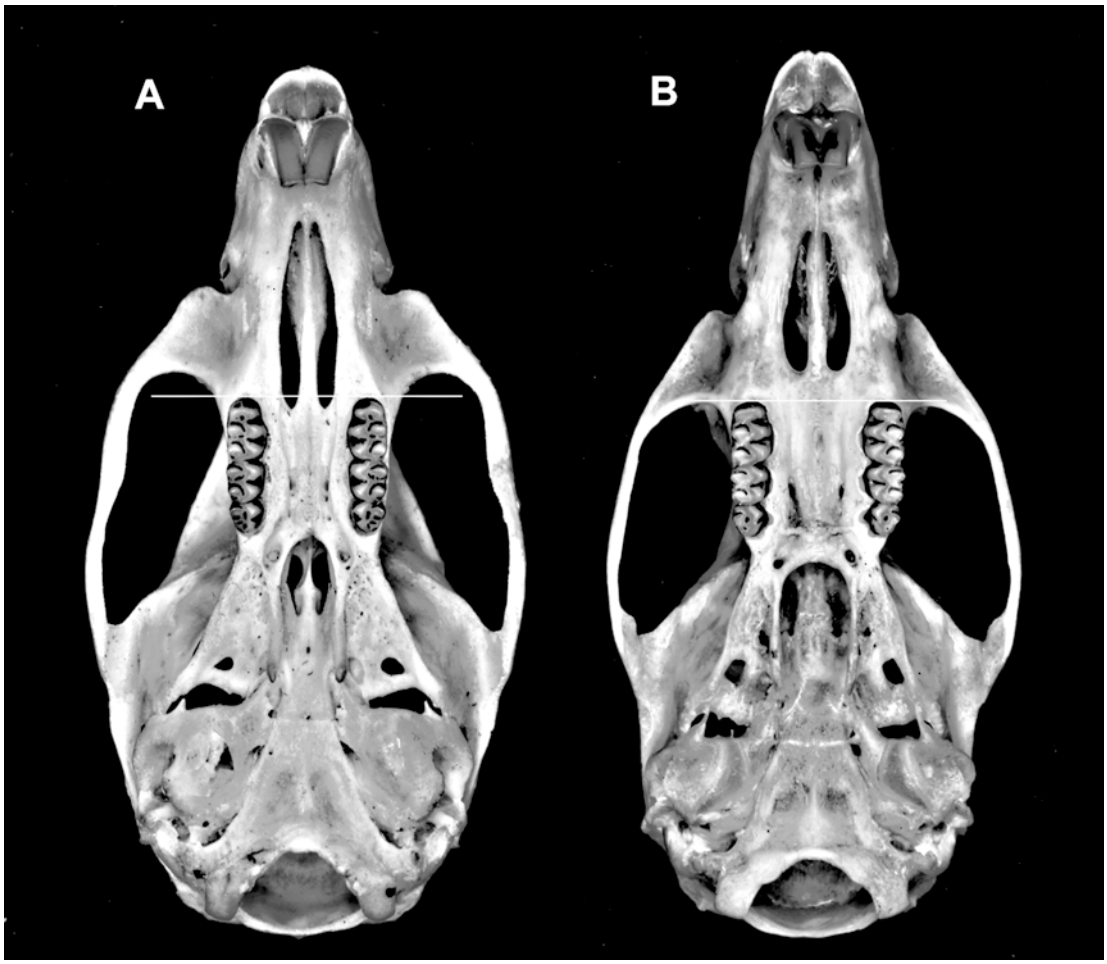


Fig. 18. Ventral views of the skull illustrating the variations in the position of the zygomatic plate relative to the first molar (character 29) and on the posterior extensions of the incisive foramina (character 31). **A,** *Oryzomys subflavus* (AMNH 134632); and **B,** *Oryzomys macconnelli* (AMNH 15341).

and right M1s (fig. 18A). All outgroups were scored with the latter condition, with the exception of *Nyctomys*. Because younger specimens usually have relatively longer foramina that reach more posteriorly than those in older specimens, this character was assessed only in adult individuals.

Character 32: *Palate short, mesopterygoid fossa extends anteriorly between the molar rows (0); or palate of intermediate length, mesopterygoid fossa extends anteriorly between the maxillary bones but not between M3s (1); or palate long, mesopterygoid fossa does not extend anteriorly between the maxillary bones (2).* This description of taxonomic variation in palatal length essentially corresponds to the classical definition of short versus long palates (e.g., Thomas, 1906; Hershkovitz, 1962) with the addition of an intermediate state (also employed by Carleton and Olson, 1999). Although taxonomic variation in palatal length is continuous, the three character-states can be unambiguously identified by the anterior extension of the mesopterygoid fossa relative to the third molars and the maxillary bones. Most oryzomyines have long palates, with the mesopterygoid fossa not extending anteriorly between the maxillary bones (state 2; fig. 20A). An intermediate-length palate, with the mesopterygoid extending anteriorly between the maxillae (fig. 20B, D), is observed

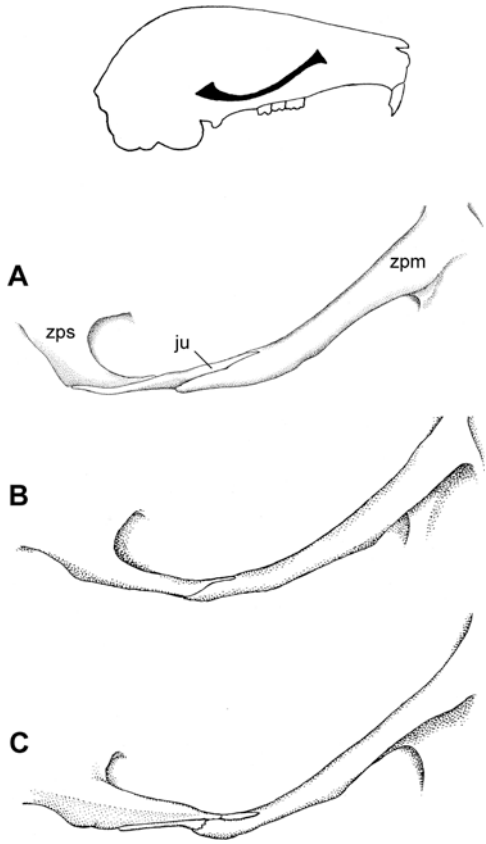


Fig. 19. Lateral views of right zygomatic plate illustrating variations in jugal morphology in oryzomyines (character 30). **A,** *Oryzomys palustris* (AMNH 242669); **B,** *Microryzomys minutus* (AMNH 260419); **C,** *Microryzomys altissimus* (AMNH 63047). Abbreviations are ju, jugal; zpm, zygomatic process of maxillary; and zps, zygomatic process of squamosal (from Carleton and Musser, 1989: fig. 15).

in specimens of *Holochilus brasiliensis*, *Melanomys*, *Microryzomys*, *Nectomys*, *Nesoryzomys swarthi*, *Oryzomys albigularis*, *O. angouya*, *O. balneator*, *O. hammondi*, *O. polius*, *O. russatus*, *O. subflavus*, and *Sigmodontomys*. All outgroups, with the exception of *Wiedomys*, have short palates; *Oryzomys levipes* is the only oryzomyine with such pattern (fig. 20C). The character is treated as ordered (0 ↔ 1 ↔ 2).

Character 33: *Bony palate flat, or with shallow lateral excavations, never with median longitudinal ridge (0); or with deep lateral troughs separated by median longitudinal ridge (1).* The bony palate of almost all oryzomyines is either flat or moderately corrugated. Conversely, the bony palates of specimens of *Holochilus* and *Lundomys* have conspicuous median longitudinal ridges separating two deep lateral troughs. I included flat and moderately corrugated palates in a single state instead of two (contra Carleton and Olson, 1999: char. 8) because several taxa display both flat and slightly corrugated conditions within analyzed samples. Carleton and Olson (1999) also considered the width of the bony palate in their character definition, but this feature varies continuously among the larger array of taxa treated in this study.

Character 34: *Posterolateral palatal pits absent (0); or one simple small foramen present at each side of the posterior palate (1); or posterolateral palatal pits always present as conspicuous perforations, usually more than one foramen, not recessed in fossae or recessed in shallow depression (2); or posterolateral palatal pits always present as perforations within deeply recessed fossa, generally with three foramina, one directed posteriorly, one anteriorly, and one dorsally (3).* The lateral surface of the posterior palate is perforated by cavities in all analyzed sigmodontines. A small simple pit is observed on each side of the palate lateral to the mesopterygoid fossa in *Oryzomys hammondi* and *Sigmodontomys aphrastus* (fig. 20B), and in all outgroups except *Peromyscus* (which lacks the pits). The pits of the remaining oryzomyines are large and conspicuous, and more than one is usually present on each side of the palate. In *Amphinectomys*, *Nectomys*, *Nesoryzomys*, and several species of *Oryzomys* (*O. albigularis*, *O. angouya*, *O. chapmani*, *O. couesi*, *O. levipes*, *O. rostratus*, *O. palustris*, *O. polius*, *O. subflavus*, and *O. xanthaeolus*), the pits, usually three on each side, are recessed in a deep fossa (state 3; fig. 20C, D). In other oryzomyines, the pits, usually one or two on each side, are at the same level of the palate or situated slightly dorsally but not recessed in deep fossae (state 2; fig. 20A). *Holochilus brasiliensis*, *Oryzomys alfaroi*, *O. megacephalus*, and *O. talamancae* are variable for this character, with exemplars with and without fossae, and thus they were scored as polymorphic (i.e., {23}). This

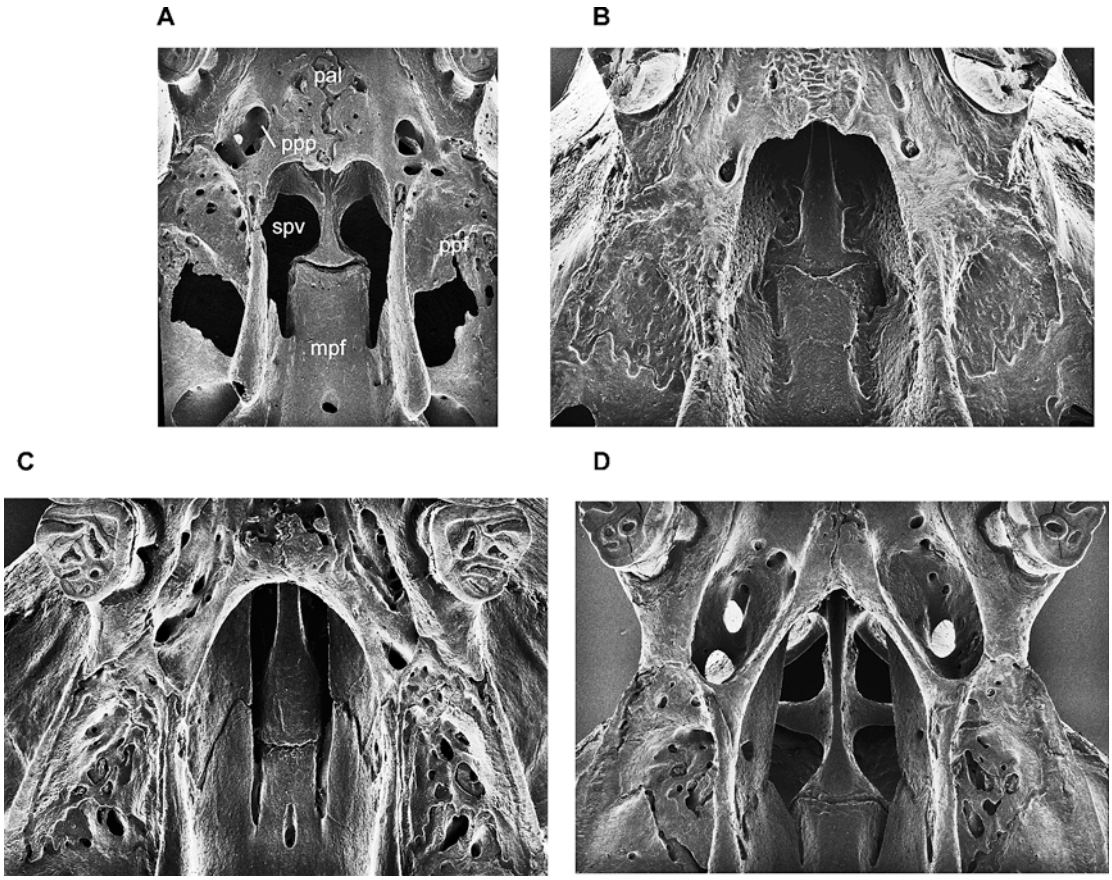


Fig. 20. Ventral views of the palatal and basicranial region illustrating the variations in the morphology of posterior palate (characters 32 and 34), parapterygoid (character 35), and sphenopalatine (character 36) in oryzomyines. **A,** *Oligoryzomys fulvescens* (AMNH 257266); **B,** *Oryzomys hammondi* (UMMZ 155827); **C,** *Oryzomys levipes* (AMNH 264193); **D,** *Oryzomys polius* (FMNH 129243). Abbreviations are mpf, mesopterygoid fossa; pal, palatine; ppf, parapterygoid fossa; ppp, posterolateral pit; spv, sphenopalatine vacuity.

character was treated as ordered (0 ↔ 1 ↔ 2 ↔ 3).

Character 35: *Parapterygoid fossae at same level as palate (0); or parapterygoid fossae dorsally excavated but not reaching level of mesopterygoid roof (1); or parapterygoid fossae deeply excavated, reaching level of mesopterygoid roof (2)*. The parapterygoid fossae of most oryzomyines are dorsally excavated above the level of the bony palate (state 1; fig. 20B, C), but they do not reach the level of the mesopterygoid roof. *Handleyomys* and *Oligoryzomys* are the only oryzomyines with flat parapterygoid fossae forming a continuous surface with the palate (fig. 20A); although the parapterygoid fossae of some specimens of *Oligoryzomys* are positioned slightly dorsally relative to the palate, the surfaces between the two bones still form a continuous slope without a sharp edge. The only oryzomyines with deeply excavated parapterygoid fossae that reach the level of the mesopterygoid roof are *Holochilus*, *Lundomys,* and *Oryzomys polius* (fig. 20D). Among the outgroups, *Peromyscus* and *Nyctomys* have flat parapterygoid fossae, whereas *Delomys*, *Thomasomys*, and *Wiedomys* display the intermediate state. The

character is treated as ordered (0 ↔ 1 ↔ 2). My scoring for several taxa (*Holochilus brasiliensis*, *Nectomys squamipes*, *Oryzomys megacephalus*, *O. palustris*, *Oligoryzomys fulvescens*, *Pseudoryzomys*, and *Zygodontomys brevicauda*) differed from that assigned by Carleton (1980: char. 23) and Steppan (1995: char. 67P), but I cannot explain the discrepancies. No information is currently available about this character for *Amphinectomys* (coded "?" in table 5).

Character 36: *Sphenopalatine vacuities present as large apertures along the presphenoid, reaching basisphenoid (0); or vacuities present but reduced, generally as narrow openings, anterior to basisphenoid-presphenoid suture (1); or vacuities absent, mesopterygoid roof totally ossified (2); or vacuities present but reduced, situated posterior to basisphenoid-presphenoid suture (3).* Most oryzomyines have either large or small sphenopalatine vacuities. Large sphenopalatine vacuities, characterized as openings that reach the basisphenoid and that are wider than the posterior expansion of the presphenoid bone (fig. 20A, D), are observed in *Holochilus*, *Nesoryzomys*, *Oligoryzomys*, *Pseudoryzomys*, *Zygodontomys cherriei*, and several species of *Oryzomys* (*O. alfaroi*, *O. angouya*, *O. chapmani*, *O. rostratus*, *O. palustris*, *O. polius*, *O. subflavus*, *O. xanthaeolus*). Reduced vacuities, characterized as openings that do not reach the basisphenoid and are narrower or of the same width of the posterior expansion of the presphenoid (fig. 20C), are observed in *Amphinectomys*, *Lundomys*, *Microryzomys*, *Neacomys*, *O. albigularis*, *Oryzomys balneator*, *O. levipes*, *O. talamancae*, and *Sigmodontomys*. The mesopterygoid roof is totally ossified (fig. 20B) in the remaining oryzomyines (table 5), except for three polymorphic species (*Nectomys squamipes*, *Oryzomys megacephalus*, and *Zygodontomys brevicauda*), which were scored accordingly (i.e., {12}). *Nyctomys* is the only taxon with vacuities restricted to the region posterior to the basisphenoid-presphenoid suture, so it was scored as a distinct state (3). This character was treated as additive, but a step matrix was employed to account for the hypothesized nonlinear pattern of transformation among states (fig. 8A). The present character description is similar to Carleton's (1980: char. 20), but my coding of certain taxa differs from his (*Oryzomys palustris* is scored here as having large vacuities, instead of intermediate; *Nectomys squamipes* and *Oryzomys megacephalus* are scored as polymorphic). The condition of the sphenopalatine vacuities was also analyzed by Steppan (1995: chars. 20S, 68P), but his scoring differs from mine for *Holochilus*, *Thomasomys*, and *Oligoryzomys fulvescens*.

Character 37: *Stapedial foramen and posterior opening of alisphenoid canal large, squamosal-alisphenoid groove and sphenofrontal foramen present (0); or stapedial foramen and posterior opening of alisphenoid canal large, squamosal-alisphenoid groove and sphenofrontal foramen absent (1); or stapedial foramen and posterior opening of alisphenoid canal small, squamosal-alisphenoid groove and sphenofrontal foramen absent, secondary branch crosses dorsal surface of pterygoid plate (2).* Different patterns of the carotid arterial circulation have been extensively discussed in the muroid literature (e.g., Bugge, 1970, 1971; Carleton, 1980; Musser and Williams, 1985; Voss, 1988, 1993), and this is one of the few morphological characters that has been interpreted consistently in sigmodontine cladistic analysis (Carleton, 1980: char. 16; Voss, 1988: char. 12; Carleton and Musser, 1989; Voss and Carleton, 1993: char. 11; Steppan, 1995: chars. 22S, 76P; Carleton and Olson, 1999: char. 14). The primitive pattern (pattern 1 of Voss, 1988; state 0 herein) is observed in *Handleyomys*, *Microryzomys*, *Neacomys minutus*, *N. spinosus*, *Zygodontomys cherriei*, *Oecomys bicolor*, *Oe. catherinae*, *Oe. trinitatis*, several species of *Oryzomys* (*O. albigularis*, *O. alfaroi*, *O. balneator*, *O. hammondi*, *O. lamia*, *O. levipes*, *O. macconnelli*, *O. rostratus*, *O. russatus*, and *O. talamancae*), and in all outgroups except *Thomasomys*. The intermediate pattern (pattern 2 of Voss, 1988; state 1 herein) is observed only in *Neacomys musseri*, *Oligoryzomys*, *Oryzomys megacephalus*, and *O. yunganus*. The last pattern (pattern 3 of Voss, 1988; state 2 herein) is observed in *Holochilus*, *Lundomys*, *Melanomys*, *Nectomys*, *Nesoryzomys*, *Oecomys concolor*, *Oe. mamorae*, several *Oryzomys* species (*O. angouya*, *O. chapmani*, *O. couesi*, *O. palustris*, *O. polius*,

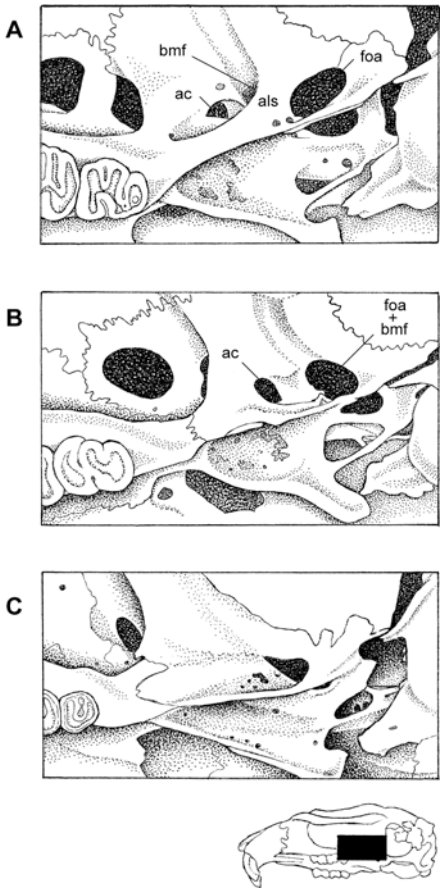


Fig. 21. Lateral view of the braincase showing variations in the foramina and associated features of the alisphenoid bone (characters 38 and 39). **A,** *Holochilus sciureus* (AMNH 210263); **B,** *Lundomys molitor* (AMNH 206393); and **C,** *Scolomys ucayalensis* (MUSM 13354). Abbreviations are ac, anterior opening of alisphenoid canal; als, alisphenoid strut; bmf, buccinator-masticatory foramen; foa, foramen ovale accessorius.

O. subflavus, *O. xanthaeolus*), *Pseudoryzomys*, *Scolomys*, *Sigmodontomys*, and *Zygodontomys brevicauda*. My observation for this character in *Nyctomys* (scored here with state 0) is at odds with those of Carleton (1980; scored with state 2) and Steppan (1995; scored as polymorphic with states 1 and 2).[6] All specimens of *Nyctomys* examined by me have a conspicuous stapedial foramen, with associated posterior opening of alisphenoid canal; almost all specimens have squamosal-alisphenoid grooves and associated sphenofrontal foramina. Two specimens of *Nyctomys* do not have obvious squamosal-alisphenoid grooves and sphenofrontal foramina, but careful inspections of the internal wall of the basicranium reveal the presence of the groove in this taxon. The character is treated as ordered (0 ↔ 1 ↔ 2). No information is currently available about this character for *Amphinectomys* (coded "?").

Character 38: *Alisphenoid strut present, buccinator-masticatory and accessory foramen ovale separate (0); or strut absent, buccinator-masticatory and foramen ovale confluent (1).* Most oryzomyines lack the alisphenoid strut (fig. 21B, C; Voss and Carleton, 1993), but well-developed struts are observed in *Oryzomys polius*, *Oryzomys levipes*, and *Holochilus* (fig. 21A). The alisphenoid strut is present in all outgroups except *Delomys* and *Wiedomys*. The condition of the strut is variable in *Pseudoryzomys*, *Oecomys bicolor*, *Oe. concolor*, *Oe. trinitatis*, *Oryzomys albigularis*, *O. lamia*, and *O. russatus*, which were scored as polymorphic. Polymorphic taxa were those having a robust strut present on both sides of the skull in at least 20% or more of examined specimens. A few (<10%) specimens of *Oligoryzomys*, *Sigmodontomys alfari*, and *Melanomys* have thin struts present on one side of the skull; these taxa were coded as lacking the strut (state 1). No information is currently available about this character for *Amphinectomys* (coded "?").

Character 39: *Anterior opening of alisphenoid canal present, large (0); or absent (1).* The alisphenoid canal has a large anterior opening in all analyzed taxa (fig. 21A, B), with the exception of *Scolomys* (fig. 21C), specimens of which either lack the aperture or have a diminutive opening in its place (Patton and da Silva, 1995: 323). No information is currently available about this character for *Amphinectomys* (coded "?").

Character 40: *Subsquamosal fenestra present (0); or fenestra vestigial or absent (1).* The subsquamosal fenestra of most oryzomyines varies from small to medium-sized, but it is never larger than the postglenoid foramen (fig. 22A, B). Departing from this condition, the subsquamosal fenestra of *Am-*

[6] The coding of this character in Steppan's (1995) matrix is inverted in relation to his character description (p. 39).

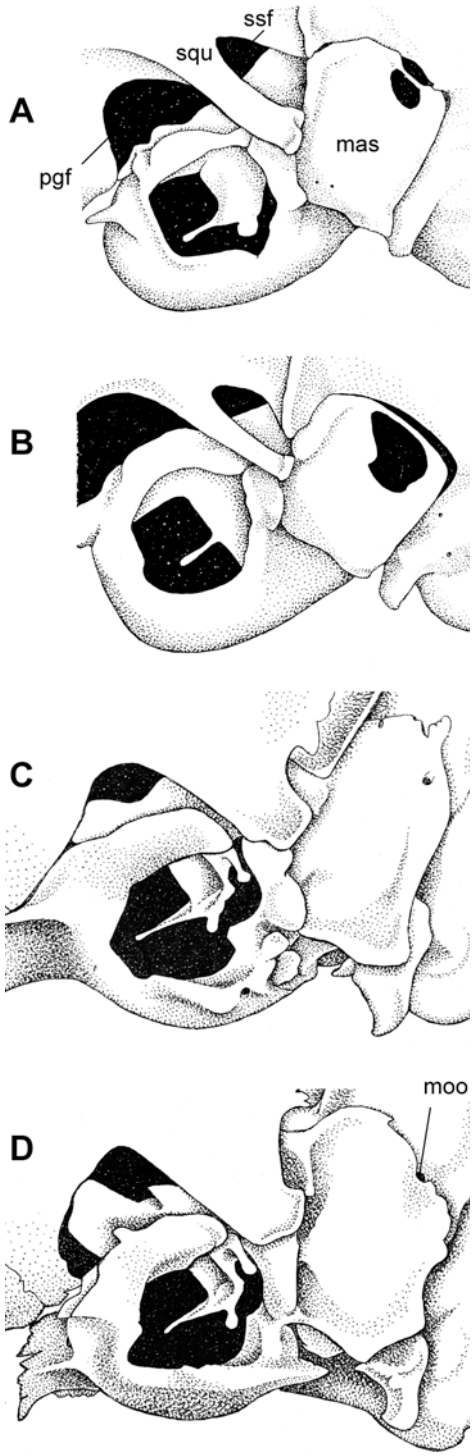


Fig. 22. Lateral view of braincase illustrating variations in the morphology of subsquamosal fenestra and mastoid bone in oryzomyines (characters 40 and 43). **A,** *Oligoryzomys microtis* (AMNH 248993); **B,** *Microryzomys minutus* (AMNH 46808); **C,** *Nectomys palmipes* (AMNH 235065); **D,** *Nectomys melanius* (AMNH 406062). Abbreviations are mas, mastoid; moo, mastoid-occipital opening; pgf, postglenoid foramen; squ, squamosal; ssf, subsquamosal fenestra (from Carleton and Musser, 1989: fig. 19; and Voss et al., 2001: fig. 47).

phinectomys, *Melanomys*, *Nectomys*, *Nesoryzomys narboroughi*, *Oryzomys hammondi*, *O. xanthaeolus*, *Sigmodontomys*, and *Zygodontomys cherriei* is vestigial, obscured internally by the lateral border of the tegmen tympani, or it is absent (fig. 22C, D). Among outgroups, the fenestra is absent in specimens of *Nyctomys*. I scored *Holochilus brasiliensis* as having a normal oryzomyine subsquamosal fenestra (state 0) contra Carleton (1980) and Steppan (1995), who considered the opening as small or reduced to a slit in this taxon.

Character 41: *Ectotympanic bullae small, exposed flange of periotic extends to internal carotid canal (0); or ectotympanic bullae intermediate, exposed wedge of periotic smaller and not contributing to wall of carotid canal (1); or ectotympanic bullae large, periotic bone mostly masked in ventral view (2).* The periotic of most oryzomyines does not reach the internal carotid canal because the ectotympanic bulla extends over and obstructs it (state 1; fig. 23A). Two arrangements depart from this pattern: the periotics of *Handleyomys*, *Microryzomys*, *Neacomys*, *Oligoryzomys*, *Oryzomys balneator*, and *O. hammondi* (plus *Nyctomys* among outgroups) advance to the carotid canal, usually contributing to the wall of the canal (state 0; fig. 23B); and the ectotympanics of *Holochilus* and *Nesoryzomys* (plus *Wiedomys* among outgroups) are enlarged, blocking the periotic from ventral view (state 2; fig. 23C). My analyzed samples of *Oecomys* (*Oe. bicolor*, *Oe. concolor*, *Oe. trinitatis*) and of *Oryzomys rostratus* included specimens with the periotic reaching or not reaching the internal carotid canal (scored as polymorphic, {01}). This character was treated as ordered (0 ↔ 1 ↔

←

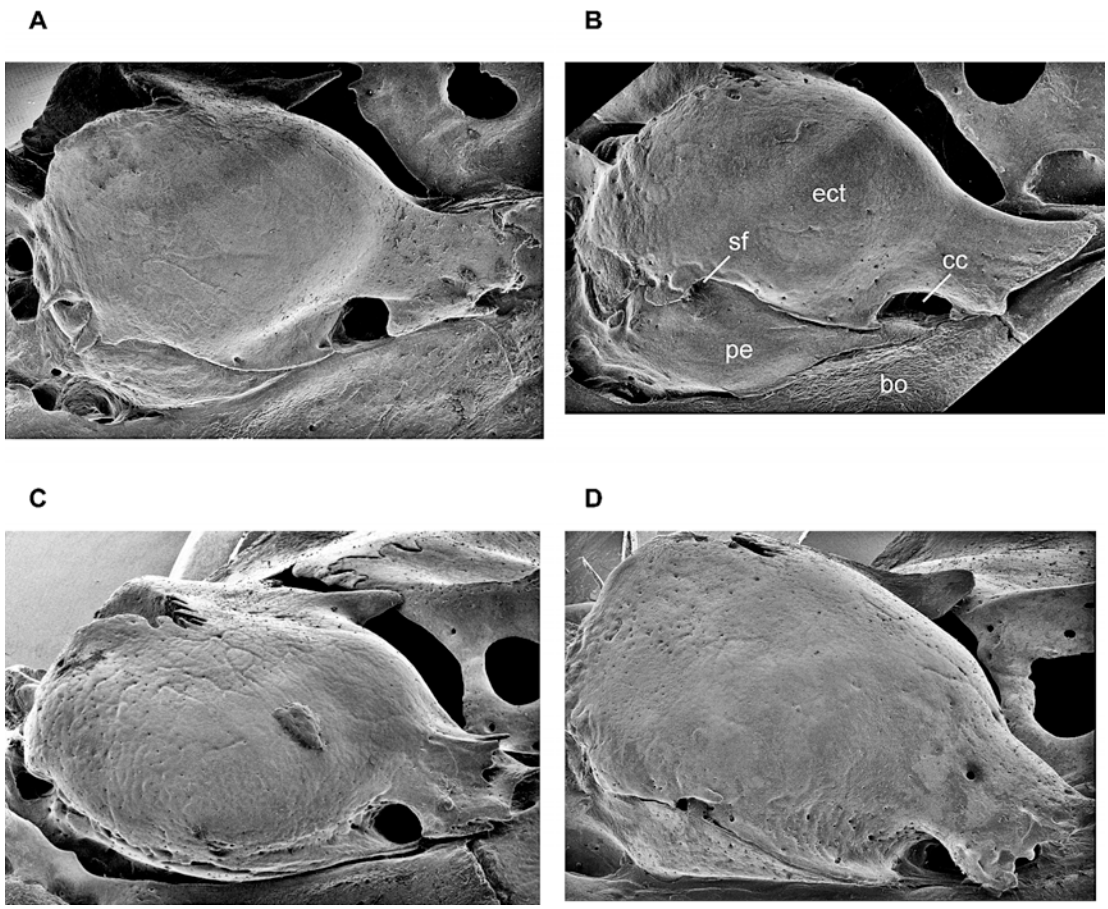


Fig. 23. Medial views of auditory bulla illustrating variations in the ectotympanic morphology (character 41). **A,** *Scolomys ucayalensis* (MUSM 13357); **B**, *Oligoryzomys fulvescens* (AMNH 257226); **C**, *Holochilus brasiliensis* (AMNH 210250); **D**, *Lundomys molitor* (AMNH 206364). Abbreviations are bo, basioccipital; cc, carotid canal; ect, ectotympanic part of auditory bulla; pe, periotic; sf, stapedial foramen.

2). My scoring for *Lundomys* differed from that assigned by Carleton and Olson (1999: char. 12): the periotic bone is visible in ventral view in all *Lundomys* specimens that I analyzed (fig. 23D). No information is currently available about this character for *Amphinectomys* (coded "?").

Character 42: *Posterior suspensory process of squamosal present and connected to the tegmen tympani (0); or posterior suspensory process absent, tegmen tympani not touching or barely in contact with squamosal (1).* All oryzomyines lack the posterior suspensory process of squamosal, a putative synapomorphy for the tribe (Voss and Carleton, 1993; Steppan, 1995). *Reithrodon* is the only other sigmodontine without the posterior suspensory process (Steppan, 1995). No information is currently available about this character for *Amphinectomys* (coded "?").

Character 43: *Mastoid completely ossified, or with a diminutive pit in the dorsal contact with the exoccipital border (0); mastoid with conspicuous fenestra (1).* The mastoids of most oryzomyines have a conspicuous dorsolateral fenestra (fig. 22B). The size of the fenestra varies from medium-sized to large, but some specimens have a small fenestra that is always enclosed by the bone, not reaching the exoccipital contact area (fig. 22A). In contrast, the mastoids of *Holochilus chacarius*, *Melanomys*, *Nectomys*,

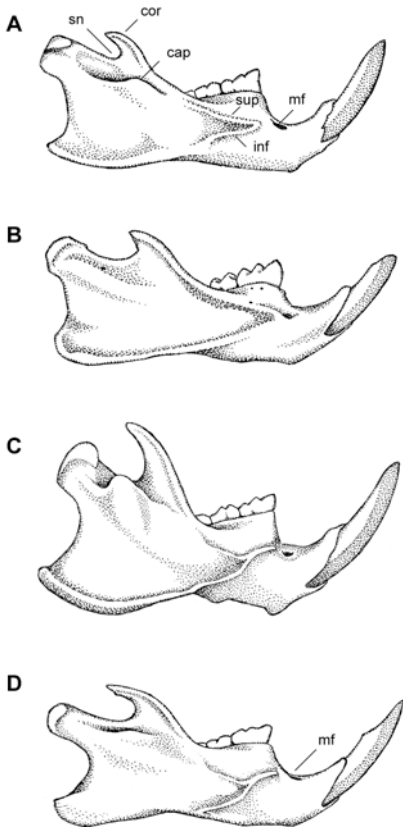


Fig. 24. Lateral views of right mandibles showing taxonomic variations in the position of the mental foramen (character 44), in development of the capsular process of the lower incisor alveolous (character 45), and in patterns of the masseteric ridges (characters 46 and 47). **A,** *Lundomys molitor* (AMNH 206363); **B,** *Oryzomys hammondi* (UMMZ 155827); **C,** *Holochilus brasiliensis* (AMNH 206383); **D,** *Zygodontomys brevicauda* (AMNH 2066641). Abbreviations are cap, capsular process of the lower incisor alveolus; cor, coronoid process; inf, inferior masseteric crest; mf, mental foramen; sn, sigmoid notch; and sup, superior masseteric crest.

Nesoryzomys, *Oecomys catherinae*, *Oryzomys hammondi*, *O. lamia*, *O. macconnelli*, *O. russatus*, *Scolomys*, *Sigmodontomys*, and *Zygodontomys* are totally ossified and lack the fenestra (fig. 22C), or have a small opening, resembling a foramen aperture, at the region of contact between the mastoid and the exoccipital (fig. 22D). My analyzed samples of seven taxa (*Neacomys spinosus*, *O. bicolor*, *O. trinitatis*, *Oryzomys albigularis, O. subflavus*, *O. talamancae*, and *O. xanthaeolus*) included specimens with and without the fenestra (scored as polymorphic). Most outgroups also have the fenestra, except *Nyctomys*. My scoring for several taxa differed from that assigned by Patton and Hafner (1983: char. 9). No information is currently available about this character for *Amphinectomys* (coded "?").

Character 44: *Mental foramen opens laterally, at body of mandible (0); or mental foramen opens dorsally, at the diastema (1).* In most oryzomyines, the mental foramen is situated laterally at the body of the mandible, usually close to the anterior end of the masseteric ridges and below the diastema (restricted here to the dorsal surface of the mandible between the first lower molar and the incisor; fig. 24C). In contrast, in *Oecomys catherinae*, *Oligoryzomys*, *Oryzomys balneator*, *O. subflavus*, and *Zygodontomys* the foramen is situated dorsally, at the diastema anterior to the m1 (fig. 24D). *Oryzomys chapmani* is polymorphic for this character. No information is currently available about this character for *Amphinectomys* (coded "?").

Character 45: *Capsular process of lower incisor alveolus absent (0); or projection present but reduced as a slight rounded elevation (1); or projection present, well developed as a conspicuous swelling with acute projection (2).* The root of the lower incisor in several sigmodontines is contained in a bony capsule on the lateral surface of the mandible (e.g., Voss, 1991: fig. 13). This capsular process exhibits a marked intraspecific variation (Steppan, 1995), which is correlated with age (older specimens have larger processes than do younger conspecifics). Differences between species are also continuous, and establishing discrete states is subtle. Extremes exist between process absent (fig. 24B) and well-developed tubercles with an acute projection (fig. 24C). Between these opposites, some taxa exhibit a subtle elevation (fig. 24A, D), which was coded as an intermediate state. Although variation was observed in the position of the tubercle, intermediate projections are usually situated ventral to the coronoid process, whereas well-developed projections are more posteriorly located. As a final criterion for state recog-

nition, the projection is always present in the juveniles of taxa with well-developed processes as adults (state 2), whereas taxa with reduced processes as adults have no trace of a process as juveniles (state 1). Most oryzomyines have a well-developed capsular process. *Handleyomys*, *Lundomys*, *Melanomys*, *Neacomys musseri*, *Nectomys squamipes*, *Oecomys catherinae*, *Oe. concolor*, *Oe. mamorae*, *Oryzomys albigularis*, *O. alfaroi*, *O. levipes*, *O. rostratus*, *O. palustris*, *O. talamancae*, *O. xanthaeolus*, *Scolomys*, and *Zygodontomys brevicauda* have small capsular processes, whereas specimens of *Oryzomys hammondi*, *O. macconnelli*, *O. megacephalus*, *O. polius*, and *O. yunganus* have none. My coding of *Handleyomys* differs from Voss et al. (2002), who reported the projection as absent. *Sigmodontomys aphrastus* is the only polymorphic taxon (coded as {01}). Outgroups are variable for this character, but the two non-sigmodontines *Nyctomys* and *Peromyscus* have the intermediate condition. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).

Character 46: *Superior and inferior masseteric ridges converge anteriorly as an open chevron (0); or anterior portion of ridges conjoined as single crest (1).* The upper and lower masseteric ridges in most oryzomyines converge anteriorly as two separate crests, joining only at their anteriormost point (Voss and Carleton, 1993; see fig. 24A). In some specimens, the ridges run closely parallel for some extent before contacting, but they are always discernible. Conversely, in *Holochilus*, *Melanomys*, *Nectomys*, *Nesoryzomys*, *Oryzomys polius*, *O. xanthaeolus*, and *Zygodontomys*, the anterior portion of the ridges is made of a single crest because the two ridges fuse to form a single masseteric crest below m1 (fig. 24C). *Sigmodontomys alfari* is polymorphic for this character. Outgroups uniformly have the open chevron pattern. No information is currently available about this character for *Amphinectomys* (coded "?").

Character 47: *Anterior edge of masseteric crests below m1 (0); or edge anterior to m1, extending to diastema (1).* Although variable among analyzed specimens, most oryzomyines have the anterior edge of the masseteric ridges below the first lower molar, usually at the procingulum (fig. 24A, B), but in specimens of *Holochilus*, *Nesoryzomys*, *Oligoryzomys*, and *Zygodontomys*, the masseteric ridges extend anterior to m1 and approach the diastema or the body of the mandible ventral to the diastema (fig. 24C, D).

Character 48: *Entoglossal process of basihyal present as small knob, basihyal arched, and thyrohyal long, greater than or equal to the length of the basihyal (0); or entoglossal process absent, basihyal straight, and thyrohyal short, less than length of basihyal (1).* All sigmodontines examined to date have the same general hyoid conformation, lacking the entoglossal process and with a straight basihyal and a short thyrohyal (Carleton, 1980; Steppan, 1995; Pacheco, 2003). Oryzomyines analyzed here also follow this pattern and contrast with the hyoid morphology observed in most neotomines and nyctomyines (including *Peromyscus* and *Nyctomys*), which possess an entoglossal process, a long thyrohyal, and an arched basihyal. This character serves as a diagnostic feature for sigmodontines (Voss, 1993; Voss and Carleton, 1993). Information on this character is missing for 27 species because hyoid bones were unavailable (coded "?" in table 5).

Dentition

Character 49: *Labial accessory root of M1 absent (0); or present (1).* Molar teeth of sigmodontines are multirooted, and taxonomic difference in the number of roots has been used extensively in sigmodontine phylogenetic analysis (Carleton, 1980; Carleton and Musser, 1989; Voss, 1991; Voss and Carleton, 1993; Steppan, 1995; Carleton and Olson, 1999). Most oryzomyines have three roots at anterior, posterior, and lingual positions on the first upper molar (M1). A fourth accessory root at the labial position is present in a variety of taxa. An accessory rootlet at central position may also be present in combination or not with the labial one (Voss and Carleton, 1993). The condition of the central accessory root is polymorphic for several taxa and may be caused by droplets of enamel left in the area of furcation of the roots during molar growth (Sicher and

Bhaskar, 1972). Therefore, I follow Voss and Carleton (1993) in coding only for the condition of the accessory labial root, which does not show intraspecific variation. Among oryzomyines, the accessory labial root of M1 is present in *Holochilus*, *Melanomys*, *Neacomys spinosus*, *Nectomys*, *Nesoryzomys*, *Oecomys*, *Oryzomys alfaroi*, *O. angouya*, *O. chapmani*, *O. couesi*, *O. rostratus*, *O. palustris*, *O. subflavus*, *O. xanthaeolus*, *Pseudoryzomys*, and *Sigmodontomys alfari*. It is absent in all other examined oryzomyines. Labial accessory roots are also present in the outgroups *Thomasomys* and *Wiedomys*. Some information for this and the next two characters was taken from the literature (in addition to the above-mentioned studies, see Hershkovitz, 1944; Voss, 1993). No information is currently available about this character for *Amphinectomys* (coded "?" in table 5).

Character 50: *Labial and lingual accessory roots of m1 absent (m1 with two roots total) (0); or labial accessory root present (three roots total) (1); or labial and lingual roots present (four roots total) (2).* On the first lower molar (m1), the number of roots varies from two to four, due to the presence or absence of accessory roots at labial and lingual positions. Among analyzed specimens, the lingual accessory root is present only in examples with the labial root, so I coded these features as a single ordered character ($0 \leftrightarrow 1 \leftrightarrow 2$). Among oryzomyines, the labial and lingual accessory roots are absent in *Microryzomys*, *Neacomys*, *Oecomys bicolor*, *Oe. catherinae*, *Oe. concolor*, *Oe. mamorae*, *Oligoryzomys*, *Oryzomys hammondi*, *O. megacephalus*, *O. polius*, *O. talamancae*, *O. yunganus*, *Scolomys*, and *Zygodontomys*; the labial accessory root is present in *Oecomys trinitatis*, *Oryzomys albigularis*, *O. angouya*, *O. balneator*, *O. lamia*, *O. levipes*, *O. macconnelli*, and *O. russatus*; and both labial and lingual accessory roots are present in *Holochilus*, *Lundomys*, *Melanomys*, *Nectomys*, *Nesoryzomys*, *Oryzomys alfaroi*, *O. chapmani*, *O. couesi*, *O. rostratus*, *O. subflavus*, *O. xanthaeolus*, *Pseudoryzomys*, and *Sigmodontomys*. The condition of the m1 accessory roots is variable in specimens of *Handleyomys* and *Oryzomys palustris* (coded as {12}). No information is currently available about this character for *Amphinectomys* (coded "?").

Character 51: *Second lower molar with two roots (0); or three roots (1).* The second lower molar (m2) of most sigmodontines is anchored by two roots, at anterior and posterior positions. By contrast, the anterior root is replaced by two smaller roots (at anterolabial and anterolingual positions) in *Handleyomys*, *Holochilus*, *Oryzomys alfaroi*, *O. chapmani*, *O. rostratus*, *O. xanthaeolus*, *Pseudoryzomys*, *Sigmodontomys alfari*, and *Zygodontomys*. *Lundomys* and *Oryzomys palustris* are polymorphic for this character. The condition of *Amphinectomys*, *Nesoryzomys swarthi*, *Oryzomys couesi*, *O. hammondi*, *O. polius*, and *Sigmodontomys aphrastus* could not be assessed (coded "?").

Character 52: *Incisors opisthodont (0); or orthodont (1).* The degree of upper incisor procumbency is defined by the position of the cutting edge of the incisor relative to the vertical-incisive plane (Hershkovitz, 1962; Steppan, 1995). Despite the gradient of incisor curvature observed among taxa, a distinct interval is observed among orthodont and opisthodont categories. Most oryzomyines, and all outgroups, have opisthodont teeth with the cutting edge terminating posteriorly to the vertical-incisive plane. *Amphinectomys*, *Handleyomys*, *Melanomys*, *Oryzomys hammondi*, *Scolomys*, and *Sigmodontomys aphrastus* have orthodont incisors with the cutting edge perpendicular to the vertical-incisive plane. No oryzomyine has proodont or hyper-opisthodont incisors (see Steppan, 1995, for definition of these categories).

Character 53: *Enamel band of upper incisors smoothly rounded, or flattened but without labial bevel (0); or band flattened medially, with distinct labial bevel (1).* The putatively derived condition (state 1) is found only in species of *Holochilus*, where medial and lateral facets create a beveled enamel surface (Voss and Carleton, 1993: fig. 12). The remaining taxa all have incisors with smoothly rounded or flattened enamel surfaces. No information is currently available about this character for *Amphinectomys* (coded "?").

Character 54: *Molars bunodont and brachydont (0); or molars planar and hypsodont*

(1). The molars of *Holochilus* are hypsodont, with the cusps situated at the same occlusal level as the central elements of the molar teeth, forming a planar surface. Remaining oryzomyines have bunodont and brachyodont molars, with the lateral apices of the cusps situated higher then the central teeth elements.

Character 55: *Labial flexi not patent, closed off by labial cingula (0); or labial flexi patent, cingula absent (1)*. The molars of all outgroups and most oryzomyines have labial cingula that close off the lateral apertures of all the labial flexi. In *Holochilus* and *Lundomys*, however, the labial flexi are patent (open), because the labial cingula are absent. No information is currently available about this character for *Amphinectomys* (coded "?").

Character 56: *Maxillary toothrows parallel (0); or anteriorly convergent (1)*. Although the direction of the toothrows appears to vary continuously among analyzed taxa, an unambiguous gap was detected between the more-or-less parallel toothrows seen in most oryzomyines and all outgroups, and the anteriorly convergent toothrow observed in *Holochilus* and *Lundomys*. No information is currently available about this character for *Amphinectomys* (coded "?").

Character 57: *Flexi of M1 and M2 do not interpenetrate (0); or flexi meet at midline, enamel overlaps (1); or flexi interpenetrate (2)*. The molars of most oryzomyines are nonlophodont, with opposite labial and lingual flexi conspicuously far from the end of the opposite flexi (e.g., fig. 25P). Several oryzomyines, however, display a certain degree of lophodonty, which varied from minimal lophodonty, where only the enamel border of the flexi reaches the end of the opposite flexi (e.g., fig. 25I), to incipient lophodonty, where flexi interpenetrate beyond the end of the opposite flexi (e.g., fig. 25H). Despite the apparent continuous nature of such variation, distinctions between the three states is unambiguous; the labial flexi (paraflexus and metaflexus) of nonlophodont taxa (state 0) are sharply curved ($\sim 90^{\circ}$) before the molar midline (e.g., fig. 25P), whereas the labial flexi of minimally lophodont taxa (state 1) are gently curved (e.g., fig. 25I). Incipiently lophodont taxa have transversely oriented paraflexi and metaflexi (e.g., fig. 25H). See the matrix in table 5 for character-state distributions among taxa. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$). No information is currently available about this character for *Amphinectomys* (coded "?").

Character 58: *Anterocone of M1 divided into labial and lingual conules by anteromedian flexus (0); or anterocone partially divided into labial and lingual conules by internal fold of procingulum, anteromedian flexus absent (1); or anterocone undivided, anteromedian flexus and internal fold of procingulum absent (2)*. The anteromedian flexus (fig. 25O, amf) is observed in all outgroup taxa and in examples of *Lundomys*, *Microryzomys* (fig. 25P), *Neacomys minutus*, *N. musseri*, *Nesoryzomys narboroughi*, *Oecomys concolor*, *Oligoryzomys* (fig. 25O), *Oryzomys albigularis* (fig. 25F), *O. angouya* (fig. 25A), *O. balneator*, *O. levipes*, *O. polius*, and *O. xanthaeolus* among oryzomyines. *Oryzomys subflavus*, *O. palustris* (fig. 25B), and *Pseudoryzomys* (fig. 25K) are the only taxa with the internal fold, which is sometimes fused with the anteroflexus. Carleton and Olson (1999) scored *Zygodontomys brevicauda* as having this last state, but I could not detect the presence of the internal fold in any exemplar of this taxon (e.g., fig. 25M). The remaining oryzomyines also have undivided anterocones (e.g., fig. 25L). Although the degree of excavation of the anteromedian flexus varies among taxa, I could not identify a clear distinction between weakly or deeply excavated states (e.g., fig. 25I vs. fig. 25O). This character was scored in young individuals because modifications of molar topography due to occlusal wear, such as the disappearance of the anteromedian flexus or the presence on an internal fold in the procingulum derived from the anteroflexus, can lead to erroneous scoring. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$). Information about this and the next 19 dental characters was not available for *Amphinectomys* and *Nesoryzomys swarthi* (coded "?" in table 5).

Character 59: *Anteroloph on M1 well-developed and discrete, reaching the labial cingulum, anteroflexus present (0); or anteroloph present but small, not reaching the*

labial cingulum, anteroflexus absent (1); or anteroloph fused with anterocone labially, anteroflexus present as small fossette (2); or anteroloph and anteroflexus absent (3). The anteroloph and anteroflexus are present and well developed among most oryzomyines (e.g., in *Oryzomys albigularis*, fig. 25F), with the following exceptions: *Lundomys* has a small anteroloph that does not reach the labial cingulum (state 1; fig. 25I); in *Melanomys*, *Nectomys*, *Oryzomys xanthaeolus*, *Scolomys*, and *Sigmodontomys*, the anteroloph is fused with the anterocone labially (state 2; fig. 25N); and in *Holochilus*, *Pseudoryzomys*, and *Zygodontomys,* the anteroloph is absent (state 3; fig. 25J). The anteroloph is present and well developed in all outgroups. Young specimens are necessary for scoring this character because modifications of molar topography due to occlusal wear can lead to erroneous scoring. Hershkovitz (1962) postulated that taxonomic variation in the development of the anteroloph is correlated with that of the mesoloph, and Carleton (1980) found a Spearman rank correlation of 94% between the condition of the anteroloph and mesoloph in a matrix that included a wide variety of New World muroids. Nevertheless, these structures show several cases of contrasting conditions, and thus they have previously been treated as separate characters in several analyses (e.g., Voss and Carleton, 1993; Steppan, 1995; Carleton and Olson, 1999). This character was treated as unordered.

Character 60: *Protostyle on M1 absent (0); or present (1).* The protostyle is absent in all analyzed taxa with the exception of *Oryzomys angouya* (fig. 25A), which has a small crest connected to the protocone.

Character 61: *Paracone of M1 connected to protocone by enamel bridge situated at posteriormost end of protocone (0); or paracone connected to protocone by enamel bridge situated at anterior portion of protocone (1); or protocone and paracone forming single dentine basin without enamel connection (2).* The paracone is connected to the posterior terminus of the protocone by an enamel bridge in several oryzomyines and in all outgroups (e.g., fig. 25C). This enamel connection also contacts the median mure in those taxa with the protocone-median mure connection (see character 63). Conversely, in several taxa the paracone and protocone are linked by an enamel bridge connected to the middle or to the anterior part of the protocone; these taxa exhibit an independent enamel connection to the median mure (e.g., fig. 25D). State 2 refers to *Zygodontomys*, in which the paracone and protocone are connected by a wide dentine surface rather than by an enamel bridge (fig. 25M). Although taxa displaying this latter pattern may have separated intercuspal dentine basins in unworn teeth (cf. Voss, 1988), they do not display a definitive connecting bridge, but rather the dentine basins are slightly obliterated by the penetration of the paraflexus. This character was analyzed in individuals with a moderate level of occlusal wear, as enamel connections are not apparent in unworn teeth. See the matrix in table 5 for character-state distributions among the remaining taxa, of which only *Oryzomys rostratus* and *O. subflavus* were scored as polymorphic (i.e., {01}). This character was treated as unordered.

Character 62: *Mesolophs on M1 and M2 well-developed, extending from the median mure to the labial cingulum, fused with mesostyle (0); or mesolophs small, not extending to labial cingulum and not fused with the mesostyle (1); or mesolophs on M1 and M2 absent (2).* Most oryzomyines have well-developed mesolophs (fig. 25B, ml). Exceptions include *Pseudoryzomys* (fig. 25K), *Lundomys* (fig. 25I), and *Holochilus brasiliensis* (fig. 25J), which have small mesolophs (state 1); and *Holochilus chacarius* and *Zygodontomys* (fig. 25M), which lack mesolophs (state 2). The mesoloph is well developed in all outgroups. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).

Character 63: *Median mure connected to protocone on M1 (0); or median mure not connected to protocone (1).* The median mure is an enamel crest connecting the anterior (protocone and paracone) and posterior (hypocone and metacone) pairs of molar cusps (fig. 25M, mm). In most oryzomyines and in all outgroups, the median mure is connected to the posterior end of the protocone, whereas the median mure is connected to the paracone in *Holochilus* (fig. 25J).

