

**PHYLOGENETIC ANALYSIS OF THE TRIBE ORYZOMYINI
(MUROIDEA: SIGMODONTINAE) BASED ON MORPHOLOGICAL
AND MOLECULAR DATA**

by

MARCELO WEKSLER

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

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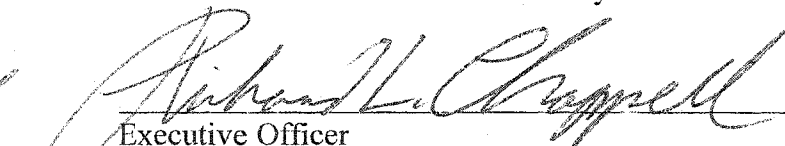
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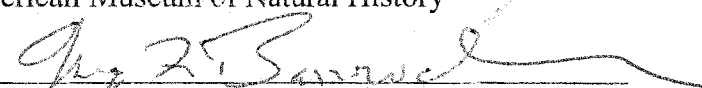
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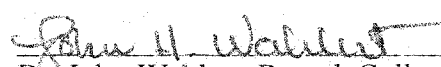
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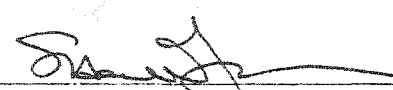
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ABSTRACT

PHYLOGENETIC ANALYSES OF THE TRIBE ORYZOMYINI (MUROIDEA: SIGMODONTINAE) BASED ON MORPHOLOGICAL AND MOLECULAR DATA

by

Marcelo Weksler

Adviser: Dr. Robert S. Voss

The present thesis provides a comprehensive hypothesis of evolutionary relationships for the Oryzomyini, the largest tribe of the Neotropical subfamily Sigmodontinae (Rodentia: Muroidea).

In the first chapter, partial sequences (1266 bp) from the first exon of the nuclear gene encoding the Interphotoreceptor Retinoid Binding Protein (IRBP) were used to infer the phylogenetic relationships among 44 species representing all 16 currently recognized genera of Oryzomyini. Monophyly of the tribe was assessed relative to 15 non-oryzomyine sigmodontine taxa. The resulting matrix included 71 taxa and 386 parsimony-informative characters. Phylogenetic analysis resulted in 16 equally parsimonious cladograms, which contained the following well-supported groups: (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 is 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 semiaquatic Oryzomys.

In the second chapter, the IRBP dataset was complemented with a morphological matrix comprised of 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, with the delineation of different states observed among oryzomyines. Separate and combined analyses were performed using the molecular and morphological datasets. 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. The systematics of the tribe and the evolution of a few pivotal characters are discussed in light of the proposed phylogeny. A new taxonomy of species currently included in the genus Oryzomys is proposed. Finally, I evaluate evolutionary and biogeographic hypotheses that are compatible with our current knowledge on oryzomyine relationships.

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**CHAPTER 1. PHYLOGENY OF NEOTROPICAL ORYZOMYINE
RODENTS (MURIDAE: SIGMODONTINAE) BASED ON THE
NUCLEAR IRBP EXON**

INTRODUCTION

The extant diversity of muroid rodents, which account for about 29% of living mammals (Wilson and Reeder, 1993), is thought to have resulted from independent radiations on separate continents throughout the world (Chaline and Mein, 1979; Carleton and Musser, 1984). One of the most impressive of these radiations is the New World subfamily Sigmodontinae, the most diverse family-level mammalian clade in the Neotropical region. The subfamily is currently divided into eight tribes, five of which – Oryzomyini, Akodontini, Abrothrichini, Phyllotini, and Thomasomyini – encompass 90% of sigmodontine species. Recognition of these tribes was originally based either on overall similarity or on ad hoc evolutionary hypotheses (e.g., Hershkovitz, 1962; Reig, 1980, 1984), but recent phylogenetic studies have started to reshape our understanding of sigmodontine relationships (e.g., Voss, 1988, 1993; Voss and Carleton 1993; Steppan, 1995; Smith and Patton, 1999).

Despite such progress, many significant problems remain, especially among the 16 genera and 100+ species currently assigned to the sigmodontine tribe Oryzomyini. Oryzomyines are ubiquitous in the Neotropics, ranging from Tierra del Fuego to Mexico and the southeastern 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). In addition, oryzomyines display a diversity of morphological adaptations and a striking degree of chromosomal divergence that make them a compelling group for comparative studies of phenotypic and cytogenetic evolution (Gardner and Patton, 1976; Carleton and Olson, 1999).

Recent phylogenetic studies involving oryzomyine rodents have employed characters systems such as morphology (Steppan, 1995, 1996, Carleton and Olson, 1999), allozymes (Dickerman and Yates, 1995) and mitochondrial DNA sequences (Myers et al., 1995; Patton and da Silva, 1995; Smith and Patton, 1999; Bonvicino and Moreira, 2001), but most aspects of oryzomyine phylogeny remain obscure. The present taxonomic composition of the tribe (Table 1) derives from the work of Voss and Carleton (1993) who included several taxa that were once classified in other sigmodontine groups, such as Pseudoryzomys and Zygodontomys (previously considered phyllotines; Hershkovitz, 1962) and Holochilus (previously considered a sigmodont; Hershkovitz, 1955). Although Voss and Carleton (1993) provided a diagnosis for Oryzomyini that listed putative morphological synapomorphies, no taxonomic comprehensive phylogenetic analysis has convincingly tested the hypothesis of tribal monophyly. Instead, previous phylogenetic studies have either assumed oryzomyine monophyly (e.g., Carleton and Olson, 1999; Dickerman and Yates, 1995; Myers et al., 1995; Patton and da Silva, 1995), or have reported conflicting results based on weak nodal support. (Steppan, 1995; Smith and Patton, 1999, Bonvicino and Moreira, 2001).

Equally problematic, relationships among oryzomyine taxa remain controversial. Phylogenetic analyses based on different sources of character data have produced incongruent hypotheses for relationships among oryzomyines (Figure 1). The causes of such incongruence are hard to identify due to differences in taxonomic sampling; to date, no study has included exemplars from all currently recognized oryzomyine genera. A dense taxonomic sampling within certain genera is also crucial. In particular, no phylogenetic analysis has retrieved Oryzomys as a monophyletic unit (e.g., Dickerman

and Yates, 1995; Patton and da Silva, 1995; Bonvicino and Moreira, 2001). Currently, several informal 'species groups' are recognized within Oryzomys (e.g., Musser et al., 1998; Patton et al., 2000; Bonvicino and Moreira, 2001), but there are few character-based analyses to support the delimitation of such groups. Likewise, several taxa formerly included as subgenera of Oryzomys (Table 1) have been elevated to generic rank due to their possession of highly distinctive morphological characters or karyotypes, but there have been few attempts to establish synapomorphies and test the monophyly of these taxa with respect to Oryzomys (e.g., Carleton and Musser, 1989 for Microryzomys and Oligoryzomys).

The goal of the present study was to undertake a comprehensive (taxon-dense) phylogenetic analysis of the tribe Oryzomyini employing DNA sequence data from the Interphotoreceptor Retinoid Binding Protein (IRBP) locus. This single-copy nuclear gene codes for a large glycoprotein that is found primarily in the interphotoreceptor matrix of the retina (Danciger et al., 1990), where it is involved in the rhodopsin cycle of light absorption (Pepperberg et al., 1993). Part of IRBP exon 1 (ca. 1.2 kb) was used to infer phylogenetic relationships among mammalian orders (Stanhope et al., 1992, 1996, 1998; Springer et al., 1999). Nevertheless, the gene also seems suitable for resolving relationships at lower taxonomic levels (Yoder and Irwin, 1999; Jansa and Voss, 2000; Suzuki et al., 2000; Michaux et al., 2002), where it shows considerably less signal saturation than more frequently used mitochondrial genes (e.g., cytochrome *b*). This paper has the following specific goals: (1) to test the monophyly of Oryzomyini and to define the contents of the tribe; (2) to place the oryzomyine clade in the larger context of sigmodontine phylogeny; (3) to resolve phylogenetic relationships among oryzomyine

taxa; (4) to test the monophyly of the genus Oryzomys; and (5) to infer the phylogenetic relationships among the several species groups within Oryzomys.

MATERIALS AND METHODS

Taxonomic Sampling

The term Oryzomyini is here applied to the clade defined by Voss and Carleton (1993). The taxonomic contents of other sigmodontine groups are also based on recent character-based analyses (Voss, 1988, 1993; Stepan, 1995; Smith and Patton, 1999). Sigmodontinae is employed in its most restricted meaning (sensu Reig, 1984), encompassing the mostly Neotropical genera in a subfamily distinct from North American neotomines and peromyscines (subfamily Neotominae), and from Central American tylomyines and nyctomyines (subfamily Tylomyinae).

All recognized genera and 44 of the ca. 100 recognized species of oryzomyines were included in the analysis (Table 2). Type species from all but two oryzomyine genera were included, as were multiple representatives of most polytypic genera for which monophyly remains to be convincingly established. A special effort was made to include a comprehensive sample of Oryzomys (sensu Musser and Carleton, 1993). All nine species groups informally recognized within the genus were included (albigularis, alfaroi, melanotis, megacephalus, nitidus, palustris, subflavus, talamancae, and xanthaeolus), as well as three species (O. balneator, O. polius, and O. angouya) which have not been assigned to any species group. Taxonomic identifications were made by the examination of museum voucher specimens by accomplished taxonomists.

Taxon sampling for the ingroup (= Sigmodontinae) was completed with exemplars from all historically recognized sigmodontine tribes: akodontines,

abrotrichines, phyllotines, sigmodontines, thomatomyines, wiedomyines, scapteromyines, and ichthyomyines. In addition, a series of unique lineages, or Sigmodontinae incertae sedis taxa (Smith and Patton, 1999) were included (Table 2). Because the position of Neotropical sigmodontines among other muroid subfamilies is poorly understood, I employed multiple outgroups including exemplars of the murid subfamilies Tylomyinae, Neotominae, Arvicolinae, Cricetinae, Calomyscinae, Mystrominae, and Murinae (Table 2). All analyses were run with unconstrained ingroup and outgroup designations (Nixon and Carpenter, 1993), and trees were subsequently rooted at the internode separating ingroup and outgroup taxa.

Molecular data

DNA was isolated for most specimens from frozen or ethanol-preserved tissues (liver, kidney, or spleen). For Lundomys molitor and Handleyomys intectus, however, DNA was extracted from skin samples of recent voucher specimens. DNA was isolated from all tissues using QiaAmp extraction kits following the manufacturer's protocol (Qiagen Inc). For skin samples, an extra-long digestion phase (> 24 h) was used, with constant replenishment of proteinase K.

Primers used in DNA amplification and sequencing are the same or slightly modified from those of Stanhope et al. (1992) and Jansa and Voss (2000). Three new primers were designed for use in sigmodontines: D2 (5' - TATCCCACATTGCCCGGCAGCA - 3'), B2 (5' - ATGAGGTGTTCCGTGTCCTG - 3'), and E2 (5' - AGCAGATGCGCAGAGCCATAGTGGT - 3'). For the majority of specimens, a two-step amplification procedure was used. A long segment (ca. 1300 bp) was first amplified from genomic DNA using primers A1 and B2. To generate fragments

of a suitable size for sequencing, the product of this reaction was used as a template in two subsequent PCR reactions, one using primer F paired with A1 and one using primer E2 paired with B2.

Initial amplifications were performed as 20 μ L reactions using either Ampli-Taq Gold polymerase (Perkin-Elmer), or HotStar Taq (Qiagen Corp.), using manufacturer-recommended concentrations of primers, unincorporated nucleotides, buffer, and MgCl₂. Reactions were performed on Perkin-Elmer 9100 or 9700 thermal cyclers using the following touchdown protocol: Three stages of 5 cycles each with denaturation at 95°C for 20 sec, annealing at 58°C, 56°C, or 54°C for 15 sec, and extension at 72°C; one stage of 23 cycles of denaturation at 95°C for 20 sec, annealing at 52°C for 15 sec, and extension at 72°C for 60 sec. All amplifications were preceded by a 95°C denaturation for 10 min. (Ampli-Taq) or 15 min. (HotStar Taq) and followed by a final extension at 72°C for 7 min. Negative controls containing no DNA were used in all batch reactions. PCR products were visualized using electrophoresis through a 2% low melting-point agarose gel (NuSieve GTG, FMC) stained with Ethidium Bromide.

For reamplification reactions, PCR products of the appropriate size were excised from the gel using a Pasteur pipette, and the gel plug was melted in 300 μ L sterile water at 73°C for 10 minutes. The resulting gel-purified product was used as a template in 30 μ L reamplification reactions using Taq polymerase (Promega). Reactions were subjected to 32 standard PCR cycles using 58°C annealing temperature.

PCR products were prepared for sequencing using the GENEclean II System (BIO 101, Inc.) and sequenced in both directions using amplification primers and dye-terminator chemistry (Applied Biosystems Inc.). Reactions were cleaned using an ethanol

(+MgCL₂) precipitation technique, and run on ABI 377 or ABI 3100 automated sequencers.

Some samples required slightly modified procedures in the amplification process, including the following: lower temperatures for the touchdown PCR (56°C to 50°C); amplification of the smaller fragments A1 + F and E2 + B2 directly from genomic DNA; and amplification of smaller overlapping fragments of 100-400 bp (primer pairs A1/I, J/F, E2/K, and L/D2). The specific protocol used for each specimen is available from the author upon request.

Data Analysis

Sequences were edited and compiled using Sequencher software (v. 3.0, Gene Codes Corporation). Base-calling ambiguities between strands were resolved by either choosing the call on the cleanest strand or using the appropriate standardized IUB ambiguity code if both strands showed the same ambiguity. Assignment of gap symbols to create primary homology hypotheses were based on the gene reading frame. For 24 taxa, small portions of the 5' or 3' ends of the sequence (average 32 bp, range 5-82 bp) were excluded because the sequence quality was poor in these regions. A total of 764 bp (out of 89,886 bp) were excluded from the analysis and coded as missing data ("?").

Departure from homogeneity of base composition across all taxa was assessed using the Chi-square test as implemented in PAUP* version 4.0b10 (Swofford, 2001). To examine the prevalence of multiple hits, saturation plots were evaluated for each substitution type (transitions and transversions) at each codon position. For each pair of taxa, the substitution divergence was plotted against total uncorrected sequence divergence (p). Because of missing data, substitution divergence was calculated by

dividing the actual number of substitutions by the sequence length of the pairwise comparison.

Phylogenetic analysis was performed in PAUP* version 4.0b10 (Swofford, 2001). Parsimony analysis was implemented with informative characters treated as unordered and equally weighted. The heuristic search option was implemented, with 100 random addition replicates and tree-bisection-reconnection (TBR) branch swapping. Only nodes with at least one unambiguous synapomorphy were retained (options PSET COLLAPSE = MINIMUM, and FILTER BEST in PAUP*). Parsimony bootstrap values (Felsenstein, 1985) were calculated with 1000 pseudoreplicates using a heuristic search with 5 random additions each, TBR branch swapping, and a maximum of 500 trees retained in each random addition replicate (2500 per bootstrap pseudoreplicate). To calculate Bremer support values (Bremer, 1988), heuristic searches (5 random-addition replicates, TBR branch swapping) were performed with a constraint placed for each node found in the consensus tree, and the ENFORCE REVERSE options on the heuristic search (HS) command in PAUP*.

Maximum likelihood analysis was performed to assess the robustness of the nodes recovered with parsimony to potential long-branch-attraction phenomena (Felsenstein, 1978). The likelihood model was selected using the strategy of nested likelihood-ratio tests (Goldman, 1993; Huelsenbeck and Rannala, 1997), in which models of nucleotide substitution with fewer parameters are successively tested against models with more parameters. A neighbor-joining (NJ) tree based on Jukes-Cantor distances (Jukes and Cantor, 1969; JC) was used to estimate the log-likelihood scores and parameters values under the following models: Jukes-Cantor (1969; JC69), Kimura (1980; K80),

Felsenstein (1981; F81), Hasegawa et al. (1985; HKY85), Rodriguez et al. (1990; GTR), and Zharkikh (1994; SYM). Starting with the JC model as the null hypothesis (one rate of substitution and equal base frequency), parameters were added and models were used as alternative hypotheses in the following order: unequal base frequencies (F81 with 3 degrees of freedoms); two types of substitutions, transitions and transversions (K80 or HKY85, $df = 1$); and six types of substitutions (SYM or GTR, $df = 4$). Two additional parameters were tested for each class of model: gamma-distributed heterogeneity of the substitution rate across sites (Yang, 1994; Γ - shape parameter) and proportion of invariant sites (1), each with one degree of freedom. The best-fit model was the one for which additional parameters no longer significantly improved the log-likelihood score, as determined by the likelihood-ratio test. Finally, I evaluated whether enforcing a molecular clock provided a better fit to the data rather than allowing for different rates across the tree. For that test, the NJ tree was rooted, and the best-fit model with the enforced clock was used as the null-hypothesis against which the best-fit model without the clock enforced was compared ($df = \text{number of taxa} - 2$). A strict Bonferroni correction was applied to the alpha level of the individual tests, in which a significance level of 0.05 was divided by 6, the number of maximum possible tests (individual $\alpha = 0.0083$). The selected model and parameters were fixed during searches. The heuristic search option was implemented with 10 random addition replicates and tree-bisection-reconnection (TBR) branch swapping. Bootstrap values for the likelihood analysis were calculated with 200 pseudoreplicates, using heuristic search with a neighbor-joining starting tree and nearest-neighbor interchange (NNI) branch swapping.

RESULTS

Sequence characteristics

Complete sequence length varied from 1263 to 1269, with all but two species having 1266 bp. The sequence of Scolomys ucayalensis has a 3 bp deletion between bases 739-748, while that of Mesocricetus auratus has a 3 bp insertion between 166-171. The insertion of gap symbols between those intervals is equivocal but unproblematic, as all possible placement sites produce the same phylogenetic topology in parsimony analyses. The consensus sequence for all species starting at position 739 consists of a GGn³ repeat (GGR GGY GGY), while Scolomys ucayalensis exhibited a GGn² repeat (GGA GGC). The placement of an insertion gap is plausible for any of the three triplets between 739-748. The results presented here are based on the insertion at positions 742-744, which gives the least number of overall steps among the three possibilities (one step less than the other two insertion positions). Mesocricetus auratus has a CAG² repeat starting at position 166, followed by a CAA triplet. Almost all other taxa have a single CAR triplet (two taxa have a CGG triplet) at position 166 followed by a CAA trinucleotide (two taxa have CYA). The placement site for gap symbols in other taxa to accommodate the extra CAG triplet of Mesocricetus between positions 166-168 or 169-171 yields the same result in terms of tree length (the second placement was used).

Average pairwise sequence divergence (uncorrected p-distance) among congeneric oryzomyine species ranged from 0 to 2.6%. (Figure 2). Species within three genera had average distances close to 1% (Oligoryzomys: average p = 1.2%, n = 10 pairwise comparisons; Neacomys: average p = 1.0%, n = 3; Oecomys: average p = 1.0%, n = 10). Two genera had lower divergence within species (Nesoryzomys: p = 0.6%, n = 1;

Zygodontomys: $p = 0.6\%$, $n = 1$), while the two species of Holochilus did not have any base pair differences between them. By contrast, Oryzomys had a much higher intrageneric average pairwise divergence ($p = 2.6\%$, $n = 120$). In fact, this value was only slightly lower than that found for the average distance between members of different oryzomyine genera ($p = 2.8\%$, $n = 800$; Figure 2). Pairwise divergence values between Zygodontomys and other oryzomyine taxa are the highest within Oryzomyini, with a maximum value of 6.1% between Z. cherriei and Oryzomys polius.

The pairwise divergence among sigmodontine taxa from different tribes had an average value of 4.6% ($n = 705$), and ranged from 2.8% between Delomys dorsalis and Phyllotis xanthopygus to 8.7% between Rheomys raptor and Zygodontomys cherriei. Distances between Rheomys raptor or Sigmodon alstoni and other sigmodontines had p values between 5.5% and 8.1% (average $p = 6.4\%$, $n = 123$). Comparisons among sigmodontine taxa of different tribes, excluding Rheomys raptor and Sigmodon alstoni, had p values between 2.8% and 6.2% (average = 4.0%, $n = 688$). Comparisons involving ingroup-outgroup pairs of taxa ranged from 6.5% (Neotoma lepida and Scapteromys tumidus) to 12.7% (Mystromys albicaudatus and Oligoryzomys fornesi), with an average of 9.2% ($n = 767$).

Saturation plots (Figure 3) indicate that there is no clear evidence of multiple substitutions (saturation) in any codon position, and thus there should be no loss of phylogenetic signal among the more divergent taxa in this analysis. All three codon positions show an almost linear increase of transitions and transversions across the range of sequence divergence examined. Even for comparisons involving taxa with higher

sequence divergence (i.e. outgroup-ingroup pairs of taxa) there is no indication of a saturation effect.

The overall base composition of IRBP sequences in this study exhibits a slight bias toward cytosine and guanine (Table 3) and is similar to the residue frequencies found for other rodents (Debry and Sagel, 2001). The bias is stronger when each codon position is analyzed individually: First codon positions are rich in guanine and extremely poor in thymine residues; second positions have elevated levels of adenine and thymine; and third positions are biased in favor of guanine and cytosine residues. Overall base composition is homogeneous across all taxa; a Chi-square test could not reject the null hypothesis of base-composition stationarity ($\chi^2 = 63.03$, $df = 210$, $p = 1.0$). The results are the same when the test is partitioned by codon position (first positions: $\chi^2 = 10.53$, $p = 1.0$; second positions: $\chi^2 = 5.74$, $p = 1.0$; third positions: $\chi^2 = 147.93$, $p = 0.99$; $df = 210$ for each test).

Parsimony analysis

The data matrix contained 588 variable sites of which 386 are parsimony-informative (Table 4). Roughly half of the variable sites in first and second codon positions were informative, compared to 70% of variable sites in third positions. Third positions contained 66% of all informative sites, while first positions contained 19% and second positions 15%. Parsimony analysis of all informative characters resulted in 16 trees of minimal length (fundamental cladograms), each with 1275 steps ($CI = 0.45$, $RI = 0.63$; only informative characters included). Levels of homoplasy, as inferred by the recovered consistency and retention indices of each position class in the most parsimonious trees, are higher for second positions and lower for first positions (Table 4).

In terms of steps per informative character, first positions have the lowest average, while third positions have the highest average. Synapomorphies accounted for 398 character changes. Unambiguous synapomorphies totaled 313 and varied from one (10 nodes) to 35 (Arvicolinae) per node. Sixty synapomorphies were in first codon positions (15%), 53 in second positions (13%), and 285 in third positions (72%). Among the 1511 character transformations, 83 corresponded to unique and unreversed synapomorphies.

Terminal branches for most outgroup taxa are longer than those for sigmodontines (Figure 4), presumably reflecting sparser taxon sampling among outgroups. The longest internal branch is the one leading to Arvicolinae, while the branch separating sigmodontines from outgroups is the third-longest internal branch. Within sigmodontines, internal branches are much shorter than external ones. The largest internal branches are the ones separating the two most basal clades, and the one separating oryzomyines from other taxa. Both ACCTRAN and DELTRAN optimizations produced the same branch length patterns.

The topology of the strict consensus ingroup tree (Figure 5) contains 55 resolved nodes out of a maximum of 68 (= 81% resolution). Of the eight polytomies found in this topology, four occurred in all fundamental cladograms (indicating lack of data), while four were due to differences in structure of fundamental cladograms (indicating character conflict, Figure 6). Sigmodontines are found to be monophyletic with high nodal support values, but they do not form a monophyletic group with either tylomyines or neotomines (Figure 4). A tree with a constrained clade containing sigmodontines, tylomyines, and neotomines, requires three extra steps. The sigmodontine taxa are split basally into two clades. The first contains Rheomys and Sigmodon, representatives of the tribes

Ichthyomyini and Sigmodontini, respectively. The IRBP data provided strong signal for this clade, with the highest level of nodal support of any recovered among non-oryzomyine sigmodontines in this analysis. The second basal clade contains the remaining sigmodontines and also received very high nodal support. This group contains three major branches, which form an unresolved polytomy in the strict consensus tree and in all fundamental cladograms, and is therefore caused by a lack of informative characters at this node.

The first of these three higher sigmodontine clade contains Thomasomys and Rhipidomys, members of the tribe Thomasomyini; Akodon and Scapteromys, members of the Akodontini; and Reithrodon. Although the structure of this clade is fully resolved, the only node with strong support is the one uniting Akodon and Scapteromys. The second higher sigmodontine clade comprises Abrothrix and Notiomys, members of the Abrothrichini; Calomys and Phyllotis, members of Phyllotini; and Wiedomys, Juliomys, Irenomys, and Delomys. The polytomy present at the base of this group is due to character conflict within the IRBP dataset because there are four possible equally-parsimonious resolutions found among the fundamental cladograms (not shown). Only the nodes subtending the tribes Abrothrichini and Phyllotini received high nodal support; the clade containing Delomys and phyllotines had moderate support.

The third higher sigmodontine clade consists of the Oryzomyini only, and is robust in terms of nodal support values and number of unambiguous synapomorphies (7). Within this tribe, the basal structure among Scolomys, Zygodontomys, and a clade containing the remaining oryzomyines is unresolved, both in the consensus tree and in all fundamental cladograms. The large group containing all oryzomyines except

Zygodontomys and Scolomys is very well-supported, and is further divided into two well-supported clades, labeled A and B in Figure 5.

Clade A contains the genera Oecomys, Handleyomys, and nine of the 16 Oryzomys species included in the analysis. The internal structure of clade A in the strict consensus topology is characterized by an extensive polytomy resulting from two solutions found in the fundamental cladograms (Figure 6A-B). Those alternative resolutions depict either (Oryzomys talamancae (O. macconnelli (O. lamia + O. russatus))) or (Handleyomys intectus (O. alfaroi + O. melanotis)) as the basal clade relative to the remaining taxa. The species of Oryzomys included in clade A are never recovered as a monophyletic group in any of the fundamental cladograms. Oecomys is always recovered as monophyletic, but with marginal nodal support. All other clades present in Clade A have moderate ($70 > \text{bootstrap support} < 85$, Bremer index > 1) to high (bootstrap support $> 85\%$, Bremer index > 3) nodal support.

Clade B contains the remaining 11 oryzomyine genera and seven Oryzomys species. Clade B is further divided into two large but poorly-supported clades. In the first of these, Microryzomys, Oligoryzomys, Neacomys, and Oryzomys balneator form a monophyletic group with negligible nodal support. Oligoryzomys and Neacomys are both recovered as monophyletic genera, with very strong bootstrap and Bremer support. A clade uniting Neacomys with Microryzomys and O. balneator is not well-supported, nor is the clade tying together the latter two taxa.

The second group within clade B consists of the remaining six species of Oryzomys scattered among the remaining eight oryzomyine genera. Within this group, the genera Holochilus and Nesoryzomys form strongly supported monophyletic groups; a

sister taxon relationship between Holochilus and Pseudoryzomys is similarly well supported, as are sister taxon relationships between Amphinectomys and Nectomys and between Melanomys and Sigmodontomys. However, the species of Oryzomys included in this clade do not form a monophyletic group. The only species of Oryzomys that form a consistent, well-supported clade are O. couesi and O. palustris. Oryzomys angouya and O. subflavus, while part of a polytomy in the consensus tree, are never each other's sister taxa in any of the fundamental cladograms (Figure 6C and D). The nodes subtending the position of the remaining species of Oryzomys – (O. polius and O. xanthaeolus) – are not well-supported. It would require an additional 6 steps to force these six species of Oryzomys to form a monophyletic group. To include O. balneator within that group would require an additional 11 steps, while to include the species of Oryzomys in Clade A would require a stunning 25 steps.

Maximum Likelihood Analysis

The nested likelihood-ratio tests selected the SYM + Γ + I model (equal base frequency, six substitution types, heterogeneity of substitution rate across sites, an estimated proportion of invariant sites, without clock enforced) as the best-fit model. Estimated parameters for the model are as follows: substitution rate matrix: 1.83 (AC), 7.74 (AG), 0.85 (AT), 1.1 (CG), 8.1 (CT), and 1 (GT); $\Gamma = 1.04$; I = 32%. The topology of the maximum likelihood tree is similar to the one recovered by the parsimony analysis, with only two differences: (1) cricetines are found as sister group to sigmodontines, instead of to arvicolines, and (2) Irenomys is found as sister group to oryzomyines, instead of to Juliomys. A tree with these modifications requires only one additional step in the parsimony analysis. The phylogenetic structure of oryzomyines found in the

likelihood analysis is identical to the solutions recovered in fundamental cladograms depicted in Figures 6B and 6C.

Bootstrap values inferred under the best-fit maximum likelihood model for ingroup clades (Figure 5) were similar to the ones found in parsimony bootstrap analysis, with a high correlation coefficient between the two values ($r = 0.96$). The largest differences between homologous bootstrap values from the two analyses were an increase of 16 percentage points for the likelihood bootstrap at the node containing Thomasomys + Rhipidomys (46% to 62%) and a decrease of 18 percentage points at the node containing Oligoryzomys stramineus and O. nigripes (52% to 34%). Nodes with parsimony bootstrap values above 70% also have likelihood bootstrap values above 70%. Twenty-three of these 26 nodes have ML and MP bootstrap values that differ by less than five percentage points.

DISCUSSION

Methodological concerns

The present study provides novel hypotheses concerning oryzomyine relationships as well as some insights on higher-level sigmodontine phylogeny. Several factors must be taken into account when assessing the level of confidence that can be placed on these results. Regarding data properties, the IRBP dataset appears to be free from several potential problems or sources of bias in phylogenetic inference. Sequence alignment of sequences is straightforward and unambiguous, with only minor problems in formulating hypotheses of primary homology. Base composition is homogeneous across taxa, without evidence of taxon attraction due to similar nucleotide-composition bias (Saccone et al., 1989; Lockhart et al., 1992). No evidence of substitution saturation

appears to be present at any codon position, thus avoiding potential loss of phylogenetic information due to excessive multiple hits (Kimura, 1982; Saitou, 1989). Parsimony and likelihood analyses recovered almost identical results with similar bootstrap values, suggesting that long-branch attraction phenomena are not affecting the topology (Felsenstein, 1978; Hendy and Penny, 1989). Similarly, outgroup sequences are not saturated in relation to ingroup taxa, which should improve confidence in the reliability of the chosen root (Wheeler, 1990; Smith 1994). Finally, IRBP provided enough character information to produce an almost completely resolved phylogeny with several strongly supported clades.

In terms of taxonomic congruence with previous studies, only one case of strong incongruence between IRBP results and morphological evidence exists (see below). Significantly, the present results show no strong incongruence with studies using mitochondrial sequences. A common feature of studies using mitochondrial genes is the saturation of the phylogenetic signal caused by multiple substitutions, especially of synonymous transitions at third-codon positions. Although some authors dismiss the potential negative effects of saturation in phylogenetic reconstruction (Björklund, 1999; Källersjö et al., 1999), the pattern retrieved from sigmodontine studies using saturated data (e.g., Smith and Patton, 1999; Bonvicino and Moreira, 2001) is consistent with predictions of low resolution and weak support for deeper nodes (Springer et al., 2001). Different algorithms (parsimony, minimum evolution, and maximum likelihood) or weighting schemes (downweighting of transitions or third-codon-position characters) are sometimes employed in those studies to circumvent the saturation problem. Unfortunately, results within this pluralistic analytical framework are not robust, with

substantial changes in tree topology depending on the algorithm or weighting scheme employed. The present results provide stronger evidence for some relationships that received low support from mitochondrial data, as well as a few incongruent hypotheses between robust IRBP clades and weakly supported mitochondrial clades.

Sigmodontine relationships

The present analysis corroborates the monophyly of the subfamily Sigmodontinae (*sensu* Reig, 1984) as a clade that excludes other New World muroid taxa – neotomines, tylomynes, and arvicolines. This result has never been found in analyses of morphological data (Carleton, 1980; Steppan, 1995), but has been recovered with analysis of mitochondrial data (Engel et al., 1998). The clade containing Rheomys and Sigmodon as the most basal sigmodontine branch is an unexpected result. Ichthyomyines and sigmodonts comprise two of the most distinctive groups of sigmodontines, being as ecologically and morphologically dissimilar from each other as they are from other sigmodontine groups. Sigmodonts are strictly terrestrial rats, living exclusively in open-vegetation formations, most commonly in grasslands in lowland habitats, and with a herbivorous diet restricted to grasses and forbs (Cameron and Spencer, 1981; Voss, 1992). By contrast, ichthyomyines are carnivorous, semi-aquatic rats, found exclusively along watercourses, most commonly along streams bordered by evergreen rain forest in montane habitats (Voss, 1988). It is clear that such a novel hypothesis linking these two taxa requires additional tests from other sources of phylogenetic data, but four points make it particularly appealing: (1) the high nodal support found for this clade and for the clade containing the remaining sigmodontines; (2) the existence of at least one putative, non-homoplastic, morphological synapomorphy (the presence of lateral crater papillae on

the phallus; Hooper, 1959; Hooper and Musser, 1964; Voss 1988); (3) the placement of Sigmodon as a basal sigmodontine in a mitochondrial phylogeny (Engel et al., 1998; no ichthyomyine taxon was included); and (4) the concordant geographical distribution of the two groups, which are restricted to Central America and northern South America (the distribution of Sigmodon extends throughout part of North America), in contrast to the distribution of all other sigmodontine groups, which are generally broadly distributed through South America and southern Central America.

The results from analysis of the IRBP data corroborate various tribal arrangements proposed by other recent phylogenetic analyses. Four clades consistent with recently redefined tribes are retrieved: Akodontini (including Scapteromys and Akodon; Smith and Patton, 1999), Abrothrichini (including Abrothrix and Notiomys; Smith and Patton, 1993, 1999), Thomasomyini (including Thomasomys and Rhipidomys, but not Delomys and Juliomys; Voss, 1993), and Phyllotini (including Calomys and Phyllotis, but not Reithrodon; Engel et al., 1998). Results from IRBP, however, are inconclusive with respect to relationships among these tribal groupings. The division of most sigmodontine taxa into three major clades (Figure 5) is strikingly similar to the results of the 'species-level' unweighted parsimony analysis of Smith and Patton (1999), especially the association of thomasomyines and akodontines in one clade and of abrothrichines and phyllotines (plus Wiedomys and Delomys) in another. Nevertheless, the sparse taxon sampling among non-oryzomyine tribes and the low support for these clades provided by IRBP and mitochondrial data prevents reliable conclusions regarding sigmodontine tribal relationships. The lack of resolution and support could reflect an evolutionary pulse of rapid cladogenesis, as suggested by authors using mitochondrial

sequences (Engel et al., 1998; Smith and Patton, 1999); however, a more detailed sampling of non-oryzomyine tribes is necessary before IRBP data can be used to test such an hypothesis.

Oryzomyini

The monophyly of the tribe Oryzomyini, as defined by Voss and Carleton (1993), is strongly corroborated by the IRBP dataset. Together with results provided by cladistic analysis of morphological characters (Steppan, 1995), the evidence for oryzomyine monophyly is much stronger than the evidence against it provided by cytochrome *b* data (Bonvicino and Moreira, 2001; see Figure 1C). The recovered oryzomyine clade includes all 14 genera assigned by Voss and Carleton (1993) plus two genera described afterwards: Amphinectomys Malygin et al., 1994, and Handleyomys Voss et al., 2002. In this context, the results from IRBP provide solid evidence for the inclusion within the Oryzomyini of several genera (e.g., Pseudoryzomys, Zygodontomys, Holochilus) that were once considered more related to other sigmodontine groups (Hershkovitz, 1955, 1962), and of Scolomys, which was not placed in the Oryzomyini by the cytochrome *b* analyses of Smith and Patton (1999).

Although the sister group to the Oryzomyini cannot be unambiguously determined from the present study, the relative position of the tribe among other sigmodontines can be addressed. First, oryzomyines are not recovered as the most basal sigmodontine clade, as suggested by Gardner and Patton (1976). Second, oryzomyines are not the sister group of all sigmodontines except Sigmodon, as was found with mitochondrial sequences (Engel et al., 1998). Third, oryzomyines are not closely related to any taxon formerly placed in the thomasomyine group, such as Thomasomys,

Rhipidomys, Delomys, and Juliomys, corroborating recent assessments of morphological character data (Voss, 1993; Steppan, 1995). Finally, any of the various sister taxa recovered for oryzomyines by Steppan (1995) or Smith and Patton (1999) are not found as such in the present analysis.

The present data provide the strongest hypothesis to date regarding the most basal relationships within Oryzomyini. Various taxa have been proposed as the basal oryzomyine lineage, including Nectomys (see Baker et al., 1983), a clade containing Microryzomys and Neacomys (see Patton and da Silva, 1995), Microryzomys (see Carleton and Olson, 1999), and a clade containing Oecomys and Oryzomys megacephalus (see Smith and Patton, 1999). Most of those hypotheses, however, were based on studies that did not include a taxonomically dense sampling of either oryzomyines or non-oryzomyine sigmodontines. In addition, these phylogenetic relationships received low levels of support from the data on which they were based. In contrast, the placement of Scolomys and Zygodontomys at the base of the oryzomyine clade, as suggested by the IRBP data, is well-supported within a densely sampled taxonomic framework (Figure 5). Nonetheless, additional analysis of other characters sources would provide a welcome test of this relationship.

The representatives of the seven species groups of Oryzomys included in clade A have been thought to be related to each other based on morphological evidence (Hershkovitz, 1966a; Musser and Williams, 1985; Musser et al., 1998), and representatives of some of these species groups (e.g., O. macconnelli, O. megacephalus, and O. yunganus) were found to be close to Oecomys in previous phylogenetic analyses (Patton and Hafner, 1983; Baker et al., 1983; Dickerman and Yates, 1995; Patton and da

Silva, 1995). Nonetheless, this is the first analysis that provides strong evidence for a distinct clade containing these taxa. The inclusion of Handleyomys in this clade and its association with Oryzomys alfaroi and O. melanotis contrasts with the lack of information provided by morphological characters, as noted by Voss et al. (2002: 20): “Indeed, no oryzomyine genus appears to exhibit any compelling pattern of synapomorphies with Handleyomys apart from those that support tribal monophyly. Likewise, none of the morphologically diverse species currently referred to Oryzomys (*sensu* Musser and Carleton, 1993) seems to show any special morphological similarity with [Handleyomys].” This reinforces the perception that evaluation of morphological data for assessment oryzomyine relationships is long overdue.

In contrast to other major oryzomyine clades within oryzomyines, the first branch within clade B has support from other sources of data. Oligoryzomys and Microryzomys share several morphological characters, although most of these were considered as oryzomyine plesiomorphies by Carleton and Musser (1989). By contrast, analyses of cytochrome *b* data have consistently recovered Neacomys and Microryzomys as sister groups (Patton and da Silva, 1995; Myers et al., 1995; Bonvicino and Moreira, 2001). Evidence for a clade containing Oligoryzomys, Neacomys, and Microryzomys is most clearly provided by the allozymic data of Dickerman and Yates (1995), who also presented a list of other data supporting this clade (op. cit., 1995: 184): “[S]imilarity in body size and proportions; similarity between Neacomys and Oligoryzomys in morphology of the glans penis and baculum (Hooper and Musser, 1964); compatibility between the standard karyotypes of Neacomys and Microryzomys with the range of diploid and fundamental numbers seen in Oligoryzomys (Gardner and Patton, 1976;

Myers and Carleton, 1981); DNA melting data showing these three [genera] to be similar genomically to the exclusion of other oryzomyines (Dickerman, 1992:184).” While most, if not all, of these features are general statements of similarity without defined hypotheses of homology and character states, they could be evaluated in the future as potential evidence for this clade.

The only case of conflict between the present study and previous ones that involves mutually well-supported clades concerns four taxa recently placed within oryzomyines. Morphological data (see Steppan, 1995, 1996; Carleton and Olson, 1999) strongly support a clade composed of four tetralophodont genera in the sequence (Zygodontomys (Pseudoryzomys (Lundomys + Holochilus))). The most parsimonious trees consistent with this pattern of relationships, however, require 19 additional IRBP substitutions than the minimum length trees. This conflict may be due to the lack of dense taxon sampling in the morphological analyses, or to homoplasy in the few morphological traits that are informative about relationships among these genera. The reevaluation of such characters with denser taxon sampling and in a combined-data analysis could provide a better understanding of this contrast between morphological and molecular results.

The clade containing Amphinectomys, Nectomys, Melanomys, Sigmodontomys, Nesoryzomys, and three species of Oryzomys (O. xanthaeolus, O. palustris, and O. couesi) is yet another new hypothesis within oryzomyine phylogenetics. Nevertheless, the close association of those taxa is not totally unexpected, given the morphological similarity of many included forms and previous evidence indicating the relatedness of some included taxa. For instance, (1) several taxa in this clade possess a series of

morphological adaptations for semi-aquatic life (Amphinectomys, Nectomys, O. palustris, and Sigmodontomys); (2) Melanomys and Sigmodontomys had been associated with Nectomys throughout their taxonomic history (Goldman, 1918; Hershkovitz, 1944); and (3) O. xanthaeolus was found close to Nesoryzomys in phenetic analysis of morphological characters (Patton and Hafner, 1983). Some of the recovered relationships within this clade corroborate previous results, including the monophyly of Nesoryzomys (Patton and Hafner, 1983), the association of O. couesi and O. palustris (Hall, 1960; Sánchez et al., 2001), and the sister group relationship of Amphinectomys and Nectomys (Malygin et al., 1994). In contrast, the close relationship of Sigmodontomys and Melanomys has never been proposed. These two taxa are dissimilar in morphological and ecological features. Melanomys is a vole-like rodent usually found in forested habitats with dense ground cover vegetation (Goodwin, 1946; Gardner, 1983), while Sigmodontomys is a larger rat, with some semiaquatic adaptations, usually associated with bodies of water such as streams and lakes (Hershkovitz, 1944; Handley, 1976; McPherson, 1985). However, Melanomys and Sigmodontomys share a similar Trans-Andean distribution throughout lower montane and lowland forested habitats in southern Central America and northwestern South America, where they are often found in sympatry (Gardner, 1983; McPherson, 1985). With the exception of Nectomys and Amphinectomys, all other taxa in this clade also possess a Trans-Andean distribution (including Nesoryzomys in the Galapagos). The resolution of the internal structure of this clade may indicate a biogeographic pattern of separate Trans vs. Cis-Andean oryzomyine radiations comparable to patterns previously reported for other groups of Neotropical organisms (e.g., Heliconius butterflies, Brower, 1996; tropidurine lizards, Harvey and

Gutberlet, 2000; various bird groups, Prum, 1988, Cracraft and Prum, 1988, Brumfield and Capparella, 1996).

“*Oryzomys*”

The present analysis provides compelling justification for the generic recognition of several taxa formerly included as subgenera of *Oryzomys* (e.g., *Microryzomys*, *Melanomys*, *Oligoryzomys*, *Oecomys*, *Sigmodontomys*, and *Nesoryzomys*). Even in its currently strict sense (Musser and Carleton, 1993), however, *Oryzomys* remains polyphyletic, a result also found in every explicit phylogenetic analysis to date (Baker et al., 1983; Patton and Hafner, 1983; Dickerman and Yates, 1995; Myers et al., 1995; Patton and da Silva, 1995; Stepan, 1995; Weksler, 1996; Bonvicino and Moreira, 2001). The phylogeny presented here indicates that *Oryzomys* should be restricted to the clade containing the *palustris* species group, here represented by *O. palustris* (type species of the genus) and *O. couesi*. Sánchez et al. (2001) listed several morphological characters that define the monophyly of this group *vis-à-vis* other *Oryzomys* species groups, but those characters should be evaluated in a broader taxonomic framework that includes additional oryzomyine genera in order to convincingly test their diagnostic value. If *Oryzomys* is thus restricted, then five additional taxa retrieved as independent lineages in clade B (“*Oryzomys*” *balneator*, “*O.*” *xanthaeolus*, “*O.*” *polius*, “*O.*” *subflavus*, and “*O.*” *angouya*) should be provided with new generic names (no genus-level name is available for the other clades of “*Oryzomys*”). Nevertheless, the low support for the phylogenetic placement of those taxa and the incongruence between the present results and previous studies suggest that a revised generic taxonomy should be based on a more comprehensive synthesis of both morphological and molecular data.