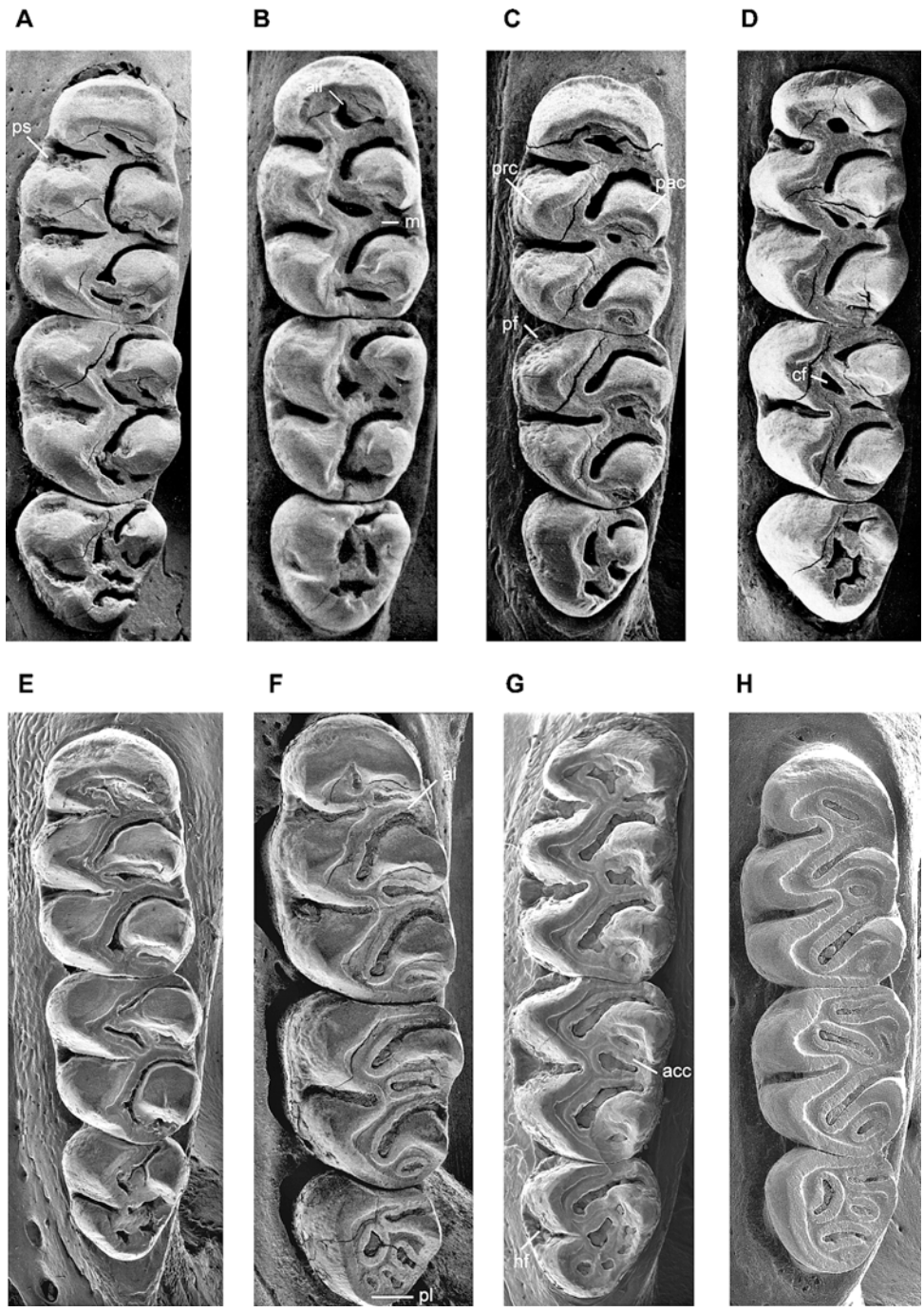
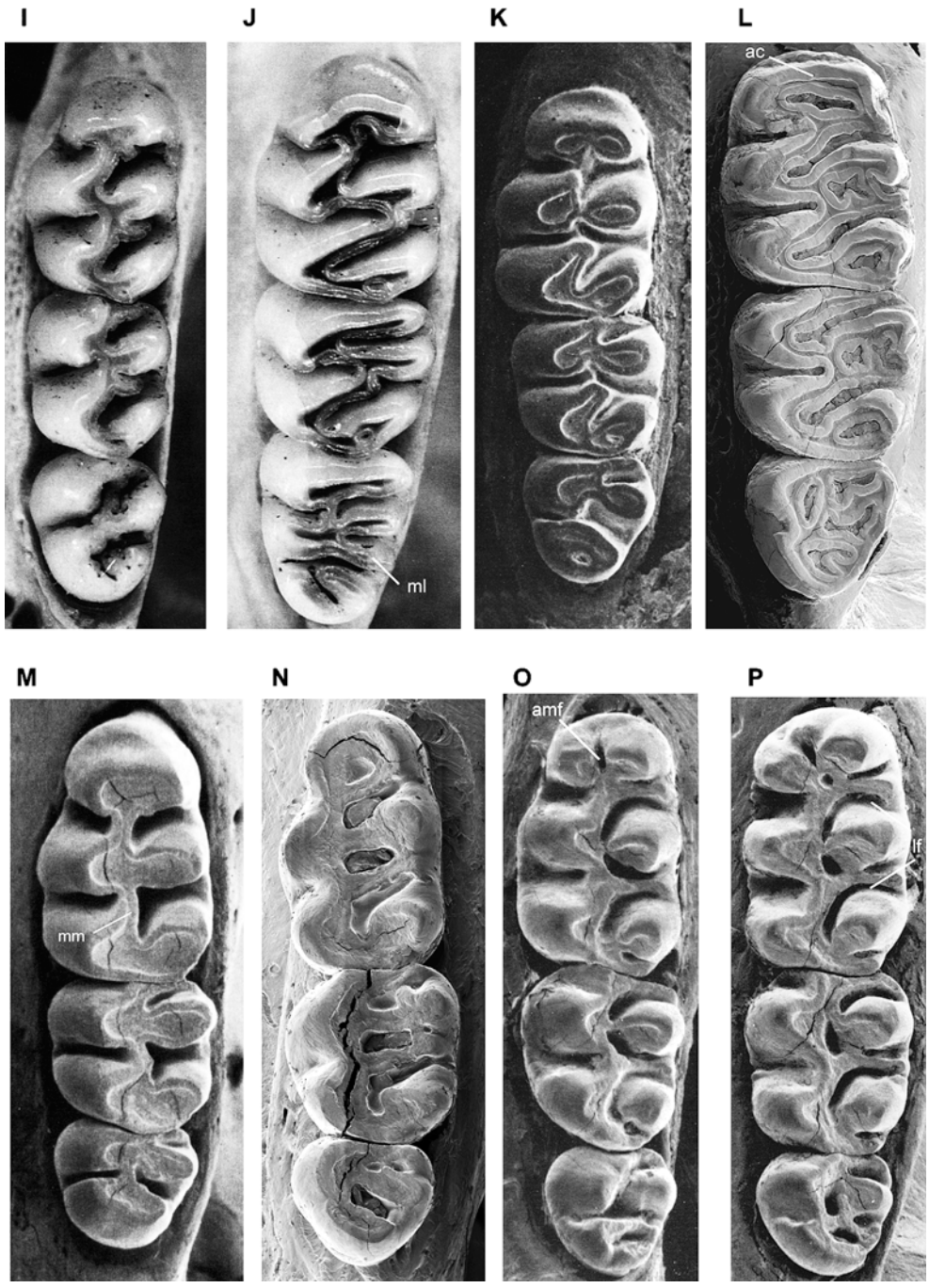


Fig. 25. Maxillary molars of oryzomyine rodents illustrating variations in characters of the occlusal surface of upper molars. **A,** *Oryzomys angouya* (AMNH 80393); **B,** *Oryzomys palustris* (AMNH234836); **C,** *Oryzomys megacephalus* (AMNH 231655); **D,** *Oryzomys macconnelli* (AMNH 131121); **E,** *Oryzomys hammondi* (UMMZ 155827); **F,** *Oryzomys albigularis* (AMNH 46495); **G,** *Oecomys trinitatis* (MUSM 15536); **H,** *Handleyomys intectus* (ICN 16074); **I,** *Lundomys molitor* (AMNH 206388); **J,** *Holochilus brasiliensis* (AMNH 206372); **K,** *Pseudoryzomys simplex* (CONN 17060);



L, *Sigmodontomys aphrastus* (UMMZ 155808); **M,** *Zygodontomys brevicauda* (AMNH 173971); **N,** *Scolomys ucayalensis* (MUSM 13357); **O,** *Oligoryzomys fulvescens* (AMNH 181446); **P,** *Microryzomys minutus* (AMNH 66527). Abbreviations are ac, anterocone; acc, accessory loph; aif, anterocone internal fold; al, anteroloph; amf, anteromedian flexus; cf, central fossette; hf, hypoflexus; lf, labial flexi; ml, mesoloph; mm, median mure; pac, paracone; pf, protoflexus; pl, posteroloph; prc, protocone; ps, protostyle.

Character 64: *Protoflexus of M2 present (0); or absent (1).* Most oryzomyines have a protoflexus on M2 (fig. 25C, pf), usually as a shallow indentation that does not attain the degree of excavation of other major folds. In contrast, the protoflexus is completely absent and the anterolingual border of M2 forms a smooth and rounded surface continuous with the protocone in *Holochilus* (fig. 25J), *Nectomys*, *Nesoryzomys narboroughi*, *Oryzomys hammondi* (fig. 25E), *O. xanthaeolus*, *Scolomys* (fig. 25N), *Sigmodontomys* (fig. 25L), and *Zygodontomys* (fig. 25M). Among outgroups, only *Wiedomys* specimens lack the protoflexus. The protoflexus can disappear with moderate wear, so younger specimens were used to score this character.

Character 65: *Paracone on M2 without accessory loph (0); or accessory loph present posterior to paracone (1).* An accessory loph is present in specimens of *Oecomys* and *Nyctomys* due to the presence of an additional fossette anterior to the mesoflexus (fig. 25G, acc). This loph is situated between the paracone and the mesoloph on M2 (and M3). All other taxa lack this accessory loph; the labial fossette of some species (see character 66) sometimes creates the impression of an accessory loph (e.g., *Oryzomys angouya*, fig. 25A), but it never reaches the labial cingulum.

Character 66: *Mesoflexus present as single internal labial fossette on M2 (0); or mesoflexus divided into labial and medial fossetti (1).* The internal fossetti observed on M2 between the mesoloph and the paracone are derived from the engulfment of the mesoflexus caused by wear of the occlusal surface. The presence of a single labial fossette, sometimes extending into the central portion of the tooth (e.g., fig. 25F), is the widespread condition among pentalophodont oryzomyines. The only taxa with an additional central fossette (fig. 25D, cf) are *Handleyomys* and several species of *Oryzomys*: *O. alfaroi*, *O. angouya*, *O. chapmani*, *O. couesi*, *O. macconnelli*, *O. rostratus*, *O. palustris*, *O. russatus*, *O. subflavus*, and *O. yunganus*. The present character is not applicable for taxa that lack a mesoflexus, such as *Holochilus chacarius* and *Zygodontomys*, and for taxa without an engulfed mesoflexus, such as *Peromyscus*, *Lundomys*, *Holochilus brasiliensis*, and *Pseudoryzomys* (coded "–" in table 5).

Character 67: *Mesoloph on M3 present and well developed (0); or absent or vestigial (1).* The mesoloph on M3 is usually present in taxa with mesolophs on M1 and M2, but some taxa do not follow this pattern. *Lundomys* and *Pseudoryzomys* have small mesolophs on M1 and M2 but not on M3 (Voss and Carleton,1993; Carleton and Olson, 1999); *Holochilus chacarius* does not have mesolophs on M1 and M2 but has one on M3 (fig. 25J); and *Scolomys* has mesolophs on M1 and M2 but lacks one on M3 (fig. 25O). All outgroups and remaining oryzomyines, with the exception of *Zygodontomys*, have a mesoloph on M3.

Character 68: *Posteroloph on M3 present (0); or absent (1).* The posteroloph is one of the first structures to lose its identity on the molar occlusal surface, joining the metacone in early stages of wear. Nevertheless, the posteroloph still can be identified on moderately worn third upper molars (M3) by the presence of an internal fossette derived from the posteroflexus. This fossette separates the metacone from the posterior rim of tooth, and thus creates an additional loph, the posteroloph. Several oryzomyine taxa have a posteroloph (fig. 25F, pl), including *Holochilus*, *Lundomys*, *Melanomys*, *Nectomys*, *Nesoryzomys narboroughi*, *Oecomys*, *Oligoryzomys*, *Pseudoryzomys*, *Sigmodontomys*, some species of *Oryzomys* (*O. albigularis*, *O. angouya*, *O. couesi*, *O. hammondi*, *O. levipes*, *O. palustris*, *O. polius*, *O. subflavus*, *O. xanthaeolus*), and *Zygodontomys brevicauda*. In several other oryzomyines, however, the metacone is the posteriormost structure on M3 (e.g., fig. 25P). Such taxa include *Handleyomys*, *Microryzomys*, *Neacomys*, *Scolomys*, most species of *Oryzomys*, and *Zygodontomys cherriei*. Among non-oryzomyine sigmodontines and outgroups, only *Peromyscus* specimens lack a posteroloph on M3.

Character 69: *Hypoflexus on M3 present, remaining excavated until later wear stages (0); or hypoflexus absent or diminutive, disappearing with little occlusal wear (1).* Most oryzomyines have a distinct hypoflexus on M3 (fig. 25G, hf) that is conspicuous in

moderately worn dentition, but usually disappears in older specimens with heavily worn teeth. Conversely, the M3 hypoflexus of several other oryzomyines is absent or diminutive even in younger specimens, never reaching the degree of excavation that this structure exhibits on M2, and it disappears in the earliest stages of molar wear (e.g., fig. 25H). My analyzed sample of *Oryzomys subflavus* included young specimens with and without the hypoflexus (scored as polymorphic, {01}). See the matrix in table 5 for character-state distributions among remaining taxa.

Character 70: *Anteromedian flexid and anteromedian fossettid absent on first lower molar (0); or anteromedian flexid absent but anteromedian fossettid present (1); or anteromedian flexid present and anteromedian fossettid absent (2).* Most analyzed taxa have an undivided m1 anteroconid with an internal enamel pit, the anteroconid internal fold or anteromedian fossettid (state 1; fig. 26G, aif). Departing from this pattern, specimens of *Thomasomys*, *Wiedomys*, *Microryzomys*, and *Oryzomys balneator* have a deep anteromedian flexid (fig. 26P, amf) dividing the anteroconid into distinct anterolabial and anterolingual conulids (state 2). The putatively plesiomorphic condition (anteroconid without anteromedian flexid or anteromedian fossettid) was observed only in specimens of *Peromyscus*. The character description is based on the assumption that the anteromedian fossettid is actually an engulfed anteromedian flexid, and is thus homologous to the latter structure (Steppan, 1995; Carleton and Olson, 1999). This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).

Character 71: *Anterolabial cingulum on m1 absent (0); or long anterolabial cingulum present (1).* A distinctive anterolabial cingulum is observed in all oryzomyines (e.g., fig. 26O, alc) except *Oryzomys lamia* and *Pseudoryzomys* (fig. 26K). The anterolabial cingulum is usually fused with the anterior labial surface of the protoconid, leaving the protoflexid as an internal fossettid. Among non-oryzomyines, the anterolabial cingulum was observed in specimens of all taxa except *Nyctomys*.

Character 72: *Ectolophid and ectostylid on m1 absent (0); or present (1).* Most oryzomyines lack an ectolophid and an ectostylid on the first and second lower molars (e.g., fig. 26J). Several oryzomyine species, however, have distinctive ectolophids and/or ectostylids. The ectolophid may be developed and reach the ectostylid (fig. 26G, el), or it can be smaller, not reaching the ectostylid, or even merged to the mesoconid. I could not sort these configurations into different states because they are observed within samples of the various species displaying the ectostylid and ectolophid. The putative apomorphic state is observed in *Nyctomys*, *Delomys*, *Thomasomys*, *Handleyomys*, *Oecomys*, and several species of *Oryzomys* (*O. albigularis*, *O. alfaroi*, *O. angouya*, *O. hammondi*, *O. levipes*, *O. macconnelli*, *O. megacephalus*, *O. talamancae*, and *O. yunganus*).

Character 73: *Mesolophids present and well developed on m1 and m2 (0); or mesolophids present in unworn dentition but small, not extending to lingual cingulum (1); or mesolophids completely absent (2).* Almost all analyzed taxa have the same condition for the mesolophid on m1/m2 and for the mesoloph on M1/M2 (character 62; see the matrix in table 5 for character-state distributions among taxa). Nonetheless, specimens of *Pseudoryzomys simplex* and *Holochilus brasiliensis* have small mesolophs on their upper molars but do not have mesolophids on their lower molars (e.g., fig. 26K), and I therefore included the two features as independent characters (following Voss and Carleton, 1993). In adult individuals with advanced molar wear, the mesolophid fuses with the entoconid, with the consequent loss of the entoflexid. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).

Character 74: *Anterolabial cingulum present on m2 (0); or absent (1).* Almost all analyzed taxa have an anterolabial cingulum present on the second lower molar (fig. 26C, ac), but the structure is absent in specimens of *Sigmodontomys alfari*. The character definition is modified from the description of Steppan (1995: char. 22P; described as procingulum on m2). In his description, Steppan (1995) defined three states: absence; cingulum appears as groove, wearing away with age; and cingulum well developed. I could not find a suitable discrete interval for

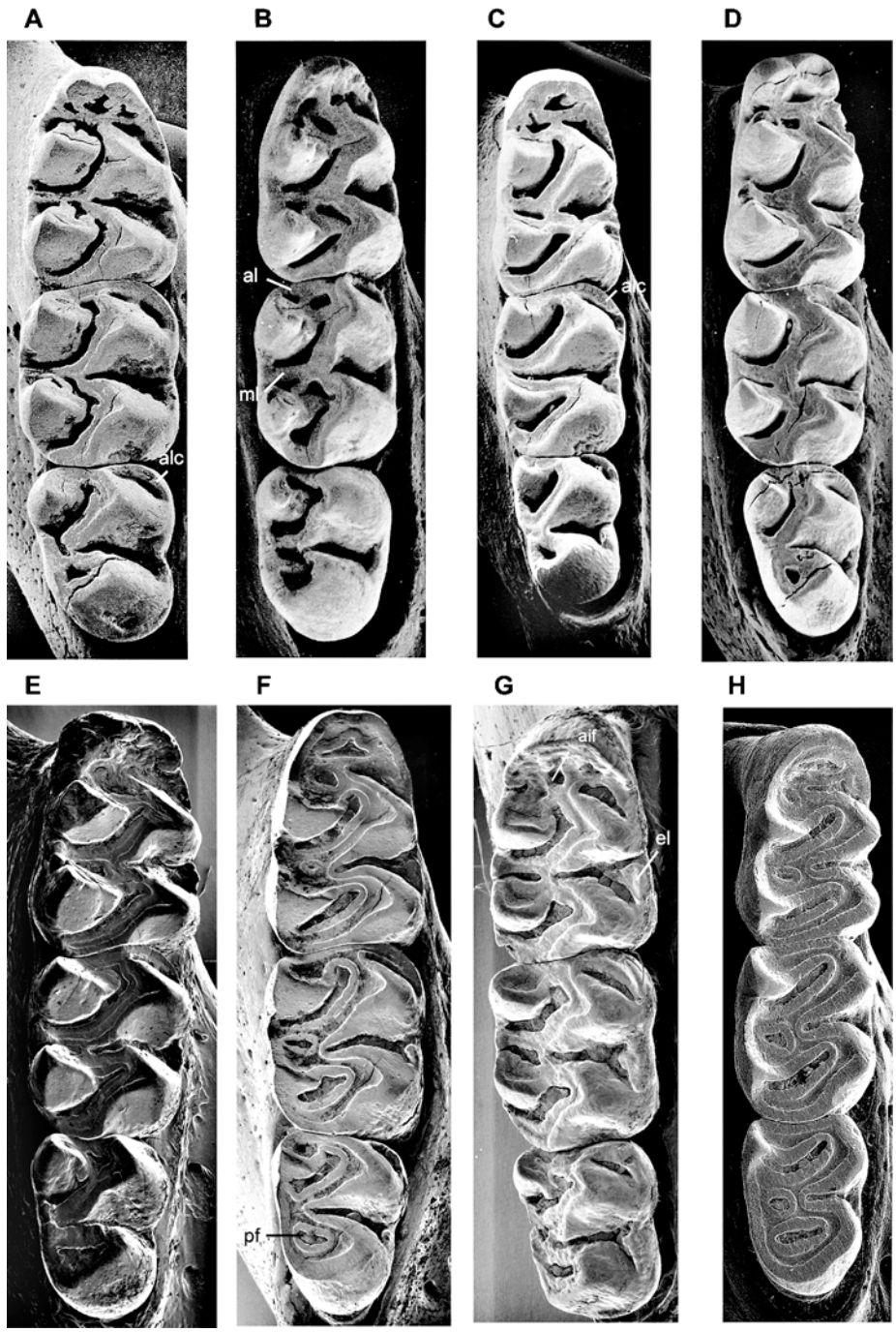
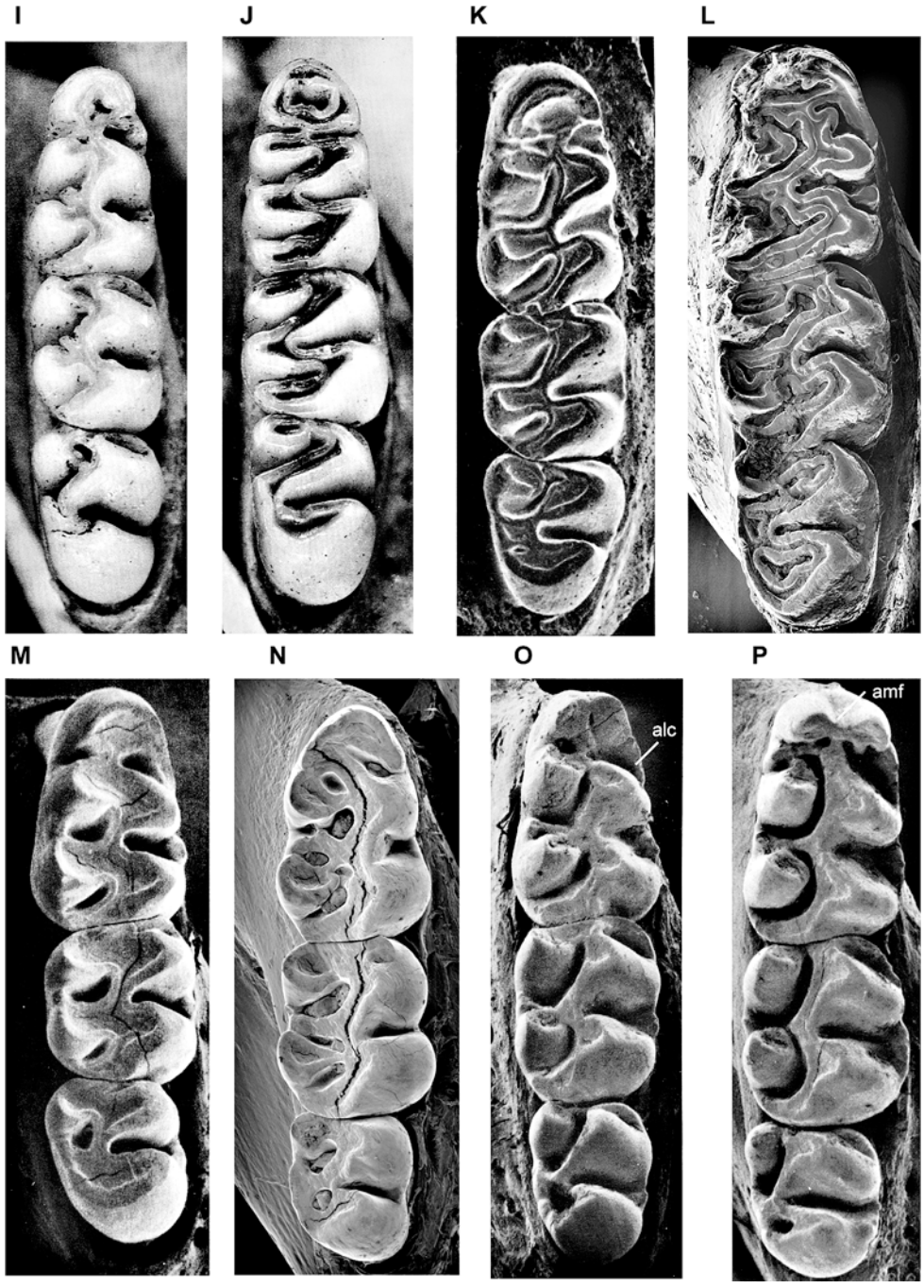


Fig. 26. Mandibular molars of oryzomyine rodents illustrating variations in characters of the occlusal surface of lower molars. **A,** *Oryzomys angouya* (AMNH 80393); **B,** *Oryzomys palustris* (AMNH234836); **C,** *Oryzomys megacephalus* (AMNH 231655); **D,** *Oryzomys macconnelli* (AMNH 131121); **E,** *Oryzomys hammondi* (UMMZ 155827); **F,** *Oryzomys albigularis* (AMNH 46495); **G,** *Oecomys trinitatis* (MUSM 15536); **H,** *Handleyomys intectus* (ICN 16074); **I,** *Lundomys molitor* (AMNH 206388); **J,** *Holochilus brasiliensis* (AMNH 206372); **K,** *Pseudoryzomys simplex* (CONN 17060);



L, *Sigmodontomys aphrastus* (UMMZ 155808); **M,** *Zygodontomys brevicauda* (AMNH 173971); **N,** *Scolomys ucayalensis* (MUSM 13357); **O,** *Oligoryzomys fulvescens* (AMNH 181446); **P,** *Microryzomys minutus* (AMNH 66527). Abbreviations are aif, anteroconid internal fold (= anteromedian fossettid); al, anterolophid; alc, anterolabial cingulum; amf, anteromedian flexid; el, ectolophid; ml, mesolophid; pf, posteroflexid.

the last two conditions, which I joined in a single state.

Character 75: *Anterolophid absent or weakly expressed on m2 and m3 (0); or anterolophid and companion metaflexid distinct (1).* A distinct anterolophid on m2 and m3 (fig. 26B, al) was observed only in *Pseudoryzomys* and three species of *Oryzomys* (*O. couesi*, *O. palustris*, and *O. polius*). The remaining taxa lack distinct anterolophids on both m2 and m3 (e.g., fig. 26D).

Character 76: *Anterolabial margin of m3 with shelflike cingulum, separated from protoconid by protoflexid (0); or anterolabial margin of m3 smoothly rounded, without cingulum, protoflexid absent (1).* Most analyzed taxa have a distinct anterolabial cingulum on m3 (fig. 26A, alc), but specimens of *Neacomys musseri*, *Nectomys squamipes*, *Oryzomys hammondi*, and *Sigmodontomys* lack the cingulum (e.g., fig. 26E). The distribution of states of the anterolabial cingulum of m3 is not identical to that of the serially homologous structure on m2, as several taxa with the cingulum present on m2 do not possess it on m3. I scored this character only in young specimens because the protoflexid disappears and the anterolabial cingulum joins the protoconid even in lightly worn teeth. I could not define discrete states related to the development of the cingulum (broad flange or narrow ridge) as did Carleton and Musser (1989: char. 16). Information about this character is not available for *Amphinectomys*, *Handleyomys*, and *Nesoryzomys swarthi* (coded "?" in table 5).

Character 77: *Posteroflexid on m3 present, well developed (0); or posteroflexid present as a small groove, obvious only in juveniles, obliterated with wear (1); or posteroflexid absent (2).* In most oryzomyines, the posteroflexid is present as a conspicuous internal fossettid on the m3, even in most old exemplars with advanced wear on teeth (fig. 26F, pf). In contrast, *Pseudoryzomys* displays a minute posteroflexid only in young individuals (fig. 26K), whereas specimens of *Holochilus*, *Lundomys*, and *Zygodontomys* lack the posteroflexid altogether, even in juveniles with unworn teeth (e.g., fig. 26J). The posteroflexid was observed in all outgroup taxa except *Peromyscus*. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).

Postcranial Skeleton

Character 78: *13 ribs present (0); or 12 ribs (1).* All oryzomyine species have a modal count of 12 ribs (see also Voss, 1993; Steppan, 1995; Voss et al., 2002; Pacheco, 2003). Although intraspecific variation in rib counts is widespread (Steppan, 1995, table 5), most outgroup taxa display 13 ribs, but *Wiedomys* has 12. The definition of this character follows Steppan (1995: char. 79P; see also Voss, 1993; Voss et al., 2002), who hypothesized that the presence of 12 ribs is a putative synapomorphy for oryzomyines. Carleton (1980: char. 36), Steppan (1995: char. 26S), and Pacheco (2003: chars. 96S, 124T) used modified definitions for this character; instead of ribs, these authors counted the number of thoracic vertebrae, also including the number of lumbar vertebrae in the character definition. In this context, taxa with 12 (rib-bearing) thoracic vertebrae have 7 lumbar vertebrae, whereas all taxa with 13 thoracics have 6 lumbars. Character information for this and the next six postcranial osteological characters is missing for several species that are not represented by complete skeletal preparations in my material, but some data were retrieved from Steppan (1995).

Character 79: *Tuberculum of first rib articulates with transverse process of first thoracic vertebra only (0); or first rib contacts transverse processes of both the first thoracic and seventh cervical vertebrae (1).* All sigmodontine rodents display the dual articulation of the first rib with the first thoracic and seventh cervical vertebrae, a synapomorphy that supports the monophyly of Sigmodontinae sensu stricto (Carleton, 1980; Voss, 1993; Voss and Carleton, 1993). Both of my nonsigmodontine outgroups, *Nyctomys* and *Peromyscus*, exhibit the putatively plesiomorphic single articulation. Information for this character is unavailable for 13 taxa not represented by suitable skeletal material in my samples (coded "?").

Character 80: *Anapophyses present on the 17th thoracico-lumbar vertebra (0); or anapophyses absent or vestigial (1).* The 17th thoracico-lumbar vertebra (TL17) is the 5th lumbar (L5) in specimens with 12 thoracic and 7 lumbar vertebrae, or the 4th lumbar

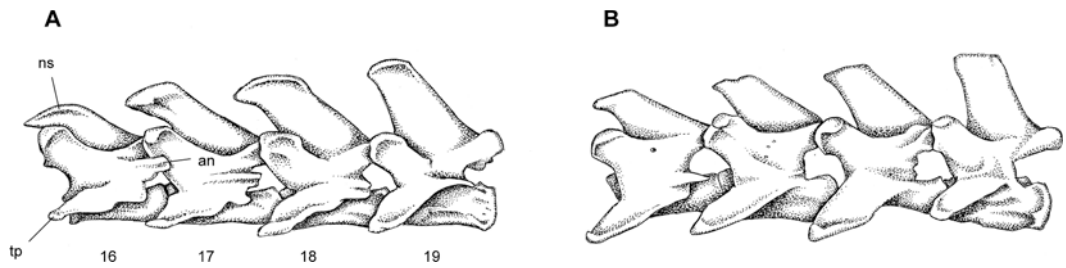


Fig. 27. Lateral view of the lumbar vertebrae showing variations in the anapophyses on the 17th thoracico-lumbar vertebra (character 80). **A**, *Nesoryzomys narboroughi* (ASNHC 8675); **B**, *Oryzomys palustris* (AMNH 219953). Abbreviations are 16–19, thoracico-lumbar vertebrae 16 to 19; an, anapophysis; ns, neural spine; tp, transverse process.

(L4) in specimens with 13 thoracics and 6 lumbars (see character 78). In both cases, TL17 is always the third-to-last lumbar. The anapophyses (or processus accessorius; Nomina Anatomica Veterinaria, 1994) are spinous processes that "leave the caudal borders of the [vertebral] pedicle and, when well developed, form a notch lateral to the caudal articular process that receives the cranial articular process of the vertebra behind" (Evans, 1993: 175). In sigmodontines, anapophyses were consistently observed on TL11–TL16 (some specimens also have vestigial anapophyses on TL10), but the condition on TL17 is taxonomically variable. Most oryzomyines, both non-sigmodontines outgroups, and *Delomys* have conspicuous anapophyses on TL17 that approach the size of the anapophyses on TL16 (fig. 27A). In contrast, specimens of *Thomasomys*, *Wiedomys*, *Melanomys*, *Microryzomys*, *Neacomys spinosus*, *Oecomys bicolor*, *Oe. mamorae*, *Oe. trinitatis*, *Oligoryzomys flavescens*, *Ol. fulvescens*, *Ol. nigripes*, *Oryzomys chapmani*, *O. couesi*, *O. megacephalus*, *O. rostratus*, *O. palustris*, *Pseudoryzomys*, *Scolomys*, and *Zygodontomys* do not have anapophyses on TL17, or they have a vestigial process much smaller than the one on TL16 (fig. 27B). Information for this character is unavailable for 18 taxa not represented by suitable skeletal material in my samples (coded "?").

Character 81: *Hemal arches absent between caudal vertebrae 2 and 3 (0); or hemal arches present, with simple posterior border (1); or present, with spinous posterior border (2).* Hemal arches (arcus hemales; Nomina Anatomica Veterinaria, 1994) are discrete ossifications that articulate with the ventral surface of the caudal ends of the second and third caudal vertebrae in some mammals (Evans, 1993; Steppan, 1995).[7] Hemal arches were observed between the second and third caudal vertebrae in almost all oryzomyines except *Scolomys* and *Nesoryzomys narboroughi* (fig. 28A). The posterior border of the hemal arch has two configurations, with or without a spinous process (fig. 28B, C, respectively). Taxa without the spinous process are *Handleyomys*, *Microryzomys*, *Neacomys spinosus*, *Oecomys bicolor*, *Oe. concolor*, *Oe. mamorae*, *Oe. trinitatis*, *Oryzomys albigularis*, *O. chapmani*, *O. levipes*, *O. macconnelli* (fig. 28B), *O. megacephalus*, *O. rostratus*, *O. russatus*, *O. talamancae*, and *O. yunganus*. The posterior spinous border is observed in the hemal arches of *Holochilus brasiliensis*, *Lundomys*, *Melanomys*, *Nectomys*, *Nesoryzomys swarthi*, *Oligoryzomys fulvescens*, *Ol. nigripes*, *Oryzomys angouya*, *O. couesi*, *O. palustris* (fig. 28C), *O. subflavus*, *O. xanthaeolus*, *Pseudoryzomys*, and *Sigmodontomys alfari*. Both species of *Zygodontomys* exhibit intraspecific variation for this feature, with all three states observed among analyzed specimens. Among outgroups, hemal arches were observed in *Wiedomys* (without posterior spinous border), whereas *Thomasomys* is polymorphic for this character (coded as {01}). This character was treated as un-

[7] I keep the term hemal arches (used by Steppan, 1995) instead of chevron bones (used by Pacheco, 2003) following current usage in mammalian anatomical literature (Evans, 1993: 174; Nomina Anatomica Veterinaria, 1994: 24).

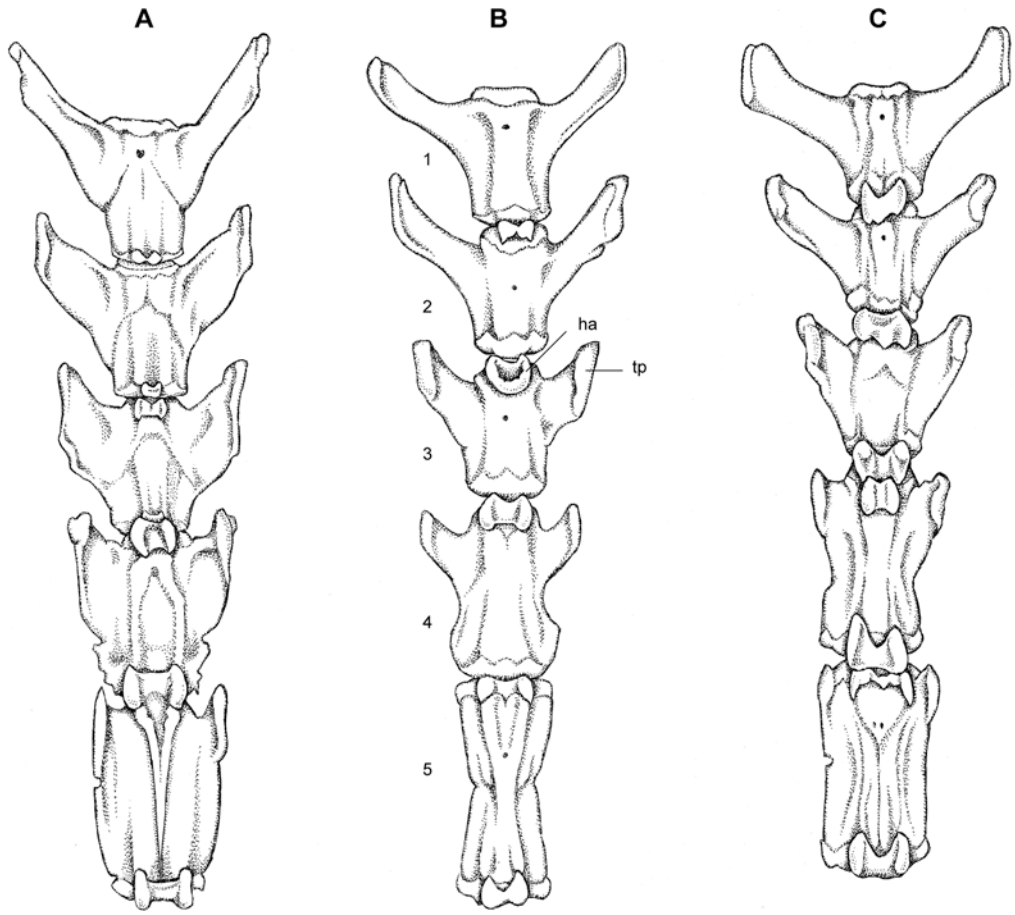


Fig. 28. Ventral view of caudal vertebrae showing taxonomic variations in the hemal arches (character 81). **A**, *Scolomys ucayalensis* (AMNH 272721). **B**, *Oryzomys macconnelli* (AMNH 257238). **C,** *Oryzomys palustris* (AMNH 219953). Abbreviations are 1–5, caudal vertebrae 1 to 5; ha, hemal arch; tp, transverse process.

ordered. Information about the condition of hemal arches is unavailable for *Amphinectomys*, *Holochilus chacarius*, *Neacomys minutus*, *N. musseri*, *Oecomys catherinae*, *Oligoryzomys flavescens*, *Ol. fornesi*, *Ol. stramineus*, *Oryzomys alfaroi*, *O. balneator*, *O. hammondi*, *O. lamia*, *O. polius*, and *Sigmodontomys aphrastus* (coded "?").

Character 82: *Entepicondylar foramen of humerus present (0); or absent (1).* The entepicondylar foramen perforates the distal end of the humerus above the medial epicondyle of most neotomines (e.g., *Peromyscus*) and all tylomyines (e.g., *Nyctomys*). The foramen is absent in all sigmodontines and might be a putative synapomorphy for the subfamily (Carleton, 1980; Voss, 1993; Voss and Carleton, 1993; Steppan, 1995; Pacheco, 2003).[8] This character could not be scored for 13 taxa without available humeri or prior literature information (coded "?").

[8] Because arvicolines also lack the entepicondylar foramen, recent molecular-based phylogenetic analyses that recover arvicolines as the sister group to sigmodontines (Jansa and Weksler, 2004) suggest that the absence of the foramen is a synapomorphy for the higher clade including both groups rather than for Sigmodontinae alone.

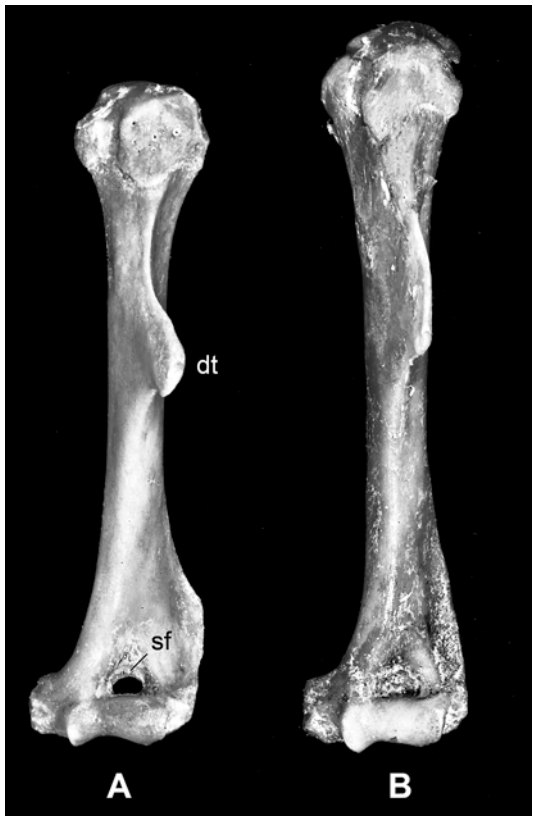


Fig. 29. Flexor surface of the humerus illustrating taxonomic variations in the supratrochlear foramen (character 83). **A,** *Nesoryzomys swarthi* (ASNHC 10003); **B,** *Oryzomys angouya* (AMNH 61850). Abbreviations are dt, deltoid tuberosity; sf, supratrochlear foramen.

Character 83: *Supratrochlear foramen in humerus absent (0); or present (1).* In contrast to the entepicondylar foramen, the supratrochlear foramen is absent in both *Peromyscus* and *Nyctomys* but present in most sigmodontines (fig. 29). The supratrochlear foramen perforates the distal portion of the humerus between the medial and lateral epicondyles and is larger than the entepicondylar foramen when both openings are present. The only sigmodontines in the current dataset without the supratrochlear foramen are *Thomasomys*, *Oecomys bicolor*, *Oe. concolor*, and *Oryzomys angouya*. This character was not scored for 20 taxa without available humeri or prior literature information (coded "?").

Character 84: *Trochlear process of calcaneum at the same level as posterior articular facet, trochlear process broad and shelflike (0); or gap between proximal edge of trochlear process and posterior articular facet, process shorter and less shelflike (1).* All sigmodontines in the present dataset, with the exception of *Thomasomys*, have a gap between the proximal edge of the trochlear process and the posterior articular facet (Carleton, 1980: fig. 16). In *Thomasomys* and both non-sigmodontine outgroups, the trochlear process is broad and shelflike and reaches the same level as the posterior articular facet. The presence of a gap (state 1) is a putative sigmodontine synapomorphy (Steppan, 1995). This character was not scored for 15 taxa without available humeri or prior literature information (coded "?").

Glans Penis

Character 85: *Lateral bacular mounds absent or diminutive (0); or present as large protuberances (1).* The tridigitate distal cartilaginous apparatus, characteristic of muroid rodents with a complex penis, is contained by the bacular mounds at the terminal crater of the glans. (Hooper, 1960, 1962; Hooper and Musser, 1964). The lateral mounds containing the lateral bacular digits are strongly developed in the vast majority of sigmodontines analyzed to date (Hooper, 1962; Hooper and Musser, 1964; Carleton, 1980; Patton and Hafner, 1983; Spotorno, 1992; Langguth and Silva Neto, 1993; Malygin and Rosmiarek, 1996). In contrast, *Nyctomys* has a central bacular mound and vestigial lateral mounds (Hooper and Musser, 1964), and *Peromyscus* lacks lateral mounds completely (Hooper, 1958). This character was not scored for 18 taxa without preserved male genitalia or prior literature information (coded "?" in table 5).

Character 86: *Large bacular cartilaginous apparatus with central digit more robust than lateral digits (0); or reduced cartilaginous apparatus with slim central digit (1).* The cartilaginous distal bacular apparatus of most oryzomyines consists of three large digits that approach or exceed half the length of the proximal bone (Hooper and Musser, 1964: table 2). The central digit in these taxa

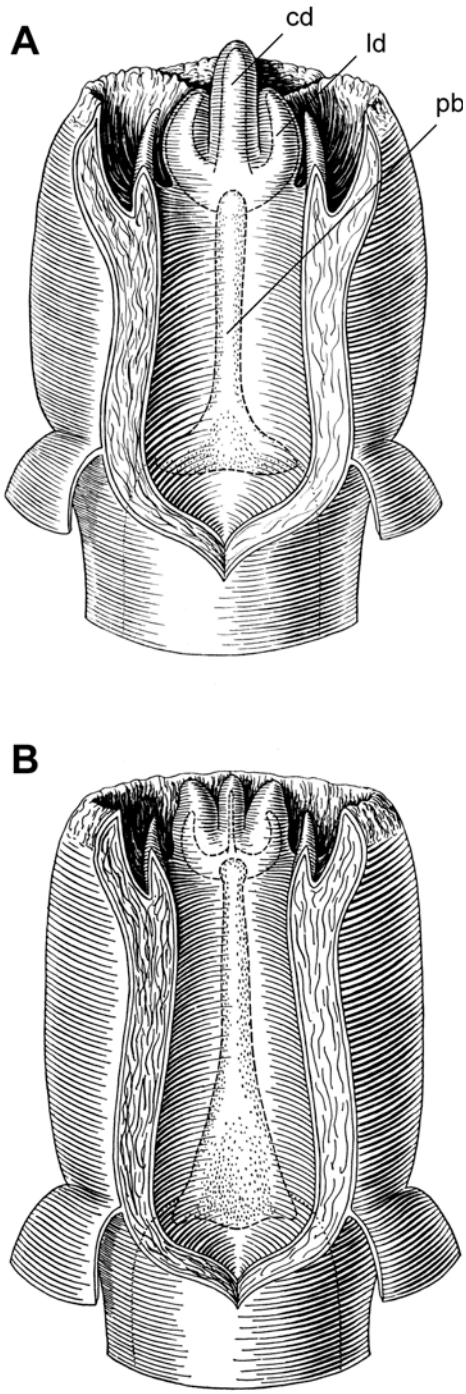


Fig. 30. Ventral views of the glans penis of oryzomyines illustrating the variations in the morphology of the bacular digits (character 86). **A,** *Oligoryzomys flavescens* (UMMZ110444); **B,** *Oryzomys alfaroi* (UMMZ P-3905). Abbreviations are cd, central digit; ld, lateral digit; pb, proximal bone (from Hooper and Musser, 1964: figs. 1, 2).

is more robust than the lateral ones (fig. 30A). In contrast, *Melanomys*, *Nesoryzomys*, *Oryzomys alfaroi*, *O. chapmani*, *O. rostratus*, *O. subflavus*, *O. xanthaeolus*, *Pseudoryzomys*, and *Sigmodontomys alfari* have a reduced tridigitate apparatus (approximately less than one-third of the proximal bone length) in which the slender central digit is less robust than the lateral digits (fig. 30B; see also Hooper and Musser, 1964; Patton and Hafner, 1983). Sigmodontine outgroups scored for this character display a robust central digit. The present character is not applicable for taxa without a tridigital apparatus (*Nyctomys* and *Peromyscus*; coded "–"). This character was not scored for 18 taxa without preserved male genitalia or prior literature information (coded "?").

Character 87: *Nonspinous tissue of crater rim does not conceal bacular mounds (0); or nonspinous tissue conceals bacular mounds (1).* Most of the exterior surface of the oryzomyine penis is densely covered with small spines, but a distinct distal band of softer tissue surrounding the crater rim is nonspinous (Hooper and Musser, 1964). In some oryzomyines (*Lundomys*, *Melanomys*, *Neacomys*, *Oligoryzomys flavescens*, *Ol. fulvescens*, *Ol. nigripes*, *Oryzomys alfaroi*, *O. balneator*, *O. chapmani*, *O. couesi*, *O. rostratus*, *O. subflavus*, *O. xanthaeolus*, and *Sigmodontomys alfari*), this band of soft nonspinous tissue is broad enough to conceal the bacular mounds, but in others (*Holochilus brasiliensis*, *Oecomys bicolor*, *Oe. concolor*, *Oe. mamorae*, *Oryzomys albigularis*, *O. angouya*, *O. levipes*, *O. macconnelli*, *O. megacephalus*, *O. palustris*, *O. talamancae*, *O. yunganus*, *Scolomys*, and *Zygodontomys*), the nonspinous tissue is less extensive and the bacular mounds are exposed. This character was not scored for 21 taxa lacking preserved male genitalia or prior literature information (coded "?"). Neither non-sigmodontine outgroup could be scored for this character

Fig. 31. Views of the dorsal papilla of the glans penis of oryzomyines illustrating variations in its condition (character 88). **A,** *Oryzomys albigularis* (CM 18663); **B,** *Oryzomys palustris* (UMMZ 110388). From Hooper and Musser (1964: fig. 2).

because bacular mounds are not developed (coded "–").

Character 88: *Dorsal papilla of glans penis spineless (0); or spinous (1)*. The dorsal and lateral surfaces of the dorsal papillae are free of spines (fig. 31A) in most examined oryzomyines, but the dorsal papilla is studded with numerous spines in *Oligoryzomys*, *Oryzomys couesi*, and *O. palustris* (fig. 31B; see also Hooper and Musser, 1964). This character is inapplicable for *Peromyscus* (in which the dorsal papilla is absent; coded "–") and was not scored for 17 taxa without preserved male genitalia or prior literature information (coded "?").

Character 89: *Subapical lobule on ventral surface of urethral processes absent (0); or present (1)*. The urethral processes are simple in most oryzomyines (fig. 32A), but a fleshy subapical lobule (fig. 32B, sl) is present on the ventral surface of each process in *Oryzomys couesi*, *O. palustris*, and *Holochilus brasiliensis* (see also Hooper, 1962; Hooper and Musser, 1964; Langguth and Silva Neto, 1993; Voss, 1988). This character is inapplicable for *Peromyscus* (in which urethral processes are absent; coded "–") and was not scored for 18 taxa lacking preserved genitalia or prior literature information (coded "?").

Male Accessory Reproductive Glands

Character 90: *Two pairs of preputial glands present (0); or one pair present (1); or preputial glands absent (2)*. One pair of preputial glands is the widespread condition among sigmodontines (Arata, 1964; Carleton, 1980; Voss and Linzey, 1981; Patton and Hafner, 1983; Carleton and Musser, 1989), but preputial glands are absent (at least macroscopically) in *Oligoryzomys fulvescens* and *Ol. nigripes* (Myers and Carleton, 1981; Voss and Linzey, 1981).[9] Among outgroups, *Nyctomys* possesses two pairs of preputial glands (Carleton, 1980; Steppan, 1995), whereas preputial glands are macroscopically absent in *Peromyscus* (Linzey and Layne, 1969). Information about this and the following seven characters are missing for 27 taxa for which no information on accessory reproductive glands is available (coded "?"). This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).

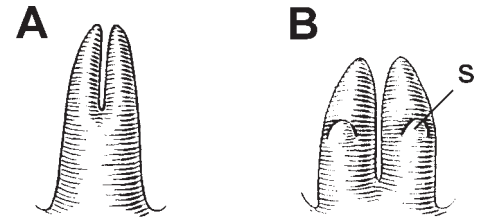


Fig. 32. Views of urethral process of the glans penis of oryzomyines illustrating variations in its morphology (character 89). **A**, *Oligoryzomys flavescens* (UMMZ 110444); **B**, *Holochilus brasiliensis* (MNHN 1166). Abbreviation is sl, subapical lobule. From Hooper and Musser (1964: figs. 1, 6).

Character 91: *Two pairs of ventral prostate glands present (0); or ventral prostate glands absent (1)*. The derived condition of this character is found only in *Nesoryzomys narboroughi* (see Patton and Hafner, 1983) and *Nyctomys* (see Voss and Linzey, 1981; contra Carleton, 1980). All remaining muroid rodents analyzed to date have at least one pair of ventral prostates, and most remaining sigmodontines have two pairs ("*Akodon*" *bogotensis* and *Thaptomys nigrita*, two taxa not analyzed herein, have a single pair; see Arata, 1964; Carleton, 1980; Voss and Linzey, 1981). Among the five specimens of *Nyctomys* dissected by Voss and Linzey (1981), four lacked the ventral prostates entirely, while in one specimen a single small pair was present. I consider this a variation within the apomorphic condition.

Character 92: *Anterior prostate glands present (0); or absent (1)*. Like the previous character, the apomorphic absence of the anterior prostate glands is found only in

[9] The specimens identified as *O. albigularis* by Voss and Linzey (1981), which also lack the preputial glands, are now referred to *O. devius* (see Musser and Carleton, 1993).

Nesoryzomys narboroughi (see Patton and Hafner, 1983) and *Nyctomys* (see Voss and Linzey, 1981; contra Carleton, 1980). All remaining taxa with available information about male accessory glands have one pair of anterior prostates (Arata, 1964; Carleton, 1980; Voss and Linzey, 1981).

Character 93: *Vesicular glands present, large, shaped like a cane or inverted "J" (0); or vesicular glands present, shaped like small diverticula (1); or vesicular glands absent (2).* The vesicular glands are usually the largest of the male glands complement, resembling J-shaped sacs (Voss and Linzey, 1981). In *Nesoryzomys narboroughi*, however, the vesicular glands are considerably smaller pear-shaped diverticulae (Patton and Hafner, 1983). The vesicular glands are absent in *Nyctomys* (Voss and Linzey, 1981; contra Carleton, 1980). This character was treated as unordered.

Character 94: *Preputial glands extend to or beyond the ventral flexure of the penis (0); or do not extend to the ventral flexure of the penis (1).* The preputial glands of all but one oryzomyine exceed the prepuce in length, reaching and sometimes extending cranially (anteriorly) beyond the ventral flexure of the penis (Voss and Linzey, 1981). The sole exception is *Neacomys spinosus*, in which the preputial glands do not reach the ventral flexure of the penis. *Oligoryzomys fulvescens* and *Ol. nigripes* could not be scored for this character because the preputial glands are absent (coded "–").

Character 95: *Dorsal prostates absent (0); or one pair present (1); or two pairs present (2).* The presence of a second pair of dorsal prostates is reported by Arata (1964) for *Sigmodontomys alfari*, the only sigmodontine taxon possessing this condition. All other oryzomyines in the present study have only one pair of dorsal prostate glands. Among outgroups, *Thomasomys* has one pair and *Nyctomys* does not have prostate glands. Voss and Linzey (1981) argued that dorsal prostatic tissue encroaches upon the lateral surface of the male reproductive tract, and hypertrophy of this portion could result in the presence of two pairs of prostate glands in *Sigmodontomys alfari*. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$).

Character 96: *Ampullary glands forming tufts of tubules that extend cranially from the base of the vas deferens (0); or ampullary glands compact, not elaborate (1).* The ampullary glands of most described oryzomyines and outgroups are compact and closely associated with the vas deferens. In contrast, the ampullary gland is composed of a series of tufts of tubules extending from the base of the vas deferens in *Oryzomys megacephalus* and *O. talamancae* (see Voss and Linzey, 1981).[10]

Character 97: *Subterminal flexure of vesicular gland rounded and smooth (0); or irregularly lobed and notched (1); or small and finger-shaped (2).* The subterminal region of the vesicular gland is smooth and rounded, not folded, in most oryzomyines and in *Thomasomys* (see Voss and Linzey, 1981). In contrast, the subterminal flexure is rough and irregular in *Oryzomys palustris*, *O. megacephalus*, *O. alfaroi,* and *O. talamancae*, whereas in *O. rostratus* it is reduced and constricted (Voss and Linzey, 1981). Patton and Hafner (1983) reported that the vesicular gland of *Nesoryzomys narboroughi* is reduced in size, pear-shaped, and smooth, but they did not specifically describe the condition of the subterminal flexure; therefore, this character was not scored for this taxon (coded "?"). *Nyctomys* could not be scored for this character because the vesicular glands are absent (coded "–"). This character was treated as unordered.

Digestive System

Character 98: *Gall bladder present (0); or absent (1).* The gall bladder is absent in all oryzomyines, a condition considered to be a diagnostic synapomorphy of the tribe (Carleton, 1980; Voss, 1991, 1993; Voss and Carleton, 1993; Steppan, 1995; Voss et al., 2002). The gall bladder is present in all outgroups for which information is available, with the exception of *Nyctomys*. Information for this character is unavailable for *Wie-*

[10] The specimens identified as *O. capito* (i.e., *O. megacephalus* in current nomenclature) by Voss and Linzey (1981) are in reality from two species: *O. megacephalus* (specimen from Trinidad) and *O. talamancae* (specimens from Panama; see Musser et al., 1998: 150); I scored both species based on Voss and Linzey's (1981) description.

domys, *Amphinectomys*, *Neacomys minutus*, *Nesoryzomys swarthi*, *Oecomys catherinae*, *Oligoryzomys fornesi*, *Ol. stramineus*, and *Oryzomys polius* (coded "?").

Character 99: *Gastric glandular epithelium of stomach limited to antrum, not extending beyond incisura angularis (0); or gastric glandular epithelium covers antrum and proximal portion of corpus near esophageal opening (1)*. Oryzomyines have the basic unilocular-hemiglandular stomach pattern characteristic of sigmodontines, with a shallow incisura angularis that does not split the stomach in two major chambers, and a glandular epithelium that covers the anterior gastric chamber or antrum (Carleton, 1973; Vorontsov, 1979). Carleton (1973) recognized two major configurations of the glandular epithelium among taxa with the unilocular-hemiglandular pattern: (1) a group with the glandular epithelium restricted to the antrum that included most sigmodontines (fig. 33A); and (2) a smaller group with glandular epithelium extending into the corpus (the posterior chamber) that included *Holochilus brasiliensis* and *Nectomys squamipes*. Subsequently, the latter condition was also described for *Microryzomys minutus* (see Carleton and Musser, 1989) and *Pseudoryzomys* (see Voss and Carleton, 1993). Among the specimens I analyzed, state 1 was observed in *Holochilus*, *Microryzomys*, *Neacomys musseri*, *Nectomys*, *Oryzomys balneator*, *Pseudoryzomys*, and *Sigmodontomys aphrastus* (fig. 33B). The remaining analyzed oryzomyines, as well as all of my outgroups, have restricted glandular epithelium (state 0). Information on the stomach morphology is not available for *Wiedomys*, *Amphinectomys*, *Neacomys minutus*, *Nesoryzomys swarthi*, *Oecomys catherinae*, *Oligoryzomys flavescens*, *O. fornesi*, *O. stramineus*, *Oryzomys angouya*, *O. lamia*, *O. levipes*, *O. polius*, *O. russatus*, and *Sigmodontomys alfari* (coded "?"). This character is inapplicable for *Peromyscus* (which has a bilocular-discoglandular stomach structure; coded "–").