Species of Oryzomys included in clade A will likewise require new genera in order to achieve a comprehensive monophyletic classification. Minimally, such new genera would contain the following taxa: (1) the megacephalus and yunganus species groups; (2) the alfaroi and melanotis species groups; (3) the talamancae and nitidus species groups (the latter represented here by “O.” macconnelli, “O.” lamia, and “O.” russatus); and (4) the albigularis species group. If the sister-taxon relationship of the alfaroi and melanotis groups with Handleyomys is corroborated by additional character analyses, members of these two groups could be transferred to the latter genus, although a new genus would better reflect the morphological distinctiveness of the alfaroi and melanotis groups in relation to Handleyomys (cf. Voss et al., 2002). Additionally, in half of the fundamental cladograms, “O.” albigularis is placed as sister taxon to the clade containing the talamancae and nitidus species groups and might be included in the same genus. Again, the degree of morphological distinctiveness of the albigularis complex may warrant the creation of a separate genus for this group of species. Obviously, further analysis with denser taxon sampling and character data from different sources is desirable before the creation of any new taxonomic entities along these lines.

CONCLUSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

The analysis of IRBP sequence data provides substantial improvement in our knowledge of oryzomyine phylogeny and reinforces the utility of slower-evolving nuclear genes in resolving relationships at lower taxonomic levels. Although the resulting phylogeny is not completely resolved, it is the best available framework for future research on the group. The assessment of oryzomyine morphological characters constitutes the natural next step prior to the creation of a biologically meaningful

taxonomic structure. In this context, the most pressing issue is the reevaluation of the genus Oryzomys, for which as many as nine new genera might be needed to achieve a monophyletic classification. Such changes must await future analyses with denser taxonomic sampling and other sources of data (such as morphology and more rapidly evolving genes) not only to achieve a fully resolved tree, but also to provide convincing for each new genus. In addition, the phylogenetic position of some fossil taxa tentatively associated with oryzomyines remains to be determined. These include Megaoryzomys from the Galapagos Islands (Lenglet and Coppois, 1979; Steadman and Ray, 1982), Megalomys from the Caribbean (Ray, 1962), and Jacobsomys from the Pliocene of tropical North America (Czaplewski, 1987). Finally, a robust character-based phylogeny would allow a reevaluation of existing scenarios for the evolutionary and biogeographic history of oryzomyines and sigmodontines (Hershkovitz, 1962, 1966b; Patterson and Pascual, 1968; Gardner and Patton, 1976; Marshall, 1979; Reig, 1980, 1984; Slaughter and Ubelaker, 1984; Jacobs and Lindsay, 1984; Baskin, 1986). Most of these scenarios are based on geographic or paleontological distributional data and stand on presently refuted hypotheses of phylogenetic relationships. The incorporation of a robust topology will provide a framework for assessing the phylogenetic assumptions and predictions of those scenarios.

TABLES

TABLE 1. Current and previous classifications of oryzomyine rodents. Number of species per genera are given in the last column.

Hershkovitz, 1944, 1955, 1960, 1962	Reig, 1980, 1984, 1986	Current (Voss and Carleton, 1993)
Oryzomyine group ^a	Oryzomyini	Oryzomyini
<u>Neacomys</u>	<u>Neacomys</u>	<u>Amphinectomys</u> ^c (1) ^d
<u>Nectomys</u>	<u>Nectomys</u>	<u>Handleyomys</u> (2)
<u>Oryzomys</u>	<u>Nesoryzomys</u>	<u>Holochilus</u> (3+)
<u>Melanomys</u> ^b	<u>Oecomys</u>	<u>Lundomys</u> (1)
<u>Microryzomys</u>	<u>Oryzomys</u>	<u>Melanomys</u> (3+)
<u>Oecomys</u>	<u>Melanomys</u>	<u>Microryzomys</u> (2)
<u>Oligoryzomys</u>	<u>Microryzomys</u>	<u>Neacomys</u> (8+)
<u>Oryzomys</u>	<u>Oligoryzomys</u>	<u>Nectomys</u> (4+)
<u>Nesoryzomys</u>	<u>Oryzomys</u>	<u>Nesoryzomys</u> (4)
<u>Sigmodontomys</u>	<u>Sigmodontomys</u>	<u>Oecomys</u> (15+)
<u>Scolomys</u>	<u>Scolomys</u>	<u>Oligoryzomys</u> (16+)
Phyllotine group	Phyllotini	<u>Oryzomys</u> (35+)
<u>Pseudoryzomys</u>	<u>Pseudoryzomys</u>	<u>Pseudoryzomys</u> (1)
<u>Zygodontomys</u>	Sigmodontini	<u>Scolomys</u> (3)
Sigmodont group	<u>Holochilus</u>	<u>Sigmodontomys</u> (2)
<u>Holochilus</u>	Incertae sedis	<u>Zygodontomys</u> (3)
	<u>Zygodontomys</u>	

^a The suprageneric groups of Hershkovitz were used as the basis for the Sigmodontine tribes erected by Vorontsov (1959). Only currently recognized oryzomyine genera are listed in the table. For example, Sigmodon is not listed under the Sigmodont group of

TABLE 1. Continued.

Herskovitz's classification, nor is Thomasomys listed under Oryzomyini in Reig's scheme.

^b The indentation of Melanomys and following genera indicate that these taxa were considered as subgenera of Oryzomys

^c Amphinectomys Malygin et al, 1994, and Handleyomys Voss et al., 2002, were described after Voss and Carleton (1993), but conform to their characterization of the tribe. These two genera plus Lundomys, described by Voss and Carleton (1993), are not included in Herskovitz's and Reig's schemes.

^d Number of species are based on Musser and Carleton (1993), with the addition of species described afterwards (listed in Patterson, 2000, and Grelle, 2002; plus new species and taxonomic modifications of Dowler et al., 2000, and Voss et al., 2001, 2002). The sign (+) after some genera (e.g., Holochilus) indicates that is very likely that the number of recognized species is underestimated.

TABLE 2. Taxa and specimens sequenced for IRBP exon 1.

Taxon ^a	Voucher no. ^b	Locality data	Genbank Accession no.
Muroid Outgroups			
Murinae			
<u>Mus musculus</u>		Genbank sequence	AF126968
Calomyscinae			
<u>Calomyscus baluchi</u>	FMNH140412	Pakistan, Malakand, Karakar Pass	AY163581
Mystromyinae			
<u>Mystromys albicaudatus</u>	DM4344	South Africa, Mgeni Vlei	AY163594
Arvicolinae			
<u>Eothenomys melanogaster</u>	USNM574329	China, Sichuan, 17 Km SSE Shimian	AY163583
<u>Microtus sikimensis</u>	USNM449126	China, Qinghai, Bei Zha Forestry Station	AY163593
Cricetinae			
<u>Mesocricetus auratus</u>		Harlan Bioproducts Laboratory Colony	AY163591
<u>Phodopus sungorus</u>	MVZ155878	no locality data recorded	AY163631
Neotominae ^c			
<u>Neotoma lepida</u>	MVZ143946	USA, California, Los Angeles County	AY163599
<u>Peromyscus maniculatus</u>	UMMZ165752	USA, Michigan, High Island	AY163630
<u>Scotinomys teguina</u>	MVZ148724	University of Michigan laboratory colony	AY163639
Tylomyinae ^c			
<u>Nyctomys sumichrasti</u>	ROM101531	El Salvador, Santa Ana, PN Montecristo	AY163603
<u>Tylomys nudicaudus</u>	ROM103590	El Salvador, Ahuachapan, El Imposible	AY163643
Sigmodontinae ^c			
Abrothrichini ^d			
<u>Abrothrix longipilis</u>	MVZ154494	Argentina, Río Negro, La Veranada	AY163577
<u>Notiomys edwardsii</u>	MVZ163067	Argentina, Río Negro, Pilcaniyeu	AY163602

TABLE 2. Continued.

Akodontini ^d			
<u>Akodon azarae</u>	GD145	Paraguay, Ñeembucu, Estancia Yacaré,	AY163578
<u>Scapteromys tumidus</u>	MVZ183267	Uruguay, Maldonado, Arroyo El Renegado	AY163637
Ichthyomyini			
<u>Rheomys raptor</u>	KU159017	Costa Rica, Puntarenas, Monteverde Reserve	AY163635
Phyllotini			
<u>Calomys lepidus</u>	MVZ171562	Peru, Puno, 6 km N Putina	AY163580
<u>Phyllotis xanthopygus</u>	MVZ182703	Argentina, Río Negro, Pilcaniyeu	AY163632
Sigmodontini			
<u>Sigmodon alstoni</u>	USNM448639	Venezuela, Apure, Hato El Frío	AY163640
Thomasomyini ^e			
<u>Rhipidomys nitela</u>	MHNS7820	Venezuela, Bolívar, San Ignacio de Yuruaní	AY163636
<u>Thomasomys baeops</u>	AMNH268146	Peru, Cajamarca, Las Ashitas	AY163642
Wiedomyini			
<u>Wiedomys pyrrhorhinos</u>	CRB1839	Brazil, Bahia, Jaborandi	AY163644
Sigmodontinae incertae sedis ^d			
<u>Delomys sublineatus</u>	FMNH141628	Brazil, São Paulo, EB Boraceia	AY163582
<u>Irenomys tarsalis</u>	MVZ184955	Argentina, Neuquen, Mallin Mula	AY163587
<u>Juliomys pictipes</u> ^f	LC59	Brazil, Minas Gerais, Parque do Caraça	AY163588
<u>Reithrodon auritus</u>	MVZ182704	Argentina, Río Negro, Las Victorias	AY163634
Oryzomyini			
<u>Amphinecomys savamis</u> ^g	MV970045	Peru, Iquitos, San Pedro	AY163579
<u>Handleyomys intectus</u> ^h	ICN16093	Colombia, Antioquia, 4 KM S El Retiro	AY163584
<u>Holochilus brasiliensis</u>	GD081	Paraguay, Ñeembucu, Estancia Santa Teresa	AY163585
<u>Holochilus chacarius</u>	GD071	Paraguay, Ñeembucu, Estancia Yacaré	AY163586
<u>Lundomys molitor</u> ⁱ	MNH4292	Uruguay, Colonia, Arroyo Cufre	AY163589

TABLE 2. Continued.

<u>Melanomys caliginosus</u>	MHNLS7698	Venezuela, Zulia, Misión Tukuko	AY163590
<u>Microryzomys minutus</u>	MVZ166666	Peru, Cuzco, 32 km NE Paucartambo	AY163592
<u>Neacomys minutus</u> ^j	AMNH272867	Peru, Loreto, Río Gálvez	AY163595
<u>Neacomys musseri</u> ^j	AMNH272676	Peru, Loreto, Río Gálvez	AY163596
<u>Neacomys spinosus</u>	MVZ155014	Peru, Amazonas, Río Cenepa	AY163597
<u>Nectomys squamipes</u>	FMNH141632	Brazil, São Paulo, Ilha do Cardoso	AY163598
<u>Nesoryzomys narboroughi</u> ^k	ASNHC8675	Ecuador, Galápagos, Isla Fernandina	AY163600
<u>Nesoryzomys swarthi</u>	ASNHC10003	Ecuador, Galápagos, Isla Santiago	AY163601
<u>Oecomys bicolor</u>	AMNH272674	Peru, Loreto, Río Gálvez	AY163604
<u>Oecomys catherinae</u> ^l	MF29	Brazil, Espírito Santo, RF C. V. Rio Doce	AY163605
<u>Oecomys concolor</u>	MVZ155005	Peru, Amazonas, Río Cenepa	AY163606
<u>Oecomys mamorae</u>	JLP16961	Brazil, Mato Grosso do Sul, Rio Vermelho	AY163607
<u>Oecomys trinitatis</u>	MUSM13320	Peru, Loreto, Río Gálvez	AY163608
<u>Oligoryzomys flavescens</u>	CRB1405	Brazil, São Paulo, Pedreira	AY163609
<u>Oligoryzomys fornesi</u> ^m	CRB747	Brazil, Goiás, Terezina de Goiás	AY163610
<u>Oligoryzomys fulvescens</u>	AMNH257262	Venezuela, Sucre, Finca Vuelta Larga	AY163611
<u>Oligoryzomys nigripes</u>	CRB1422	Brazil, São Paulo, Pedreira	AY163612
<u>Oligoryzomys stramineus</u> ⁿ	MNRJ46406	Brazil, Goiás, Terezina de Goiás	AY163613
<u>Oryzomys albigularis</u>	AMNH268125	Peru, Cajamarca, Las Ashitas	AY163614
<u>Oryzomys alfaroi</u>	ROM101537	El Salvador, Santa Ana, PN Montecristo	AY163615
<u>Oryzomys angouya</u> ^o	MNRJ50234	Brazil, Rio de Janeiro, Teresopolis	AY163616
<u>Oryzomys balneator</u>	AMNH268144	Peru, Cajamarca, 4 km W of Chaupe	AY163617
<u>Oryzomys couesi</u>	TTU37749	Mexico, Jalisco, Chamela	AY163618
<u>Oryzomys lamia</u>	MNRJ46654	Brazil, Goiás, Chapada dos Veadeiros	AY163619
<u>Oryzomys macconnelli</u>	AMNH272678	Peru, Loreto, Río Gálvez	AY163620
<u>Oryzomys megacephalus</u> ^p	MHNLS8061	Venezuela, Bolívar, San Ignacio de Yuruaní	AY163621

TABLE 2. Continued.

<u>Oryzomys palustris</u>	TTU75311	USA, Texas, Freesto	AY163623
<u>Oryzomys polius</u>	FMNH129243	Peru, Amazonas, Balsas	AY163624
<u>Oryzomys melanotis</u>	ROM101843	El Salvador, Ahuachapan, El Imposible	AY163622
<u>Oryzomys russatus</u>	ORG67	Brazil, Rio de Janeiro, Garrafão	AY163625
<u>Oryzomys subflavus</u>	MNRJ61665	Brazil, Minas Gerais, Fazenda Canoas	AY163626
<u>Oryzomys talamancae</u>	USNM449894	Panama, Bocas del Toro, Tierra Oscura	AY163627
<u>Oryzomys xantheolus</u>	MVZ145533	Peru, Arequipa, 4.5 mi E Acari	AY163628
<u>Oryzomys yunganus</u>	CMNH76926	Suriname, Saramacca, Tafelberg	AY163629
<u>Pseudoryzomys simplex</u>	GD065	Paraguay, Ñeembucu, Estancia Yacaré	AY163633
<u>Scolomys ucayalensis</u>	AMNH272721	Peru, Loreto, Río Gálvez	AY163638
<u>Sigmodontomys alfari</u>	USNM449895	Panama, Bocas del Toro, Isla San Cristobal	AY163641
<u>Zygodontomys brevicauda</u>	AMNH257321	Venezuela, Sucre, Finca Vuelta Larga	AY163645
<u>Zygodontomys cherriei</u> ^a	USNM448665	Venezuela, Zulia, Misión Tukuko	AY163646

^a Unless otherwise indicated, taxonomy follows Musser and Carleton (1993)

^b Museum and collectors acronyms as follows: AMNH, American Museum of Natural History; ASNHC, Angelo State Natural History Collections; CMNH, Carnegie Museum of Natural History; CRB, Cibeles R. Bonvicino, voucher at MNRJ; DM, Durban Museum, South Africa; FMNH, Field Museum of Natural History; GD, Guillermo D'Elia; ICN, Instituto de Ciencias Naturales, Bogotá, Colombia; JLP, James L. Patton, voucher at UFMG (Mammal Collection, Universidade Federal de Minas Gerais, Brazil); KU, University of Kansas Natural History Museum; LC, Leonora Costa, voucher at UFMG; MF, Monica Fonseca, voucher at UFMG; MHNLS, Museo de Historia Natural La Salle, Caracas, Venezuela; MNHN, Museo Nacional de Historia Natural, Montevideo, Uruguay; MNRJ, Museu Nacional, Rio de Janeiro, Brazil; MV, Michael Valqui, voucher

TABLE 2. Continued.

at MUSM (Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru); MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; ORG, Laboratorio de Vertebrados, Universidade Federal do Rio de Janeiro, Brazil, voucher at MNRJ; ROM, Royal Ontario Museum; TTU, Museum of Texas Tech University; UMMZ, Museum of Zoology, University of Michigan; USNM, National Museum of Natural History

^c Sensu Reig (1984)

^d Sensu Smith and Patton (1999)

^e Sensu Voss (1993)

^f = Wilfredomys pictipes; Gonzáles (2000)

^g = Malygin et al, 1994

^h = Oryzomys intectus; Voss et al. (2002)

ⁱ = Holochilus magnus; Voss and Carleton (1993)

^j Patton et al. (2000)

^k = Nesoryzomys indefessus; Dowler et al. (2000)

^l = Oecomys trinitatis; J. Patton, personal communication

^m = Oligoryzomys microtis; Bonvicino and Weksler (1998)

ⁿ Bonvicino and Weksler (1998)

^o = Oryzomys ratticeps; Musser et al. (1998)

^p = Oryzomys capito; Musser et al. (1998)

^q = Zygodontomys brevicauda; R. Voss, personal communication

TABLE 3. Range and average (in parentheses) of base composition (percentage) for each codon position across all taxa.

Position	A	C	G	T
First	20.0-22.8 (21.6)	27.8-30.0 (28.9)	36.3-38.8 (37.2)	11.1-13.1 (12.4)
Second	25.5-27.7 (26.8)	23.2-24.9 (24.2)	17.6-19.3 (18.3)	29.8-31.7 (30.7)
Third	10.8-18.7 (16.5)	28.9-38.3 (31.0)	29.0-38.3 (31.4)	12.6-23.3 (21.1)
All	19.2-22.8 (21.6)	27.1-30.7 (28.0)	27.9-31.7 (29.0)	18.4-22.2 (21.4)

TABLE 4. Tree statistics and homoplasy indices for each codon position of IRBP.

Position	Number of variable characters	Number of informative characters	CI	RI	Num. Steps (mean)
First	140	73	0.51	0.71	1.91
Second	89	57	0.44	0.50	2.22
Third	359	256	0.44	0.63	2.91
All	588	386	0.45	0.63	2.57

FIGURES

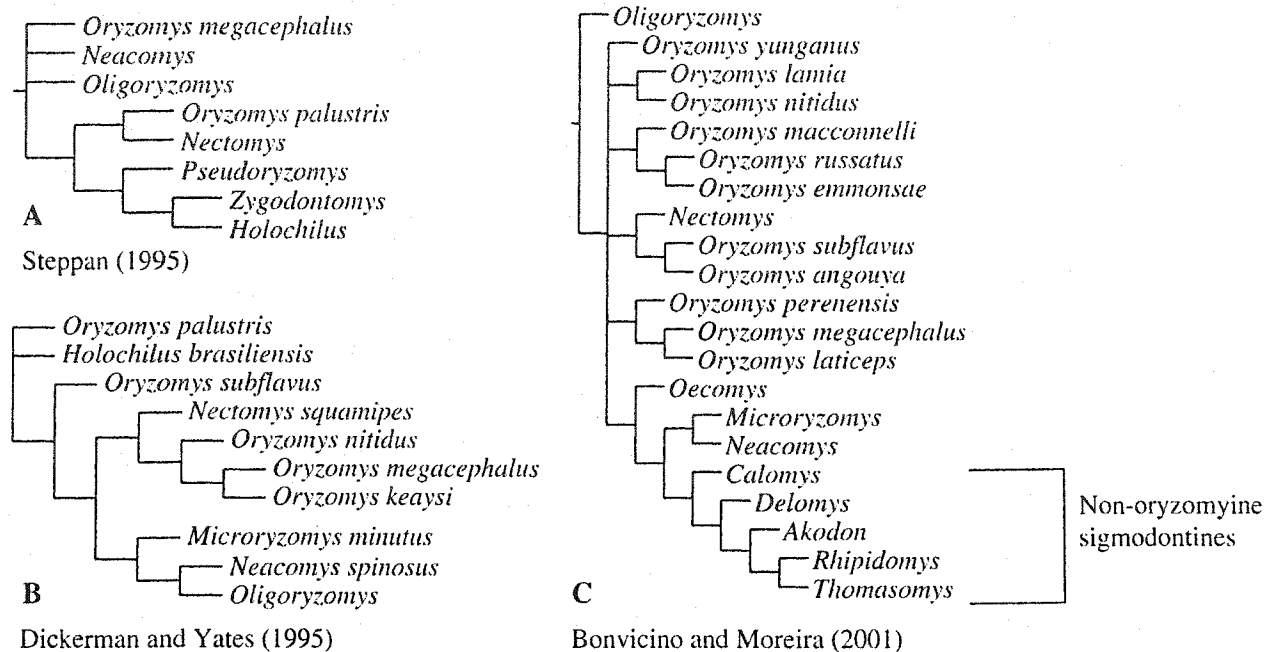


Figure 1. Three previous hypotheses of oryzomyine relationships, updated to conform with current taxonomic usage and pruned of non-oryzomyines outgroups. For simplicity, species-level taxonomic sampling is not illustrated for monophyletic genera in these analyses. (A) Portion of sigmodontine phylogeny based on morphological characters (Steppan, 1995), of which only 11 were informative about oryzomyine relationships; (B) phylogeny based on electrophoretic allozymes (Dickerman and Yates, 1995; 19 parsimony-informative loci); (C) phylogeny based on cytochrome *b* sequences (Bonvicino and Moreira, 2001). Other topologies recovered from cytochrome *b* display the same pattern of low resolution (Myers et al., 1995) or are highly incongruent with this one (Patton and da Silva, 1995; Smith and Patton, 1999).

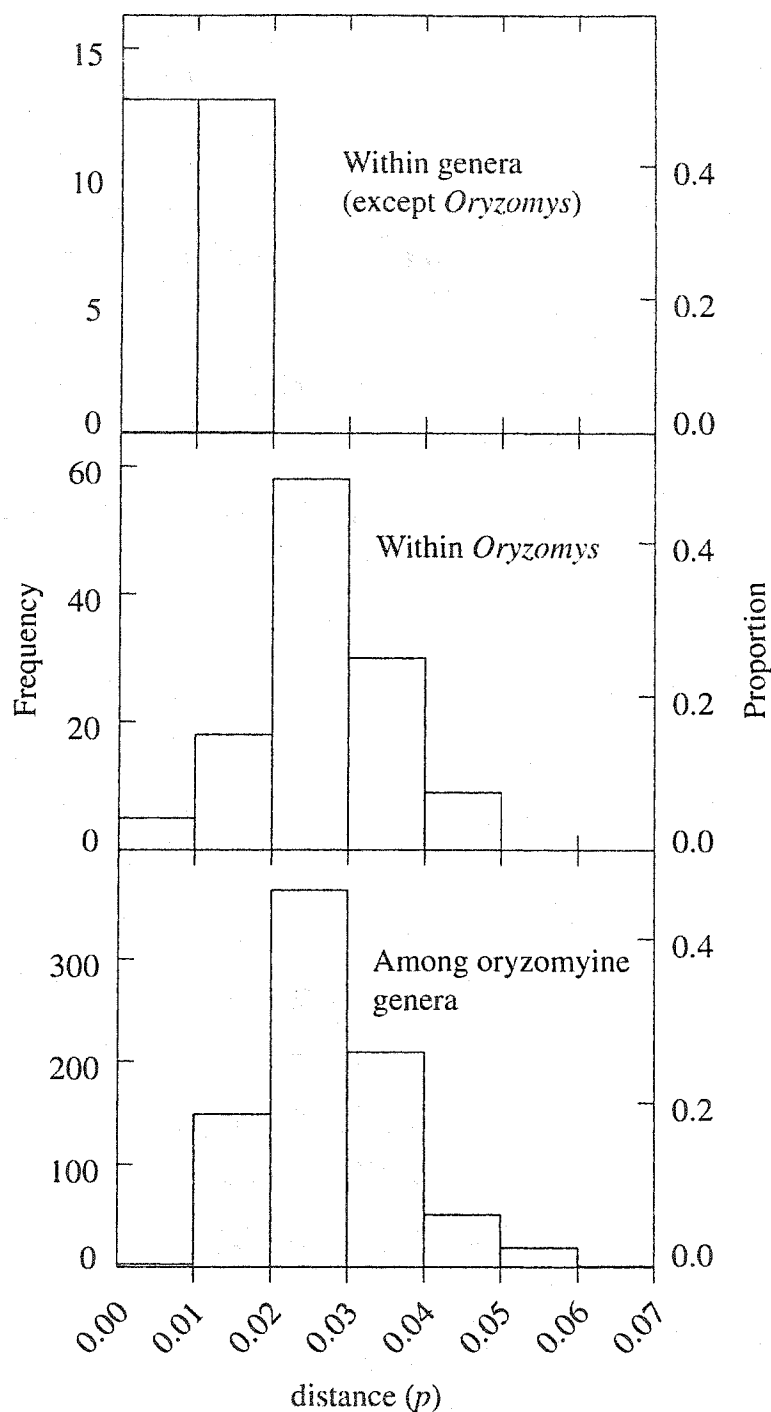


Figure 2. Pairwise sequence divergence (p) at three taxonomic levels. Six genera were used for the upper histogram: *Zygodontomys*, *Oecomys*, *Oligoryzomys*, *Neacomys*, *Holochilus*, and *Nesoryzomys*. However, the level of pairwise species divergence within *Oryzomys* (middle histogram) is equivalent to that observed among species in different oryzomyine genera (lower histogram).

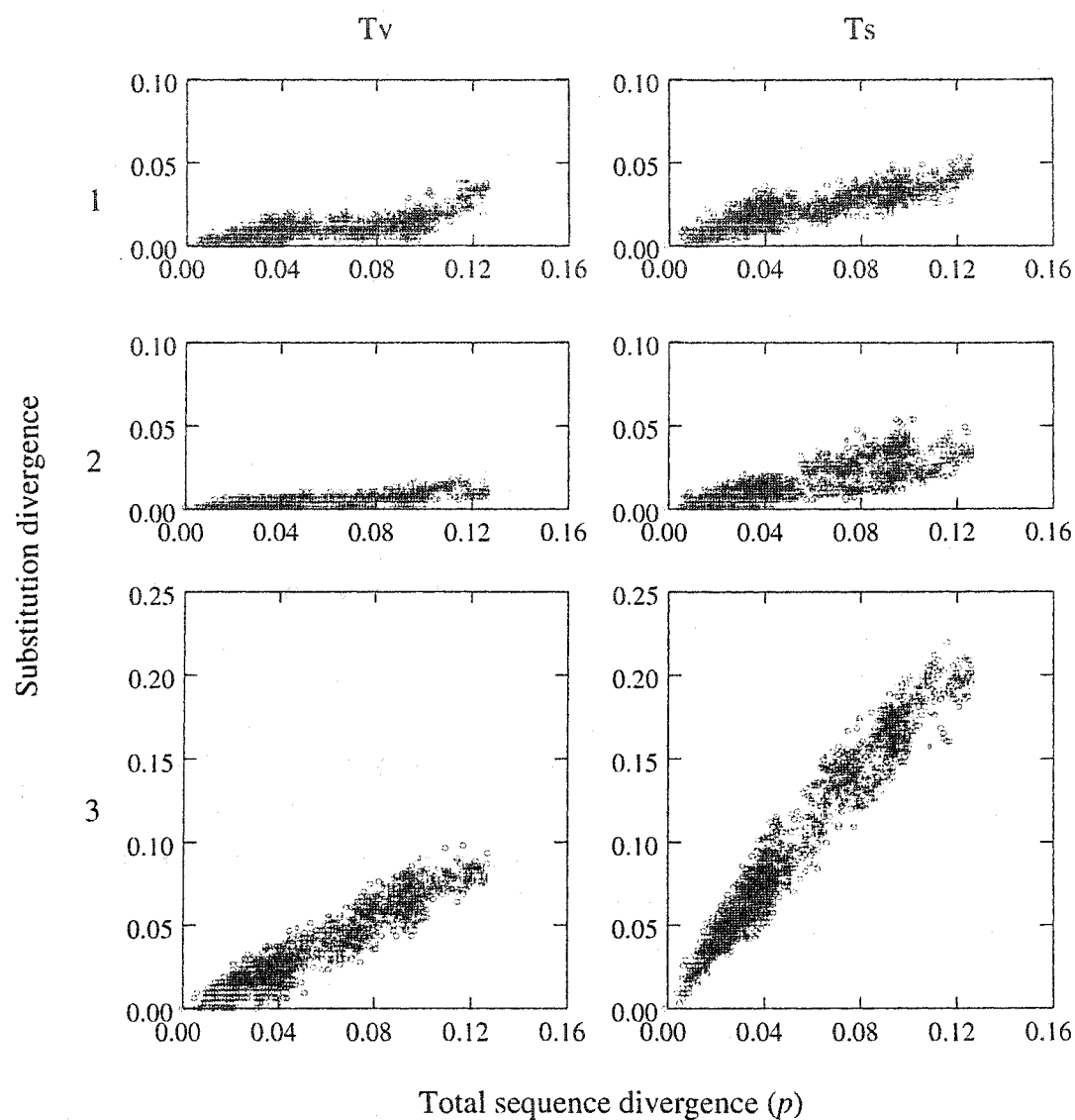


Figure 3. Saturation plots for transversion (tv) and transition (ti) substitutions per partition (codon position) for the 71 muroid sequences included in this study. Each graph is the plot of the frequency of inferred substitution type (Y-axes) versus uncorrected pairwise sequence divergence (X-axes). There is no sign of saturation for any combination of codon position and substitution type, even in comparisons between outgroup and ingroup taxa.

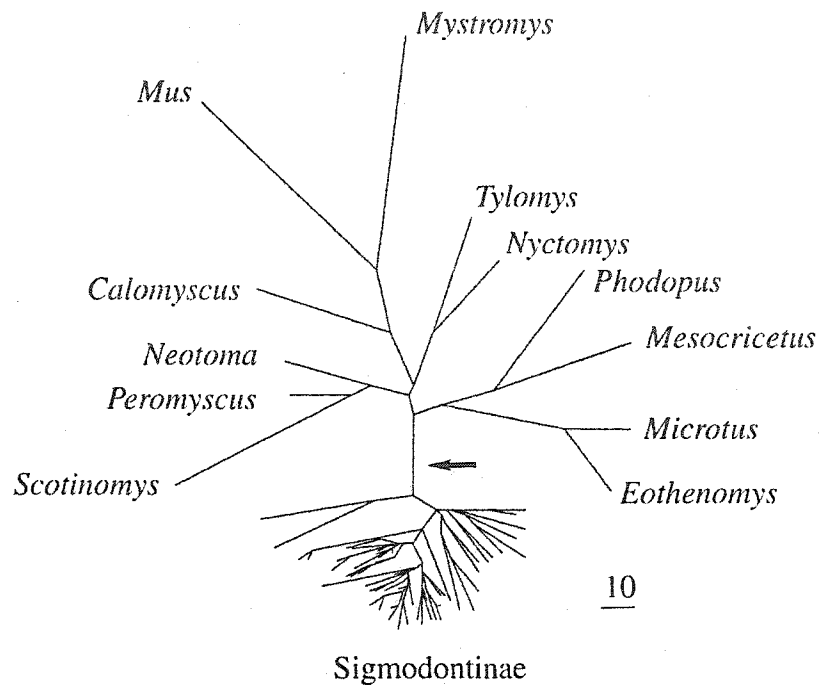


Figure 4. One of 16 undirected networks of muroid relationships based on parsimony analysis of IRBP sequences. Branch lengths are drawn proportional to reconstructed character changes (base substitutions) based on ACCTRAN optimization. DELTRAN optimization produced a similar branch length pattern, as well as the maximum likelihood tree. For greater clarity, sigmodontine terminals are not labeled. The inferred position of the sigmodontine root is indicated by the arrow. Note that sigmodontines, neotomines (Neotoma, Scotinomys and Peromyscus), and tylomyines (Tylomys and Nyctomys) do not form a monophyletic group. Rather, the sister group of sigmodontines in this topology is the clade composed by cricetines (Phodopus and Mesocricetus) and arvicolines (Microtus and Eothenomys). Bootstrap and Bremer support for outgroups relationships are low, however, with the exception of subfamilial nodes.

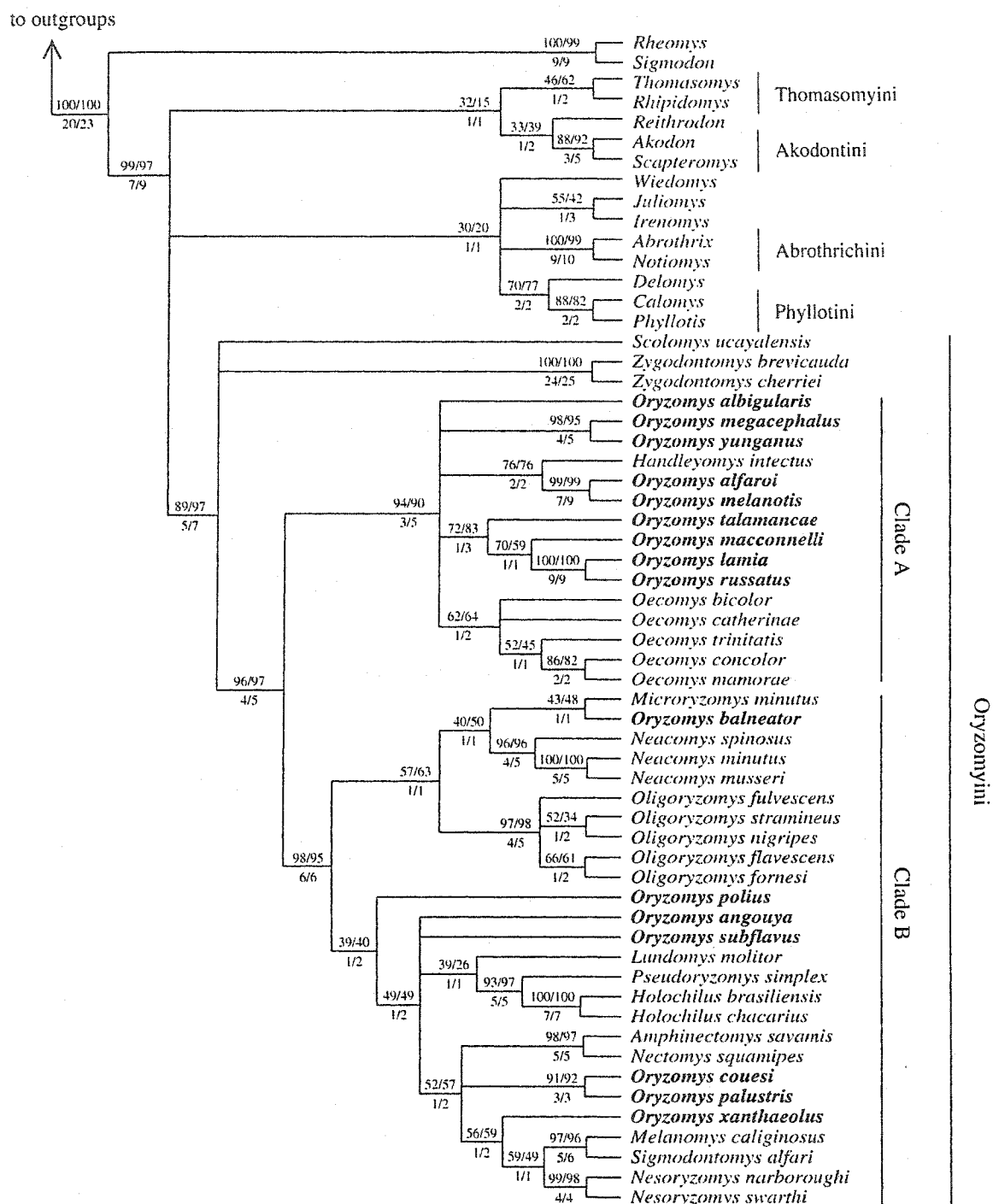


Figure 5. Strict consensus of 16 most parsimonious trees resulting from cladistic parsimony analysis of IRBP DNA sequences (parsimony-informative characters = 386, tree length = 1275, CI = 0.45, RI = 0.63). Tree is pruned to show only ingroup (Sigmodontinae) relationships. Numbers above and below branches refer to the following values: parsimony bootstrap / likelihood bootstrap (above branches), Bremer index /

number of unambiguous character changes (below branches). Non-oryzomyine terminals are labeled as generic exemplars and only tribes with two or more taxa are indicated as such. Species currently assigned to the genus Oryzomys are in boldface.

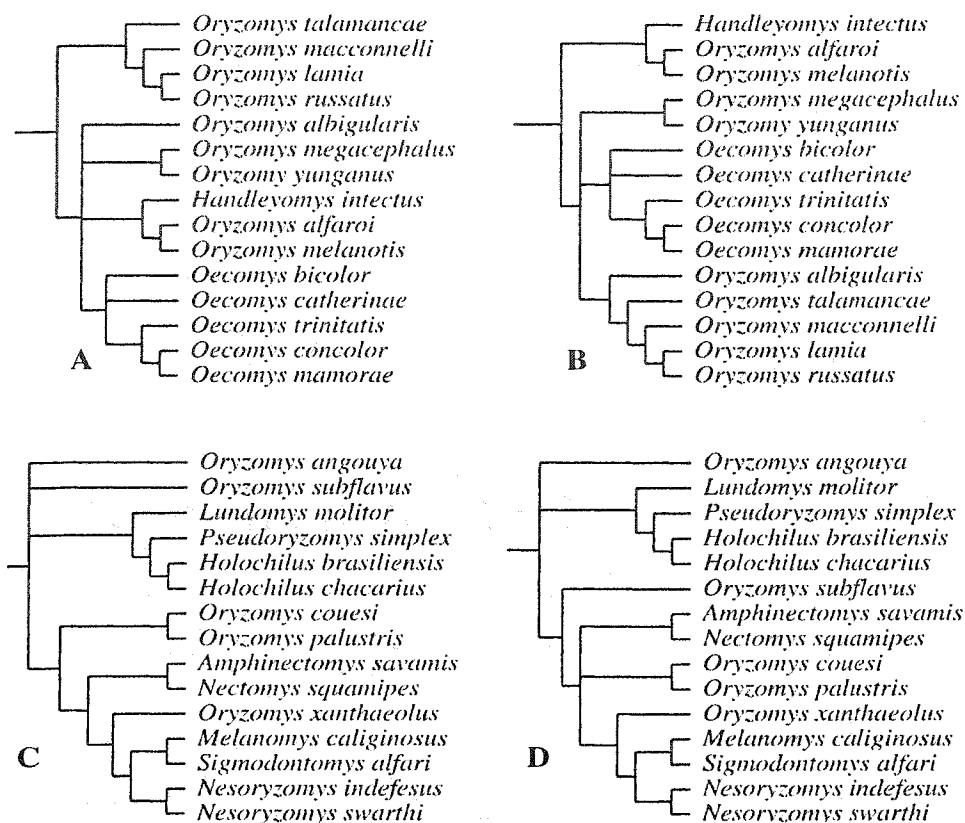


Figure 6. Subtrees of the different solutions for oryzomyine clades recovered in the fundamental cladograms. The conflicting solutions resulted in some of the polytomies displayed in the consensus tree (Figure 5). (A and B) Solutions for relationships within Clade A of Figure 5; each solution was found in 8 fundamental cladograms. (C and D) Solutions for relationships within Clade B of Figure 5; each solution was found in 8 fundamental cladograms. The maximum likelihood analysis resulted in a tree congruent with resolutions B and C.

**CHAPTER 2. PHYLOGENETIC RELATIONSHIPS OF THE
ORYZOMYINI (MUROIDEA: SIGMODONTINAE): SEPARATE
AND COMBINED ANALYSES OF MORPHOLOGICAL AND
MOLECULAR DATA**

INTRODUCTION

Sigmodontine rodents --- the monophyletic group that includes almost all South American muroids and excludes North American neotomines and tylomyines (Reig, 1980; Jansa and Weksler, 2004) --- have challenged students of mammalian systematics for the past two centuries. The result of 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 are now 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 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 the group resilient to rigorous phylogenetic hypothesis-testing. Systematic research over the last several decades, however, has improved our understanding of sigmodontine relationships at all taxonomic levels (e.g., Voss, 1988; Voss, 1991; Smith and Patton, 1993; Voss, 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 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 somewhat resembling common 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 cursorial, but some species display marked specializations for arboreal or semi-aquatic 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'Elia, 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 summarized previous hypotheses of intratribal relationships. A summary of genera included in Oryzomyini is provided in Appendix 1.

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; 1917a) further divided the pentalophodont genera (i.e., taxa with the mesoloph/ id) 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 to be made.

Other authors, however, have not regarded the differences in palatal morphology as a sufficient character for separating oryzomyines from thomasomyines and 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 oryzomyine genera were placed by Hershkovitz (1955, 1962) in other suprageneric groups because they were tetralophodont (i.e., lacking mesoloph /id). 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 descents 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, 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 only 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 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 (Appendix 1). 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).

“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.” (Herskovitz, 1944: 13).

“[except] for the presence of intermediate forms, typical Oryzomys and subgenus Oecomys might well be treated as generically distinct.” (Herskovitz, 1960: 521).

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 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 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 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 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 (1983) data, and recovered a far less resolved topology. Their strict consensus of

10,000 shortest tree (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 non-homoplasious) 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 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 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 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, but most have been based on small sets of taxa. Patton and Hafner (1983), for example, presented allozymic evidence suggesting that Oryzomys bauri is more closely related to O. xantheolus than to Nesoryzomys or to Oryzomys palustris. In a more inclusive analysis, 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). 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 relationships (fig. 7), which tend to be poorly supported by bootstrap and other resampling measures with values below 50%.

Weksler (2003) published the only phylogenetic study of oryzomyines accomplished to date using a nuclear gene sequences. In that study, parsimony and likelihood analyses were performed 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 groups, 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 semiaquatic Oryzomys. The results of these analyses are detailed in chapter 1.

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 2) 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; 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 (Appendix 1; table 1). 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 guess work. 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, 2003; Weksler, 2003) have made it possible to rationally select phylogenetic exemplars among the morass of congeneric forms.

The main 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 presented in chapter I of this volume (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. A new taxonomy of species currently included in the genus Oryzomys is proposed. Finally, I evaluate evolutionary and biogeographic hypotheses that are compatible with current knowledge of oryzomyine relationships.

MATERIAL AND METHODS

Taxonomic sampling and morphological character scoring

The designated ingroup for all of the 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 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 extant oryzomyine genera, consisting of 49 of the 116 currently recognized oryzomyine species (table 3).

Type species from all but three genera (Handleymys, 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) and were used to root the tree. The last three are pentapododont sigmodontines previously regarded as closely related to oryzomyines (Hershkovitz, 1962; Stepan, 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 2.

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 78-79; Stepan, 1995), glans

penis (85-89; Hooper and Musser, 1964; Carleton, 1980), and digestive tract (98-99; Carleton, 1973; Voss, 1991). Nevertheless, subsequent 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; however it does 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; Carleton and Musser, 1989; Voss, 1991; Braun, 1993; Steppan, 1993; Voss and Carleton, 1993; Steppan, 1995; 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 description 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 the majority of 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 (non-polymorphic) taxa. An annotated list of all analyzed characters, including rejected characters, is provided in Appendix 3.

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 resulting from lack of specimens with appropriate material or as "-" if resulting from inapplicable comparisons. Multistate characters were treated as ordered if anatomically intermediates could be recognized among the set of alternative conditions.

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 (referred hereafter 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 1,000 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 reconstruction (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 reduce the number of fundamental trees to a minimal conservative set¹.

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 ↔ 1 ↔ 2), but cost matrices were applied to three 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 Mabey 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 reported in appendices 4 and 5 for the morphology-only and combined analyses, respectively. To calculate Bremer support values (or Decay Index, DI; Bremer, 1988), 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 the **ENFORCE REVERSE** options on the heuristic search command in PAUP*. Jackknife values (JK; Farris et al., 1996) were calculated from analyzed 1,000 pseudoreplicated

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

datasets using heuristic searches with 10 random-additions replicates and TBR branch swapping; a maximum of 200 trees were retained in each random-addition replicate (for a total of 2,000 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 were 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 (referred hereafter 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 8 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 a pectoral pair. 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. swarthi².