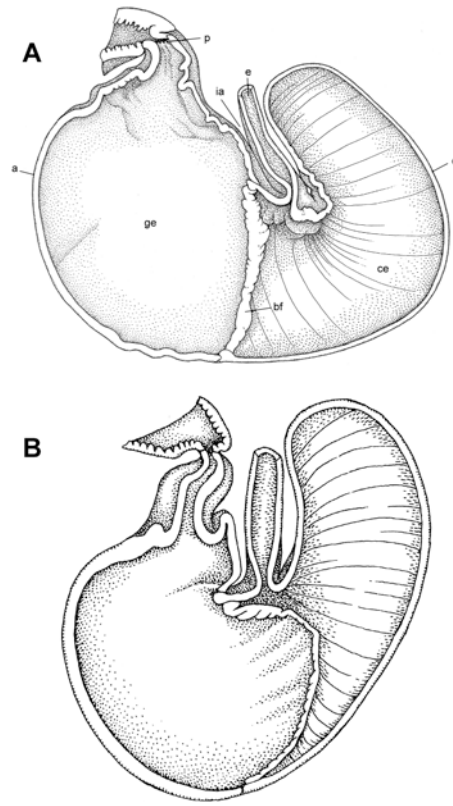


Fig. 33. Ventral views of oryzomyine stomachs (in midfrontal section) illustrating variations in the extent of gastric glandular epithelium (character 99). **A**, *Oryzomys palustris* (AMNH 239256); **B,** *Oligoryzomys microtis* (AMNH 263328). Abbreviations are a, antrum; bf, bordering fold; c, corpus; ce, cornified squamous epithelium; e, esophagus; ge, glandular epithelium; ia, incisura angularis; p, pylorus (from Carleton and Musser, 1989: fig. 28).

Summary of Morphological Dataset

The final morphological dataset consists of 99 characters out of 350 originally examined features (table 6). The dataset includes 16 characters based on external morphology; 32 characters of the skull and mandible; 29 dental characters; 7 postcranial characters; and 10 characters from the phallus, accessory male reproductive glands, and digestive system (table 6). Ninety-one characters are parsimony-informative, and the remaining eight are autapomorphic for oryzomyine taxa. Sixty-four characters are binary, 25 describe simple additive transformations, 2 describe complex (i.e., based on step matrices) additive transformations, and 8 describe nonadditive (unordered) transformations. The data matrix (table 5) has $54 \times 99 = 5346$ cells, of which 590 (11%)

TABLE 6
Character Information Summary

Character system	No. examined	No. included (% of examined)	Invariant	Metric character	Continuous trait	Autapomorphic for outgroups	Other[a]	Not observed
External morphology	52	16 (31)	16	3	8	2	3	4
Cranium and mandible	136	32 (24)	35	3	25	5	22	14
Dentition	88	29 (33)	18	2	13	2	16	8
Postcranium	16	7 (44)	5	1	2	1	—	—
Phallus	34	5 (15)	11	6	3	8	—	—
Accessory male reproductive glands	13	8 (62)	4	—	1	—	1	—
Digestive tract and other soft anatomy	11	2 (18)	2	—	—	2	—	5
Total	350	99 (28)	91	15	52	20	42	31

[a] Other reasons for character exclusion, which include rampant polymorphism (intraspecific variation), ambiguous characterization, nonreplicable results, characters not applicable to present set of taxa, complete covariation with other character, and structure or states not identified.

are scored as missing ("?"), 17 (0.3%) are scored as inapplicable ("–"), and 70 (1%) are scored as polymorphic. Data completeness for most terminal taxa range from 78 to 100% (table 4); however, *Nesoryzomys swarthi* was scored for only 63% of characters, and only 32% were coded for *Amphinectomys savamis*.

Phylogenetic Results

Morphology-Only Analyses: A heuristic analysis of the morphological data matrix with polymorphic entries analyzed as composites (CO) resulted in one most parsimonious tree of 522 steps (CI = 0.25, RI = 0.63; table 7) consistent with the assumption of ingroup (oryzomyine) monophyly (fig. 34). After rooting the tree using *Nyctomys* and *Peromyscus*, the basal tree structure depicts the sequence (*Thomasomys* (*Delomys* (*Wiedomys* + Oryzomyini))). Oryzomyines are split basally into two major clades, the first with 28 and the second with 21 taxa. The first clade contains the genera *Handleyomys*, *Microryzomys*, *Neacomys*, *Oecomys*, *Oligoryzomys*, *Scolomys*, *Zygodontomys*, and 10 of the 19 analyzed species of *Oryzomys*. The second clade is composed of *Amphinectomys*, *Holochilus*, *Lundomys*, *Melanomys*, *Nesoryzomys*, *Pseudoryzomys*, *Nectomys*, *Sigmodontomys,* and the remaining nine *Oryzomys* species. Of the eight genera with multiple representatives, only *Oryzomys* and *Sigmodontomys* are not recovered as monophyletic.

The first oryzomyine clade is divided basally into two large subclades. In the first, *Scolomys* and *Zygodontomys* form a monophyletic group (labeled A in fig. 34) that is sister to the group containing *Microryzomys*, *Neacomys*, *Oligoryzomys*, and *Oryzomys balneator* (labeled C). *Neacomys* and *Oligoryzomys* are both recovered as monophyletic genera, and the latter is the sister group to a clade formed by *Microryzomys* and *Oryzomys balneator*. The second oryzomyine clade (labeled B*) contains *Handleyomys*, *Oecomys,* and eight species of *Oryzomys*. *Oecomys* is recovered as monophyletic, with *O. hammondi* as its sister group. Going up the tree, a clade with the three species of the *nitidus* species group (*O. macconnelli*, *O. russatus* and *O. lamia*) is joined by *O. yunganus* and then by a clade with *O. megacephalus*, *O. talamancae*, *O. albigularis*, *O. levipes*, and *Handleyomys*. The latter genus is the sister group of the *albigularis* species group (*O. albigularis* and *O. levipes*).

Oryzomys polius appears as the sister group to the remaining members of a second large group (labeled D* in fig. 34). The next branch contains *O. angouya*, and the remaining taxa are split into two clades. The first clade contains *O. subflavus* as the most basal taxon, followed by (1) the *alfaroi* group of *Oryzomys*—*O. chapmani*, *O. alfaroi* and *O.*

TABLE 7
Summary of Phylogenetic Analyses

	No. of terminal taxa	No. of ingroup taxa	No. of informative characters	No. of MPT[a]	Tree length	CI[b]	RI[c]	Resolved nodes[d]
IRBP 1[e]	69	44	386	16	1512	0.45	0.63	56 (85%)
IRBP only	49	44	204	4	667	0.55	0.71	36 (78%)
Morphology CO[f]	54	49	91	1	522	0.25	0.63	51 (100%)
Morphology TS[g]	54	49	91	22	693	0.22	0.62	31 (61%)
Combined CO	54	49	295	2	1214	0.38	0.65	50 (98%)
Combined TS	54	49	295	9	1388	0.34	0.64	46 (90%)
Combined, reduced[h]	49	44	295	8	1174	0.40	0.65	42 (92%)

[a] Most parsimonious trees.
[b] Consistency index, excluding uninformative characters.
[c] Retention index.
[d] Resolved nodes in consensus tree; 100 × resolved nodes/(number of taxa – 3).
[e] Analysis of Weksler (2003).
[f] Polymorphic entries treated as composite states.
[g] Polymorphic entries treated as states with transformation series.
[h] Analysis excluding five taxa without IRBP data.

rostratus—of which the latter two appear as sister species; (2) the *palustris* group of *Oryzomys* (*O. palustris* and *O. couesi*); and (3) a clade containing *Pseudoryzomys*, *Lundomys*, and *Holochilus*, with the latter two as sister taxa. Another clade contains *Nesoryzomys* as the most basal taxon, followed by six taxa in the sequence (*Oryzomys xanthaeolus* (*Amphinectomys* (*Melanomys* (*Sigmodontomys aphrastus* (*S. alfari* + *Nectomys*))))).

A heuristic analysis of the morphological data with polymorphic entries analyzed as transformation series (TS) resulted in 22 most parsimonious trees of 693 steps each (CI = 0.22, RI = 0.62). The consensus tree (fig. 35) is the least resolved among the analyzed datasets, with only 31 of 51 (61%) resolved nodes and major polytomies between and within the major oryzomyine clades. The TS tree differs from the CO tree in several important aspects: (1) clade A is not recovered in the consensus tree, appearing in only in a few fundamental cladograms; (2) *Amphinectomys* appears as the sister taxon of *Handleyomys* within clade B*; (3) the *alfaroi* group of *Oryzomys* is recovered within clade B*; and (4) *Sigmodontomys* is recovered as monophyletic. Nevertheless, many relationships are congruent between the two analyses, including: (1) monophyly of Oryzomyini; (2) monophyly of clade C; (3) the three tetralophodont taxa *Pseudoryzomys*, *Holochilus*, and *Lundomys* and the *palustris* group of *Oryzomys* form a clade; (4) *Oryzomys polius* as basal member of clade D*; and (5) *Nectomys* and *Sigmodontomys* form a clade. Additionally, clades B* and D* are similar between the two analyses, with only minor differences in taxa content, and the monophyletic genera recovered in the CO analysis are also observed in the TS tree. Note also that all nodes at which the two analyses conflict are weakly supported in both trees.

IRBP-Only Analysis: A heuristic analysis of the IRBP dataset resulted in four equally parsimonious trees of 667 steps (CI = 0.55, RI = 0.71; table 7). The consensus topology (fig. 36) is identical to that previously recovered by Weksler (2003: fig. 5) when pruned of the outgroup taxa not included here. Within oryzomyines, a basal polytomy involving *Scolomys*, *Zygodontomys*, and a clade containing all of the remaining ingroup taxa is present in the consensus tree and in all fundamental cladograms. The largest group in this trichotomy is further divided into two clades. The first (labeled B in fig. 36) contains the genera *Oecomys*, *Handleyomys*, and 9 of the 16 analyzed species of *Oryzomys*. The internal structure of clade B in the strict consensus topology is characterized by a five-fold

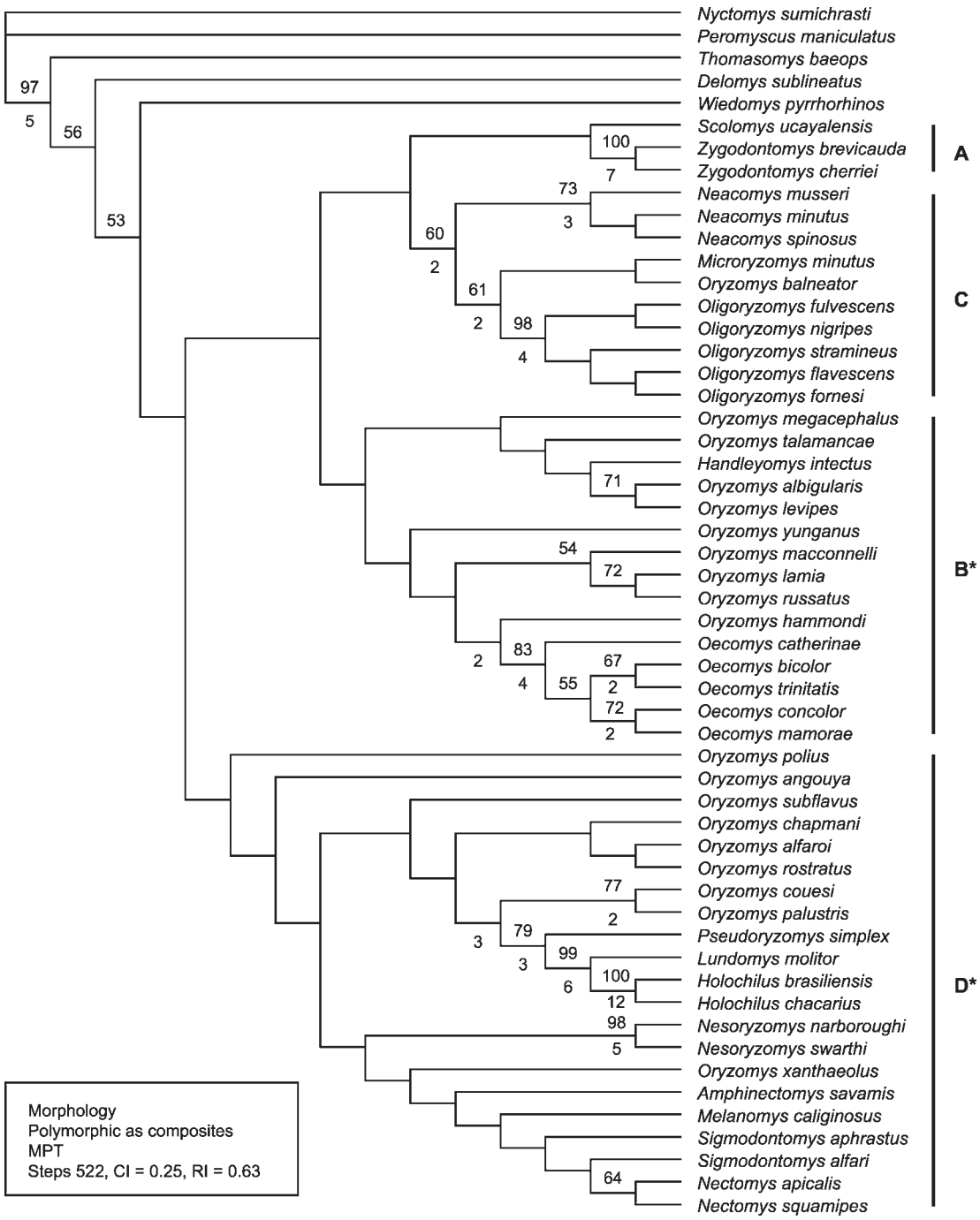


Fig. 34. Single most parsimonious tree resulting from cladistic parsimony analysis of 99 morphological characters (parsimony-informative characters = 91, tree length = 522, CI = 0.25, RI = 0.63). Polymorphic data were treated as composite entries. Numbers above and below branches refer to jackknife resampling percentage (> 50%) and decay index (> 1), respectively. Letters A, B*, C, and D* define clades discussed in the text.

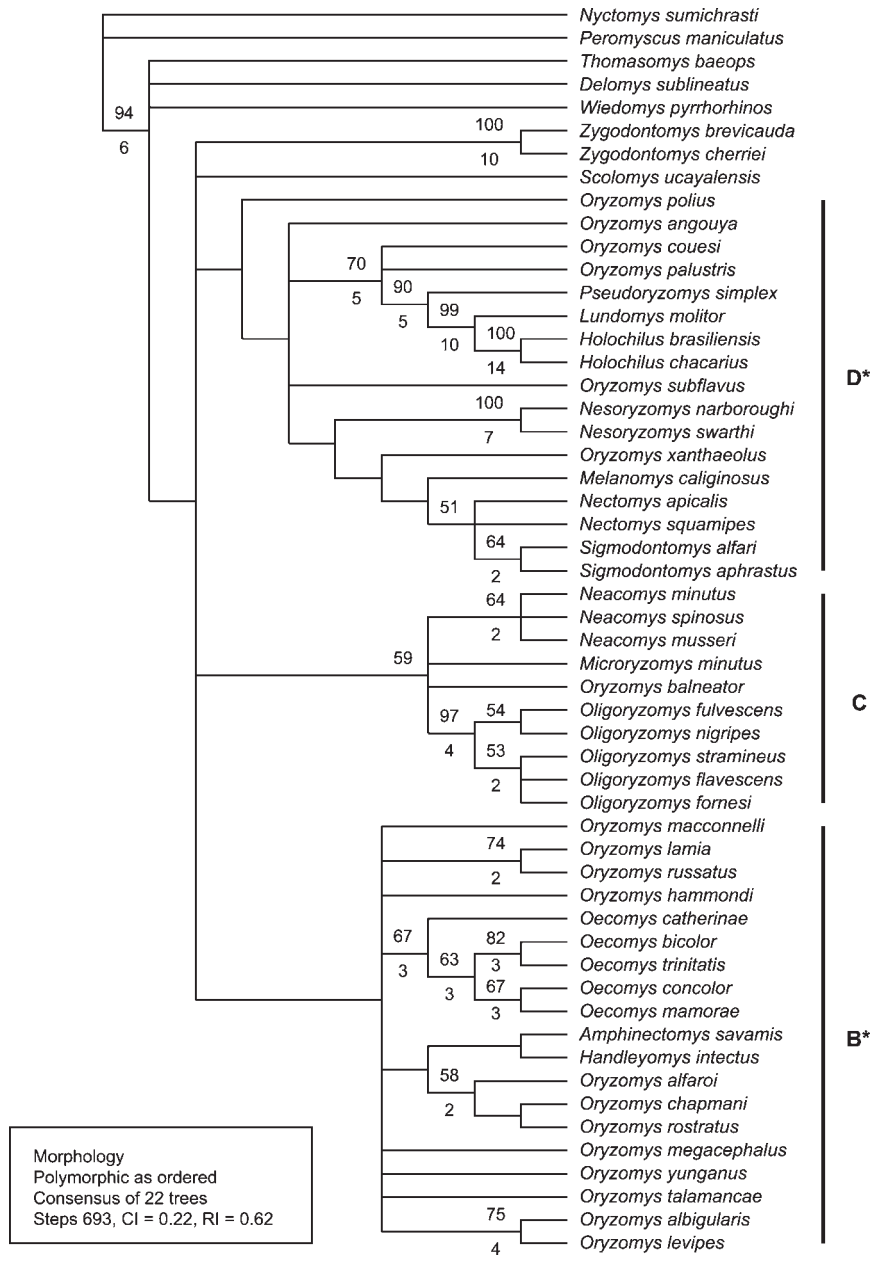


Fig. 35. Strict consensus of 22 minimum-length trees resulting from cladistic parsimony analysis of 99 morphological characters (parsimony-informative characters = 91, tree length = 693, CI = 0.22, RI = 0.62). Polymorphic data were treated as transformations series. Numbers above and below branches refer to jackknife resampling percentage (> 50%) and decay index (> 1), respectively. Letters B*, C, and D* define clades discussed in the text.

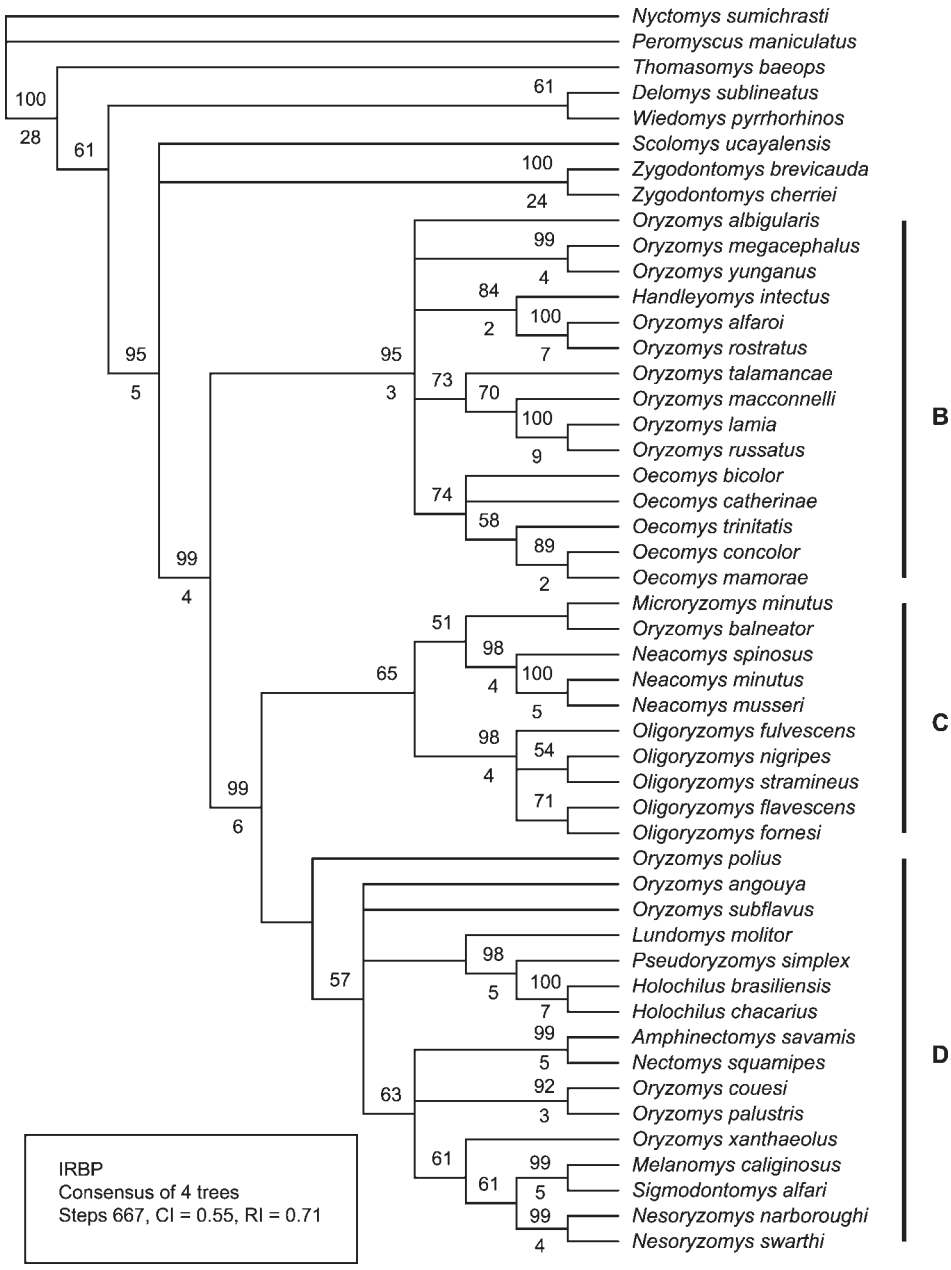


Fig. 36. Strict consensus of four minimum-length trees resulting from parsimony analysis of IRBP sequences (parsimony-informative characters = 204, tree length = 667, CI = 0.55, RI = 0.71). Numbers above and below branches refer to jackknife resampling percentage (> 50%) and decay index (> 1), respectively. Letters B, C, and D define clades discussed in the text.

polytomy resulting from two solutions found in the fundamental cladograms, which depict either (*Oryzomys talamancae* (*O. macconnelli* (*O. lamia* + *O. russatus*))) or (*Handleyomys intectus* (*O. alfaroi* + *O. rostratus*)) as the basal clade relative to the remaining taxa.

The second major group, containing the remaining 11 oryzomyine genera and 7 species of *Oryzomys,* is divided into two clades. The first (labeled C) contains *Microryzomys*, *Oligoryzomys*, *Neacomys*, and *Oryzomys balneator*. The second (labeled D) consists of six species of *Oryzomys* interspersed among eight other genera. Within this group, (1) *Oryzomys polius* appears as the sister group to remaining species, and (2) three pairs of genera are recovered as sister groups: *Holochilus* + *Pseudoryzomys*, *Amphinectomys* + *Nectomys*, and *Melanomys* and *Sigmodontomys*. The species of *Oryzomys* included in this clade are not recovered as monophyletic.

COMBINED ANALYSES: A heuristic search of the combined data analyzed with CO polymorphic entries resulted in two most parsimonious trees of 1214 steps (CI = 0.38, RI = 0.65; table 7). Oryzomyines are again recovered as monophyletic, and *Wiedomys* is again its sister group (fig. 37). *Oryzomys hammondi* appears as the sister group of remaining oryzomyines, followed by the clade containing *Scolomys* and *Zygodontomys* (labeled clade A in fig. 37). The basal phylogenetic structure of remaining oryzomyines is similar to the one recovered by the IRBP-only analysis, with three large clades (labeled B, C, and D) containing 17, 10, and 18 species each. Clades C and D appear as sister groups. Within clade B, the clade containing the *albigularis* species group (*O. albigularis* and *O. levipes*) plus *O. talamancae* is recovered as sister group of the (*O. megacephalus* + *O. yunganus*) clade. Going up the tree, this clade is joined by a cluster containing *Handleyomys* and three species of *Oryzomys* (*O. rostratus*, *O. chapmani*, and *O. alfaroi*) and then by the monophyletic *Oecomys*. *Oryzomys chapmani* is found as the sister species to *O. rostratus;* the three species of the *nitidus* species group (*O. macconnelli*, *O. russatus,* and *O. lamia*) form a clade that is the sister group of the remaining species.

Within clade C, *Microryzomys* and *Oryzomys balneator* are recovered as sister groups and are joined successively by the monophyletic genera *Oligoryzomys* and *Neacomys*. *Oryzomys polius* appears as the sister group to remaining members in clade D, which is then split into two subclades. The first contains two species of *Oryzomys* (*O. palustris* and *O. couesi*) as the sister group to the clade containing *Pseudoryzomys*, *Lundomys*, and *Holochilus*, with the latter two as sister groups. The phylogenetic sequence of the second subclade starts with *Oryzomys angouya*, followed by *O. subflavus*, *Nesoryzomys*, and *O. xanthaeolus*. Nested within the subclade, (*Amphinectomys* + *Nectomys*) and (*Melanomys* + *Sigmodontomys*) are sister groups. *Nectomys* is recovered as monophyletic, but *Sigmodontomys* is not: *S. aphrastus* is recovered as the sister group of *Melanomys*, and the two are joined to *S. alfari*.

The polytomy present in the consensus tree (fig. 37) is the result of different arrangements within the genus *Oligoryzomys* in the fundamental cladograms: *O. fulvescens* is recovered either as the sister group of the (*O. fornesi* + *O. flavescens*) clade or as the sister group of the (*O. stramineus* + *O. nigripes*) clade.

Heuristic search of combined datasets with polymorphic entries analyzed as TS resulted in nine most parsimonious trees of 1388 steps (CI = 0.34, RI = 0.64). The consensus tree (fig. 38) resembles the CO combined tree, having six differences: (1) *hammondi* is within clade B; (2) the basal topology of major oryzomyines clades is unresolved; (3) the internal topology of clade B is unresolved; (4) *Microryzomys* and *O. balneator* do not form a monophyletic group; (5) *Oligoryzomys* is the basal taxon in clade C; and (6) *O. angouya* is the sister group of all members of clade D except *O. polius*. The polytomies present in the consensus tree (fig. 38) are the result of (1) different arrangements within the *Sigmodontomys-Melanomys* clade; (2) different ordering of *xanthaeolus* and *Nesoryzomys*; (3) different positioning of *O. hammondi* within clade B, either as sister group to *Oecomys* or as the most basal taxon in clade B; and (4) different positioning of clade A, either as basal to all oryzomyines or as sister group to clade B.

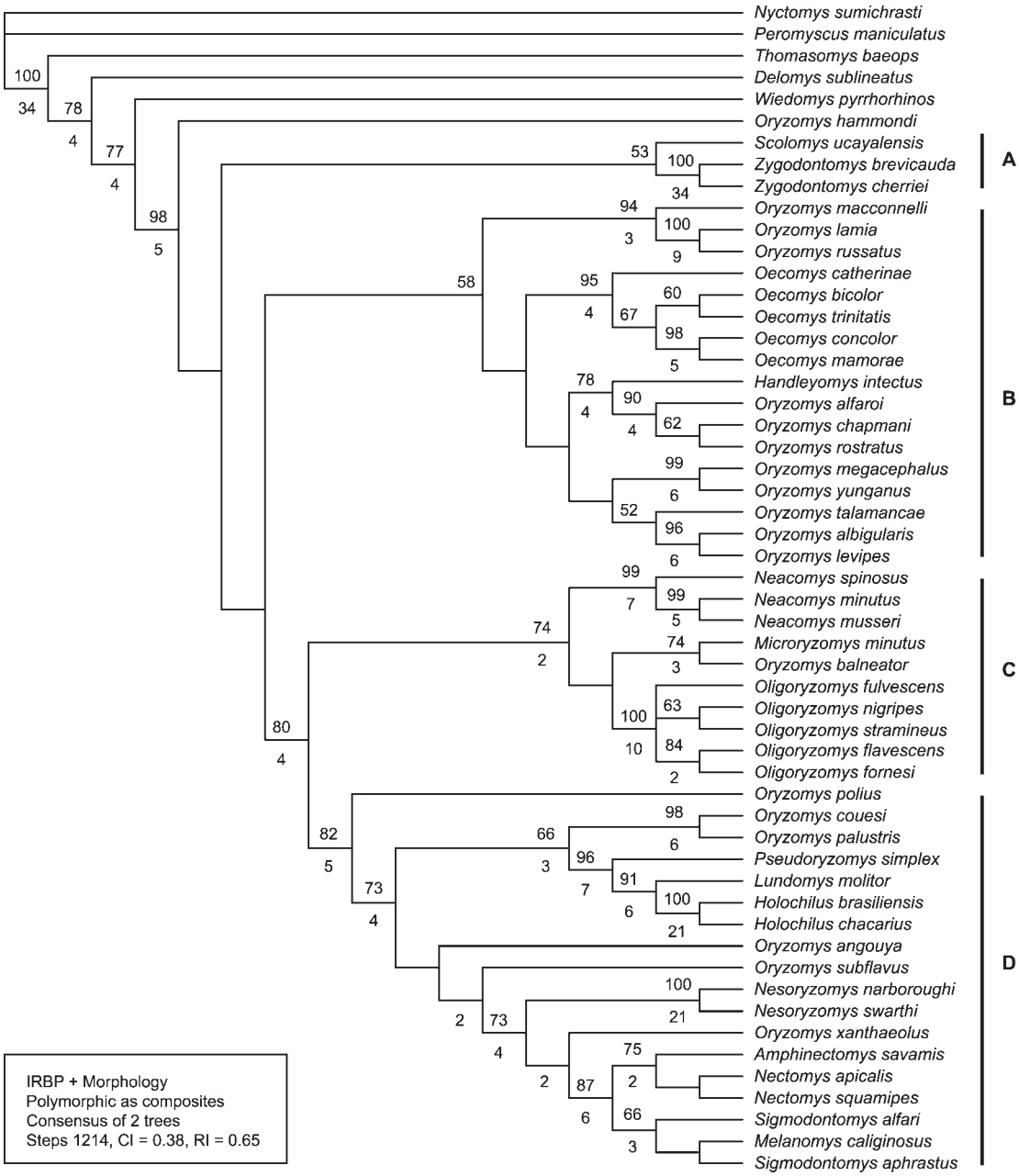


Fig. 37. Strict consensus of two minimum-length trees resulting from parsimony analysis of morphological and IRBP data (parsimony-informative characters = 295, tree length = 1214, CI = 0.38, RI = 0.65). Polymorphic data were treated as composite entries. Numbers above and below branches refer to jackknife resampling percentage (> 50%) and decay index (> 1), respectively. Letters A, B, C, and D define clades discussed in the text.

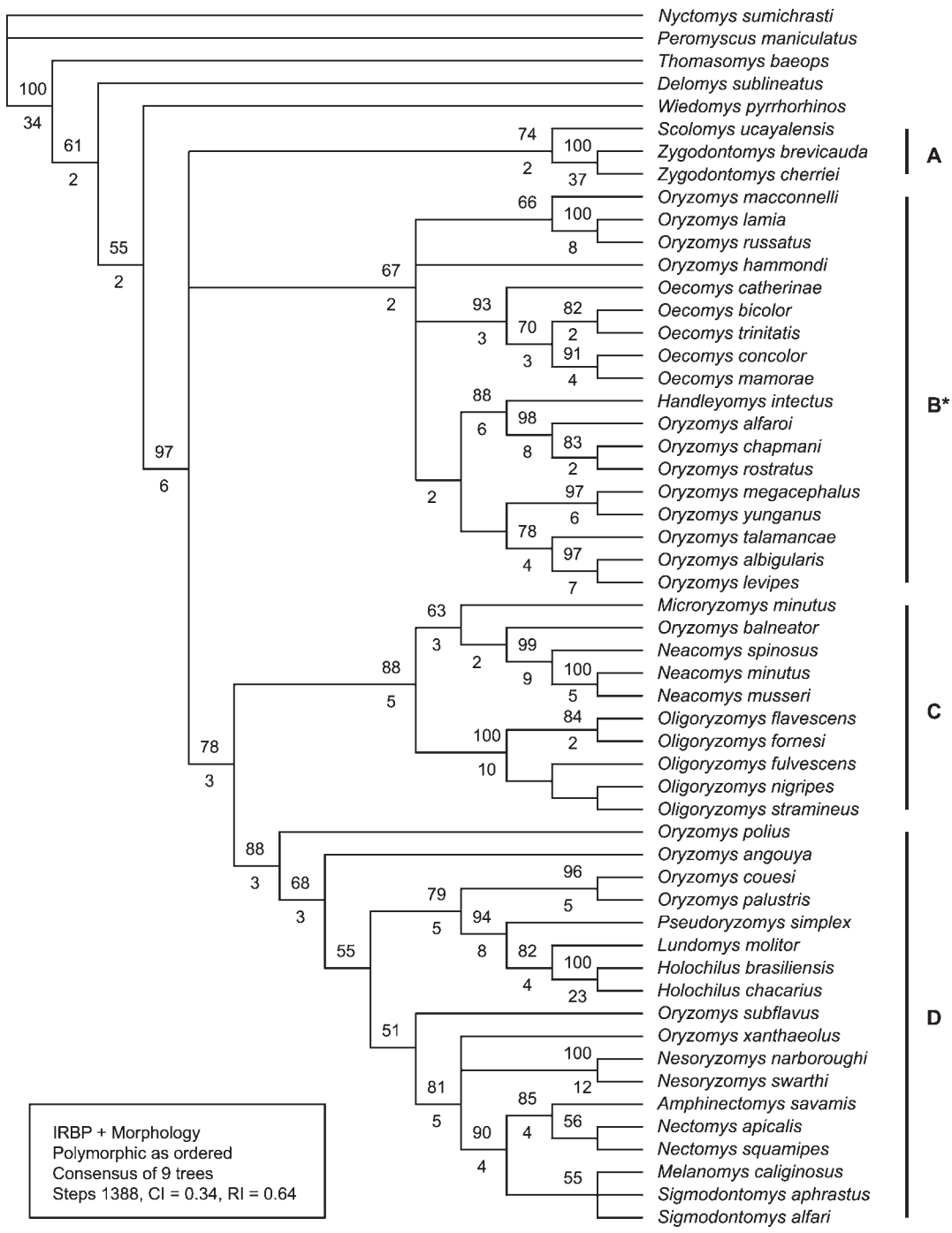


Fig. 38. Strict consensus of nine minimum-length trees resulting from parsimony analysis of morphological and IRBP data (parsimony-informative characters = 295, tree length = 1388, CI = 0.34, RI = 0.64). Polymorphic data were treated as transformations series. Numbers above and below branches refer to jackknife resampling percentage (> 50%) and decay index (> 1), respectively. Letters A, B*, C, and D define clades discussed in the text.

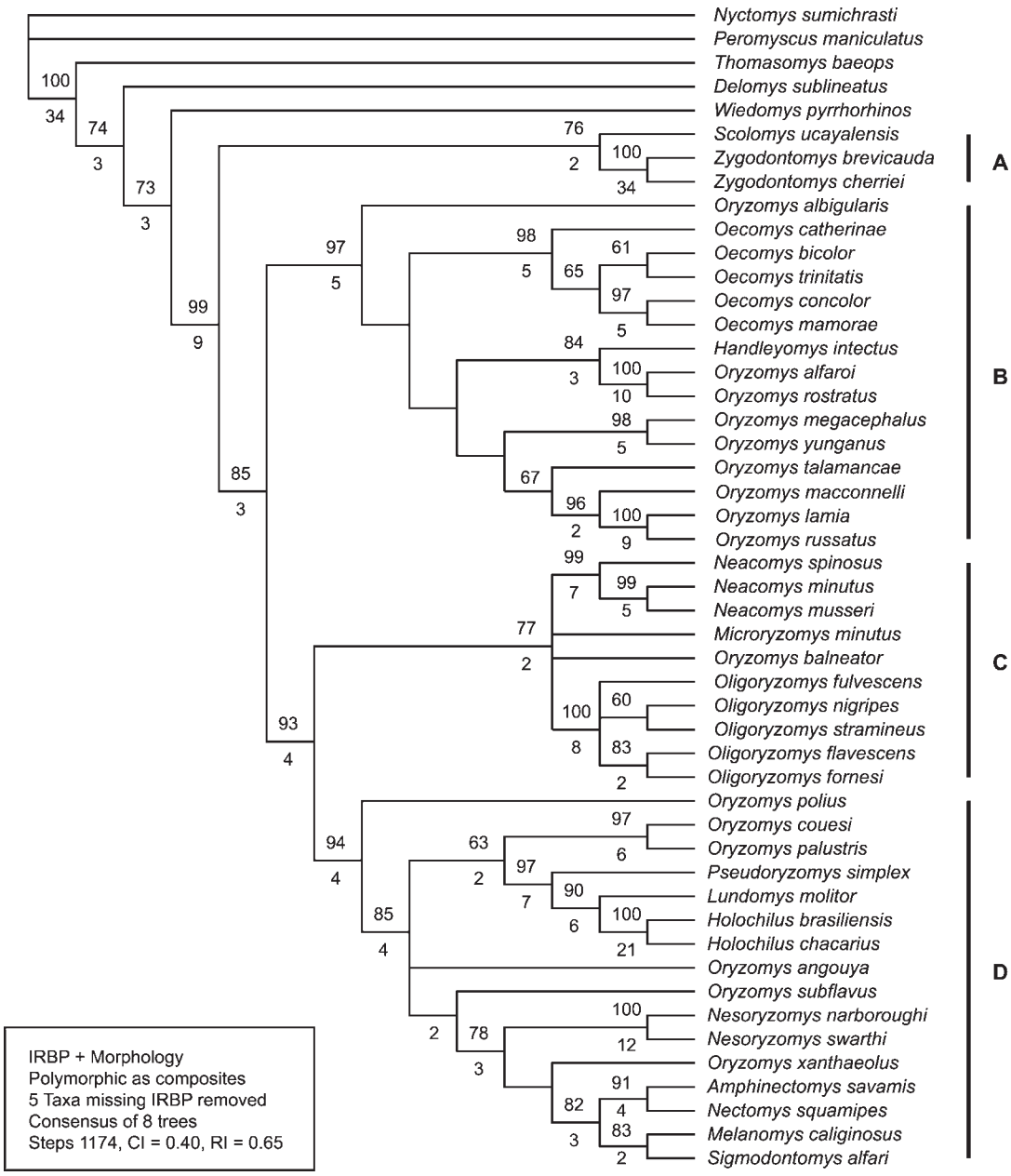


Fig. 39. Strict consensus of eight minimum-length trees resulting from parsimony analysis of morphological and IRBP characters, excluding taxa without sequence data (parsimony-informative characters = 295, tree length = 1174, CI = 0.40, RI = 0.65). Polymorphic data were treated as composite entries. Numbers above and below branches refer to jackknife resampling percentage (> 50%) and decay index (> 1), respectively. Letters A, B, C, and D define clades discussed in the text.

A node-by-node description of all groups recovered in the combined analysis with CO coding for polymorphisms (fig. 37) is presented in appendix 3.

REDUCED ANALYSIS: Heuristic search of the reduced dataset (i.e., excluding the five oryzomyines without molecular sequences) resulted in eight most parsimonious trees of 1174 steps (CI = 0.40, RI = 0.65; table 7). The recovered trees and the consensus cladogram (fig. 39) are similar to those retrieved by the CO combined analysis, except for three changes: (1) in clade B, *Oryzomys albigularis* is recovered as the most basal taxon, while the *nitidus* group is recovered as sister group to *O. talamancae* (i.e., *O. albigularis* and the *nitidus* group swap places); (2) in clade C, *O. balneator* and *Microryzomys* are not recovered as sister taxa, and instead are placed in a polytomy with *Oligoryzomys* and *Neacomys*; and (3) in clade D, *Oryzomys angouya* is recovered in a polytomy also containing the two major subclades of clade D.

NODAL SUPPORT

Nodal support values for the morphological trees are generally low. For instance, in the CO analysis (fig. 34), 34 nodes (67% of resolved nodes) collapse in trees that are one step longer, 6 additional nodes (12%) collapse in trees that are two steps longer, and 4 more nodes (8%) collapse in trees that are three steps longer. Only 7 nodes (14% of the total) have a decay index greater than three. Resampling values were also low: 28 nodes (55%) have jackknife values below 50%, and 17 nodes (33%) have jackknife values between 50 and 85%, while the remaining 6 nodes (12% of the total) have jackknife values higher than 85%.

Nodal support values for the IRBP tree (fig. 36) are considerably higher. Seventeen nodes (47%) collapse in trees that are one step longer, 2 additional nodes (6%) collapse in trees that are two steps longer, and 2 more nodes (6%) collapse in trees that are three steps longer. Fifteen nodes (42% of the total) have a decay index greater than three. Jackknife values show higher support: 2 nodes (6%) have jackknife values below 50%, and 15 nodes (42%) have jackknife values between 50 and 85%, while the remaining 19 nodes (53% of the total) have jackknife values higher than 85%.

Nodal support values for the combined CO analysis indicate that most of the 50 resolved nodes in the consensus tree (fig. 37) are at least moderately well supported. Only 16 nodes (32%) collapse in trees that are one step longer, 5 additional nodes (10%) collapse in trees that are two steps longer, and 4 more nodes (8%) collapse in trees that are three steps longer. The remaining 25 nodes (50% of the total) have a decay index greater than 3. Jackknife resampling suggests a similar pattern of support. Eleven nodes (22%) have jackknife values below 50%, and 20 nodes (40%) have jackknife values between 50 and 85%, while the remaining 19 nodes (38% of the total) have jackknife values higher than 85%. Nodal support is slightly higher in the TS analysis (fig. 38): 8 nodes (18%) collapse in trees that are one step longer, 8 additional nodes (18%) collapse in trees that are two steps longer, and 6 more nodes (13%) collapse in trees that are three steps longer. The remaining 23 nodes (51% of the total) have a decay index greater than three. In terms of resampling values, only 5 nodes (11%) have jackknife values below 50%, and 20 nodes (44%) have jackknife values between 50 and 85%, while the remaining 20 nodes (44% of the total) have jackknife values higher than 85%.

The effect of taxon removal in the reduced analysis is visible in nodal support values: 7 nodes (18% of the total) have jackknife values increased by at least 10%, 3 of them more then 20%. Twenty-three nodes (61%) have minimal changes in jackknife values (differences between −3% and +3%), while 4 nodes (11%) decreased at least 4%. The maximum increase in jackknife values was 39% (from 58 to 97%; clade B), while the maximum decrease was 5% (from 87 to 82%; *Amphinectomys* + *Nectomys* + *Melanomys* + *Sigmodontomys*).

DISCUSSION

EFFECTS OF DIFFERENT CODINGS OF POLYMORPHIC DATA

The different codings for polymorphic characters produced similar topologies, espe-

Node	Taxon content	1	2	3	4	5	6
1	Sigmodontinae	100	100	100	100	97	94
2	1 – *Thomasomys*	78	61	74	61	56	
3	Oryzomyini +*Wiedomys*	77	55	73		53	46
4	Oryzomyini	98	97	99	95	47	44
5	4 – *Oryzomys hammondi*	28		X	X		
6	Clade A	53	74	76		17	
7	*Zygodontomys*	100	100	100	100	100	100
8	Clades B + C + D	49		85	99		
9	Clade B	58	67[a]	97	95		<5[b]
10	*nitidus* group	94	66	96	70	54	
11	*Oryzomys lamia* + *O. russatus*	100	100	100	100	72	74
12	Clade B – *nitidus* group	7	<5[a]				
13	*Oecomys*	95	93	98	74	83	67
14	*Oecomys* – *Oe. catherinae*	67	70	65		55	63
15	*Oecomys bicolor* + *Oe. trinitatis*	60	82	61		67	82
16	*Oecomys mamorae* + *Oe. concolor*	98	91	97	89	72	67
17	Clade B – *nitidus* group and *Oecomys*	12	<5[a]				
18	*Handleyomys* + *O. chapmani* + *O. alfaroi* + *O. rostratus*	78	88	84	84		
19	*O. chapmani* + *O. alfaroi* + *O. rostratus*	90	98	100[c]	100[c]	44	58
20	*Oryzomys chapmani* + *O. rostratus*	62	83	X	X		15
21	*Oryzomys talamancae* + *albigularis* group + *megacephalus* group	20	23				
22	*Oryzomys megacephalus* + *O. yunganus*	99	96	98	99		
23	*O. talamancae* + *Oryzomys levipes* + *O. albigularis*	52	78				
24	*Oryzomys levipes* + *O. albigularis*	96	97	X	X	71	75
25	Clades C + D	80	78	93	100		
26	Clade C	74	88	77	65	60	59
27	*Neacomys*	99	99	99	96	73	64
28	*Neacomys minutus* + *N. musseri*	99	99	99	100		
29	Clade C – *Neacomys*	49				61	
30	*Microryzomys* + *Oryzomys balneator*	74			48	70	
31	*Oligoryzomys*	100	100	100	98	98	97
32	*Oligoryzomys nigripes* + *Ol. stramineus*	63	39	60	54		
33	*Oligoryzomys flavescens* + *Ol. fornesi*	84	84	83	71	31	
34	Clade D	82	88	94	41		<5[d]
35	Clade D – *Oryzomys polius*	73	68	85	57		12
36	*Pseudoryzomys* + *Lundomys* + *Holochilus* + *palustris* group	66	79	63		46	70
37	*palustris* group	98	97	97	92	77	
38	*Pseudoryzomys* + *Lundomys* + *Holochilus*	96	94	97	44	79	90
39	*Holochilus* + *Lundomys*	91	82	90		99	99
40	*Holochilus*	100	100	100	100	100	100
41	*Oryzomys angouya* + *O. subflavus* + *Nesoryzomys* + *O. xanthaeolus* + *Amphinectomys* + *Nectomys* + *Sigmodontomys* + *Melanomys*	18					
42	*Oryzomys subflavus* + *Nesoryzomys* + *O. xanthaeolus* + *Amphinectomys* + *Nectomys* + *Sigmodontomys* + *Melanomys*	31	51	40			<5[d]
43	Node 42 – *Oryzomys subflavus*	73	81	78		15	8[d]
44	*Nesoryzomys*	100	100	100	99	98	100
45	Node 43 – *Nesoryzomys*	47		41		22	<5[d]
46	*Amphinectomys* + *Nectomys* + *Melanomys* + *Sigmodontomys*	87	90	82		36	51[d]
47	*Amphinectomys* + *Nectomys*	75	85	91	99		
48	*Nectomys*	49	56	X	X	64	
49	*Sigmodontomys* + *Melanomys*	66	55	83	99		
50	*Melanomys* + *Sigmodontomys aphrastus*	46		X	X		

Fig. 40. Changes in monophyly, resolution, and support in the different analyses for nodes recovered in the combined (CO) analysis. Each column corresponds to one of the six analyses described in the text: 1, combined data, CO coding for polymorphic entries; 2, combined data, TS coding; 3, reduced analysis; 4, IRBP only; 5, morphology only, CO coding; 6, morphology only, TS coding. White squares indicate that the taxon was monophyletic in all most parsimonious trees (MPTs) for a particular analysis, squares with hatching indicate monophyly in some but not all MPTs, and black squares indicate polyphyly or paraphyly in all MPTs. Squares with an X indicate that the clade could not be recovered in the IRBP-only or reduced analysis because it lacked sequence data. The value within each box indicates the jackknife percentage. Superscript letters indicate: a, with *Oryzomys hammondi*; b, with *O. hammondi* and *Amphinectomys*; c, *O. chapmani* not included because it lacks IRBP sequences; d, without *Amphinectomys*.

cially in the combined trees, as expected by the low number of polymorphic cells in the matrix (1%). The major difference was the lack of resolution of the consensus tree derived from the morphology-only TS analysis (fig. 35). Different codings had little impact on nodal support (fig. 40), with TS coding providing slightly higher values for most nodes, as expected from the retention of more phylogenetic information in this kind of coding (Mabee and Humphries, 1993).

In the morphology-only analyses, both codings placed some taxa in unexpected positions. In the CO analysis, the *alfaroi-chapmani-rostratus* clade is found nested within clade D*, while the TS analysis placed *Amphinectomys* within clade B*. All of these unexpected arrangements received low nodal support and none was recovered in the combined (TS or CO) or IRBP analyses. The major difference in the combined analyses using different polymorphism coding was the position of *O. hammondi*, recovered either as the sister group of all oryzomyines (CO coding) or as a member of clade B* (TS coding). The latter placement was recovered in the morphology-only analyses with both CO and TS coding.

The remaining discussion is based on the consensus tree of the combined analysis with polymorphic data treated as composites (fig. 37). The differences in topology recovered by the two treatments of polymorphic data do not affect any of the interpretations presented below, except as noted.

Effects of Missing Data on Topology and Support

Neither *Amphinectomys*, which could be scored for only one-third of all morphological characters, nor the five taxa without IRBP sequences behaved as wildcard taxa (Nixon and Wheeler, 1992; Kearney, 2002) in the combined analysis. All had secured positions, not floating on the fundamental cladograms as the result of alternative optimizations of question marks, leading to a well-resolved strict consensus tree. Removal of the five taxa without IRBP sequences in the reduced analysis, however, affected the tree topology, as it reduced the resolution of two major clades (C and D) and changed the structure of another (clade B). Nevertheless, almost all of these changes involved clades with low nodal support.

Removal of the taxa with missing data, however, had a marked effect in nodal support for several oryzomyine lineages. Foremost among these changes were the percentile increases for resampling support of the major oryzomyine lineages; for example, the jackknife support of clade A increased from 53 to 74%; clade B, from 58 to 96%; clade D, from 82 to 94%; clade (B + C + D), from 49 to 78%; and clade (C + D), from 80 to 92% (fig. 40). Support for clade C did not change significantly (jackknife from 74 to 77%), as this is the only major oryzomyine clade without missing data. Other significant increases were observed in nodes closer to the tips in which terminal taxa were removed; for example, *Nectomys* + *Amphinectomys* (*N. apicalis* removed), jackknife support increase from 75 to 89%; *Melanomys* + *Sigmodontomys* (*S. aphrastus* removed), from 66 to 84%.

Among the six taxa with large amounts of missing data, three were recovered in noncontroversial positions within oryzomyines. *Nectomys apicalis* was found as the sister group to *Nectomys squamipes*; *Oryzomys levipes* was found together with *O. albigularis*, conforming to the expectation of the *albigularis* species group (Patton et al., 1990; Musser and Carleton, 1993; Percequillo, 2003); and *O. chapmani* clustered with *O. rostratus* and *O. alfaroi*, compatible with the presumably close association of these species (Goldman, 1918; Musser and Carleton, 1993). In contrast, *Amphinectomys*, *Sigmodontomys aphrastus,* and *Oryzomys hammondi* have distinct and sometimes unexpected placements in the different analyses. *Amphinectomys* appears as the sister group to *Nectomys* in the combined analysis, but in the morphology-only tree it is placed as the sister group to the clade *Melanomys* + *Sigmodontomys* + *Nectomys* (CO analysis) or within clade B (TS analysis). *Sigmodontomys aphrastus* is not found as the sister species to *Sigmodontomys alfari* in either CO morphology-only or combined analyses, but is in the TS analysis of morphological data. Instead, the two species form a paraphyletic sequence relative to *Nectomys* in the mor-

phology-only analysis and to *Melanomys* in the combined analysis. Finally, *Oryzomys hammondi* is placed as the most basal oryzomyine in the CO combined tree, and as the sister group to *Oecomys* in the morphology-only and TS combined analyses.

Dataset Comparison

The IRBP and morphological datasets produced a similar number of equally most parsimonious trees and number of resolved nodes in their separated analyses despite differences in the number of informative characters (204 vs. 91 for IRBP and morphology, respectively). Furthermore, both datasets contributed equally to the structure of the combined tree, with each data partition having 30 nodes recovered in their separate analyses and in the combined consensus cladogram. On the other hand, the IRBP dataset was much less homoplasious than was the morphology dataset, as measured by ensemble CI and RI values. This pattern contradicts the expectation of higher homoplasy for the dataset with more characters (Sanderson and Donoghue, 1989; Sanderson, 1991) and indicates that the molecular dataset had more phylogenetic signal than did the morphological partition, despite similar levels of phylogenetic resolution. This is also reflected in the higher values of nodal support recovered for the nodes in the IRBP analysis and in the resolution of the most conflicting hypothesis between the datasets favoring the IRBP solution in the combined tree.

The resulting trees from the morphological and IRBP separate analyses exhibit topological differences that imply phylogenetic conflict. Nevertheless, node-by-node comparisons of nodal support values reveal only one case of conflicting relationships between well-supported clades in the separate analyses, or "hard" incongruence—the incompatibility between well-defined patterns of morphological versus molecular synapomorphies (Voss and Jansa, 2003). The sister group of *Holochilus* is *Pseudoryzomys* in the IRBP-only analysis and *Lundomys* in the morphology-only analysis, both solutions with jackknife values $> 95\%$ and a decay index > 6. The combined tree favors the morphological solution because there are 15 morphological synapomorphies for *Holochilus* + *Lundomys* hypothesis versus 7 IRBP synapomorphies for *Holochilus* + *Pseudoryzomys*. The lack of molecular synapomorphies for *Lundomys* and *Holochilus* might be due to differential evolutionary rates between molecules and morphology. Additional data on other molecular markers, as well as denser sampling, are necessary for the resolution of this conflict. All remaining cases of conflict between morphology and IRBP clades involved weak supported nodes from one or both datasets. No other clade that was moderately or highly supported (with a decay index >2 and/or jackknife support values $>70\%$) in either analysis was incongruent with any equivalently supported node in the other.

Major differences of higher-level relationships between separate analyses are (1) *Zygodontomys* and *Scolomys* as advanced oryzomyines in the morphology tree and as the most basal oryzomyines in the IRBP tree; (2) the recovery of the (*O. alfaroi* + *O. rostratus* + *O. chapmani*) clade within clade D* in the morphology tree (but not in the TS analysis) and within clade B in the IRBP tree; and (3) the closer relationship between clades B* and C in the morphology tree and between clades C and D in the IRBP tree. In each case, the nodal support for the morphology solutions was low, while the support for IRBP solutions was high, and in each case the combined tree favored the IRBP resolution.

Although the higher-level topology of the ingroup was resolved toward the IRBP solution, most of the conflicts observed within the major oryzomyines clades were resolved toward morphological hypotheses. Thus, the sister group relationship between the (*Microryzomys* + *Oryzomys balneator*) clade and *Oligoryzomys* is also observed in the morphology-only tree, instead of the most parsimonious IRBP arrangement of *Neacomys* as the sister group to (*Microryzomys* + *Oryzomys balneator*) clade (but observed also in the combined TS analysis). Likewise, the placement of the *Oryzomys palustris* species group closer to the (*Pseudoryzomys* + *Holochilus* + *Lundomys*) clade, instead of to the (*Nectomys* + *Melanomys* +

Sigmodontomys + *Nesoryzomys* + *Amphinectomys*) clade, was the favored morphological solution. Finally, 38% of the nodes present in the combined tree were also recovered in both separated analyses of IRBP and morphology, and 30 of 45 nodes (66%)[11] have both morphological and molecular synapomorphies, indicating that there is a considerable amount of phylogenetic agreement between the datasets, which the recovery of similar major oryzomyine clades (B, C, and D) indicates.

Oryzomyine Synapomorphies

Voss and Carleton (1993) proposed five oryzomyine synapomorphies: (1) presence of a pectoral pair of mammae; (2) long palate with prominent posterolateral pits; (3) absence of alisphenoid strut; (4) absence of posterior suspensory process of the squamosal attached to tegmen tympani; (5) and absence of gall bladder. Steppan (1995) recovered four additional oryzomyine synapomorphies: (1) nasals extending posterior to lacrimal; (2) 12 thoracic vertebrae; (3) absence of hemal arches; and (4) fewer than 36 caudal vertebrae (character not included in the present study). Surprisingly, the unconnected tegmen tympani was the only one of these traits also recovered here as an unambiguous oryzomyine synapomorphy. The absence of the gall bladder is recovered only in DELTRAN optimization because the condition of the gall bladder is unknown in *Wiedomys*.

Absence of the posterior suspensory process of squamosal connected to the tegmen tympani was also the only oryzomyine synapomorphy recovered in both morphology-only and combined analyses, and it was the only synapomorphy recovered as both unreversed and unique. *Reithrodon* is the only sigmodontine taxon outside the Oryzomyini with unconnected tegmen tympani (Voss and Carleton, 1993; Steppan, 1995; Pacheco, 2003). This similarity, however, is due to convergence, as *Reithrodon* is not the sister group of oryzomyines (Steppan, 1995; Smith and Patton, 1999; D'Elía, 2003; Weksler, 2003). Four other unambiguous oryzomyine synapomorphies were recovered in the combined analysis: absence of ungual tufts on D1; long incisive foramina passing M1, undivided anterocone on M1, and medial enamel bridge connection between paracone and protocone on M1. Nevertheless, they were reversed several times within oryzomyines. In addition, they occur in several groups outside oryzomyines (see Steppan [1995] and Pacheco [2003] for distribution of some of these characters in non-oryzomyine taxa).

Reconstruction of ancestral states for the proposed oryzomyine synapomorphies in the combined tree indicates that transformation occurred prior to or after the branch leading to oryzomyines. The extended posterior terminus of the nasal appeared as a synapomorphy within oryzomyines, while five other traits were shared with non-oryzomyines: absence of alisphenoid strut and presence of pectoral mammae are shared with *Wiedomys* and *Delomys*; and long palate with complex posterolateral pits, presence of 12 thoracic vertebrae, and presence of hemal arches are shared with *Wiedomys*. Nevertheless, these recovered transformation patterns may be misleading because of the rarefied sampling of non-oryzomyine taxa and of the uncertainty for the oryzomyine sister group. For instance, *Wiedomys* is also recovered as the sister group to oryzomyines in Steppan (1995), who first suggested that some of the proposed oryzomyine synapomorphies could actually be synapomorphies for the clade uniting oryzomyines and *Wiedomys*. However, in a previous IRBP analysis with denser sigmodontine taxonomic sampling (Weksler, 2003), *Wiedomys* was not recovered as the sister group to oryzomyines. Consequently, the characteristics shared by *Wiedomys* and oryzomyines would appear as homoplasic apomorphies for each taxon.

Additional analyses are necessary for the confident designation of the other oryzomyine synapomorphies, but for at least one of the traits proposed by Voss and Carleton (1993), the presence of pectoral mammae, recent evidence indicates that it is not an oryzomyine synapomorphy, but rather a ple-

[11] Among the 50 recovered nodes in the combined consensus cladogram, 5 nodes are directly connected to taxa without IRBP data, and thus cannot have molecular synapomorphies.

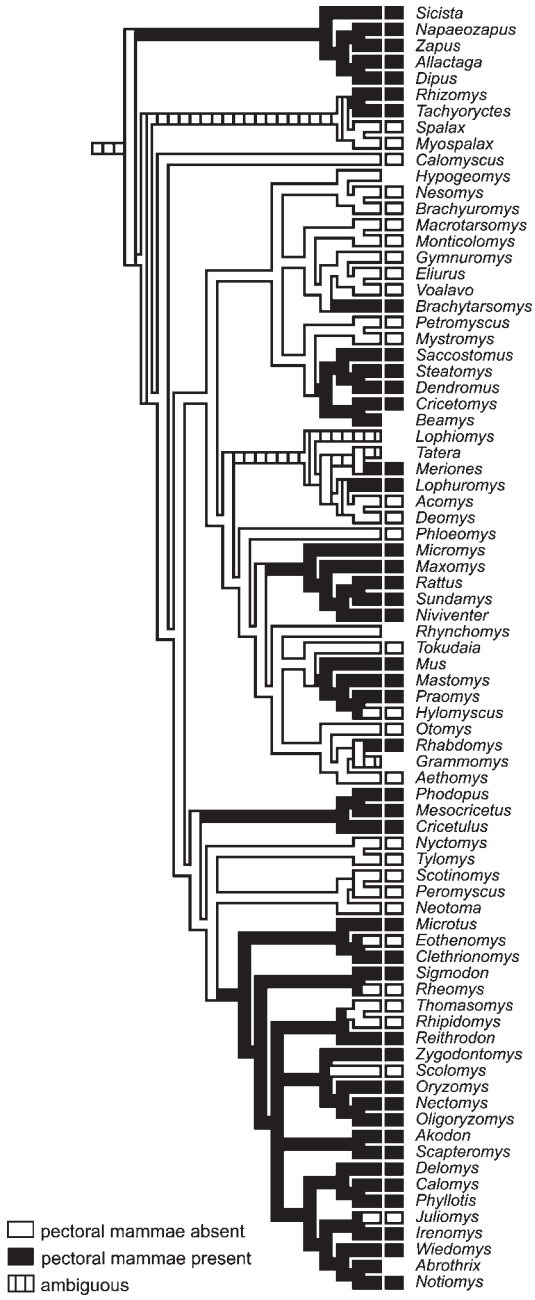


Fig. 41. Evolution of the pectoral mammae in muroid rodents inferred from optimization of character 1 on the consensus tree from Jansa and Weksler (2004). In addition to the AMNH collection, the following sources were consulted for the assessment of presence or absence of the pectoral mammae: Ellerman (1941), Arvy (1974), Carleton (1980), Voss (1988, 1991, 1992, 1993), Patton and da Silva (1995), Goodman et al. (1999), Nowak (1999), Carleton and Goodman (2000), Lecompte et al. (2002), and Pacheco (2003).

siomorphy for sigmodontines. The addition of the pectoral pair was interpreted by Voss (1993) and Voss and Carleton (1993) as a derived condition within sigmodontines because the outgroups used for establishing character polarity, peromyscines and nyctomyines, do not have the pectoral pair. Nevertheless, pectoral mammae are present in almost all other muroid subfamilies (Arvy, 1974). The reconstruction of patterns of character change in a recent comprehensive muroid phylogeny (Jansa and Weksler, 2004) shows the presence of pectoral mammae as the ancestral condition for the sigmodontines (fig. 41). Thus, the absence of the pectoral pair in several sigmodontines lineages, such as ichthyomyines, thomasomyines, and abrothrichines, should be interpreted as apomorphic. Within oryzomyines, character reconstruction patterns indicated that the absence of the pectoral pair in *Handleyomys* and *Scolomys* was caused by two independent losses, as in both morphology-only and combined analyses these two genera were never recovered as sister taxa.

Oryzomyine Relationships

Most of the phylogenetic results of the combined analysis were either in agreement with previous phylogenies or contradicted earlier results that are weakly supported. The combined cladogram contained many strongly supported clades previously recovered in the IRBP-only analysis of Weksler (2003). Foremost are recognitions of the three higher-level major clades with most oryzomyines (clades B, C, and D), their interrelationships, and the basal position of *Scolomys* and *Zygodontomys* in the tribe. Notwithstanding, the combined analysis displayed several new hypotheses of intergeneric relationships, chiefly the union of *Scolomys* and *Zygodontomys* in a monophyletic group, and the internal topology of clades B, C, and D. The phylogenetic results also indicated that many groupings of oryzomyine taxa,

←

previously recognized in formal classifications as genera (*Zygodontomys*, *Oligoryzomys*, *Oecomys*, *Nesoryzomys*, *Holochilus*, *Neacomys*, *Nectomys*) or informally as species groups within *Oryzomys* (*albigularis*, *nitidus*, *palustris*), are monophyletic. Finally, the results corroborate the polyphyly of *Oryzomys* and suggest that *Sigmodontomys* is paraphyletic.

Scolomys and *Zygodontomys* were securely placed as basal oryzomyines in the IRBP-only and combined CO analysis. In the morphology-only and combined TS analyses the two genera were recovered as sister taxa with moderate support in the latter analysis, which increased in the reduced analysis. The recovery of this clade and its position at a basal branch within oryzomyines were unexpected. *Scolomys* and *Zygodontomys* are two of the most distinctive clades of oryzomyines, and they are ecologically and morphologically dissimilar from one another. Whereas species of *Scolomys* are strictly forest-dwelling (Patton and da Silva, 1995; Gómez-Laverde et al., 2004), species of *Zygodontomys* are highly specialized for savannas and other open vegetation formations (Voss, 1991). The IRBP divergence of both lineages was also high, suggesting an early split within oryzomyine evolution. Although the clade lacks IRBP synapomorphies, analyses using faster-evolving mitochondrial genes have also recovered it (Garcia, 1999). This suggests an early cladogenetic event between the *Scolomys* and *Zygodontomys* lineages after the appearance of the *Scolomys-Zygodontomys* ancestor.

The other three large clades (B, C, and D) recovered in the combined analyses received support from the previous IRBP analysis (Weksler, 2003). Nevertheless, relationships within the major clades are still not well-supported, especially among the lineages in clade B. Further analyses are needed for the corroboration of the present results. With the delimitation of these clades being well secured here, separate analyses of each clade with denser taxon sampling and using varied sources of data, such as morphology and nuclear and mitochondrial genes, will allow resolution of their interrelationships.

The "*Oryzomys*" Problem

The present analysis provides compelling justification for the current generic recognition of several taxa formerly included as subgenera of *Oryzomys* (e.g., *Microryzomys*, *Melanomys*, *Oligoryzomys*, *Oecomys*, *Sigmodontomys*, and *Nesoryzomys*). The results also present convincing evidence for the polyphyly of *Oryzomys* in its currently strict sense (i.e., Musser and Carleton, 1993), a result also congruent with previous phylogenetic analyses (Baker et al., 1983; Patton and Hafner, 1983; Dickerman and Yates, 1995; Myers et al., 1995; Patton and da Silva, 1995; Steppan, 1995; Weksler, 1996; Percequillo, 1998; Bonvicino and Moreira, 2001; Bonvicino and Moreira, 2001; Andrade and Bonvicino, 2003; Weksler, 2003). None of the cladograms recovered from morphological, molecular, or combined data analyzed here retrieved any clade resembling *Oryzomys* in its currently recognized form.

Dispersion of the different *Oryzomys* clades over the tree was extensive, and a new taxonomic classification is obviously needed for the genus. Because the required modifications involve procedures beyond the scope of the present study, such as the designation of type species, listing of valid species (and synonyms) referred to each new genera, morphological diagnoses, and comparisons with closely related clades, the new genera are being described elsewhere (Weksler, Percequillo, and Voss, in prep.) Below, I discuss possible taxonomic arrangements.

The new classification should be compatible with the recovered phylogeny and preferably cause the least possible change in the current oryzomyine nomenclature. In addition, the new arrangement should try to recognize distinctive and diagnosable clades. The preferred arrangement is restriction of *Oryzomys* to the *palustris* group (table 2) and erection of new genera for remaining species groups or isolated species. Thus, 11 new genera would be created (fig. 42), each encompassing one (*nitidus*, *albigularis*, *talamancae*, *subflavus*, *xanthaeolus*) or multiple (*melanotis* + *alfaroi* + *chapmani*; *yunganus* + *megacephalus*) species groups, or species recovered as independent from all other *Oryzomys* (*angouya*, *polius*, *balneator*, *hammondi*).

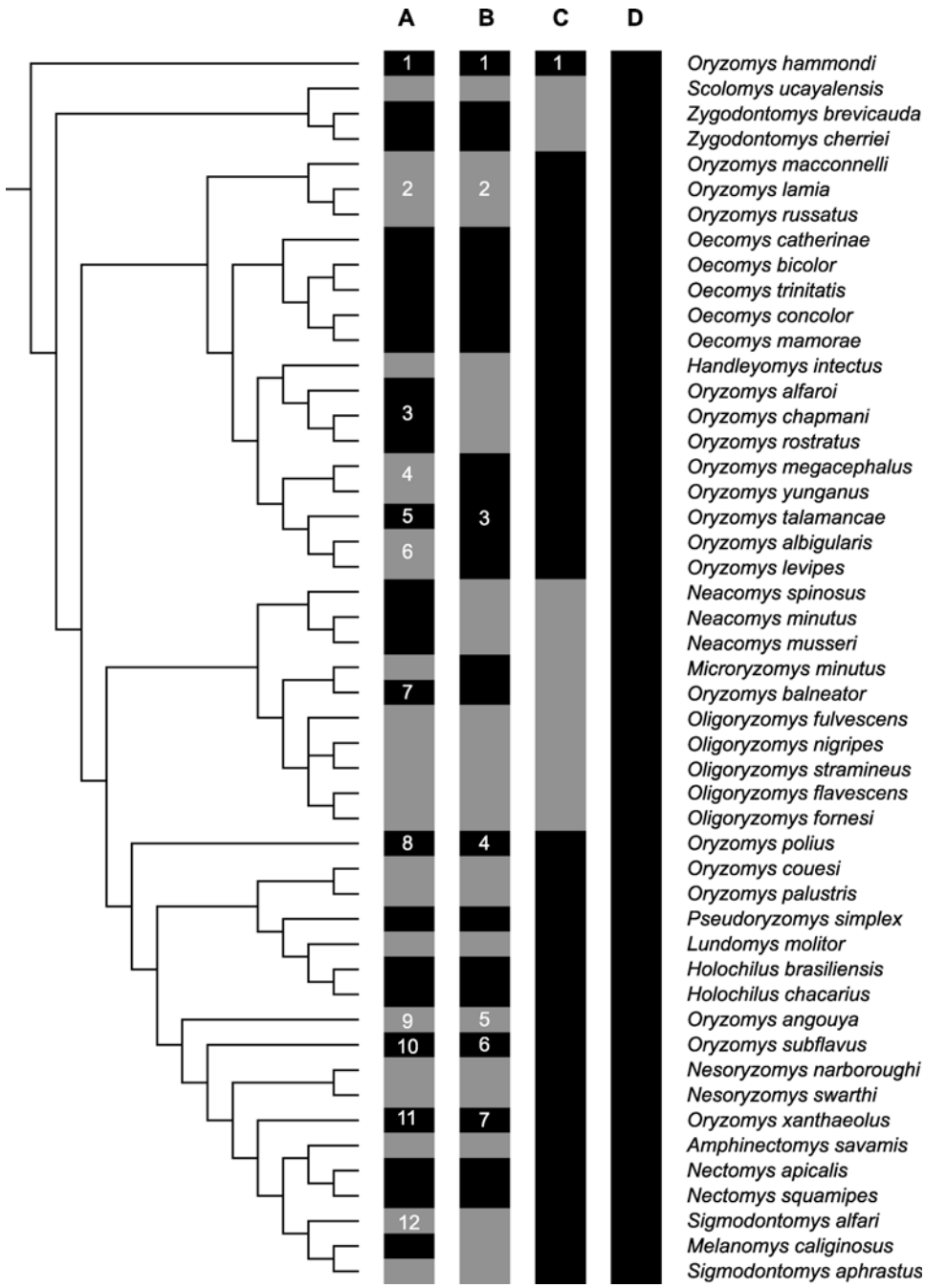


Fig. 42. Combined tree illustrating four possible arrangements for a new oryzomyine taxonomy. The bars indicate generic limits and numbers within the bars indicate new genera. In arrangement A, each major lineage of *Oryzomys* is placed in different and new genera. In arrangement B, several *Oryzomys* lineages are incorporated into existing genera, while independent lineages are placed in new genera. In arrangement C, each major oryzomyine lineage (clades A, B, C, and D, and *O. hammondi*) is designated as a genus. Finally, in arrangement D, all oryzomyines are placed under a single genus, reflecting the overdispersion of members of *Oryzomys* in the tribe. See text for further details.

Other nomenclatural arrangements might provide fewer nomenclatural changes, at least in terms of creation of new names (fig. 42). For example, some species or groups of species could be absorbed into sister genera, such as the inclusion of *balneator* in *Microryzomys*, or of *melanotis*, *chapmani*, and *alfaroi* groups in *Handleyomys*. These changes, however, would otherwise change the taxonomic composition of these two genera that have detailed, unambiguous, and distinctive diagnoses (Carleton and Musser, 1989; Voss et al., 2002). Another possible change in the proposed nomenclatural arrangement is the inclusion of *albigularis* and *talamancae* in a single genus (fig. 42). Nevertheless, the sister group relationship of these two species groups is not well secured, as demonstrated by different placements of *talamancae* in individual analyses of morphology and molecular data, and of the low nodal support in the combined tree. Clearly, other taxonomic arrangements are also possible, such as delimiting each major oryzomyine clade (especially B, C, and D) or each big clade within these major groups as new genera. Nevertheless, the inclusion of a variety of morphotypes and distinctive evolutionary and ecological variants would render such huge genera less useful to research of adaptation, biogeography, faunal diversification, and other topics, resulting in a classification with less heuristic value (Wheeler, 2004).

Oryzomyine Evolution

Oryzomyini is the most diverse tribe within the sigmodontine radiation, and this diversity is reflected in morphological and ecological variation observed among the taxa analyzed in this study. The scant available published information on oryzomyine ecology and natural history suggests that most oryzomyines are medium-sized, unspecialized, forest-dwelling, omnivorous rats, with nocturnal and cursorial habits (e.g., Flemming, 1970, 1971; Wolfe, 1982; Ernest, 1986; Janos et al., 1995; Musser et al., 1998; Nowak, 1999; Patton et al., 2000; Voss et al., 2001; Guabloche et al., 2002; Voss et al., 2002). Nevertheless, there are several conspicuous anatomical and ecological deviations from this generalized *bauplan*, which I interpret below in light of the recovered phylogeny.

TABLE 8
Size of Oryzomyines as Measured by Head-and-Body Length (HBL)

Genus/species group	HBL range (mm)	Source
hammondi	173–203	BMNH specimens
Scolomys	84–105	Emmons and Feer, 1997; Nowak, 1999
Zygodontomys	95–155	Nowak, 1999
Handleyomys	80–130	Voss et al., 2002
Oecomys	90–176	Hershkovitz, 1960; Voss et al., 2001
alfaroi	97–122	Hershkovitz, 1960; Musser et al., 1998
talamancae	99–142	Musser et al., 1998
nitidus	110–172	Musser et al., 1998
megacephalus	99–158	Musser et al., 1998
yunganus	84–142	Musser et al., 1998
albigularis	110–174	USNM specimens
melanotis	96–120	USNM specimens
chapmani	102–116	USNM specimens
Microryzomys	62–99	Carleton and Musser, 1989
Neacomys	64–100	Nowak, 1999; Voss et al., 2001
Oligoryzomys	70–111	Bonvicino and Weksler, 1998; Nowak, 1999
balneator	80–100	AMNH specimens
Amphinectomys	190	Malygin et al., 1994
Holochilus	123–211	Voss and Carleton, 1993
Lundomys	160–230	Voss and Carleton, 1993
Melanomys	100–153	Allen, 1913; USNM specimens
Nectomys	135–254	Hershkovitz, 1944; Voss et al., 2001
Nesoryzomys	100–200	Nowak, 1999
Pseudoryzomys	103–127	Voss and Myers, 1991
Sigmodontomys alfari	120–152	Hershkovitz, 1944
Sigmodontomys aphrastus	152	Harris, 1932
subflavus	113–200	Musser et al., 1998; Langguth and Bonvicino, 2002
polius	138–164	Osgood, 1913; FMNH specimens
xanthaeolus	101–133	USNM specimens
palustris	105–150	USNM specimens
angouya	153–180	Geise, 1995

Size: Of the 31 genera, species groups, or isolated oryzomyine lineages recovered in the analysis, 16 have species with the adult range of head-and-body length (HBL) between 90

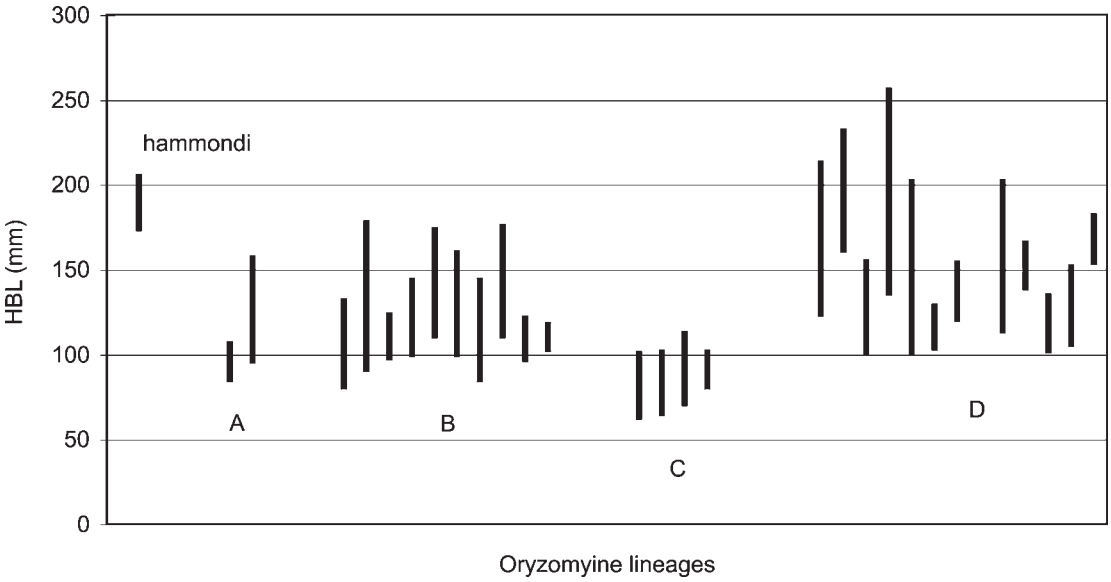


Fig. 43. Chart illustrating the difference in size of oryzomyine lineages as measured by the head-and-body length (HBL). Sources of the measurements are found in table 8.

and 175 mm (considered medium-sized; table 8). Two additional groups have HBL between 100 and 200 mm (considered large-medium) and two others have HBL between 80 and 145 (small-medium). Five groups are composed of small taxa, with HBL between 60 and 110 mm, while six groups are composed of large taxa, with HBL between 150 and 260 mm (some *Nectomys* and *Holochilus* can be as small as 125 mm, but are probably young adults). Thus 71 of 116 oryzomyines (61%) are either medium, small-medium, or large-medium in size, 29 (25%) are small-sized, and 16 (14%) are large-sized.

Inspection of body size distribution among the major oryzomyine lineages (fig. 43) reveals that all members of clade B are medium- or small-medium-sized, all members of clade C are small-sized, and all members of clade D are medium, large-medium, or large in size. *O. hammondi* is a large rat, while clade A includes both medium and small taxa. Reconstruction of size transformation in the recovered phylogeny (fig. 44) shows that the putative primitive condition for oryzomyines is that of a medium-sized rat. There are two transformations into the small class (*Scolomys* and clade B) and four transformations into the large class (*hammondi*, *Lundomys* + *Holochilus*, *angouya*, and *Amphinectomys* + *Nectomys*).

ARBOREAL AND SEMIAQUATIC SPECIALIZATIONS: *Oecomys* is the only oryzomyine taxon with obvious specializations for arboreal life. Although species belonging to other oryzomyine clades (such *Oligoryzomys* and the *subflavus* group of *Oryzomys*) are sometimes reported to have some arboreal capacity (Alho, 1982; Fonseca and Redford, 1984; Alho and Villela, 1985; Mares et al., 1986), most individuals of these taxa are collected on the ground (Mares et al., 1989; Bonvicino et al., 2005). In contrast, various studies have shown that *Oecomys* specimens are found mostly, and sometimes exclusively, in trees, often as high as 15–20 m above the ground (Hershkovitz, 1960; Mares et al., 1989; Patton et al., 2000; Voss et al., 2001). The main adaptations for arboreal life observed in *Oecomys* include: more robust and compact hindfeet, with lateral broadening of the metatarsus; first and fifth digits more powerful and opposable; and plantar pads modified for grasping (Hershkovitz, 1960). These features are also observed in other arboreal sigmodontine rodents (e.g., *Rhipidomys*).

In contrast, semiaquatic (amphibious) specializations are observed in seven oryzo-

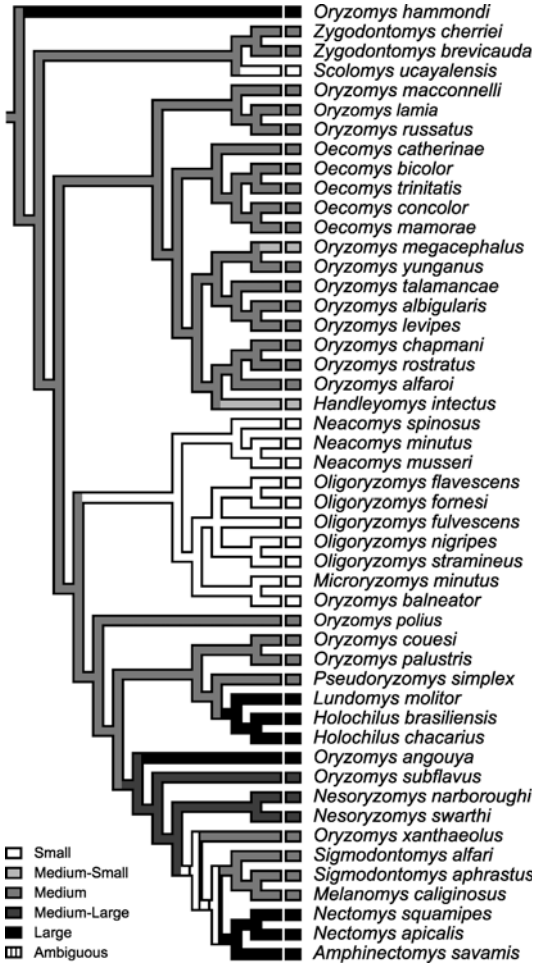


Fig. 44. Evolution of size in oryzomyines inferred from the optimization of five size categories (see text) on the consensus tree of the combined analysis. The ambiguous optimization is due to differences in interpretation of the character under ACCTRAN or DELTRAN.

myine taxa: *Amphinectomys*, *Nectomys*, *Lundomys*, *Holochilus*, *Sigmodontomys alfari*, *Pseudoryzomys*, and in the *palustris* group of *Oryzomys*. The degrees of morphological adaptations of these taxa are proportionate to the amount of time the animals spend in water and to the type of activities performed there (i.e., foraging and nestbuilding; Stein, 1988). Specimens of *Holochilus*, *Lundomys*, *Amphinectomys*, and *Nectomys*, which are found almost exclusively alongside bodies of freshwater, display well-developed interdigital webbing and natatory fringes, whereas *Oryzomys palustris*, *Pseudoryzomys simplex*, and *Sigmodontomys alfari*, which are less dependent on water bodies, have reduced interdigital webbing and do not display natatory fringes. The same pattern is observed in relation to the size of these rats: *Holochilus*, *Amphinectomys*, *Nectomys*, and *Lundomys* are the largest living oryzomyines, while *Sigmodontomys*, *O. palustris*, and *Pseudoryzomys* are all medium-sized rodents. This size gradient is in agreement with the hypotheses of larger body size for semiaquatic small mammals (Wolff and Guthrie, 1985).

All semiaquatic oryzomyines are members of clade D, where they are divided into two lineages: (1) the *palustris* group, *Pseudoryzomys*, *Lundomys*, and *Holochilus*; and (2) *Amphinectomys*, *Nectomys*, and *Sigmodontomys alfari*, together with the terrestrial *S. aphrastus* and *Melanomys caliginosus*. Reconstruction of ancestral states of the characters related to the semiaquatic habitus (fig. 45) indicates that such adaptations occurred at least twice within oryzomyines. Natatory fringes appeared in the last common ancestor (LCA) of *Lundomys* and *Holochilus* and in the LCA of *Amphinectomys* and *Nectomys*. Optimizations of interdigital webbing transformations, however, are ambiguous (fig. 45). In ACCTRAN optimization, interdigital webs evolved twice and were lost twice: small membranes (not extending to first interphalangeal joints) appeared in the LCA of the *palustris* group + *Lundomys* + *Holochilus* + *Pseudoryzomys*, and in the LCA of *Amphinectomys* + *Nectomys* + *Melanomys* + *Sigmodontomys*; well-developed webs (extending to or beyond first interphalangeal joints) appeared in the LCA of *Lundomys* + *Holochilus*, and in the LCA of *Amphinectomys* + *Nectomys*; webs were lost in the lineage leading to *Oryzomys couesi* and in the LCA of *Melanomys* + *Sigmodontomys aphrastus*. In DELTRAN optimization, webbing appeared five times and was not lost in any lineage: small webs appeared in the LCA of *Lundomys* + *Holochilus* + *Pseudoryzomys*, and independently in the lineages leading to *O. palustris* and *Sigmodontomys alfari*, whereas large webs appeared in the LCA of *Holochilus* + *Lundomys* and in the LCA of

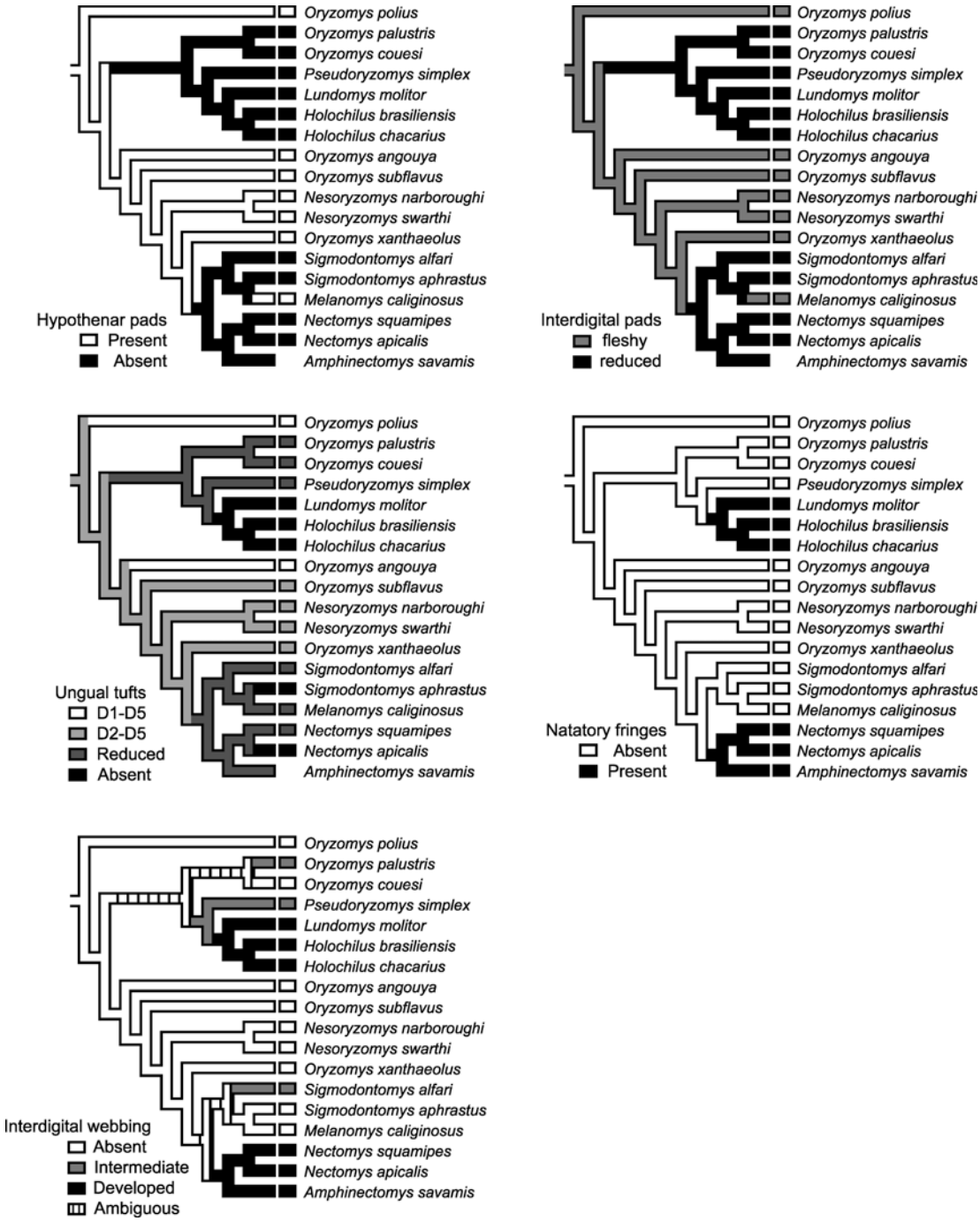


Fig. 45. Evolution of five hindfoot characters related to riparian life-style inferred from optimization of characters 4, 5, 7, 8, and 9 on the consensus tree from the combined analysis. The condition for *Amphinectomys* is unknown for the first three characters. Ambiguous optimization is due to differences in interpretation of the character under ACCTRAN or DELTRAN.

Nectomys + *Amphinectomys*. Note that in ACCTRAN optimization, the sequence of modifications of the two hindfoot specializations follow the same pattern in the two semiaquatic clades, with the appearance of small webs preceding the synchronous development of long webs and natatory fringes.

Other hindfoot characters also seem to be influenced by the transition to a semiaquatic mode of life (fig. 45). Hypothenar pads, interdigital pads, and ungual tufts, for example, are all reduced or lost in semiaquatic taxa. Changes in these characters are synchronous with ACCTRAN-optimized changes in known semiaquatic specializations. Interdigital pads and ungual tufts were reduced, and hypothenar pads were lost in the LCA of the *Oryzomys palustris* group + *Lundomys* + *Holochilus* + *Pseudoryzomys*, and in the LCA of *Amphinectomys* + *Nectomys* + *Melanomys* + *Sigmodontomys*. Ungual tufts were lost in the LCA of *Lundomys* + *Holochilus* and in the lineage leading to *Nectomys apicalis*.[12] Functional morphological research might shed light on the role (if any) of these features in semiaquatic locomotion.

HABITAT: Twenty-one oryzomyine clades, encompassing 61% of all oryzomyine species, are found exclusively in forest environments, especially in ombrofilous forest. Five forest-dwelling clades (*Nectomys*, *Oecomys*, *angouya*, *nitidus*, and *megacephalus*) are also distributed in open vegetation biomes, such as the Cerrado and Llanos, but are mostly found in forest patches within open vegetation, such as gallery forests and "cerradão" (Alho et al., 1986; Mares et al., 1986; Nitikman and Mares, 1987; Mares et al., 1989; Bonvicino et al., 1996, 1998; Talamoni and Dias, 1999; Lacher and Alho, 2001). Five other oryzomyine clades representing 10% of oryzomyine species, however, are found only in open-vegetation biomes: *Lundomys* in the Pampas; *Pseudoryzomys* in the Cerrado, Caatinga, and Chaco; *Zygodontomys* in the Llanos and other northern South American and Central American savannas; and the *xanthaeolus* group of *Oryzomys* and *Nesoryzomys* in the dry coastal biomes of Western Peru, Ecuador, and the Galapagos Islands (Patton and Hafner, 1983; Voss, 1991; Voss and Myers, 1991; Voss and Carleton, 1993; Dowler et al., 2000; Guabloche et al., 2002). Finally, species of five clades (28% of oryzomyine species) are found in both forest and nonforest

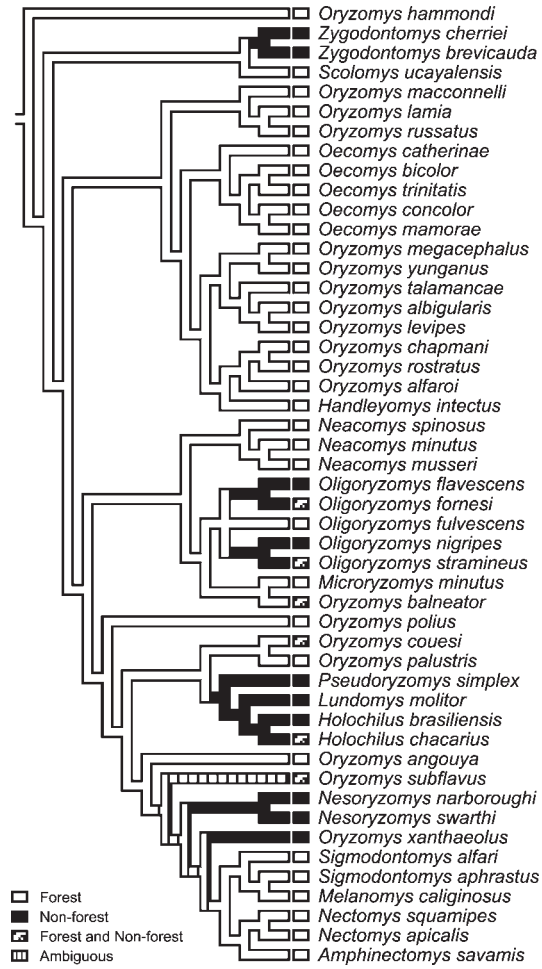


Fig. 46. Evolution of oryzomyine habitat type inferred from the optimization of two environmental categories (see text) on the consensus tree of the combined analysis. The ambiguous optimization is due to differences in interpretation of the character under ACCTRAN or DELTRAN.

[12] This is the only discrepancy between these characters, but other species of *Nectomys* also lack ungual tufts, and the primitive condition for the genus is probably absence of tufts. The condition in *Amphinectomys* is unknown, but if this taxon lacks ungual tufts, the pattern of concordance will also be perfect for this character.

environments: *Holochilus*, *Microryzomys*, *Oligoryzomys*, *palustris*, and *subflavus*.

Forest-dwelling taxa occur in all oryzomyine lineages (fig. 46), whereas exclusively open-vegetation dwellers are found only in clades A and D. All members of clade B are exclusively sylvan taxa, while clades A, B, and D contain both types. Reconstruction of this feature in the recovered cladogram (fig. 46) indicates that the ancestral oryzomyine was a forest-dwelling taxon, and that invasions of open-vegetation environments occurred at least four times in oryzomyine evolution.

Three other significant modifications from the generalized oryzomyine *bauplan* are observed in restricted clades: the volelike appearance of *Zygodontomys*, *Melanomys* and *Handleyomys* species (Allen, 1913; Voss, 1991; Voss et al., 2001); the spiny pelage of *Scolomys* and *Neacomys*; and the hypsodonty of *Holochilus* molars (modified for intake of grass; Hershkovitz, 1955). Members of 11 lineages retained the primitive, unspecialized morphotype: *S. aphrastus*, *O. polius*, *nitidus* group, *subflavus* group, *albigularis* group, *talamancae* group, *alfaroi* group, *chapmani* group, *melanotis* group, *megacephalus* group, and *yunganus* group. As expected, all of these taxa, with the exception of *S. aphrastus*, are currently part of *Oryzomys*, highlighting, in a phylogenetic framework, the notion of the genus as a wastebasket group of unspecialized, mostly forest-dwelling, rats. As inferred by the reconstruction on the combined tree of size and the ecological adaptations discussed above, evolutionary niche shifts occurred de novo in different clades of these unspecialized oryzomyines. In turn, lineages that went through such evolutionary transitions are now among the most speciose oryzomyine clades assigned to genera: *Oligoryzomys* (16 spp.), *Oecomys* (15 spp.), *Nectomys* (8 spp.), and *Neacomys* (8 spp.). This indicates the conquest of different ecological roles in South American biomes that opened the possibilities for further diversification of oryzomyines.

Biogeography

The evaluation of the recovered phylogeny using methods of biogeographical analysis (e.g., Wiley, 1987; Bremer, 1992; Ronquist, 1994; Bremer, 1995; Ronquist, 1997; Hausdorf, 1998; Ronquist, 1998) is beyond the scope of this study because many oryzomyines species were omitted, obscuring potentially important patterns found in the internal clades (Ronquist, 1996). Nevertheless, the present phylogeny provides a heuristic framework for assessing previous oryzomyine biogeographic scenarios, as well as a basis for future inquiries in oryzomyine biogeography. In this section, I also summarize the current knowledge on distributional patterns, fossil record, and molecular dating for the tribe.

The first step in biogeographic analysis is delimitation of the distributional areas that will serve as discrete entities in the elaboration of workable hypotheses (Humphries and Parenti, 1999). Most oryzomyine genera and species groups can be classified into three general distribution patterns as delineated below.

Trans-Andean Distribution (fig. 47): This category encompasses taxa primarily distributed in lower-montane and lowland habitats west of the Andes, such as trans-Andean lowland rainforests (Voss and Emmons, 1996) and the arid coastal region of Peru and Ecuador (including the Galapagos Islands). Nine oryzomyine taxa are found in such trans-Andean landscapes: *Melanomys*, *Sigmodontomys*, *Nesoryzomys*, and six groups of *Oryzomys* (*palustris*, *talamancae*, *melanotis*, *alfaroi*, *chapmani*, and *xanthaeolus*). The *chapmani* and *melanotis* groups are restricted to forests of Central America and Mexico (Goldman, 1918), whereas *Nesoryzomys* occurs only in the Galapagos Islands (Dowler et al., 2000), and the *xanthaeolus* group occurs in both the Galapagos Islands and in the Pacific littoral zone of Peru and Ecuador (Patton and Hafner, 1983). The remaining trans-Andean taxa are found in forests from northwestern South America into Central America, or in the case of the *palustris* group, in the United States (Allen, 1913; Goldman, 1918; Hall, 1981; Musser and Carleton, 1993; Carleton and Musser, 1995; Voss and Emmons, 1996; Musser et al., 1998; Sanchez-H. et al., 2001).

Andean Distribution (fig. 47): This category encompasses taxa found only in

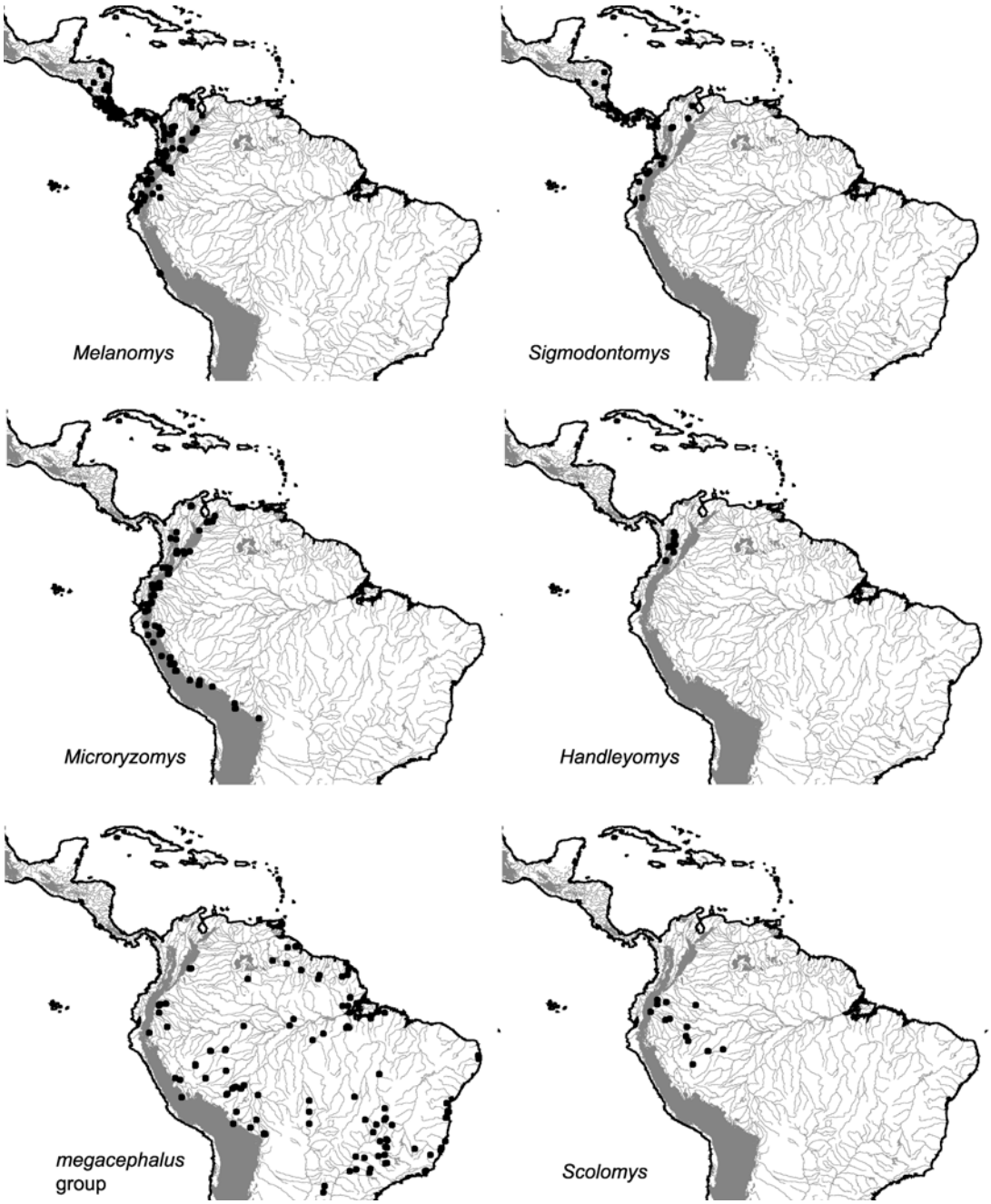


Fig. 47. Examples of the three distribution categories defined in the text: trans-Andean (top), Andean (middle), and cis-Andean. Locality data are from: Allen (1913) and Weksler (in prep.) for *Melanomys*; Musser et al. (1998) for *Sigmodontomys*; Carleton and Musser (1989) for *Microryzomys*; Voss et al. (2002) for *Handleyomys*; Musser et al. (1998) and Weksler et al. (1999) for *megacephalus* group; Gómez-Laverde et al. (2004) for *Scolomys*.

Andean habitats such as montane forest and Paramos, usually on both sides of the cordillera and above 1500–2000 m. Six taxa are found exclusively or primarily in the Andes mountains: *Microryzomys*, *Handleyomys*, and four groups of *Oryzomys* (*albigularis*, *balneator*, *hammondi*, and *polius*). *Microryzomys* and the *albigularis* group are widely distributed in the Andes, from central Bolivia to northern Venezuela (Carleton and Musser, 1989; Patton et al., 1990; Musser and Carleton, 1993; Percequillo, 2003). The four remaining taxa have restricted range: *Handleyomys* is found in cloud forest of the Colombian Occidental and Central Cordilleras (Voss et al., 2002); *O. balneator* occurs in lower montane forest in both west and east slopes of the Andes in Ecuador and Peru (Musser et al., 1998); *O. hammondi* is known from a single locality from Ecuadorian western Andes (Thomas, 1913; specimens from UMMZ); and *O. polius* is known from a few localities from the eastern Peruvian Andes (Osgood, 1913; specimens from AMNH and FMNH).

Cis-Andean Distribution (fig. 47): This category encompasses taxa primarily distributed in lowland or lower montane biomes east of the Andes, such as Amazon, Atlantic and coastal Venezuelan rainforests, Llanos, Cerrado, Chaco, Pampas, and Caatinga. This category includes 15 taxa: *Nectomys*, *Amphinectomys*, *Holochilus*, *Lundomys*, *Pseudoryzomys*, *Neacomys*, *Oecomys*, *Scolomys*, and five groups of *Oryzomys* (*megacephalus*, *yunganus*, *nitidus*, *angouya*, and *subflavus*). *Lundomys*, *Pseudoryzomys*, and the *angouya* and *subflavus* groups occur only in southeast South America (central and eastern Brazil, Bolivia, Paraguay, Uruguay, and Argentina) (Voss and Myers, 1991; Musser and Carleton, 1993; Voss and Carleton, 1993; Percequillo, 1998; Langguth and Bonvicino, 2002; Bonvicino, 2003). *Holochilus*, *Nectomys*, *Oecomys*, and the *megacephalus* and *nitidus* groups are widely distributed in the Amazon basin, eastern Andean piedmont, and southeast South America (Hershkovitz, 1944, 1955, 1960; Musser et al., 1998; Percequillo, 1998; Weksler et al., 1999; Patton et al., 2000). *Neacomys* and the *yunganus* group occur throughout Amazonia (Musser et al., 1998; Patton et al., 2000; Voss et al., 2001), whereas *Amphinectomys* and *Scolomys* are found only in western Amazonia (Malygin et al., 1994; Patton and da Silva, 1995; Gómez-Laverde et al., 2004).

As expected in such simplifications, the geographic range of various taxa blurs the exact limits of the three categories. One species of the *albigularis* group, *O. devius*, is found in the highlands of Costa Rica and Panama (Carleton and Musser, 1995; Percequillo, 2003). One species of *Oecomys* (*Oe. bicolor*) and two species of *Neacomys* (*N. tenuipes* and *N. pictus*) are found in eastern Panama and western Colombia (Hall, 1981; Musser and Carleton, 1993); another species of *Oecomys* (*Oe. trinitatis*) reaches Costa Rica. Two species of *Nectomys* (*N. magdalenae* and *N. grandis*) are found in the inter-Andean valleys of the Magdalena and Cauca Rivers (Hershkovitz, 1944; Bonvicino, in prep.). One species of the *yunganus* group (*Oryzomys tatei*) is restricted to the eastern Andean piedmont (Musser et al., 1998) and could be considered an Andean taxon. *Sigmodontomys* and *Melanomys* occur in a few localities at the coastal Venezuelan forests east of the Andes, and *Melanomys* also occurs in some localities in the eastern Ecuadorian Andes piedmont (Voss and Emmons, 1996). In each of these cases, however, taxa have restricted distributions outside their main geographic category, and I assume this is a result of secondary, recent range expansion.

In contrast, two taxa could not be effectively categorized into the patterns. *Oligoryzomys* is distributed from Mexico to Terra del Fuego, being found east, west, and at the Andes mountains (Carleton and Musser, 1989; Patton et al., 1990; Carleton and Musser, 1995). *Zygodontomys* is widely distributed in open vegetation biomes of northern South America and eastern Central America, occurring east and west of the Andes (Voss, 1991). The species of these two genera are treated individually in the present analysis. *Zygodontomys cherriei* has trans-Andean distribution, whereas *Z. brevicauda* is distributed east of the Cordillera de Mérida (Voss, 1991). Among *Oligoryzomys* species, *O. fulvescens* is distributed from Mexico to the eastern Amazon basin in Brazil; remaining species are encompassed in the cis-

Andean category, being restricted to southeastern South America.

The two major methodological categories currently in use in taxon biogeography (sensu Hovenkamp, 1997) can be divided in "projection-rule biogeography" and "vicariant biogeography" (Seberg, 1988). These approaches are considered separately bellow.

VICARIANCE BIOGEOGRAPHY: No major vicariance scenario has been proposed for the biogeographic history of oryzomyines, or for any other sigmodontine tribe. The most obvious vicariance scenario for oryzomyines would be related to the Andean uplift, with the separation of trans- and cis-Andean lineages (van der Hammen, 1974). Molecular clock estimates for the initial diversification of oryzomyines point to a period between 5 and 9 mybp. This time range is based on the bounds estimated for the diversification of all sigmodontine lineages except sigmodonts and ichthyomyines by Steppan et al. (2004) using four nuclear genes, as well as on estimates for the origin of the oryzomyine lineage by Engel et al. (1998) using 1340 bp of the mitochondrial genome. Smith and Patton (1999: fig. 10) also placed the origin of oryzomyines in this period in their analysis of cytochrome *b* sequences. This time boundary is also congruent with the time estimated by DNA-DNA hybridization for the divergence of *Akodon* and *Oryzomys* (Catzeflis et al., 1993). If these estimates are corroborated in future studies that use better calibration points and denser taxonomic sampling, then oryzomyines could have been affected by the final orogenic surge of the Andes between 3 and 5 mybp (Irving, 1975; Simpson, 1979; Kellogg, 1984; Helmens and van der Hammen, 1994), a scenario proposed for other neotropical groups such as *Heliconius* butterflies (Brower, 1996), sand flies (Arrivillaga et al., 2002), tropidurine lizards (Harvey and Gutberlet, 2000), and various bird groups (Cracraft and Prum, 1988; Prum, 1988; Brumfield and Capparella, 1996).

The cis- and trans-Andean patterns, however, do not show correspondence to the major oryzomyine lineages (fig. 48). Instead, each major lineage displays all or most of the described biogeographic patterns. Clades B and D contain Andean, cis-Andean, and trans-Andean taxa, whereas clade C has Andean and cis-Andean taxa; clade A has cis-Andean and trans-Andean taxa. Even within each lineage, the distribution categories are not grouped into monophyletic units (fig. 48). In clade A, the two cis-Andean species are paraphyletic. In clade B, two unrelated taxa, *Handleyomys* and the *albigularis* group, have Andean distribution; three trans-Andean taxa (*O. chapmani*, *O. alfaroi*, and *O. rostratus*) are grouped, but a fourth taxon, *O. talamancae*, is not included in this clade; and the cis-Andean taxa form a paraphyletic grade. In clade C, the two Andean taxa (*Microryzomys* and *O. balneator*) do form a clade, but the cis-Andean taxa are observed within three clades: one formed by *Neacomys* and two subclades of *Oligoryzomys*. Finally, cis- and trans-Andean taxa of clade D are dispersed over several lineages. Only two clades in the present analysis follow a cis–trans-Andean sister-group pattern: the *palustris* (trans) and tetralophodont (cis) clade, and the *Melanomys* + *Sigmodontomys* (trans) and *Amphinectomys* + *Nectomys* (cis) clade. A third clade that follows this pattern is recovered with moderate support by the IRBP analysis, containing the *talamancae* (trans) and *nitidus* (cis) groups.

It is clear from the above patterns (or lack of thereof) that any analytical methodology within the vicariance framework will have to include several cases of over-Andean dispersal within oryzomyine phylogeny.

PROGRESSION RULE BIOGEOGRAPHY: The center of origin concept was once ousted from historical biogeography (Croizat et al., 1974; Nelson and Platnick, 1981), but several procedures (Bremer, 1992, Ronquist, 1994, 1997; Hausdorf, 1998) have tried to reinstate it in cladistic framework under the label "ancestral area methodologies" (Ebach, 1999; Crisci, 2001). The basic premise of these methods is the progression rule of Hennig (1966), which Bremer (1994: 255–256) rephrased as "(1) areas positionally more plesiomorphic (present on 'deep' branches) in a cladogram of a particular group are more likely parts of the ancestral area for that group than are positionally more apomorphic areas and (2) areas represented on numerous branches of the cladogram are more likely parts of the ancestral

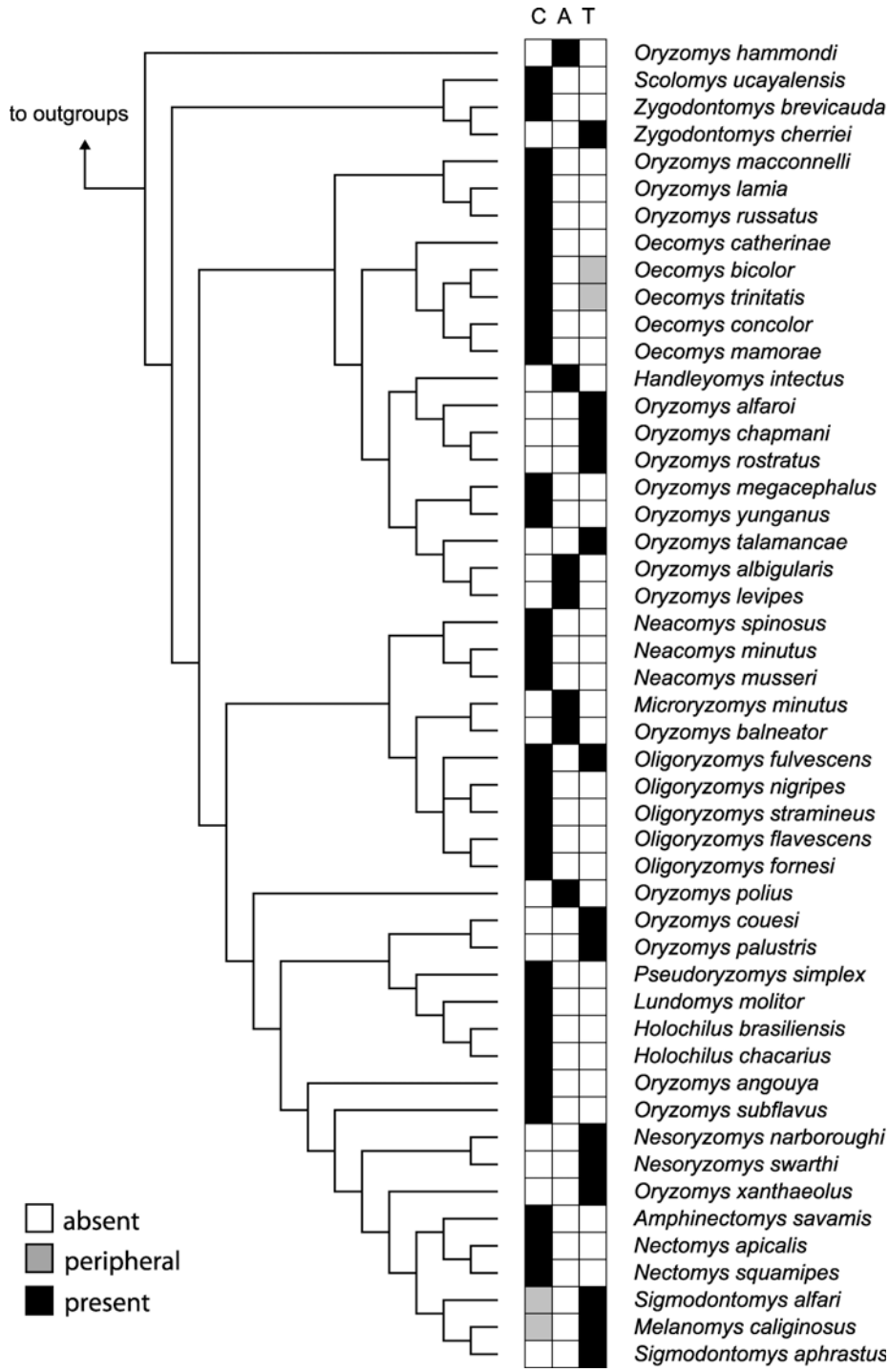


Fig. 48. Biogeographic patterns of oryzomyines plotted on the consensus tree from the combined analysis. See text for definition of the three geographic categories. Letters on the top of the figure refer to **C**, cis-Andean; **A**, Andean; and **T**, trans-Andean distribution.

area than are areas represented on a few branches.''