My scoring of several taxa is at odds with some observations in the literature. Stepan (1995, table 6; also Gyldenstolpe, 1932), for example, stated that Neacomys has only six mammae (lacking the pectoral pair) but 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 Stepan (1995) reported as having six mammae, whereas I observed eight mammae (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 the postaxial mammae of most oryzomyines, but as there seems to be a continuous variation in the position of this pair among other oryzomyines, it is impossible to falsify the hypothesis that the ‘thoracic’ mammae of Scolomys and the ‘postaxial’ 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 ↔ 1 ↔ 2)³.

² Available specimens of congeners Nesoryzomys darwini and N. indefessus displayed 8 mammae.

³ Analyses with the condition of each mammae loci treated as a separated binary character arrived at the same phylogenetic results.

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 proximal region in 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 the claws, have been extensively cited in sigmodontine phylogenetic studies (see character 7), but the presence or absent of the tufts on the manus has only been recently employed (cf. Pacheco, 2003). 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 the 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 hind foot, the thenar and hypothenar pads (figs. 9A and B). In contrast, the hind foot of Holochilus, Lundomys, Nectomys, Scolomys, Sigmodontomys, Pseudoryzomys, Oryzomys palustris, and O. couesi have only a conspicuous thenar pad, the hypothenar pad being absent or vestigial⁴ (fig. 9C). Oryzomys yunganus is polymorphic for this trait (see Musser et al., 1998: 58). No information is currently available about pad morphology of pads in Amphinectomys (coded "?" in table 5).

Character 5: Plantar pads on hind feet 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: character 77; Carleton and Musser, 1989: character 2; Voss and Carleton, 1993: character 3). Nevertheless, I preferred to recognize the configuration of Scolomys as conflicting, rather than intermediary, and kept each trait as separated characters. This character was treated as ordered (0 ↔ 1 ↔ 2) to reflect the morphoclinal aspect of the development of

⁴ Vestigial structures are usually encompassed with the absent states. In those case, exemples of the same taxon display both absent/vestigial structure, as opposed to taxa displaying always present devepoed

pads. No information is currently available about pad morphology in Amphinectomys (coded "?").

Character 6: Plantar surface of hind feet smooth, without well-developed squamae (0); or plantar surface covered with squamae (1). The sole of the hind foot of most oryzomyines is continuously covered with small scale-like 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 Handleiomys, 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 hind foot as an 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). Most oryzomyines have thick ungual tufts on dII-dV of the hind feet, 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

structures.

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 (eg. 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 exist 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 ↔ 1 ↔ 2 ↔ 3). No information is currently available about ungual tufts in Amphinectomys (coded "?").

Character 8: Natatory fringes on hind feet absent (0); or present (1). Natatory fringes are continuous combs of stiff hairs along the plantar margins and sometimes between the digits of the hindfoot (Voss, 1988, fig. 7). The semi-aquatic taxa Amphinectomys, Holochilus, Lundomys, and Nectomys are the only oryzomyines to

exhibit natatory fringes. Among other sigmodontines, natatory are also present in ichthyomyines, but these were not included in this study.

Character 9: Interdigital webbing on hind feet 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 webbing are present between digits I to 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 hind feet 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 hind foot depends on the color and density of the covering hairs. Although white, gray, and brown hindfeet each include a range of subtly different colors, 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 surface.

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 employed is correlated with the bicolored/indistinctly bicolored/distinctly bicolored description of some authors (e.g., Stepan, 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, macroscopically obvious (1). The tails of muroid rodents always have some hair, usually consisting of at least 3 bristles emerging from the margin of each scale. Short hairs and low hair density give the tail a naked, scaly appearance; this is the pattern observed in most oryzomyines. In contrast, Nesoryzomys and all outgroups except Delomys and Thomasomys have tails with longer, denser hairs; such tails appear to be densely furred and to lack visible scales (even when viewed under the stereomicroscope). I could not distinguish an intermediate 'slightly furred' state that has sometimes been recognized in sigmodontine phylogenetics (e.g., Patton and Hafner, 1983; Stepan, 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 and Abrawayaomys (genera not included in this study), are the only sigmodontines with spiny pelage; however, the presence of dorsal spines is recurrent among other muroids subfamilies (e.g., in Acomys, Echiothrix, Maxomys, Platacanthomys, and Tokudaia) and among non-muroid rodents (e.g., Heteromyinae, Echimyidae 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 lack of obvious countershading. This character was treated as ordered (0 ↔ 1 ↔ 2).

Character 16: Subauricular patches absent (0); or present (1). Subauricular patches, areas of whitish coloration immediately ventral to the base of each pinna, are rare among oryzomyines, occurring only in examples of Nesoryzomys and Oryzomys albigularis. Among analyzed outgroups, subauricular patches were observed only 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 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 (figs. 11A and C). A small number of taxa, however, could not be placed unequivocally in one or the other state and are scored as polymorphic: Thomasomys, Wiedomys, Oligoryzomys nigripes, Oryzomys angouya, O. xanthaeolus, Sigmodontomys alfari, and Zygodontomys. The distribution of character-states among remaining taxa is recorded in table 5. Because of ontogenetic variation in nasal extension, only adult specimens were employed in coding this character (see also Steppan, 1995: characters 9S and 46P).

Character 20: 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). Like 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 (figs. 11A and C). The latter 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 ({12}): Melanomys caliginosus, Oryzomys alfaroi, O. xanthaeolus, and Sigmodontomys alfari. Some correlation exist 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 ↔ 1 ↔ 2)

Character 21: Lacrima equally contacting maxillary and frontal bones (0); or lacrima contacting mainly maxillary (1). In most oryzomyines, and in all outgroups, each lacrimal bone 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 bone 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. palustris, O. xanthaeolus, Pseudoryzomys, Scolomys, and Sigmodontomys. I observed both conditions among

specimens of *Oryzomys angouya* and *O. megacephalus*, which were scored as polymorphic ({01}).

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 by authors as "amphoral" or "hourglass-shaped", whereas in the two last 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 non-linear 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: character 24; Patton and Hafner, 1983: characters 13 and 14; Carleton and Musser, 1989: character 6; Voss, 1993: character 6; Voss and Carleton, 1993: character 7; Stepan, 1995: characters 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: character 4), with an additional intermediate condition (state 3) to accommodate Pseudoryzomys (scored as state 1 by Carleton and Olson, 1999). Another difference in the present coding scheme is the consideration of supraorbital crests as a distinct feature; the development of temporal ridges (considered here strictly as the ridges at the parietal-squamosal suture) is not taken into account. The rationale for considering interorbital shape and supraorbital ornamentation as a single character, instead of breaking into 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, frontal-squamosal suture exposed (0); or postorbital ridge present and concealing frontal-squamosal suture in most old specimens (1). The postorbital ridge is a

vertical bony ridge extending from the contact between the frontal and parietal to above the zygomatic root of the squamosal, following the frontal-squamosal 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: Fronto-squamosal suture continuous with the fronto-parietal suture, dorsal facet of frontal never in contact with squamosal (0); or fronto-squamosal suture anterior to fronto-parietal 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 (figs. 14A and B). In Holochilus, Melanomys, Nectomys, Oryzomys hammondi, and Sigmodontomys, however, the fronto-squamosal suture is situated anterior to the fronto-parietal 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 dorsal-lateral edges about the squamosal root of the zygomatic arch (0); or parietals deeply expanded onto lateral surface of the braincase (1). The parietals of Amphinectomys, Microrizomys, 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 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 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 longer than posterior border of frontals, in contact with squamosal (0); interparietal strap-shaped, nearly as long as posterior border of frontals, but not in contact with squamosal (1); or interparietal wedge-shaped, about half as long 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 ({12}). This character was treated as ordered (0 ↔ 1 ↔ 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. 17A). Pseudoryzomys, Lundomys, and Holochilus, however, have deeper zygomatic notches because the anterodorsal margin of the 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. 17B). 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 Stepan (1995: characters 8S and 43P; also Patton and Hafner, 1983: characters 11 and 12). This character was treated as ordered (0 ↔ 1 ↔ 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 were consequently scored as polymorphic for this character. The distribution of character-states among remaining taxa is recorded in table 5. Character definition taken from Carleton and Olson (1999: character 2), which is similar to Stepan (1995: characters 6S and 42P). My scoring for Zygodontomys brevicauda, and Oryzomys megacephalus, however, differed from that assigned by Stepan (1995).

Character 30: Jugal present and large, maxillary and squamosal processes of the zygoma non 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, and Oryzomys balneator, 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 ↔ 1 ↔ 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 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 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 (figs. 20B and D), is observed 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: Palatal bridge flat, or with shallow lateral excavations, never with median longitudinal ridge (0); or with deep lateral troughs separated by median longitudinal ridge (1). The palatal bridge of almost all oryzomyines is either flat or moderately corrugated. Conversely, the palatal bridges 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: character 8) because several taxa display both flat and slightly corrugated conditions within analyzed samples. Carleton and Olson (1999) also considered the width of the palatal bridge 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; figs. 20C and 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 were scored as polymorphic ({23}). This 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, but they do not reach the level of the mesopterygoid roof (state 1; figs. 20B and C). 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 ($0 \leftrightarrow 1 \leftrightarrow 2$). 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: character 23) and Stepan (1995: character 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 (figs. 20A and 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 the polymorphic species (Nectomys squamipes, Oryzomys megacephalus, and Zygodontomys brevicauda) which were scored accordingly ({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 non-linear pattern of transformation among states (fig. 8A). The present character description is similar to Carleton's (1980: character 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 Stepan (1995: characters 20S and 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., Guthrie, 1963; 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: character 16; Voss, 1988: character 12; Carleton and Musser, 1989; Voss and Carleton, 1993: character 11; Steppan, 1995: characters 22S and 76P; Carleton and Olson, 1999: character 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, 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 state 1 and 2)⁵. 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

⁵ The coding of this character in Steppan's (1995) matrix is inverted in relation to his character description (p. 39).

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 "?" in table 5).

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 (figs. 21B and 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 ({01}). 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 ($\leq 10\%$) 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 "?" in table 5).

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 (figs. 21A and 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 "?" in table 5).

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 (figs. 22A and B). Departing from this condition, the subsquamosal fenestra of Amphinectomys, Melanomys, Nectomys, Nesoryzomys narboroughi, Oryzomys hammondi, O. xantheolus, Sigmodontomys, and Zygodontomys cherriei is vestigial, obscured internally by the lateral border of the tegmen tympani, or is absent (figs. 22C and 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 Stepan (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 obstruct 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 the internal carotid canal (scored as polymorphic {01}). This

character was treated as ordered (0 ↔ 1 ↔ 2). My scoring for Lundomys differed from that assigned by Carleton and Olson (1999: character 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 "?" in table 5).

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 "?" in table 5).

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 dorso-lateral fenestra (fig. 22A). The size of the fenestra varies from medium-sized to large, but some specimens have a small fenestra that is enclosed by the bone, not reaching the exoccipital contact area (fig. 22B). In contrast, the mastoids of Holochilus chacarius, Melanomys, Nectomys, Nesoryzomys, Oecomys catherinae, Oryzomys hammondi, O. lamia, O. macconnelli, O. russatus, Scolomys, Sigmodontomys, and Zygodontomys are totally ossified, without 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: character 9), but I cannot explain the discrepancies. No information is currently available about this character for Amphinectomys (coded "?" in table 5).

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 "?" in table 5).

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), but variation is also correlated with age (older specimens have larger processes than younger conspecifics). Difference between species is 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 (figs. 24A and 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 recognition, 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. 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 ↔ 1 ↔ 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 actually contacting, but 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 have uniformly the open chevron pattern. No information is currently available about this character for Amphinectomys (coded "?" in table 5).

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 (figs. 24A and 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 (figs. 24C and 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; Stepan, 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 2 characters was taken from literature (in addition to above mentioned studies, 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 2 to 4, 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 ↔ 1 ↔ 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, O. 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 alfaro, 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 "?" in table 5).

Character 51: Second lower molar with 2 roots (0); or 3 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 antero-labial and antero-lingual positions) in Handleyomys, Holochilus, Oryzomys alfaro, O. chapmani, O. rostratus, O. xanthaeolus, Pseudoryzomys, Sigmodontomys alfari, and Zygodontomys. Lundomys and Oryzomys palustris are polymorphic for this character, whereas Amphinectomys, Nesoryzomys swarthi, Oryzomys couesi, O.

hammondi, O. polius, and Sigmodontomys aphrastus could not be assessed for this character (scored as missing, "?").

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, Handleiomys, 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 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 "?" in table 5).

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 than 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 "?" in table 5).

Character 56: Maxillary tooth rows parallel (0); or anteriorly convergent (1). Although the direction of the tooth rows appears to vary continuously among analyzed taxa, an unambiguous gap was detected between the more or less parallel tooth rows seen in most oryzomyines and all outgroups, and the anteriorly convergent tooth row observed in Holochilus and Lundomys. No information is currently available about this character for Amphinectomys (coded "?" in table 5).

Character 57: Flexi of M1 and M2 do interpenetrate (0); or flexi meet at midline, enamel overlaps (1); or flexi interpenetrate (2). The molars of most oryzomyines are non-lophodont, with opposite labial and lingual flexi conspicuously far from each other end (e.g., fig. 25P). Several oryzomyines, however, display a certain degree of lophodonty, that varied from minimal lophodonty, where only the enamel border of the flexi reach 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 non-lophodont 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 transversally oriented paraflexi and metaflexi (e.g., fig. 25H). See matrix in table 5 for character-states distribution among taxa. This character was treated as ordered ($0 \leftrightarrow 1 \leftrightarrow 2$). No information is currently available about this character for Amphinectomys (coded "?" in table 5).

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 (fig. 25I), 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 if the anteromedian flexus varies among taxa, I could not identify a clear distinction between ‘weakly’ or ‘deeply’ excavated states (e.g., figs. 25I versus 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. Character treated as ordered (0 ↔ 1 ↔ 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 fossete (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 xantheolus, 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 have previously been treated as separate characters in several analyses (e.g., Voss and

Carleton, 1993; Stepan, 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, and these taxa exhibit an independent enamel connection to the median mure (e.g., fig. 25D). State 2 refer to *Zygodontomys*, in which the paracone and protocone are connected by a wide dentine surface rather than 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 matrix in table 5 for character-states distribution among the remaining taxa, of which

only Oryzomys rostratus and O. subflavus were scored as polymorphic ({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 ↔ 1 ↔ 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).

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 fossete 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.

Character 66: Mesoflexus present as single internal labial fossete on M2 (0); or mesoflexus divided into labial and medial fosseti (1). The internal fosseti observed on M2 between the mesoloph and the paracone are derived from the engulfment of the mesoflexus caused by wear of occlusal surface. The presence of a single labial fossete, 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 fossete (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 fossete derived from the posteroflexus. This fossete 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 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). See matrix in table 5 for character-states distribution among remaining taxa.

Character 70: Anteromedian flexid and anteromedian fossetid absent on first lower molar (0); or anteromedian flexid absent but anteromedian fossetid present (1); or anteromedian flexid present and anteromedian fossetid absent (2). Most analyzed taxa have an undivided m1 anteroconid with an internal enamel pit, the anteromedian fossetid (state 1; fig. 26G, af). Departing from this pattern, specimens of Thomasomys, Wiedomys, Microrizomys, 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 fossetid) was observed only in specimens of Peromyscus. The character description is based on the assumption that the anteromedian fossetid is actually an engulfed anteromedian flexid, and thus homologous to the latter structure (Steppan, 1995; Carleton and Olson, 1999). Character treated as ordered (0 ↔ 1 ↔ 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 protostylid, leaving the protoflexid as an

internal fossetid. Among non-oryzomyines, the anterolabial cingulum was not observed in specimens of 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 reaching the ectostylid (fig. 26G, el), or 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, Oryzomys 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 matrix in table 5 for character-states distribution among taxa). Nonetheless, specimens of Pseudoryzomys simplex and Holochilus brasiliensis have small mesolophids 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. Character treated as ordered (0 ↔ 1 ↔ 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 Stepan (1995: character 22P; described as procingulum on m2). In his description, Stepan (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 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 shelf-like 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 Neacomys musseri, Nectomys squamipes, Oryzomys hammondi, Sigmodontomys aphrastus, and S. alfari 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: character 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 fossetid on the m3, even in most old exemplars with advanced teeth wear (fig. 26F, pf). In contrast, Pseudoryzomys display 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. Character treated as ordered (0 ↔ 1 ↔ 2).

Post-cranial 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: character 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: character 36), Steppan (1995: character 26S), and Pacheco (2003: characters 96S and 124T) employed 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 seven lumbar vertebrae, whereas all taxa with 13 thoracics have six lumbar. Character information for this and the next 6 post-cranial 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 non-sigmodontine outgroups, Nyctomys and Peromyscus, exhibit the plesiomorphic single articulation. Information for this character is unavailable for 13 taxa not represented by suitable skeletal material in my samples (coded "?" in table 5).

Character 80: Anapophyses present on the 17th thoracico-lumbar vertebra (0); or anapophyses absent or vestigial (1). The 17th thoracico-lumbar vertebrae (TL17) is the 5th lumbar (L5) in specimens with 12 thoracic and 7 lumbar vertebrae, or the 4th lumbar (L4) in specimens with 13 thoracics and 6 lumbar (see character 78). In both cases, TL17 is always the third-to-last lumbar. The anapophyses (or processus accessorius; ICVAN, 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 to 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, Microrhizomys, 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 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 "?" in table 5).

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; ICVAN, 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; Stepan, 1995)⁶. 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 (figs. 28B and C, respectively). Taxa without the spinous process are Handleyomys, Microrhizomys, 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,

⁶ I keep the term hemal arches (used by Stepan, 1995) instead of chevron bones (used by Pacheco, 2003) following current usage in mammalian anatomical literature (Evans, 1993: 174; ICVAN, 1994: 24).

Melanomys, Nectomys, Nesoryzomys swarthi, Oligoryzomys fulvescens, Ol. nigripes, Oryzomys angouya, O. couesi, O. palustris (fig. 28C), O. subflavus, O. xanthacolus, Pseudoryzomys, and Sigmodontomys alfari. Both species of Zygodontomys exhibit intraspecific variation for this feature, with all three states observed among analyzed specimens (scored {012}). Among outgroups, hemal arches were observed in Wiedomys (without posterior spinous border), whereas Thomasomys is polymorphic for this character ({01}). This character was treated as unordered. 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 "?" in table 5).

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)⁷. This character could not be scored for 13 taxa without available humeri or prior literature information (coded "?" in table 5).

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

⁷ 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.

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 "?" in table 5).

Character 84: Trochlear process of calcaneum at the same level as posterior articular facet, trochlear process broad and shelf-like (0); or gap between proximal edge of trochlear process and posterior articular facet, process shorter and less shelf-like (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 shelf-like 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 "?" in table 5).

Glans penis

Character 85: Lateral bacular mounds absent or diminutive (0); or present as large protuberances (1). The bacular mounds in the terminal crater of the glans contain the distal cartilaginous apparatus of muroid rodents with a complex (tridigitate) penis (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 mounds but has 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 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 "?" in table 5).

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. 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) nonspinous tissue is less extensive and the bacular mounds are exposed. This character was scored for 21 taxa lacking preserved male genitalia or prior literature information (coded "?" in table 5). Neither non-sigmodontine outgroup could be scored for this character because bacular mounds are not developed (coded "-" in table 5).

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 palustris and O. couesi (fig. 31B; see also Hooper and Musser, 1964). This character is inapplicable for Peromyscus (in which the dorsal papillae is absent; coded "-") and was not scored for 17 taxa without preserved male genitalia or prior literature information (coded "?" in table 5).

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 "?" in table 5).

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 Oryzomys albigularis, Oligoryzomys fulvescens, and Ol. nigripes (Myers and Carleton, 1981; Voss and Linzey, 1981). . 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 "?" in table 5). This character was treated as ordered (0 ↔ 1 ↔ 2).

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 muroids 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 Nesoryzomys narboroughi (Patton and Hafner, 1983) and Nyctomys (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).

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. Oryzomys albigularis and Oligoryzomys fulvescens 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 have 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.

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. albigularis (see Voss and Linzey, 1981).

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. albigularis, 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 do 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, an apomorphic condition considered 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 Wiedomys, 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 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 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 unavailable 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 "-").

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 589 (11%) are scored as missing ("?"), 18 (0.3%) are scored as inapplicable ("-"), and 71 (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 521 steps (CI = 0.25, RI = 0.63) 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 remaining taxa are split into two clades. The first clade contains O. subflavus the as most basal taxon, followed by (1) the alfaroi group of Oryzomys --- O. chapmani, O. alfaroi and O. 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 seven 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 out of 51 resolved nodes (61%) 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*; and (3) the alfaroi group of Oryzomys is recovered within clade B*. Nevertheless, many relationships are congruent between the two analyses, including: (1) monophyly of Oryzomyini; (2) monophyly of clade C; (3) the clade containing the three tetralophodont taxa Pseudoryzomys, Holochilus, and Lundomys plus

the palustris group of Oryzomys; and (4) Oryzomys polius as basal member of clade D*. Additionally, clades B* and D* are similar between the two analyses, with only minor differences in taxa content, and the TS analysis recovered the same monophyletic genera of the CO tree. It is also noteworthy that all nodes at which the two analyses conflict are weakly supported in both trees.

Phylogenetic results - 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). The consensus topology (fig. 36) is identical to that previously recovered by Weksler (2003; fig. 5 of chapter 1) 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 nine of the 16 analyzed species of Oryzomys. The internal structure of clade B in the strict consensus topology is characterized by a five-fold 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 Microrizomys, Oligoryzomys, Neacomys, and Oryzomys balneator. The second (labeled D) consists of 6 species of Oryzomys interspersed among 8 other genera. Within this

group, (1) Oryzomys polius appears as the sister group to remaining species; (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.

Phylogenetic results - Combined analyses

A heuristic search of the combined data analyzed with composite polymorphic entries (CO) resulted in two most-parsimonious trees of 1214 steps (CI=0.38, RI=0.65). 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 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. The albigularis species group (O. albigularis and O. levipes) 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.

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, 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 transformation series (TS) resulted in 9 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 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.

Phylogenetic results - Reduced analysis

Heuristic search of the reduced dataset (i.e., excluding the five oryzomyines without molecular sequences) resulted in 2 most-parsimonious trees of 1175 steps (CI=0.40, RI=0.65). The recovered trees, and the consensus cladogram (fig. 39), are identical to the results of the combined analysis after deleted taxa are pruned from the trees.

Nodal support

Nodal support values for the morphological trees are generally low. For instances, in the CO analysis (fig. 34), thirty-four nodes (67% of resolved nodes) collapse in trees that are 1 step longer, six additional nodes (12%) collapse in trees that are 2 steps longer, and four more nodes (8%) collapse in trees that are 3 steps longer. Only seven nodes (14% of the total) have decay index > 3. Resampling values were also low: 28 nodes (55%) have jackknife values below 50% and 17 nodes (33%) have jackknife values between 50-85%, while the remaining six 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 1 step longer, two additional nodes (6%) collapse in trees that are 2 steps longer, and two more nodes (6%) collapse in trees that are 3 steps longer. Fifteen nodes (42% of the total) have decay index > 3. Jackknife values show higher support: two nodes (6%) have jackknife values below 50% and 15

nodes (42%) have jackknife values between 50-85%, 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 sixteen nodes (32%) collapse in trees that are 1 step longer, five additional nodes (10%) collapse in trees that are 2 steps longer, and four more nodes (8%) collapse in trees that are 3 steps longer. The remaining 25 nodes (50% of the total) have decay index > 3 . Jackknife resampling suggest a similar pattern of support. Eleven nodes (22%) have jackknife values below 50% and 20 nodes (40%) have jackknife values between 50-85%, 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 1 step longer, 8 additional nodes (18%) collapses in trees that are 2 steps longer, and 6 more nodes (13%) collapse in trees that are 3 steps longer. The remaining 23 nodes (51% of the total) have decay index > 3 . In terms of resampling values, only 5 nodes (11%) have jackknife values below 50% and 20 nodes (44%) have jackknife values between 50-85%, 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: nine nodes (20% of the total) have jackknife values increased by at least 10 percentage points, three of them more then 20 percentage points. Thirty nodes (66%) have minimal changes in jackknife (differences between -3 and 3 percentage points), while six nodes (13%) decreased at least four percentage points. The maximum increase in jackknife values was 38 percentage points (from 58% to 96%; 'Clade B'), while the

maximum decrease was 10 percentage points (from 52% to 42%; talamancae + albigularis groups).

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 3.8 and 3.9 list all morphological synapomorphies for the morphology-only and combined analyses, respectively). The effects of the TS coding for polymorphic characters is presented as changes in topology or in support in the morphology-only or combined analyses. The effect of exclusion of taxa without IRBP sequence is presented only as changes in support values in the reduced analysis, as the topology of the reduced tree is identical to the complete one pruned from excluded taxa. 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'Elia, 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 thomatomyine 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'Elia, 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'Elia, 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 hind foot digits (7), incisive foramina 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'Elia, 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'Elia, 2003; but see Garcia, 1999), but the position of Scolomys as basal oryzomyine is secured in both combined and IRBP-only analyses (see also Weksler, 2003). In 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 do not reach 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 mesolophs (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 display 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 anapophysis 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; 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 6 species recognized for the group (table 1) 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 3 roots in the first lower molar is the least homoplasious among them, observed additionally in the Oryzomys albigularis group, Oryzomys angouya, Microroryzomys, 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: no change.

Remarks: Neither morphology nor IRBP provide phylogenetic signal for a robust resolution of the basal structure of clade B. Nevertheless, in the nitidus groups is recovered as the basal group in clade B 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, 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: no change.

Remarks: Neither morphology nor IRBP provide 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 fosseti at mesoflexus position (66).

Molecular synapomorphies: 3.

TS coding: increased nodal support in combined analysis. In the morphology-only, 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 Handleyomys plus the alfaroi-rostratus-chapmani clade possesses a series of compelling morphological synapomorphies, especially the number of roots of the second lower molars, 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, are long considered associated (Goldman, 1918), but besides a previous IRBP analysis (Weksler, 2003) no phylogenetic evidence have 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 as close taxa since Merriam (1901) recognized the melanotis and chapmani species groups, the last including O. rhabdops (member of the alfaroi group), and Goldman (1918) recognized the melanotis and alfaroi groups, the last including O. chapmani and O. saturator. 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: no change.

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 have 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 anapophysis 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: no change.

Remarks: O. talamancae is recovered as the sister group of the nitidus species group in the IRBP-only analysis with moderate nodal support. Additional data is 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 throughout sigmodontine history (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 5 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 persists for the group (A. R. Percequillo, per. comm.).

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 ('Clade C' and 'Clade 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 signal for the sister group relationship of clades C and D, the IRBP evidence pointing for this relationship is overwhelming (Weksler, 2003). Supplementary morphological characters are needed to

providing additional corroboration and a more robust 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 (Patton 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 one 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 four 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: no change.

Remarks: In the IRBP-only and TS combined analyses, Neacomys, Microryzomys and O. balneator form a clade (see also Weksler, 2003). Although the conflict between morphology and molecular data is resolved towards the morphology 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: no change.

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 analyses.

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 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 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 diminute, 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 (in press).

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 do not reach M1 (31), complex posterolateral palatal pits (34), large sphenopalatine vacuities (36), derived carotid circulation pattern 2 (37), 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 fosseti 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 hind foot 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 5 morphological synapomorphies uniting the O. palustris group (O. palustris and O. couesi) and the tetralophodont taxa Lundomys, Holochilus, and Pseudoryzomys are hind foot characters believed to be semiaquatic specializations.

IRBP-only analysis place 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 scope 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 with (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 hind foot 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 tooth row (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 anapophysis 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 as Holochilus' sister group with high nodal support. The sheer number of morphological characters

uniting Lundomys and Holochilus overwhelms the unexpected strong molecular signal pointing to the Pseudoryzomys-Holochilus closer relatedness. 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 data also show 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), postorbital ridge present (23), frontosquamosal suture anterior to frontoparietal (24), incisive foramina 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: 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 anapophysis present on TL17 (80).

Molecular synapomorphies: none.

TS coding: clade not recovered.

Reduced analysis: no change.

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 xantheolus, 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 fossete 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, 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 xantheolus, Amphinectomys, Nectomys, Sigmodontomys, and Melanomys.

Nodal support: JK = 47%, DI = 2.

Partitioned evidence: clade recovered in the morphology-only analysis but not in the morphology-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 diminute, hypoflexus (69).

Molecular synapomorphies: none.

TS coding: clade recovered in some fundamental cladograms of combined analysis.

Reduced analysis: no change.

Remarks: Oryzomys xantheolus 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 morphology-only analysis.

Morphological synapomorphies: hypothenar pad absent (4), pes with extremely small interdigital pads (5), ungual tufts absent on D1, sparse in remaining hind foot digits (7), tail unicolored (11), incisive foramina reach M1 (31), reduced sphenopalatine vacuities (36), flexi meet at midline on M1 (57), M1 with undivided anterocone (58), 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. xantheolus, and the O. palustris group (fig. 36). Nevertheless, the combination of morphological and molecular data

unexpectedly increase the nodal support for this clade (e.g., jackknife support in the combined tree increases to 87% from 36% in morphology-only tree), despite the lack of a single unambiguous molecular synapomorphy (2 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); analyses of cytochrome b gene placed Nectomys together with Scolomys (Patton and da Silva, 1995); Nesoryzomys and Holochilus (Smith and Patton, 1999); and 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 is likely the result of the high quantity of missing information. The overwhelming molecular signal points to the sister group relationship of Amphinectomys and Nectomys relationship, 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 alfari 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 (Herskovitz, 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 (Herskovitz, 1944). Nevertheless, no explicit phylogenetic analysis had demonstrated Nectomys

monophyly. The low nodal support of the combined analysis is probably caused by the lack of IRBP sequence by N. alfari.

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 corroborate 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); 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 (an young specimen) by Ray (1962; see Musser and Carleton, 1993). Detailed taxonomic considerations of this puzzling taxon will be provided elsewhere (McCain and Weksler, in prep.).

DISCUSSION

Effects of different codings of polymorphic data

The different codings for polymorphic characters produced similar topologies, especially in the combined tree, 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 or TS coding.

The remaining discussion will be 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 when 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. The removal of the 5 taxa without IRBP sequences in the reduced analysis also did not affect tree topology, indicating that the missing data does not have an apparent effect in the determination of phylogenetic relationships in the present analysis.

Removal of these taxa, however, had a marked effect in nodal support for several oryzomyine lineages. Foremost among these changes were the percentile increase 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, e.g., 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 amount of missing data, three were recovered in non-controversial 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); and O. chapmani clustered with O. rostratus and O. chapmani, 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 morphology-only or combined analyses. Instead, the two species form a paraphyletic sequence relative to Nectomys in the morphology-only and to Melanomys in the combined analyses. 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 the 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 analysis and in the combined consensus cladogram. On the other hand, the IRBP dataset was much less homoplasious than 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 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 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 reveals 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 above 95% and decay index above 6. The combined tree favors the morphological solution because there are 15 morphological synapomorphies for Holochilus + Lundomys hypothesis, against 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, and 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 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 is high, and in each case the combined tree favored the IRBP resolution.

While the higher-level topology of the ingroup was resolved toward the IRBP solution, most of the conflict observed within the major oryzomyines clades were resolved towards 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 out of 45⁸ nodes (66%) have both morphological and molecular synapomorphies, indicating that there is a considerable amount of phylogenetic

⁸ 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.

agreement between the datasets --- the recovery of similar major oryzomyine clades (B, C, and D) is indicative of that.

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. Stepan (1995) recovered four additional oryzomyine synapomorphies: (6) nasals extending posterior to lacrimal; (7) 12 thoracic vertebra; (8) absence of hemal arches; and (9) fewer than 36 caudal vertebrae (character not included in the present study). Surprisingly, the unconnected tegmen tympani was the only one among 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.

The 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 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; Stepan, 1995; Pacheco, 2003). This similarity, however, is due to convergence, as Reithrodon is not the sister group of oryzomyines (Stepan, 1995; Smith and Patton, 1999; D'Elia, 2003; Weksler, 2003). Four other unambiguous oryzomyine synapomorphies were recovered in the combined analysis: absence of ungual tufts on D1; long incisive foramina reaching

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 indicate 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 posterolateral pits, presence 12 thoracic vertebra, 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 oryzomyines synapomorphies could actually be synapomorphies for the clade uniting oryzomyines and Wiedomys. However, in a previous IRBP analysis with denser 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 homoplastic 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 plesiomorphy 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 is the recognition 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 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 was an unexpected result. Scolomys and Zygodontomys are two of the most distinctive clades of oryzomyines, as 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, 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 overwhelming 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 well secured here, separated analyses of each clade with denser taxon sampling and employing varied sources of data, such as morphology, 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; Stepan, 1995; Weksler, 1996; 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 recovered 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. 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 the restriction of Oryzomys to the palustris group (table 1), 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).

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 into Microryzomys, or of melanotis, chapmani, and alfaroi groups into 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 the 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 researches interested in adaptation, biogeography, faunal diversification and

other topics, resulting in less heuristic classification (Wheeler, 2004). The new genera will be described elsewhere.

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; 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.

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 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 out of 116 oryzomyines (61%) are either medium, small-medium, or large-medium sized, 29 (25%) are small sized, and 16 (14%) are large sized.

The 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 sized. *O. hammondi*, is a large rat, while clade A possess 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), the majority of individuals of these taxa are collected on the ground (Mares et al., 1989; Bonvicino et al., in press). 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 hind feet, 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 specializations are observed in 7 oryzomyine taxa: Amphinectomys, Nectomys, Lundomys, Holochilus, Sigmodontomys alfari, Pseudoryzomys, and in the palustris group of Oryzomys. The degree of morphological adaptations of these taxa are in proportion 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 waterbodies, 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, 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 Nectomys + Amphinectomys. It is worth noting that in ACCTRAN optimization, the sequence of modifications of the two hind foot 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 and 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 apicalis⁹. 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; Bonvicino et al., 1998; Talamoni and Dias, 1999; Lacher and Alho, 2001). Five other oryzomyine clades, however, representing 10% of oryzomyine species, 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 America 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 (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 non-forest 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

⁹ 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.

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 vole-like 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 eleven 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. Unsurprisingly, 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 waste-basket group of ‘unspecialized’ mostly forest-dwelling rats. As inferred by the reconstruction of size and the ecological adaptations discussed above in the combined tree, 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 species), 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 the 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:

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 and in Pacific littoral

zone of Peru and Ecuador (Patton and Hafner, 1983). The remaining trans-Andean taxa are found in forests from the 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 Andean habitats such as montane forest and Paramos, usually on both sides of the cordillera and above 1,500-2,000 m. Six taxa are found exclusively or primarily on 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). 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 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, Caatinga, etc. 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 southern 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; 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 Amphinecomys, 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). 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 interandean valleys of the Magdalena and Cauca rivers (Hershkovitz, 1944; Bonvicino, in prep.). The yunganus and nitidus groups have species restricted to eastern Andean piedmont --- Oryzomys tatei and O. nitidus, respectively (Weksler, 1996; Musser et al., 1998) --- and could be considered as 'Andean taxa'. 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 will be 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 below.

'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 MYA. 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 4 nuclear genes; and 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 place the origin of oryzomyines in this period in their analysis of cytochrome *b* sequences. This time bound 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 using better calibration points and denser taxonomic sampling, then oryzomyines could have been affected by the final orogenic surge of the Andes between 3-5 MYA (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. 6.4.). 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. 6.4). 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 area than are areas represented on a few branches".

This methodological formulations fits well to biogeography of sigmodontines, as scenarios for the group have relied heavily on the center of origin concept, with an strong dispersalist element. Almost all 'classical' sigmodontine biogeographic scenarios agree that oryzomyines, as all sigmodontines, are descendants from a 'proto-sigmodontine' ancestor (s) that invaded (i.e., dispersed to) South America from North America in the late Cenozoic (Simpson, 1950; Hershkovitz, 1966b; Patterson and Pascual, 1968; Hershkovitz, 1969, 1972; 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 of South America are from the Pleistocene (Steppan, 1996; Pardiñas, 2002). Steppan (1996) estimated the age of Holochilus primigenus from Bolivia at between 0.7-1 MYA. Forms of Holochilus, Lundomys, Nectomys, and Oligoryzomys were retrieved from the Ensenadense (Early-medium 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 some time before the Pleistocene. In turn, the lower bound for oryzomyines in South America is unknown; Oryzomyines (and Sigmodontines in general) are absent from the middle Miocene (13 MYA) 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 MYA.

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; Baskin, 1989) are unfounded. Oryzomys? pliocaenicus from the Miocene (Hemphillian) of Kansas (Hibbard, 1939) is "...generically indeterminate, but may represent Bensonomys" (Baskin, 1986): 295; see also (Herskovitz, 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). =Bensonmymys 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 undoubted oryzomyines present in the North American fossil record are referred to Oryzomys fossilis (= Oryzomys 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 MYA) and Chapadmalalan (3.5-4 MYA), respectively (Pardiñas et al., 2002), whereas fossils of =Prosigmodon and Sigmodon are present in North America in the Hemphillian (6.8 MYA) and Blancan (3.3 MYA), respectively (Martin, 1979; Czaplewski, 1987; Korth, 1994). Thus, fossil data by itself does 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, an eastern Andean (fig. 48): Scolomys, nitidus group, Neacomys, and Oryzomys polius for clades A, B, C, and D, respectively. The same conclusion was attained by studies of tribal relationships based on cytochrome b (Smith and Patton, 1999; D'Elia, 2003). Central American (trans-Andean) taxa are always recovered deeply nested within the major lineages.

Given the estimated time for initial diversification of oryzomyine based on molecular studies, the oryzomyine ancestor must have arrived in South America prior to the formation of the Panamanian land-bridge at 2.8 MYA (Marshall, 1985) by over water dispersal. 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 (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,

i.e., 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 non-synchronous dispersion of various oryzomyine lineages from northern South America in a time frame 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 as 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 invasion 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 pre-montane forests of the Northern Andes and the Western Amazon lowlands forests. All basal taxa within each lineages --- 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).

TABLES

TABLE 1. Species groups within the genus *Oryzomys*. Species included in the present analysis are marked with ‘*’.

Group	Species	Group	Species	Group	Species
<u>albigularis</u> ^{a, b, c, d, e, f, g}	<u><i>O. albigularis</i></u> * <u><i>O. auriventer</i></u> <u><i>O. devius</i></u> <u><i>O. keaysi</i></u> <u><i>O. levipes</i></u> * <u><i>O. meridensis</i></u> <u><i>O. caracolus</i></u>	<u>nitidus</u> ^{a, b, h, i, j}	<u><i>O. emmonsae</i></u> <u><i>O. lamia</i></u> * <u><i>O. legatus</i></u> <u><i>O. macconnelli</i></u> * <u><i>O. nitidus</i></u> <u><i>O. russatus</i></u> *	<u>palustris</u> ^{a, k, l}	<u><i>O. couesi</i></u> * <u><i>O. dimidiatus</i></u> <u><i>O. gorgasi</i></u> <u><i>O. nelsoni</i></u> <u><i>O. palustris</i></u> *
<u>megacephalus</u> ^{a, h, m, n}	<u><i>O. megacephalus</i></u> * <u><i>O. oniscus</i></u> <u><i>O. perenensis</i></u> <u><i>O. seuanezi</i></u>	<u>subflavus</u> ^{a, p, q}	<u><i>O. maracajuensis</i></u> <u><i>O. marinhos</i></u> <u><i>O. subflavus</i></u> * <u><i>O. scotti</i></u> <u><i>O. andersoni</i></u>	<u>xanthaeolus</u> ^{a, r, s}	<u><i>O. bauri</i></u> <u><i>O. galapagoensis</i></u> <u><i>O. xanthaeolus</i></u> *
<u>chapmani</u> ^a	<u><i>O. chapmani</i></u> * <u><i>O. saturator</i></u>	<u>melanotis</u> ^{a, k}	<u><i>O. melanotis</i></u> <u><i>O. rostratus</i></u> *	<u>alfaroi</u> ^{a, k}	<u><i>O. alfaroi</i></u> * <u><i>O. rhabdops</i></u>
<u>yunganus</u> ^h	<u><i>O. tatei</i></u> <u><i>O. yunganus</i></u> *	<u>talamancae</u> ^h	<u><i>O. boliviensis</i></u> <u><i>O. talamancae</i></u> *	species without known relationships ^a	<u><i>O. angouya</i></u> * <u><i>O. balneator</i></u> * <u><i>O. hammondi</i></u> * <u><i>O. polius</i></u> *

Sources, 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, A. R. Percequillo (pers. com.); 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).

TABLE 2. Taxonomic categories of 6 oryzomyine genera in key taxonomic checklists.

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

TABLE 3. Taxonomic diversity of extant oryzomyine genera and number of included species per taxon. Species groups are listed for Oryzomys.

Genera	Number of species	Number of included species
<u>Amphinectomys</u>	1	1
<u>Handleyomys</u>	2	1
<u>Holochilus</u>	4	2
<u>Lundomys</u>	1	1
<u>Melanomys</u>	3	1
<u>Microryzomys</u>	2	1
<u>Neacomys</u>	8	3
<u>Nectomys</u>	8	2
<u>Nesoryzomys</u>	4	2
<u>Oecomys</u>	15	5
<u>Oligoryzomys</u>	16	5
<u>Oryzomys</u>	43	19
<u>albigularis</u>	7	2
<u>alfaroi</u>	2	1
<u>chapmani</u>	2	1
<u>megacephalus</u>	4	1
<u>melanotis</u>	2	1
<u>nitidus</u>	6	3
<u>palustris</u>	5	2
<u>subflavus</u>	5	1
<u>talamancae</u>	2	1
<u>xanthaeolus</u>	3	1
<u>yunganus</u>	2	1
unknown position	4	4
<u>Pseudoryzomys</u>	1	1
<u>Scolomys</u>	2	1
<u>Sigmodontomys</u>	2	2
<u>Zygodontomys</u>	3	2
Total	116	49

TABLE 4. Summary of taxon - character matrix. Character systems from which information are 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	Missing IRBP
<u>Nyctomys sumichrasti</u>	0	3	97		
<u>Peromyscus maniculatus</u>	4	6	90		
<u>Delomys sublineatus</u>	13	0	87	PE, GL	
<u>Thomasomys baeops</u>	3	0	97		
<u>Wiedomys pyrrhorhinos</u>	12	0	88	GL, DS	
<u>Amphinectomys savamis</u>	67	0	32	DE, PS, PE, GL, DS	
<u>Handleyomys intectus</u>	16	0	84	PE, GL	
<u>Holochilus brasiliensis</u>	0	1	99		
<u>Holochilus chacarius</u>	21	1	78	PS, PE, GL	
<u>Lundomys molitor</u>	8	1	91	GL	
<u>Melanomys caliginosus</u>	1	0	99		
<u>Microryzomys minutus</u>	3	0	97		
<u>Neacomys minutus</u>	22	0	78	PS, PE, GL, DS	
<u>Neacomys musseri</u>	16	0	84	PS, GL	
<u>Neacomys spinosus</u>	1	0	99		
<u>Nectomys apicalis</u>	15	0	85	PE, GL	X
<u>Nectomys squamipes</u>	5	0	95		
<u>Nesoryzomys narboroughi</u>	5	0	95		
<u>Nesoryzomys swarthi</u>	37	0	63	DE, PE, GL, DS	
<u>Oecomys bicolor</u>	8	0	92	GL	
<u>Oecomys catherinae</u>	23	0	77	PS, PE, GL, DS	
<u>Oecomys concolor</u>	1	0	99		
<u>Oecomys mamorae</u>	10	0	90	GL	
<u>Oecomys trinitatis</u>	12	0	88	GL	
<u>Oligoryzomys flavescens</u>	11	0	89	GL	
<u>Oligoryzomys fornesi</u>	21	0	79	PE, GL, DS	
<u>Oligoryzomys fulvescens</u>	0	1	99		
<u>Oligoryzomys nigripes</u>	8	0	92		
<u>Oligoryzomys stramineus</u>	23	0	77	PS, PE, GL, DS	
<u>Oryzomys albigularis</u>	1	1	98		
<u>Oryzomys alfaroi</u>	7	0	93	PS	
<u>Oryzomys angouya</u>	2	0	98		
<u>Oryzomys balneator</u>	16	0	84	PS, GL	
<u>Oryzomys chapmani</u>	10	0	90	GL	X

TABLE 4. Continued.