This methodological formulation fits well to biogeography of sigmodontines, as scenarios for the group have relied heavily on the center of origin concept, with a strong dispersalist element. Almost all classical sigmodontine biogeographic scenarios agree that oryzomyines, as all sigmodontines, are descendants from proto-sigmodontine ancestors that invaded (i.e., dispersed to) South America from North America in the late Cenozoic (Simpson, 1950; Hershkovitz, 1966b, 1969, 1972; Patterson and Pascual, 1968; Patterson and Pascual, 1972; Savage, 1974; Baskin, 1978 1986; Marshall, 1979; Reig, 1980; Simpson, 1980; Jacobs and Lindsay, 1984; Reig, 1984; Slaughter and Ubelaker, 1984; Reig, 1986; Czaplewski, 1987; Baskin, 1989). The South American fossil record strongly corroborates this hypothesis, as sigmodontine rodents suddenly appear in the well-known Argentinean fossil sequence at the Pliocene (Montehermosan and Chapadmalalan; Pardiñas et al., 2002).

The major disagreements between these dispersalist scenarios are the time of the dispersion and the place of the initial diversification for the sigmodontine groups (i.e., the place of the ancestral area of the group). Scenarios range from an early arrival (early or middle Miocene, 15–24 mybp) of a primitive stock of muroids in South America by waif dispersal or island hopping across the Bolivar Trough, and further radiation in the South American continent (e.g., Hershkovitz, 1966b; Reig, 1980, 1984), to a relatively recent entrance (Early or Middle Pliocene 2.5–4 mybp) of an already diversified sigmodontine stock through the Panama Isthmus (e.g., Patterson and Pascual, 1968; Patterson and Pascual, 1972; Baskin, 1986; Baskin, 1989; Czaplewski, 1987).

The oryzomyine fossil record is extremely poor and cannot provide, by itself, any evidence for the timing or the place of such initial radiation. The earliest oryzomyines in the South American fossil record are from the Pleistocene (Steppan, 1996; Pardiñas et al., 2002). Steppan (1996) estimated the age of *Holochilus primigenus* from Bolivia at between 0.7 and 1 mybp. Forms of *Holochilus*, *Lundomys*, *Nectomys*, and *Oligoryzomys* were retrieved from the Ensenadense (Early-Middle Pleistocene of Argentina; Pardiñas et al., 2002). All these taxa are placed at advanced, or apomorphic, positions in the tree, suggesting that diversification of the tribe must have occurred before the Pleistocene. Oryzomyines (and Sigmodontines in general) are absent from the middle Miocene (13 mybp) Honda group of La Venta, the richest Miocene tropical fossil deposit in South America (Kay and Madden, 1997). Sampling for small vertebrates at this site has been exemplary, as indicated by the recovery of examples of small mammals groups, such as echimyid rodents (Walton, 1997) and didelphid marsupials (Goin, 1997), that are often captured alongside oryzomyines in present-day tropical forest biomes (Voss and Emmons, 1996). Thus, based on this strong negative evidence, the upper bound for oryzomyine absence in South America is about 13 mybp.

The North American record also does not provide clues for timing and place of oryzomyine diversification. Previous suggestions that *Oryzomys* is present in the Pliocene or even Miocene in North America (Jacobs and Lindsay, 1984; Baskin, 1986, 1989) are unfounded. *Oryzomys*? *pliocaenicus* from the Miocene (Hemphilian) of Kansas (Hibbard, 1939) is ''generically indeterminate, but may represent *Bensonomys*'' (Baskin, 1986: 295; see also Hershkovitz, 1966b: 737). ?*Oryzomys* from the Miocene (Hemphillian) of Oregon (Shotwell, 1970) is more closely related to ''*Peromyscus*'' *pliocenicus*, putatively an ancestral to the fossil neotomine †*Repomys* (see May, 1981; Baskin, 1986). ''*Oryzomys*'' from the Early Pliocene (Blancan) of New Mexico (May *in* Jacobs and Lindsay, 1984; Repenning and May, 1986) is ''close dentally to †*Jacobsomys* and †*Symmetrodontomys* and might belong to the genus †*Jacobsomys*'' (Czaplewski, 1987: 194). †*Bensonomys* and †*Symmetrodontomys* were placed by McKenna and Bell (1997, following Musser, in lit.) in the Peromyscini tribe, whereas †*Jacobsomys* was tentatively assigned to sigmodontines sensu lato (i.e., sensu Carleton and Musser, 1984) as Sigmodontinae incertae sedis. The earliest confirmed oryzomyines present in the North American fossil record are referred to *Oryzomys fossilis* (= *Oryz-*

omys palustris), from the Pleistocene of Florida, Georgia, Kansas, and Texas (Hibbard and Taylor, 1960; Dalquest, 1962; Hibbard, 1963; Webb, 1974; Kurten and Anderson, 1980; Webb and Wilkins, 1984; Hulbert and Pratt, 1998). All fossil localities of *O. palustris* with a more precise dating are from middle (Rancholabrean; 0.3 mybp) and late (Sangamonian; 0.13 mybp) Pleistocene deposits (Webb, 1974; Webb and Wilkins, 1984).

Fossils from other sigmodontine tribes, in turn, are present in both North and South American Pliocene. Fossils of Phyllotini and Akodontini are present in South America in the Montehermosan (4–5 mybp) and Chapadmalalan (3.5–4 mybp), respectively (Pardiñas et al., 2002), whereas fossils of †*Prosigmodon* and *Sigmodon* are present in North America in the Hemphillian (6.8 mybp) and Blancan (3.3 mybp), respectively (Martin, 1979; Czaplewski, 1987; Korth, 1994). Thus, fossil data alone do not provide much evidence for the ancestral area of oryzomyines.

Application of the progression rule to the current phylogeny suggests a South American ancestral area for oryzomyines. The most basal taxon for each lineage is cis-Andean or, in case of clade D, eastern Andean (fig. 48): *Scolomys*, *nitidus* group, *Neacomys*, and *Oryzomys polius* for clades A, B, C, and D, respectively. Central American (trans-Andean) taxa are always recovered deeply nested within the major lineages.

Given the estimated time for initial diversification of oryzomyines based on molecular studies, the oryzomyine ancestor must have arrived in South America prior to the formation of the Panamanian land bridge at 3.5–4.0 mybp (Coates et al., 1992; Ibaraki, 1997) by over-water dispersal (but see Coates et al., 2004, for new evidence pointing to a collision of the Central American arc with South America at 7.1 mybp). The capability of oryzomyines to undertake long-distance water dispersal is well known (Carleton and Olson, 1999). Oryzomyines are known from volcanic islands without former subaerial connections to the South American plate, such as the Galapagos Islands (*Nesoryzomys* and *Oryzomys bauri*) and Fernando de Noronha (†*Noronhomys*). These islands are situated at 1000 km and 310 km, respectively, from South America, a distance far exceeding the one among the stepping-stone connections that existed between the North and South American plates since the Miocene (Donnelly, 1992).

Thus, there is no phylogenetic indication that the immediate precursor of oryzomyines was in Central America as previously proposed (Patterson and Pascual, 1968, 1972; Baskin, 1978, 1986; Marshall, 1979; Simpson, 1980; Jacobs and Lindsay, 1984; Czaplewski, 1987; Baskin, 1989; Engel et al., 1998). Such a hypothesis would involve several ad hoc events of dispersal and extinction. The principal argument used for a North American diversification of oryzomyines was the supposed presence of members of the tribe (among other sigmodontines) in the North American Tertiary fossil record, that is, before the formation of the Panamanian land bridge. As discussed above, no undisputed fossil oryzomyine is known from the Tertiary of North America.

Current oryzomyine diversity in Central and North America is more likely a product of independent colonizations made by the different clades within oryzomyines that are currently found in that area (*Zygodontomys*, *alfaroi-melanotis-chapmani*, *talamancae*, *Oligoryzomys*, *palustris*, *Melanomys*, and *Sigmodontomys*). This scenario is similar to the one proposed by Hershkovitz (1966b), who suggested nonsynchronous dispersion of various oryzomyine lineages from northern South America in a timeframe ranging from before the completion of the Panamanian bridge to recent times. The *palustris* group was included by Hershkovitz in his "Stratum III: Old South American Migrants in North American", which "returned over water routes to Middle America [during the Pliocene] and differentiated significantly [in situ]" (Hershkovitz, 1966: 733). *Melanomys*, *Sigmodontomys*, *talamancae*, *alfaroi*, *Zygodontomys*, and *Oligoryzomys* were considered members of "Stratum IV: Late South American Migrants in Middle America", which "spread over Panamanian land-bridge into Middle America [during Pleistocene]; [with] low grade subspeciation" (Hershkovitz, 1966: 737). *Oryzomys melanotis* and *Sigmodontomys aphrastus* were of doubtful position.

Hershkovitz (1966) also included in the recent migrants group some taxa that were considered here as with borderline distribution in Central America, such as *albigularis*, *Oecomys*, and *Neacomys*.

A slightly different scenario is the concomitant range expansion of all the independent oryzomyine lineages into Central America after the completion of the Panamanian land bridge, without over-water dispersal events in the Pliocene. Such invasion would be second only to the Didelphidae dispersal into Central America as part of the ''Great American Interchange'' in terms of number of genera, and would be the most successful in terms of species diversity. Much of the oryzomyine radiation is restricted to tropical North America, with only one taxon extending into the Nearctic region, a pattern also observed in other groups of South American invaders such as Didelphidae, Echimyidae, and Xenarthra (Webb and Wilkins, 1984). Some of the invading oryzomyine groups have experienced larger in situ diversification, such as the *alfaroi-melanotis-chapmani* clade, the *palustris* group, and *Oligoryzomys* (Hershkovitz, 1966b; Hall, 1981; Carleton and Musser and 1995), whereas others appear to be in early stages of dispersion into Central America, especially those cis-Andean taxa with minimal distribution in Central America, such as *Neacomys* and *Oecomys*.

A more precise location of the oryzomyine ancestral area in South America requires delimitation of smaller units for analysis than the three general categories provided here. Two areas are likely candidates: the region of premontane forests of the northern Andes and the western Amazon lowland forests. All basal taxa within each lineage—*Neacomys*, *polius*, *hammondi*, the *nitidus* group, and *Scolomys*—are distributed in the western Amazon and/or submontane Andes. The few biogeographical analyses done with oryzomyine genera or species groups also placed western Amazon/eastern Andes taxa as basal to their own lineages (Costa, 2003). In contrast, taxa restricted to other South American landscapes, such as southeastern South America (*Lundomys*, *Pseudoryzomys*, *subflavus* and *angouya* groups), are situated farther from the oryzomyine root in the present phylogeny and in lower level analyses (Patton et al., 2001; Costa, 2003).

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APPENDIX 1

Specimens Examined

Specimens are from the American Museum of Natural History unless otherwise designated (ASNHC, Angelo State Natural History Collections, San Angelo; FMNH, Field Museum of Natural History, Chicago; GD, Guillermo D'Elía; KU, University of Kansas Natural History Museum, Lawrence, KS; MNRJ, Museu Nacional, Rio de Janeiro, Brazil; MUSM, Museo de Historia Natural, Universidade Nacional Mayor de San Marcos, Lima, Peru; MVZ, Museum of Vertebrate Zoology; UC, Univeristy of California–Berkeley; UMMZ, Museum of Zoology, University of Michigan, Ann Arbor; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC).

Nyctomys sumichrasti

Skin and skull: BELIZE: Toledo, Rio Grande, 1.9 km. ENE Big Fall Bridge (256834); COSTA RICA: Talamanca, Cavita (25973); MEXICO: Oaxaca, 5 mi. W Chiltepec (190330); Tehuantepec, Santo Domingo Guzman (3101–4, 2425–6 [skull numbers]); NICARAGUA: Rio Tuma (29550). *Skeleton:* BELIZE: Toledo, Rio Grande, 1.9 km ENE Big Fall Bridge (256834); MEXICO: Oaxaca, 5 mi. W Chiltepec (190330). *Fluid:* Unknown locality: (130310). *Roots:* HONDURAS: Lepaera, Gracias (129804).

Peromyscus maniculatus

Skin and skull: CANADA: Alberta, Thoral Creek (122566); GREENLAND: Labrador, Indian Harbor (91111 [skin only]). USA: Arizona, Navajo Co., Mesa Top (122826); Colorado, Alamosa Co., 9 mi. E Center (137741–2, 137763; 137738–9, 137744); Utah, San Juan Co., Navajo Mt. (125945–6). *Skeleton:* USA: Arizona, Navajo Co., Mesa Top (122826); Colorado, Alamosa Co., 9 mi. E Center (137741–2, 137763); Utah, San Juan Co., Navajo Mt. (125945–6). *Fluid:* USA: Connecticut, Byram River Gorge Reservoir (232248), and Stonington (232249).

Delomys sublineatus

Skin and skull: BRAZIL: São Paulo, E.B. Boracéia (FMNH 141628), and Casa Grande (USNM 460535–7, USNM 462075, USNM 484222–3, USNM 484225–6).

Thomasomys baeops

Skin and skull: ECUADOR: El Oro, Taraguacocha (47629, 47632–3, 47635, 47637–8, 47640–2, 47699). PERU: Cajamarca, Las Ashitas (268146 [skin only]). *Skeleton:* ECUADOR: El Oro, Taraguacocha (47699). *Fluid:* ECUADOR: Napo, near Papallacta (248499–50).

Wiedomys pyrrhorhinos

Skin and skull: BRAZIL: Bahia, Palmeiras, Sítio Ananaz (MNRJ 18749–50); Paraíba, Princêsa Isabel, Sítio Prancozinho (MNRJ 18587); Pernambuco, Triunfo, Sítio Peri-Peri (MNRJ 18746); Pernambuco, Bodocó (USNM 304584); Exú (USNM 555760); Garanhuns, Sítio Cajarana (MNRJ 60735); unknown locality (USNM 538306, USNM 538314, USNM 538382, USNM 538386–8). *Skeleton:* unknown locality (USNM 538306, USNM 538314, USNM 538382, USNM 538386–8). *Fluid:* Unknown locality (USNM 537470).

Handleyomys intectus

Skin and skull: COLOMBIA: Cauca, El Roble (32931–2, 33021).

Holochilus brasiliensis

Skin, skull, and skeleton: URUGUAY: Canelones, Banada de Tropa Vieja (206362); Soriano, 3 km E Cardona (206371–2, 206374–6, 206379, 206383); Tacuarembo, Rio Negro, Isla Sanchez Chica, ca. 16 km WSW San Jorge (206390; 206391 [skull only]). *Fluid:* PARAGUAY: Ñeembecu, Estancia Santa Teresa (GD 081).

Holochilus chacarius

Skin and skull: ARGENTINA: Formosa, Riacho Pilaga (USNM 236321–4 [USNM 236322 ski only]); PARAGUAY: unknown locality (USNM 4949; USNM 11010 [skull only]). *Fluid:* PARAGUAY: unknown locality (USNM 11009–10).

Lundomys molitor

Skin, skull, and skeleton: URUGUAY: Canelones, Banada de Tropa Vieja (206363–4); Soriano, 3 km E Cardona (206368, 206380; 206373, 206388 [skin and skull only]), Trienta y Tres, 25 km WSW Trienta y Tres, Rio Olimar Chico (206392; 206393 [skin and skull only]). *Fluid:* URUGUAY: Soriano, 3 km E Cardona (206373, 206388). *Roots:* URUGUAY: Canelones, Banada de Tropa Vieja (206365).

Melanomys caliginosus

Skin and skull: COLOMBIA: Magdalena, Manyanares (15497); ECUADOR: Manabi, Cuaque (66331, 66333–4, 66338–40); Pichincha, Gualea (46691, 46694, 46696); Pichincha, La

Palma, Cotache (46717). *Skeleton:* COLOMBIA: Magdalena, Manyanares (15497), Santa Marta (USNM 280606, USNM 280690); PANAMA: Bocas Del Toro, Isla San Cristobal (USNM 449888), Peninsula Valiente (USNM 578385), Tierra Oscura (USNM 449890). *Roots:* COLOMBIA, Cauca, Munchique (32408), Puerto Viejo (36826). COSTA RICA: El Sauce (250414); Puntarenas, Palmar (139414, 139425); ECUADOR: Esmeraldas (33215); Loja, Rio Casagna (193995); NICARAGUA: Rio Tuma (USNM 29532); Toro Rapids (136936). PANAMA: Bocas Del Toro, Isla Colon (USNM 464881); Darien, Tacaruna (USNM 37931), Cana (USNM 178667).

Microryzomys minutus

Skin and skull: ECUADOR: Canari, Chical (63034, 63037); Canari, San Antonio (67561, 67563); Pichincha, Cañon Rio Pita (66571, 66573–4); PERU: Cuzco, 32 km NE Poncartambo (MVZ 166666); Cuzco, 3 km E Amaybamba (MVZ 173975); Junin, Tarama, 22 mi. E Tarama (231070); VENEZUELA: Mérida, Paramo de Los Conejos (96168). *Skeleton:* BOLIVIA, Cochabamba, 31 km W Comarapa (260419); Santa Cruz, Serrania Siberia (264142). *Fluid:* ECUADOR: Tungurahua, San Francisco (63385, 63386); Napo, near Papallacta (248278). *Roots:* VENEZUELA: Tachira, Buena Vista (USNM 442214).

Neacomys minutus

Skin, skull, and fluid: PERU: Loreto, Rio Galvez, Nuevo San Juan (272869, MUSM 13311–3).

Neacomys musseri

Skin, skull, and fluid: PERU: Loreto, Rio Galvez, Nuevo San Juan (272712, 272719 [skull only], 272676, 272687 [skull only], MUSM 13308, MUSM 13310).

Neacomys spinosus

Skin and skull: PERU: Amazonas, Rio Cenepa, vicinity of Huampami (MVZ 155014); Loreto, Boca Rio Curaray (71518, 71523–4, 71526–9, 71531, 71533, 71536); Puno, Inca Mines (15810 [skin only]). *Skeleton:* BOLIVIA: Santa Cruz, San Rafael de Amboro (261987–91).

Nectomys apicalis

Skin and skull: ECUADOR: Napo, Oriente, San José (68187–8); Pastaza, Sarayacu (67327); PERU: Cuzco, Kiteni, Rio Urubamba (MVZ 166700); Loreto, Boca Del Rio Curaray (71911–2, 71915–7, 71919). *Skeleton:* PERU: Loreto, Boca Del Rio Curaray (71911). *Fluid:* PERU: Junin, Tarma (232648). *Roots:* ECUADOR, Napo, San Jose (68194); Pastaza, Sayacu (67375); Zamora (47825).

Nectomys squamipes

Skin and skull: BRAZIL: Minas Gerais, Rio Caparaó (80397); Minas Gerais, Serra do Caparaó, Fazenda Cardoso (61854–6, 6185–8); São Paulo, Itapetininga (USNM 484163–75), Ilha do Cardoso (FMNH 141630, FMNH 141632).

Nesoryzomys narboroughi

Skin, skull, and skeleton: ECUADOR: Galápagos Islands, Isla Fernandina (ASNHC 8675; USNM 364937–9 [not skin], USNM 259552).

Nesoryzomys swarthi

Skin, skull, and skeleton: ECUADOR: Galápagos Islands, Isla Santiago (ASNHC 10003).

Oecomys bicolor

Skin and skull: ECUADOR: Pastaza, Canelos (67502 [skin only]); PERU: Cuzco, Pagoreni (USNM 582885–6), Tangoshiari (USNM 588041); Loreto, Rio Galvez, Nuevo San Juan (268257–8, 272710, 272724 [skull only], 272727 [skull only], 272674, 273096, MUSM 11210, MUSM 13315 [skin only], MUSM 13317, MUSM 13318 [skull only]);Madre De Dios, Rio Manu (USNM 559396), Rio Tambopata (USNM 530921); Pasco, Oxapampa (USNM 364505–7). *Skeleton:* PERU: Cuzco, Pagoreni (USNM 582885). *Fluid:* BOLIVIA: Beni, boca del Rio Biata (262852); FRENCH GUIANA: Les Nouragues (269823); PERU: Loreto, Rio Galvez, Nuevo San Juan (272724, 272727, MUSM 13318). *Roots:* BRAZIL: Amazonas, Taurarate (78634); Pará, Recreio (95987).

Oecomys catherinae

Skin and skull: BRAZIL: Bahia, Ilheus (USNM 304561).

Oecomys concolor

Skin and skull: BOLIVIA: Santa Cruz, El Refugio (USNM 588189–90); VENEZUELA: T.F. Amazonas, Boca Mavaca (USNM 406017), Acanana (USNM 406022), San Juan (USNM 409863, USNM 418444 [skull only]), and Tamatama (USNM 409880, USNM 416712 [skull only]). *Skeleton:* VENEZUELA: Aragua, Rancho Grande (USNM 399535). *Fluid:* COLOMBIA: Vaupes, El Dorado on Rio Vaupes (212419).

Oecomys mamorae

Skin and skull: BOLIVIA: Beni, Rio Itenez (209987, 210023), San Joaquin (USNM 391302), and San Ramon (460430); Chuquisaca, Camiri (USNM 277602), Tihumayu (USNM 290906), and Tola Orko (USNM

271581–2); Santa Cruz, Ayacucho (USNM 390655), Cordillera (USNM 390654), Velasco (USNM 390656, USNM 391301); BRAZIL: Mato Grosso, Fazenda Acurizal (USNM 531278 [skull only]). *Skeleton:* BOLIVIA: Beni, Rio Itenez (209987, 210023). *Fluid:* BOLIVIA: Beni, Rio Ibare (211719), Rio Mamore (211723); Santa Cruz, 3.5 km W of Estacion Pailon (260420). BRAZIL: Mato Grosso, Fazenda Acurizal (USNM 531278).

Oecomys trinitatis

Skin and skull: PERU: Loreto, Rio Galvez, Nuevo San Juan (273112, 273119, 273122, MUSM 15535–7, MUSM 15539, MUSM 13320). *Skeleton:* Trinidad, Bush Bush Forest (206784). *Roots:* Trinidad, Cumaca (169721), North Manzanilla (186474).

Oligoryzomys flavescens

Skin and skull: BRAZIL: São Paulo, Casa Grande (USNM 484124–5) and Itapetininga (USNM 484124–37 [USNM 484134–5 skin only]). *Skeleton:* URUGUAY: Rocha, 22 km SE Lascano (205997–206001).

Oligoryzomys fornesi

Skin and skull: PARAGUAY: Misiones, San Ignacio (USNM 390122).

Oligoryzomys fulvescens

Skin and skull: VENEZUELA: Aragua, Camp Rafael Rangel (USNM 314173, USNM 317716–7, 317719–20, USNM 317724–7); Distrito Federal, Alto No Leon (USNM 374326) and Los Venados (USNM 371167); Mérida, Santa Rosa (USNM 387872); Sucre, Finca Vuelta Larga (257251–2, 257256, 257258–9, 257262–6); Yaracuy, Urama (USNM 374693). *Skeleton:* VENEZUELA: Sucre, Finca Vuelta Larga (257262–6). *Fluid:* VENEZUELA: Portuguesa, La Arenosa, (266918, 266920, 266922–6).

Oligoryzomys nigripes

Skin and skull: BRAZIL: Mato Grosso do Sul, Maracajú (134899; 134541–3, 134545, 134551, 134833, 134838, 134900, 134902); Minas Gerais, Viçosa (USNM 541500); São Paulo, Mogi–Guassu (USNM 526774–5) and Barragem (USNM 542930–6). *Skeleton:* BRAZIL: Mato Grosso do Sul, Maracajú (134899).

Oligoryzomys stramineus

Skin and skull: BRAZIL: Ceará, Santanópole (USNM 304583); Pernambuco, Exú (USNM 528416).

Oryzomys albigularis

Skin and skull: ECUADOR: El Oro, El Chiral (46484–5, 46489–90, 46493, 46495–6, 46500, 48040, 48042); Loja, Alamor (48233 [skin only]); PERU, Cajamarca, Las Ashitas (268125 [skin only]). *Skeleton:* Peru, unknown locality (231911). *Fluid:* ECUADOR: Pichincha, 2.5 km N Guarumal (248275–6); PERU: Cajamarca, (268115, 268120); Cajamarca, Las Ashitas (268126–7); Cajamarca, Las Juntas (268131–3). *Roots:* ECUADOR: El Oro, El Chiral (46486–8, 46491, 46498), Salvias (47812).

Oryzomys alfaroi

Skin and skull: COSTA RICA: Cartago, Tuis (9613); Puntarenas, Canas Gordas (142424–5, 142426 [skin only], 142427, 142429–30, 142436–8). *Fluid:* COSTA RICA: unknown locality (9633–4, 9636, 9638–9); ECUADOR: Pichincha, Mindo (248496). *Roots:* COLOMBIA: Cauca, Las Lomitas (322717); ECUADOR: Mojanda (46752), Puente de Chimbo (62310, 62347); Guayas, Cerro Manglar Alto (66346).

Oryzomys angouya

Skin and skull: BRAZIL: Minas Gerais, Serra do Caparaó, Fazenda Cardoso (61850); Morro do Ferro, 25 km S Poços de Caldas (207953–5 [skull only]); Sao Paulo, Piquete (36497); PARAGUAY: Guaira, Villarica (66784); Itapua, Trinidad (36513); Misiones, 5 km by road ENE Ayolas (248407–8, 248409, 248411). *Skeleton:* BRAZIL: Minas Gerais, Serra do Caparaó, Fazenda Cardoso (61850). *Fluid:* BRAZIL: Minas Gerais, Morro do Ferro, 25 km S Poços de Caldas (207953–5).

Oryzomys balneator

Skin and skull: ECUADOR: El Oro, El Chiral (47585–9, 47592–3, 47595); PERU: Cajamarca, 4 km W Chaupe (268137, 268144). *Fluid:* ECUADOR: Canar, El Chiral (68519); PERU: Cajamarca, 4 km W of Chaupe (268134–5, 268139, 268141, 268143).

Oryzomys chapmani

Skin and skull: MEXICO: Oaxaca, 16 mi SSW La esperanza (254698–700); Tamaulipas, Rancho del Cielo (148108–10, 148111, 148102–14, 148116, 148169). *Skeleton:* MEXICO: Oaxaca, 16 mi SSW La esperanza (254698–700). *Fluid:* MEXICO: Oaxaca, Ixtlan, Vista Hermosa (213658, 214841, 214908–9); Vera Cruz, Coyame (166936 [penis only]).

Oryzomys couesi

Skin, skull, and skeleton: MEXICO: Oaxaca, 5 mi E San Gabriel Mistepec (190292, 190294, 190296–7, 190299–300, 190305–6, 190311,

190318); *Fluid:* GUATEMALA: Lake Peten (144763, 144965, 144968, 145029–30); Zacapa, Cabanas, Quebrada Honda (265862).

Oryzomys hammondi
Skull and fluid: ECUADOR, Pichincha, Mindo (UMMZ 155827).

Oryzomys lamia
Skin and skull: BRAZIL: Goiás, Anápolis (134644–5, 134667, 134772, 134677, 134763).

Oryzomys levipes
Skin and skull: BOLIVIA: La Paz, Nequejahuira (72117, 72657–62, 72664, 72669), Rio Unduavi (264726); Santa Cruz, Serrania Siberia (264192–3); PERU: Cuzco, 54 km NE Paucartambo (MVZ 171468). *Skeleton:* BOLIVIA: La Paz, Rio Unduavi (264726); Santa Cruz, Serrania Siberia (264192–3). *Fluid:* BOLIVIA: La Paz, Rio Unduavi (264728–9).

Oryzomys macconnelli
Skin and skull: BRAZIL: Pará, Capim, km 94 on BR 14 (203405, 203408–10); PERU: Loreto, Rio Galvez, Nuevo San Juan (273100, MUSM 15241–2); VENEZUELA: Bolivar, 5.2 km NE San Ignacio de Yuruani (257236 [skull only], 257237–8). *Skeleton:* VENEZUELA: Bolivar, 5.2 km NE San Ignacio de Yuruani (257236–8). *Fluid:* BRAZIL: Amazonas, Serra da Neblina (246136). PERU: Huanuco, Cerros del Sira (241641); Loreto, Rio Galvez, Nuevo San Juan (273100); VENEZUELA: Bolivar, 5.2 km NE San Ignacio de Yuruani (257236).

Oryzomys megacephalus
Skin, skull, and skeleton: FRENCH GUIANA, Paracou, Near Sinnamary (266514 [not skeleton], 266518 [not skeleton], 266521 [not skeleton], 266523 [not skeleton], 266494); GUIANA: Kartabo (41927); VENEZUELA: Bolivar, 5.2 km NE San Ignacio de Yuruani (257230–3). *Fluid:* FRENCH GUIANA, Paracou, Near Sinnamary (266514, 266518, 266521, 266523). *Roots:* GUIANA: Kartabo (41914), Minehaha Cr. (36340).

Oryzomys palustris
Skin, skull, and skeleton: USA: Florida, Highlands Co., Lake Placid, Archbold Biological Station (219953, 250167, 252718–9, 253214–5, 253217–8, 253220); Florida, Collier Co., Fakahatchee Strand (252717), Rookery Bay Sanctuary (UMMZ 124636 [not skeleton]). *Fluid:* USA: Georgia, Liberty Co., St. Catherine's Island (239257–60, 239263–4).

Oryzomys polius
Skin,skull, and skeleton: PERU: Amazonas, 19 km by road E Balsas (FMNH 129242–3 [skin and skull only]); Cajamarca, Chaupe (64054), San Ignacio (64055–6).

Oryzomys rostratus
Skin and skull: MEXICO: San Luis Potosi, El Salto (172915, 172969, 174626, 177193), 22 mi W Ciudad Valles (254713–7); Vera Cruz, N Shore Lake Catemaco (174628); Vera Cruz, Pasa Nueva (17140 [skin only], 17164). *Skeleton:* MEXICO: San Luis Potosi, 22 mi W Ciudad Valles (254713–7). *Fluid:* MEXICO: Oaxaca, Juchitan, Santa Maria Chimalya (231967).

Oryzomys russatus
Skin and skull: BRAZIL: Minas Gerais, Fazenda Cardozo (61835, 61837); São Paulo, Casa Grande (USNM 485001–11). *Skeleton:* BRAZIL: Minas Gerais, Fazenda Cardozo (61835). *Roots:* BRAZIL: São Paulo, Ubatuba (USNM 304598); PARAGUAY: Caaguazu, Sommerfeld Colony No. 11 (USNM 293147).

Oryzomys subflavus
Skin and skull: BRAZIL: Goiás, Anápolis (134577–8, 134632, 134639–40, 134650, 134660, 134785); Minas Gerais, Juramento, Fazenda Canoas (MNRJ 61665–6). *Skeleton:* BRAZIL: Minas Gerais, Juramento, Fazenda Canoas (MNRJ 61665–6). *Fluid:* BRAZIL: Goiás, Anápolis (202660–2).

Oryzomys talamancae
Skin and skull: ECUADOR, Esmeraldas, Cuaque (64733, 64773–5, 64777, 64779–80, 64782, 64785, 67900); PANAMA: Bocas del Toro, Tierra Oscura (USNM 449894). *Skeleton:* PANAMA: Bocas del Toro, Tierra Oscura (USNM 449894); VENEZUELA: Zulia, Mision Tukuko (USNM 448600, USNM 448607–9). *Fluid:* ECUADOR: Manabi, Bahia de Caraquez, Rio Briseno (66229–31, 66239), Pata de Pajaro (66236–7).

Oryzomys xanthaeolus
Skin and skull: ECUADOR: El Oro, Pasage (61313, 61315, 61318, 61321); El Oro, Portovelo (47740–1, 47745–6); Guayas, Chongoncito (63254); Loja, Casagna (47733). *Skeleton:* ECUADOR: El Oro, Pasage (61313); El Oro, Portovelo (47745). Los Rios, Hacienda Santa Teresita (USNM 534364), Puerto Nuevo (USNM

534367), Vinces (USNM 534369); PERU: Ica, El Ingenio (USNM 277565) and Nasaca (USNM 277568). *Fluid:* ECUADOR: Manabi, Bahia de Caraquez, Rio Briseno (66221–8), El Destino (66333); PERU: Llampa (USNM 302989–91), Chasquitambo (USNM 302992).

Oryzomys yunganus

Skin and skull: FRENCH GUIANA: Paracou, Near Sinnamary (266495–6, 266503); VENEZUELA: Bolivar, Auyantepui (130948, 130952, 130955, 130959, 131096, 131104, 131126). *Skeleton:* PERU: Pasco, San Pablo (231666). *Fluid:* BOLIVIA: Santa Cruz, Rio Saguayo (262079, 262081); FRENCH GUIANA: Paracou, Near Sinnamary (266495).

Pseudoryzomys simplex

Skin and skull: BOLIVIA: Beni, Estacion Biologica del Beni (262048), San Joaquin (USNM 364749); Santa Cruz, Velasco (USNM 390668). Skeleton: BOLIVIA: Beni, Estacion Biologica del Beni (262048).

Scolomys ucayalensis

Skin and skull: PERU: Loreto, Rio Galvez, Nuevo San Juan (272668, 272686, 272697, 272706, 272708, 272721, MUSM 13356–61). *Skeleton:* PERU: Loreto, Rio Galvez, Nuevo San Juan (272721). *Fluid:* PERU: Loreto, Rio Galvez, Nuevo San Juan (272686, 272697, 272706, 272708, MUSM 13356–8).

Sigmodontomys alfari

Skin and skull: COSTA RICA: Cartago, Santa Teresa, Peralta (123305, 141877); NICARAGUA: Rio Grande (28547, 28549); PANAMA: Bocas del Toro, Isla San Cristobal, Bocatorito (USNM 449895); Darien, Tacarcuna (37901, 37904, 37908–9, 37912, 37914). *Skeleton:* PANAMA: Bocas del Toro, Isla San Cristobal, Bocatorito (USNM 449895). *Roots:* PANAMA: Darien, Tacarcuna (34191, 37903, 37906, 37910–1, 37914).

Sigmodontomys aphrastus

Skin and skull: COSTA RICA: Monteverde Cloud Forest Reserve (KU 161003, KU 159021); ECUADOR, Pichincha, Mindo (UMMZ 155808 [skull only]); PANAMA: Chiriqui, San Felix (USNM 541200–1). *Fluid:* ECUADOR, Pichincha, Mindo (UMMZ 155808).

Zygodontomys brevicauda

Skin, skull, and skeleton: TRINIDAD AND TOBAGO: Trinidad, Soldado Rock (206640, 206645–7, 206649–50, 206655, 206657–8, 206660). VENEZUELA: Bolivar, Uruyen (135454 [skin only]; Sucre, Finca Vuelta Larga (257322 [skin only]). *Fluid:* VENEZUELA: Portuguesa, La Hoyada, near Guanarito (266935–6, 266941, 266944–5, 266947, 266950).

Zygodontomys cherriei

Skin and Skull: COSTA RICA: Puntarenas, Boruca (11727–8, 11730, 11732, 11736–40, 11752); VENEZUELA: La fortuna, San Miguel (132831 [skin only]). *Fluids:* COLOMBIA: Bolivar, 1 km NW Boquillas (255818–9).

APPENDIX 2

Summary of Characters

The following list of characters was drawn from previous phylogenetic analyses of sigmodontines at various taxonomic levels. Suitable characters from oryzomyine taxonomic studies are also listed. Most characters were assessed in the present taxon set; some characters are marked as not observed because material was not available or because I did not have access to the original character description in time. I organized the characters in terms of general morphological systems (external morphology, skull and mandible, dentition, postcranial skeleton, and bacular and soft anatomy characters). I subdivided each system into more specific classes (e.g., vibrissae, mammae, hindfeet). This division is sometimes subjective but it serves as a guide when going through specimens. Numerals before the characters reflect this structure.

All previous studies in which the character was employed are listed. I tried to maintain the original character descriptions, and I indicate when characters were modified (most of the ones included in the present analyses). When two or more similar descriptions of the same structure are available in the literature, I usually include the first, or sometimes the clearest description. Characters employed in the present study are marked with an asterisk (*) and are referred to by their numbers in the description (followed by #). Reasons for rejection of characters are indicated, which include: no variation among included taxa, metric characters, continuous traits (including characters related to distance, size, shape, and color) without distinctive discrete interval between states, rampant polymorphism (intraspecific variation), ambiguous characterization, unreplicable results, autapomorphies for non-oryzomyines, characters not applicable in the present set of taxa, complete covariation with other characters, and

structure or states not identified. Several of these features are informative taxonomic characters, but they were unsuitable for coding cladistic characters in the present analysis.

1. External Morphology

1.1. Vibrissae

1.1.1. *Superciliary, genal, and mysticacial vibrissae extended well beyond ears (0); or vibrissae reach pinnae but rarely extend beyond (1)* (Musser et al., 1998: 320; see also Luna, 2002: chars. 1, 2 and 4; Pacheco, 2003: char. 17T; Voss, 2003: 16–17). Rejected: continuous trait; in addition, the relative position of the end of the vibrissae to the pinnae also depends on the size of the pinnae and of the rostrum.

1.1.2. *Superciliary vibrissae present (0); or absent (1)* (Voss, 1988: char. 6). Rejected: invariant (present).

1.1.3. *Genal 1 vibrissae present (0); or absent (1)* (Luna, 2002: char. 3; Pacheco, 2003: chars. 8S and 15T; Voss, 2003: 16–17). Rejected: invariant (present).

1.1.4. *Genal 2 vibrissae present (0); or absent (1)* (Pacheco, 2003: chars. 9S and 16T). Not observed. I could not determine with confidence the character-state for most taxa because absence may be due to the poor condition of skin vouchers (see Pacheco, 2003). Apparently, genal 2 vibrissae are present only in *Oecomys bicolor* and *O. catherinae*.

1.1.5. *Carpal vibrissae distinctly longer than metacarpal pads (0); or shorter, inconspicuous or absent (1)* (Pacheco, 2003: char. 10S). Rejected: invariant (long).

1.1.6. *Calcaneal vibrissae present (0); or absent (1)* (Pacheco, 2003: char. 11S). Rejected: invariant (present).

1.2. Mammary Glands

*1.2.1. *Four mammae present in inguinal and abdominal pairs (0); or six mammae in inguinal, abdominal, and postaxial pairs (1); or eight mammae in inguinal, abdominal, postaxial, and pectoral pairs (2)* (Carleton, 1980: char. 79; Voss, 1993: 24; Voss and Carleton, 1993: char. 5; Steppan, 1995[13]: char. 35S; Luna, 2002: char. 23; Voss et al., 2002: 18; Pacheco, 2003: chars. 12S–15S and 23T). Included: #1. Note: Some of those characterizations included more states not observed in the present analysis (e.g., 10 mammae).

1.3. Manus

*1.3.1. *Claws of manus small, not extending much beyond digital pads, not keeled (0); or claws long, extending conspicuously beyond digit pads and ventrally, keeled for about half their length (1)* (modified from Steppan, 1995: char. 85P; Pacheco, 2003: chars. 1S and 2T). Included: #2.

1.3.2. *Hypothenar pad of manus separate, not fused with third interdigital pad (0); or hypothenar and third interdigital pads fused (1); or hypothenar and thenar pads fused with adjacent third and first interdigital pads, respectively (2)* (Voss, 1988: char. 7). Rejected: invariant (pad separate).

1.3.3. *Second digit of manus distinctly longer than fifth (0); or second and fifth digits subequal (1)* (Pacheco, 2003: chars. 2S and 3T). Rejected: continuous trait; although some taxa (e.g., *Oecomys bicolor*, *Nyctomys sumichrasti*) have the second and fifth digits with subequal length, the condition observed in several other taxa form a gradation from subequal to distinctly longer (e.g., *Oryzomys megacephalus*, *Oecomys mamorae*, *Oryzomys talamancae*, *Oryzomys albigularis*, *Thomasomys*).

*1.3.4. *Ungual tufts at base of manual claws present and long (0); or reduced or absent (1)* (Pacheco, 2003: char. 1T). Included: #3.

1.3.5. *Pollex bears a nail (0); or clawed (1)* (Olds and Anderson, 1989: char. 12). Rejected: invariant (nail present).

1.3.6. *Phalange 1 of pollex (dI of manus) long and slender (0); or short and wide (1)* (Pacheco, 2003: 102S). Not observed.

1.4. Pes

*1.4.1. *Hypothenar pad of pes present (0); or absent or vestigial (1)* (Voss, 1993: 24; Voss et al., 2002: 18; Pacheco, 2003: chars. 4S and 7T; Luna, 2002: char. 5). Included: #4. This and the following character (1.4.2.) have also been treated as a single multistate character (Carleton, 1980: char. 77; Carleton and Musser, 1989: char. 2; Voss and Carleton, 1993: char. 3; Braun, 1993: char. 2 [part]; Carleton and Olson, 1999: char. 38).

*1.4.2. *Plantar pads on hindfeet large and fleshy, interdigitals 1–4 set close together, often in contact (0); or pads smaller but still fleshy,*

[13] Steppan (1993) presents an almost identical character set to Steppan (1995); it is not included here. The only differences is the absence in Steppan (1993) of two characters related to posterior extension of nasals and premaxillae (Steppan 1995: characters 46P and 47P).

interdigitals 1 and 4 displaced proximally relative to 2 and 3 (1); or interdigital pads distributed as in state 1 but extremely small and with low relief (2) Included: #5; see note on previous character (1.4.1).

1.4.3. *Hypothenar pad extending distally beyond proximal base of the first interdigital pad (0); or intermediate to first and thenar pad (1)* (Steppan, 1995: char. 87P; see also Luna, 2002: chars. 7 and 8; Pacheco, 2003: chars. 8T, 9T, and 10T). Rejected: continuous trait.

1.4.4. *Thenar pad present (0); or absent (1)* (Braun, 1993: char. 2 [part]). Rejected: invariant (present).

*1.4.5. *Plantar surface of hindfeet smooth, without well-developed squamae (0); or plantar surface covered with squamae (1)* (Luna, 2002: char. 14; Pacheco, 2003: chars. 6S and 6T). Included: #6.

*1.4.6. *Ungual tufts present on all claws of hindfoot as a uniform thick sheath extending to or beyond claw tip (0); or tufts absent on digit I (dI), present on dII–dV as a uniform thick sheath extending to or beyond claw tip (1); or tufts absent on dI, present as sparse cover and with few hairs extending beyond the claw tip on dII–dV (2); or tufts extremely reduced or absent on all claws (3)* (modified from Patton and Hafner, 1983: char. 15; Carleton and Musser, 1989: char. 4; Voss, 1993: 24; Voss and Carleton, 1993: char. 1; Musser et al., 1998: 320; Carleton and Olson, 1999: char. 36; Voss et al., 2002: 18; Pacheco, 2003: chars. 3S and 4T [part]). Included: #7.

*1.4.7. *Natatory fringes on hindfeet absent (0); or present (1)* (Voss, 1988: char. 8; Voss and Carleton, 1993: char. 2; Carleton and Olson, 1999: char. 37). Included: #8.

*1.4.8. *Interdigital webbing on hindfeet absent (0); or present but small, not extending to first interphalangeal joint of any digit (1); or present and long, extending to or beyond first interphalangeal joints of digits II, III, and IV (2)* (Patton and Hafner, 1983: char. 19; Carleton and Musser, 1989: char. 3; Braun, 1993: char. 4; Voss and Carleton, 1993: char. 4; Carleton and Olson, 1999: char. 39; Luna, 2002: char. 9; Pacheco, 2003: chars. 7S and 11T). Included: #9.

1.4.9. *Plantar surface naked or only lightly furred on heel (0); or plantar surface densely furred to thenar pad (1); or plantar surface densely furred to first interdigital pad (2); or plantar surface entirely fur-covered or nearly so (3)* (Carleton, 1980: char. 78; Braun, 1993: char. 1; see also Patton and Hafner, 1983: char. 18; Steppan, 1995: chars. 33S and 88P; Luna, 2002: char. 15; Pacheco, 2003: char. 5S). Rejected: autapomorphy for *Peromyscus* (Carleton's coding).

*1.4.10. *Dorsal surface of hindfeet densely covered with white hairs, feet appear solid white (0); or dorsal surface sparsely covered with short silvery hairs, feet appear grayish white or pale tan (1); or dorsal surface covered with dark hairs, feet appear brown (2)* Included: #10. Modified from Musser et al. (1998: 320).

1.4.11. *Hindfoot short and broad (0); or long and narrow (1); or long and broad (2)* (Patton and Hafner, 1983: char. 16). Rejected: ambiguous characterization.

1.4.12. *Relative hindfoot length (mean hindfoot length divided by mean head-and-body length)* (Olds and Anderson, 1989: char. 10; Braun, 1993: char. 7). Rejected: metric character.

1.4.13. *Dark metatarsal patches absent (0); or present (1)* (Pacheco, 2003: char. 5T). Rejected: invariant (absent).

1.4.14. *Nail on hallux absent (0); or present (1)* (Luna, 2002: char. 12; Pacheco, 2003: char. 12T). Rejected: invariant (absent).

1.4.15. *Hallux (d1 of pes) not reaching base of digit 2 (0); or reaching base of digit 2 (1); or extending beyond base of digit 2* (Patton and Hafner, 1983: char. 17; see also Voss, 1988: char. 14 [part]; Pacheco, 2003: chars. 103S and 13T). Rejected: continuous trait. Note: Steppan (1995: char. 86P) characterized the length of d1 relative to d5; Carleton and Olson (1999: char. 40) joined the relative length of d1 and d5 in a single character.

1.4.16. *Metatarsals II–V slightly longer than V; nail of fifth digit extends to terminal phalanx of fourth digit (0); or metatarsals II–V conspicuously longer than V; nail of fifth digit extends to second phalanx of fourth digit (1)* (Carleton and Musser, 1989: char. 1; see also Voss, 1988: char. 14 [part]; Luna, 2002: char. 10; Pacheco, 2003: chars. 104S and 14T). Rejected: continuous trait. See note in previous character (4.2.9).

1.5. Tail

*1.5.1. *Ventral surface of tail covered with dark hairs (0); or covered with hairs with dark basal band and white distal band (1); or covered with white hairs (2)* (modified from Patton and Hafner, 1983: char. 20; Musser and Williams, 1985: 19; Voss, 1988: char. 3; Steppan, 1995: char. 89P; Musser et al., 1998: 320; Luna, 2002:

char. 16; Pacheco, 2003: char. 25T). Included: #11.

*1.5.2. *Tail densely furred, scales not visible even at higher magnification (0); or tail sparsely furred, scales macroscopically obvious (1)* (modified from Patton and Hafner, 1983: char. 21; Steppan, 1995: char. 90P; see also Luna, 2002: char. 17). Included: #12.

1.5.3. *Scales in tail heavy and large (0); or light and small (1)* (Patton and Hafner, 1983: char. 22). Rejected: ambiguous characterization.

1.5.4. *Tail pencil absent (0); or present (1)* (Braun, 1993: char. 3; Luna, 2002: char. 19; Pacheco, 2003: chars. 17S and 27T). Rejected: invariant (absent).

1.5.5. *Relative tail length (mean tail length divided by mean head-and-body length)* (Olds and Anderson, 1989: char. 4; Braun, 1993: char. 5; Luna, 2002: char. 18). Rejected: metric character.

1.5.6. *Coloration of tail uniform from the base to tip (0); or tip of tail consistently white (1); or more than one-third of the tail white (2)* (Pacheco, 2003: char. 26T). Rejected: dorsal tail coloration, invariant (uniform).

1.6. Pelage

*1.6.1. *Dorsal and ventral fur without grooved spines (0); or with grooved spines (1)* (Patton and Hafner, 1983: char. 23; Luna, 2002: char. 21; Pacheco, 2003: char. 21T). Included: #13.

*1.6.2. *Ventral fur with plumbeous or dark gray base (0); or ventral fur without plumbeous base (1)* Included: #14.

*1.6.3. *Dorsal and ventral colors sharply delimited, dorsum much darker than pale ventral surface, resulting in conspicuous countershading (0); or dorsal and ventral colors subtly delimited, dorsum slightly darker than ventral surface, resulting in weak countershading (1); or limits of dorsal and ventral colors indistinct, ventral surface dark, countershading absent (2)* (modified from Voss, 1988: char. 2; Steppan, 1995: char. 91P; Luna, 2002: char. 20; Pacheco, 2003: char. 20T). Included: #15.

1.6.4. *Nose not reddish (0); or nose reddish and sharply contrasting with rest of head (1)* (Pacheco, 2003: chars. 16S and 19T). Rejected: autapomorphy for *Wiedomys*.

1.6.5. *Upperparts bright tawny, ochraceous tones along sides of head and body (0); or brownish tawny with burnished tones, only slightly brighter along sides of head and body (1)* (Musser and Williams, 1985: 19; Musser et al., 1998: 320). Rejected: continuous trait.

1.6.6. *Underparts bright whitish gray to nearly solid white, cream highlights (0); or grayish white (1); or dark gray, slightly infused with white or pale buff (2)* (Musser et al., 1998: 320). Rejected: continuous trait.

1.6.7. *Pectoral streaks absent (0); or present (1)* (Steppan, 1995: char. 92P; see also Pacheco, 2003: char. 22T). Rejected: invariant (absent).

1.6.8. *Pelage glossy and grizzled-brownish, composed of wool hairs, buff-painted awns and guard hairs (0); or pelage dull and gray-black, composed of wool hairs and few, fine scattered guard hairs (1)* (Voss, 1988: char. 1). Rejected: not applicable.

1.6.9. *Preauricular patches absent (0); or present (1)* (Braun, 1993: char. 8). Rejected: invariant (absent).

1.6.10. *Postauricular patches absent (0); or present (1)* (Braun, 1993: char. 9). Rejected: invariant (absent).

*1.6.11. *Subauricular patches absent (0); or present (1)* (Braun, 1993: char. 10). Included: #16.

1.7. Pinnae

1.7.1. *Antitragus and pinnae broad (0); or narrow to moderate size (1)* (Pacheco, 2003: char. 18T). Not observed.

1.7.2. *Pinnae present and large, visible above the fur of the head (0); or present but small, concealed beneath the fur of the head, or absent (1)* (Voss, 1988: char. 5; see also Luna, 2002: char. 5). Rejected: invariant (pinnae present and large).

1.7.3. *Relative ear length (mean ear length divided by mean head-and-body length)* (Olds and Anderson, 1989: char. 13; Braun, 1993: char. 6; Steppan, 1995: char. 34S). Rejected: metric character.

1.7.4. *Ears scarcely covered by hair (0); or densely covered by hair (1)* (Luna, 2002: char. 22). Not observed.

1.8. Integument: Miscellaneous

1.8.1. *Philtrum present (0); or absent (1)* (Voss, 1988: char. 4). Rejected: invariant (present).

1.8.2. *Anus a simple orifice flush with the inguinal surface, not protuberant (0); or anus slightly protuberant, usually half the size of male or female prepuce (1); or anus conspicuously protuberant, usually approaching the size of prepuce or longer (2)* (Pacheco, 2003: char. 24T). Rejected: invariant (not protuberant).

2. Skull

2.1. Anterior Dorsum

*2.1.1. *Rostral tube absent (0); or present (1)* (Voss, 1993: 24; Voss et al., 2002: 18; Pacheco, 2003: chars. 18S and 28T; Voss, 2003: 16–17; see also Steppan, 1995: char. 37P; Luna, 2002: char. 38). Included: #17.

2.1.2. *Nasal width less than minimum interorbital distance of dorsal surface of rostrum (1); or greater than or equal to minimum interorbital distance of dorsal surface of rostrum (1)* (Steppan, 1995: char. 48P; Luna, 2002: char. 24). Rejected: continuous trait.

2.1.3. *Nasal bones long, produced anteriorly beyond the premaxillae to conceal the incisors and nasal orifice in dorsal view (0); or nasals short, truncated behind premaxillae to expose the incisors and nasal orifice in dorsal view* (Voss, 1988: char. 10). Rejected: invariant (nasals long).

*2.1.4. *Nasals with blunt posterior margin, finishing in an open angle (0); or nasals with acutely pointed terminus, finishing informing a sharp angle (1).* Included: #18. See also Braun (1993: char. 29).

*2.1.5. *Nasals short, not extending posteriorly beyond the triple-point suture between the maxillary, frontal, and lacrimal (0); or long, extending posteriorly well beyond the maxillary-frontal-lacrimal suture (1)* (modified from Steppan, 1995: chars. 9S and 46P; see also Luna, 2002: chars. 25 and 26; Pacheco, 2003: chars. 19S and 29T). Included: #19.

*2.1.6. *Premaxillaries long, extending posteriorly beyond the nasals (0); or shorter, extending posteriorly to about the same level as the nasals (1); or very short, terminating anterior to the nasals (2)* (Steppan, 1995: chars. 10S and 47P; see also Pacheco, 2003: chars. 20S and 30T). Included: #20.

2.1.7. *Gnathic process absent (0); or present, small or vestigial (1); or present, developed as a continuation of the rostral tube (2)* (Luna, 2002: char. 31). Not observed.

2.2. Orbital Region Dorsum

*2.2.1. *Lacrimal equally contacting maxillary and frontal bones (0); or lacrimal contacting mainly maxillary (1)* (modified from Goldman, 1918: 13). Included: #21.

2.2.2. *Lacrimal bone scarcely evident dorsally (0); or lacrimal bears a shelf projecting into preorbital region (1)* (Carleton, 1980: char. 27). Rejected: invariant (scarcely evident).

2.2.3. *Mediodorsal fusion of frontal complete (0); or partially open or vascularized (1); or distinct and consistent fontanelle present (2)* (Steppan, 1995: char. 53P). Rejected: invariant (complete fusion).

*2.2.4. *Interorbital region symmetrically constricted (''hourglass-shaped'' or ''amphoral''), with rounded supraorbital margins (0); or interorbital region symmetrically constricted with squared supraorbital margins (1); or interorbital region symmetrically constricted with conspicuously beaded supraorbital margins (2); or interorbital region convergent anteriorly (''cuneate'') with weakly beaded supraorbital margins (3); or interorbital region convergent anteriorly with well-developed supraorbital crests (4)* (modified from Carleton, 1980: char. 24; Steadman and Ray, 1982: 10; Patton and Hafner, 1983: chars. 13 and 14; Carleton and Musser, 1989: char. 6; Olds and Anderson, 1989: char. 26; Braun, 1993: chars. 17, 18, and 19; Voss, 1993: 24; Voss and Carleton, 1993: char. 7; Steppan, 1995: chars. 11S, 49P, 50P, and 51P; Carleton and Olson, 1999: char. 4; Luna, 2002: chars. 28 and 29; Voss et al., 2002: 18; Pacheco, 2003: chars. 28S, 43T, and 59T; Voss, 2003: 16–17). Included: #22

2.2.5. *Supraorbital knobs absent (0); or small swellings or knobs on anterior supraorbital region, just posterior to lacrimal (1)* (Steppan, 1995: char. 52P). Rejected: invariant (absent).

2.2.6. *Supraorbital foramina on the lateral surface of the frontal within the orbital fossae (0); or foramina on the dorsal surface of the frontals between the orbital fossae (1)* (Voss, 1988: char. 11). Rejected: invariant (foramina on lateral surface).

*2.2.7. *Postorbital ridge absent, posterior orbital wall without conspicuous relief, frontosquamosal suture exposed (0); or postorbital ridge present and concealing frontosquamosal suture in most old specimens (1)* (Voss and Carleton, 1993: char. 8; Carleton and Olson, 1999: char. 5; Pacheco, 2003: chars. 29S and 46T). Included: #23.

2.2.8. *Postorbital process absent (0); or present (1)* (Carleton, 1980: char. 26; Luna, 2002: char. 35). Rejected: invariant (absent).

2.2.9. *Lacrimal posterior projection absent (0); or present (1)* (Pacheco, 2003: char. 38T). Rejected: invariant (absent).

2.2.10. *Interorbital region narrow (0); or intermediate (1); or broad (2)* (Pacheco, 2003: char. 44T). Rejected: continuous trait.