<u>Oryzomys couesi</u>	10	0	90	GL	
<u>Oryzomys hammondi</u>	23	0	77	PS, PE, GL	X
<u>Oryzomys lamia</u>	22	0	78	PS, PE, GL	
<u>Oryzomys levipes</u>	10	0	90	GL	X
<u>Oryzomys macconnelli</u>	8	0	92	GL	
<u>Oryzomys megacephalus</u>	0	0	100		
<u>Oryzomys rostratus</u> ^a	1	0	99		
<u>Oryzomys palustris</u>	0	0	100		
<u>Oryzomys polius</u>	22	0	78	PS, PE, GL, DS	
<u>Oryzomys russatus</u>	14	0	86	PE, GL	
<u>Oryzomys subflavus</u>	8	0	92	GL	
<u>Oryzomys talamancae</u>	9	0	91	GL	
<u>Oryzomys xantheolus</u>	9	0	91	GL	
<u>Oryzomys yunganus</u>	11	0	89	GL	
<u>Pseudoryzomys simplex</u>	8	1	91	GL	
<u>Scolomys ucayalensis</u>	9	0	91	GL	
<u>Sigmodontomys alfari</u>	2	0	98		
<u>Sigmodontomys aphrastus</u>	22	0	78	PS, PE, GL	X
<u>Zygodontomys brevicauda</u>	0	1	99		
<u>Zygodontomys cherriei</u>	0	1	99		

a: Weksler (2003) wrongly reported Oryzomys melanotis from El Salvador. In reality, it is Oryzomys rostratus, the same 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.

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

Taxon	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890
<u>Nyctomys sumichrasti</u>	0000000001	0001000000	0400000000	1001030001	0000100000
<u>Peromyscus maniculatus</u>	1000010000	2000001001	0000010000	0000000000	1010100000
<u>Delomys sublineatus</u>	2000110001	1100001001	0000010110	0001010100	1011000100
<u>Thomasomys baeops</u>	1000001001	01001100A2	0000110011	0001122000	1010200111
<u>Wiedomys pyrrhorhinos</u>	2000010001	00001000A2	0300010100	0101100100	2010000?11
<u>Amphinectomys savamis</u>	???????121	?100000002	14?0020110	1203?1???1	???01?0???
<u>Handleyomys intectus</u>	1000101001	0100100012	1000A20111	1202020100	011010011C
<u>Holochilus brasiliensis</u>	2011213121	0100100001	1211110201	111D202000	2110211112
<u>Holochilus chacarius</u>	?011213121	0100100001	1211110201	1212202000	2100211?12
<u>Lundomys molitor</u>	2111213121	0100100011	0100110211	0212212100	1110100102
<u>Melanomys caliginosus</u>	2000112002	010020001C	1401120111	1102122101	1100110?12
<u>Microryzomys minutus</u>	2000111001	1100200011	0000011002	1102110100	0110200100
<u>Neacomys minutus</u>	2000111001	0111000012	0400010101	1202110100	0110200?00
<u>Neacomys musseri</u>	2000111001	0111000012	0400010101	1202111100	0110100?00
<u>Neacomys spinosus</u>	2000111001	0111000012	0400010101	1202110100	01A0200?10
<u>Nectomys apicalis</u>	2011213121	0100100112	0401120111	1103122101	1100210112
<u>Nectomys squamipes</u>	2001212121	0100100112	1401110111	11031C2101	1100110112
<u>Nesoryzomys narboroughi</u>	?000111000	2000110001	1100110111	0203102101	2100211112
<u>Nesoryzomys swarthi</u>	?000111000	1000110001	1100110110	0103102100	2100211112
<u>Oecomys bicolor</u>	2000001001	0101000001	1400110001	1202120A00	A1A0200?10
<u>Oecomys catherinae</u>	2000001001	0100000001	0400110011	1202120100	1101100?10
<u>Oecomys concolor</u>	2000001001	0101100001	0400110001	1202122A00	A110100?10
<u>Oecomys mamorae</u>	2000011001	0101100001	040011000C	1202122100	1110100?10
<u>Oecomys trinitatis</u>	2000001001	0100000001	1400110001	1202120A00	A1A0200?11
<u>Oligoryzomys flavescens</u>	2000111001	1100100011	0000010102	1202001100	0111201?00
<u>Oligoryzomys fornesi</u>	2000111001	1100100011	0000010102	1202001100	0111201?00
<u>Oligoryzomys fulvescens</u>	2000111001	1100100011	0000010102	1202001100	0111201100
<u>Oligoryzomys nigripes</u>	2000111001	11000000A1	0000010102	1202001100	0111201100
<u>Oligoryzomys stramineus</u>	2000111001	1100000011	0000010102	1202001100	0111201?00
<u>Oryzomys albigularis</u>	2000101001	1100010001	0000A10112	1103110A00	11A0100101
<u>Oryzomys alfaroi</u>	2000101001	210000000C	0300A10111	120D100100	1110100?12
<u>Oryzomys angouya</u>	2000110001	11000000A1	A1001C0111	0103102100	1110200?11
<u>Oryzomys balneator</u>	2000111001	0101000012	0000010002	1102110100	0111200?01
<u>Oryzomys chapmani</u>	2000101001	0100000001	0300A101A1	1203102100	111A200?12
<u>Oryzomys couesi</u>	2001212001	1100100001	1400120101	0203122100	1110200?12
<u>Oryzomys hammondi</u>	200010200?	0100100001	0301110010	1101120101	0100000?00

TABLE 5. Continued.

<u>Oryzomys lamia</u>	2000101001	2100000012	0300010112	1202120A00	1100200?01
<u>Oryzomys levipes</u>	2000101001	1100000001	1100AC0111	1003110000	1110100?01
<u>Oryzomys macconnelli</u>	2000101001	2100000001	0300AC0111	1202120100	1100000101
<u>Oryzomys megacephalus</u>	2000101001	1100000001	A100010111	120D1C1100	1110000100
<u>Oryzomys palustris</u>	2011212011	2100000011	1400120101	0203102100	111010011C
<u>Oryzomys polius</u>	2000110000	2100100001	0400120111	0103202000	1110010100
<u>Oryzomys rostratus</u>	2000111001	1100000001	0300010101	1203100100	A110100?12
<u>Oryzomys russatus</u>	2000101001	2100000001	0300010111	1102120A00	1100200101
<u>Oryzomys subflavus</u>	2000111001	1100000001	04001C010C	0103102101	11A1200112
<u>Oryzomys talamancae</u>	2000101001	1100000001	0300A10111	120D110100	11A0100?00
<u>Oryzomys xanthaeolus</u>	2000111001	11000000AC	14001C01A1	0203102101	11A0110112
<u>Oryzomys yunganus</u>	200A101001	2100000001	0300010111	1202121100	1110000?00
<u>Pseudoryzomys simplex</u>	2001212011	2100000011	1300110201	0202102A00	1110200112
<u>Scolomys ucayalensis</u>	1001111001	0110100112	1300020000	1202122110	1100100100
<u>Sigmodontomys alfari</u>	2001212012	01000000AC	140111010C	1102112101	11002A0112
<u>Sigmodontomys aphrastus</u>	2001203002	0100200112	1401110000	1101112101	1100A00?12
<u>Zygodontomys brevicauda</u>	2000111001	11001000A1	040002011C	02021B2100	1101101100
<u>Zygodontomys cherriei</u>	2000101001	11001000A1	0400020111	0202100101	1101211100

TABLE 5. Continued.

Taxon	5555555555 1234567890	6666666666 1234567890	7777777777 1234567890	8888888888 1234567890	9999999999 123456789
<u>Nyctomys sumichrasti</u>	0000000000	0000100001	0100000000	00000--000	112000-10
<u>Peromyscus maniculatus</u>	0000000000	00100-0110	1010002000	00000----2	000????0-
<u>Delomys sublineatus</u>	0000002000	0000000001	1100000010	0111??????	????????00
<u>Thomasomys baeops</u>	0000000000	0000000002	1100000011	A1001??101	00001?000
<u>Wiedomys pyrrhorhinos</u>	0000000000	0001000002	1000000111	111110?00?	??????????
<u>Amphinectomys savamis</u>	?1?0??????	??????????	??????????	??????????	??????????
<u>Handleyomys intectus</u>	1100002200	0000010111	11000?011?	111???????	????????10
<u>Holochilus brasiliensis</u>	1011112230	01110-0001	1020002110	2111101011	000011011
<u>Holochilus chacarius</u>	1011112230	02110-0001	10200021??	??????????	????????11
<u>Lundomys molitor</u>	A000111010	01000-1001	1010002110	211110000?	????????10
<u>Melanomys caliginosus</u>	0100000220	1001000011	1000000111	2111110001	000011010
<u>Microryzomys minutus</u>	0000000000	1000000102	1000000111	11111??0?1	000011011
<u>Neacomys minutus</u>	0000000000	1000000111	1000000???	??????0???	??????????
<u>Neacomys musseri</u>	0000000000	1000000111	1000010???	????10000?	????????11
<u>Neacomys spinosus</u>	0000000200	1000000111	1000000111	1111100001	000111010
<u>Nectomys apicalis</u>	0000001220	0001000011	100001011?	21?1??????	????????11
<u>Nectomys squamipes</u>	0000001220	0001000001	100000011?	21?110???	000011011
<u>Nesoryzomys narboroughi</u>	0000000000	1001000001	1000000110	011111??01	111?11?10
<u>Nesoryzomys swarthi</u>	?000000???	??????????	????????110	2111??????	??????????
<u>Oecomys bicolor</u>	0000001200	0000100011	1100000111	1101101001	????????10
<u>Oecomys catherinae</u>	0000001200	0000100001	1100000???	??????????	??????????
<u>Oecomys concolor</u>	0000001000	0000100001	1100000110	1101101001	000011010
<u>Oecomys mamorae</u>	0000001200	0000100001	1100000111	111?10100?	????????10
<u>Oecomys trinitatis</u>	0000001200	0000100001	1100000111	111110????	????????10
<u>Oligoryzomys flavescens</u>	0000000000	1000000011	1000000111	?11?100101	????????1?
<u>Oligoryzomys fornesi</u>	0000000000	1000000011	10000001??	??????????1	??????????
<u>Oligoryzomys fulvescens</u>	0000000000	1000000001	1000000111	2111100102	000-11010
<u>Oligoryzomys nigripes</u>	0000000000	1000000001	1000000111	211?100102	????????10
<u>Oligoryzomys stramineus</u>	0000000000	1000000011	1000000???	??????????	??????????
<u>Oryzomys albigularis</u>	0000002000	0000000011	110000011?	1111101002	000-10110
<u>Oryzomys alfaroi</u>	1000000200	1000010111	11000001??	????110001	000011110
<u>Oryzomys angouya</u>	0000000001	1000010001	1100000110	2101101001	00001101?
<u>Oryzomys balneator</u>	0000000000	1000000102	1000000???	????10000?	????????11
<u>Oryzomys chapmani</u>	1000000200	1000010111	1000000111	111?11000?	????????10
<u>Oryzomys couesi</u>	?000000200	1000010001	1000100111	211110011?	????????10
<u>Oryzomys hammondi</u>	?100002200	1001000001	1100010???	??????????	????????10

TABLE 5. Continued.

<u>Oryzomys lamia</u>	0000001200	0000000101	0000000???	???????????	?????????1?
<u>Oryzomys levipes</u>	0000002000	0000000011	1100000110	111110100?	?????????1?
<u>Oryzomys macconnelli</u>	0000001200	1000010101	1100000110	111110100?	?????????10
<u>Oryzomys megacephalus</u>	0000000200	0000000101	1100000111	1111101001	000010110
<u>Oryzomys palustris</u>	A000000100	1000010001	1000100111	2111101111	000011110
<u>Oryzomys polius</u>	?000000000	0000000011	10001001??	???????????	???????????
<u>Oryzomys rostratus</u>	1000000200	A000010111	1000000111	1111110001	000011210
<u>Oryzomys russatus</u>	0000001200	0000010101	1000000110	1111???????	?????????1?
<u>Oryzomys subflavus</u>	0000000100	A0000100A1	1000000110	211111000?	?????????10
<u>Oryzomys talamancae</u>	0000002200	0000000111	1100000110	111110100?	?????????10
<u>Oryzomys xantheolus</u>	1000000020	1001000011	1000000110	211?11000?	?????????10
<u>Oryzomys yunganus</u>	0000001200	0000010111	110000011?	111?10100?	?????????10
<u>Pseudoryzomys simplex</u>	1000000130	11000-1001	0020001111	211111?001	?????????11
<u>Scolomys ucayalensis</u>	0100000220	1001001111	1000000111	01111?100?	?????????10
<u>Sigmodontomys alfari</u>	1000001220	0001000011	1001010110	2111110001	000?2101?
<u>Sigmodontomys aphrastus</u>	?100002220	0001000011	1000110???	???????????	?????????11
<u>Zygodontomys brevicauda</u>	1000000230	22010-1001	1020002111	?111101001	000011010
<u>Zygodontomys cherriei</u>	1000000230	22010-1101	1020002111	?111101001	000011010

TABLE 6. Character information summary.

Character system	# Examined	# Included (% of examined)	Invariant	Metric character	Continuous trait	Autapo- morphic 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

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

TABLE 7. Summary of phylogenetic analyses.

	Number of terminal taxa	Number of ingroup taxa	Number of informative characters	Number of MPT ^e	Tree length	CI ^f	RI ^h	Resolved nodes ⁱ
IRBP 1 ^a	69	44	386	16	1512	0.45	0.63	56 (85%) ^f
IRBP-only	49	44	204	4	667	0.55	0.71	36 (78%)
Morphology CO ^b	54	49	91	1	521	0.25	0.63	51 (100%)
Morphology TS ^c	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 ^d	49	44	295	2	1175	0.4	0.65	45 (98%)

Legend. **a**, analysis of Weksler (2003); **b**, polymorphic entries treated as composite states; **c**, polymorphic entries treated as states with transformation-series; **d**, analysis excluding 5 taxa without IRBP data; **e**, most-parsimonious trees; **f**, consistency index, excluding uninformative characters; **g**, retention index; **h**, resolved nodes in consensus tree; **i**, 100*resolved nodes/(number of taxa-3).

TABLE 8. Size of oryzomyine as measured by head-and-body length (HBL).

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

FIGURES

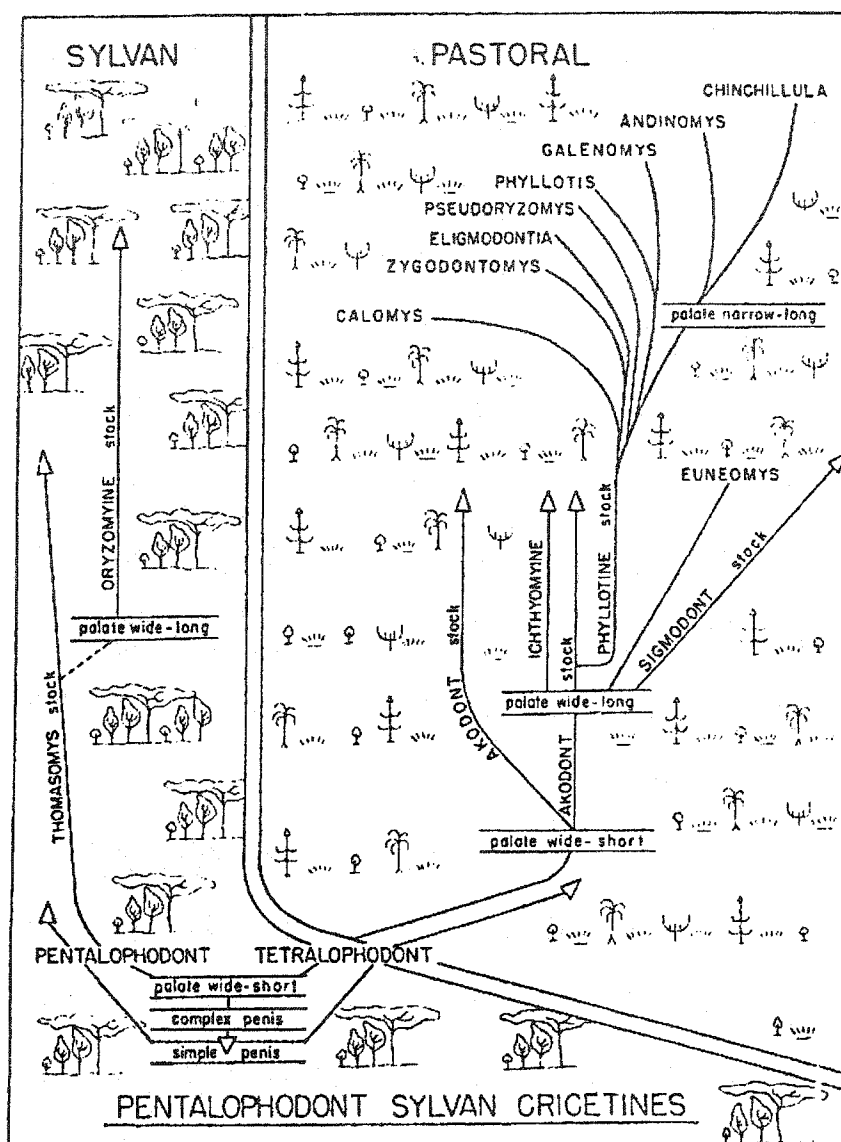


Figure 1. Evolutionary scenario for the radiation of sigmodontines (Herskovitz, 1962; reproduced from fig. 2). Note the position of *Zygodontomys* and *Pseudoryzomys* within the phyllotine radiation. *Holochilus* was included by Herskovitz (1955, 1962) in the “sigmodont” group. The original caption read: “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.”

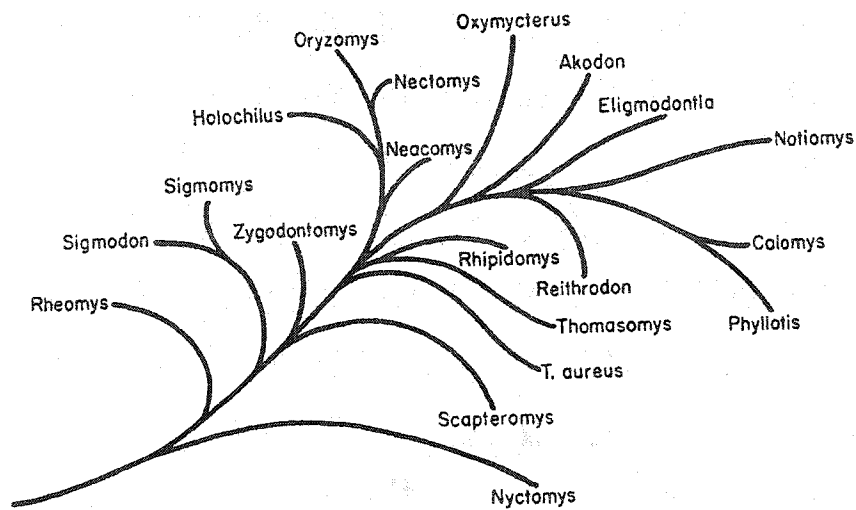


Figure 2. Relationships among Neotropical muroid rodents based on characters from the glans penis (Hooper and Musser, 1964; reproduced from fig. 8B). Note the inclusion of Holochilus in a clade with other oryzomyines. Species of “Oryzomys” represented in Hooper and Musser’s study included forms now referred 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.”

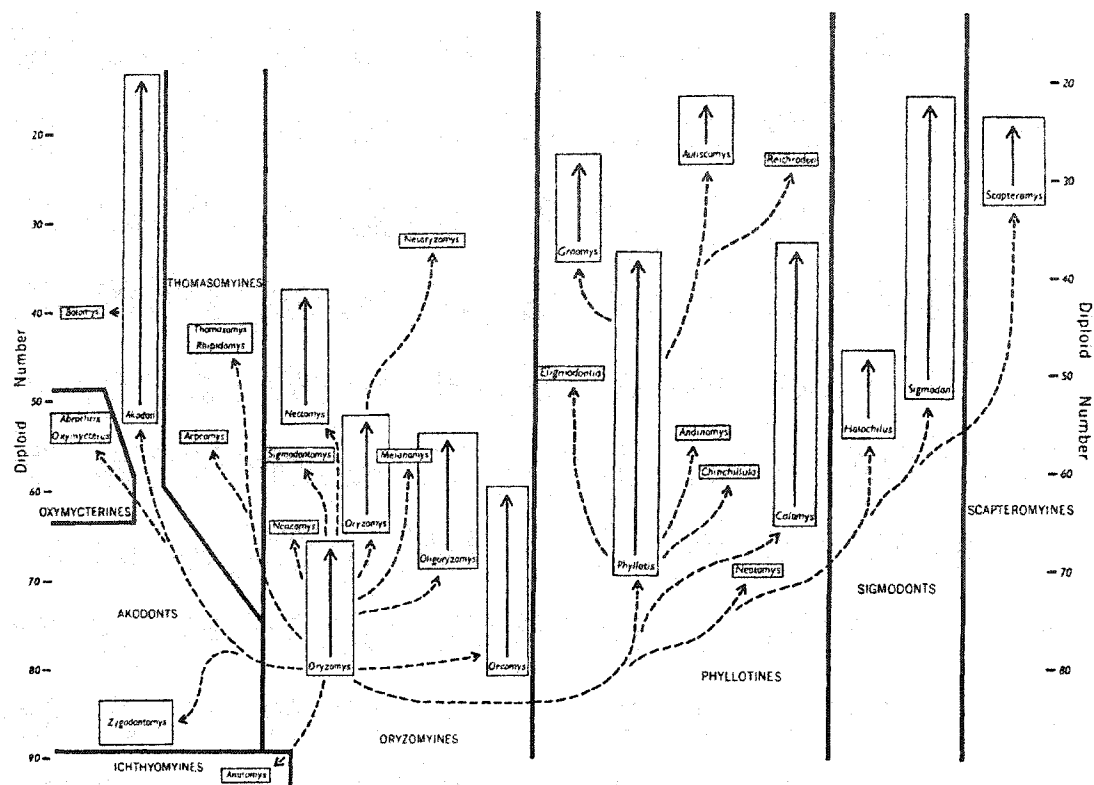


Figure 3. Interrelationships and evolutionary scenario for the karyotypic evolution of sigmodontines (Gardner and Patton, 1976; reproduced from fig. 10). Oryzomyines were postulated to be the basal group from which other sigmodontine groups originated. Note the exclusion of *Zygodontomys* (which included *Bolomys* in then-current usage) and *Holochilus* from oryzomyines. The original caption reads: "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."

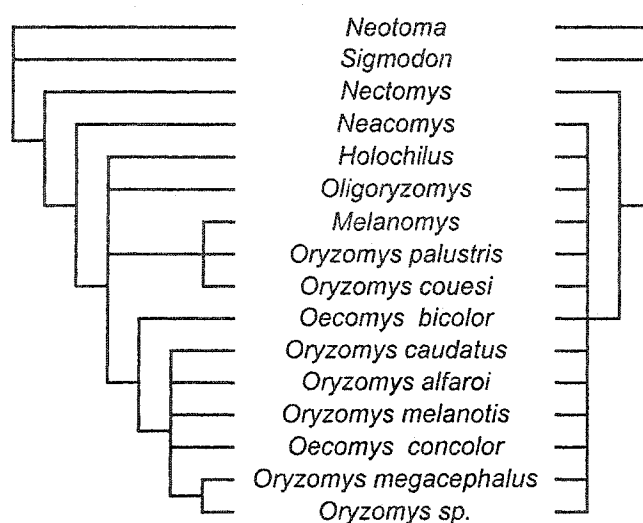


Figure 4. Hypotheses of relationships among oryzomyine rodents based on G-banded chromosome morphology (Baker et al., 1983), with generic taxonomy updated to reflect current usage. The matrix consisted of 14 oryzomyine taxa, one non-oryzomyine sigmodontine (*Sigmodon hispidus*) and one neotomine (*Neotoma 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. The taxonomy has updated to reflect current usage.

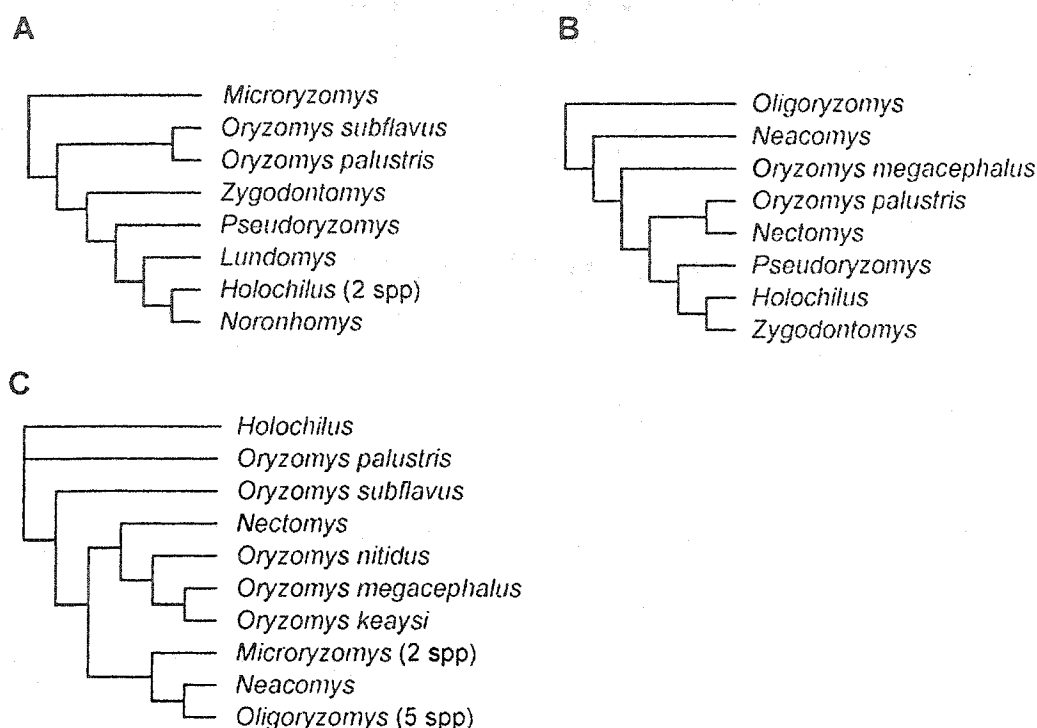


Figure 5. Hypotheses of relationships among oryzomyine rodents based on morphological characters and allozymic data. For simplicity, species-level taxonomic sampling is not illustrated in these condensed diagrams, except for that were genera not recovered as monophyletic groups. The taxonomy has been 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 fig. his 19). The tree on which this diagram was based was recovered in an parsimony analysis using a dummy character included to favor sigmodontine monophyly. Analysis without such character (Steppan, 1995, fig. 20) recovers a basal polytomy involving *Neacomys*, *Oligoryzomys*, *Oryzomys megacephalus*, and the clade containing remaining oryzomyines; and *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 5 algorithms (binary parsimony, multistate parsimony, Fitch-Margoliash, frequency parsimony, and maximum likelihood). Holochilus was used to root the tree.

Figure 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, $CI=0.277$, $RI=0.7529$) display a wide polytomy, which include several clades of sigmodontines. **Oryzomyine** taxa are shown in bold type.

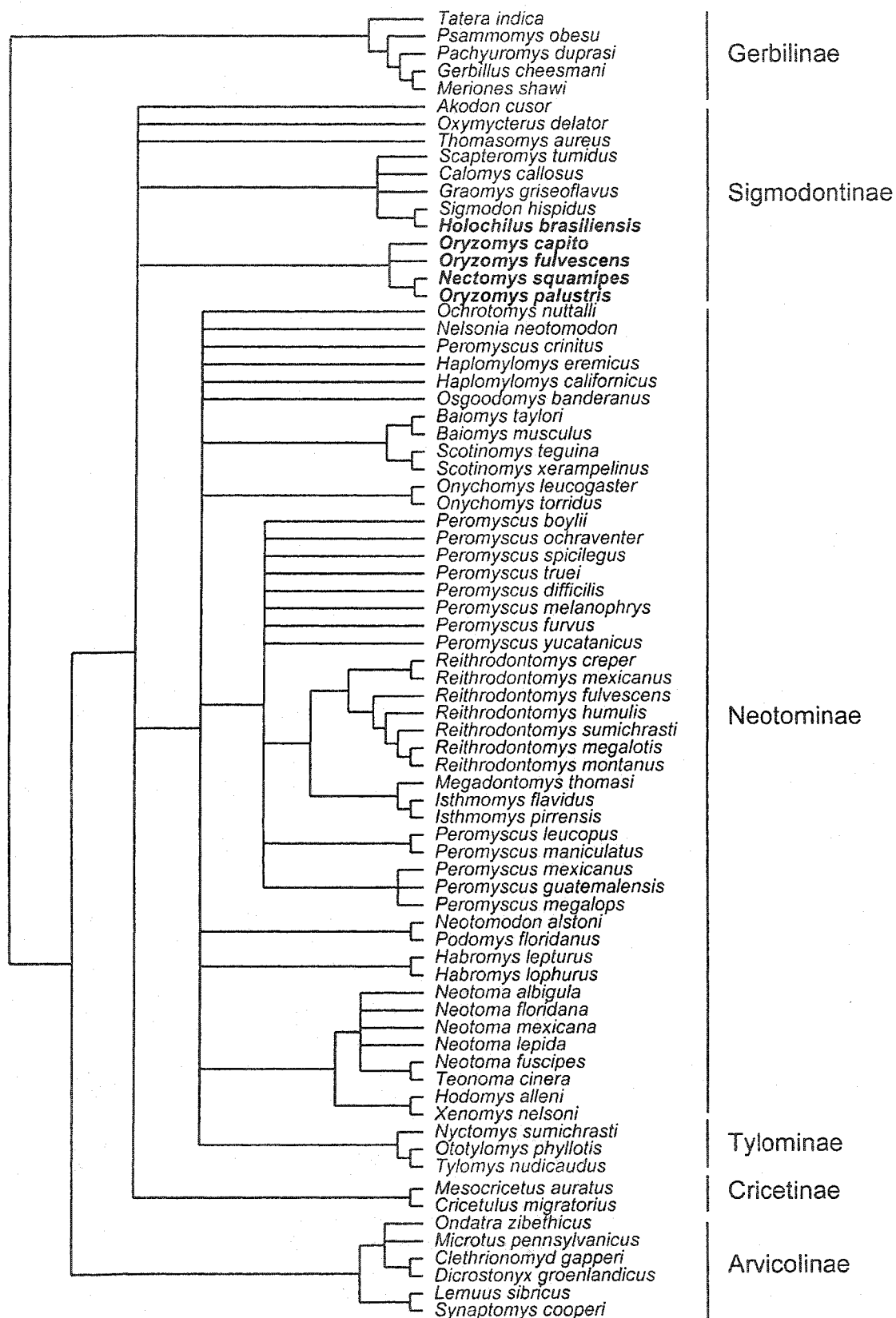


Figure 6.

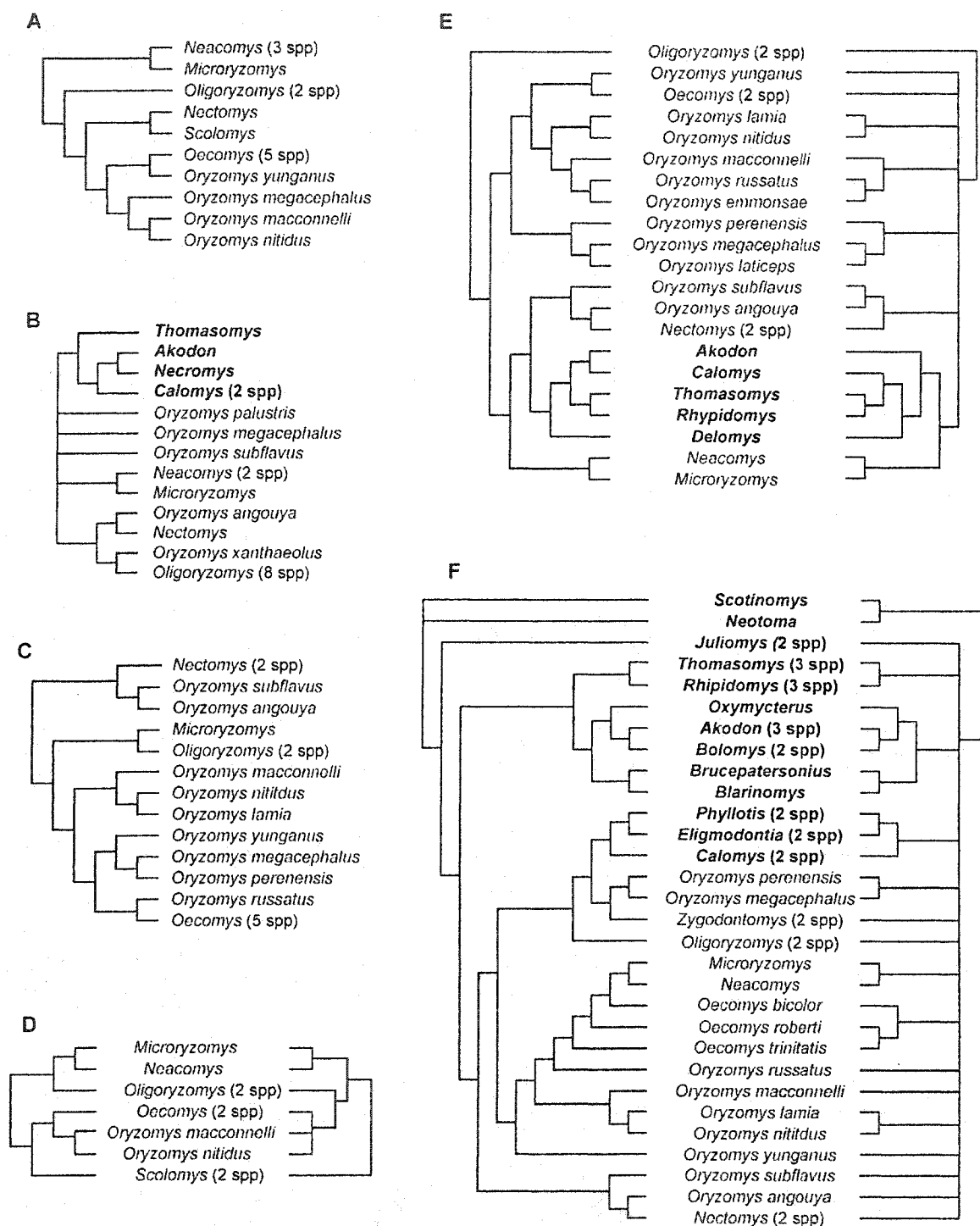


Figure 7. Hypotheses of relationships among oryzomyine rodents based on the mitochondrial gene cytochrome *b*. For simplicity, species-level taxonomic sampling is not illustrated in these condensed diagrams, except for genera that were not recovered as monophyletic groups. The taxonomy in all of these trees has been updated to reflect

current usage. Non-oryzomyine taxa are in bold. **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 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 2 most parsimonious trees obtained by unweighted parsimony analysis of all nucleotide substitutions. The tree is rooted with one murine (Mus musculus) as designated outgroup (not shown). **C**, Analysis based on 801 bp (Andrade and Moreira, 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 3 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 maximum likelihood 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 parsimony 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 included 2 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). Non-oryzomyine taxa are italicized. 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).

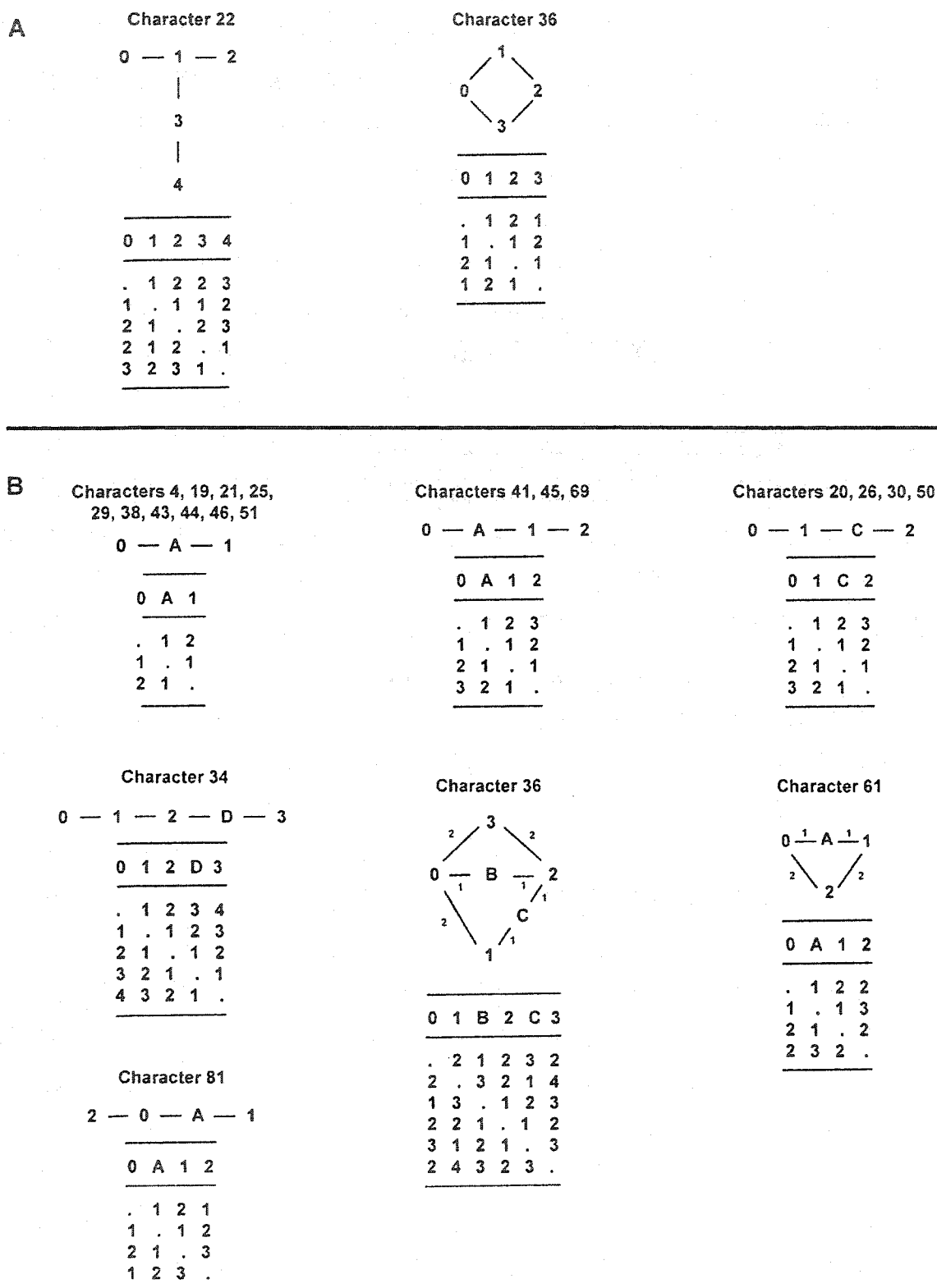


Figure 8. Transformation series and step matrices for characters with complex change patterns (A) and for characters with polymorphic data entries in the analysis of polymorphism as transformations series (B).

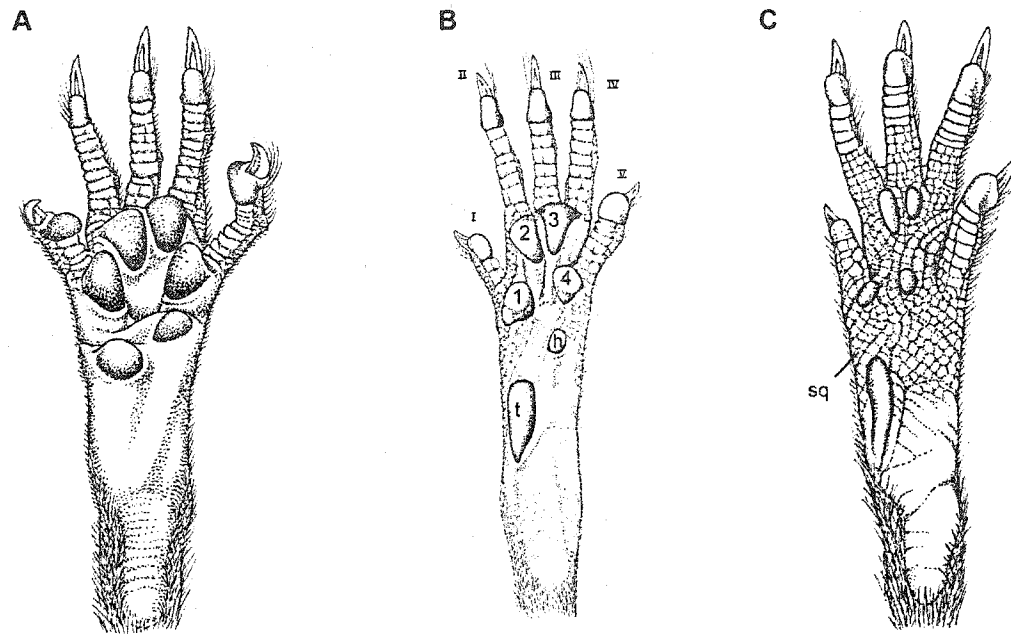


Figure 9. Plantar views of the left hind foot illustrating variation in the hypothenar pad (character 4), interdigital pads (character 5), and plantar surface texture (character 6). **A**, *Oecomys auyantepui* (AMNH 267595), showing the hypothenar pad, developed interdigital pads, and smooth plantar surface; **B**, *Handleyomys intectus* (AMNH 16092) showing the hypothenar pad, small 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.

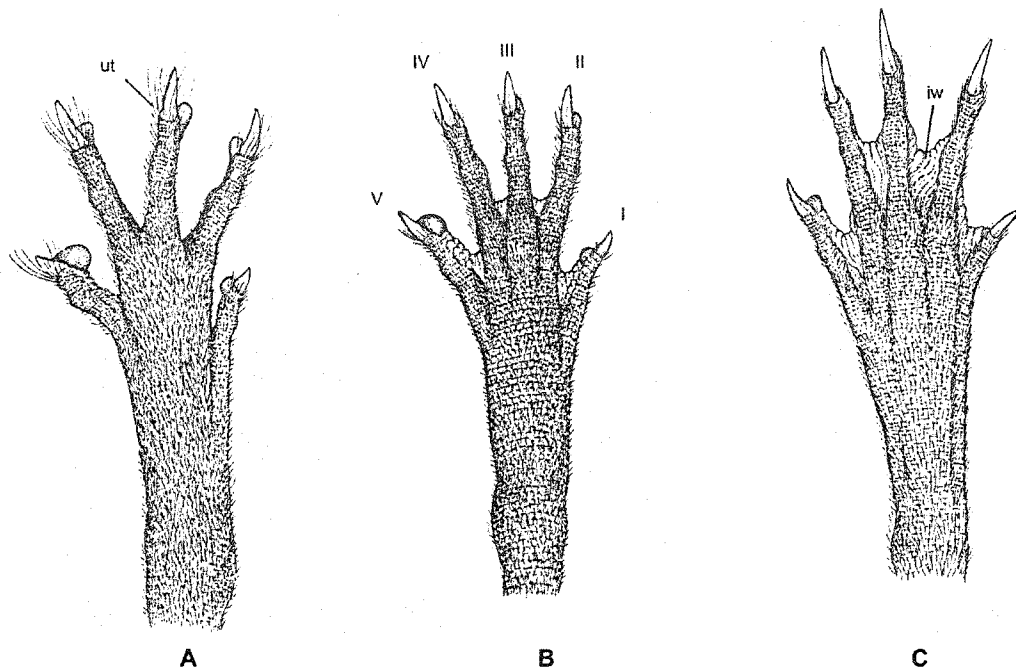


Figure 10. Dorsal views of left hind foot illustrating variation in the ungual tufts (character 7) and interdigital web (character 9). **A**, *Oryzomys megacephalus* (AMNH 262085), with developed ungual tufts and without interdigital webbing; **B**, *Oryzomys palustris* (AMNH 239260), with sparse ungual 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.

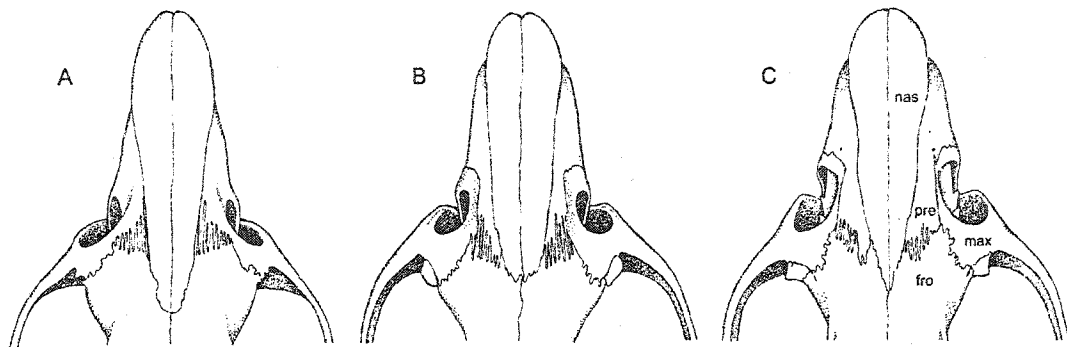


Figure 11. Dorsal views of rostrum illustrating variation in the posterior morphology of the nasal (characters 18 and 19) and premaxillary (character 20). **A**, *Handleyomys intectus* (ICN 16074), showing the blunt posterior nasal terminus extending beyond maxillary-frontal suture and the premaxillaries 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 maxillary-frontal suture and the premaxillaries terminating anterior to the nasal. Abbreviations are **fro**, frontal; **max**, maxillary; **nas**, nasal; and **pre**, premaxillary.

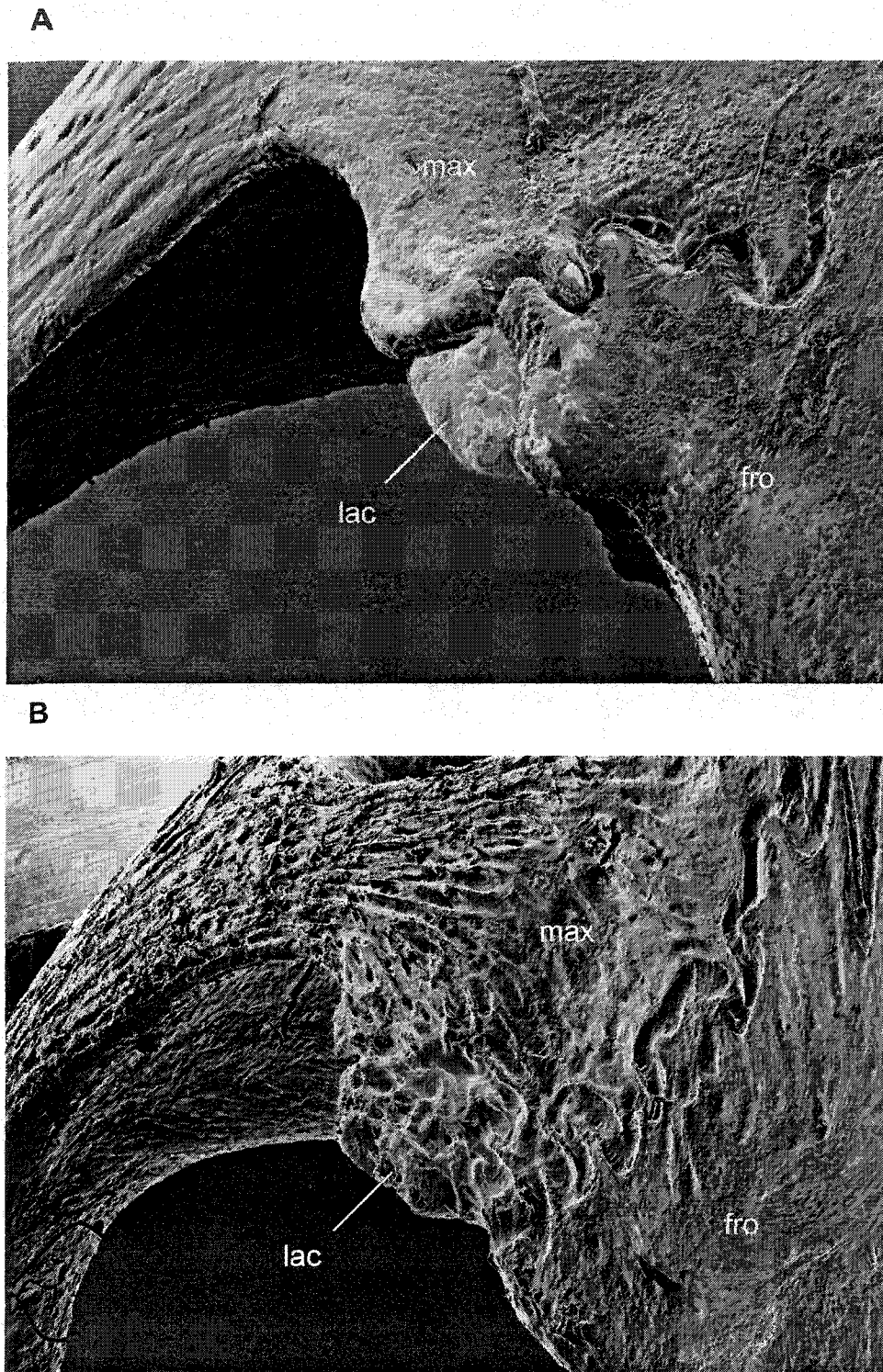


Figure 12. Dorsal views of lachrymal bone illustrating the variation in its contact with maxillary and frontal (character 21). **A**, *Oryzomys balneator* (AMNH 47593); and **B**, *Oecomys bicolor* (AMNH 272674). Abbreviations are **fro**, frontal; **lac**, lacrimal; and **max**, maxillary.

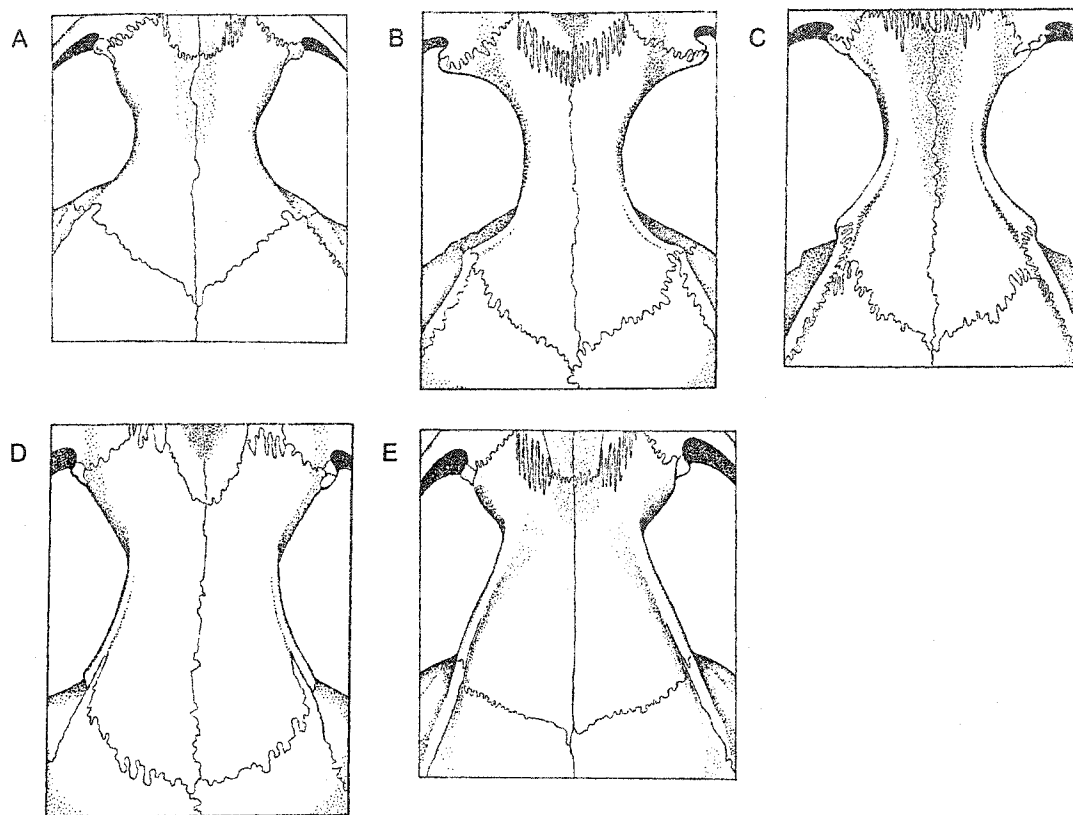


Figure 13. Dorsal views of interorbital region illustrating the variation in its shape (character 22). **A**, Handleymys fuscatus (ICN 12703); **B**, Nesoryzomys narboroughi (ASNHC 8675); **C**, Holochilus brasiliensis (AMNH 206372); **D**, Oryzomys lamia (AMNH 134763); and **E**, Oryzomys palustris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

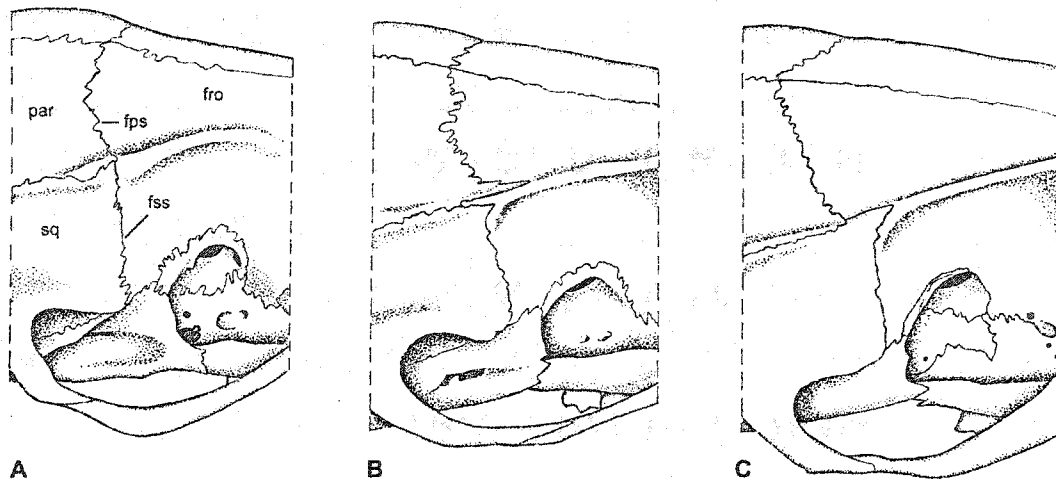


Figure 14. Lateral views of fronto-squamosal and fronto-parietal sutures illustrating variation in their contact (character 24). **A**, *Oryzomys alfaroi* (AMNH 142424); **B**, *Oryzomys macconnelli* (AMNH 262033); and **C**, *Melanomys caliginosus* (AMNH 66331). Abbreviations are **fro**, frontal; **fss**,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

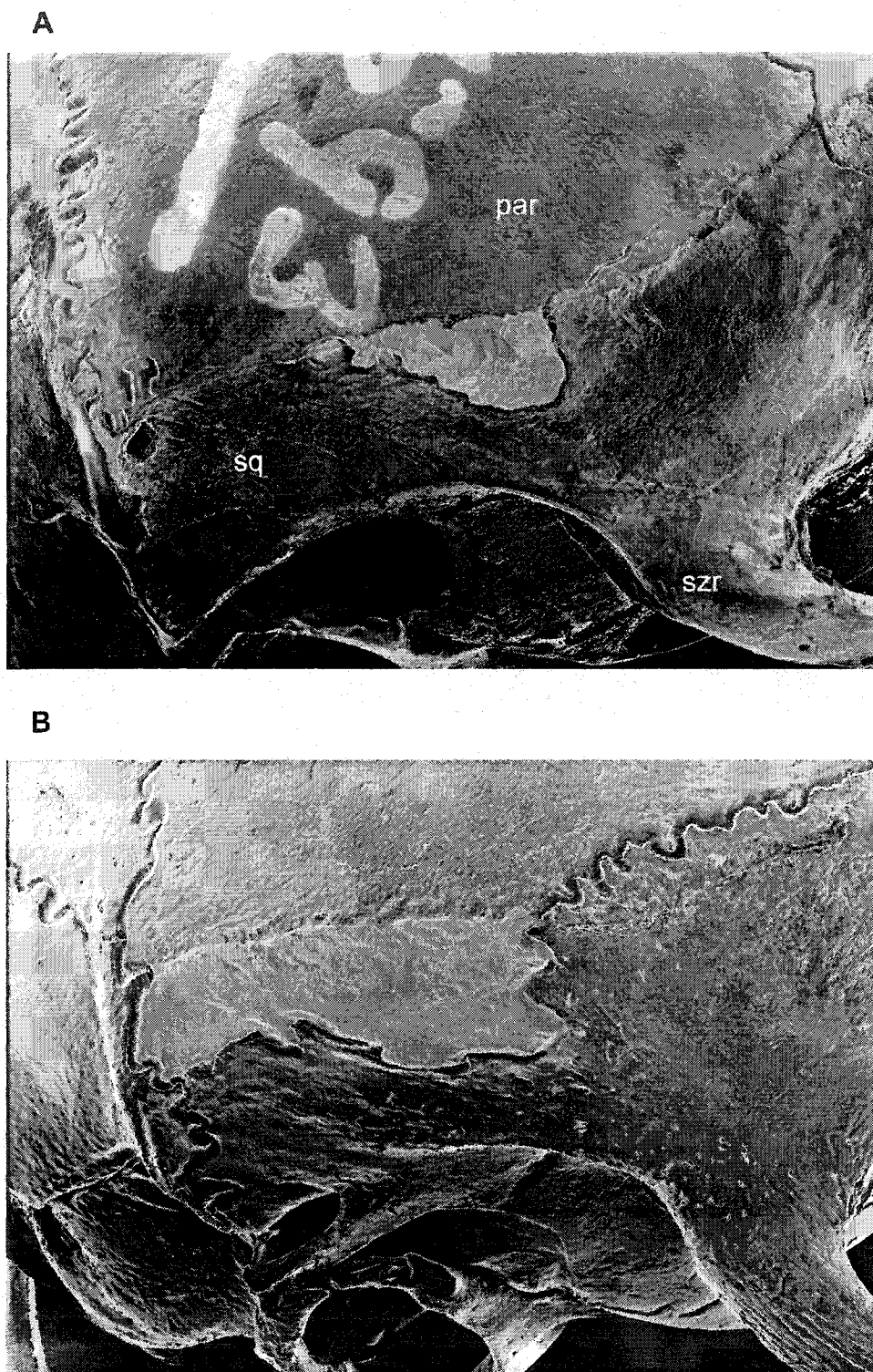


Figure 15. Lateral views of braincase illustrating variation in the lateral expansion of the parietal (character 25). **A**, *Oryzomys balneator* (AMNH 47593); **B**, *Oecomys bicolor* (AMNH 272674). Abbreviations are **par**, parietal; **sq**, squamosal; and **szi**, squamosal zygomatic root.

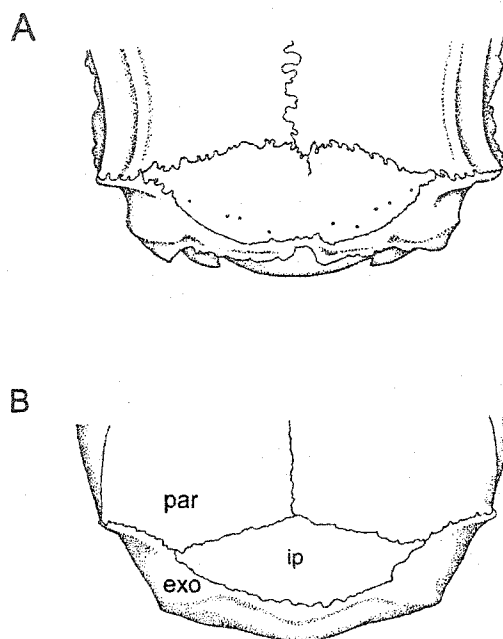


Figure 16. Dorsal views of occipital region illustrating the variation of interparietal morphology (character 26). **A**, *Nectomys melanius* (MNHN 1981.1296); **B**, *Handleyomys intectus* (ICN 16079). Abbreviations are **exo**, exoccipital; **ip**, interparietal; and **par**, parietal (from Voss et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

Figure 17. Lateral views of the rostral and zygomatic regions illustrating the variation in the zygomatic plate and notch (character 28). **A**, Oryzomys palustris (AMNH 242523); **B**, Microryzomys minutus (AMNH 46808); **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.

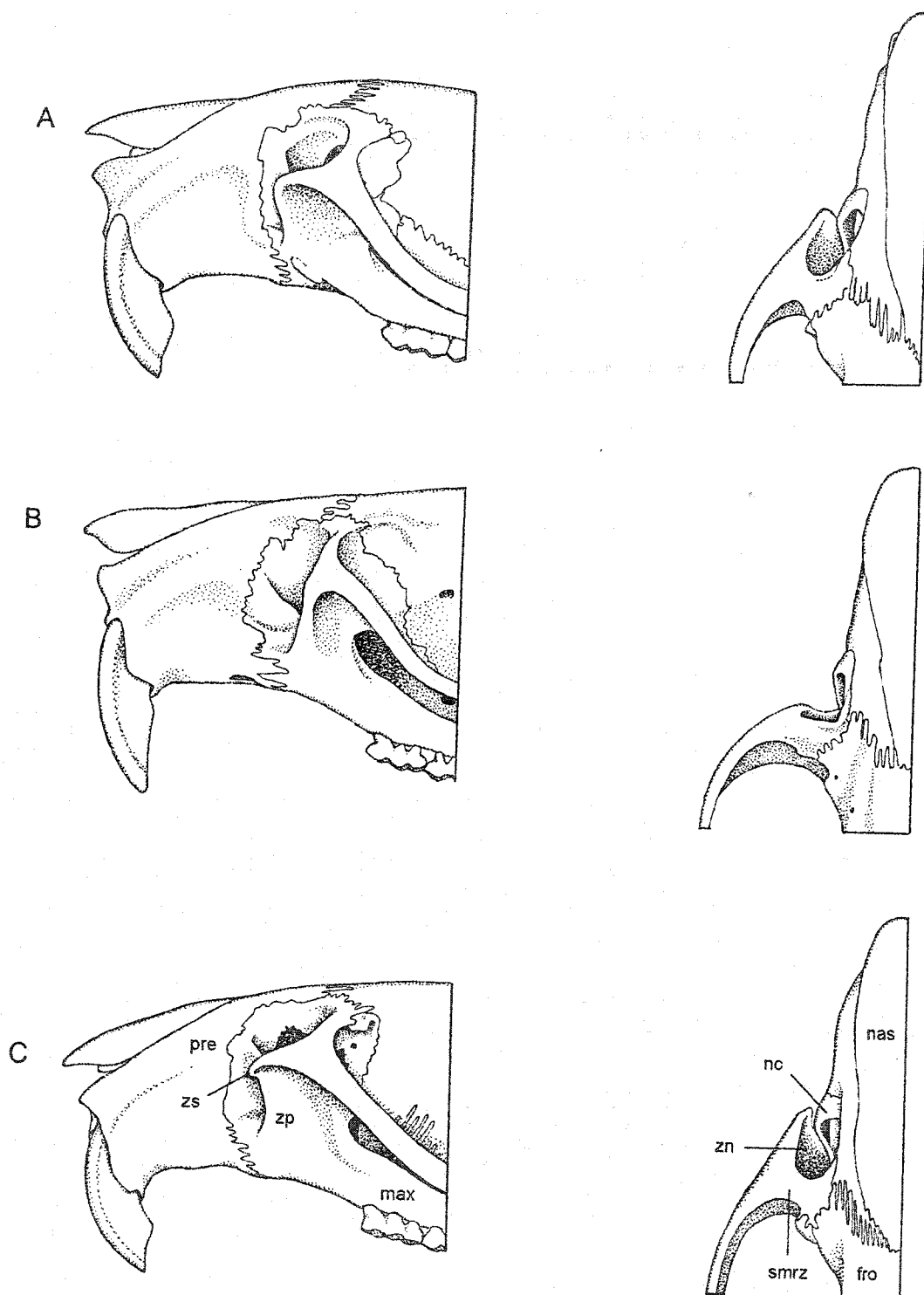


Figure 17.

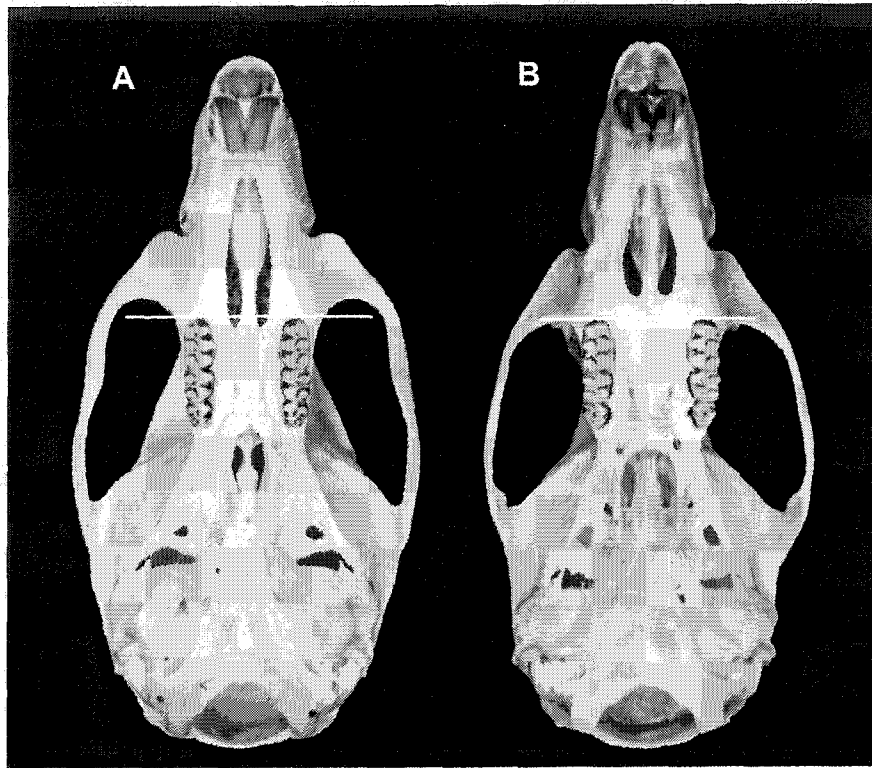


Figure 18. Ventral views of the skull illustrating the variation in the position of the zygomatic plate relative to the first molar (character 29) and on the posterior extensions of the incisive foramina (character 31). A, *Oryzomys subflavus* (AMNH 134632); and B, *Oryzomys macconnelli* (AMNH 15341).

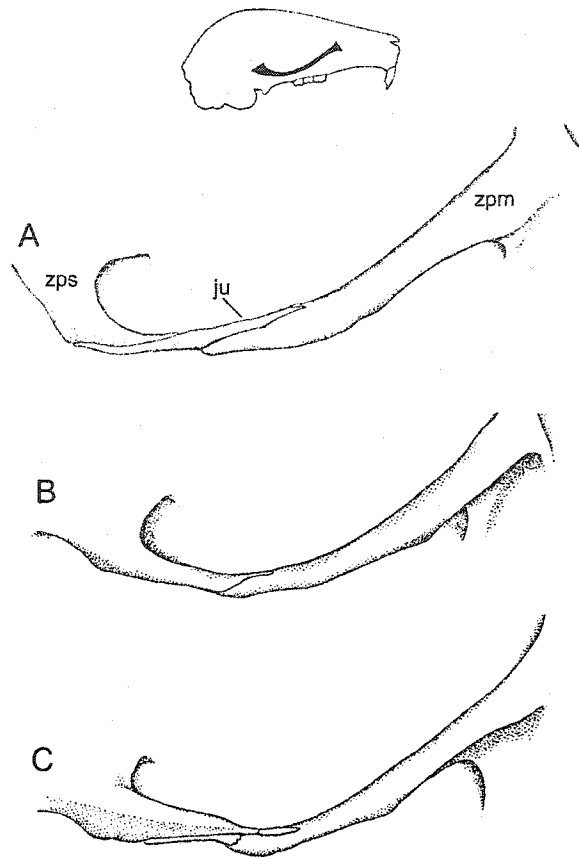


Figure 19. Lateral views of right zygomatic plate illustrating variation on jugal morphology in oryzomyines (character 30). **A**, *Oryzomys palustris* (AMNH 242669); **B**, *Microroryzomys minutus* (AMNH 260419); **C**, *Microroryzomys altissimus* (AMNH 63047). Abbreviations are **ju**, jugal; **zpm**,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

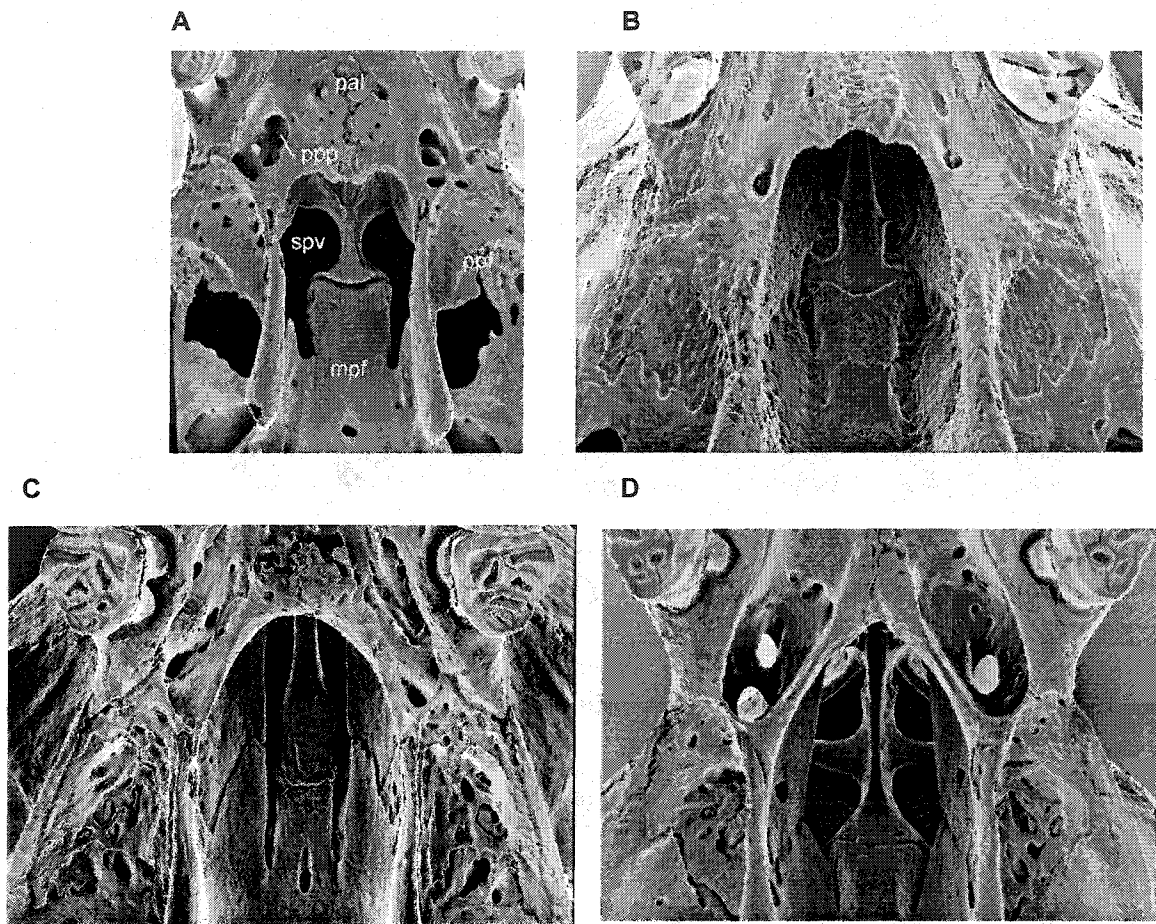


Figure 20. Ventral views of the palatal and basicranial region illustrating the variation in the morphology of posterior palate (characters 32 and 34), parapterygoid (character 35), and sphenopalatine (character 36) in oryzomyines. **A**, *Oligoryzomys fulvescens* (AMNH 257266); **B**, *Oryzomys hammondi* (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.

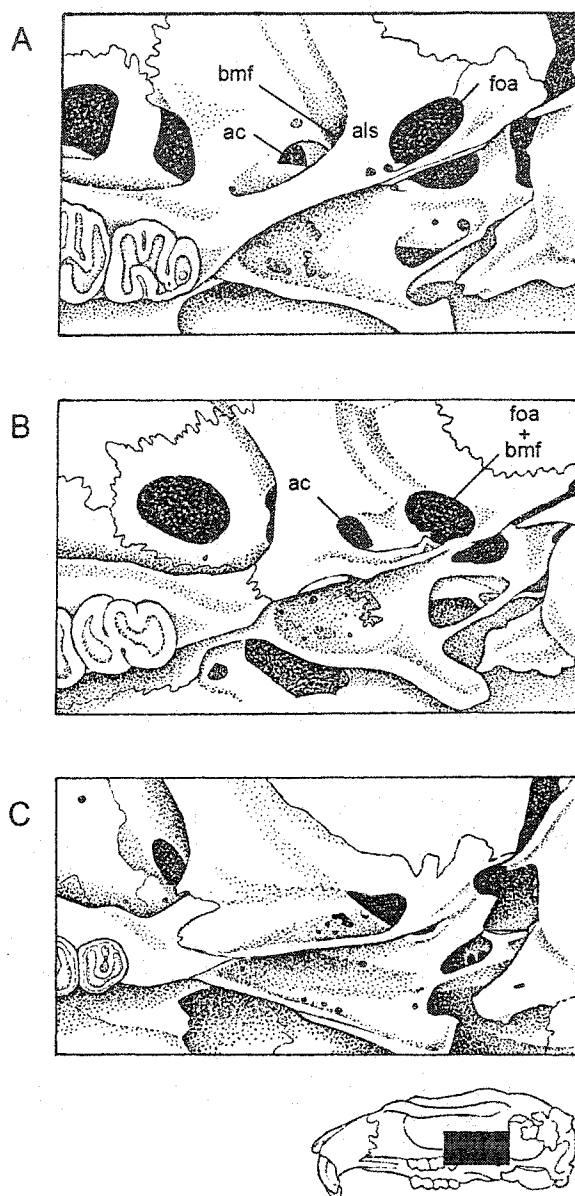


Figure 21. Lateral view of the braincase showing variation in the foramina and associated features of the alisphenoid bone (characters 38 and 39). **A**, *Holocheilus sciureus* (AMNH 210263); **B**, *Lundomys molitor* (AMNH 206393); and **C**, *Scolomys ucayalensis* (MUSM 13354). Abbreviations are **als**,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

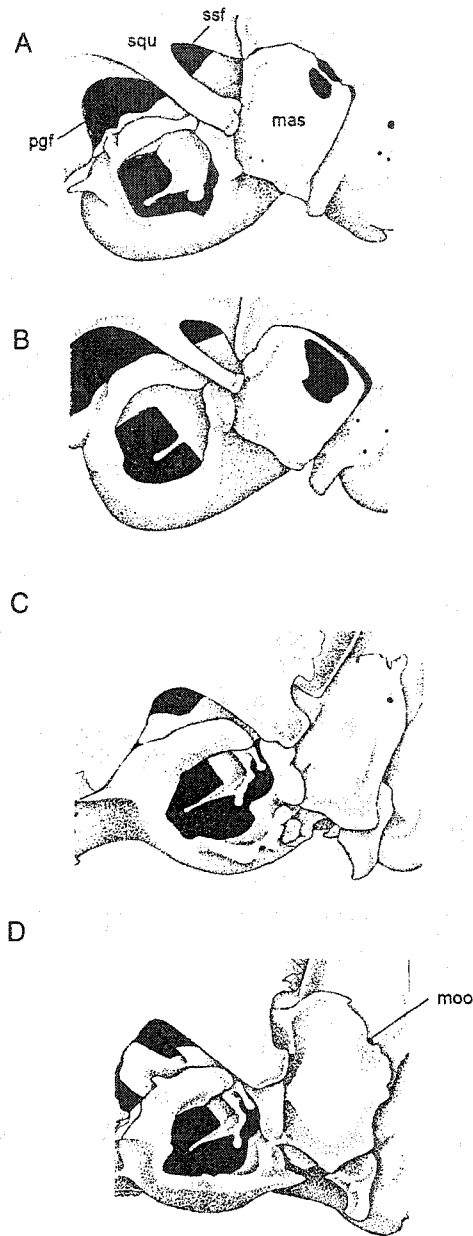


Figure 22. Lateral view of braincase illustrating variation on the morphology of subsquamosal fenestra and mastoid bone in oryzomyines (character 40 and 43). **A**, *Oligoryzomys microtis* (AMNH 248993); **B**, *Microrizomys minutus* (AMNH 46808); **C**, *Nectomys palmipes* (AMNH 235065); **D**, *Nectomys melanius* (AMNH 406062). Abbreviations are **mas**, mastoid; **moo**, mastoid-occipital opening; **pgf**, posglenoid formamen; **ssf**, subsquamosal fenestra; **squ**, squamosal (from Carleton and Musser, 1993: fig. 19; and Voss et al., 2001: fig. 47).

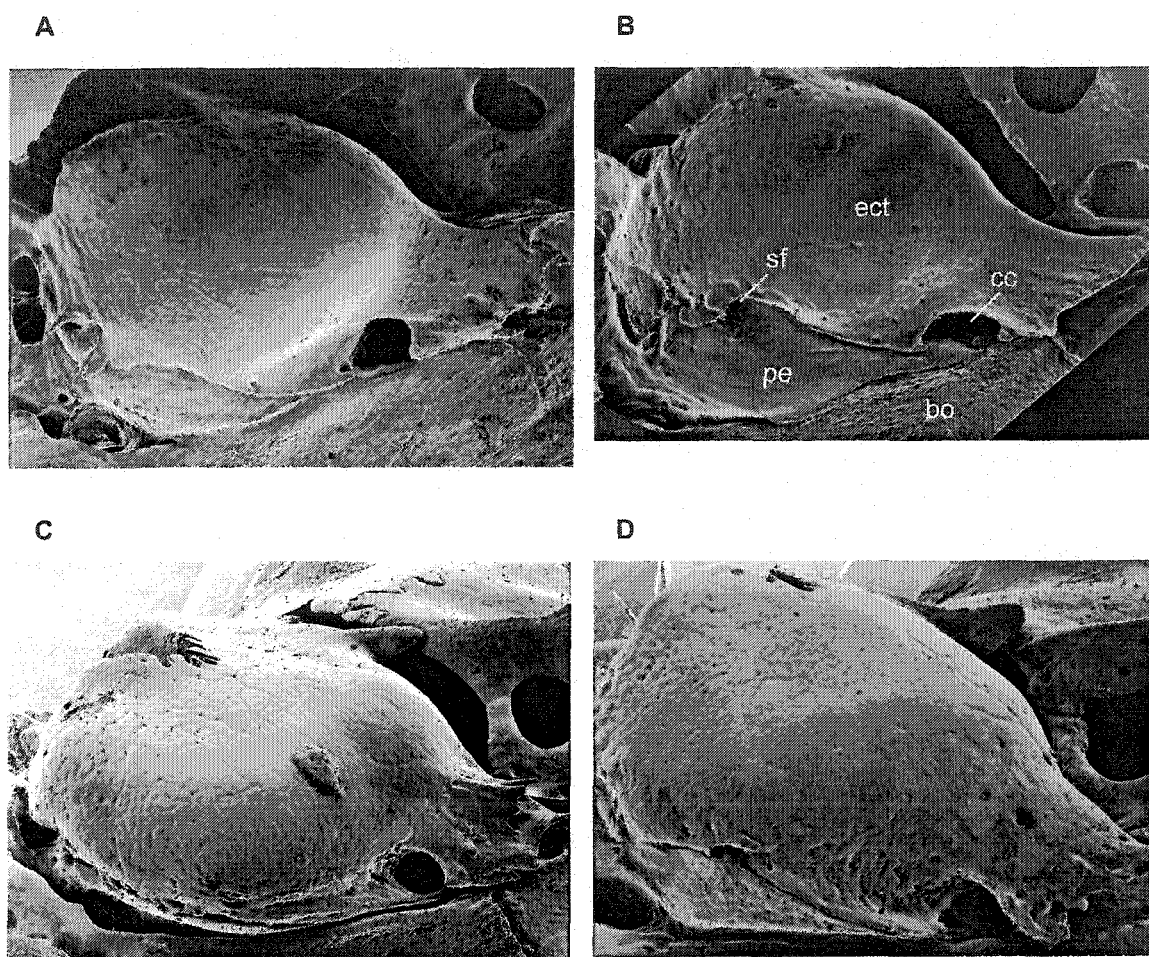


Figure 23. Medial views of auditory bulla illustrating variation on the ectotympanic morphology (character 41). **A**, *Scolomys ucayalensis* (MUSM 13357); **B**, *Oligoryzomys fulvescens* (AMNH 257226); **C**, *Holochilus brasiliensis* (AMNH 210250); **D**, *Lundomys molitor* (AMNH 206364). Abbreviations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

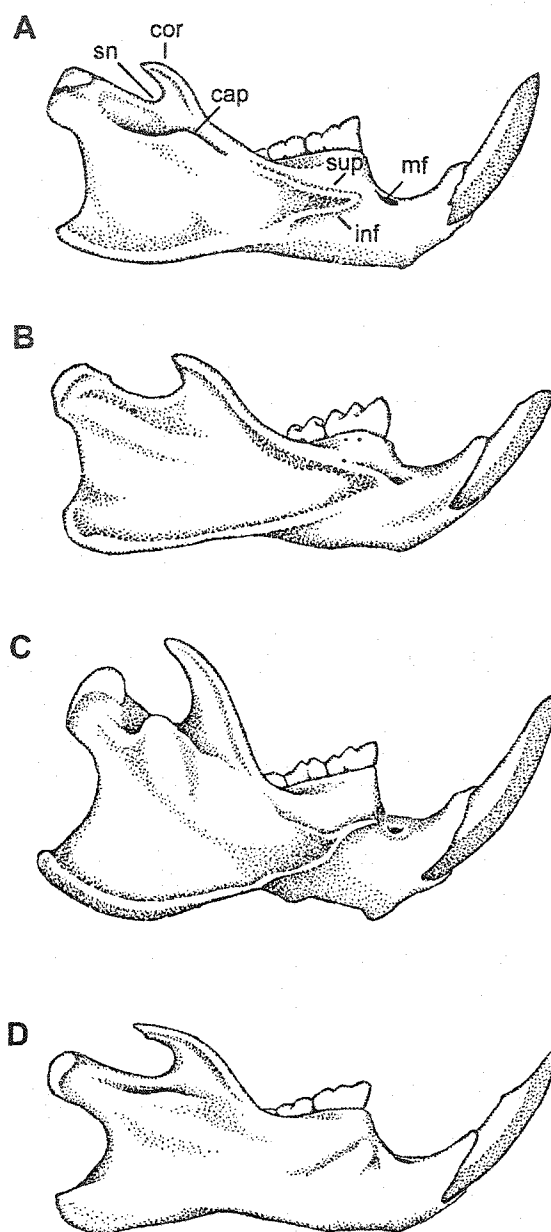


Figure 24. Lateral views of right mandibles showing taxonomic variation in the position of the mental foramen (character 44), in development of the capsular process of the lower incisor alveolus (character 45), and in patterns of the masseteric ridges (character 46 and 47). **A**, *Lundomys molitor* (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.

Figure 25. Maxillary molars of oryzomyine rodents illustrating variation in characters of the occlusal surface of upper molars. **A**, Oryzomys angouya (AMNH 80393); **B**, Oryzomys palustris (AMNH 234836); **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 fossete; **hf**, hypoflexus; **lf**, labial flexi; **ml**, mesoloph; **mm**, median mure; **pac**, paracone; **pf**, protoflexus; **pl**, posteroloph; **prc**, protocone; **ps**, protostyle.

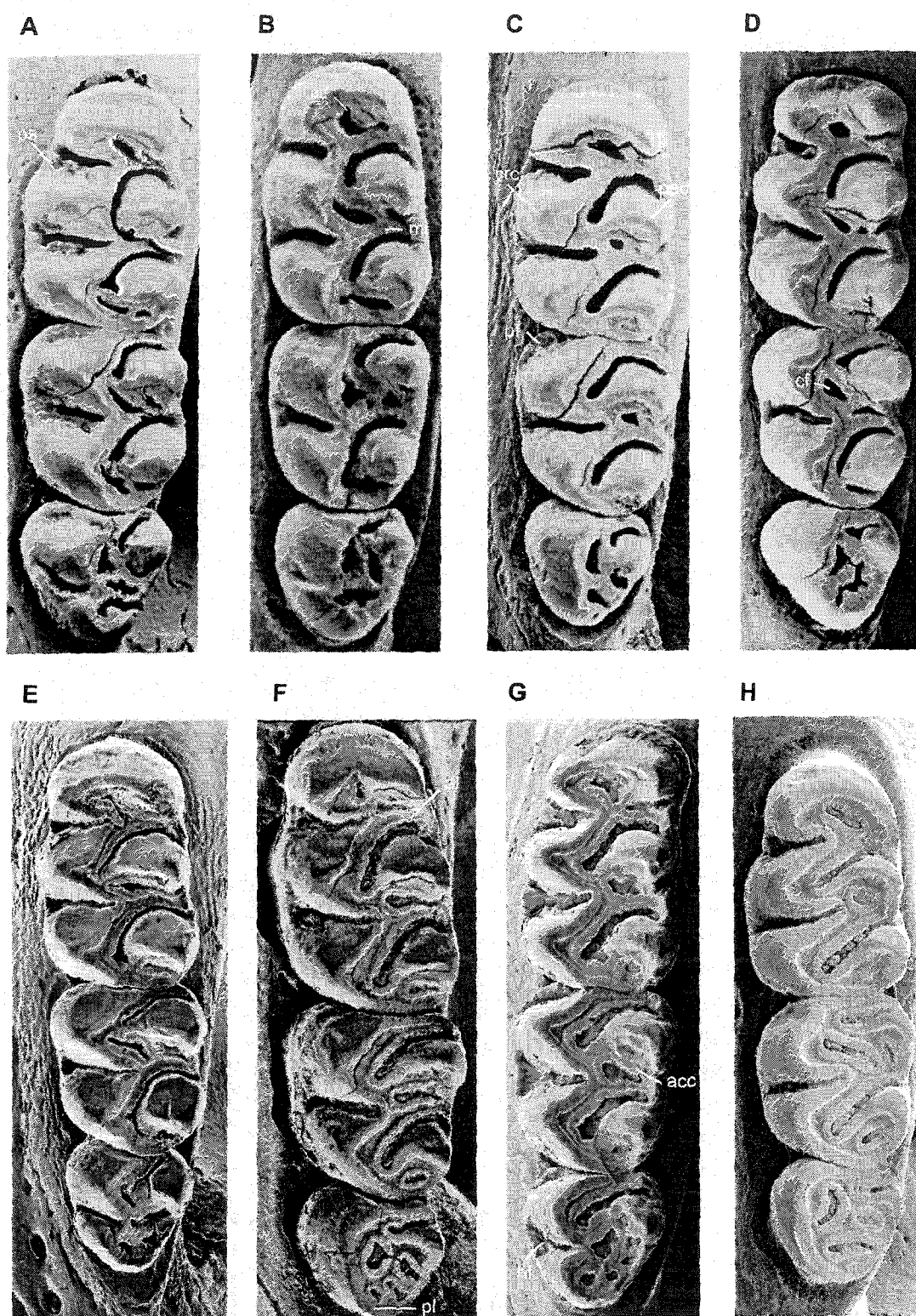


Figure 25.