2.2.11. *Interfrontal fontanella absent (0); or present (1)* (Pacheco, 2003: char. 45T). Rejected: invariant (absent).

2.2.12. *Depression along median suture of frontals deep (0); or shallow (1); or absent (1)* (Steadman and Ray, 1982: 10). Rejected: continuous variation.

2.3. Posterior Dorsum

2.3.1. *Suprasquamosal foramen present (0); or absent (1)* (Pacheco, 2003: char. 35S). Rejected: autapomorphy for *Peromyscus*.

2.3.2. *Frontoparietal suture rounded, edge of frontal convex (0); or suture straight or slightly sigmoidal to concave (1)* (Steppan, 1995: chars. 12S and 54P; see also Braun, 1993: char. 21). Rejected: ambiguous characterization; I could not detect the distinct states.

2.3.3. *Frontoparietal suture as obtuse angle (0); or as acute or right angle.* (Steppan, 1995: char. 55P). Rejected: invariant (obtuse angle).

*2.3.4. *Frontosquamosal suture at same plane of the frontoparietal suture lateral terminus, forming a continuous suture line; dorsal facet of frontal never in contact with squamosal (0); or frontosquamosal suture anterior to frontoparietal suture lateral terminus, leading to an area of contact between dorsal facet of frontal and squamosal (1)* Included: #24.

*2.3.5. *Parietals restricted to the dorsal surface of the braincase, or slightly expanded below the lateral edges of the dorsal at about the squamosal root of the zygomatic arch (0); or parietals deeply expanded onto lateral surface of the braincase (1)* (modified from Musser et al., 1998: 321; see also Luna, 2002: char. 36; Pacheco, 2003; char. 40S). Included: #25.

*2.3.6. *Interparietal wider than posterior border of frontals, in contact with squamosal (0); interparietal strap-shaped, nearly as wide as posterior border of frontals, but not in contact with squamosal (1); or interparietal wedge-shaped, about half as wide as posterior border of frontals, not in contact with squamosal (2)* (modified from Carleton and Musser, 1989: char. 9; Olds and Anderson, 1989: char. 28; Carleton and Olson, 1999: char. 6; Steppan, 1995: char. 14S; Luna, 2002: chars. 34 and 37; Pacheco, 2003: chars. 37S, 38S, and 58T). Included: #26.

2.3.7. *Ratio of interparietal–parietal length less than 0.43 (0); or between 0.43 and 0.70 (1); or greater than 0.70 (2)* (Steppan, 1995: chars. 13S and 56P; see also Braun, 1993: char. 22; and Pacheco, 2003: char. 39S). Rejected: metric character.

*2.3.8. *Basicranial flexion weakly pronounced, foramen magnum oriented mostly caudad (0); or strongly pronounced, foramen magnum oriented mostly posteroventrally (1)* (Carleton and Musser, 1989: char. 8). Included: #27.

2.3.9. *Skull flat or slightly convex (0); or markedly convex dorsally (1)* (Braun, 1993: char. 20). Rejected: ambiguous characterization.

2.3.10. *Lambdoidal crest square, occiput flat (0); or lambdoidal crest square, occiput rounded (1)* (Patton and Hafner, 1983: char. 10). Rejected: continuous trait.

2.4. Zygomata

*2.4.1. *Zygomatic plate narrow and zygomatic notch indistinct; anterior border of plate flat, below or slightly in front of anterior margin of antorbital bridge (0); or plate broad with moderate or deep notch; anterodorsal margin smoothly rounded, conspicuously anterior to superior maxillary root of zygoma (1); or plate broad and notch conspicuous; anterodorsal margin produced as a sharp corner or spinous process, conspicuously anterior to superior maxillary root of zygoma (2); or plate narrow and zygomatic notch absent; anterior margin of zygomatic plate conspicuously posterior to superior maxillary root of zygoma (3)* (modified from Carleton and Olson, 1999: char. 1; see also Carleton, 1980: char. 25; Olds and Anderson, 1989: chars. 29 and 31; Braun, 1993: chars. 27 and 28; Steppan, 1995: chars. 8S and 43P; Patton and Hafner, 1983: chars. 11 and 12; Carleton and Musser, 1989: char. 5; Voss, 1993: 24; Voss and Carleton, 1993: char. 6; Luna, 2002: chars. 27, 40–42; Voss et al., 2002: 18; Pacheco, 2003: chars. 21S, 22S, and 31T; Voss, 2003: 16–17). Included: #28.

*2.4.2. *Posterior margin of zygomatic plate situated anterior to the alveolus of M1 (0); or approximately even with the alveolus of M1 (1)* (Carleton and Olson, 1999: char. 2; Luna, 2002: char. 32; Pacheco, 2003: chars. 68S and 84T; see also Braun, 1993: char. 24; Steppan, 1995: chars. 6S and 42P). Included: #29.

2.4.3. *Zygomatic plate inclined $<20^\circ$ in frontal view (0); or $>20^\circ$ (1)* (Steppan, 1995: char. 44P). Rejected: continuous trait.

2.4.4. *Zygomatic plate vertical (0); or slanted backward from the base.* (Pacheco, 2003: chars. 24S and 33T). Rejected: invariant (vertical).

2.4.5. *Anterior bridge of root of zygomata lying well below dorsal surface of rostrum (one-fourth to one-half less than rostrum height, as measured from the midpoint between height of zygomatic spine and anteriormost border of orbit (0); or anterior bridge below rostrum (displaced less than one-fourth rostrum height) (1); or insertion high, close on dorsal surface of rostrum (less than one-*

eighth) or posterior surface of bridge joins at dorsal level of surface (2) (Steppan, 1995: chars. 5S and 41P; see also Luna, 2002: char. 31; Pacheco, 2003: char. 39T). Rejected: unreplicable results. Also, continuous trait.

*2.4.6. *Jugal present and large, maxillary and squamosal processes of the zygoma not overlapping (0); or jugal present and small, maxillary and squamosal processes overlapping, but not in contact (1); or jugal absent, or reduced to slivers of bones, maxillary and squamosal processes in contact (2)* (modified from Carleton and Musser, 1989: char. 7; Carleton and Olson, 1999: char. 3; Pacheco, 2003: chars. 30S, 31S, and 47T). Included: #30.

2.4.7. *Posterior extension of jugal borders glenoid fossa (0); or jugal does not approach the glenoid fossa (1)* (Pacheco, 2003: char. 32S). Rejected: invariant (jugal borders glenoid fossa).

2.4.8. *Zygomata little expanded, greatest width less than distance from posterior part of nasals to anterior border of supraoccipital (0); or zygomata well expanded, greatest width greater than or equal to distance from posterior part of nasals to anterior border of supraoccipital.* (Braun, 1993: char. 25; see also Pacheco, 2003: char. 41T). Rejected: continuous trait.

2.4.9. *Zygomatic arches parallel-sided (0); or slightly divergent posteriorly (1)* (Luna, 2002: char. 30). Rejected: continuous trait.

2.4.10. *Zygomatic plate close to skull, the plate parallel to wall of rostrum (0); or conspicuous angle separates plate from skull (1)* (Luna, 2002: char. 44). Rejected: ambiguous characterization.

2.4.11. *Zygomatic plate narrow (0); or broad (1)* (Pacheco, 2003: chars. 23S and 32T). Rejected: continuous trait.

2.4.12. *Notch between maxillary zygomatic process and lacrimal bone absent (0); or present (1)* (Pacheco, 2003: char. 37T). Rejected: invariant (absent).

2.4.13. *Squamosal roots of zygomatic arch not expanding laterally, joining braincase at oblique angle (0); or roots laterally expanded, joining the braincase more perpendicularly (1)* (Pacheco, 2003: char. 40T). Rejected: continuous trait.

2.4.14. *Zygomatic arch low, the ventral margin of arches reaches orbital floor or lower (0); or arches high, ventral margin dips to a point slightly above orbital floor (1); or arches very high, the ventral margin of the arch placed above the orbital floor by half the orbital region.* (Pacheco, 2003: char. 42T). Rejected: continuous trait.

2.4.15. *Anterior border of zygomatic plate more or less planar (0); or slightly concave (1); or concave (2); or deeply concave (3)* (Braun, 1993: char. 23). Rejected: ambiguous characterization.

2.5. Lateral Skull

2.5.1. *90–135° angle formed relative to palatine plane by the premaxillo-maxillary suture on the lateral surface of rostrum and below antorbital foramen (0); or suture nearly horizontal at ventral end, sharply angled (≤90°) in middle of rostrum.* (Steppan, 1995: char. 45P; see also Braun, 1993: char. 26; Pacheco, 2003: char. 35T). Rejected: invariant (90–135° angle).

2.5.2. *Masseteric tubercle absent (0); or present (1)* (Steppan, 1995: char. 7S; Luna, 2002: char. 33; Pacheco, 2003: chars. 25S, 26S, and 34T). Rejected: invariant (absent).

2.5.3. *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)* (Pacheco, 2003: chars. 43S and 48T). Rejected: invariant (dorsal to M2).

2.5.4. *Ethmoturbinals absent or small (0); or distinct, moderate (1); or large and inflated (2)* (Pacheco, 2003: chars. 44S and 49T). Rejected: unreplicable results.

2.5.5. *Sphenopalatine foramen absent or nearly ossified (0); or present, small to moderate size (1); or present, large (2)* (Steppan, 1995: char. 75P). Rejected: rampant intraspecific variation.

2.5.6. *Infraorbital foramen with narrow lumen (0); or lumen moderately open (1); or lumen wide (2)* (Pacheco, 2003: chars. 27S and 36T). Rejected: invariant (narrow lumen).

2.5.7. *Infraorbital fontanels absent (0); or present (1)* (Braun, 1993: char. 30). Rejected: structure not identified.

2.5.8. *Dorsal projection of alisphenoid well developed (0); or moderate (1)* (Pacheco, 2003: char. 45S). Rejected: invariant (moderate).

2.5.9. *Optic foramen moderate or large, placed dorsal to at least half the length of M3 (0); or foramen small, placed posterodorsal to M3.* (Pacheco, 2003: char. 50T). Not observed.

2.5.10. *Ventral swelling in the region of the premaxillo-maxillary suture absent (0); or present (1)* (Steppan and Pardiñas, 1998: char. 103).[14] Not observed.

2.5.11. *Nasolacrimal capsule anterior or subequal to anterior margin of zygomatic plate (0);*

[14] The first 98 characters of Steppan and Pardinãs (1998) are the same of Steppan (1995).

or well anterior to anterior margin of zygomatic plate (1); or absent (2) (Luna, 2002: char. 43). Rejected: continuous trait; also, characterization relies on another variable trait (length of zygomatic plate).

2.6. Incisive Foramina

*2.6.1. *Posterior margins of incisive foramina conspicuously projecting between first molars (0); or terminating anteriorly or at the front of first molar alveoli (1)* (modified from Carleton and Musser, 1989: char. 10; see also Patton and Hafner, 1983: char. 2; Olds and Anderson, 1989: char. 18; Voss and Carleton, 1993: char. 9; Steppan, 1995: chars. 4S and 38P; Carleton and Olson 1999: char. 7; Luna, 2002: char. 62; Pacheco, 2003: chars. 48S and 62T; Voss, 2003: 16–17). Included: #31.

2.6.2. *Separation of anterior apexes of incisive foramina <80% separation of posterior apexes (0); or separation of anterior apexes 80–100% of posterior apexes (1)* (Steppan, 1995: char. 40P). Rejected: continuous trait.

2.6.3. *Incisive foramina teardrop-shaped with lateral margins expanded posteriorly (0); or lateral margins evenly rounded (1); or lateral margins straight and parallel (2)* (Patton and Hafner, 1983: char. 1). Rejected: continuous trait.

2.6.4. *Ethmoid portion of the incisive foramina with length equal to or less than half of the incisive foramina length, and width less than the foramina width (0); or ethmoid portion with length equal to about three-fourths of the foramina length, and width less than the foramina width (1); or ethmoid portion with length encompassing the foramina total length, and width more than the foramina width (2)* (Patton and Hafner, 1983: char. 4). Rejected: continuous trait.

2.6.5. *Maxillary septum of incisive foramina length less than or equal to one-half incisive foramina length (0); or septum length one-half to four-fifths of incisive foramina (1); or length more than four-fifths incisive foramina.* (Steppan, 1995: char. 39P; Pacheco, 2003: chars. 49S and 63T). Rejected: continuous trait; also, unreplicable results.

2.6.6. *Maxillary septum of incisive foramina very narrow (0); or moderately broad (1); or very broad (2)* (Patton and Hafner, 1983: char. 3). Rejected: continuous trait.

2.6.7. *Incisive foramina broad, length/width ratio less than 3 (0); or narrow, length/width ratio equal or greater than 3 (1)* (Luna, 2002: char. 61). Rejected: metric character.

2.7. Palate

2.7.1. *Palatal breadth wide, the distance between the protocones of the first upper molar exceeds the length of the first molars (0); or palate narrow, the distance between protocones is subequal to the length of the first molar or less (1)* (Pacheco, 2003: chars. 51S and 65T; see also Braun, 1993: char. 11; Voss, 2003: 16–17). Rejected: continuous trait; in addition, the relative breadth of the palate is described in terms of another trait, the length of first molar, that is certainly variable among taxa.

*2.7.2. *Palate short, mesopterygoid fossa extends anteriorly beyond M3 (0); or palate medium, mesopterygoid fossa extends between M3 and posterior margin of the maxillary bone (1); or palate long, mesopterygoid fossa does not extend beyond posterior margin of the maxillary bone (2)* (modified from Carleton and Olson, 1999: char. 9; see also Steadman and Ray, 1982: 10; Patton and Hafner, 1983: char. 6; Carleton and Musser, 1989: char. 11 [part]; Olds and Anderson, 1989: char. 16; Voss, 1991: char. 1; Braun, 1993: char. 12; Voss, 1993: 24; Steppan, 1995: chars. 21S and 70P; Luna, 2002: char. 64; Voss et al., 2002: 18; Pacheco, 2003: chars. 50S and 64T). Included: #32.

*2.7.3. *Bony palate flat, or with shallow lateral excavations, never with median longitudinal ridge (0); or with deep lateral troughs separated by a median longitudinal ridge (1)* (modified from Carleton and Olson, 1999: char. 8; see also Steppan, 1995: char. 72P; Luna, 2002: char. 67). Included: #33.

2.7.4. *Posterior portion of bony palate either smooth or slightly thickened and bumpy (0); or medial bony mound present with slight lateral protuberances (1); or medial bony mound present with discrete bony projections extending laterally but not in contact with sides of bony palate (2); or medial bony mound present with discrete bony projection in contact or fused with sides of bony palate (3)* (Musser et al., 1998: 74). Rejected: rampant intraspecific variation.

2.7.5. *Medial process of posterior palate absent (0); or present (1)* (Steppan, 1995: char. 71P; see also Luna, 2002: char. 65; Pacheco, 2003: char. 66T). Rejected: rampant intraspecific variation.

2.7.6. *Palatine suture straight (0); or convoluted (1)* (Pacheco, 2003: char. 53S). Not observed.

2.7.7. *Maxillary palatal pits absent (0); or present in the maxillary bone (1)* (Pacheco, 2003: chars. 54S and 68T). Rejected: rampant intraspecific variation.

2.7.8. *Pair of round foramina at junction of the maxillary and palatine bones, or occasionally a pair of larger foramina accompanied by one or two minute bones (0); or pair of oblong foramina, substantially penetrating both the maxillary and palatine bones (1); or pair of larger foramina and many tiny foramina perforating hard palate (2)* (Carleton, 1980: char. 22; Braun, 1993: char. 13). Rejected: invariant (simple pair)

*2.7.9. *Posterolateral palatal pits absent (0); or one simple small foramen present at each side of the posterior palate (1); or posterolateral palatal pits always present as conspicuous perforations, usually more than one foramen, not recessed in fossae or recessed in shallow depression (2); or posterolateral palatal pits always present as perforations within deeply recessed fossa, generally with three foramina, one directed posteriorly, one anteriorly, and one dorsally (3)* (modified from Carleton, 1980: char. 21; Steadman and Ray, 1982: 10; Patton and Hafner, 1983: char. 5; Carleton and Musser, 1989: char. 11 [part]; Olds and Anderson, 1989: char. 17; Voss, 1993: 24; Carleton and Olson, 1999: char. 10; Luna, 2002: char. 68; Voss et al., 2002: 18; Pacheco, 2003: chars. 52S and 67T). Included: #34.

2.7.10. *Posterolateral palatal pits anterior to mesopterygoid fossa (0); or pits posterior to anterior border of mesopterygoid fossa (1)* (Steppan, 1995: char. 73P; Luna, 2002: char. 69). Rejected: correlated with character #34.

2.7.11. *Molar-bearing portion of maxillae low and rectangular (0); or deep with conspicuous triangular shape (1)* (Pacheco, 2003: char. 69T). Not observed.

2.7.12. *Maxillary at posterior base of M3 normal (0); or swollen (1)* (Pacheco, 2003: char. 70T). Not observed.

2.7.13. *Anterior palatine foramina not recessed or furrowed (0); or recessed in a trough or furrow (1); or deeply recessed (2)* (Braun, 1993: char. 14). Not observed.

2.8. Ventral Pterygoid Region

2.8.1. *Mesopterygoid fossa parallel sided, U-shaped (0); or posteriorly convergent, horseshoe-shaped (1); or posteriorly divergent, V-shaped (2)* (Steppan, 1995: char. 19S; see also Luna, 2002: char. 70; Pacheco, 2003: chars. 57S and 75T). Rejected: continuous trait.

2.8.2. *Posterior width of mesopterygoid fossa 1.5 times the anterior width (0); or between 1.5 and 2.4 times larger (1); or more than 2.4 times larger (2)* (Steppan, 1995: char. 66P; see also Luna, 2002: char. 71). Rejected: continuous trait.

2.8.3. *Mesopterygoid and parapterygoid fossae subequal in size (0); or mesopterygoid fossa distinctly narrower than adjacent parapterygoid fossae (1)* (Olds and Anderson, 1989: char. 20A; Steppan, 1995: chars. 18S and 64P; see also Pacheco, 2003: chars. 56S and 74T). Rejected: autapomorphy for *Peromyscus*.

*2.8.4. *Parapterygoid fossae at same level as palate (0); or parapterygoid fossae dorsally excavated but not reaching level of mesopterygoid roof (1); or parapterygoid fossae deeply excavated, reaching level of mesopterygoid roof (2)* (modified from Carleton, 1980: char. 23; Olds and Anderson, 1989: char. 20B; Braun, 1993: char. 15; Steppan, 1995: char. 67P; Carleton and Olson, 1999: char. 11 [part]; Luna, 2002: char. 73). Included: #35.

2.8.5. *Parapterygoid fossa rectangular (0); or triangular (1)* (Pacheco, 2003: chars. 58S and 72T). Rejected: ambiguous characterization.

2.8.6. *Posterior width of parapterygoid <1.5 times anterior width (0); or between 1.5 and 2.4 times (1); or >2.4 times (2)* (Steppan, 1995: char. 65P). Rejected: continuous trait.

*2.8.7. *Sphenopalatine vacuities present as large apertures along the presphenoid, reaching basisphenoid (0); or vacuities present but reduced, generally as narrow openings, anterior to basisphenoid-presphenoid suture (1); or vacuities absent, mesopterygoid roof totally ossified (2); or vacuities present but reduced, situated posterior to basisphenoid-presphenoid suture (3)* (modified from Carleton, 1980: char. 20; see also Olds and Anderson, 1989: char. 21; Steppan, 1995: chars. 20S and 68P; Patton and Hafner, 1983: char. 7; Voss, 1993: 24; Luna, 2002: char. 72; Voss et al., 2002: 18; Pacheco, 2003: chars. 55S and 71T). Included: #36.

2.8.8. *Orbital wings of presphenoid anterior to a distinct constriction of the presphenoid (0); or wings posterior to maximum constriction (1)* (Steppan, 1995: char. 69P). Rejected: unreplicable results.

2.8.9. *Bony ridges at lateral edge of parapterygoid pronounced (0); or not defined, lateral sides of parapterygoid fossae smooth (1)* (Luna, 2002: char. 75). Rejected: invariant (present).

2.8.10. *Parapterygoid vacuity absent or faint (0); or distinct (1)* (Pacheco, 2003: char. 73T). Not observed

2.9. General Basicranium

*2.9.1. *Stapedial foramen and posterior opening of alisphenoid canal large, squamosal-alisphenoid groove and sphenofrontal foramen present (0); or stapedial foramen and posterior opening of alisphenoid canal large, squamosal-*

alisphenoid groove and sphenofrontal foramen absent (1); or stapedial foramen and posterior opening of alisphenoid canal small, squamosal-alisphenoid groove and sphenofrontal foramen absent, secondary branch crosses dorsal surface of pterygoid plate (2) (Carleton, 1980: char. 16; Voss, 1988: char. 12; Carleton and Musser, 1989: char. 13; Voss, 1993: 24; Voss and Carleton, 1993: char. 11; Steppan, 1995: chars. 22S and 76P; Musser et al., 1998: 321; Carleton and Olson, 1999: char. 14; Luna, 2002: chars. 47, 48, 74, and 78; Voss et al., 2002: 18; Pacheco, 2003: chars. 34S and 52T; Voss, 2003: 16–17). Included: #37.

*2.9.2. *Alisphenoid strut present, buccinator-masticatory and accessory foramen ovale separate (0); or strut absent, buccinator-masticatory and foramen ovale confluent (1)* (Carleton, 1980: char. 17; Musser and Williams, 1985: 19; Voss, 1991: char. 2; Voss, 1993: 24; Voss and Carleton, 1993: char. 10; Steppan, 1995: chars. 23S and 78P; Musser et al., 1998: 321; Carleton and Olson, 1999: char. 13; Luna, 2002: char. 45; Pacheco, 2003: chars. 33S and 51T; Voss, 2003: 16–17). Included: #38.

*2.9.3. *Anterior opening of alisphenoid canal present, large (0); or absent (1)* Included: #39. See also Patton and da Silva (1995: 323).

2.9.4. *Foramen ovale larger than medial lacerate foramen (0); or foramina subequal in size (1); or foramen ovale smaller than medial lacerate foramen (2)* (Patton and Hafner, 1983: char. 8; see also Luna, 2002: char. 63). Rejected: rampant intraspecific variation; also, continuous trait.

2.9.5. *Postglenoid foramen absent (0); or present, small (1); or present, large (2)* (Carleton, 1980: char. 18; Luna, 2002: char. 55). Rejected: plesiomorphic condition found only in *Nyctomys*.

*2.9.6. *Subsquamosal fenestra present (0); or fenestra vestigial or absent (1)* (modified from Carleton, 1980: char. 19; Steppan, 1995: chars. 17S and 61P; Luna, 2002: chars. 54 and 56; Pacheco, 2003: chars. 41S and 56T [part]). Included: #40.

2.9.7. *Subsquamosal fenestra level with squamosal root of zygomatic arch (0); or fenestra placed distinctly below the squamosal root of the zygomatic arch.* (Pacheco, 2003: char. 57T). Not observed.

2.9.8. *Hamular process absent (i.e., subsquamosal fenestra absent) (0); or process broad along entire length, subsquamosal fenestra often reduced (1); or bridge reduced in thickness, posterior terminus appears flattened (2); or posterior end reduced as well, not greatly thicker than bridge (3)* (Steppan, 1995: char. 60P; see also Luna, 2002: chars. 50 and 53; Pacheco, 2003: chars. 42S and 56T [part]). Rejected: correlated with character #43.

2.9.9. *Hamular process attached to mastoid tubercle and part of anterior lamina of petrosal (0); or attached to periotic and mastoid tubercle, and part of anterior lamina of petrosal (1); or attached to periotic only (2)* (Luna, 2002: char. 51). Not observed.

2.9.10. *Petromastoid bony tube for the stapedial artery present (0); or absent (1)* (Pacheco, 2003: char. 66S). Rejected: invariant (present).

2.9.11. *Tentorium cerebellum present as crest of low relief (0); or present as a small, thin flange (1); or present as a large, broad lamina (2)* (Carleton, 1980: char. 34). Rejected: invariant (present).

2.9.12. *Hypoglossal foramen level with or anterior to the paraoccipital process (0); or posterior to the paraoccipital process (1)* (Pacheco, 2003: char. 59S). Rejected: invariant (level).

2.9.13. *Squamosal absent (0); or present (1)* (Steppan, 1995: char. 16S). Rejected: autapomorphy for *Nyctomys*.

2.9.14. *Internal carotid artery not exposed (0); or exposed.* (Pacheco, 2003: char. 53T). Rejected: invariant (not exposed).

2.9.15. *Alisphenoid squamosal posterior margin without notch (0); or notch present (1)* (Pacheco, 2003: char. 76T). Rejected: invariant (notch absent).

2.9.16. *Foramen ovale accessory not visible in ventral view (0); or almost completely visible from ventral view (1)* (Luna, 2002: char. 76). Rejected: invariant (not visible).

2.10. Bullae

*2.10.1. *Ectotympanic bullae small, exposed flange of periotic extends to internal carotid canal (0); or ectotympanic bullae intermediate, exposed wedge of periotic smaller and not contributing to wall of carotid canal (1); or ectotympanic bullae large, periotic bone mostly masked in ventral view (2)* (Carleton and Olson, 1999: char. 12; see also Carleton and Musser, 1989: char. 12; Steppan 1995: char. 62P; Luna, 2002: char. 66; Pacheco, 2003: char. 77T). Included: #41.

2.10.2. *Inflation of tympanic bullae (i.e.,(length × depth of bulla)/total length of skull) less than 48% (0); or between 49 and 61% (1); or between 62 and 80% (2); or greater than 80% (3)* (Carleton, 1980: char. 33; see also Braun, 1993: char. 16; Voss, 2003: 16–17). Rejected: metric character.

2.10.3. *Orientation of anterior border of auditory bulla oblique when viewed ventrally (0); or transverse (1); or rounded (2)* (Steppan, 1995: char. 57P). Rejected: continuous trait.

2.10.4. *Stapedial spine of auditory bulla circular to ovoid in cross section (0); or laterally appressed against auditory bulla, not smoothly rounded in cross section (1)* (Steppan, 1995: char. 59P; see also Luna, 2002: char. 58; Pacheco, 2003: char. 78T). Rejected: invariant (circular to ovoid).

2.10.5. *Eustachian tube does not reach posterior lobe of pterygoid process (0); or tube subequal to posterior lobe of pterygoid process, does not extend anterior to the base of process (1); or tube extends anteriorly past base of pterygoid process (2)* (Steppan, 1995: char. 63P; see also Luna, 2002: char. 79). Rejected: unreplicable results.

2.10.6. *Dorsal aperture of ectotympanic ring loosed (0); or open (1)* (Pacheco, 2003: chars. 46S and 60T; see also Luna, 2002: char. 52). Rejected: rampant intraspecific variation.

*2.10.7. *Posterior suspensory process of squamosal present and connected to the tegmen tympani (0); or posterior suspensory process absent, tegmen tympani not touching or barely in contact with squamosal (1)* (Voss, 1993: 24; Voss and Carleton, 1993: char. 12; Steppan, 1995: chars. 15S and 58P; Luna, 2002: char. 49; Voss et al., 2002: 18; Pacheco, 2003: chars. 36S and 54T). Included: #42.

2.10.8. *Mastoid bullae small, unmodified (0); or moderately inflated (1); or large, greatly inflated (2)* (Carleton, 1980: char. 32). Rejected: invariant (small mastoid bullae).

*2.10.9. *Mastoid completely ossified, or with diminutive pit in the dorsal contact with the exoccipital border (0); mastoid with conspicuous fenestra (1)* (modified from Patton and Hafner, 1983: char. 9; Luna, 2002: char. 59). Included: #43.

2.10.10. *Supraoccipital process long (0); or short (1)* (Pacheco, 2003: char. 47S). Rejected: invariant (long).

2.10.11. *Sinus groove present on tegmen tympani (0); or absent (1)* (Pacheco, 2003: char. 55T; see also Luna, 2002: char. 57). Rejected: correlated with character #42.

2.10.12. *Ectotympanic not expanded laterally (0); or distinctly expanded laterally (1)* (Pacheco, 2003: char. 61T). Rejected: autapomorphy for *Wiedomys* (see Pacheco, 2003).

2.11. Auditory Apparatus

2.11.1. *Malleus and incus exposed in lateral view (0); or largely concealed (1)* (Luna, 2002: char. 60; Pacheco, 2003: char. 61S) Rejected: invariant (exposed).

2.11.2. *Accessory tympanum absent, anterior and posterior lamina complete (0); or present, small, only anterior lamina eroded (1); or present and large (2)* (Carleton, 1980: char. 31). Rejected: invariant (present and large).

2.11.3. *Malleus perpendicular (0); or parallel (1)* (Carleton, 1980: char. 30; see also Pacheco, 2003: char. 63S). Rejected: invariant (parallel).

2.11.4. *Cephalic process of malleus exhibits a thin but distinct crest that continues to the crest of the cephalic peduncle of malleus (0); or cephalic process lacks a crest, but crest present in the cephalic peduncle of malleus (1)* (Pacheco, 2003: char. 65S). Not observed.

2.11.5. *Orbicular apophysis of malleus present, as bony knob or spur (0); or absent (1)* (Voss, 1988: char. 13; Pacheco, 2003: char. 62S). Rejected: invariant (present).

2.11.6. *Processus brevis of incus with base thick, usually short, tip pointed or knoblike, more robust in appearance (0); or base narrow, usually long and tapering to a pointed tip, delicate in appearance (1)* (Pacheco, 2003: chars. 64S and 81T). Rejected: continuous trait.

2.11.7. *Malleus lamina broad, squarelike (0); or narrow, rectangular shape (1)* (Pacheco, 2003: char. 79T). Rejected: ambiguous characterization.

2.11.8. *Ventral margin of malleus lamina shallow (0); or with a distinct deep ridge and fossa (1)* (Pacheco, 2003: char. 80T). Rejected: invariant (shallow).

2.12. Jaw

2.12.1. *Mandible with a cricetine morphotype (0); or New World muroid morphotype (1)* (Pacheco, 2003: char. 88S) Rejected: invariant (New World morphotype).

2.12.2. *Mandibular ramus shallow, leading edge of ascending ramus oriented more obliquely, sigmoid notch straight and shallow (0); or mandibular ramus deep, leading edge of ascending ramus oriented more vertically, sigmoid notch rounded and deep (1)* (Carleton and Olson, 1999: char. 16). Rejected: unreplicable results.

2.12.3. *Coronoid process above maximum height of mandibular condyle (0); or subequal (1); or below mandibular condyle (2)* (Steppan, 1995: char. 34P; see also Luna, 2002: char. 80; Pacheco, 2003: char. 120T). Rejected: continuous trait.

2.12.4. *Condylar process level with angular process (0); or condylar process extending*

posteriorly beyond the angular process (1) (Luna, 2002: char. 82; Pacheco, 2003: char. 119T). Rejected: continuous trait.

2.12.5. *Angular process of dentary directed posteriorly in the same plane as the ascending ramus (0); or directed laterally away from plane of the ascending ramus (1)* (Carleton, 1980: char. 28). Rejected: invariant (directed posteriorly).

2.12.6. *Medioventral process of mandibular ramus absent, ramus rounded when viewed ventrally or not sharply angled (0); or process weakly present, or ramus sharply angled, near 90° (1); or process distinct (2)* (Steppan, 1995: char. 36P; Luna, 2002: char. 87). Rejected: structure not identified.

*2.12.7. *Mental foramen opens laterally, at body of mandible (0); or mental foramen opens dorsally, at the diastema (1)* Included: #44. See also Pacheco (2003: chars. 90S and 116T).

*2.12.8. *Capsular process of lower incisor alveolus absent (0); or projection present but reduced as a slight rounded elevation (1); or projection present, well developed as a conspicuous swelling with acute projection (2)* (modified from Voss, 1991: 26–27; Voss and Carleton, 1993: 17–18; see also Braun, 1993: char. 31; Voss, 1993: 19; Steppan, 1995: char. 33P; Luna, 2002: char. 84; Voss et al., 2002: 18; Pacheco, 2003: chars. 91S and 118T; Voss, 2003: 16–17). Included: #45.

*2.12.9. *Superior and inferior masseteric ridges converge anteriorly as an open chevron (0); or anterior portion of ridges conjoined as single crest (1)* (Voss and Carleton, 1993: 18–19; Carleton and Olson, 1999: char. 15; see also Steppan 1995: char. 35P; Luna, 2002: char. 86). Included: #46.

*2.12.10. *Anterior edge below m1 (0); or edge anterior to m1, extending to diastema (1)* (Pacheco, 2003: chars. 89S and 115T). Included: #47.

2.12.11. *Retromolar region shallow, as a groove (0); or present, deep in a fossa (1)* (Luna, 2002: char. 85; Pacheco, 2003: chars. 92S and 121T). Not observed.

2.12.12. *First lower molar alveolus and diastema form a straight and acute angle (0); or angle is obtuse, more open (1); or angle is very obtuse, much closer to horizontal (2)* (Pacheco, 2003: char. 117T). Not observed.

2.12.13. *Ventral margin of mandible slightly concave (0); or conspicuously horizontal (1)* (Pacheco, 2003: char. 122T). Not observed.

2.12.14. *Angular notch shallow (0); or deep (1)* (Luna, 2002: chars. 81 and 83). Rejected: continuous trait.

2.13. Hyoid

*2.13.1. *Entoglossal process of basihyal present as small knob, basihyal arched, and thyrohyal long, greater than or equal to the length of the basihyal (0); or entoglossal process absent, basihyal straight, and thyrohyal short, less than length of basihyal (1)* (Carleton, 1980: char. 29; Pacheco, 2003: char. 60S). Included: #48.

3. Dentition

3.1. Molar Roots

*3.1.1. *Labial accessory root of M1 absent (0); or present (1)* (Carleton, 1980: char. 9; Carleton and Musser, 1989, char. 19 [part]; Voss, 1991: char. 6; Voss and Carleton, 1993: char. 22; Steppan, 1995: chars. 4P and 5P; Carleton and Olson, 1999: char. 32; Pacheco, 2003: chars. 85S and 111T) Included: #49.

3.1.2. *Single large lingual root on upper first molar (0); or intermediate lingual root (1); or two roots present (2); or rootless, ever-growing teeth (3)* (Carleton, 1980: char. 8; Pacheco, 2003: chars. 86S and 112T). Rejected: invariant (single large root).

3.1.3. *Upper second molar with single, large, lingual root (0); or with intermediate root (1); or two roots (2); or rootless, ever-growing teeth (3)* (Carleton, 1980: char. 10). Rejected: invariant (single large root).

3.1.4. *Upper third molar with three roots (0); or two roots (1); or one root (2); or rootless, ever-growing teeth (3)* (Carleton, 1980: char. 11; Steppan, 1995: char. 6P; Pacheco, 2003: char. 113T). Rejected: invariant (three roots).

*3.1.5. *Labial and lingual accessory roots of m1 absent (m1 with two roots total) (0); or only labial accessory root present (three roots total) (1); or labial and lingual roots present (four roots total) (2)* (Carleton, 1980: chars. 12 and 13; Carleton and Musser, 1989, char. 19 [part]; Voss, 1991: char. 7; Voss and Carleton, 1993; char. 23; Steppan, 1995, char. 7P; Carleton and Olson, 1999, char. 33). Included: #50.

*3.1.6. *m2 with 2 roots(0); or 3 roots(1)* (Carleton, 1980: char. 14; Steppan, 1995: char. 8P; Pacheco, 2003: chars. 87S and 114T). Included: #51.

3.1.7. *m3 with 2 roots (0); or 3 roots (1)* (Carleton, 1980: char. 15; Steppan, 1995: char. 9P). Rejected: correlated with character #51.

3.2. Incisors

*3.2.1. *Incisors opisthodont (0); or orthodont (1)* (modified from Voss, 1993: 24; Braun,

1993: char. 33; Steppan, 1995: char. 2P; Luna, 2002: char. 88; Pacheco, 2003: chars. 67S and 82T; Voss, 2003: 16–17). Included: #52.

3.2.2. *Upper incisor with straight internal dentine fissure (0); or dentine fissure curved at the anterior end in lingual direction, comma-shaped (1); or dentine fissure tripartite, Y-shaped (2)* (Steppan, 1995: char. 3P; Luna, 2002: char. 88). Rejected: unreplicable results (all looked the same).

*3.2.3. *Enamel band of upper incisors smoothly rounded, or flattened but without labial bevel (0); or band flattened medially, with distinct labial bevel (1)* (Voss and Carleton 1993: char. 13; Carleton and Olson, 1999: char. 17). Included: #53.

3.2.4. *Grooves on upper incisors absent (0); or fine striae present (1); or one mediolateral shallow groove (2); or one mediolateral groove and one small shallow groove on midline (3); or one involuted groove on lateral corner (4)* (Steppan, 1995: char. 1P; see also Carleton, 1980: char. 7; Braun, 1993: char. 32; Luna, 2002: char. 90). Rejected: invariant (absent).

3.2.5. *Upper incisors not flexed inwardly toward midline (0); or incisors flexed toward midline (2)* (Braun, 1993: char. 34). Rejected: ambiguous characterization.

3.2.6. *Wear surface of incisors more-or-less flat, facing backward (0); or wear surface of incisors oriented medially (1)* (Pacheco, 2003: char. 83T). Rejected: invariant (flat).

3.3. Upper Molars

*3.3.1. *Molars bunodont and brachydont (0); or molars planar and hypsodont (1)* (modified from Carleton, 1980: char. 4; Braun, 1993: char. 39; Carleton and Musser, 1989: char. 5; Voss and Carleton, 1993: char. 14; Carleton and Olson, 1999: char. 18; Pacheco, 2003: chars. 76S and 85T; Voss, 2003: 16–17). Included: #54.

*3.3.2. *Labial flexi not patent, closed off by labial cingula (0); or labial flexi patent, cingula absent (1)* Included: #55. See also Luna (2002: char. 101) and Pacheco (2003: char. 74S).

3.3.3. *Principal cusps of upper molars arranged in opposite labial-lingual pairs (0); or alternating in anteroposterior position (1)* (Voss, 1991: char. 3; Voss and Carleton, 1993: char. 15 [part]; Carleton and Olson, 1999: char. 19 [part]). Rejected: continuous trait.

*3.3.4. *Maxillary toothrows parallel (0); or anteriorly convergent (1)* (Steppan, 1995: char. 74P; see also Braun, 1993: char. 35; Luna, 2002: char. 77). Included: #56.

*3.3.5. *Flexi of M1 and M2 do not interpenetrate (0); or flexi meet at midline, enamel overlaps (1); or flexi interpenetrate (2)* (Steppan, 1995: char. 13P; see also Voss, 1993: 24; Luna, 2002: chars. 92 and 93; Voss et al., 2002: 18; Pacheco, 2003: chars. 77S and 86T). Included: #57.

3.3.6. *Ratio of toothrow length/ skull length* (Braun, 1993: char. 36). Rejected: metric character.

3.3.7. *Size of teeth relative to size of entire skull large (0); or intermediate (1); or small (2)* (Steadman and Ray, 1982: 10). Rejected: ambiguous characterization.

3.3.8. *Molars crested (0); planar or slightly terraced (1)* (Braun, 1993: char. 38). Rejected: correlated with character #52.

3.3.9. *Major and primary folds of upper molars not compressed anteroposteriorly (0); or compressed (1)* (Braun, 1993: char. 40). Not observed.

3.3.10. *Index of molar complexity (score based on presence/absence of several features such as mesoloph, anteroloph, enteroloph)* (Carleton: 1980: char. 1). Rejected: not applicable (each feature was scored separately).

3.4. M1 and M2

*3.4.1. *Anterocone of M1 divided into labial and lingual conules by anteromedian flexus (0); or anterocone partially divided into labial and lingual conules by internal fold of procingulum, anteromedian flexus absent (1); or anterocone undivided, anteromedian flexus and internal fold of procingulum absent (2)* (modified from Carleton, 1980, char. 2; Carleton and Musser, 1989: char. 15 [part]; Braun, 1993: char. 41; Voss, 1993: 24; Steppan, 1995: char. 10P; Carleton and Olson, 1999: char. 20; Luna, 2002: char. 94; Voss et al., 2002: 18; Pacheco, 2003: chars. 69S and 87T;). Included: #58.

3.4.2. *Anterolabial and anterolingual conules subequal (0); or anterolingual conule distinctly reduced, about half size or less of the anterolabial conule (1)* (Pacheco, 2003: chars. 70S and 88T; see also Carleton and Musser, 1989: char. 15 [part]; Luna, 2002: char. 95). Rejected: autapomorphy for *Wiedomys*. Note: A reduced anterolingual conule is observed in other taxa (e.g., *Microryzomys*; cf. Carleton and Musser, 1989), but only *Wiedomys* displays an extreme reduction of that structure; remaining taxa have a gradient of sizes.

*3.4.3. *Anteroloph on M1 well developed and discrete, reaching the labial cingulum, anteroflexus present (0); or anteroloph present but small, not reaching the labial cingulum, anteroflexus absent (1); or anteroloph fused with anterocone labially, anteroflexus present as small*

fossette (2); or anteroloph and anteroflexus absent (3) (modified from Voss and Carleton, 1993: char. 18; Steppan, 1995: char. 12P; Carleton and Olson, 1999: char. 23; Pacheco, 2003: chars. 90T–92T). Included: #59.

*3.4.4. *Protostyle on M1 absent (0); or present (1)* Included: #60. See also Pacheco (2003: char. 96T).

*3.4.5. *Paracone of M1 connected to protocone by enamel bridge situated at posteriormost end of protocone (0); or paracone connected to protocone by enamel bridge situated at anterior portion of protocone (1); or protocone and paracone forming single dentine basin without enamel connection (2)* Included: #61.

3.4.6. *Metaloph on M1 and M2 absent (0); present (1)* (Pacheco: 2003: char. 71S). Rejected: invariant (absent).

*3.4.7. *Mesolophs on M1 and M2 well developed, extending from the median mure to the labial cingulum, fused with mesostyle (0); or mesolophs small, not extending to labial cingulum and not fused with the mesostyle (1); or mesolophs on M1 and M2 absent (2)* (Voss and Carleton, 1993: char. 16; see also Olds and Anderson, 1989: char. 32; Voss, 1991: char. 5; Steppan, 1995: char. 1P; Carleton and Olson, 1999: char. 30; Luna, 2002: chars. 91, 96, and 97; Pacheco, 2003: char. 72S). Included: #62.

3.4.8. *Paralophule on M1 absent (0); or present (1)* (Luna, 2002: char. 102). Rejected: invariant (absent).

3.4.9. *Posteroloph on M1 and M2 present (0); or absent (1)* (modified from Carleton and Olson, 1999: char. 24; Luna, 2002: char. 100). Rejected: invariant (present).

*3.4.10. *Median mure connected to protocone on M1 (0); or median mure not connected to protocone (1)* Included: #63.

*3.4.11. *Protoflexus of M2 present (0); or absent (1)* (Voss and Carleton, 1993: char. 19; Carleton and Olson, 1999: char. 25; see also Steppan, 1995: char. 21P; Pacheco, 2003: chars. 75S and 97T). Included: #64.

*3.4.12. *Paracone on M2 without accessory loph (0); or accessory loph present posterior to paracone (1)* Included: #65.

*3.4.13. *Mesoflexus present as single internal labial fossette on M2 (0); or mesoflexus divided into labial and medial fossetti (1)* (Musser and William, 1985: 19; Musser et al., 1998: 321). Included: #66.

3.4.14. *Enteroloph and enterostyle on M1 and M2 absent (0); or only enterostyle present (1); or both enteroloph and enterostyle present (2)* (Luna, 2002: char. 103). Rejected: invariant (both absent).

3.4.15. *Procingulum anterior edge of M1 without additional edge (0); or with additional edge accompanied by an accessory lophule (1)* (Pacheco, 2003: char. 89T). Rejected: rampant intraspecific variation.

3.4.16. *Paraloph on M1 oriented perpendicularly to 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)* (Pacheco, 2003: char. 93T). Rejected: not applicable (paraloph absent; paracone?).

3.4.17. *Hypoflexus on M1 narrow (0); or broad (1)* (Pacheco, 2003: char. 94T). Rejected: ambiguous characterization.

3.4.18. *Hypoflexus width similar to mesoflexus on M2 (0); or distinctly narrower than mesoflexus (1)* (Pacheco, 2003: char. 95T). Not observed.

3.4.19. *Mesostyle on M1 present (0); or absent (1)* (Steppan, 1995: char. 11P). Rejected: correlated with character #62.

3.4.20. *Paraflexus on M2 well developed (0); or reduced (1); or absent (2)* (Steppan and Pardiñas, 1998: char. 99). Rejected: invariant (well developed)

3.4.21. *Hypoflexus on M2 oblique, directed toward the paraflexus (0); or transverse (1)* (Steppan and Pardiñas, 1998: char. 100). Not observed.

3.4.22. *Anteroloph on M2 present (0); or absent or vestigial (1)* (Braun, 1993: char. 43). Rejected: invariant (present).

3.4.23. *Second upper molar width <0.91 length (0); or width >0.91 length (1)* (Steppan, 1995: char. 3S). Rejected: continuous trait.

3.5. M3

*3.5.1. *Mesoloph on M3 present and well developed (0); or absent or vestigial (1)* (Voss and Carleton, 1993: char. 17; Carleton and Olson, 1999: char. 22; Pacheco, 2003: char. 73S). Included: #67.

*3.5.2. *Posteroloph on M3 present (0); or absent (1)* Included: #68.

3.5.3. *Metacone of M3 tuberculate (0); or shallow (1)* (Pacheco, 2003: char. 84S). Rejected: autapomorphy for *Nyctomys*.

*3.5.4. *Hypoflexus on M3 present, remaining excavated until later wear stages (0); or hypoflexus absent or diminutive, disappearing with little occlusal wear (1)* (modified from Steppan, 1995: chars. 23P and 26P; Pacheco, 2003: char. 98T). Included: #69.

3.5.5. *No rotation of hypoflexus and mesoflexus axes of M3 relative to M2 (0); or axes rotated relative to M2 (1)* (Steppan, 1995: char. 27P). Rejected: continuous trait.

3.5.6. *No reduction of mesoflexus on M3 relative to M2 (0); or reduced relative to M2 (1); or highly reduced relative to M2, to absent (2)* (Steppan, 1995: char. 24P). Rejected: continuous trait.

3.5.7. *No posterior shift of mesoflexus on M3 relative to M2 (0); or posterior shift relative to M2 (1)* (Steppan, 1995: char. 25P). Rejected: continuous trait.

3.5.8. *Anteroloph on M3 moderately or well developed (0); or reduced (1); or absent or vestigial (2)* (Braun, 1993: char. 44). Rejected: invariant (present).

3.5.9. *Upper and lower third molars subequal in size to second molars, principal coronal features of posterior half of third molars recognizable (0); or noticeably smaller than second molars, posterior half of third molars more reduced.* (Carleton and Musser, 1989: char. 18; also Carleton and Olson, 1999: char. 34). Rejected: continuous trait.

3.5.10. *Third upper molar length <0.63 length M2 (0); or between 0.63 and 0.96 (1); or >0.96 length M2 (2)* (Steppan, 1995: char. 2S; see also Olds and Anderson, 1989: char. 41). Rejected: continuous trait.

3.5.11. *Third upper molar length <0.205 alveolar length of molar toothrow (0); or between 0.205 and 0.25 (1); or >0.25 (2)* (Steppan, 1995: char. 32P; see also Braun, 1993: char. 37). Rejected: continuous trait.

3.5.12. *Second secondary fold (= posteroflexus) of M3 present and well developed (0); or present as an enamel island or confluent with second primary fold (= metaflexus) (1); or absent or obsolete (2)* (Braun, 1993: char. 45). Rejected: correlated with character #68.

3.5.13. *Second minor fold of M3 present and well developed (0); or present as a notch (1); or absent (2)* (Braun, 1993: char. 46). Rejected: not applicable.

3.6. m1

3.6.1. *Primary cusps on m1 opposite in position (0); or cusps intermediate (1); or opposite (2)* (Carleton, 1980: char. 3; Voss, 1991: char. 4; Steppan, 1995: char. 16P; Pacheco, 2003: char. 78S). Rejected: continuous trait.

*3.6.2. *Anteromedian flexid and anteromedian fossettid absent on first lower molar (0); or anteromedian flexid absent but anteromedian fossettid present (1); or anteromedian flexid present and anteromedian fossettid absent (2)* (modified from Voss and Carleton, 1993: char. 20; Steppan, 1995: char. 17P; Carleton and Olson; 1999: char. 26; Luna, 2002: char. 88; Pacheco, 2003: chars. 81S, 99T, and 100T). Included: #70.

*3.6.3. *Anterolabial cingulum on m1 absent (0); or long anterolabial cingulum present (1)* (Steppan, 1995: chars. 14P and 15P; see also Luna, 2002: char. 98; Pacheco, 2003: chars. 79S and 102T). Included: #71.

3.6.4. *Procingulum on m1 attached by anterior murid (0); or procingulum separated, murid cut by opposing flexids (1)* (Steppan, 1995: char. 18P). Rejected: invariant (attached).

*3.6.5. *Ectolophid and ectostylid on m1 absent (0); or present (1)* (Voss, 1993: 24; Luna, 2002: char. 104; Pacheco, 2003: char. 101T). Included: #72.

3.6.6. *Metaflexid on m1 appressed (0); or open (1)* (Pacheco, 2003: char. 80S). Not observed.

*3.6.7. *Mesolophids present and well developed on m1 and m2 (0); or mesolophids present in unworn dentition but small, not extending to lingual cingulum (1); or mesolophids completely absent (2)* (Voss and Carleton, 1993: char. 21; Carleton and Olson, 1999: char. 27; see also Pacheco, 2003: chars. 83S and 105T). Included: #73.

3.6.8. *Posterolophid on m1 clearly defined as a discrete entity from the hypoconid (0); or boundaries of the posterolophid and hypoconid indistinct, the two continuous as a broad loph across the rear margin of the tooth (1)* (Carleton and Olson, 1999: char. 28). Rejected: unidentifiable states.

3.6.9. *Metalophid anteromedially oriented to the murid on m1 (0); or metalophid with double connections, one oriented anteromedially to the murid and the other oriented anteroposteriorly (1); or a metalophid anteroposteriorly oriented that closes the anterolingual cingulum (2)* (Pacheco, 2003: char. 103T). Not observed.

3.6.10. *Entolophid perpendicularly oriented to the murid on m1–m2 (0); or anteromedially oriented to the mesolophid-murid angle or the base of mesolophid (1); or oriented to the mesolophid (2)* (Pacheco, 2003: char. 104T). Not observed.

3.6.11. *Posteroflexid narrow and oblique on m1–m2 (0); or broad and semicircular (1)* (Pacheco, 2003: char. 108T). Not observed.

3.6.12. *Molar flexus (flexids) not crenellated (0); or crenellated (1)* (Pacheco, 2003: char. 110T). Rejected: invariant (not crenellated).

3.6.13. *Posterolophid/posterostylid on m1 absent (0); or intermediate, posteroflexid*

present as groove, or obvious in juvenile, absent with strong wear (1); or distinct at all ages. (Steppan, 1995: char. 19P). Rejected: invariant (present).

3.6.14. *Procingulum of m1 with no torsion (0); or moderate torsion (1); or strong torsion (2)* (Steppan and Pardiñas, 1998: char. 101) Not observed.

3.7. m2 and m3

*3.7.1. *Anterolabial cingulum present on m2 (0); or absent (1)* (Steppan, 1995: char. 22P; Pacheco, 2003: char. 107T). Included: #74.

3.7.2. *Hypoflexid on m2 short (0); or elongate (1)* (Musser et al., 1998: 169) Rejected: correlated with character #66.

*3.7.3. *Anterolophid absent or weakly expressed on m2 and m3 (0); or anterolophid and companion metaflexid distinct (1)* (Carleton and Musser, 1989: char. 16). Included: #75.

3.7.4. *Lower m2 posteroflexid and m3 entoflexid open to lingual margin of tooth (0); or lingual folds isolated as enamel islands on m2 (posterofossettid) and m3 (entofossettid), respectively (1)* (Carleton and Olson, 1999: char. 31). Rejected: unidentifiable states.

*3.7.5. *Anterolabial margin of m3 with shelflike cingulum, separated from protoconid by protoflexid (0); or anterolabial margin of m3 smoothly rounded, without cingulum, protoflexid absent (1)* (Carleton and Musser, 1989: char. 17; Carleton and Olson, 1999: char. 29). Included: #76.

*3.7.6. *Posteroflexid on m3 present, well developed (0); or posteroflexid present as a small groove, obvious only in juveniles, obliterated with wear (1); or posteroflexid absent (2)* (modified from Steppan, 1995: char. 20P; Pacheco, 2003: char. 82S). Included: #77.

3.7.7. *Opposing flexi on m3 do not meet (0); or flexi meet, median mure cut (1)* (Steppan, 1995: char. 31P). Rejected: invariant (do not meet).

3.7.8. *Mesoflexid on m3 not reduced relative to m2 (0); or reduced relative to m2 (1); or highly reduced relative to m2, to absent (2)* (Steppan, 1995: char. 28P; also Carleton, 1980: char. 5 [part]). Rejected: continuous trait.

3.7.9. *Mesoflexid on m3 no shifted relative to m2 (0); or anterior shift relative to m2 (1)* (Steppan, 1995: char. 29P; see also Carleton, 1980: char. 5 [part]). Rejected: continuous trait.

3.7.10. *Hypoflexid on m3 not shifted relative to m2 (0); or posterior shift relative to m2 (1)* (Steppan, 1995: char. 30P; see also Carleton, 1980: char. 5 [part]). Rejected: continuous trait.

3.7.11. *Lower third molar shorter than second molars, reduction principally evident in posterior half such that serial enamel homologies may be obscured (0); or m3 subequal in size to second molars, principal coronal features of posterior half of third molars recognizable (1); or m3 longer than second molars (2)* (Carleton and Olson, 1999: char. 35; see also Steppan and Pardiñas, 1998: char. 102). Rejected: continuous trait.

3.7.12. *Entoconid on m3 absent (0); or present (1)* (Pacheco, 2003: char. 109T). Rejected: invariant (absent).

3.7.13. *Mesolophid on m3 conspicuous (0); or indistinct (1)* (Pacheco, 2003: char. 106T). Rejected: rampant intraspecific variability.

3.7.14. *Ratio of lower third molar to length of molar row >30% (0); or between 29 and 24% (1); or <23% (2)* (Carleton, 1980: char. 6). Rejected: metric character.

3.7.15. *m3 with two distinct enameled lobes, the entoconid-hypoconid cusp pair comprising a large posterior moiety of the tooth (0); or m3 a simple peglike tooth, the entoconid-hypoconid cusp pair absent or reduced to a small conule (1)* (Voss, 1988: char. 9). Rejected: invariant (entoconid-hypoconid present).

4. Postcranial Skeleton

4.1. Ribs and Vertebrae

*4.1.1. *13 ribs (0); or 12 ribs (1)* (Steppan, 1995: char. 79P; see also Carleton, 1980: char. 36; Voss, 1993: 24; Steppan, 1995: char. 26S; Voss et al., 2002: 18; Pacheco, 2003: chars. 96S and 124T). Included: #78.

4.1.2. *Neural spine of second cervical vertebra (C2) not significantly enlarged (0); or enlarged, distinct knob (1); or very enlarged into distinct keel, plow-shaped, may overlap C3 (2)* (Steppan, 1995: char. 82P). Rejected: invariant (not significantly enlarged).

4.1.3. *Neural spine of second cervical vertebra (C2) does not overlap C3 (0); or does overlap C3 (excluding situation where height is very enlarged) (1)* (Steppan, 1995: char. 83P). Rejected: invariant (does not overlap).

*4.1.4. *Tuberculum of first rib articulates with transverse process of first thoracic vertebra only (0); or first rib contacts transverse processes of both the first thoracic and seventh cervical vertebrae (1)* (Carleton, 1980: char. 39; Steppan, 1995: char. 25S; Pacheco, 2003: char. 95S). Included: #79.

4.1.5. *Spine on second thoracic vertebra present (0); or absent (1)* (Carleton, 1980: char. 38). Rejected: invariant (present).

4.1.6. *Neural spine on second thoracic vertebra (T2) at least twice as long as nearby spines (0); or spine short on T2, longer on T3 (1)* (Steppan, 1995: char. 81P). Rejected: invariant (T2 have longest spine).

*4.1.7. *Anapophyses present on the 17th thoracico-lumbar vertebra (0); or anapophyses absent or vestigial (1)* Included: #80.