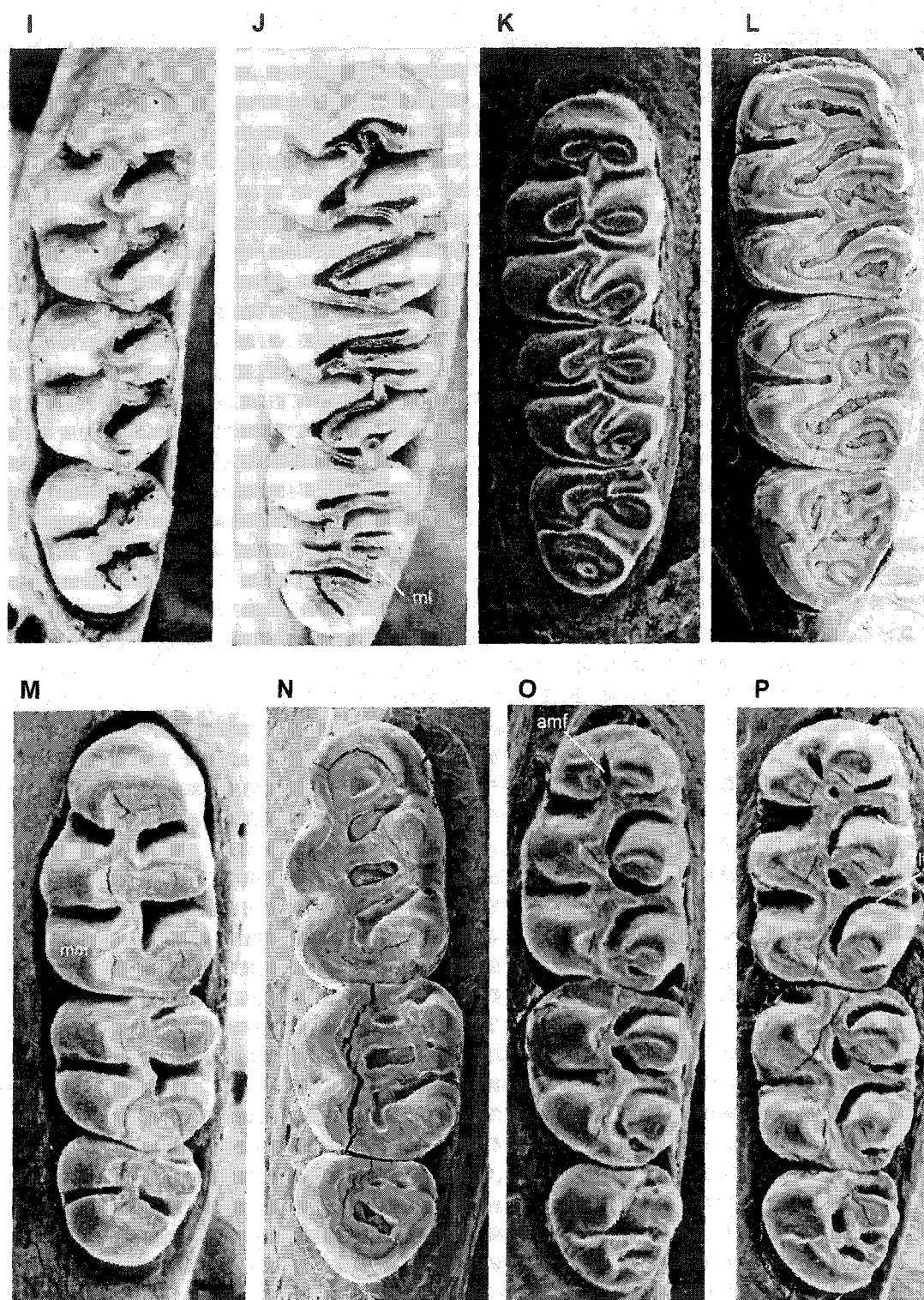


Figure 25. (Continued)

Figure 26. Mandibular molars of oryzomyine rodents illustrating variation 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 **amf**, anteromedian flexid; **aif**, anteroconid internal fold; **alc**, anterolabial cingulum; **el**, ectolophid; **ml**, mesolophid; **al** anterolophid; **pf**, posteroflexid.

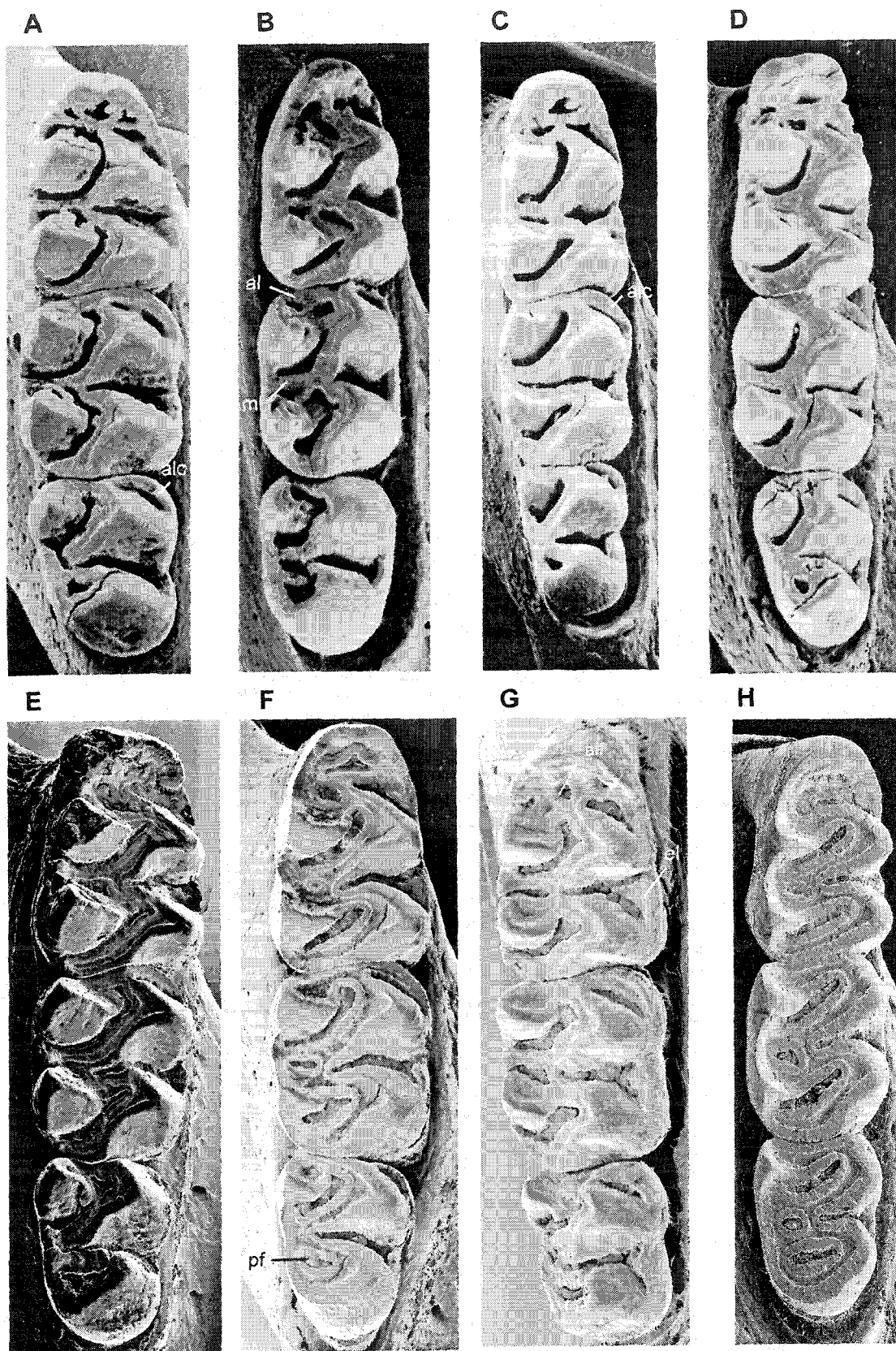


Figure 26.

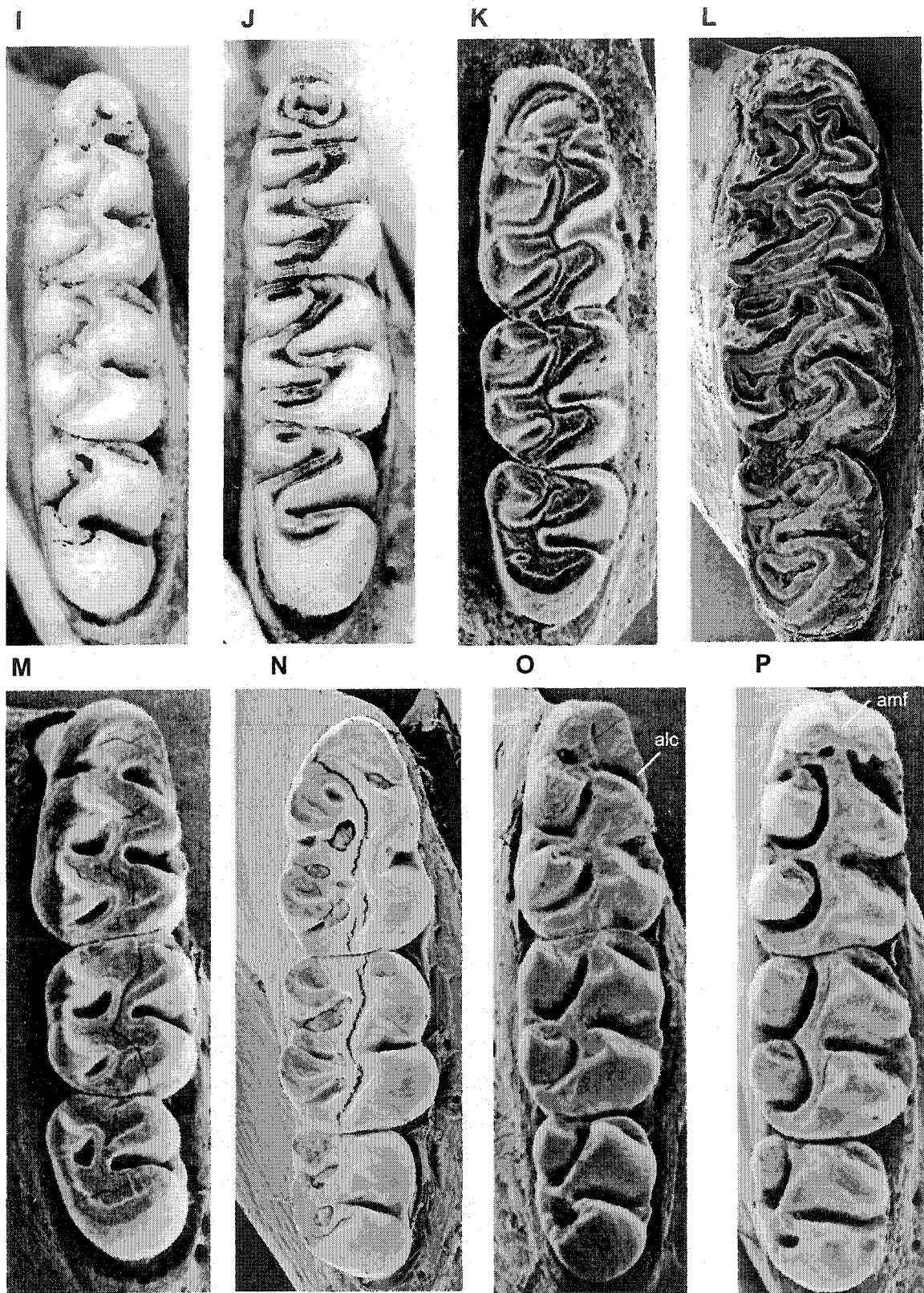


Figure 26. (Continued)

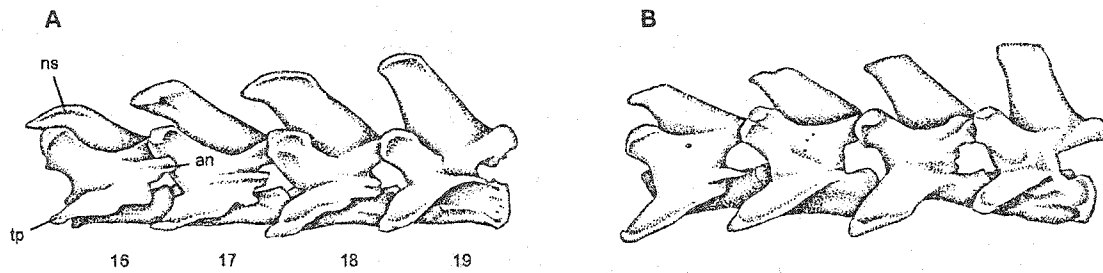


Figure 27. Lateral view of the lumbar vertebrae showing variation on the anapophysis on the 17th thoracico-lumbar vertebra (character 80). **A**, *Nesoryzomys narboroughi* (ASNHC 8675); **B**, *Oryzomys palustris* (AMNH 219953). Abbreviations are **16-19**, thoracico-lumbar vertebrae 16 to 19; **an**,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

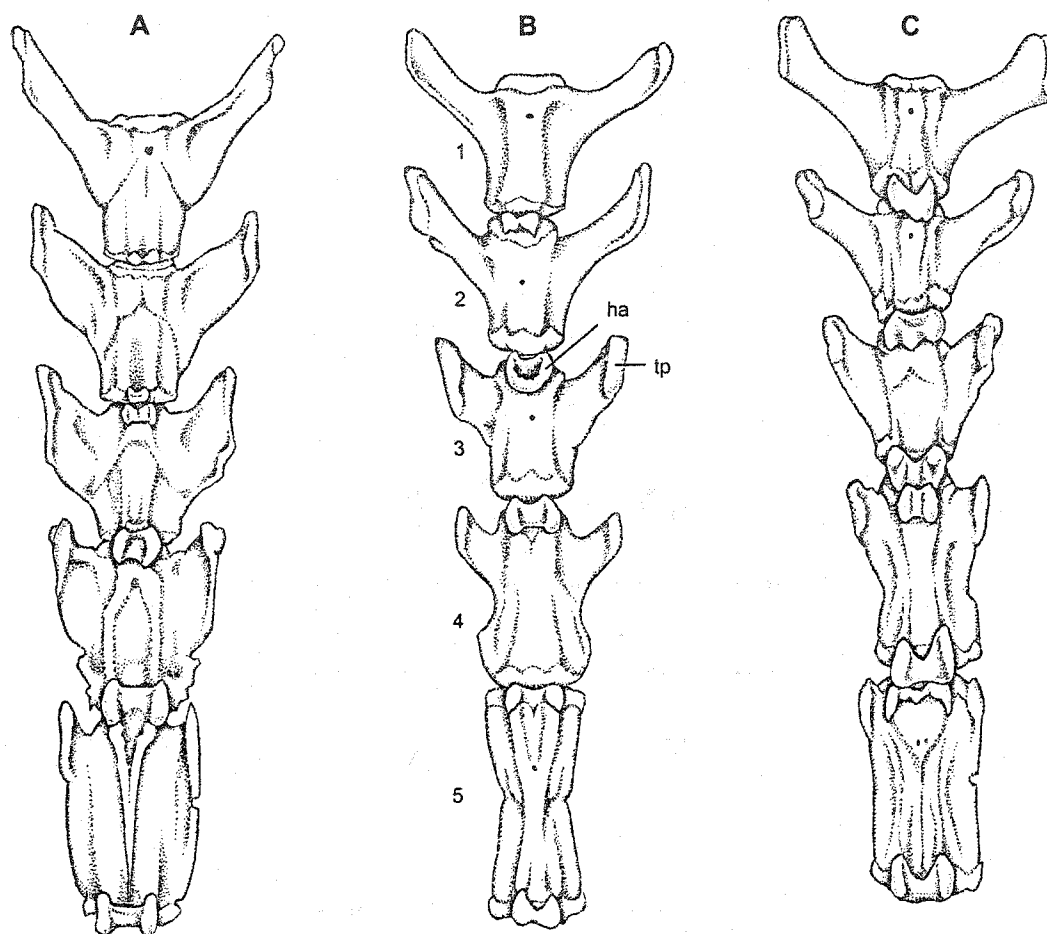


Figure 28. Ventral view of caudal vertebrae showing taxonomic variation in the hemal arches (character 81). A, *Scolomys ucayalensis* (AMNH 272721). B, *Oryzomys macconnelli* (AMNH 257238). C, *Oryzomys palustris* (AMNH 219953). Abbreviations are 1-5, caudal vertebrae 1 to 5; ha, hemal arch; tp, transverse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

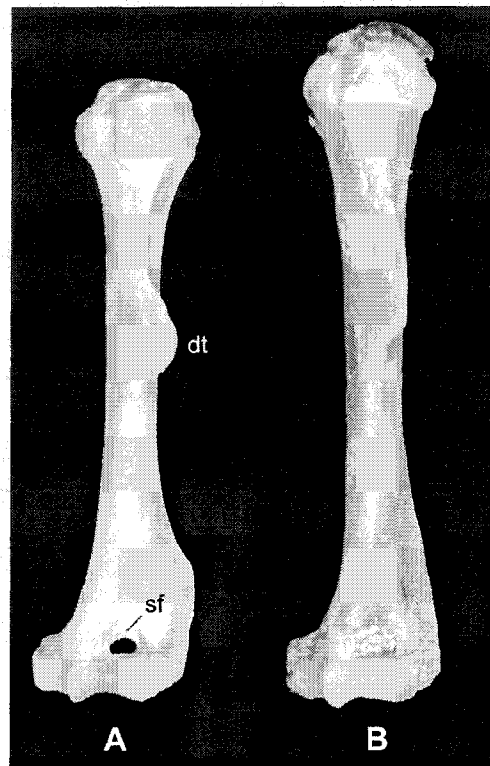


Figure 29. Flexor surface of the humerus illustrating taxonomic variation in the supratrochlear foramen (character 83). **A**, *Nesoryzomys swarthii* (ASNHC 10003); **B**, *Oryzomys angouya* (AMNH 61850). Abbreviations are **dt**, deltoid tuberosity; **sf**, supratrochlear foramen.

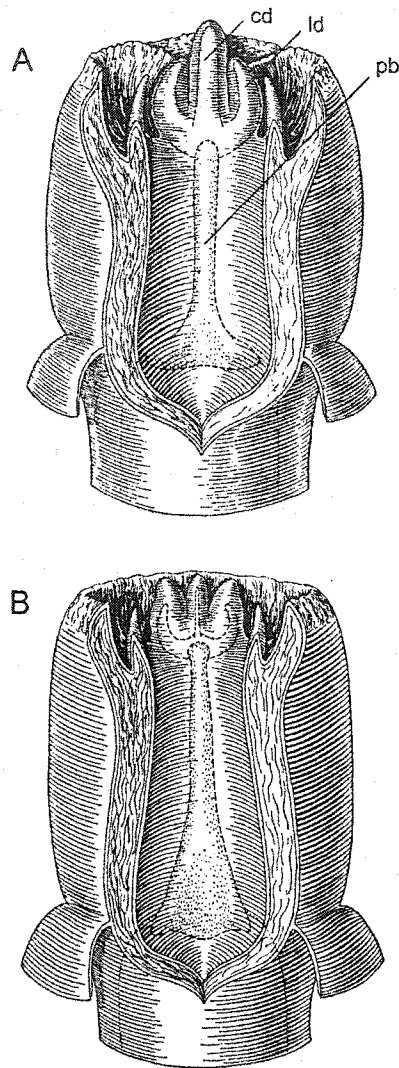


Figure 30. Ventral views of the glans penis of oryzomyines illustrating the variation on the morphology of the bacular digits (character 86). **A**, *Oligoryzomys flavescens* (UMMZ110444); **B**, *Oryzomys alfaroi* (UMMZ P-3905). Abbreviations are **cd**, central digit; **ld**, lateral digit; **pb**,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

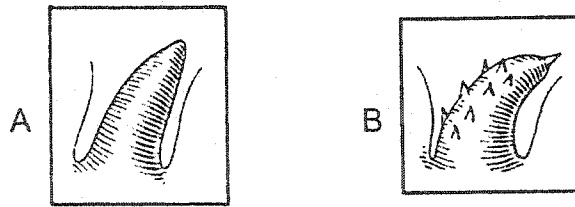


Figure 31. Views of the dorsal papilla of the glans penis of oryzomyines illustrating the variation in its condition (character 88). A, Oryzomys albigularis (CM 18663); B, Oryzomys palustris (UMMZ 110388). From Hooper and Musser (1964: fig. 2).

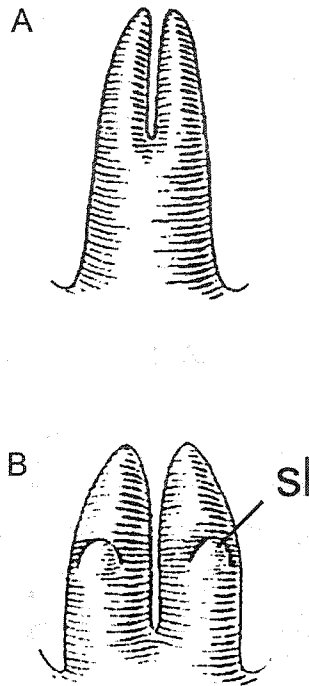


Figure 32. Views of urethral process of the glans penis of oryzomyines illustrating variation on its morphology (character 89). A, Oligoryzomys flavescens (UMMZ 110444); B, Holochilus brasiliensis (MNHN 1166). Abbreviation is sl, subapical lobule. From Hooper and Musser (1964: figs. 1 and 6).

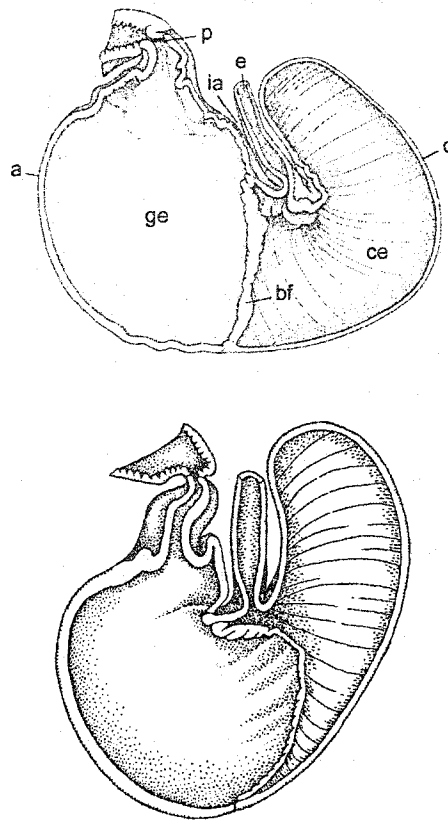


Figure 33. Ventral views of oryzomyine stomachs (in midfrontal section) illustrating variation in the extent of gastric glandular epithelium (character 99). **A**, Oryzomys palustris (AMNH 239256); **B**, Oligoryzomys microtis (AMNH 263328). Abbreviations are: **a**, antrum; **bf**, bordering fold; **c**,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

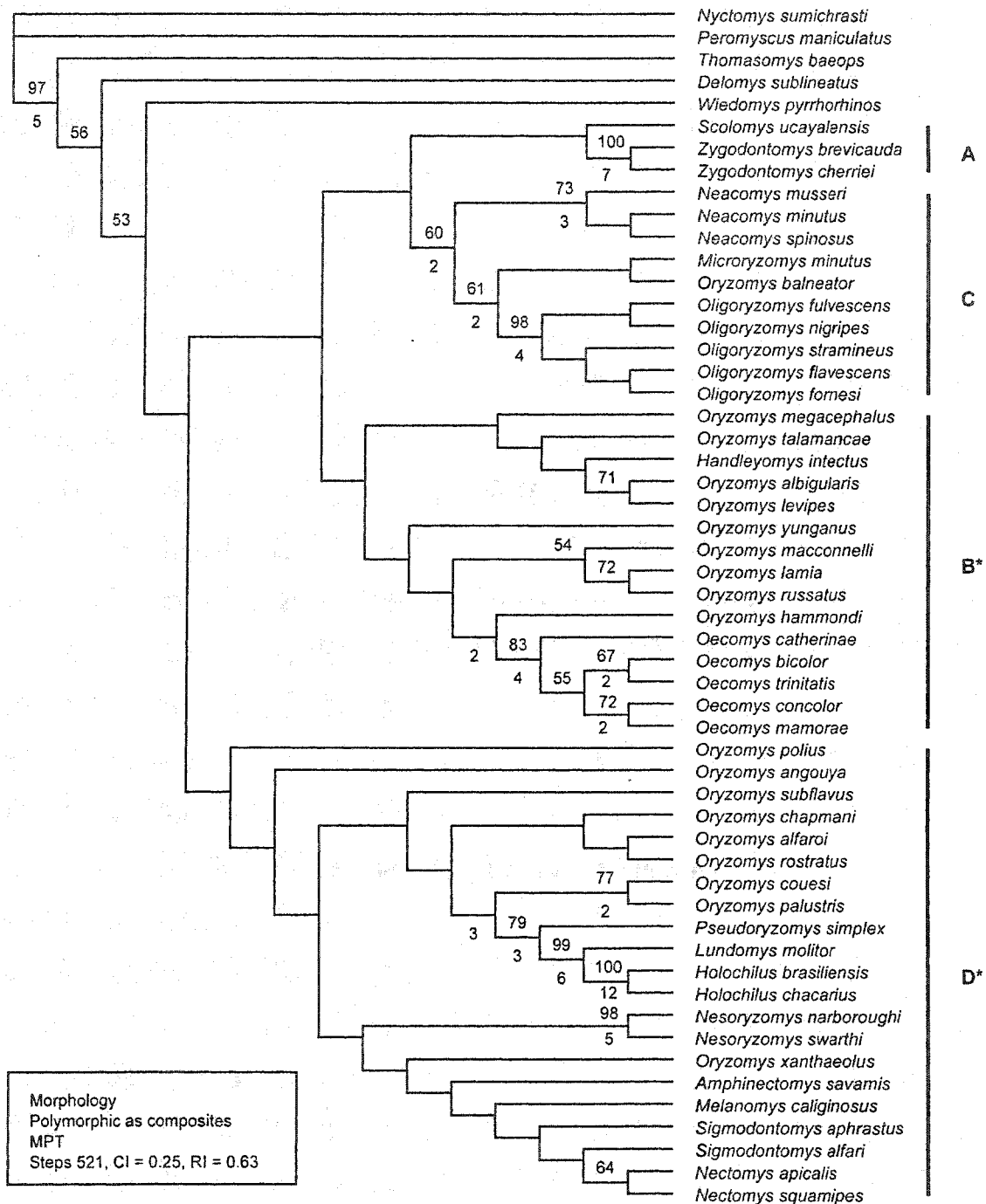


Figure 34. Single most parsimonious tree resulting from cladistic parsimony analysis of 99 morphological characters (parsimony-informative characters = 91, tree length = 521, CI = 0.25, RI = 0.63). Polymorphic data were treated as composite entries. Numbers above and below branches refer to jackknife resampling percentage (> 50%) and decay index (> 1), respectively. Letters A, B*, C, and D* define clades discussed in the text.

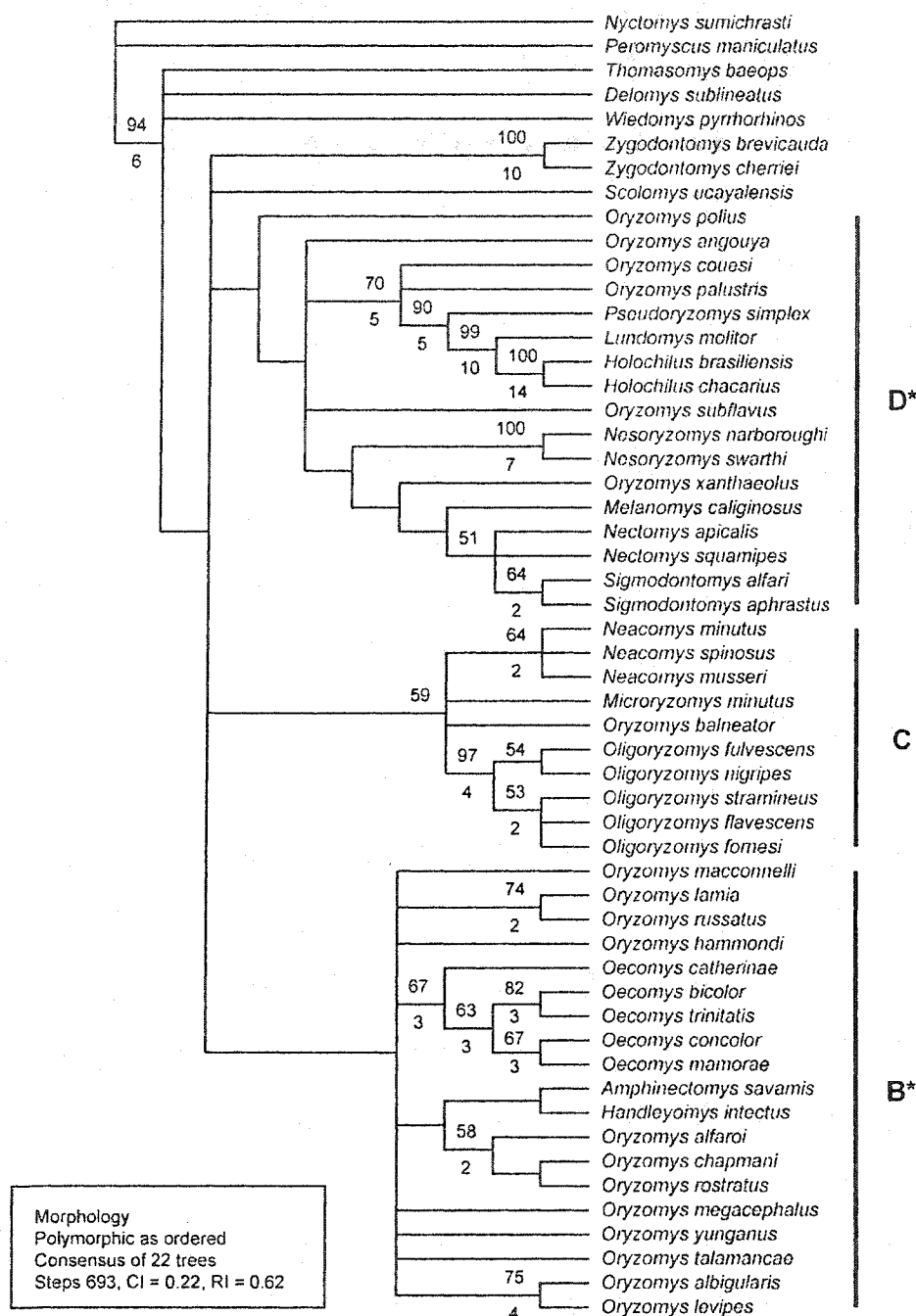


Figure 35. Strict consensus of 22 minimum length trees resulting from cladistic parsimony analysis of 99 morphological characters (parsimony-informative characters = 91, tree length = 693, CI = 0.22, RI = 0.62). Polymorphic data were treated as transformations series. Numbers above and below branches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

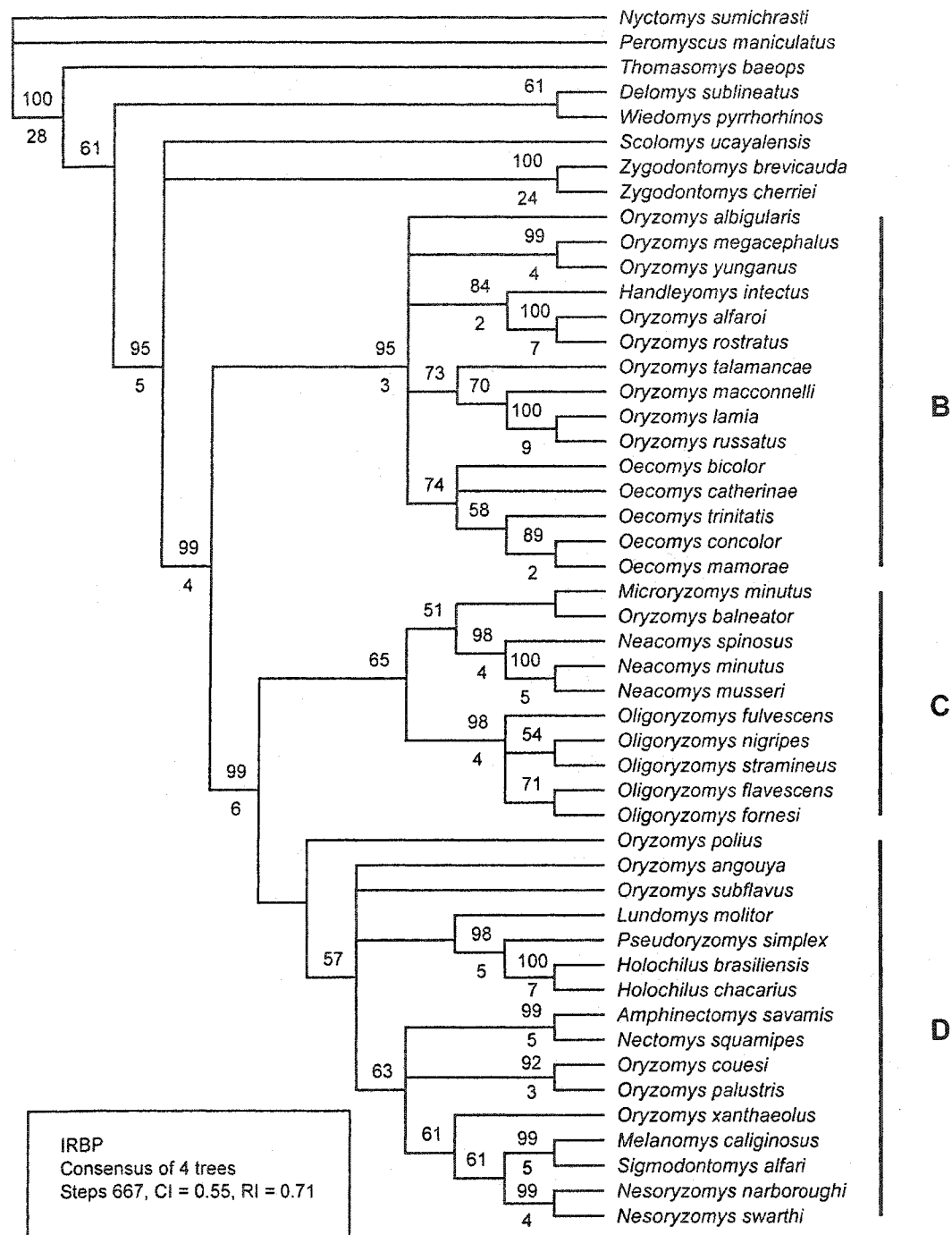


Figure 36. Strict consensus of 4 minimum length trees resulting from parsimony analysis of IRBP sequences (parsimony-informative characters = 204, tree length = 667, CI = 0.55, RI = 0.71). Numbers above and below branches refer to jackknife resampling percentage (> 50%) and decay index (> 1), respectively. Letters B, C, and D define clades discussed in the text.

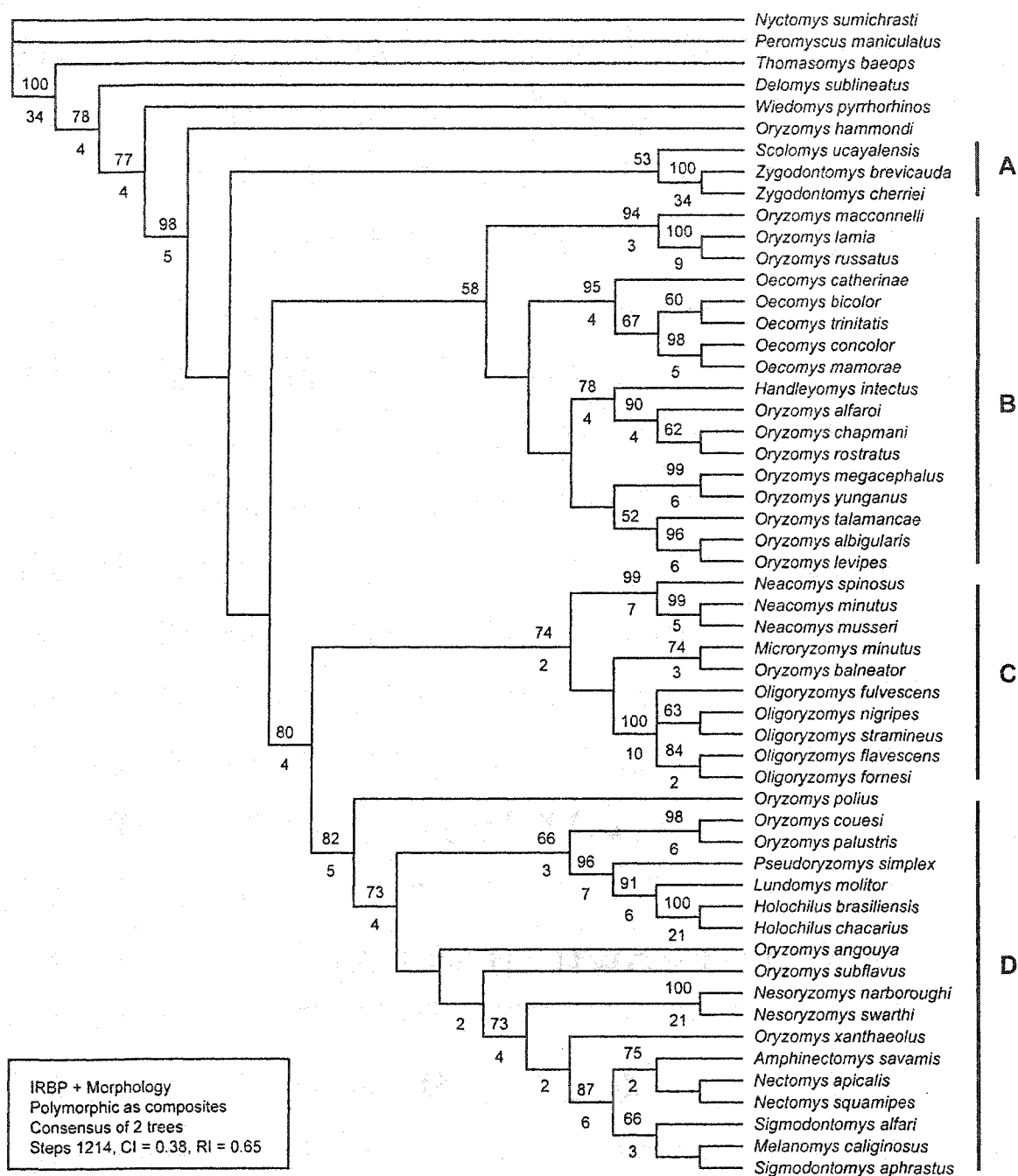


Figure 37. Strict consensus of 2 minimum length trees resulting from parsimony analysis of morphological and IRBP data (parsimony-informative characters = 295, tree length = 1214, CI = 0.38, RI = 0.65). Polymorphic data were treated as composite entries. Numbers above and below branches refer to jackknife resampling percentage (> 50%) and decay index (> 1), respectively. Letters A, B, C, and D define clades discussed in the text.

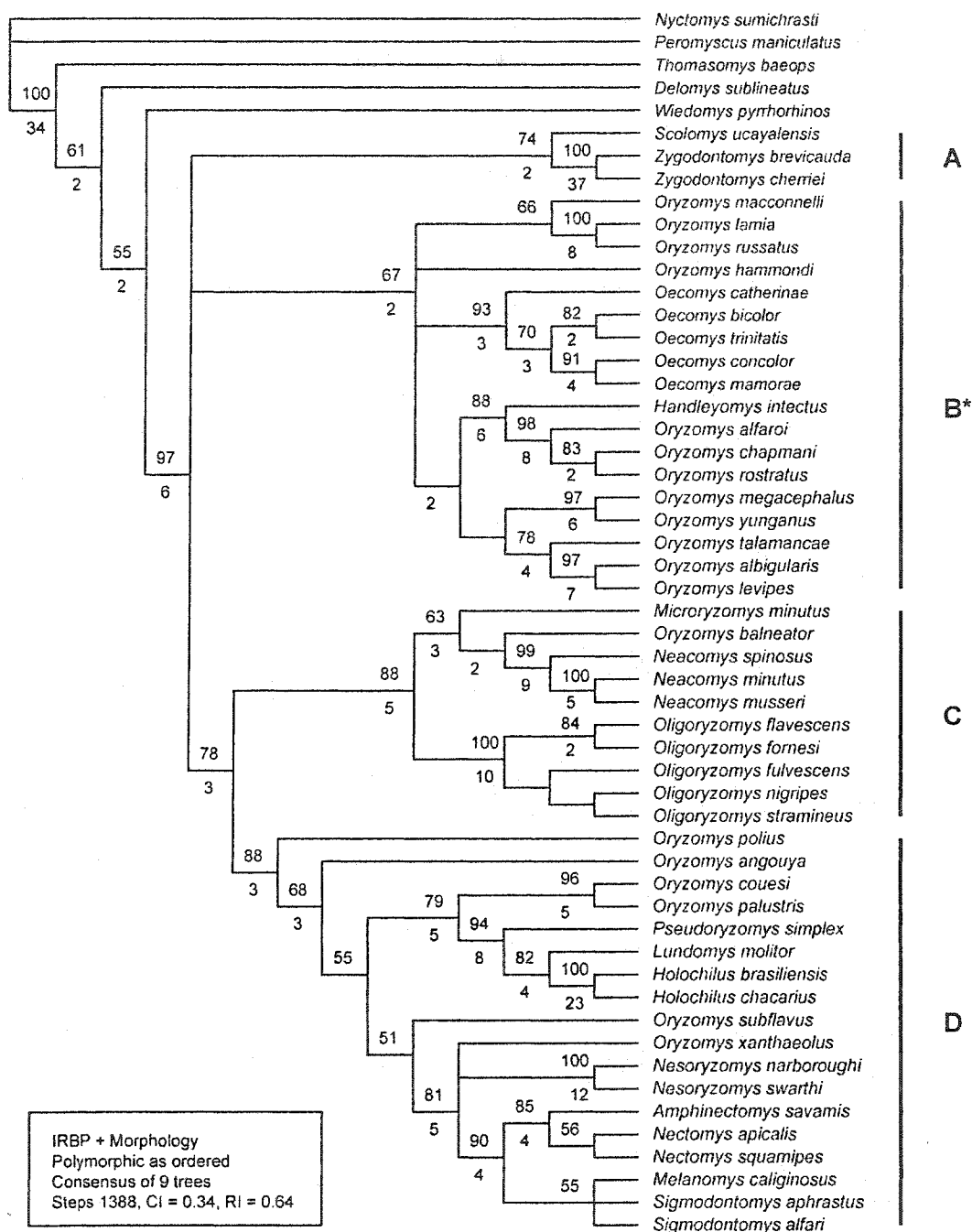


Figure 38. Strict consensus of 3 minimum length trees resulting from parsimony analysis of morphological and IRBP data (parsimony-informative characters = 295, tree length = 1384, CI = 0.34, RI = 0.64). Polymorphic data were treated as transformations series. Numbers above and below branches refer to jackknife resampling percentage (> 50%) and decay index (> 1), respectively. Letters A, B, C, and D define clades discussed in the text.