*4.1.8. *Hemal arches absent between caudal vertebrae 2 and 3 (0); or hemal arches present, with simple posterior border (1); or present, with spinous posterior border (2)* (Steppan, 1995: char. 28S; Pacheco, 2003: chars. 98S, 99S, and 126T). Included: #81.

4.1.9. *Number of caudal vertebrae: 21–25 (0); or 26–30 (1); or 31–35 (2); or 36–40 (3)* (Carleton, 1980: char. 37; Steppan, 1995: chars. 27S and 80P; Pacheco, 2003: chars. 97S and 125). Rejected: continuous trait.

4.2. Limbs

4.2.1. *Third scapular fossa absent (0); or present (1)* (Carleton, 1980: char. 41). Rejected: invariant (absent).

*4.2.2. *Entepicondylar foramen of humerus present (0); or absent (1)* (Carleton, 1980: char. 35; Steppan, 1995: char. 29S; Pacheco, 2003: char. 93S). Included: #82. Note: states are inverted in Steppan's matrix.

*4.2.3. *Supratrochlear foramen in humerus absent (0); or present (1)* (Steppan, 1995: char. 30S; Pacheco, 2003: chars. 94S and 123T). Included: #83.

4.2.4. *Distance from condyle of humerus to notch of deltoid tuberosity <59% of total humerus length (0); or ≥59 (1)* (Steppan, 1995: char. 84P). Rejected: continuous trait (and invariant: less than 59%).

4.2.5. *Fusion of tibia-fibula: <30% (0); or between 31 and 36% (1); or between 37 and 41% (2) or >42% (3)* (Carleton, 1980: char. 42). Rejected: metric character.

*4.2.6. *Trochlear process of calcaneum at the same level as posterior articular facet, trochlear process broad and shelflike (0); or gap between proximal edge of trochlear process and posterior articular facet, process shorter and less shelflike (1)* (Carleton, 1980: char. 40; Steppan, 1995: char. 32S; Pacheco, 2003: chars. 100S and 127T). Included: #84.

4.2.7. *Peroneal process of fifth metatarsal equal with or proximal to the distal edge of calcaneum (articular surface with the cuboid) (0); or fifth metatarsal not proximal to cuboid/calcaneum articulation (1)* (Steppan, 1995: char. 31S; Pacheco, 2003: chars. 101S and 128T). Rejected: autapomorphy for *Nyctomys*.

5. Phallus and Soft Anatomy

5.1. Phallus: Body

5.1.1. *Entire body of glans covered with spiny investure (0); or one-half to three-quarters of body spiny (1); or less than one-half of body spiny (2); or body wholly denuded of spines (3)* (Carleton, 1980: char. 52; Pacheco, 2003: char. 133T). Rejected. *Sigmodontomys alfari* has only four-fifths of the glans body covered with spines (Hooper and Musser, 1964), but I could not determine if this condition is similar to the one reported by Pacheco (2003) for *T. baeops*, which has spines in a "reduced region". Remaining taxa with study material have the entire glans body covered with spines.

5.1.2. *Grooves on glans penis body shallow or absent (0); or distinct but usually extend no more than half the body (1); or deep, extend beyond half the length of body (2)* (Pacheco, 2003: chars. 105S and 134T; the coding follows the latter character; the former has only two states, absent to shallow or present). Rejected: continuous trait.

5.1.3. *Body of glans surface not corrugated (0); or corrugated (1)* (Carleton, 1980: char. 54). Rejected: invariant (not corrugated).

5.1.4. *Dorsal lappets absent (0); or present (1)* (Carleton, 1980: char. 56). Rejected: autapomorphy for *Peromyscus*.

5.1.5. *Ventral lappets absent (0); or present (1)* (Carleton, 1980: char. 57). Rejected: autapomorphy for *Peromyscus*.

5.1.6. *Spines on internal crater wall absent (0); or present (1)* (Carleton, 1980: char. 53). Rejected: invariant (absent).

5.1.7. *Urinary meatus terminal, or nearly so (0); or subterminal (1)* (Carleton, 1980: char. 55; Pacheco, 2003: char. 111S). Rejected: plesiomorphic condition found only in *Nyctomys* (see Hooper and Musser, 1964).

5.1.8. *Crater hood of glans absent (0); or present (1)* (Carleton, 1980: char. 61). Rejected: invariant (absent).

5.1.9. *Ventral shield absent (0); or present (1)* (Carleton, 1980: char. 62; Pacheco, 2003: char. 109S). Rejected: invariant (absent).

5.1.10. *Lateral troughs present (0); or absent (1)* Rejected: autapomorphy for *Nyctomys*.

5.1.11. *Crater rim uniform (0); or multiply divided (1)* (Pacheco, 2003: char. 135T). Rejected: autapomorphy for *Thomasomys*.

5.1.12. *Dorsal and ventral margin of crater rim about same height (0); or dorsal margin distinctly longer than ventral margin (1)* (Pacheco, 2003: char. 136T). Rejected: invariant (same height).

5.1.13. *Notch on midventral margin of crater rim absent (0); or present (1)* (Pacheco, 2003: char. 137T). Rejected: invariant (absent).

5.2. Bacular Mounds and Digits

*5.2.1. *Lateral bacular mounds absent or diminutive (0); or present as large protuberances (1)* (Carleton, 1980: char. 60; Steppan, 1995: char. 36S; Pacheco, 2003: char. 107S; see also Voss, 1988: char. 18). Included: #85.

5.2.2. *Lateral bacular mound simple, not triple curved (0); or complexly curved, triple curved (1)* (Pacheco, 2003: chars. 108S and 139T). Rejected: invariant (simple mounds)

5.2.3. *Hooks on lateral mounds absent (0); or present (1)* (Steppan, 1995: char. 95P). Rejected: invariant (absent).

5.2.4. *Knob on dorsal surface of lateral mounds absent (0); or present (1)* (Steppan, 1995: char. 96P). Rejected: invariant (absent).

*5.2.5. *Large bacular cartilaginous apparatus with central digit more robust than lateral digits (0); or reduced cartilaginous apparatus with slim central digit shorter than laterals (1)* Included: #86.

5.2.6. *Medial bacular mound extending slightly distal to lateral bacular mounds (0); or remarkably long, well beyond lateral bacular mounds (1)* (Pacheco, 2003: char. 138T). Rejected: continuous trait.

5.2.7. *Lateral mounds not visible, tips placed deep in crater (0); or visible, tips extending to crater rim or just beyond (1); or large and distinctly visible, tips extending beyond crater rim (2)* (Pacheco, 2003: char. 140T). Rejected: continuous trait.

5.2.8. *Spines on lateral mounds absent (0); or present (1)* (Pacheco, 2003: char. 141T). Rejected: invariant (absent).

*5.2.9. *Nonspinous tissue of crater rim does not conceal bacular mounds (0); or nonspinous tissue conceals bacular mounds (1) Nonspinous* Included: #87.

5.3. Dorsal Papilla and Urethral Process

*5.3.1. *Dorsal papilla of glans penis spineless (0); or spinous (1)* Included: #88.

5.3.2. *Lateral papillae of glans penis absent (0); or present (1)* (see also Pacheco, 2003: char. 113S). Rejected: invariant (absent).

5.3.3. *Urethral process spineless (0); or spiny (1)* (modified from Carleton, 1980: char. 58; Pacheco, 2003: chars. 112S and 142T). Rejected: autapomorphy for *Thomasomys*.

5.3.4. *Urethral process with three main lobules (0); or two main lobules (1)* Rejected: autapomorphy for *Nyctomys*.

*5.3.5. *Subapical lobule on ventral surface of urethral processes absent (0); or present (1)* Included: #89.

5.3.6. *Dorsal papilla present (0); or absent (1)* (Carleton, 1980: char. 59; Pacheco, 2003: chars. 110S and 143T). Rejected: autapomorphy for *Peromyscus*.

5.4. Phallus: Ratios

5.4.1. *Ratio of glans penis length/width* (Carleton, 1980: char. 63; Pacheco, 2003: char. 106S). Rejected: metric character.

5.4.2. *Ratio of baculum length/width* (Carleton, 1980: char. 64). Rejected: metric character.

5.4.3. *Ratio of baculum length/glans penis length* (Carleton, 1980: char. 66). Rejected: metric character.

5.4.4. *Ratio of crater depth/length of glans penis* (Carleton, 1980: char. 67). Rejected: metric character.

5.4.5. *Ratio of lateral mounds length/medial mound length* (Steppan, 1995: char. 94P). Rejected: metric character.

5.4.6. *Ratio of cartilaginous tip length/bacular length* (Carleton, 1980: char. 65; Steppan, 1995: char. 93P). Rejected: metric character.

5.5. Male Accessory Glands

*5.5.1. *Two pairs of preputial glands present (0); or one pair present (1); or preputial glands absent (2)* (Carleton, 1980: char. 68; Steppan, 1995: chars. 37S and 97P; Pacheco, 2003: chars. 114S, 115S, and 144T). Included: #90.

*5.5.2. *Two pairs of ventral prostate glands present (0); or ventral prostate glands absent (1)* (modified from Carleton, 1980: chars. 69 and 70; see also Pacheco, 2003: chars. 116S and 145T). Included: #91.

*5.5.3. *Anterior prostate glands present (0); or absent (1)* (modified from Carleton, 1980: char. 72). Included: #92.

*5.5.4. *Vesicular glands present, large, shaped like a cane or inverted "J" (0); or vesicular glands present, shaped like small diverticula (1); or vesicular glands absent (2)* (modified from Carleton, 1980: char. 75). Included: #93.

5.5.5. *Lateral ventral prostate larger than medial (0); or ventral prostates of equal size (1); medial ventral larger than laterals (2)* (Pacheco, 2003: char. 145T). Rejected: continuous trait.

5.5.6. *Bulbo-urethral glands present, normal size (0); or present, large (1); or present, huge (2)* (Carleton, 1980: char. 73). Rejected: invariant (present, normal size).

5.5.7. *Ampullaries present (0); or absent (1); or present, elaborate and filamentous (2); or present, elaborate and coiled (3)* (Carleton, 1980: char. 74). Rejected: invariant (present, normal).

5.5.8. *Ampullae of ductus deferens absent (0); or present (1)* (Carleton, 1980: char. 76). Rejected: invariant (absent).

*5.5.9. *Preputial glands extend to or beyond the ventral flexure of the penis (0); or do not extend to the ventral flexure of the penis (1)* Included: #94.

*5.5.10. *Dorsal prostates absent (0); or one pair present (1); or two pairs present (2)* (modified from Carleton, 1980: char. 71). Included: #95.

*5.5.11. *Ampullary glands forming tufts of tubules that extend cranially from the base of the vas deferens (0); or ampullary glands compact, not elaborate (1)* Included: #96.

*5.5.12. *Subterminal flexure of vesicular gland rounded and smooth (0); or irregularly lobed and notched (1); or small and finger-shaped (2)* Included: #97.

5.6. Digestive Tract

*5.6.1. *Gall bladder present (0); or absent (1)* (Carleton, 1980: char. 49; Voss, 1988: char. 17; Voss, 1991: char. 8; Voss, 1993: 24; Voss and Carleton, 1993: 25; Steppan, 1995: chars. 38S and 98P; Voss et al., 2002: 18; Pacheco, 2003: chars. 122S and 132T). Included: #98.

5.6.2. *Incisura angularis shallow, stomach unilocular (0); or incisura angularis deeply developed, stomach bilocular (1)* (Carleton, 1980: char. 47; Pacheco, 2003: chars. 120S and 131T). Rejected: autapomorphy for *Peromyscus*.

5.6.3. *Gastric epithelium hemiglandular (0); or discoglandular (1)* (modified from Carleton, 1980: char. 46; see also Voss, 1988: char. 16; Steppan, 1995: chars. 39S and 40S; Voss et al., 2002: 16; Pacheco, 2003: chars. 118S, 119S, and 130T). Rejected: autapomorphy for *Peromyscus*.

*5.6.4. *Gastric glandular epithelium of stomach limited to antrum, not extending beyond incisura angularis (0); or gastric glandular epithelium covers antrum and proximal portion of corpus near esophageal opening (1)* (Carleton and Musser, 1989: char. 20; Voss and Carleton, 1993: char. 24). Included: #99.

5.6.5. *Sulcus on greater curvature of stomach absent (0); or present (1)* (Carleton, 1980: char. 48; Pacheco, 2003: char. 121S). Rejected: invariant (absent).

5.6.6. *Coils of the large intestine absent, or one or two coils present (0); or three or four coils (1); or five or six coils (2); or seven or more coils (3)* (Carleton, 1980: char. 50). Not observed.

5.6.7. *Caecum moderately long, simple internally (0); or short, simple sac (1); or long, elaborate infolding (2)* (Carleton, 1980: char. 51). Not observed.

5.7. Miscellaneous

5.7.1. *Anterior longitudinal ridge complete, high relief; generally separating inflexi labii superioris (0); or ridge complete, low relief; inflexi labii superioris generally in contact (1); or ridge absent; inflexi labii superioris in broad contact (2)* (Carleton, 1980: char. 44). Not observed.

5.7.2. *Three complete and four incomplete palatal ridges (0); or three complete and five to nine incomplete palatal ridges (1); two complete and five incomplete palatal ridges (2); or two complete and four incomplete palatal ridges (3)* (Carleton, 1980: char. 45; Pacheco, 2003: char. 129T). Not observed.

5.7.3. *Internal cheek pouches absent or poorly developed (0); or present (1)* (Carleton, 1980: char. 43; Pacheco, 2003: char. 117S). Rejected: invariant (absent).

5.7.4. *Omohyoid muscle present (0); or absent (1)* (Voss, 1988: char. 15). Not observed.

APPENDIX 3

Description of Nodes

A node-by-node description of all groups recovered in the combined analysis with CO coding for polymorphisms (fig. 37) is presented below. Included are the definition of the node, the nodal support as represented by jackknife (JK) resampling support and decay index (DI), and the unambiguous morphological and molecular synapomorphies (appendices 4 and 5 list all morphological synapomorphies for the morphology-only and combined analyses, respectively). The effects of the TS coding for polymorphic characters and of exclusion of taxa without IRBP sequence are presented as changes in topology or in support in the morphology-only or combined analyses. Figure 40 summarize the pattern of recovery of the clades and their jackknife support in the different analyses.

Node 1

Composition: Sigmodontinae (sensu Reig, 1984).

Nodal support: JK = 100%, DI = 34.

Partitioned evidence: clade recovered in both morphology-only and IRBP-only analyses.

Morphological synapomorphies: furred tail (12), zygomatic plate anterior to M1 alveolus (29), derived hyoid pattern (48), first rib articulates with CE7 and TL1 (79), humerus without entepicondylar foramen (82), lateral bacular mounds present (85), and dorsal prostates present (95).

Molecular synapomorphies: 34, including 16 unique and unreversed.

TS coding: no change.

Reduced analysis: no change.

Remarks: Monophyly of the subfamily Sigmodontinae sensu Reig (1984), i.e., excluding neotomines, peromyscines, and tylomyines, has been amply demonstrated in recent phylogenetic analyses using IRBP dataset (D'Elía, 2003; Weksler, 2003; Jansa and Weksler, 2004). Most of the morphological synapomorphies listed above for the subfamily were recognized in previous studies (Carleton, 1980; Voss, 1993; Steppan, 1995); the characters related to the tail and to the zygomatic plate, however, need to be reassessed in analyses with denser sampling.

Node 2

Composition: Sigmodontinae minus *Thomasomys*.

Nodal support: JK = 78%, DI = 4.

Partitioned evidence: clade recovered in both morphology-only and IRBP-only analyses.

Morphological synapomorphies: eight mammae (1), pes with squamate plantar surface (6), broad zygomatic plate (28), alisphenoid strut absent (38), capsular process of lower incisor alveolus absent (45), humerus with supratrochlear foramen (83), and subequal proximal edge of trochlear process and posterior articular facet of calcaneum (84).

Molecular synapomorphies: 2, including 1 unique and unreversed.

TS coding: reduction of nodal support.

Reduced analysis: slight reduction of nodal support.

Remarks: Monophyly of the thomasomyine group sensu Hershkovitz (1962; 1966a) (i.e., including *Delomys* and *Thomasomys* among others) was first contested by Voss (1993) and subsequently refuted by recent phylogenetic analyses with dense taxon sampling (Smith and Patton, 1999; D'Elía, 2003; Weksler, 2003).

Node 3

Composition: *Wiedomys* + Oryzomyini.

Nodal support: JK = 77%, DI = 4.

Partitioned evidence: clade recovered in the morphology-only analysis but not in the IRBP-only analysis.

Morphological synapomorphies: weakly cuneate interorbit with small crests (22), medium palate (32), M2 without protoflexus (64), and 12 ribs (78).

Molecular synapomorphies: none.

TS coding: reduction of nodal support.

Reduced analysis: no change.

Remarks: The sister group relationship between *Wiedomys* and oryzomyines was also recovered in the morphological analysis of Steppan (1995; see fig. 5B), which included a larger sample of other sigmodontine tribes. Molecular studies, however, strongly challenge these results (Smith and Patton, 1999; D'Elía, 2003; Weksler, 2003).

Node 4

Composition: Oryzomyini.

Nodal support: JK = 98%, DI = 5.

Partitioned evidence: clade recovered in both morphology-only and IRBP-only analyses.

Morphological synapomorphies: ungual tufts absent on D1, developed in remaining hindfoot digits (7), incisive foramina do not reach M1 (31), tegmen tympani absent (42), M1 with undivided anterocone (58), enamel connection between paracone and protocone at middle of protocone on M1 (61).

Molecular synapomorphies: no change can be unambiguously assigned to node 4 because *Oryzomys hammondi*, the first taxon to branch off within the Oryzomyini, lacks IRBP data. Eight molecular synapomorphies are found when ACCTRAN optimization is employed; the same synapomorphies are recovered in the reduced analysis.

TS coding: no change.

Reduced analysis: Decay index increases to 9.

Remarks: Corroboration for oryzomyine monophyly sensu Voss and Carleton (1993) comes from analyses using morphological data (Steppan, 1995) and nuclear genes (Weksler, 2003). Studies employing cytochrome *b*, however, fail to recover such group (Smith and Patton, 1999; Bonvicino and Moreira, 2001; Bonvicino et al., 2003; D'Elía, 2003). As discussed by Weksler (2003), these results are probably due to the saturation of the phylogenetic signal in this rapid-evolving mitochondrial gene.

Node 5

Composition: Oryzomyini minus *Oryzomys hammondi*.

Nodal support: JK = 28%, DI = 1.

Partitioned evidence: none; *O. hammondi* is recovered as the sister group of *Oecomys*, well nested within oryzomyines, in the morphology-only analysis. *O. hammondi* does not have IRBP

data and consequently was not included in the IRBP-only and reduced analyses.

TS coding: *O. hammondi* is recovered within clade B* in both combined and morphology-only analyses.

Morphological synapomorphies: long palate (32), simple posterolateral palatal pits (34), reduced capsular process of lower incisor alveolus (45), and M3 without posteroloph (68).

Remarks: The position of *O. hammondi* among oryzomyines is unarguably the least secure in the present analysis. The hypothesis of *O. hammondi* as the most basal oryzomyine should be viewed with caution because of the lack of strong support for the basal relationships of oryzomyines, and because of the contradictory results of the different analyses. Nevertheless, the basal position could explain why *O. hammondi* has always been regarded as an oryzomyine with obscure relationships (e.g., Hershkovitz, 1948; Hershkovitz, 1970; Musser and Carleton, 1993).

Node 6

Composition: *Zygodontomys* and *Scolomys* (clade A).

Nodal support: JK = 53%, DI = 1.

Partitioned evidence: clade recovered in the morphology-only analysis but not in the IRBP-only analysis.

Morphological synapomorphies: narrow interparietal (26) and absence of mesoloph on M3 (67).

Molecular synapomorphies: none.

TS coding: increased nodal support in the combined analysis; clade not recovered in the morphology-only analysis.

Reduced analysis: increased nodal support.

Remarks: *Scolomys* has most of the morphological synapomorphies that characterize the oryzomyines (Voss and Carleton, 1993; Gómez-Laverde et al., 2004), but morphological characters do not present evidence about its relationship within the tribe. Analyses of cytochrome *b* data recover *Scolomys* outside oryzomyines (Smith and Patton, 1999; D'Elía, 2003; but see Garcia, 1999), but the position of *Scolomys* as a basal oryzomyine is secured in both combined and IRBP-only analyses (see also Weksler, 2003). On the other hand, evidence for the clustering of *Scolomys* and *Zygodontomys* in a monophyletic group comes mostly from morphological data.

Node 7

Composition: *Zygodontomys*.

Nodal support: JK = 100%, DI = 34.

Partitioned evidence: clade recovered in both morphology-only and IRBP-only analyses.

Morphological synapomorphies: tail slightly bicolored (11), strongly cuneate interorbit with overhanging crests (22), incisive foramina pass M1 (31), mental foramen located at diastema (44), masseteric crests reach anterior to m1 procingulum (47), m2 with 3 roots (51), protocone and paracone forming single dentine basin without enamel connection on M1 (61), M1 and M2 without mesolophs (62), m1 and m2 without mesolophids (73), and m3 without posteroflexid (77).

Molecular synapomorphies: 25, including 15 unique and unreversed.

TS coding: no change.

Reduced analysis: no change.

Remarks: The placement of *Zygodontomys* as a basal oryzomyine is well secured by combined and IRBP-only results (see also Weksler, 2003). Corroboration of *Zygodontomys* monophyly is an expected result (cf. Voss, 1991; Bonvicino et al., 2003). Previously regarded as a subspecies of *Z. brevicauda* (see Voss, 1991), *Z. cherriei* displays an impressive number of morphological (7) and molecular (8) differences to *Z. brevicauda* and is considered here as distinct species.

Node 8

Composition: Oryzomyini minus *O. hammondi*, *Zygodontomys*, and *Scolomys*.

Nodal support: JK = 49%, DI = 1.

Partitioned evidence: clade recovered in the IRBP-only analysis but not in the morphology-only analysis.

Morphological synapomorphies: M2 with protoflexus (64).

Molecular synapomorphies: 5, including 2 unique and unreversed.

TS coding: *O. hammondi* is recovered within clade B* in both combined and morphology-only analyses.

Reduced analysis: increased nodal support.

Remarks: Although morphological evidence for this "core oryzomyine" clade is meager, it receives high nodal support from the molecular data (see also Weksler, 2003).

Node 9

Composition: *Handleyomys*, *Oecomys*, and 11 species of *Oryzomys* belonging to 8 groups: *alfaroi*, *melanotis* (*O. rostratus*), *chapmani*, *albigularis* (*O. albigularis* and *O. levipes*), *megacephalus*, *yunganus*, *talamancae*, and *nitidus* (*O. lamia*, *O. macconnelli*, and *O. russatus*). (clade B).

Nodal support: JK = 58%, DI = 1.

Partitioned evidence: clade recovered in the IRBP-only analysis but not in the morphology-only analysis. A similar clade is recovered in the

latter analysis, in which *O. alfaroi*, *O. rostratus*, and *O. chapmani* are excluded and *O. hammondi* is included.

Morphological synapomorphies: pes with smooth plantar surface (6), and flexi meet at midline on M1 (57).

Molecular synapomorphies: 4, including 2 unique.

TS coding: *O. hammondi* is also included in clade B* in the combined and morphology-only analyses. *Amphinectomys* is also included in clade B* in the morphology-only analysis.

Reduced analysis: increased nodal support.

Remarks: Previous morphological, molecular, and allozymic studies recovered results partially consistent with clade B. Phenetic morphological analyses cluster *Oecomys*, the *nitidus* and *megacephalus* groups, but not the *albigularis* group (Patton and Hafner, 1983). Patton and da Silva (1995) found a clade including *Oecomys*, *Oryzomys yunganus*, *O. megacephalus*, *O. nitidus*, and *O. macconnelli* using both weighted parsimony and distance analyses of cytochrome *b*. Finally, analysis of allozymic data (Dickerman and Yates, 1995) recovered a clade containing *O. albigularis*, *O. nitidus*, and *O. megacephalus*.

Node 10

Composition: *Oryzomys nitidus* species group (*O. lamia*, *O. macconnelli*, and *O. russatus*).

Nodal support: JK = 94%, DI = 3.

Partitioned evidence: clade recovered in both morphology-only and IRBP-only analyses.

Morphological synapomorphies: tail strongly bicolored (11), m1 with 3 roots (50), and anapophyses present on TL17 (80).

Molecular synapomorphies: 4, including 1 unique.

TS coding: clade recovered in the combined analysis and in some fundamental cladograms of the morphology-only analysis.

Reduced analysis: no change.

Remarks: The *nitidus* group of species has been recognized early in *Oryzomys* taxonomic history (Thomas, 1901), but only recently it has been shown as a monophyletic group (Weksler, 1996; Percequillo, 1998; Musser et al., 1998). Phylogenetic analyses based on cytochrome *b* data have failed to recover the group (Bonvicino and Moreira, 2001), probably due to phylogenetic signal saturation. The six species recognized for the group (table 2) display a distinctive set of characters relative to other *Oryzomys* species complexes, but only three unambiguous morphological synapomorphies characterize the group, all of them homoplasious within the Oryzomyini. The presence of three roots in the first lower molar is the least homoplasious among them, observed additionally in the *Oryzomys albigularis* group, *Oryzomys angouya*, *Microryzomys*, and *Oecomys trinitatis*.

Node 11

Composition: *Oryzomys lamia* and *O. russatus*.

Nodal support: JK = 100%, DI = 9.

Partitioned evidence: clade recovered in both morphology-only and IRBP-only analyses.

Morphological synapomorphies: developed capsular process of lower incisor alveolus (45), m1 without ectolophid (72).

Molecular synapomorphies: 9, including 5 unique and unreversed.

TS coding: no change.

Reduced analysis: no change.

Remarks: *O. lamia* was considered a junior synonym of *O. russatus* by Musser et al. (1998), but the impressive number of morphological (6) and molecular (9) differences between the two species warrants the recognition of species status to each taxon, as proposed by Bonvicino et al. (1999).

Node 12

Composition: *Handleyomys*, *Oecomys*, and 8 species of *Oryzomys* belonging to 7 groups: *alfaroi*, *melanotis* (*O. rostratus*), *chapmani*, *albigularis* (*O. albigularis* and *O. levipes*), *megacephalus*, *yunganus*, and *talamancae* (clade B minus *nitidus* group).

Nodal support: JK = 7%, DI = 1.

Partitioned evidence: none.

Morphological synapomorphies: none.

Molecular synapomorphies: 2.

TS coding: clade recovered in some fundamental cladograms of combined analysis.

Reduced analysis: clade not recovered.

Remarks: Neither morphology nor IRBP provides phylogenetic signal for a robust resolution of the basal structure of clade B. Nevertheless, the *nitidus* group is recovered as the basal group in clade B in most analyses. Additional characters are needed to formulate a solid phylogenetic hypothesis for members of this clade.

Node 13

Composition: *Oecomys*.

Nodal support: JK = 95%, DI = 4.

Partitioned evidence: clade recovered in both morphology-only and IRBP-only analyses.

Morphological synapomorphies: pes with extremely developed interdigital pads (5),

strongly cuneate interorbit with overhanging crests (22), parietal with deep lateral expansion (25), narrow zygomatic plate (28), M2 with accessory loph to paracone (65), M3 with posteroloph (68).

Molecular synapomorphies: 2.

TS coding: no change.

Reduced analysis: no change.

Remarks: Monophyly of *Oecomys* was suggested by chromosomal data (Gardner and Patton, 1976) and supported by analyses of mitochondrial genes (Patton and da Silva, 1995; Andrade and Bonvicino, 2003) and nuclear genes (Weksler, 2003). *Oecomys* is the only oryzomyine taxon with morphological specializations for arboreal life, with several of them serving as synapomorphies for the genus.

Node 14

Composition: *Oecomys bicolor*, *Oe. trinitatis*, *Oe. mamorae*, and *Oe. concolor*.

Nodal support: JK = 67%, DI = 1.

Partitioned evidence: clade recovered in the morphology-only analysis but not in the IRBP-only analysis.

Morphological synapomorphies: zygomatic plate at same level as M1 alveolus (29).

Molecular synapomorphies: none.

TS coding: no change.

Reduced analysis: clade found in both combined and morphology-only analyses.

Remarks: The basal position of *Oe. catherinae* within *Oecomys* needs to be substantiated by supplementary characters and additional analyses employing denser taxonomic sampling.

Node 15

Composition: *Oecomys bicolor* and *Oe. trinitatis*.

Nodal support: JK = 60%, DI = 1.

Partitioned evidence: clade recovered in the morphology-only analysis but not in the IRBP-only analysis.

Morphological synapomorphies: lacrimal articulates mainly with maxillary (21) and developed capsular process of lower incisor alveolus (45).

Molecular synapomorphies: none.

TS coding: increased nodal support.

Reduced analysis: no change.

Node 16

Composition: *Oecomys concolor* and *Oe. mamorae*.

Nodal support: JK = 98%, DI = 5.

Partitioned evidence: clade recovered in both morphology-only and IRBP-only analyses.

Morphological synapomorphies: subtle countershading (15) and derived carotid circulation pattern 2 (37).

Molecular synapomorphies: 2, including 1 unique and unreversed.

TS coding: slight decrease in nodal support.

Reduced analysis: no change.

Remarks: The sister group relationship between *Oecomys concolor* and *Oe. mamorae* is the only phylogenetic hypothesis within *Oecomys* strongly supported by both molecular and morphological data.

Node 17

Composition: *Handleyomys* and 8 species of *Oryzomys* belonging to 7 groups: *alfaroi*, *melanotis* (*O. rostratus*), *chapmani*, *albigularis* (*O. albigularis* and *O. levipes*), *megacephalus*, *yunganus*, and *talamancae*.

Nodal support: JK = 12%, DI = 1.

Partitioned evidence: none.

Morphological synapomorphies: M3 without hypoflexus (or diminutive) (69) and subterminal flexure of vesicular gland irregularly lobed (97).

Molecular synapomorphies: none.

TS coding: clade recovered in the combined analysis and in some fundamental cladograms of the morphology-only analysis.

Reduced analysis: clade not recovered.

Remarks: Neither morphology nor IRBP provides phylogenetic signal for a robust resolution of the internal structure of clade B. Additional characters are needed to formulate a solid phylogenetic hypothesis for members of this clade.

Node 18

Composition: *Handleyomys*, *Oryzomys alfaroi*, *O. chapmani*, and *O. rostratus*.

Nodal support: JK = 78%, DI = 4.

Partitioned evidence: clade recovered in the IRBP-only analysis but not in the morphology-only analysis.

Morphological synapomorphies: presence of labial accessory root on m1 (50), m2 with 3 roots (51), and M2 with two fossetti at mesoflexus position (66).

Molecular synapomorphies: 3.

TS coding: increased nodal support in combined analysis. In the morphology-only analysis, *Handleyomys* is found as the sister group of *Amphinectomys*; the two are then connected to the *alfaroi-chapmani-rostratus* clade.

Reduced analysis: no change.

Remarks: In the previous analysis of IRBP sequences, *Handleyomys* also appears as the

sister group to the *alfaroi* and *melanotis* species groups of *Oryzomys* in a highly supported clade (Weksler, 2003). Morphological data by itself does not corroborate the position of *Handleyomys* as the sister group of the *alfaroi-melanotis-chapmani* complex—in the CO morphology-only tree, *Handleyomys* appears as the sister group to the *Oryzomys albigularis* group. Nevertheless, the signal provided by IRBP data is not falsified by the morphological data; in fact, the clade including *Handleyomys* and the *alfaroi-rostratus-chapmani* groups has a series of compelling morphological synapomorphies in the combined tree; particularly, the number of roots of the second lower molars is unique among taxa within clade B.

Node 19

Composition: *Oryzomys alfaroi*, *O. chapmani*, and *O. rostratus*.

Nodal support: JK = 90%, DI = 4.

Partitioned evidence: clade recovered in the morphology-only analysis. *O. chapmani* lacks IRBP sequence data, but *O. alfaroi* and *O. rostratus* are recovered as sister groups in the IRBP-only analysis.

Morphological synapomorphies: large sphenopalatine vacuities (36), flexi not interpenetrating on M1 (57), and enamel bridge connection between paracone and protocone at middle of protocone on M1 (61).

Molecular synapomorphies: 9, including 4 unique and unreversed.

TS coding: increased nodal support.

Reduced analysis: no change.

Remarks: The three species groups, *chapmani*, *alfaroi*, and *melanotis*, have long been considered to be associated (Goldman, 1918), but besides a previous IRBP analysis (Weksler, 2003), no phylogenetic evidence has been previously presented for their close relationship. In the CO morphology-only tree, this clade is recovered within clade D*, but the TS analysis places it within clade B*.

Node 20

Composition: *Oryzomys chapmani* and *O. rostratus*.

Nodal support: JK = 62%, DI = 1.

Partitioned evidence: none; *O. rostratus* is recovered as the sister group of *O. alfaroi* in the morphology-only analysis. *O. chapmani* does not have IRBP data and consequently was not included in the IRBP-only and reduced analyses.

Morphological synapomorphies: m1 without ectolophid (72).

TS coding: increased nodal support in the combined analysis.

Remarks: Relationships within the *alfaroi-melanotis-chapmani* complex warrants further analyses with denser taxonomic sampling. The *chapmani* and *alfaroi* species groups have been considered to be close taxa since Merriam (1901) recognized the *melanotis* and *chapmani* species groups, with the latter including *O. rhabdops* (member of the *alfaroi* group), and Goldman (1918) recognized the *melanotis* and *alfaroi* groups, with the latter including *O. chapmani* and *O. saturatior*. Musser and Carleton (1993), however, asserted that the *alfaroi* group may be more closely related to the *melanotis* complex.

Node 21

Composition: Five species of *Oryzomys* belonging to 4 groups: *albigularis* (*O. albigularis* and *O. levipes*), *megacephalus*, *yunganus*, and *talamancae*.

Nodal support: JK = 20%, DI = 1.

Partitioned evidence: none.

Morphological synapomorphies: tail slightly bicolored (11) and ampullary glands forming tufts of tubules (96)

Molecular synapomorphies: none.

TS coding: clade recovered in the combined analysis and in some fundamental cladograms of the morphology-only analysis.

Reduced analysis: clade not recovered.

Node 22

Composition: *Oryzomys megacephalus* and *O. yunganus*.

Nodal support: JK = 99%, DI = 6.

Partitioned evidence: clade recovered in the IRBP-only analysis but not in the morphology-only analysis.

Morphological synapomorphies: derived carotid circulation pattern 1 (37) and absence of capsular process of lower incisor alveolus (45).

Molecular synapomorphies: 5, including 2 unique and unreversed.

TS coding: clade recovered in the combined analysis and in some fundamental cladograms of the morphology-only analysis.

Reduced analysis: no change.

Remarks: The two morphological synapomorphies observed for this clade are unique transformations among members of clade B. In particular, the carotid circulation pattern 1 displayed by species of the *yunganus* and *megacephalus* groups is observed only in a few other oryzomyines such as *Oligoryzomys* and in *Neacomys musseri*. The closeness of *yunganus* and *megacephalus* groups has been recognized before. For example, Musser et al. (1998: 323) stated that "[members] of the *Oryzomys megacephalus* and *O. yunganus* groups seem much

alike compared with the other [*Oryzomys* species groups]. Were it not for the distinction between the two provided by molar occlusal patterns, we would confidently include *O. yunganus* and *O. tatei* [= *yunganus* group] along with *O. megacephalus* and *O. laticeps* [*megacephalus* group sensu Musser et al., 1998] in one group apart from the trans-Andean species, which seem to form a tight morphological cluster despite their striking external differences, and members of the *O. nitidus* group".

Node 23

Composition: *Oryzomys talamancae*, *O. albigularis*, and *O. levipes*.

Nodal support: JK = 52%, DI = 1.

Partitioned evidence: none.

Morphological synapomorphies: reduced sphenopalatine vacuities (36), flexi deeply interpenetrating on M1 (57), and anapophyses present on TL17 (80).

Molecular synapomorphies: 4, including 1 unique among oryzomyines.

TS coding: clade recovered in the combined analysis and in some fundamental cladograms of the morphology-only analysis.

Reduced analysis: clade not recovered.

Remarks: *O. talamancae* is recovered as the sister group of the *nitidus* species group in the IRBP-only and reduced analyses, with moderate nodal support. Additional data are needed to resolve the conflict that results in a poorly supported hypothesis, although nodal support is higher in the TS combined analysis.

Node 24

Composition: *Oryzomys albigularis* species group (*O. albigularis* and *O. levipes*).

Nodal support: JK = 96%, DI = 6.

Partitioned evidence: clade recovered in the morphology-only analysis. *O. levipes* does not have IRBP data and consequently was not included in the IRBP-only and reduced analyses.

Morphological synapomorphies: amphoral interorbit with square edges (22), medium palate (32), m1 with 3 roots (50), M1 with deeply divided anterocone (58), and M3 with posteroloph (68).

TS coding: no change.

Remarks: The *albigularis* group has been recognized since the early classification of sigmodontines (Goldman, 1918; Hershkovitz, 1944; Cabrera, 1961; Gardner and Patton, 1976; Patton et al., 1990; Musser and Carleton, 1993; Aguilera et al., 1995; Marquez et al., 2000), but monophyly of the group has not been demonstrated so far. Musser and Carleton (1993) recognized five species for the group, *O. albigularis*, *O. auriventer*, *O. devius*, *O. keaysi*, and *O. levipes*, based on Gardner and Patton (1976), Gardner (1983), and Patton et al. (1990). There is karyological and morphometric evidence for the recognition of two Venezuelan species, *O. caracolus* and *O. meridiensis* (Aguilera et al., 1995; Márquez et al., 2000). One unnamed karyotypic form is known from Venezuela (Aguilera et al., 1995), and several other alpha taxonomic problems persist for the group (Percequillo, 2003).

Node 25

Composition: *Neacomys*, *Microryzomys*, *Oligoryzomys*, *Pseudoryzomys*, *Lundomys*, *Holochilus*, *Nesoryzomys*, *Amphinectomys*, *Nectomys*, *Sigmodontomys*, *Melanomys*, and 7 species of *Oryzomys*: *O. balneator*, *O. polius*, *O. couesi*, *O. palustris*, *O. subflavus*, *O. angouya*, and *O. xanthaeolus* (clades C and D).

Nodal support: JK = 80%, DI = 4.

Partitioned evidence: clade recovered in the IRBP-only analysis but not in the morphology-only analysis.

Morphological synapomorphies: M1 with deeply divided anterocone (58).

Molecular synapomorphies: 5, including 3 unique and unreversed.

TS coding: clade recovered only in the combined analysis.

Reduced analysis: increased nodal support.

Remarks: Despite the lack of strong morphological signals for the sister group relationship of clades C and D, the IRBP evidence for this relationship is overwhelming (Weksler, 2003). Supplementary morphological characters are needed for additional corroboration and a better morphological diagnosis for the clade.

Node 26

Composition: *Neacomys*, *Microryzomys*, *Oligoryzomys*, and *Oryzomys balneator* (clade C).

Nodal support: JK = 74%, DI = 2.

Partitioned evidence: clade recovered in both IRBP-only analysis and morphology-only analyses.

Morphological synapomorphies: nasals reaching posteriorly to maxillary-frontal suture at lacrimal (19), zygomatic plate subequal to M1 alveolus (29), and small ectotympanic (41).

Molecular synapomorphies: 1 substitution.

TS coding: no change.

Reduced analysis: no change.

Remarks: Clade C is the only higher-level oryzomyine clade recovered unchanged in all analyses. Previous phylogenetic analyses also recovered *Neacomys* in monophyletic groups with *Microryzomys* and/or *Oligoryzomys* (Pat-

ton and Hafner, 1983; Dickerman and Yates, 1995; Patton and da Silva, 1995; Myers et al., 1995; Smith and Patton, 1999; Bonvicino and Moreira, 2001; Bonvicino et al., 2003).

Node 27

Composition: *Neacomys*.

Nodal support: JK = 99%, DI = 7.

Partitioned evidence: clade recovered in both IRBP-only analysis and morphology-only analyses.

Morphological synapomorphies: spiny pelage (13), totally white ventral hairs (14), premaxillaries terminating anterior to nasal (20), and M3 without hypoflexus (69).

Molecular synapomorphies: 4, including 1 unique and unreversed.

TS coding: no change.

Reduced analysis: no change.

Remarks: A fifth *Neacomys* morphological apomorphy, preputial glands not extending to ventral flexure of penis (94), is recovered in ACCTRAN optimization and is unique among oryzomyines. Optimization is ambiguous because information for this character is known only for *Neacomys spinosus*. If other *Neacomys* species are found to display the same condition for the character, this will be a unique morphological synapomorphy for the genus.

Node 28

Composition: *Neacomys minutus* and *N. musseri*.

Nodal support: JK = 99%, DI = 5.

Partitioned evidence: clade recovered in the IRBP-only analysis but not in the morphology-only analysis.

Morphological synapomorphies: none.

Molecular synapomorphies: 5, including 4 unique and unreversed.

TS coding: no change.

Reduced analysis: no change.

Remarks: The morphology-only tree recovered *N. spinosus* as the sister group of *N. minutus*, but with low nodal support. Both *Neacomys minutus* and *N. musseri* are small-sized species, contrasted to the large *N. spinosus*.

Node 29

Composition: *Microryzomys*, *Oligoryzomys*, and *Oryzomys balneator* (clade C minus *Neacomys*).

Nodal support: JK = 49%, DI = 1.

Partitioned evidence: clade recovered in the morphology-only analysis but not in the IRBP-only analysis.

Morphological synapomorphies: jugal absent (30).

Molecular synapomorphies: none.

TS coding: clade recovered in some fundamental cladograms of the morphology-only analysis.

Reduced analysis: clade recovered in some fundamental cladograms.

Remarks: In the IRBP-only and TS combined analyses, as well as in some fundamental cladograms of the reduced analysis, *Neacomys*, *Microryzomys*, and *O. balneator* form a clade (see also Weksler, 2003). Although the conflict between morphological and molecular data is resolved toward the morphological solution (i.e., *Oligoryzomys* as the sister group to the (*Microryzomys* + *O. balneator*) clade), neither arrangement receives strong support from the data. Additional characters are needed for the resolution of the internal relationships within this clade.

Node 30

Composition: *Microryzomys* and *Oryzomys balneator*.

Nodal support: JK = 74%, DI = 3.

Partitioned evidence: clade recovered in both IRBP-only and morphology-only analyses.

Morphological synapomorphies: narrow zygomatic plate (28), medium palate (32), presence of anteromedian flexid on m1 procingulum (70; unique among oryzomyines), and extended gastric glandular epithelium.

Molecular synapomorphies: 1 substitution.

TS coding: clade recovered in some fundamental cladograms of the morphology-only analysis.

Reduced analysis: clade recovered in some fundamental cladograms.

Remarks: The presence of the anteromedian flexid on m1 procingulum is a unique synapomorphy among oryzomyines. The close relationship between *Microryzomys* and *O. balneator* was first recovered in a previous IRBP-based phylogenetic analysis (Weksler, 2003).

Node 31

Composition: *Oligoryzomys*.

Nodal support: JK = 100%, DI = 10.

Partitioned evidence: clade recovered in both IRBP-only analysis and morphology-only analysis.

Morphological synapomorphies: flat parapterygoid (35), large sphenopalatine vacuities (36), derived carotid circulation pattern 1 (37), masseteric crests reaching anterior to m1 procingulum (47), M3 with posteroloph (68), and glans penis with spinous dorsal papilla (88).

Molecular synapomorphies: 4, including 2 unique and unreversed.

TS coding: no change.

Reduced analysis: no change.

Remarks: Monophyly of *Oligoryzomys* has been previously supported by morphological data (Carleton and Musser, 1989), analyses of allozymes (Dickerman and Yates, 1995), mitochondrial genes (Myers et al., 1995), and nuclear genes (Weksler, 2003). Among the recovered synapomorphies for the genus, the spinous dorsal papilla in the glans penis is homoplasious only with the *Oryzomys palustris* group, while the pattern 1 of the carotid circulation is observed only in the *Oryzomys yunganus* + *O. megacephalus* clade and in *Neacomys musseri*.

Node 32

Composition: *Oligoryzomys nigripes* and *Ol. stramineus*.

Nodal support: JK = 63%, DI = 1.

Partitioned evidence: clade recovered in the IRBP-only analysis but not in the morphology-only analysis.

Morphological synapomorphies: none.

Molecular synapomorphies: 2, including 1 unique and unreversed.

TS coding: no change.

Reduced analysis: no change.

Remarks: *Ol. fulvescens* is recovered as the sister taxon to *Ol. nigripes* in the morphology-only analysis.

Node 33

Composition: *Oligoryzomys flavescens* + *Ol. fornesi*.

Nodal support: JK = 84%, DI = 2.

Partitioned evidence: clade recovered in both IRBP-only and morphology-only analyses.

Morphological synapomorphies: M3 without, or with diminutive, hypoflexus (69).

Molecular synapomorphies: 2 unique and unreversed transformations.

TS coding: increased nodal support in the morphology-only analysis.

Reduced analysis: no change.

Remarks: *Ol. flavescens* and *Ol. fornesi* have similar karyotypes (Bonvicino and Weksler, 1998) and were included in the *microtis-flavescens* group of *Oligoryzomys* by Weksler and Bonvicino (2005).

Node 34

Composition: *Pseudoryzomys*, *Lundomys*, *Holochilus*, *Nesoryzomys*, *Amphinectomys*, *Nectomys*, *Sigmodontomys*, *Melanomys*, and 6 species of *Oryzomys*: *O. polius*, *O. couesi*, *O. palustris*, *O. subflavus*, *O. angouya*, and *O. xanthaeolus* (clade D).

Nodal support: JK = 82%, DI = 5.

Partitioned evidence: clade recovered in the IRBP-only analysis but not in the morphology-only analysis.

Morphological synapomorphies: strongly bicolored tail (11), parietal with deep lateral expansion (25), incisive foramina pass M1 (31), complex posterolateral palatal pits (34), large sphenopalatine vacuities (36), derived carotid circulation pattern 2 (37), and M3 with posteroloph (68).

Molecular synapomorphies: 2, including 1 unique among oryzomyines.

TS coding: clade recovered in the combined analysis. In the morphology-only analysis, a similar clade, but without *Amphinectomys*, is recovered.

Reduced analysis: increased resampling values.

Remarks: In the CO morphology-only analysis, clade D (clade D* in fig. 34) contains three species of *Oryzomys*—*O. alfaroi*, *O. rostratus*, and *O. chapmani*—that are recovered in clade B in the combined and IRBP analyses. Among morphological synapomorphies for clade D, the derived carotid pattern is unreversed within the clade.

Node 35

Composition: clade D minus *Oryzomys polius*.

Nodal support: JK = 73%, DI = 4.

Partitioned evidence: clade recovered in the IRBP-only analysis but not in the morphology-only analysis.

Morphological synapomorphies: M1 with labial root (49), m1 with accessory rootlets (50), and M2 with labial and lingual fossetti at mesoflexus position (66).

Molecular synapomorphies: 2, including 1 unique and unreversed.

TS coding: increased nodal support in the combined analysis.

Reduced analysis: increase nodal support.

Remarks: *Oryzomys polius* is recovered in a similar position in the morphology-only analysis, as the sister group to the remaining taxa of clade D* (fig. 34). *O. polius* has been an enigmatic species since its description; Osgood (1913) stated that "this species is not closely related to any [other *Oryzomys*] with which I have been able to compare". Its position as the most basal member of clade D (or D* in the morphological analysis) indicates that it is a unique lineage within oryzomyines.

Node 36

Composition: *Pseudoryzomys*, *Lundomys*, *Holochilus*, *Oryzomys palustris*, and *O. couesi*.

Nodal support: JK = 66%, DI = 3.

Partitioned evidence: clade recovered in the morphology-only analysis but not in the IRBP-only analysis.

Morphological synapomorphies: hypothenar pad absent (4), pes with extremely small interdigital pads (5), ungual tufts absent on D1, sparse in remaining hindfoot digits (7), zygomatic plate at same level as M1 alveolus (29), and M1 with anterocone divided by internal fold (58).

Molecular synapomorphies: none.

TS coding: increased nodal support.

Reduced analysis: no change.

Remarks: Three of the five morphological synapomorphies uniting the *O. palustris* group (*O. palustris* and *O. couesi*) and the tetralophodont taxa *Lundomys*, *Holochilus*, and *Pseudoryzomys* are hindfoot characters thought to be semiaquatic specializations. IRBP-only analysis places the *O. palustris* group within the other major clade within clade D, the one formed by *Nectomys*, *Nesoryzomys*, and associated taxa (fig. 36). Thus, the conflict between IRBP and morphology signal might be resolved in the morphology solution due to possible convergent structures.

Node 37

Composition: *Oryzomys palustris* species group (*O. palustris* and *O. couesi*).

Nodal support: JK = 98%, DI = 6.

Partitioned evidence: clade recovered in both IRBP-only and morphology-only analyses.

Morphological synapomorphies: narrow interparietal (26), m2 and m3 with anterolophid (75), glans penis with spinous dorsal papilla (88), and urethral process of glans penis with subapical process (89).

Molecular synapomorphies: 4, including 2 unique and unreversed.

TS coding: clade recovered only in the combined analysis.

Reduced analysis: no change.

Remarks: The *palustris* group has long been accepted in *Oryzomys* systematics (Merriam, 1901; Goldman, 1918; Hershkovitz, 1971; Musser and Carleton, 1993; Sanchez-H. et al., 2001). Five species are recognized for the group: *O. couesi*, *O. dimidiatus*, *O. gorgasi*, *O. nelsoni*, and *O. palustris*. The latter is the type species of *Oryzomys*, and thus the strict concept of the genus *Oryzomys* is restricted to this clade.

Node 38

Composition: *Pseudoryzomys*, *Lundomys*, and *Holochilus*.

Nodal support: JK = 96%, DI = 7.

Partitioned evidence: clade recovered in both IRBP-only and morphology-only analyses.

Morphological synapomorphies: zygomatic spine present (28), simple posterolateral palatal pits (34), M1 without anteroloph (59), reduced mesolophs on M1 and M2 (62), and reduced posteroflexid on m3 (77).

Molecular synapomorphies: 1.

TS coding: no change.

Reduced analysis: no change.

Remarks: Analyses of morphological and nuclear data also recovered a clade containing *Holochilus*, *Lundomys*, and *Pseudoryzomys*, and †*Noronhomys* (Voss and Carleton, 1993; Steppan, 1996; Carleton and Olson, 1999; Weksler, 2003).

Node 39

Composition: *Holochilus* + *Lundomys*.

Nodal support: JK = 91%, DI = 6.

Partitioned evidence: clade recovered in the morphology-only analysis but not in the IRBP-only analysis.

Morphological synapomorphies: ungual tufts absent on forefeet digits (3), ungual tufts absent on hindfoot digits (7), natatory fringes present (8), developed interdigital webbing (9), tail unicolored (11), amphoral interorbit with square edges (22), palatine median longitudinal ridge present (33), deeply excavated parapterygoid (35), lateral cingula absent on molars (55), posteriorly divergent maxillary toothrow (56), flexi meet at midline on M1 (57), enamel bridge connection between paracone and protocone at posteriormost end of protocone on M1 (61), m3 without posteroflexid (77), and anapophyses present on TL17 (80).

Molecular synapomorphies: none

TS coding: no change.

Reduced analysis: no change.

Remarks: The arrangement within the (*Lundomys* + *Pseudoryzomys* + *Holochilus*) clade differs among trees. In the IRBP-only results, *Pseudoryzomys* is recovered with high nodal support as the sister group of *Holochilus*. The sheer number of morphological characters uniting *Lundomys* and *Holochilus* overwhelms the unexpected strong molecular signal pointing to the closer relatedness of *Pseudoryzomys-Holochilus*. Previous morphological studies also recovered *Holochilus* closer to *Lundomys* than to *Pseudoryzomys* (Voss and Carleton, 1993; Steppan, 1996; Carleton and Olson, 1999), while the previous analysis of molecular data also shows *Holochilus* closer to *Pseudoryzomys* than to *Lundomys* (Weksler, 2003).

Node 40

Composition: *Holochilus*

Nodal support: JK = 100%, DI = 21.

Partitioned evidence: clade recovered in both IRBP-only and morphology-only analyses.

Morphological synapomorphies: amphoral interorbit with developed beads (22), postorbit-

al ridge present (23), frontosquamosal suture anterior to frontoparietal (24), incisive foramina do not reach M1 (31), alisphenoid strut present (38), large ectotympanic (41), single-crest anterior masseteric ridges (46), masseteric crests reach anterior to m1 procingulum (47), incisors with labial bevel (53), molars hypsodont (54), flexi deeply interpenetrating on M1 (57), M1 with undivided anterocone (58), median mure not connect to protocone on M1 (63), and M2 without protoflexus (64).

Molecular synapomorphies: 7, including 4 unique and unreversed.

TS coding: no change.

Reduced analysis: no change.

Remarks: The association of *Holochilus* within oryzomyines was first suggested by glans penis data (Hooper and Musser, 1964), but its position within Oryzomyini has been only recently secured (Voss and Carleton, 1993; Steppan, 1995; Weksler, 2003). Monophyly of *Holochilus* is well secured, with several synapomorphies vis-à-vis other oryzomyines (Voss and Carleton, 1993).

Node 41

Composition: *Oryzomys angouya*, *O. subflavus*, *Nesoryzomys*, *O. xanthaeolus*, *Amphinectomys*, *Nectomys*, *Sigmodontomys*, and *Melanomys*.

Nodal support: JK = 18%, DI = 1.

Partitioned evidence: none.

Morphological synapomorphies: tail slightly bicolored (11) and anapophyses present on TL17 (80).

Molecular synapomorphies: none.

TS coding: clade not recovered.

Reduced analysis: clade recovered in some fundamental cladograms.

Remarks: The two main clades within clade D recovered in the combined analysis—(1) *Oryzomys palustris* group, *Lundomys*, *Pseudoryzomys*, and *Holochilus*, and (2) *Nesoryzomys* + *Oryzomys xanthaeolus* + *O. subflavus* + *O. angouya* + *Amphinectomys* + *Nectomys* + *Melanomys* + *Sigmodontomys*—have low nodal support. *O. angouya* and *O. subflavus* are not part of this second major clade in the partitioned analyses. Additional characters are needed to formulate a solid phylogenetic hypothesis for the basal structure of clade D.

Node 42

Composition: *Oryzomys subflavus*, *Nesoryzomys*, *O. xanthaeolus*, *Amphinectomys*, *Nectomys*, *Sigmodontomys*, and *Melanomys*.

Nodal support: JK = 31%, DI = 2.

Partitioned evidence: none.

Morphological synapomorphies: vestigial subsquamosal fenestra (40) and slim central bacular digit (86).

Molecular synapomorphies: 1.

TS coding: clade recovered only in the combined analysis.

Reduced analysis: no change.

Remarks: Additional characters are needed to provide more support for the internal topology of clade D.

Node 43

Composition: *Nesoryzomys*, *Oryzomys xanthaeolus*, *Amphinectomys*, *Nectomys*, *Sigmodontomys*, and *Melanomys*.

Nodal support: JK = 73%, DI = 4.

Partitioned evidence: clade recovered in the morphology-only analysis and in some fundamental cladograms of IRBP-only analysis.

Morphological synapomorphies: single-crest anterior masseteric ridges (46), M2 without protoflexus (64), and M2 with single labial fossette at mesoflexus position (66).

Molecular synapomorphies: 4.

TS coding: no change.

Reduced analysis: slight increase in nodal support.

Remarks: This is one of the few higher-level nodes within clade D with a moderate support. This clade is also recovered in both partitioned analysis, although the *palustris* group is also included in some fundamental cladograms of the IRBP analysis. *Nesoryzomys* is found as the sister group to the clade containing *Sigmodontomys* and *Melanomys* in the IRBP-only analysis.

Node 44

Composition: *Nesoryzomys*.

Nodal support: JK = 100%, DI = 11.

Partitioned evidence: clade recovered in both IRBP-only and morphology-only analyses.

Morphological synapomorphies: dorsal surface of pes solid white (10), scaly tail (12), subtle countershading (15), subauricular patches present (16), large ectotympanic (41), masseteric crests reach anterior to m1 procingulum (47).

Molecular synapomorphies: 5, including 1 unique and unreversed.

TS coding: no change.

Reduced analysis: no change.

Remarks: Monophyly of *Nesoryzomys* is well corroborated by morphological and molecular data (Patton and Hafner, 1983; Weksler, 2003).