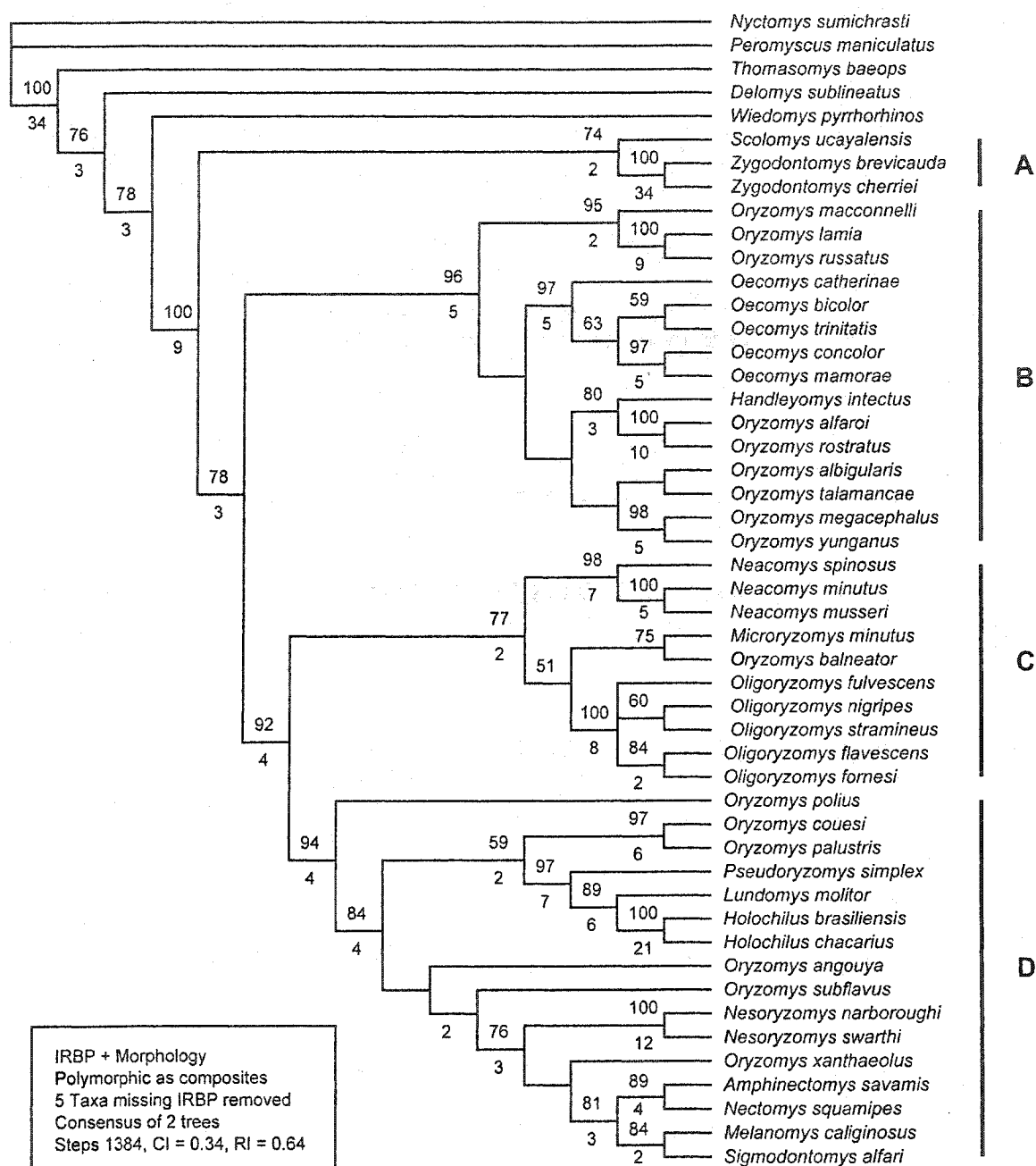


Figure 39. Strict consensus of 2 minimum length trees resulting from parsimony analysis of morphological and IRBP characters, excluding taxa without sequence data (parsimony-informative characters = 295, tree length = 1175, CI = 0.40, RI = 0.65). Polymorphic data were treated as composite entries. Numbers 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.

Major clades

Node 3 (Oryzomyini + Wiedomys)

77	55	78
53	46	

Node 4 (Oryzomyini)

98	97	100
47	44	95

Node 5 (Oryzomyini minus O. hammondi)

28		X
		X

Node 6 (Clade A)

53	74	74
17		

Node 8 (B + C + D)

49		78
		99

Node 9 (Clade B)

58	67 ^a	96
	<5 ^b	95

a. with O. hammondi
b. with O. hammondi and Amphinectomys

Node 25 (C + D)

80	78	92
		100

Node 26 (Clade C)

74	88	77
60	59	65

Node 34 (Clade D)

82	88	94
	<5*	41

* without Amphinectomys

combined CO	combined TS	reduced
morpho CO	morpho TS	IRBP

	node absent
	node present
X	not applicable (taxa lack IRBP)
	present in some fundamental cladograms

Figure 40. Changes in monophyly, resolution, and support for higher-level oryzomyine taxa in the different analyses. Each square corresponds to one of the six analyses described in the text (see legend in lower left corner). White squares indicate that the taxon was monophyletic in all most parsimonious trees for a particular analysis, squares with hatching indicate monophyly in some but not all most-parsimonious trees), and black squares indicate polyphyly or paraphyly in all most-parsimonious trees. Squares with an X indicate that the clade could not be recovered in the IRBP-only or reduced analysis because lack of sequence data. The value within each box indicates the jackknife percentage.

Clade BNode 12 (Clade B minus nitidus group)

7	<5*	9

* with O. hammondi

Node 17

12	<5 ^a	9

a. with O. hammondib. with O. hammondi and AmphinectomysNode 18 (Handleomys + alfaroi + chapmani + rostratus)

78	88	80
		84

Node 19 (alfaroi + chapmani + rostratus)

90	98	100*
44	58	100*

* chapmani was not included because it lacks IRBP sequencesNode 21 (albigularis + talamacae + megacephalus)

20	23	15

Clade CNode 29 (O. balneator + Microryzomys + Oligoryzomys)

49		51
61		

Node 30 (O. balneator + Microryzomys)

74		75
70		48

Clade DNode 35 (Clade D minus O. polius)

73	68	84
	12	57

Node 36 (Tetralophodont + palustris group)

66	79	59
46	70	

Node 38 (Tetralophodont)

96	94	97
79	90	44

Node 39 (Lundomys + Holochilus)

91	82	89
99	99	

Node 41

18		17

Node 42

31	51	40
	<5*	

* without Amphinectomys**Figure 40. (Continued)**

Clade D (continued)

Node 43

73	81	76
15	8*	

* without Amphinectomys

Node 45

47		41
22	<5*	

* without AmphinectomysNode 46 (Amphinectomys +
Nectomys + Melanomys +
Sigmodontomys)

87	90	81
36	51*	

* without AmphinectomysNode 47 (Amphinectomys +
Nectomys)

75	85	89
		99

Node 49 (Sigmodontomys +
Melanomys)

66	55	84
		44

GeneraNode 7 (Zygodontomys)

100	100	100
100	100	100

Node 13 (Oecomys)

95	93	97
83	67	74

Node 27 (Neacomys)

99	99	98
73	64	96

Node 31 (Oligoryzomys)

100	100	100
98	97	98

Node 40 (Holochilus)

100	100	100
100	100	100

Node 44 (Nesoryzomys)

100	100	100
98	100	99

Node 48 (Nectomys)

49	56	X
64		X

Figure 40. (Continued)

Oryzomys species groupsNode 10 (nitidus)

94	66	95
54		70

Node 22 (megacephalus +
yunganus)

99	96	98
		99

Node 23 (talamancae +
albigularis)

52	78	42

Node 24 (albigularis)

96	97	X
71	75	X

Node 37 (palustris)

98	97	97
77		92

**Miscellaneous clades not
recovered in the
combined analysis**talamancae + nitidus

		73

Micoryzomys + O.
balneator + Neacomys

	63	
		48

Oecomys + O. hammondi

		X
34		X

palustris + Nesoryzomys +
O. xanthaeolus +
Amphinectomys + Nectomys
+ Melanomys +
Sigmodontomys

		63

Figure 40. (Continued)

Figure 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 used for the 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).

2 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 100

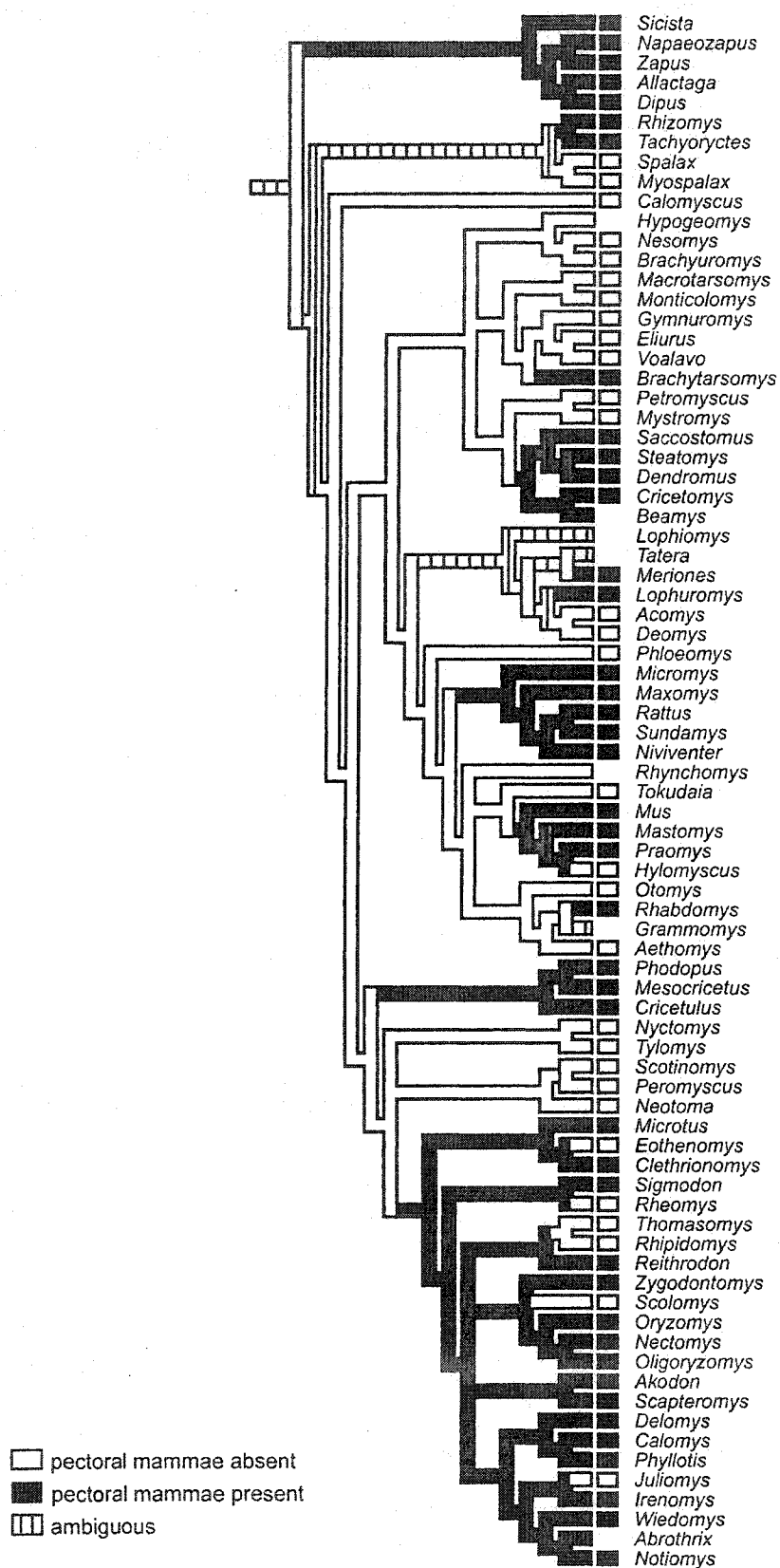


Figure 41.

Figure 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 over-dispersion of members of Oryzomys in the tribe. See text for further details.

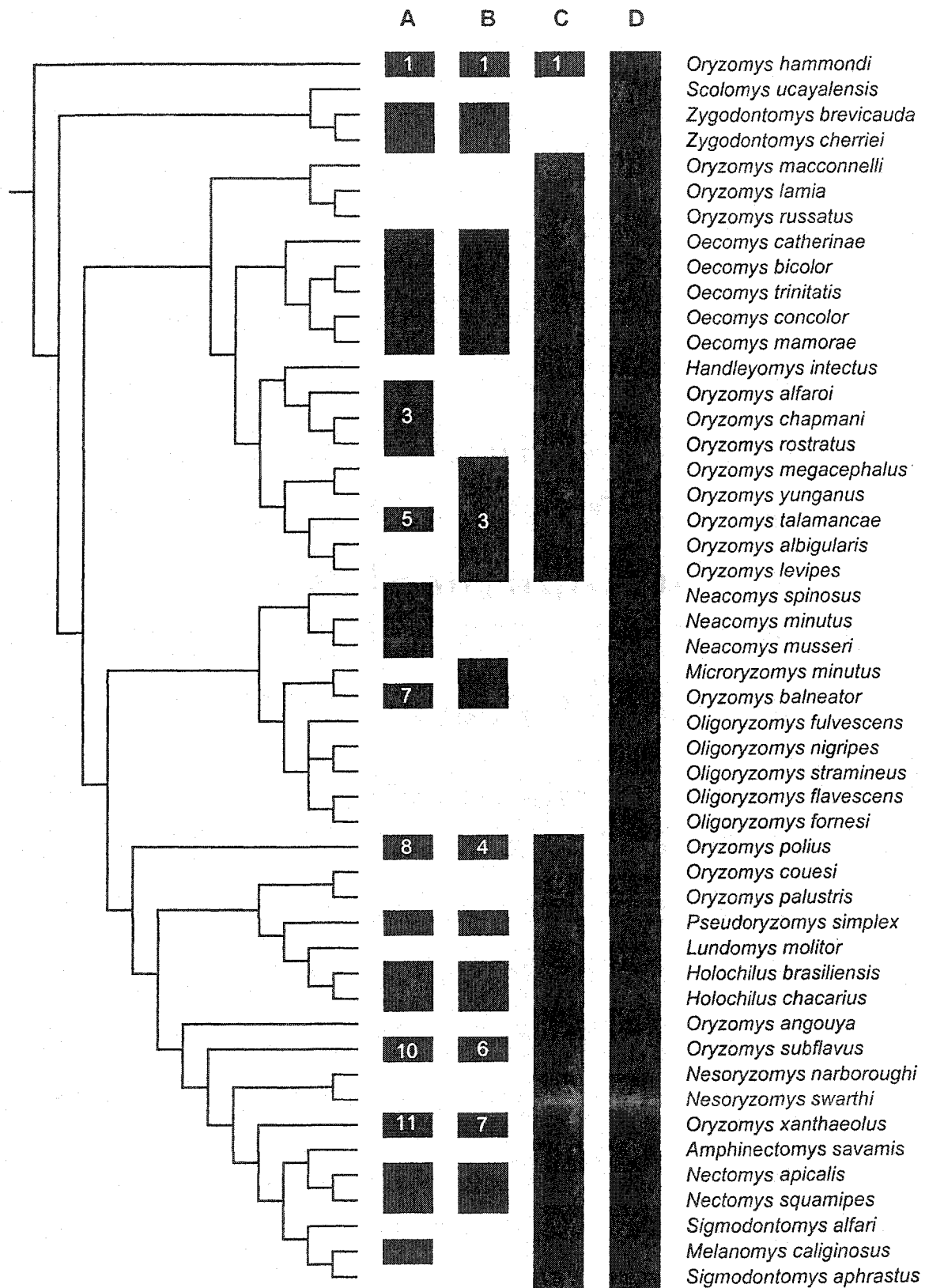


Figure 42.

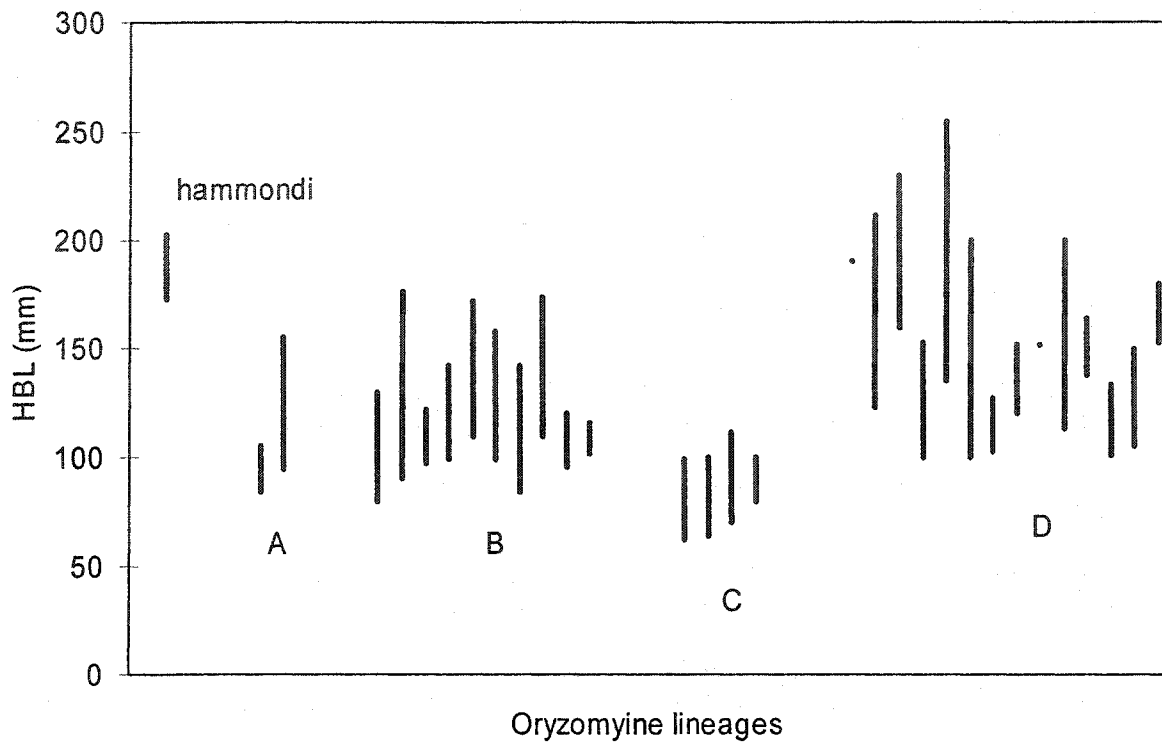


Figure 43. Chart illustrating the difference in size of oryzomyine lineages as measured by the head-and-body length (HBL). Sources of the measurements are found in table 9.

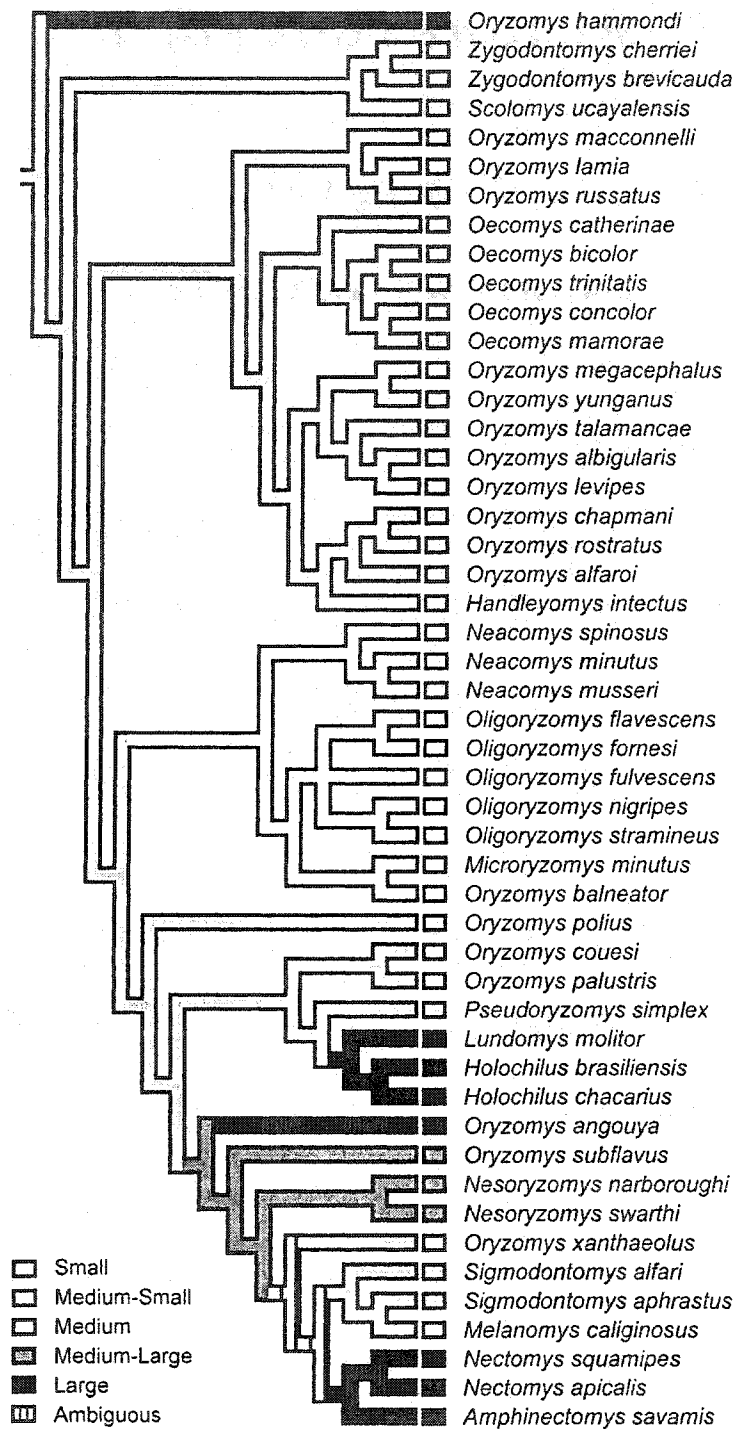


Figure 44. Evolution of size in oryzomyines inferred from the optimization of 5 size categories (see text) on the consensus tree of the combined analysis. The ambiguous optimization is due to differences in interpretation of the character under ACCTRAN or DELTRAN.

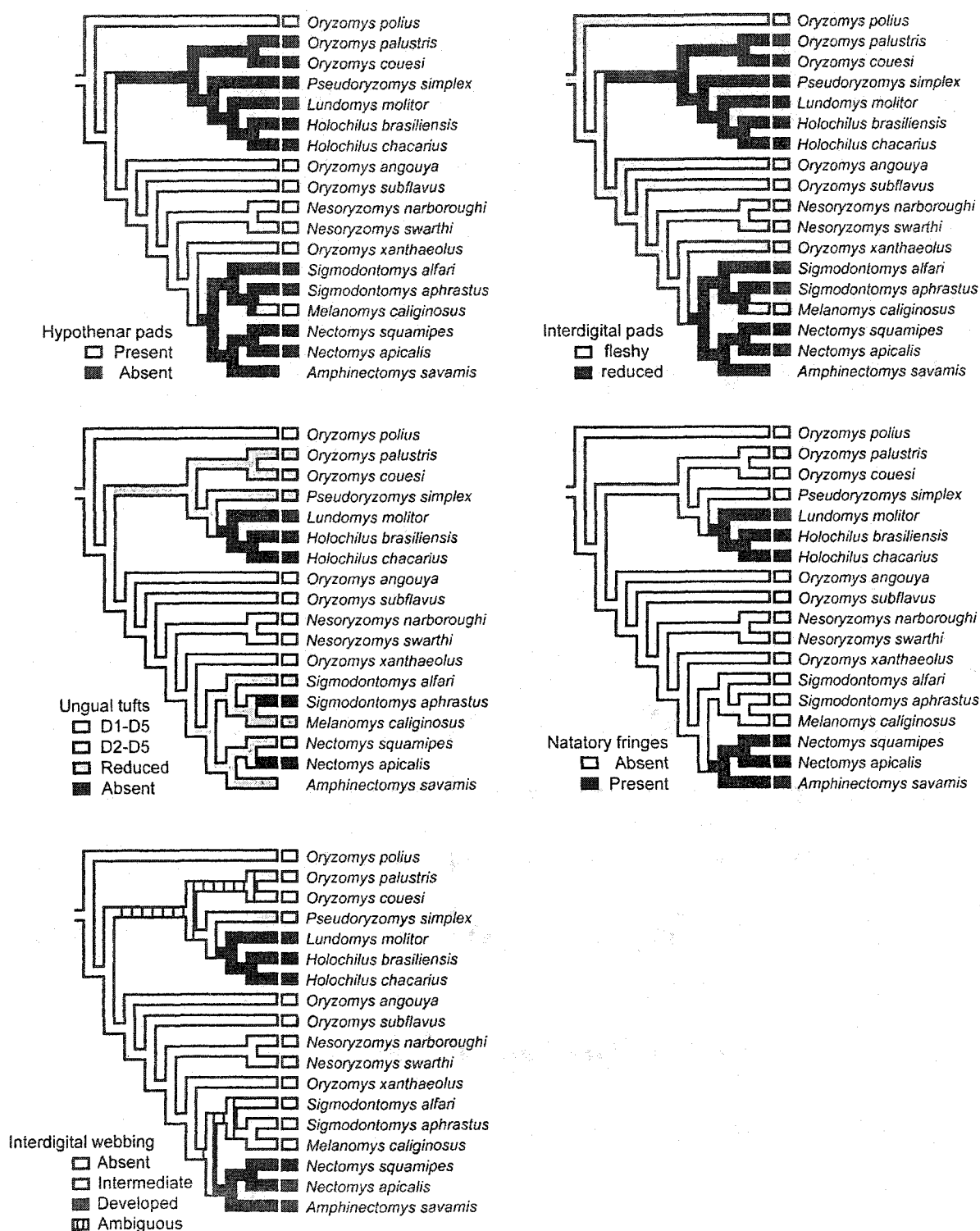


Figure 45. Evolution of 5 hindfoot characters related to riparian life style inferred from optimization of characters 4, 5, 7, 8, and 9 on the consensus tree from the combined analysis. The condition for *Amphinectomys* is unknown for the first 3 characters.

Ambiguous optimization is due to differences in interpretation of the character under ACCTTRAN or DELTRAN.

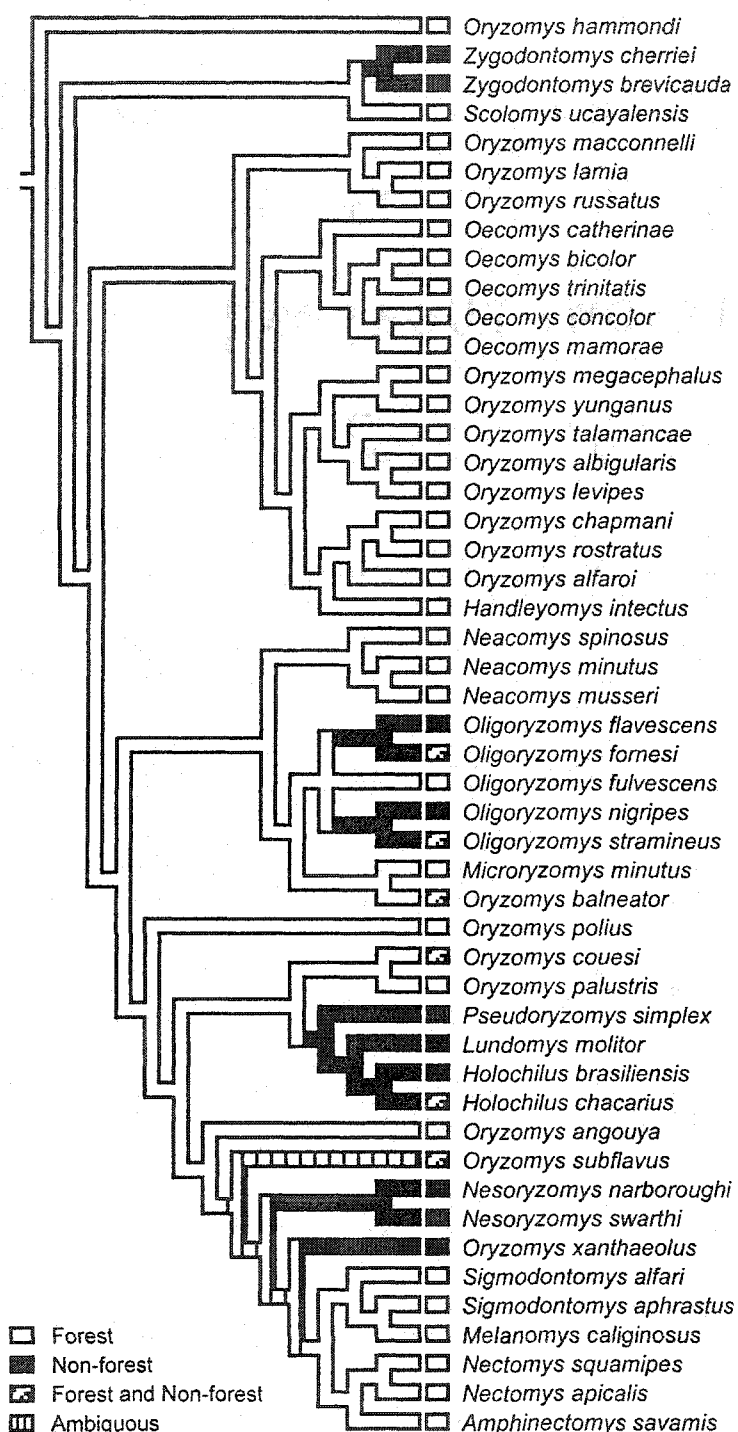


Figure 46. Evolution of oryzomyine habitat type inferred from the optimization of two environmental categories (see text) on the consensus tree of the combined analysis. The ambiguous optimization is due to differences in interpretation of the character under ACCTRAN or DELTRAN.

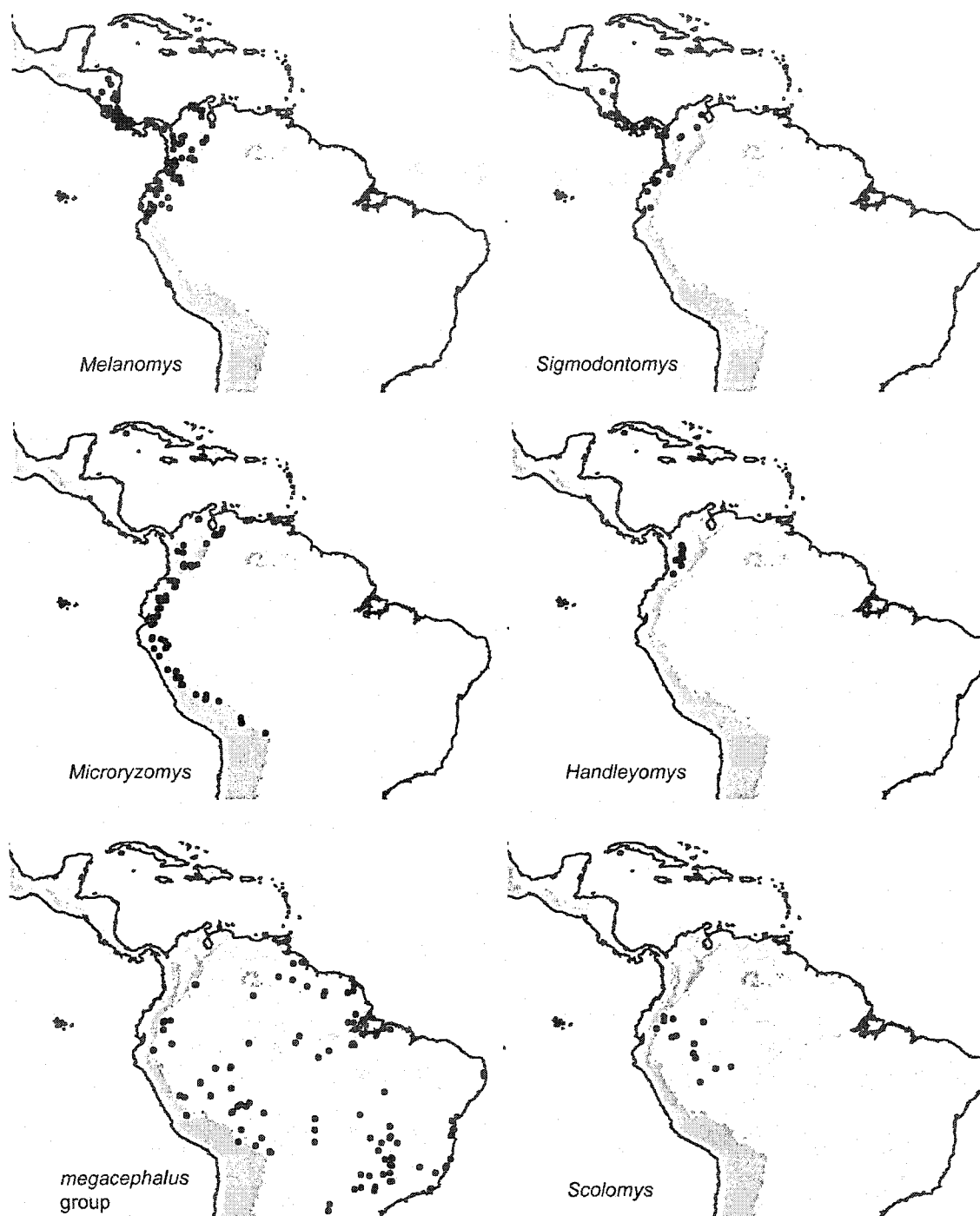


Figure 47. Examples of the three distribution categories defined in the text: trans-Andean (top), Andean (middle), and cis-Andean. Locality data are from: Allen (1913) and Weksler (in prep.) for Melanomys; Musser et al. (1998) for Sigmodontomys; Carleton and Musser (1989) for Microryzomys; Voss et al.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

(1998) and Weksler et al. (1999) for megacephalus group; Gómez-Laverde et al. (2004) for Scolomys.

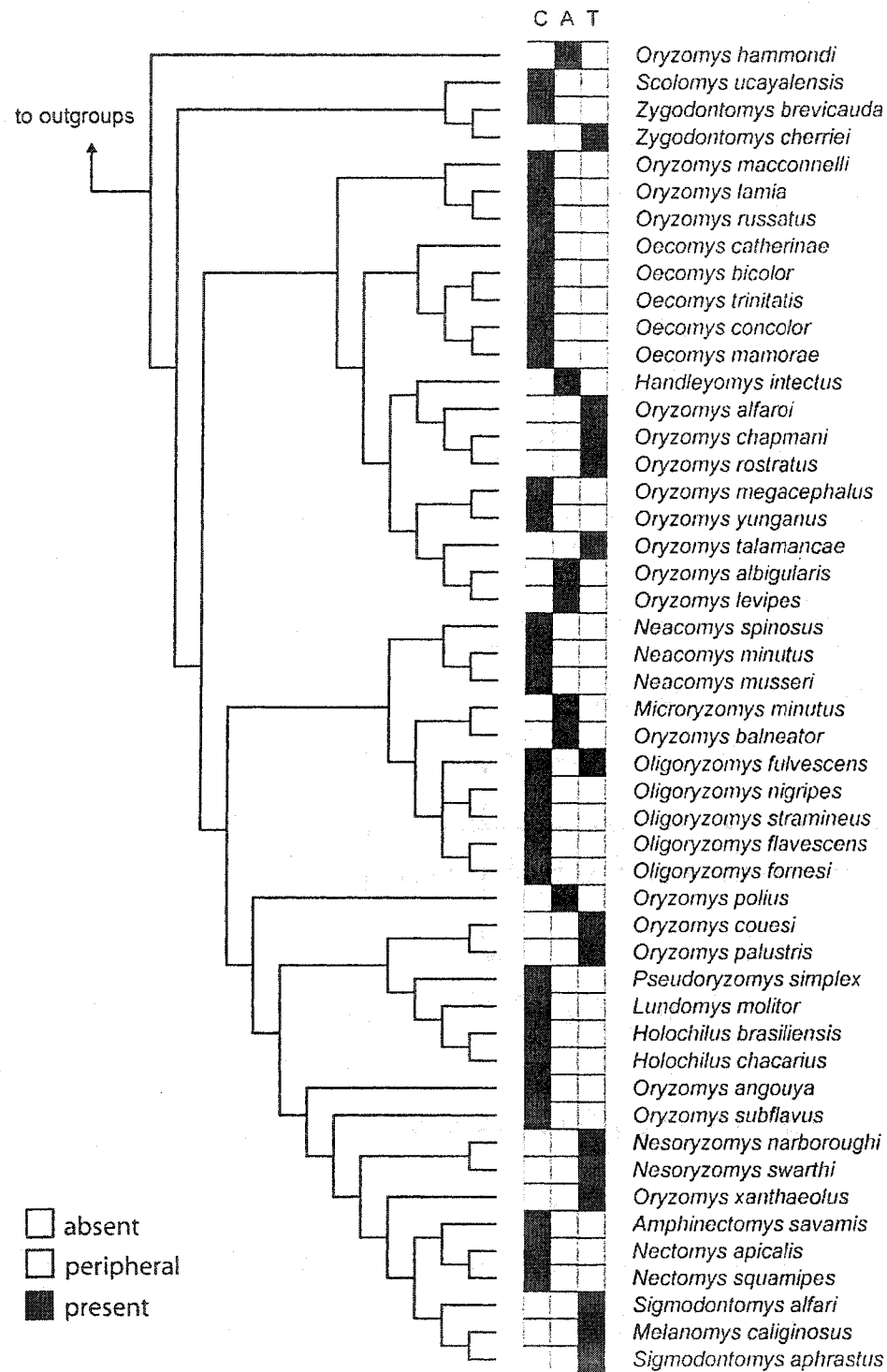


Figure 48. Interpretation of biogeographic history of oryzomyines inferred from the optimization of three geographic categories (see text) on the consensus tree from the combined analysis. The ambiguous optimization is due to differences in interpretation of the character under ACCTRAN or DELTRAN. Letters on the top of the figure refer to C, cis-Andean; A, Andean; and T, trans-Andean distribution.

APPENDIX 1. SYNOPSIS OF ORYZOMYINE GENERA

The first described oryzomyine species were Mus megacephalus Fischer, 1814 (= Oryzomys megacephalus), Mus angouya Fischer, 1814 (= Oryzomys angouya), and Mus nigripes Olfers, 1818 (= Oligoryzomys nigripes), based on the detailed description of the Paraguayan fauna by Azara (1801). Since then, 360 names have been erected for the 116 species currently recognized as oryzomyines (Tate, 1932a, b, c, d; Musser and Carleton, 1993; Patterson, 2000; Voss et al., 2001; Grelle, 2002; Langguth and Bonvicino, 2002; Bonvicino, 2003; Brooks et al., 2004). The 16 oryzomyine genera are presented below in chronological order of description, with a brief summary of their taxonomic history, distribution, species diversity, general biology, and an assessment of their monophyly.

Holochilus Brandt, 1835 (marsh rats)

Marsh rats are large (HBL = 160-230 mm) semiaquatic rats, usually found close to bodies of water such as marshes, swamps, and streams, and are distributed in South America, east of the Andes in Colombia, eastern Ecuador, eastern Perú, the Guianas, Brazil, Bolivia, Uruguay, Paraguay, and Northern Argentina (Hershkovitz, 1955; Voss and Carleton, 1993; Nowak, 1999). Three species are currently recognized (Musser and Carleton, 1993): H. brasiliensis, H. sciureus, and H. chacarius; nonetheless, the genus has not been recently revised and significant morphological and karyological variation suggest that more taxa might be incorporated within H. sciureus and H. brasiliensis (Weksler, in prep.).

Holochilus was the first described oryzomyine genus. Brandt (1835) erected Holochilus as a subgenus of Mus Linnaeus 1758, the period all-encompassing genus for muroid rodents. Subsequently, Holochilus was raised to generic level by Wagner (1842),

and Thomas (1884; 1896). Wagner (1842) observed the similarity, especially of the molar occlusal topology, between Holochilus and Sigmodon, an opinion latter firmly validated by Hershkovitz (1955). 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). Assumption of generic monophyly is unproblematic because all Holochilus species share a distinctive morphology, with several putative synapomorphies, vis-à-vis other oryzomyines (Voss and Carleton, 1993).

Oryzomys Baird, 1857 (rice rats)

Oryzomys includes small to large (HBL 85-200 mm) mice and rats that are ubiquitous in the neotropical region, occurring in a variety of habitats, such as forests, marshes, and grasslands. Oryzomys has the oddest geographical distribution of any sigmodontine genus, and arguably of any Neotropical mammalian genus: in addition to its wide distribution in the Neotropical region, from Northern Argentina to Mexico (second only to Oligoryzomys, another oryzomyine genus), it is only one of two sigmodontine genera that also occur in the Nearctic region, reaching southern New Jersey and Pennsylvania (Hall, 1981; Wolfe, 1982); and is also only one of two terrestrial mammals occurring in the Galapagos Islands (Dowler et al., 2000). In addition, Oryzomys species were present in historical times in several other islands, such as the Maria Madre Island (recently extirpated; Alvarez Castaneda and Mendez, 2003) and Jamaica (extirpated in the 19th century; Allen, 1942).

Baird (1857) erected Oryzomys as a subgenus of Hesperomys, and included only Hesperomys palustris Harlan, 1837. Oryzomys was raised to full generic status by Coues

(1890), and was the default genus for description of any South American cursorial and pentadactylodont species in late 19th, early 20th century. Oryzomys is currently the largest sigmodontine genus, with 44 recognized species (table 1), many of them described in the past decade (Musser et al., 1998; Weksler et al., 1999; Langguth and Bonvicino, 2002; Bonvicino, 2003; Brooks et al., 2004).

Several species groups are recognized within the genus (table 1). The first author to divide Oryzomys in such groups was Merriam (1901), who recognized 4 species groups of North and Central American Oryzomys: (1) palustris-mexicanus group (= palustris group); (2) chapmani group (including forms currently allocated in the chapmani and alfaroi groups); (3) melanotis group; and (4) fulvescens group (= Oligoryzomys). Several other groups were latter proposed, and most have been recognized as monophyletic groups in phylogenetic analysis (see references in table 1). In addition to such species groups, a few species remain without known relationships within the genus, referred here as unique lineages.

Nectomys Peters, 1861 (water rats)

Nectomys are large (HBL = 135-255 mm), semiaquatic rats, usually found close to streams in lowland forests and grasslands (Voss and Emmons, 1996; Emmons and Feer, 1997; Nowak, 1999). Five species are currently recognized (Musser and Carleton, 1993; Bonvicino et al., 1996; Patton et al., 2000; Voss et al., 2001): Nectomys apicalis, N. melanius, N. palmipes, N. rattus, N. squamipes. An ongoing review of the genus, however, recognizes three additional species: N. garleppii, N. grandis, and N. magdalenae, plus two undescribed species from western Amazonia (Bonvicino, in prep.). Nectomys is widespread in South America, occurring in the interandean valleys of the

Magdalena and Cauca rivers, throughout Amazonia in Peru, Bolivia, Colombia, Venezuela, Brazil, Ecuador, the Guianas, southwards to NE Argentina, Paraguay, Uruguay, and SE Brazil, from sea level to ca. 2,000 m. Nectomys is also present in the Island of Trinidad and in the coastal islands of Southeastern Brazil (Hershkovitz, 1944; Musser and Carleton, 1993; Bonvicino, 1994).

Peters (1861) erected the genus Nectomys based on Mus squamipes Brants, 1827. He observed similarity between Nectomys and Holochilus in the morphology of hind foot (intradigital webbing) and tail (degree of squamation), as well as in molar proportions and folding pattern. Nevertheless, Peters (1861) erected the new genus because Nectomys had separated lips, opposed to the supposedly (erroneously) fused lips of Holochilus. Potamys Liais, 1872 is a junior synonym. Thomas (1896) included Nectomys in Holochilus based on external characters, but reversed his opinion a year later (Thomas, 1897). Assumption of generic monophyly for the genus is unproblematic because all Nectomys species share singular 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).

Zygodontomys Allen, 1897 (cane rats)

Zygodontomys are medium (HBL = 95-155 mm) cursorial rats found in nonforest habitats in Central America and South America north of the Amazon from southeastern Costa Rica, Panama, Colombia, Venezuela, Suriname, French Guiana, Guyana, and northern Brazil, and are also found in continental-shelf islands in Panama, Trinidad and Tobago and Venezuela (Voss, 1991). The last revision of the genus (Voss, 1991)

recognized two species, Zygodontomys brunneus and Z. brevicauda, the latter with 3 subspecies. Variation in karyotype (Mattevi et al., 2002; Bonvicino et al., 2003) and morphology (Voss, 1991), however, suggest that the subspecies might deserve full species status (Z. cherriei, Z. brevicauda, and Z. microtinus).