Node 45

Composition: *Oryzomys xanthaeolus*, *Amphinectomys*, *Nectomys*, *Sigmodontomys*, and *Melanomys*.

Nodal support: JK = 47%, DI = 2.

Partitioned evidence: clade recovered in the morphology-only analysis but not in the IRBP-only analysis.

Morphological synapomorphies: reduced capsular process of lower incisor alveolus (45), anteroloph joined to anterocone by labial cingulum on M1 (59), and M3 without, or with diminutive, hypoflexus (69).

Molecular synapomorphies: none.

TS coding: clade recovered in some fundamental cladograms of combined analysis.

Reduced analysis: no change.

Remarks: *Oryzomys xanthaeolus* is found as the sister group to the clade including *Nesoryzomys*, *Sigmodontomys*, and *Melanomys* in the IRBP-only analysis.

Node 46

Composition: *Amphinectomys*, *Nectomys*, *Sigmodontomys*, and *Melanomys*.

Nodal support: JK = 87%, DI = 6.

Partitioned evidence: clade recovered in the morphology-only analysis but not in the IRBP-only analysis.

Morphological synapomorphies: hypothenar pad absent (4), pes with extremely small interdigital pads (5), ungual tufts absent on D1, sparse in remaining hindfoot digits (7), tail unicolored (11), incisive foramina do not reach M1 (31), reduced sphenopalatine vacuities (36), flexi meet at midline on M1 (57), M1 with undivided anterocone (58), and enamel bridge connection between paracone and protocone at posteriormost end of protocone on M1 (61).

Molecular synapomorphies: none.

TS coding: clade not recovered in the morphology-only analysis (*Amphinectomys* is excluded).

Reduced analysis: reduced nodal support.

Remarks: *Amphinectomys*, *Nectomys*, *Sigmodontomys*, and *Melanomys* are solely united by morphological characters; in the IRBP-only tree, these four taxa are recovered in a clade that also contains *Nesoryzomys*, *O. xanthaeolus*, and the *O. palustris* group (fig. 36). Nevertheless, the combination of morphological and molecular data unexpectedly increases the nodal support for this clade (e.g., jackknife support in the combined tree increases to 87% from 36% in the morphology-only tree), despite the lack of a single unambiguous molecular synapomorphy (two synapomorphies are observed in ACCTRAN optimization). Students of sigmodontine taxonomy have previously considered *Nectomys* to be close to *Melanomys* (see Goodman, 1918), *Sigmodontomys* (see Hershkovitz, 1944), and *Amphinectomys* (see Malygin et al., 1994). Phylogenetic analyses, however, recovered conflicting results: analysis of cytogenetic data placed *Nectomys* as the sister group of all oryzomyines (Baker et al., 1983; Voss and Carleton, 1993); analyses of morphological characters placed *Nectomys* together with *Oryzomys palustris* (Patton and Hafner, 1983; Steppan, 1995; Weksler, 1996); analysis of allozyme data placed *Nectomys* as the sister group of a clade including *Oryzomys nitidus*, *O. megacephalus*, and *O. keaysi* (Dickerman and Yates, 1995); and analyses of cytochrome *b* placed *Nectomys* together with *Scolomys* (Patton and da Silva, 1995), *Nesoryzomys* and *Holochilus* (Smith and Patton, 1999), or *Oryzomys subflavus* and *O. angouya* (Myers et al., 1995; Bonvicino and Moreira, 2001; Andrade and Bonvicino, 2003; Bonvicino et al., 2003).

Node 47

Composition: *Amphinectomys* and *Nectomys*.

Nodal support: JK = 75%, DI = 2.

Partitioned evidence: clade recovered in the IRBP-only analysis but not in the morphology-only analysis.

Morphological synapomorphies: natatory fringes present (8).

Molecular synapomorphies: 6, including 1 unique and unreversed.

TS coding: clade recovered only in the combined analysis.

Reduced analysis: increased nodal support.

Remarks: *Amphinectomys* and *Nectomys* were also recovered as sister taxa, with high nodal support, in the previous analysis of IRBP sequences (Weksler, 2003). The different position of *Amphinectomys* in the morphology-only analyses likely results from much missing information. The overwhelming molecular signal points to the sister group relationship of *Amphinectomys* and *Nectomys*, corroborating the assessment of Malygin et al. (1994), based on external, cranial, and karyotypic features.

Node 48

Composition: *Nectomys*.

Nodal support: JK = 49%, DI = 1.

Partitioned evidence: clade recovered in the morphology-only analysis. *Nectomys apicalis* does not have IRBP data and consequently was not included in the IRBP-only and reduced analyses.

TS coding: clade recovered in the combined analysis and in some fundamental cladograms of the morphology-only analysis.

Morphological synapomorphies: subtle countershading (15) and pointed nasal posterior terminus (18).

Remarks: Monophyly of *Nectomys* is uncontested, mainly because all *Nectomys* species share unique cranial and integumental characters (Hershkovitz, 1944; Bonvicino, 1994; Patton et al., 2000; Voss et al., 2001). *Nectomys* species are so similar to each other that at one point all forms were placed as subspecies under a single species (Hershkovitz, 1944). Nevertheless, no explicit phylogenetic analysis has demonstrated *Nectomys* monophyly. The low nodal support of the combined analysis is probably caused by the lack of IRBP sequence by *N. apicalis*.

Node 49

Composition: *Sigmodontomys* + *Melanomys*.

Nodal support: JK = 66%, DI = 3.

Partitioned evidence: clade recovered in the IRBP-only analysis but not in the morphology-only analysis.

Morphological synapomorphies: dorsal surface of pes brown (10) and simple posterolateral palatal pits (34).

Molecular synapomorphies: 6, including 1 unique and unreversed.

TS coding: decreased nodal support in combined analysis.

Reduced analysis: increased resampling values.

Remarks: Weksler (2003), based on IRBP data, first advanced the hypothesis of a close relationship between *Sigmodontomys* and *Melanomys*. The present analysis strongly corroborates that assessment, providing morphological synapomorphies for that relationship. Although morphological data alone did not recover *Sigmodontomys* as the sister group of *Melanomys*, they still were recovered in proximity in a clade that included additionally only *Nectomys* (fig. 34). *Melanomys* has been previously linked to *Sigmodontomys* (as a subgenus of *Nectomys*; Goodman, 1918), but previous phylogenetic analyses recovered different results: analysis of cytogenetic data placed *Melanomys* in a clade with *Oryzomys palustris* and *O. couesi* (Baker et al., 1983; but see Voss and Carleton, 1993, fig. 4); and analyses of morphological characters placed *Melanomys* as the sister group to a clade containing *Oryzomys albigularis*, *O. keaysi*, and *Oligoryzomys destructor* (Patton and Hafner, 1983). In the previous analysis of IRBP sequences, *Melanomys* appears as the sister group of *Sigmodontomys* in a highly supported clade (Weksler, 2003).

Node 50

Composition: *Melanomys* + *Sigmodontomys aphrastus*.

Nodal support: JK = 46%, DI = 1.

Partitioned evidence: none; *S. aphrastus* does not have IRBP data and consequently was not included in the IRBP-only and reduced analyses.

TS coding: clade recovered in some fundamental cladograms of combined analysis.

Morphological synapomorphies: no countershading (15) and orthodont incisors (52).

Remarks: *Sigmodontomys* appears as paraphyletic in all CO analyses, but it recovered as monophyletic in some fundamental cladograms of combined TS analysis and in the TS morphology-only analysis. Nodal support for these arrangements are weak, and *Sigmodontomys* is recovered as monophyletic in trees one step longer in the morphology-only and combined CO analyses. *S. aphrastus* has always been regarded as an enigmatic taxon, being linked variously to *Nectomys* (see Hershkovitz, 1944) or to *Oryzomys hammondi* (see Hershkovitz, 1948; Carleton and Musser, 1995). Its current placement in the genus *Sigmodontomys* was not based on character-based study, but rather on an assessment of the holotype of *S. aphrastus* (a young specimen) by Ray (1962; see Musser and Carleton, 1993).

APPENDIX 4
Character Transformations in Morphological Tree

Character transformations in morphological tree with polymorphisms analyzed as composites. Char. indicates character number; CI, consistency index; and Opt., optimization method (in which optimizations are indicated by A, ACCTRAN; D, DELTRAN; and U, unambiguous).

Node	Taxon content	Char.	CI	Opt.	Change	Description
1	Sigmodontinae	12	0.33	U	0 → 1	furred tail
		29	0.10	U	0 → 1	zygomatic plate anterior to M1 alveolus
		48	1.00	U	0 → 1	derived hyoid
		79	1.00	U	0 → 1	first rib articulates with CE7 and TL1
		82	1.00	U	0 → 1	humerus without entepicondylar foramen
		85	1.00	U	0 → 1	lateral bacular mounds present
		95	1.00	U	0 → 1	dorsal prostates present
		35	0.33	A	0 → 1	excavated parapterygoid
		80	0.11	A	0 → 1	anapophyses absent on TL17
		96	0.50	A	0 → 1	compact ampullary glands
2	1 – *Thomasomys*	1	0.50	U	1 → 2	eight mammae
		6	0.13	U	0 → 1	pes with squamate plantar surface
		28	0.33	U	0 → 1	broad zygomatic plate
		38	0.25	U	0 → 1	alisphenoid strut absent
		45	0.11	U	1 → 0	capsular process of lower incisor alveolus absent
		83	0.25	U	0 → 1	humerus with supratrochlear foramen
		84	1.00	U	0 → 1	subequal proximal edge of trochlear process and posterior articular facet of calcaneum
		5	0.40	A	0 → 1	pes with regular interdigital pads
		11	0.12	A	0 → 1	tail slightly bicolored
3	2 – *Delomys*	22	0.18	U	0 → 3	weakly cuneate interorbit with small crests
		32	0.17	U	0 → 1	medium palate
		72	0.17	U	1 → 0	m1 without ectolophid
		78	1.00	U	0 → 1	12 ribs
		81	0.33	U	0 → 1	hemal arches present on CA2–3
		36	0.19	A	1 → 0	large sphenopalatine vacuities
		98	0.50	A	0 → 1	gall bladder absent
		35	0.33	D	0 → 1	excavated parapterygoid
4	Oryzomyini	30	0.20	U	0 → 1	jugal reduced, constricted centrally
		34	0.33	U	1 → 2	simple posterolateral palatal pits
		37	0.13	U	0 → 1	derived carotid circulation 1
		42	1.00	U	0 → 1	tegmen tympani absent
		5	0.40	D	0 → 1	pes with regular interdigital pads
		11	0.12	D	0 → 1	tail slightly bicolored
		96	0.50	D	0 → 1	compact ampullary glands
		98	0.50	D	0 → 1	gall bladder absent
5	Clade B* + 6	7	0.33	U	0 → 1	ungual tufts absent on D1, developed in remaining hindfoot digits
		31	0.17	U	0 → 1	incisive foramina do not reach M1
		32	0.17	U	1 → 2	long palate
		68	0.14	U	0 → 1	M3 without posteroloph
		36	0.19	A	0 → 1	reduced sphenopalatine vacuities
		58	0.12	A	0 → 2	M1 with undivided anterocone
6	Clade A + clade C	19	0.14	U	0 → 1	nasals reach posterior to maxillary-frontal suture
		45	0.11	U	0 → 1	reduced capsular process of lower incisor alveolus
		61	0.29	U	0 → 1	enamel bridge connection between paracone and protocone at middle of protocone on M1
		29	0.10	A	1 → 0	zygomatic plate at same level as M1 alveolus
		80	0.11	D	0 → 1	anapophyses absent on TL17

APPENDIX 4
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
7	Clade A	15	0.11	U	0 → 1	subtle countershading
		26	0.25	U	1 → 2	narrow interparietal
		43	0.17	U	1 → 0	completely ossified mastoid
		64	0.20	U	0 → 1	M2 without protoflexus
		67	0.33	U	0 → 1	M3 without mesoloph
		37	0.13	A	1 → 2	derived carotid circulation 2
		59	0.60	A	0 → 2	anteroloph joined to anterocone by labial cingulum on M1
		81	0.33	A	1 → 0	hemal arches absent on CA2–3
		58	0.12	D	0 → 2	M1 with undivided anterocone
8	*Zygodontomys*	22	0.18	U	3 → 4	strongly cuneate interorbit with overhanging crests
		31	0.17	U	1 → 0	incisive foramina pass M1
		36	0.19	U	1 → 0	large sphenopalatine vacuities
		44	0.17	U	0 → 1	mental foramen located at diastema
		47	0.50	U	1 → 2	masseteric crests reach anterior to m1 procingulum
		51	0.20	U	0 → 1	m2 with 3 roots
		61	0.29	U	1 → 2	protocone and paracone forming single dentine basin without enamel connection on M1
		62	0.50	U	0 → 2	M1 and M2 without mesolophs
		73	0.33	U	0 → 2	m1 and m2 without mesolophids
		77	0.33	U	0 → 2	m3 without posteroflexid
		29	0.10	A	0 → 1	zygomatic plate anterior to M1 alveolus
		59	0.60	A	2 → 3	M1 without anteroloph
		59	0.60	D	0 → 3	M1 without anteroloph
9	Clade C	41	0.29	U	1 → 0	small ectotympanic
		87	0.25	U	1 → 0	bacular mounds not covered by rim of nonspinous tissue
		45	0.11	A	1 → 2	developed capsular process of lower incisor alveolus
		58	0.12	A	2 → 0	M1 with deeply divided anterocone
		29	0.10	D	1 → 0	zygomatic plate at same level as M1 alveolus
10	*Neacomys*	11	0.12	U	1 → 0	tail unicolored
		13	0.50	U	0 → 1	spiny pelage
		14	0.20	U	0 → 1	totally white ventral hairs
		20	0.22	U	1 → 2	premaxillaries anterior to terminus of nasal
		22	0.18	U	3 → 4	strongly cuneate interorbit with overhanging crests
		69	0.09	U	0 → 1	M3 without hypoflexus (or diminutive)
		94	1.00	A	0 → 1	preputial glands do not extend to the ventral flexure of the penis
11	*Neacomys minutus*	37	0.13	U	1 → 0	primitive carotid circulation
	+ *N. spinosus*	45	0.11	D	1 → 2	developed capsular process of lower incisor alveolus
12	26: *Neacomys*	22	0.18	U	3 → 0	amphoral interorbit with rounded edges
		30	0.20	U	1 → 2	jugal absent
		44	0.17	A	0 → 1	mental foramen located at diastema
		45	0.11	D	1 → 2	developed capsular process of lower incisor alveolus
13	*Microryzomys* +	28	0.33	U	1 → 0	narrow zygomatic plate
	Oryzomys	32	0.17	U	2 → 1	medium palate
	balneator	37	0.13	U	1 → 0	primitive carotid circulation
		70	0.50	U	1 → 2	m1 with anteromedian flexid
		99	0.20	U	0 → 1	extended gastric glandular epithelium
14	*Oligoryzomys*	35	0.33	U	1 → 0	flat parapterygoid
		36	0.19	U	1 → 0	large sphenopalatine vacuities

APPENDIX 4
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
		47	0.50	U	1 → 2	masseteric crests reach anterior to m1 procingulum
		68	0.14	U	1 → 0	M3 with posteroloph
		88	0.33	U	0 → 1	glans penis with spinous dorsal papilla
		81	0.33	A	1 → 2	hemal arches with spinous posterior border
		44	0.17	D	0 → 1	mental foramen located at diastema
15	*Oligoryzomys nigripes* + *Ol. fulvescens*	90	0.50	U	1 → 2	preputial glands absent
		81	0.33	D	1 → 2	hemal arches with spinous posterior border
16	*Oligoryzomys flavescens* + *Ol. fornesi* + *Ol. stramineus*	69	0.09	U	0 → 1	M3 without hypoflexus (or diminutive)
17	*Oligoryzomys flavescens* + *Ol. fornesi*	15	0.11	U	0 → 1	subtle countershading
18	Clade B*	6	0.13	U	1 → 0	pes with smooth plantar surface
		72	0.17	U	0 → 1	m1 with ectolophid
		57	0.20	A	0 → 1	flexi meet at midline on M1
		58	0.12	D	0 → 2	M1 with undivided anterocone
19	*Oryzomys megacephalus* + *O. talamancae* + *Handleyomys* + *O. albigularis* + *O. levipes*	96	0.50	U	1 → 0	ampullary glands forming tufts of tubules
		97	0.50	U	0 → 1	subterminal flexure of vesicular gland irregularly lobed
		22	0.18	A	3 → 1	amphoral interorbit with square edges
20	*Oryzomys talamancae* + *Handleyomys* + *O. albigularis* + *O. levipes*	37	0.13	U	1 → 0	primitive carotid circulation
		45	0.11	U	0 → 1	reduced capsular process of lower incisor alveolus
		69	0.09	U	0 → 1	M3 without hypoflexus (or diminutive)
		57	0.20	A	1 → 2	flexi deeply interpenetrating on M1
		80	0.11	A	1 → 0	anapophyses present on TL17
		90	0.50	A	1 → 2	preputial glands absent
		57	0.20	D	0 → 2	flexi deeply interpenetrating on M1
21	*Handleyomys* + *Oryzomys albigularis* + *O. levipes*	50	0.25	U	0 → 1	m1 with 3 roots
		21	0.13	A	0 → 1	lacrimal articulates mainly with maxillary
		22	0.18	A	1 → 0	amphoral interorbit with rounded edges
		22	0.18	D	3 → 1	amphoral interorbit with square edges
22	*Oryzomys albigularis* + *O. levipes*	32	0.17	U	2 → 1	medium palate
		34	0.33	U	2 → 3	complex posterolateral palatal pits
		58	0.12	U	2 → 0	M1 with deeply divided anterocone
		68	0.14	U	1 → 0	M3 with posteroloph
		38	0.25	A	1 → 0	alisphenoid strut present
23	*Oryzomys yunganus* + 24	11	0.12	U	1 → 2	tail strongly bicolored
		36	0.19	U	1 → 2	completely ossified sphenopalatine
		66	0.17	A	0 → 1	M2 with labial and lingual fossetti at mesoflexus position
		57	0.20	D	0 → 1	flexi meet at midline on M1
24	25 + 27	37	0.13	U	1 → 0	primitive carotid circulation
		43	0.17	U	1 → 0	completely ossified mastoid
25	*nitidus* group	50	0.25	U	0 → 1	m1 with 3 roots
		80	0.11	A	1 → 0	anapophyses present on TL17
26	*Oryzomys lamia* + *O. russatus*	45	0.11	U	0 → 2	developed capsular process of lower incisor alveolus
		72	0.17	U	1 → 0	m1 without ectolophid

APPENDIX 4
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
27	*Oryzomys*	11	0.12	U	2 → 0	tail unicolored
	hammondi +	25	0.20	U	0 → 1	parietal with deep lateral expansion
	Oecomys	28	0.33	U	1 → 0	narrow zygomatic plate
		68	0.14	U	1 → 0	M3 with posteroloph
		66	0.17	A	1 → 0	M2 with single labial fossette at mesoflexus position
28	*Oecomys*	5	0.40	U	1 → 0	pes with extremely developed interdigital pads
		22	0.18	U	3 → 4	strongly cuneate interorbit with overhanging crests
		45	0.11	U	0 → 1	reduced capsular process of lower incisor alveolus
		49	0.14	U	0 → 1	M1 with labial root
		65	0.50	U	0 → 1	M2 with accessory loph to paracone
29	28 – *Oecomys*	29	0.10	U	1 → 0	zygomatic plate at same level as M1 alveolus
	catherinae	14	0.20	A	0 → 1	totally white ventral hairs
		43	0.17	A	0 → 1	mastoid with large fenestra
30	*Oecomys bicolor* +	21	0.13	U	0 → 1	lacrimal articulates mainly with maxillary
	Oe. trinitatis	45	0.11	U	1 → 2	developed capsular process of lower incisor alveolus
		80	0.11	D	0 → 1	anapophyses absent on TL17
31	*Oecomys concolor*	15	0.11	U	0 → 1	subtle countershading
	+ *Oe. mamorae*	37	0.13	U	0 → 2	derived carotid circulation 2
		14	0.20	D	0 → 1	totally white ventral hairs
		43	0.17	D	0 → 1	mastoid with large fenestra
32	Clade D*	25	0.20	U	0 → 1	parietal with deep lateral expansion
		34	0.33	U	2 → 3	complex posterolateral palatal pits
		37	0.13	U	1 → 2	derived carotid circulation 2
		80	0.11	A	1 → 0	anapophyses present on TL17
		81	0.33	A	1 → 2	hemal arches with spinous posterior border
		36	0.19	D	1 → 0	large sphenopalatine vacuities
33	32: *Oryzomys*	45	0.11	U	0 → 2	developed capsular process of lower incisor alveolus
	polius	49	0.14	U	0 → 1	M1 with labial root
		50	0.25	U	0 → 1	m1 with 3 roots
		61	0.29	U	0 → 1	enamel bridge connection between paracone and protocone at middle of protocone on M1
		66	0.17	A	0 → 1	M2 with labial and lingual fossetti at mesoflexus position
		81	0.33	D	1 → 2	hemal arches with spinous posterior border
34	33: *Oryzomys*	7	0.33	U	0 → 1	ungual tufts absent on D1, developed in remaining hindfoot digits
	angouya	50	0.25	U	1 → 2	m1 with 4 roots
		86	0.25	U	0 → 1	slim central bacular digit
		87	0.25	U	1 → 0	bacular mounds not covered by rim of nonspinous tissue
		32	0.17	A	1 → 2	long palate
		40	0.38	A	0 → 2	vestigial subsquamosal fenestra
35	*Oryzomys*	29	0.10	U	1 → 0	zygomatic plate at same level as M1 alveolus
	subflavus + 36	58	0.12	U	0 → 1	M1 with anterocone divided by internal fold
		97	0.50	A	0 → 1	subterminal flexure of vesicular gland irregularly lobed
		66	0.17	D	0 → 1	M2 with labial and lingual fossetti at mesoflexus position
36	37 + 39	51	0.20	U	0 → 1	m2 with 3 roots
		80	0.11	U	0 → 1	anapophyses absent on TL17
		11	0.12	A	1 → 2	tail strongly bicolored
		40	0.38	A	2 → 0	subsquamosal fenestra present

APPENDIX 4
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
		32	0.17	D	1 → 2	long palate
37	*O. chapmani* + *O. alfaroi* + *O. rostratus*	31	0.17	U	0 → 1	incisive foramina do not reach M1
		58	0.12	U	1 → 2	M1 with undivided anterocone
		68	0.14	U	0 → 1	M3 without posteroloph
		69	0.09	U	0 → 1	M3 without hypoflexus (or diminutive)
		81	0.33	U	2 → 1	hemal arches with simple posterior border
		6	0.13	A	1 → 0	pes with smooth plantar surface
		25	0.20	A	1 → 0	parietal without lateral expansion
38	*O. alfaroi* + *O. rostratus*	37	0.13	U	2 → 0	primitive carotid circulation
		45	0.11	U	2 → 1	reduced capsular process of lower incisor alveolus
39	*Oryzomys* sensu stricto + 41	4	0.33	U	0 → 1	hypothenar pad absent
		5	0.40	U	1 → 2	pes with extremely small interdigital pads
		7	0.33	U	1 → 2	ungual tufts absent on D1, sparse in remaining hindfoot digits
		21	0.13	U	0 → 1	lacrimal articulates mainly with maxillary
		9	0.29	A	0 → 1	intermediate interdigital webbing
		19	0.14	A	0 → 1	nasals reach posterior to maxillary-frontal suture
		86	0.25	A	1 → 0	long central bacular digit
40	*Oryzomys* sensu stricto	22	0.18	U	3 → 4	strongly cuneate interorbit with overhanging crests
		26	0.25	U	1 → 2	narrow interparietal
		75	0.33	U	0 → 1	m2 and m3 with anterolophid
		88	0.33	U	0 → 1	glans penis with spinous dorsal papilla
		89	0.50	U	0 → 1	urethral process of glans penis with subapical process
		86	0.25	D	1 → 0	long central bacular digit
41	*Pseudoryzomys* + *Lundomys* + *Holochilus*	28	0.33	U	1 → 2	zygomatic spine present
		34	0.33	U	3 → 2	simple posterolateral palatal pits
		59	0.60	U	0 → 3	M1 without anteroloph
		62	0.50	U	0 → 1	M1 and M2 with reduced mesolophs
		77	0.33	U	0 → 1	m3 with reduced posteroflexid
		67	0.33	A	0 → 1	M3 without mesoloph
		73	0.33	A	0 → 2	m1 and m2 without mesolophids
		97	0.50	A	1 → 0	subterminal flexure of vesicular gland rounded and smooth
		99	0.20	A	0 → 1	extended gastric glandular epithelium
		9	0.29	D	0 → 1	intermediate interdigital webbing
		73	0.33	D	0 → 1	m1 and m2 with small mesolophids
42	*Holochilus* + *Lundomys*	3	0.33	U	0 → 1	ungual tufts absent on forefeet digits
		7	0.33	U	2 → 3	ungual tufts absent on hindfoot digits
		8	0.33	U	0 → 1	natatory fringes present
		9	0.29	U	1 → 2	developed interdigital webbing
		15	0.11	U	0 → 1	subtle countershading
		22	0.18	U	3 → 1	amphoral interorbit with square edges
		33	1.00	U	0 → 1	palatine median longitudinal ridge present
		35	0.33	U	1 → 2	deeply excavated parapterygoid
		55	1.00	U	0 → 1	lateral cingula absent on molars
		56	1.00	U	0 → 1	posteriorly divergent maxillary toothrow
		57	0.20	U	0 → 1	flexi meet at midline on M1
		61	0.29	U	1 → 0	enamel bridge connection between paracone and protocone at posteriormost end of protocone on M1
		77	0.33	U	1 → 2	m3 without posteroflexid
		80	0.11	U	1 → 0	anapophyses present on TL17
		11	0.12	A	2 → 0	tail unicolored

APPENDIX 4
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
		11	0.12	D	1 → 0	tail unicolored
		86	0.25	D	1 → 0	long central bacular digit
43	*Holochilus*	22	0.18	U	1 → 2	amphoral interorbit with developed beads
		23	1.00	U	0 → 1	postorbital ridge present
		24	0.33	U	0 → 1	frontosquamosal suture anterior to frontoparietal
		31	0.17	U	0 → 1	incisive foramina do not reach M1
		38	0.25	U	1 → 0	alisphenoid strut present
		41	0.29	U	1 → 2	large ectotympanic
		46	0.20	U	0 → 1	single-crest anterior masseteric ridges
		47	0.50	U	1 → 2	masseteric crests reach anterior to m1 procingulum
		53	1.00	U	0 → 1	incisors with labial bevel
		54	1.00	U	0 → 1	molars hypsodont
		57	0.20	U	1 → 2	flexi deeply interpenetrating on M1
		58	0.12	U	1 → 2	M1 with undivided anterocone
		63	0.50	U	0 → 1	median mure not connected to protocone on M1
		64	0.20	U	0 → 1	M2 without protoflexus
		19	0.14	A	1 → 0	nasals reach anterior to maxillary-frontal suture
		67	0.33	A	1 → 0	M3 with mesoloph
		87	0.25	A	0 → 1	bacular mounds covered by rim of nonspinous tissue
		89	0.50	A	0 → 1	urethral process of glans penis with subapical process
		73	0.33	D	1 → 2	m1 and m2 without mesolophids
		99	0.20	D	0 → 1	extended gastric glandular epithelium
44	*Nesoryzomys* + *Oryzomys xanthaeolus* + *Amphinectomys* + *Nectomys* + *Sigmodontomys* + *Melanomys*	21	0.13	U	0 → 1	lacrimal articulates mainly with maxillary
		43	0.17	U	1 → 0	completely ossified mastoid
		46	0.20	U	0 → 1	single-crest anterior masseteric ridges
		64	0.20	U	0 → 1	M2 without protoflexus
		66	0.17	A	1 → 0	M2 with single labial fossette at mesoflexus position
45	*Nesoryzomys*	10	0.40	U	1 → 0	dorsal surface of pes solid white
		12	0.33	U	1 → 0	scaly tail
		15	0.11	U	0 → 1	subtle countershading
		16	0.33	U	0 → 1	subauricular patches present
		22	0.18	U	3 → 1	amphoral interorbit with square edges
		41	0.29	U	1 → 2	large ectotympanic
		47	0.50	U	1 → 2	masseteric crests reach anterior to m1 procingulum
		91	0.50	A	0 → 1	ventral prostates absent
		92	0.50	A	0 → 1	anterior prostates absent
		93	1.00	A	0 → 1	vesicular glands present with small diverticula
46	44 – *Nesoryzomys*	22	0.18	U	3 → 4	strongly cuneate interorbit with overhanging crests
		45	0.11	U	2 → 1	reduced capsular process of lower incisor alveolus
		59	0.60	U	0 → 2	anteroloph joined to anterocone by labial cingulum on M1
		69	0.09	U	0 → 1	M3 without hypoflexus (or diminutive)
		20	0.22	A	1 → 2	premaxillaries anterior to terminus of nasal
		26	0.25	A	1 → 2	narrow interparietal
		40	0.38	D	0 → 2	vestigial subsquamosal fenestra
47	46 – *Oryzomys xanthaeolus*	31	0.17	U	0 → 1	incisive foramina do not reach M1
		36	0.19	U	0 → 1	reduced sphenopalatine vacuities

APPENDIX 4
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
		52	0.20	U	0 → 1	orthodont incisors
		7	0.33	A	1 → 2	ungual tufts absent on D1, sparse in remaining hindfoot digits
		11	0.12	A	1 → 0	tail unicolored
		58	0.12	A	0 → 2	M1 with undivided anterocone
		20	0.22	D	1 → 2	premaxillaries anterior to terminus of nasal
48	*Melanomys* + *Sigmodontomys* + *Nectomys*	10	0.40	U	1 → 2	dorsal surface of pes brown
		19	0.14	U	0 → 1	nasals reach posterior to maxillary-frontal suture
		24	0.33	U	0 → 1	frontosquamosal suture anterior to frontoparietal
		34	0.33	U	3 → 2	simple posterolateral palatal pits
		15	0.11	A	0 → 2	no countershading
		32	0.17	A	2 → 1	medium palate
		7	0.33	D	1 → 2	ungual tufts absent on D1, sparse in remaining hindfoot digits
		11	0.12	D	1 → 0	tail unicolored
		15	0.11	D	0 → 1	subtle countershading
		58	0.12	D	0 → 2	M1 with undivided anterocone
49	*Sigmodontomys* + *Nectomys*	4	0.33	U	0 → 1	hypothenar pad absent
		5	0.40	U	1 → 2	pes with extremely small interdigital pads
		57	0.20	U	0 → 1	Flexi meet at midline on M1
		61	0.29	U	1 → 0	enamel bridge connection between paracone and protocone at posteriormost end of protocone on M1
		76	0.25	U	0 → 1	m3 without anterolabial cingulum
		99	0.20	U	0 → 1	extended gastric glandular epithelium
		18	0.33	A	0 → 1	pointed nasal posterior terminus
		26	0.25	A	2 → 1	long interparietal
		29	0.10	A	1 → 0	zygomatic plate at same level as M1 alveolus
50	*Sigmodontomys alfari* + *Nectomys*	9	0.29	U	0 → 1	intermediate interdigital webbing
		52	0.20	U	1 → 0	opisthodont incisors
		15	0.11	A	2 → 1	subtle countershading
		45	0.11	A	1 → 2	developed capsular process of lower incisor alveolus
51	*Nectomys*	8	0.33	U	0 → 1	natatory fringes present
		9	0.29	U	1 → 2	developed interdigital webbing
		10	0.40	U	2 → 1	dorsal surface of pes pale
		34	0.33	U	2 → 3	complex posterolateral palatal pits
		29	0.10	A	0 → 1	zygomatic plate anterior to M1 alveolus
		36	0.19	A	1 → 2	completely ossified sphenopalatine
		86	0.25	A	1 → 0	long central bacular digit
		18	0.33	D	0 → 1	pointed nasal posterior terminus

APPENDIX 5
Character Transformations in Combined Tree

Character transformations in the combined tree with polymorphisms analyzed as composites. Char. indicates character number; CI, consistency index; Opt., optimization method (in which optimizations are indicated by A, ACCTRAN; D, DELTRAN; and U, unambiguous).

Node	Taxon content	Char.	CI	Opt.	Change	Description
1	Sigmodontinae	12	0.33	U	0 → 1	furred tail
		29	0.09	U	0 → 1	zygomatic plate anterior to M1 alveolus
		48	1.00	U	0 → 1	derived hyoid
		79	1.00	U	0 → 1	first rib articulates with CE7 and TL1
		82	1.00	U	0 → 1	humerus without entepicondylar foramen
		85	1.00	U	0 → 1	lateral bacular mounds present
		95	1.00	U	0 → 1	dorsal prostates present
		15	0.13	A	0 → 1	subtle countershading
		35	0.33	A	0 → 1	excavated parapterygoid
		80	0.13	A	0 → 1	anapophyses absent on TL17
		96	0.50	A	0 → 1	compact ampullary glands
2	1 – *Thomasomys*	1	0.50	U	1 → 2	8 mammae
		6	0.13	U	0 → 1	pes with squamate plantar surface
		28	0.29	U	0 → 1	Broad zygomatic plate
		38	0.25	U	0 → 1	alisphenoid strut absent
		45	0.11	U	1 → 0	capsular process of lower incisor alveolus absent
		83	0.25	U	0 → 1	humerus with supratrochlear foramen
		84	1.00	U	0 → 1	subequal proximal edge of trochlear process and posterior articular facet of calcaneum
		5	0.33	A	0 → 1	Pes with regular interdigital pads
3	2 – *Delomys*	22	0.17	U	0 → 3	weakly cuneate interorbit with small crests
		32	0.17	U	0 → 1	medium palate
		64	0.25	U	0 → 1	M2 without protoflexus
		78	1.00	U	0 → 1	12 ribs
		72	0.14	A	1 → 0	m1 without ectolophid
		81	0.40	A	0 → 1	hemal arches present on CA2–3
		98	0.50	A	0 → 1	gall bladder absent
		15	0.13	D	0 → 1	subtle countershading
		35	0.33	D	0 → 1	excavated parapterygoid
		80	0.13	D	0 → 1	anapophyses absent on TL17
4	Oryzomyini	7	0.30	U	0 → 1	ungual tufts absent on D1, developed in remaining hindfoot digits
		31	0.17	U	0 → 1	incisive foramina do not reach M1
		42	1.00	U	0 → 1	tegmen tympani absent
		58	0.12	U	0 → 2	M1 with undivided anterocone
		61	0.22	U	0 → 1	enamel bridge connection between paracone and protocone at middle of protocone on M1
		36	0.16	A	1 → 2	completely ossified sphenopalatine
		43	0.14	A	1 → 0	completely ossified mastoid
		5	0.33	D	0 → 1	pes with regular interdigital pads
		98	0.50	D	0 → 1	gall bladder absent
5	4 – *Oryzomys hammondi*	32	0.17	U	1 → 2	long palate
		34	0.38	U	1 → 2	simple posterolateral palatal pits

APPENDIX 5
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
		45	0.11	U	0 → 1	reduced capsular process of lower incisor alveolus
		68	0.14	U	0 → 1	M3 without posteroloph
		30	0.22	A	0 → 1	jugal reduced, constricted centrally
		96	0.50	D	0 → 1	compact ampullary glands
6	Clade A	26	0.25	U	1 → 2	narrow interparietal
		67	0.33	U	0 → 1	M3 without mesoloph
		19	0.11	A	0 → 1	nasals reach posterior to maxillary-frontal suture
		37	0.13	A	0 → 2	derived carotid circulation 2
		59	0.60	A	0 → 2	anteroloph joined to anterocone by labial cingulum on M1
		81	0.40	A	1 → 0	hemal arches absent on CA2–3
		43	0.14	D	1 → 0	completely ossified mastoid
		72	0.14	D	1 → 0	m1 without ectolophid
7	*Zygodontomys*	11	0.13	U	0 → 1	tail slightly bicolored
		22	0.17	U	3 → 4	strongly cuneate interorbit with overhanging crests
		31	0.17	U	1 → 0	incisive foramina pass M1
		44	0.17	U	0 → 1	mental foramen located at diastema
		47	0.50	U	1 → 2	masseteric crests reach anterior to m1 procingulum
		51	0.20	U	0 → 1	m2 with 3 roots
		61	0.22	U	1 → 2	protocone and paracone forming single dentine basin without enamel connection on M1
		62	0.50	U	0 → 2	M1 and M2 without mesolophs
		73	0.33	U	0 → 2	m1 and m2 without mesolophids
		77	0.33	U	0 → 2	m3 without posteroflexid
		36	0.16	A	2 → 0	large sphenopalatine vacuities
		59	0.60	A	2 → 3	M1 without anteroloph
		30	0.22	D	0 → 1	jugal reduced, constricted centrally
		36	0.16	D	1 → 0	large sphenopalatine vacuities
		59	0.60	D	0 → 3	M1 without anteroloph
8	5 – Clade A	64	0.25	U	1 → 0	M2 with protoflexus
		43	0.14	A	0 → 1	mastoid with large fenestra
		30	0.22	D	0 → 1	jugal reduced, constricted centrally
		81	0.40	D	0 → 1	hemal arches present on CA2–3
9	Clade B	6	0.13	U	1 → 0	pes with smooth plantar surface
		57	0.14	U	0 → 1	flexi meet at midline on M1
		61	0.22	A	1 → 0	enamel bridge connection between paracone and protocone at posteriormost end of protocone on M1
		72	0.14	A	0 → 1	m1 with ectolophid
		36	0.16	D	1 → 2	completely ossified sphenopalatine
10	*nitidus* group	11	0.13	U	0 → 2	tail strongly bicolored
		50	0.18	U	0 → 1	m1 with 3 roots
		80	0.13	U	1 → 0	anapophyses present on TL17
		66	0.17	A	0 → 1	M2 with labial and lingual fossetti at mesoflexus position
11	*Oryzomys lamia* + *O. russatus*	45	0.11	U	1 → 2	developed capsular process of lower incisor alveolus
		72	0.14	U	1 → 0	m1 without ectolophid

APPENDIX 5
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
		61	0.22	D	1 → 0	enamel bridge connection between paracone and protocone at posteriormost end of protocone on M1
12	13 + 18	49	0.14	A	0 → 1	M1 with labial root
		61	0.22	D	1 → 0	enamel bridge connection between paracone and protocone at posteriormost end of protocone on M1
13	*Oecomys*	5	0.33	U	1 → 0	pes with extremely developed interdigital pads
		22	0.17	U	3 → 4	strongly cuneate interorbit with overhanging crests
		25	0.20	U	0 → 1	parietal with deep lateral expansion
		28	0.29	U	1 → 0	narrow zygomatic plate
		65	0.50	U	0 → 1	M2 with accessory loph to paracone
		68	0.14	U	1 → 0	M3 with posteroloph
		49	0.14	D	0 → 1	M1 with labial root
14	13 – *Oecomys catherinae*	29	0.09	U	1 → 0	zygomatic plate at same level as M1 alveolus
		14	0.20	A	0 → 1	totally white ventral hairs
15	*Oecomys bicolor* + *Oe. trinitatis*	21	0.13	U	0 → 1	lacrimal articulates mainly with maxillary
		45	0.11	U	1 → 2	developed capsular process of lower incisor alveolus
16	*Oecomys mamorae* + *Oe. concolor*	15	0.13	U	0 → 1	subtle countershading
		37	0.13	U	0 → 2	derived carotid circulation 2
		14	0.20	D	0 → 1	totally white ventral hairs
17	18 + 21	69	0.09	U	0 → 1	M3 without hypoflexus (or diminutive)
		97	0.67	U	0 → 1	subterminal flexure of vesicular gland irregularly lobed
18	*Handleyomys* + *O. chapmani* + *O. alfaroi* + *O. rostratus*	50	0.18	U	0 → 1	m1 with 3 roots
		51	0.20	U	0 → 1	m2 with 3 roots
		66	0.17	U	0 → 1	M2 with labial and lingual fossetti at mesoflexus position
		86	0.25	A	0 → 1	slim central bacular digit
		87	0.20	A	1 → 0	bacular mounds not covered by rim of nonspinous tissue
		49	0.14	D	0 → 1	M1 with labial root
19	*O. chapmani* + *O. alfaroi* + *O. rostratus*	36	0.16	U	2 → 0	large sphenopalatine vacuities
		57	0.14	U	1 → 0	flexi not interpenetrating on M1
		61	0.22	U	0 → 1	enamel bridge connection between paracone and protocone at middle of protocone on M1
		34	0.38	A	2 → 3	complex posterolateral palatal pits
		50	0.18	D	1 → 2	m1 with 4 roots
		86	0.25	D	0 → 1	slim central bacular digit
		87	0.20	D	1 → 0	bacular mounds not covered by rim of nonspinous tissue
20	*Oryzomys chapmani* + *O. rostratus*	72	0.14	U	1 → 0	m1 without ectolophid
		29	0.09	A	1 → 0	zygomatic plate at same level as M1 alveolus
		97	0.67	A	1 → 2	subterminal flexure of vesicular gland small and finger-shaped
		34	0.38	D	2 → 3	complex posterolateral palatal pits
21	22 + 23	11	0.13	U	0 → 1	tail slightly bicolored

APPENDIX 5
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
		96	0.50	U	1 → 0	ampullary glands forming tufts of tubules
		49	0.14	A	1 → 0	M1 without labial root
22	*Oryzomys megacephalus* + *O. yunganus*	37	0.13	U	0 → 1	derived carotid circulation 1
		45	0.11	U	1 → 0	capsular process of lower incisor alveolus absent
23	*O. talamancae* + *O. levipes* + *O. albigularis*	36	0.16	U	2 → 1	reduced sphenopalatine vacuities
		57	0.14	U	1 → 2	flexi deeply interpenetrating on M1
		80	0.13	U	1 → 0	anapophyses present on TL17
		34	0.38	A	2 → 3	complex posterolateral palatal pits
		90	0.45	A	1 → 2	preputial glands absent
24	*Oryzomys levipes* + *O. albigularis*	22	0.17	U	3 → 1	amphoral interorbit with square edges
		32	0.17	U	2 → 1	medium palate
		50	0.18	U	0 → 1	m1 with 3 roots
		58	0.12	U	2 → 0	M1 with deeply divided anterocone
		68	0.14	U	1 → 0	M3 with posteroloph
		38	0.25	A	1 → 0	alisphenoid strut present
		34	0.38	D	2 → 3	complex posterolateral palatal pits
25	Clade C + clade D	58	0.12	U	2 → 0	M1 with deeply divided anterocone
		22	0.17	A	3 → 4	strongly cuneate interorbit with overhanging crests
		36	0.16	A	2 → 1	reduced sphenopalatine vacuities
		45	0.11	A	1 → 2	developed capsular process of lower incisor alveolus
		87	0.20	A	1 → 0	bacular mounds not covered by rim of nonspinous tissue
		72	0.14	D	1 → 0	m1 without ectolophid
26	Clade C	19	0.11	U	0 → 1	nasals reach posterior to maxillary-frontal suture
		29	0.09	U	1 → 0	zygomatic plate at same level as M1 alveolus
		41	0.29	U	1 → 0	small ectotympanic
		45	0.11	D	1 → 2	developed capsular process of lower incisor alveolus
		87	0.20	D	1 → 0	bacular mounds not covered by rim of nonspinous tissue
27	*Neacomys*	13	0.50	U	0 → 1	spiny pelage
		14	0.20	U	0 → 1	totally white ventral hairs
		20	0.22	U	1 → 2	premaxillaries anterior to terminus of nasal
		69	0.09	U	0 → 1	M3 without hypoflexus (or diminutive)
		94	1.00	A	0 → 1	preputial glands do not extend to the ventral flexure of the penis
		22	0.17	D	3 → 4	strongly cuneate interorbit with overhanging crests
28	*Neacomys minutus* + *N. musseri*	99	0.17	A	0 → 1	extended gastric glandular epithelium
29	26 – *Neacomys*	30	0.22	U	1 → 2	jugal absent
		11	0.13	A	0 → 1	tail slightly bicolored
		22	0.17	A	4 → 0	amphoral interorbit with rounded edges
		44	0.17	A	0 → 1	mental foramen located at diastema
		22	0.17	D	3 → 0	amphoral interorbit with rounded edges
30	*Microryzomys* + *Oryzomys balneator*	28	0.29	U	1 → 0	narrow zygomatic plate
		32	0.17	U	2 → 1	medium palate

APPENDIX 5
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
		70	0.50	U	1 → 2	m1 with anteromedian flexid
		99	0.17	U	0 → 1	extended gastric glandular epithelium
31	*Oligoryzomys*	35	0.33	U	1 → 0	flat parapterygoid
		36	0.16	U	1 → 0	large sphenopalatine vacuities
		37	0.13	U	0 → 1	derived carotid circulation 1
		47	0.50	U	1 → 2	masseteric crests reach anterior to m1 procingulum
		68	0.14	U	1 → 0	M3 with posteroloph
		88	0.33	U	0 → 1	glans penis with spinous dorsal papilla
		11	0.13	D	0 → 1	tail slightly bicolored
		44	0.17	D	0 → 1	mental foramen located at diastema
32	*Oligoryzomys nigripes* + *Ol. stramineus*	none				
33	*Oligoryzomys flavescens* + *Ol. fornesi*	69	0.09	U	0 → 1	M3 without hypoflexus (or diminutive)
34	Clade D	11	0.13	U	0 → 2	tail strongly bicolored
		25	0.20	U	0 → 1	parietal with deep lateral expansion
		31	0.17	U	1 → 0	incisive foramina pass M1
		34	0.38	U	2 → 3	complex posterolateral palatal pits
		36	0.16	U	1 → 0	large sphenopalatine vacuities
		37	0.13	U	0 → 2	derived carotid circulation 2
		68	0.14	U	1 → 0	M3 with posteroloph
		32	0.17	A	2 → 1	medium palate
		81	0.40	A	1 → 2	hemal arches with spinous posterior border
35	34 – *Oryzomys polius*	49	0.14	U	0 → 1	M1 with labial root
		66	0.17	U	0 → 1	M2 with labial and lingual fossetti at mesoflexus position
		21	0.13	A	0 → 1	lacrimal articulates mainly with maxillary
		50	0.18	A	0 → 2	m1 with 4 roots
		45	0.11	D	1 → 2	developed capsular process of lower incisor alveolus
		50	0.18	D	0 → 1	m1 with 3 roots
		81	0.40	D	1 → 2	hemal arches with spinous posterior border
36	37 + 38	4	0.25	U	0 → 1	hypothenar pad absent
		5	0.33	U	1 → 2	pes with extremely small interdigital pads
		7	0.30	U	1 → 2	ungual tufts absent on D1, sparse in remaining hindfoot digits
		29	0.09	U	1 → 0	zygomatic plate at same level as M1 alveolus
		58	0.12	U	0 → 1	M1 with anterocone divided by internal fold
		9	0.33	A	0 → 1	intermediate interdigital webbing
		19	0.11	A	0 → 1	nasals reach posterior to maxillary-frontal suture
		32	0.17	A	1 → 2	long palate
		51	0.20	A	0 → 1	M2 with 3 roots
		21	0.13	D	0 → 1	lacrimal articulates mainly with maxillary

APPENDIX 5
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
		50	0.18	D	1 → 2	M1 with 4 roots
37	*Oryzomys* sensu stricto	26	0.25	U	1 → 2	narrow interparietal
		75	0.33	U	0 → 1	m2 and m3 with anterolophid
		88	0.33	U	0 → 1	glans penis with spinous dorsal papilla
		89	0.50	U	0 → 1	urethral process of glans penis with subapical process
		22	0.17	A	4 → 3	weakly cuneate interorbit with small crests
		97	0.67	A	0 → 1	subterminal flexure of vesicular gland irregularly lobed
38	*Pseudoryzomys* + *Lundomys* + *Holochilus*	28	0.29	U	1 → 2	Zygomatic spine present
		34	0.38	U	3 → 2	simple posterolateral palatal pits
		59	0.60	U	0 → 3	M1 without anteroloph
		62	0.50	U	0 → 1	M1 and M2 with reduced mesolophs
		77	0.33	U	0 → 1	m3 with reduced posteroflexid
		67	0.33	A	0 → 1	M3 without mesoloph
		73	0.33	A	0 → 2	m1 and m2 without mesolophids
		99	0.17	A	0 → 1	extended gastric glandular epithelium
		9	0.33	D	0 → 1	intermediate interdigital webbing
		22	0.17	D	3 → 4	strongly cuneate interorbit with overhanging crests
		51	0.20	D	0 → 1	m2 with 3 roots
		73	0.33	D	0 → 1	m1 and m2 with small mesolophids
39	*Holochilus* + *Lundomys*	3	0.33	U	0 → 1	ungual tufts absent on forefeet digits
		7	0.30	U	2 → 3	ungual tufts absent on hindfoot digits
		8	0.50	U	0 → 1	natatory fringes present
		9	0.33	U	1 → 2	developed interdigital webbing
		11	0.13	U	2 → 0	tail unicolored
		22	0.17	U	3 → 1	amphoral interorbit with square edges
		33	1.00	U	0 → 1	palatine median longitudinal ridge present
		35	0.33	U	1 → 2	deeply excavated parapterygoid
		55	1.00	U	0 → 1	lateral cingula absent on molars
		56	1.00	U	0 → 1	posteriorly divergent maxillary toothrow
		57	0.14	U	0 → 1	flexi meet at midline on M1
		61	0.22	U	1 → 0	enamel bridge connection between paracone and protocone at posteriormost end of protocone on M1
		77	0.33	U	1 → 2	m3 without posteroflexid
		80	0.13	U	1 → 0	anapophyses present on TL17
40	*Holochilus*	22	0.17	U	1 → 2	amphoral interorbit with developed beads
		23	1.00	U	0 → 1	postorbital ridge present
		24	0.25	U	0 → 1	frontosquamosal suture anterior to frontoparietal
		31	0.17	U	0 → 1	incisive foramina do not reach M1
		38	0.25	U	1 → 0	alisphenoid strut present
		41	0.29	U	1 → 2	large ectotympanic
		46	0.20	U	0 → 1	single-crest anterior masseteric ridges
		47	0.50	U	1 → 2	masseteric crests reach anterior to m1 procingulum
		53	1.00	U	0 → 1	incisors with labial bevel
		54	1.00	U	0 → 1	molars hypsodont

APPENDIX 5
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
		57	0.14	U	1 → 2	flexi deeply interpenetrating on M1
		58	0.12	U	1 → 2	M1 with undivided anterocone
		63	0.50	U	0 → 1	median mure not connected to protocone on M1
		64	0.25	U	0 → 1	M2 without protoflexus
		19	0.11	A	1 → 0	nasals reach anterior to maxillary-frontal suture
		67	0.33	A	1 → 0	M3 with mesoloph
		87	0.20	A	0 → 1	bacular mounds covered by rim of nonspinous tissue
		89	0.50	A	0 → 1	urethral process of glans penis with subapical process
		73	0.33	D	1 → 2	m1 and m2 without mesolophids
		99	0.17	D	0 → 1	extended gastric glandular epithelium
41	*Oryzomys angouya*	11	0.13	U	2 → 1	tail slightly bicolored
	+ *O. subflavus* +	80	0.13	U	1 → 0	anapophyses present on TL17
	Nesoryzomys + *O.*	32	0.17	D	2 → 1	medium palate
	xanthaeolus +					
	Amphinectomys +					
	Nectomys +					
	Sigmodontomys +					
	Melanomys					
42	*Oryzomys subflavus*	40	0.43	U	0 → 2	vestigial subsquamosal fenestra
	+ *Nesoryzomys* + *O.*	86	0.25	U	0 → 1	slim central bacular digit
	xanthaeolus +	43	0.14	A	1 → 0	completely ossified mastoid
	Amphinectomys +	50	0.18	D	1 → 2	m1 with 4 roots
	Nectomys +	87	0.20	D	1 → 0	bacular mounds not covered by rim of nonspinous tissue
	Sigmodontomys +					
	Melanomys					
43	42 – *Oryzomys*	46	0.20	U	0 → 1	single-crested anterior masseteric ridges
	subflavus	64	0.25	U	0 → 1	M2 without protoflexus
		66	0.17	U	1 → 0	M2 with single labial fossette at mesoflexus position
		21	0.13	D	0 → 1	lacrimal articulates mainly with maxillary
		43	0.14	D	1 → 0	completely ossified mastoid
44	*Nesoryzomys*	10	0.50	U	1 → 0	dorsal surface of pes solid white
		12	0.33	U	1 → 0	scaly tail
		15	0.13	U	0 → 1	subtle countershading
		16	0.33	U	0 → 1	subauricular patches present
		41	0.29	U	1 → 2	large ectotympanic
		47	0.50	U	1 → 2	masseteric crests reach anterior to m1 procingulum
		22	0.17	A	4 → 1	amphoral interorbit with square edges
		91	0.50	A	0 → 1	ventral prostates absent
		92	0.50	A	0 → 1	anterior prostates absent
		93	1.00	A	0 → 1	vesicular glands present with small diverticula
		22	0.17	D	3 → 1	amphoral interorbit with square edges
45	43 – *Nesoryzomys*	45	0.11	U	2 → 1	reduced capsular process of lower incisor alveolus
		59	0.60	U	0 → 2	anteroloph joined to anterocone by labial cingulum on M1
		69	0.09	U	0 → 1	M3 without hypoflexus (or diminutive)

APPENDIX 5
(Continued)

Node	Taxon content	Char.	CI	Opt.	Change	Description
		19	0.11	A	0 → 1	nasals reach posterior to maxillary-frontal suture
		20	0.22	A	1 → 2	premaxillaries anterior to terminus of nasal
		22	0.17	D	3 → 4	strongly cuneate interorbit with overhanging crests
46	45 – *Oryzomys xanthaeolus*	4	0.25	U	0 → 1	hypothenar pad absent
		5	0.33	U	1 → 2	pes with extremely small interdigital pads
		7	0.30	U	1 → 2	ungual tufts absent on D1, sparse in remaining hindfoot digits
		11	0.13	U	1 → 0	tail unicolored
		31	0.17	U	0 → 1	incisive foramina do not reach M1
		36	0.16	U	0 → 1	reduced sphenopalatine vacuities
		57	0.14	U	0 → 1	flexi meet at midline on M1
		58	0.12	U	0 → 2	M1 with undivided anterocone
		61	0.22	U	1 → 0	enamel bridge connection between paracone and protocone at posteriormost end of protocone on M1
		9	0.33	A	0 → 1	intermediate interdigital webbing
		24	0.25	A	0 → 1	frontosquamosal suture anterior to frontoparietal
		76	0.20	A	0 → 1	m3 without anterolabial cingulum
		99	0.17	A	0 → 1	extended gastric glandular epithelium
		20	0.22	D	1 → 2	premaxillaries anterior to terminus of nasal
47	*Amphinectomys* + *Nectomys*	8	0.50	U	0 → 1	natatory fringes present
		9	0.33	A	1 → 2	developed interdigital webbing
		26	0.25	A	1 → 2	narrow interparietal
		86	0.25	A	1 → 0	long central bacular digit
		9	0.33	D	0 → 2	developed interdigital webbing
48	*Nectomys*	15	0.13	U	0 → 1	subtle countershading
		18	0.33	U	0 → 1	pointed nasal posterior terminus
		36	0.16	A	1 → 2	completely ossified sphenopalatine
		19	0.11	D	0 → 1	nasals reach posterior to maxillary-frontal suture
		24	0.25	D	0 → 1	frontosquamosal suture anterior to frontoparietal
		99	0.17	D	0 → 1	extended gastric glandular epithelium
49	*Sigmodontomys* + *Melanomys*	10	0.50	U	1 → 2	dorsal surface of pes brown
		34	0.38	U	3 → 2	simple posterolateral palatal pits
		29	0.09	A	1 → 0	zygomatic plate at same level as M1 alveolus
		24	0.25	D	0 → 1	frontosquamosal suture anterior to frontoparietal
50	*Melanomys* + *Sigmodontomys aphrastus*	15	0.13	U	0 → 2	no countershading
		52	0.20	U	0 → 1	orthodont incisors
		9	0.33	A	1 → 0	interdigital webbing absent
		80	0.13	A	0 → 1	anapophyses absent on TL17
		19	0.11	D	0 → 1	nasals reach posterior to maxillary-frontal suture

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

ERRATUM

Although every effort is made to minimize printed errors in our publication series, a few inevitably escape our attention. The following substantive correction applies to Bulletin number 296, issued February 16, 2006:

Title page (page 1):

In the title, for "ORYZOMINE" read "ORYZOMYINE"

The error occurred in the editorial process and was not the fault of the author.