Allen (1897) described the genus Zygodontomys based on Oryzomys cherriei Allen, 1895. Allen (1897: 38) considered Zygodontomys and Oryzomys similar in terms of cranial characters, but the striking differences in external aspect - which resembled Sigmodon - and molar topography between the two taxa were considered sufficient to describe Zygodontomys as a new genus. Species of Zygodontomys share several putative apomorphic characters (Voss, 1991) and have similar, distinctive karyotypes (Mattevi et al., 2002; Bonvicino et al., 2003). Thus, assumption of monophyly for the genus is unproblematic, and partial corroboration for that comes from phylogenetic analysis of cytochrome *b* sequences (Bonvicino et al., 2003).

Sigmodontomys Allen, 1897 (rice water rats)

Sigmodontomys are medium-large (HBL = 115-150 mm) rats with subtly developed semiaquatic adaptations (Hershkovitz, 1944; Handley, 1976; Nowak, 1999) distributed over trans-Andean lowland and lower montane forest, as well as Coastal Venezuelan forests, in Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela and Ecuador (Hall, 1981; McPherson, 1985; Musser and Carleton, 1993; Voss and Emmons, 1996). Two species are currently recognized for the genus (Musser and Carleton, 1993), Sigmodontomys alfari and S. aphrastus, but evidence for generic monophyly of Sigmodontomys is tenuous, if not non-existent, as no character-based study was used to place S. aphrastus and S. alfari in the same genus.

Allen (1897) provided a detailed description of Sigmodontomys and compared it with Sigmodon and Oryzomys, but the only statement about Sigmodontomys relationships was that "...the enamel pattern of the molars is somewhat intermediate between that of Sigmodon and Oryzomys..." (Allen, 1897: 38-39). Sigmodontomys was placed as a subgenus of Nectomys by Goldman (1913) and was followed by subsequent authors (Gyldenstolpe, 1932; Tate, 1932c; Ellerman, 1941; Cabrera, 1961; see table 2). Gardner and Patton (1976) suggested that Sigmodontomys was closer to Oryzomys than to Nectomys, and transferred it to the former genus. Musser and Carleton (1993) cautiously raised it again to generic level, noting "...the need to refine [Sigmodontomys] relationships to Oryzomys proper." (Musser and Carleton, 1993: 748).

Neacomys Thomas, 1900 (bristly mice)

Neacomys are very small (HBL = 64-100 mm) cursorial mice with spiny pelage, found throughout the Amazon basin in Brazil, Colombia, Perú, Ecuador, Bolivia, Venezuela, Guyana, Surinam, and French Guiana and West of the Andes from Easternmost Panama to Ecuador and Venezuela, where they occur in lowland, premontane, and lower montane rainforest below about 1500 m elevation (Emmons and Feer, 1997; Nowak, 1999). Eight species are currently recognized for the genus (Musser and Carleton, 1993; Patton et al., 2000; Voss et al., 2001): Neacomys dubosti, N. guianae, N. minutus, N. musseri, N. paracou, N. pictus, N. spinosus, and N. tenuipes.

Thomas (1900) described Neacomys based on Hesperomys spinosus Thomas, 1882. The author cited the lack of intermediaries between soft-furred species of Oryzomys and the 'Acomys-like' Hesperomys spinosus as justification for the erection of the genus. In his lackluster description, Thomas provided general characters - "...skull is

low and broad ... interparietal of medium size ...bullae small ...[molars proportionally] small..." - or characters also shared with some species of Oryzomys - "...supraorbital edges distinctly but not excessively beaded ...palatal foramina unusually short..."

(Thomas, 1900: 153). Thomas clearly considered Neacomys as a close ally to Oryzomys, especially because of the "...molars [with] typical Oryzomys structure..." (Thomas, 1900: 153). Assumption of generic monophyly is unproblematic because all Neacomys species share singular cranial and integumental characters, in particular the spiny investure (Patton et al., 2000; Voss et al., 2001). Reciprocal monophyly between Neacomys and Scolomys, the other oryzomyine spinous taxon, has been amply demonstrated (Patton and da Silva, 1995; Smith and Patton, 1999; Weksler, 2003).

Oligoryzomys Bangs, 1900 (pigmy rice rats)

Oligoryzomys are very small (HBL = 70-110 mm) cursorial mice, found in a wide range of habitats from northeastern Mexico to extreme southern Chile and Argentina, in forests, grasslands, and semi-arid environments, from sea level to around 3,500 m (Goldman, 1918; Hall, 1981; Carleton and Musser, 1989; Emmons and Feer, 1997; Nowak, 1999). O. victus is known from the Saint Vincent Island and Martinique in the Lesser Antilles (Lorvelec et al., 2001). Sixteen species are currently recognized for the genus (Musser and Carleton, 1993; Carleton and Musser, 1995; Bonvicino and Weksler, 1998): Oligoryzomys andinus, Ol. arenalis, Ol. chacoensis, Ol. delticola, Ol. destructor, Ol. flavescens, Ol. fornesi, Ol. fulvescens, Ol. griseolus, Ol. longicaudatus, Ol. magellanicus, Ol. microtis, Ol. nigripes, Ol. stramineus, Ol. vegetus, and Ol. victus (presumably extinct). Ongoing taxonomic studies of the genus, however, reveal that at least two karyotypic forms belong to unnamed taxa (Weksler and Bonvicino, in press).

Bangs (1900) erected Oligoryzomys as a subgenus of Oryzomys, and included on it the several species of “pigmy Oryzomys” (including O. dryas humilior, a junior synonym of Microryzomys minutus). He considered “...true that in important characters the group [i.e., Oligoryzomys] differs little from true Oryzomys, but the small size and very delicate built throughout, including the skull, distinguish its members from the large rat-like species, with heavy ridged skulls, of true Oryzomys” (Bangs, 1900: 94-95).

Oligoryzomys was variously considered a full genus, subgenus or synonym of Oryzomys (table 2), and its status as full genus was established only recently (Carleton and Musser, 1989; see below). Monophyly of Oligoryzomys is partially 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).

Melanomys Thomas, 1902 (dusky rice rats)

Melanomys are medium (HBL = 100-140 mm) vole-like rats, usually found in forested habitats with dense ground cover vegetation (Goodwin, 1946; Gardner, 1983; Nowak, 1999), and are distributed from Honduras southward throughout Nicaragua, Costa Rica, and Panama to northern South America, in Colombia, Ecuador, and Peru. (Allen, 1913; Goldman, 1918; Hall, 1981; Musser and Carleton, 1993). Three species are currently recognized (Musser and Carleton, 1993): Melanomys caliginosus, M. robustulus, and M. zunigae. The genus, however, has not been recently revised; Allen (1913), the last reviewer, described significant variation and recognized several subspecies within M. caliginosus.

Thomas (1902) erected Melanomys as a subgenus of Oryzomys. Although Allen (Allen 1913), raised it to full generic status, Melanomys was usually treated as subgenus

of Oryzomys (Goldman, 1918; Tate, 1932b; Ellerman, 1941; Hershkovitz, 1944; Cabrera, 1961; Hooper and Musser, 1964; Gardner and Patton, 1976; Honacki et al., 1982; see table 2). Musser and Carleton (1993) cautiously raised it again to generic level, noting that its relationship to Oryzomys "...deserves more rigorous, character-based, phylogenetic substantiation" (Musser and Carleton, 1993: 708). Assumption of generic monophyly is unproblematic because all Melanomys species share a distinctive morphology, with several putative synapomorphies, vis-à-vis other oryzomyines (Allen, 1913; Gardner and Patton, 1976).

Nesoryzomys Heller, 1904 (galapagos rice rats)

Nesoryzomys are medium (HBL = 100-200 mm) rats endemic to the Galapagos Islands (Patton and Myers, 1983; Novak, 1999; Dowler, 2003). Five species are currently recognized (Dowler et al., 2000): Nesoryzomys darwini, N. fernandinae (extinct during the Holocene), N. indefessus, N. swarthi, and N. narboroughi (sometimes considered as subspecies of N. indefessus, e.g., Novak, 1999).

Heller (1904) described the genus Nesoryzomys based on N. narboroughi Heller, 1904. Heller (1904: 241) considered Nesoryzomys to be similar to Oryzomys, but with several striking cranial differences. Ellerman (1941) followed the suggestion of Goldman (1918) and placed Nesoryzomys as a subgenus of Oryzomys, but morphological, chromosomal and allozymic evidence convincingly support the distinctiveness between Nesoryzomys and other Oryzomys groups (Beaufort, 1963; Niethammer, 1964; Gardner and Patton, 1976; Patton and Hafner, 1983). Although information for these character systems is from a single Nesoryzomys species, N. narboroughi, all species of the genus have similar external and craniodental morphology. Evidence for Nesoryzomys

monophyly comes from phenetic analysis of such characters (Patton and Hafner, 1983), and was partially corroborated with cladistic analysis of molecular data (Weksler, 2003).

Oecomys Thomas, 1906 (arboreal rice rats)

Oecomys are small to medium (HBL = 71-176 mm) rats with several arboreal specializations, usually found in forested habitats (Hershkovitz, 1960; Emmons and Feer, 1997; Nowak, 1999). Oecomys are distributed from easternmost Costa southward throughout Panama, Colombia, Ecuador, Peru, Venezuela, Guianas, Bolivia, Brazil and Paraguay. Fifteen species are currently recognized (Musser and Carleton, 1993):

Oecomys auyentepui, Oe. bicolor, Oe. catherinae, Oe. cleberi, Oe. concolor, Oe. flavicans, Oe. mamorae, Oe. paricola, Oe. phaeotis, Oe. rex, Oe. roberti, Oe. rutilus, Oe. speciosus, Oe. superans, Oe. trinitatis. The genus, however, has not been recently revised. Partial corroboration for generic monophyly is provided by phylogenetic analyses of cytochrome *b* (Patton and da Silva, 1995; Andrade and Bonvicino, 2003) and IRBP (Weksler, 2003) sequences.

Thomas (1906) erected Oecomys as a subgenus of Oryzomys to include several arboreal forms previously included in Rhipidomys with the palate morphology and mammae formula similar to Oryzomys. Thomas (1909) raised it to full generic status and was followed by some authors (e.g., Gyldenstolpe, 1932; Tate, 1932d). Nevertheless, Goldman (1918), Ellerman (1941) and Hershkovitz (1960) again placed it as subgenus of Oryzomys, and were followed by subsequent checklists (table 2). Gardner and Patton (1976) provided karyotypic evidence for the distinctiveness of Oecomys from other oryzomyine groups, and Musser and Carleton (1993) recognized it as a full genus, but

caution for the lack of "...convincing substantiation from phylogenetic perspective". (Musser and Carleton, 1993: 715).

Microryzomys Thomas, 1917 (diminutive rice rats)

Microryzomys are very small (HBL = 60-100 mm), cursorial mice, found in intermediate to high elevations habitats, such as montane forest and Paramos, over the Andes in West-Central Bolivia, Perú, Ecuador, Colombia (including the Sierra Nevada de Santa Marta) and Venezuela (including the Caribbean Coastal Ranges), usually between 2,000 to 4,000 meters (Carleton and Musser, 1989). Two species are currently recognized (Carleton and Musser, 1989): Microryzomys minutus and M. altissimus.

Microryzomys was described as a subgenus of Oryzomys by Thomas (1917b), as remained as such (table 2) until Carleton and Musser (1989) provided a set of characters that substantiate it as a genus apart from Oryzomys. Thallomyscus Thomas, 1926 is a junior synonym. Assumption of generic monophyly is unproblematic because the two Microryzomys species share the same suite of singular cranial and integumental characters.

Scolomys Anthony, 1924 (spiny mice)

Spiny mice are small (HBL = 85-105 mm), cursorial mice, found in lowland forests of western Amazon in northern Peru, southern Peru, western Brazil, and Ecuador (Gómez-Laverde et al., 2004). The last revision of the genus (Gómez-Laverde et al., 2004) recognized two species, Scolomys ucayalensis and S. melanops.

Anthony (1924) described the genus Scolomys based on Scolomys melanops Anthony, 1924. Anthony (1924: 3) considered Scolomys and Neacomys similar in terms of external characters, but the striking differences in cranial traits between the two taxa

were considered sufficient to describe Scolomys as a new genus. Monophyly of the genus has been demonstrated by morphological and molecular data (Patton and da Silva, 1995; Gómez-Laverde et al., 2004).

Pseudoryzomys Hershkovitz, 1962 (false rice rats)

Pseudoryzomys are medium-sized (HBL = 100-130 mm) rats found in open vegetation environments of Central South America, in Northernmost Argentina, Central and Northeastern Brazil, Paraguay, and Bolivia (Voss and Myers, 1991). Pseudoryzomys simplex is the only recognized species of the genus (Voss and Myers, 1991).

Hershkovitz (1959) erected Pseudoryzomys based on Oryzomys wavrini (= Pseudoryzomys simplex), but his description did not comply with the International code of Zoological Nomenclature rules (Pine and Wetzel, 1975). The genus was properly described in Hershkovitz's (1962) revision of phyllotine rodents. Although its position among sigmodontine tribes has been long debated (e.g., Hershkovitz, 1962; Olds and Anderson, 1989; Braun, 1993), Pseudoryzomys displays the suite of synapomorphies that define the oryzomyines sensu Voss and Carleton (1993).

Lundomys Voss and Carleton, 1993 (Lund's marsh rats)

Voss and Carleton (1993) described the genus Lundomys based in part on a former species of Holochilus (H. magnus Hershkovitz 1955) and on a supposedly fossil species (Hesperomys molitor Winge, 1887). Lundomys are large (HBL = 160-230 mm), semiaquatic rats, found close to bodies of water such as swamps and streams in Uruguay and Southern Brazil (Hershkovitz, 1955; Voss and Carleton, 1993; Novak, 1999).

Lundomys molitor is the only recognized species of the genus (Voss and Carleton, 1993).

Amphinectomys Malygin, Aniskin, Isaev, and Milishnikov, 1994 (peruvian water rats)

Malygin et al. (1994) described the genus Amphinectomys. Based on morphological and karyological characters, and in ecological features, the authors proposed Amphinectomys to be allied to Sigmodontomys and, especially, Nectomys. Amphinectomys (Peruvian water rats) are large (HBL = 190 mm), semiaquatic rats, found close to streams in lowland forests and is known from only two localities in eastern Peruvian Amazonia (Malygin et al., 1994; Valqui and Weksler, in prep.). Amphinectomys savamis is the single described species of the genus (Malygin et al., 1994).

Handleyomys Voss, Gómez-Laverde, and Pacheco, 2002 (Handley's rice rats)

Handleyomys are small (HBL = 80-130 mm) rats endemic to the Cloud Forests of the Occidental and Central Cordilleras (northern Andes) in Colombia (Voss et al., 2002). The two species of Handleyomys, H. fuscatus and H. intectus, display most of the putative synapomorphies of the Oryzomyini (Voss et al., 2002), and recent analyses corroborate its inclusion in the tribe (Pacheco, 2003; Weksler, 2003).

Voss et al. (2002) showed several synapomorphic characters that clearly place Handleyomys within the tribe Oryzomyini, but the authors could not find any oryzomyine taxa with phylogenetic affinities to Handleyomys. The two species share a unique and distinctive combination of morphological characters within the sigmodontines (Voss et al., 2002), and thus the assumption of generic monophyly is unproblematic.

APPENDIX 2. EXAMINED SPECIMENS

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); 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 Berkeley; UMMZ - Museum of Zoology, University of Michigan, Ann Arbor; USNM - National Museum of Natural History, Smithsonian Institution, Washington D.C.).

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, Thorval 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 bacops

Skin and skull: ECUADOR: El Oro, Taraguacocha (47629, 47632, 47633, 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, Princesa 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); Tacuarembó, 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: Manabí, Cuaque (66331, 66333, 66334, 66338, 66339, 66340); Pichincha, Guala (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, 61857, 61858); 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 [ski 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, Tauraraté (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 484124-25) 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 317724-27); 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, Santanópolis (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:** COLOMBIA: Meta, Macarena (142161, 142164, 142167); **ECUADOR:** El Oro, El Chiral (46486-8, 46491, 46498).

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, 47586, 47587-9, 47597-3, 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 Mistepéc (190292, 190294, 190296-7, 190299, 190300, 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, 134664-5, 134667, 134772, 134677, 134763).

Oryzomys levipes

Skin and skull: BOLIVIA: La Paz, Nequejahuiria (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: BOLIVIA: Beni, Boca del Rio Baures (209948, 209950-3, 209958, 210016-8); VENEZUELA: Bolivar, 5.2 km NE San Ignacio de Yuruani (257230-3). **Fluid:** BOLIVIA: Beni, Rio Itenez (209965, 209978); Santa Cruz, Rio Saguayo (262084-6). **Roots:** PERU: Pasco, Rio Nevati (213497, 213509, 239964, 239966, 239979, 239982)

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 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 and 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 russatus

Skin and skull: BRAZIL: Minas Geraes, Fazenda Cardozo (61835, 61837); São Paulo, Casa Grande (USNM 485001-11). **Skeleton:** BRAZIL: Minas Geraes, 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), Vines

(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: Llampá (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, 37909,

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 and 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 3. SUMMARY OF CHARACTERS

The characters listed below were employed in previous phylogenetic analyses involving sigmodontines, regardless of the taxonomic level they were aimed. Some characters included in taxonomic studies within oryzomyines are also listed. Most characters were assessed in the present taxon set; some characters are marked as not observed because I did not have access to the description in time, or because material was not available. I organize the characters in terms of general morphological system (external morphology, skull and mandible, dentition, post-cranial skeleton, and bacular and soft anatomy characters). I subdivide each system into more specific classes (e.g., vibrissae, mammae, hind feet, etc.). This division is sometimes subjective, but serves as a guide when going through specimens. Numerals before the characters follow the order of this structure.

I include all previous studies in which the character was employed. I tried to maintain original descriptions, and I indicate when characters were modified (most of the 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 actually employed in the present study are marked with an asterisk (*) and referred by their numbers in the description (followed by #). Reasons for rejection of characters are indicated, and 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, non-replicable results,

autapomorphies for non-oryzomyines, characters not applicable in the present set of taxa, complete covariation with other character, and structure or states not identified. Several of these features are informative taxonomic characters, but they were unsuitable for the coding of 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: characters 1, 2 and 4; Pacheco, 2003: character 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: character 6). Rejected: invariant (present).

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

1.1.4. Genal 2 vibrissae present (0); or absent (1). (Pacheco, 2003: characters 9S and 16T). Not observed. I could not determine with confidence the character-state for the majority of taxa because absence may be due to poor condition skin vouchers (see Pacheco, 2003). Apparently, it is only present 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: character 10S). Rejected: invariant (long).

1.1.6. Calcaneal vibrissae present (0); or absent (1). (Pacheco, 2003: character 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: character 79; Voss, 1993: 24; Voss and Carleton, 1993: character 5; Steppan, 1995¹⁰: character 35S; Luna, 2002: character 23; Voss et al., 2002: 18; Pacheco, 2003: characters 12S to 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: character 85P; Pacheco, 2003: characters 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: character 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: characters 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

¹⁰ Steppan (1993) presents an almost identical character set to Steppan (1995) and 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).

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: character 1T). Included: #3.

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

1.3.5. 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: characters 4S and 7T; Luna, 2002: character 5). Included: #4. This and the following character (1.4.2.) have also been treated as a single multistate character (Carleton, 1980: character 77; Carleton and Musser, 1989: character 2; Voss and Carleton, 1993: character 3; Braun, 1993: character 2 [part]; Carleton and Olson, 1999: character 38). See page XX.

***1.4.2. Plantar pads on hind feet 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).** 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: character

87P; see also Luna, 2002: characters 7 and 8; Pacheco, 2003: characters 8T, 9T, and 10T). Rejected: continuous trait.

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

Rejected: invariant (present).

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

***1.4.6. Ungual tufts present on all claws of hind foot as an 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: character 15; Carleton and Musser, 1989: character 4; Voss, 1993: 24; Voss and Carleton, 1993: character 1; Musser et al., 1998: 320; Carleton and Olson, 1999: character 36; Voss et al., 2002: 18; Pacheco, 2003: character 3S and 4T [part]). Included: #7.

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

***1.4.8. Interdigital webbing on hind feet 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: character 19; Carleton and Musser, 1989: character 3; Braun, 1993: character 4;

Voss and Carleton, 1993: character 4; Carleton and Olson, 1999: character 39; Luna, 2002: character 9; Pacheco, 2003: characters 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: character 78; Braun, 1993: character 1; see also Patton and Hafner, 1983: character 18; Steppan, 1995: characters 33S and 88P; Luna, 2002: character 15; Pacheco, 2003: character 5S). Rejected: autapomorphy for Peromyscus (Carleton's coding).

*1.4.10. Dorsal surface of hind feet 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. Hind foot short and broad (0); or long and narrow (1); or long and broad (2). (Patton and Hafner, 1983: character 16). Rejected: ambiguous characterization.

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

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

1.4.14. Nail on hallux absent (0); or present (1). (Luna, 2002: character 12; Pacheco, 2003: character 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: character 17; see

also Voss, 1988: character 14 [part]; Pacheco, 2003: characters 103S and 13T). Rejected: continuous trait. Note : Steppan (1995: character 86P) characterizes the length of d1 relative to d5; Carleton and Olson (1999: character 40) joins 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: character 1; see also Voss, 1988: character 14 [part]; Luna, 2002: character 10; Pacheco, 2003: characters 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: character 20; Musser and Williams, 1985: 19; Voss, 1988: character 3; Steppan, 1995: character 89P; Musser et al., 1998: 320; Luna, 2002: character 16; Pacheco, 2003: characters 25T). Included: #11.

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

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

1.5.4. Tail pencil absent (0); or present (1). (Braun, 1993: character 3; Luna, 2002: character 19; Pacheco, 2003: characters 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: character 4; Braun, 1993: character 5; Luna, 2002: character 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 1/3 of the tail white (2). (Pacheco, 2003: character 26T). Rejected: if 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: character 23; Luna, 2002: character 21; Pacheco, 2003: character 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: character 2; Stepan, 1995: character 91P; Luna, 2002: character 20; Pacheco, 2003: character 20T). Included: #15.

1.6.4. Nose non-reddish (0); or nose reddish and sharply contrasting with rest of head (1). (Pacheco, 2003: characters 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: character 92P; see also Pacheco, 2003: character 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: character 1). Rejected: not applicable.

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

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

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

1.7. Pinnae

1.7.1. Antitragus and pinnae broad (0); or narrow to moderate size (1). (Pacheco, 2003: character 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: character 5; see also Luna, 2002: character 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: character 13; Braun, 1993: character 6; Steppan, 1995: characters 34S). Rejected: metric character.

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

1.8. Integument Miscellaneous

1.8.1. Philtrum present (0); or absent (1). (Voss, 1988: character 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: character 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: characters 18S and 28T; Voss, 2003: 16-17; see also Steppan, 1995: character 37P; Luna, 2002: character 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: character 48P; Luna, 2002: character 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: character 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: character 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: characters 9S and 46P; see also Luna, 2002: characters 25 and 26; Pacheco, 2003: characters 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: characters 10S and 47P; see also Pacheco, 2003: characters 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: character 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. Lacrima bone scarcely evident dorsally (0); or lacrima bears a shelf projecting into preorbital region (1). (Carleton, 1980: character 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: character 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: character 24; Steadman and Ray, 1982: 10; Patton and Hafner, 1983: characters 13 and 14; Carleton and Musser, 1989: character 6; Olds and Anderson, 1989: character 26; Braun, 1993: characters 17, 18, and 19; Voss, 1993: 24; Voss and Carleton, 1993: character 7; Steppan, 1995: characters 11S, 49P, 50P, and 51P; Carleton and Olson, 1999: character 4; Luna, 2002: characters 28 and 29; Voss et al., 2002: 18; Pacheco, 2003: characters 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 lacrima (1). (Steppan, 1995: character 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: character 11). Rejected: invariant (foramina on lateral surface).

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

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

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

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

2.2.11. Interfrontal fontanella absent (0); or present (1). (Pacheco, 2003: character 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: character 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: characters 12S and 54P; see also

Braun, 1993: character 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: character 55P). Rejected: invariant (obtuse angle).

*2.3.4. Fronto-squamosal suture at same plane of the fronto-parietal suture lateral terminus, forming a continuous suture line; dorsal facet of frontal never in contact with squamosal (0); or fronto-squamosal suture anterior to fronto-parietal 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 dorsal-lateral edges 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: character 36; Pacheco, 2003; character 40S). Included: #25.

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

2.3.7. Ratio of interparietal/ parietal length less than 0.43 (0); or between 0.43-0.70 (1); or greater than 0.70 (2). (Steppan, 1995: character 13S and 56P; see also Braun,

1993: character 22; and Pacheco, 2003: character 39S). Rejected: metric character.

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

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

2.3.10. Lambdoidal crest square, occiput flat (0); or lambdoidal crest square, occiput rounded (1). (Patton and Hafner, 1983: character 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: character 1; see also Carleton, 1980: character 25; Olds and Anderson, 1989: characters 29 and 31; Braun, 1993: characters 27 and 28; Steppan, 1995: characters 8S and 43P; Patton and Hafner, 1983: characters 11 and 12; Carleton and Musser, 1989: character 5; Voss, 1993: 24; Voss and Carleton, 1993: character 6; Luna, 2002: characters 27, 40-42; Voss et al., 2002: 18; Pacheco, 2003: characters 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: character 2; Luna, 2002: character 32; Pacheco, 2003: characters 68S and 84T; see also Braun, 1993: character 24; Stepan, 1995: characters 6S and 42P). Included: #29.

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

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

2.4.5. Anterior bridge of root of zygomata lying well below dorsal surface of rostrum ($1/4 - 1/2$ 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 $< 1/4$ rostrum height) (1); or insertion high, close on dorsal surface of rostrum ($< 1/8$) or posterior surface of bridge joins at dorsal level of surface (2). (Stepan, 1995: characters 5S and 41P; see also Luna, 2002: character 31; Pacheco, 2003: character 39T). Rejected: non-replicable results. Also, continuous trait.

*2.4.6. Jugal present and large, maxillary and squamosal processes of the zygoma non 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: character 7; Carleton and Olson, 1999: character 3; Pacheco, 2003: characters 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: character 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: character 25; see also Pacheco, 2003: character 41T). Rejected: continuous trait.

2.4.9. Zygomatic arches parallel-sided (0); or slightly divergent posteriorly (1). (Luna, 2002: character 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: character 44). Rejected: ambiguous characterization.

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

2.4.12. Notch between maxillary zygomatic process and lacrimal bone absent (0); or present (1). (Pacheco, 2003: character 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 perpendicular (1). (Pacheco, 2003: character 40T). Rejected: continuous trait.

2.4.14. Zygomatic arch low, the ventral margin of arches reach orbital floor or lower (0); or arches high, ventral margin dip 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: character 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: character 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 ($\leq 90^\circ$) in middle of rostrum. (Steppan, 1995: character 45P; see also Braun, 1993: character 26; Pacheco, 2003: character 35T).

Rejected: invariant (90-135° angle).

2.5.2. Masseteric tubercle absent (0); or present (1). (Steppan, 1995: character 7S; Luna, 2002: character 33; Pacheco, 2003: characters 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: characters 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: characters 44S and 49T). Rejected: non-replicable results.

2.5.5. Sphenopalatine foramen absent or nearly ossified (0); or present, small to moderate size (1); or present, large (2). (Steppan, 1995: character 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: characters 27S and 36T). Rejected: invariant (narrow lumen).

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

2.5.8. Dorsal projection of alisphenoid well developed (0); or moderate (1). (Pacheco, 2003: character 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: character 50T). Not observed.

2.5.10. Ventral swelling in the region of the premaxillo-maxillary suture absent (0); or present (1). (Steppan and Pardinãs, 1998: character 103¹¹). Not observed.

2.5.11. Nasolacrimal capsule anterior or subequal to anterior margin of zygomatic plate (0); or well anterior to anterior margin of zygomatic plate (1); or absent (2). (Luna, 2002: character 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: character 10; see also Patton and Hafner, 1983: character 2; Olds and Anderson, 1989: character 18; Voss and Carleton, 1993: character 9; Steppan, 1995: characters 4S and 38P; Carleton and Olson 1999: character 7;

¹¹ The first 98 characters of Steppan and Pardinãs (1998) are the same of Steppan (1995).

Luna, 2002: character 62; Pacheco, 2003: characters 48S and 62T; Voss, 2003: 16-17).

Included: #31.

2.6.2. Separation of anterior apices of incisive foramina < 80% separation of posterior apices (0); or separation of anterior apices 80-100% of posterior apices (1). (Steppan, 1995: character 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: character 1). Rejected: continuous trait.

2.6.4. Ethmoid portion of the incisive foramina with length equal or less to half of the incisive foramina length, and width less than the foramina width (0); or ethmoid portion with length equal to ca. 3/4 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: character 4). Rejected: continuous trait.

2.6.5. Maxillary septum of incisive foramina length $\leq 1/2$ incisive foramina length (0); or septum length $1/2 - 4/5$ of incisive foramina (1); or length $> 4/5$ incisive foramina. (Steppan, 1995: character 39P; Pacheco, 2003: characters 49S and 63T). Rejected: continuous trait; also, non-replicable results.

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

2.6.7. Incisive foramina broad, length/width ratio less than three (0); or narrow, length/width ratio equal or greater than three (1). (Luna, 2002: character 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: characters 51S and 65T; see also Braun, 1993: character 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: character 9; see also Steadman and Ray, 1982: 10; Patton and Hafner, 1983: character 6; Carleton and Musser, 1989: character 11 [part]; Olds and Anderson, 1989: character 16; Voss, 1991: character 1; Braun, 1993: character 12; Voss, 1993: 24; Stepan, 1995: characters 21S and 70P; Luna, 2002: character 64; Voss et al., 2002: 18; Pacheco, 2003: characters 50S and 64T;). Included: #32.

*2.7.3. Palatal bridge 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: character 8; see also Stepan, 1995: character 72P; Luna, 2002: character 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: character 71P; see also Luna, 2002: character 65; Pacheco, 2003: character 66T).

Rejected: rampant intraspecific variation.

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

2.7.7. Maxillary palatal pits absent (0); or present in the maxillary bone (1). (Pacheco, 2003: characters 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: character 22; Braun, 1993: character 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: character 21; Steadman and Ray, 1982: 10; Patton and Hafner, 1983: character 5; Carleton and

Musser, 1989: character 11 [part]; Olds and Anderson, 1989: character 17; Voss, 1993: 24; Carleton and Olson, 1999: character 10; Luna, 2002: character 68; Voss et al., 2002: 18; Pacheco, 2003: characters 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: character 73P; Luna, 2002: character 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: character 69T). Not observed.

2.7.12. Maxillary at posterior base of M3 normal (0); or swollen (1). (Pacheco, 2003: character 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: character 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: character 19S; see also Luna, 2002: character 70; Pacheco, 2003: characters 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 - 2.4 larger (1); or more than 2.4 times larger (2). (Steppan, 1995: character 66P; see also Luna, 2002: character 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: character 20A; Stepan, 1995: characters 18S and 64P; see also Pacheco, 2003: characters 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: character 23; Olds and Anderson, 1989: character 20B; Braun, 1993: character 15; Stepan, 1995: character 67P; Carleton and Olson, 1999: character 11 [part]; Luna, 2002: character 73). Included: #35.

2.8.5. Parapterygoid fossa rectangular (0); or triangular (1). (Pacheco, 2003: characters 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). (Stepan, 1995: character 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: character 20; see also Olds and Anderson, 1989: character 21; Stepan, 1995: characters 20S and 68P; Patton and Hafner, 1983: character 7; Voss, 1993: 24; Luna, 2002: character 72; Voss et al., 2002: 18; Pacheco, 2003: characters 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: character 69P). Rejected: non-replicable 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: character 75). Rejected: invariant (present).

2.8.10. Parapterygoid vacuity absent or faint (0); or distinct (1). (Pacheco, 2003: character 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: character 16; Voss, 1988: character 12; Carleton and Musser, 1989: character 13; Voss, 1993: 24; Voss and Carleton, 1993: character 11; Steppan, 1995: characters 22S and 76P; Musser et al., 1998: 321; Carleton and Olson, 1999: character 14; Luna, 2002: characters 47, 48, 74, and 78; Voss et al., 2002: 18; Pacheco, 2003: characters 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: character 17; Musser and Williams, 1985: 19; Voss, 1991: character

2; Voss, 1993: 24; Voss and Carleton, 1993: character 10; Steppan, 1995: characters 23S and 78P; Musser et al., 1998: 321; Carleton and Olson, 1999: character 13; Luna, 2002: characters 45; Pacheco, 2003: characters 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: character 8; see also Luna, 2002: character 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: character 18; Luna, 2002: character 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: character 19; Steppan, 1995: character 17S and 61P; Luna, 2002: characters 54 and 56; Pacheco, 2003: characters 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: character 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: character 60P; see also Luna, 2002: characters 50 and 53; Pacheco, 2003: character 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: character 51). Not observed.

2.9.10. Petromastoid bony tube for the stapedial artery present (0); or absent (1). (Pacheco, 2003: character 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: character 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: character 59S). Rejected: invariant (level).

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

2.9.14. Internal carotid artery non-exposed (0); or exposed. (Pacheco, 2003: character 53T). Rejected: invariant (non-exposed).

2.9.15. Alisphenoid squamosal posterior margin without notch (0); or notch present (1). (Pacheco, 2003: character 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: character 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: character 12; see also Carleton and Musser, 1989: character 12; Steppan 1995: character 62P; Luna, 2002: character 66; Pacheco, 2003: character 77T). Included: #41.

2.10.2. Inflation of tympanic bullae (i.e., length X depth of bulla / total length of skull) less than 48% (0); or between 49-61% (1); or between 62-80% (2); or greater than 80% (3). (Carleton, 1980: character 33; see also Braun, 1993: character 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: character 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: character 59P; see also Luna, 2002: character 58; Pacheco, 2003: character 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: character 63P; see also Luna, 2002: character 79). Rejected: non-replicable results.

2.10.6. Dorsal aperture of ectotympanic ring loosed (0); or open (1). (Pacheco, 2003: characters 46S and 60T; see also Luna, 2002: character 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: character 12; Steppan, 1995: characters 15S and 58P; Luna, 2002: character 49; Voss et al., 2002: 18; Pacheco, 2003: characters 36S and 54T). Included: #42.

2.10.8. Mastoid bullae small, unmodified (0); or moderately inflated (1); or large, greatly inflated (2). (Carleton, 1980: character 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: character 9; Luna, 2002: character 59). Included: #43.

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

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

2.10.12. Ectotympanic not expanded laterally (0); or distinctly expanded laterally (1). (Pacheco, 2003: character 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: character 60; Pacheco, 2003: character 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: character 31). Rejected: invariant (present and large).

2.11.3. Malleus perpendicular (0); or parallel (1). (Carleton, 1980: character 30; see also Pacheco, 2003: character 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: character 65S). Not observed.

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

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

2.11.7. Malleus lamina broad, square-like (0); or narrow, rectangular shape (1). (Pacheco, 2003: character 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: character 80T). Rejected: invariant (shallow).

2.12. Jaw

2.12.1. Mandible with a cricetine morphotype (0); or New-World murid morphotype (1). (Pacheco, 2003: character 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: character 16). Rejected: non-replicable results.

2.12.3. Coronoid process above maximum height of mandibular condyle (0); or subequal (1); or below mandibular condyle (2). (Steppan, 1995: character 34P; see also Luna, 2002: character 80; Pacheco, 2003: character 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: character 82; Pacheco, 2003: character 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: character 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: character 36P; Luna, 2002: character 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: characters 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: character 31; Voss, 1993: 19; Steppan, 1995: character 33P; Luna, 2002: character 84; Voss et al., 2002: 18; Pacheco, 2003: characters 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: character 15; see also Steppan 1995: character 35P; Luna, 2002: character 86). Included: #46.

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

2.12.11. Retromolar region shallow, as a groove (0); or present, deep in a fossa (1). (Luna, 2002: character 85; Pacheco, 2003: characters 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 close to horizontal (2). (Pacheco, 2003: character 117T). Not observed.

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

2.12.14. Angular notch shallow (0); or deep (1). (Luna, 2002: characters 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: character 29; Pacheco, 2003: character 60S). Included: #48.

3. Dentition

3.1. Molar Roots

*3.1.1. Labial accessory root of M1 absent (0); or present (1). (Carleton, 1980: character 9; Carleton and Musser, 1989, character 19 [part]; Voss, 1991: character 6; Voss and Carleton, 1993: character 22; Stepan, 1995, characters 4P and 5P; Carleton and Olson, 1999, character 32; Pacheco, 2003: characters 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, evergrowing teeth (3). (Carleton, 1980: character 8; Pacheco, 2003: characters 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, evergrowing teeth (3). (Carleton, 1980: character 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, evergrowing teeth (3). (Carleton, 1980: character 11; Stepan, 1995: character 6P; Pacheco, 2003: character 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: characters 12 and 13; Carleton and Musser, 1989, character 19 [part]; Voss, 1991: character 7; Voss and Carleton, 1993; character 23; Stepan, 1995, character 7P; Carleton and Olson, 1999, character 33). Included: #50.

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

3.1.7. m3 with 2 roots (0); or 3 roots (1). (Carleton, 1980: character 15; Stepan, 1995: character 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: character 33; Stepan, 1995: character 2P; Luna, 2002: character 88; Pacheco, 2003: characters 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). (Stepan, 1995: character 3P; Luna, 2002: character 88). Rejected: non-replicable 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, character 13; Carleton and Olson, 1999, character 17). Included: #53.

3.2.4. Grooves on upper incisors absent (0); or fine striae present (1); or 1 mediolateral shallow groove (2); or 1 mediolateral groove and 1 small shallow groove on midline (3); or 1 involuted groove on lateral corner (4). (Stepan, 1995: character 1P; see

also Carleton, 1980: character 7; Braun, 1993: character 32; Luna, 2002: character 90).

Rejected: invariant (absent).

3.2.5. Upper incisors not flexed inwardly toward midline (0); or incisors flexed toward midline (2). (Braun, 1993: character 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: character 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: character 4; Braun, 1993: character 39; Carleton and Musser, 1989: character 5; Voss and Carleton, 1993: character 14; Carleton and Olson, 1999: character 18; Pacheco, 2003: characters 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: character 101) and Pacheco (2003: character 74S).

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

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

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

3.3.6. Ratio of toothrow length / skull length. (Braun, 1993: character 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: character 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: character 40). Not observed.

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

3.4. M1 & 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, character 2; Carleton and Musser, 1989, character 15 [part]; Braun, 1993: character 41; Voss, 1993: 24; Steppan, 1995, character 10P; Carleton and Olson, 1999, character 20;

Luna, 2002: character 94; Voss et al., 2002: 18; Pacheco, 2003: characters 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: characters 70S and 88T; see also Carleton and Musser, 1989: character 15 [part]; Luna, 2002: character 95). Rejected: autapomorphy for Wiedomys. Note: A reduced anterolingual conule is observed in other taxa (e.g., Microrhizomys; cf. Carleton and Musser, 1989), but only Wiedomys display an extreme reduction of that structures; remaining taxa have a gradient of size.

***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 fossete (2); or anteroloph and anteroflexus absent (3).** (modified from Voss and Carleton, 1993: character 18; Stepan, 1995: character 12P; Carleton and Olson, 1999: character 23; Pacheco, 2003: characters 90T to 92T).

Included: #59.

***3.4.4. Protostyle on M1 absent (0); or present (1).** Included: #60. See also Pacheco (2003: character 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, character 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: character 16; see also Olds and Anderson, 1989: character 32; Voss, 1991: character 5; Stepan, 1995: character 1P; Carleton and Olson, 1999: character 30; Luna, 2002: characters 91, 96, and 97; Pacheco, 2003: character 72S). Included: #62.

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

3.4.9. Posteroloph on M1 and M2 present (0); or absent (1). (modified from Carleton and Olson, 1999: character 24; Luna, 2002: character 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: character 19; Carleton and Olson, 1999: character 25; see also Stepan, 1995: character 21P; Pacheco, 2003: characters 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 fossete on M2 (0); or mesoflexus divided into labial and medial fosseti (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: character 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: character 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: character 93T). Rejected: not applicable (paraloph absent; paracone?).

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

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

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

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

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

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

3.4.23. Second upper molar width < 0.91 length (0); or width > 0.91 length (1). (Steppan, 1995: character 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: character 17; Carleton and Olson, 1999: character 22; Pacheco, 2003: character 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: character 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: characters 23P and 26P; Pacheco, 2003: character 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: character 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: character 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: character 25P). Rejected: continuous trait.

3.5.8. Anteroloph on M3 moderately or well developed (0); or reduce (1); or absent or vestigial (2). (Braun, 1993: character 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: character 18; also Carleton and Olson, 1999: character 34). Rejected: continuous trait.

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

3.5.11. Third upper molar length < 0.205 alveolar length of molar tooth row (0); or between 0.205-0.25 (1); or > 0.25 (2). (Steppan, 1995: character 32P; see also Braun, 1993: character 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: character 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: character 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: character 3; Voss, 1991: character 4; Steppan, 1995: character 16P; Pacheco, 2003: character 78S). Rejected: continuous trait.

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

*3.6.3. Anterolabial cingulum on m1 absent (0); or long anterolabial cingulum present (1). (Stepan, 1995: characters 14P and 15P; see also Luna, 2002: character 98; Pacheco, 2003: characters 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). (Stepan, 1995: character 18P). Rejected: invariant (attached).

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

3.6.6. Metaflexid on m1 appressed (0); or open (1). (Pacheco, 2003: character 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: character 21; Carleton and Olson, 1999: character 27; see also Pacheco, 2003: characters 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: character 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 antero-posteriorly (1); or a metalophid antero-posteriorly oriented that closes the anterolingual cingulum (2). (Pacheco, 2003: character 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: character 104T). Not observed.

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

3.6.12. Molar flexus (-ids) not crenellated (0); or crenellated (1). (Pacheco, 2003: character 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: character 19P). Rejected: invariant (present).

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

3.7. m2 & m3

***3.7.1.** Anterolabial cingulum present on m2 (0); or absent (1). (Steppan, 1995: character 22P; Pacheco, 2003: character 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: character 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: character 31). Rejected: unidentifiable states.

*3.7.5. Anterolabial margin of m3 with shelf-like cingulum, separated from protoconid by protoflexid (0); or anterolabial margin of m3 smoothly rounded, without cingulum, protoflexid absent (1). (Carleton and Musser, 1989: character 17; Carleton and Olson, 1999: character 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: character 20P; Pacheco, 2003: character 82S). Included: #77.

3.7.7. Opposing flexi on m3 do not meet (0); or flexi meet, median mure cut (1). (Steppan, 1995: character 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: character 28P; also Carleton, 1980: character 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: character 29P also Carleton, 1980: character 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: character 30P also Carleton, 1980: character 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: character 35; see also Steppan and Pardinã, 1998: character 102). Rejected: continuous trait.

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

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

3.7.14. Ratio of lower third molar to length of molar row > 30% (0); or between 29 to 24% (1); < 23% (2). (Carleton, 1980: character 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 cups pair absent or reduced to a small conule (1). (Voss, 1988: character 9). Rejected: invariant (entoconid-hypoconid present).

4. Postcranial Skeleton

4.1. Ribs & vertebrae

*4.1.1. 13 ribs (0); or 12 ribs (1). (Steppan, 1995: character 79P; see also Carleton, 1980: character 36; Voss, 1993: 24; Steppan, 1995: character 26S; Voss et al., 2002: 18; Pacheco, 2003: characters 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: character 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: character 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: character 39; Steppan, 1995: character 25S; Pacheco, 2003: character 95S). Included: #79.

4.1.5. Spine on second thoracic vertebra present (0); or absent (1). (Carleton, 1980: character 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: character 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: character 28S; Pacheco, 2003: characters 98S, 99S, 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: character 37; Steppan, 1995: characters 27S and 80P; Pacheco, 2003: characters 97S and 125). Rejected: continuous trait.

4.2. Limbs

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

*4.2.2. Entepicondylar foramen of humerus present (0); or absent (1). (Carleton, 1980: character 35; Steppan, 1995: character 29S; Pacheco, 2003: character 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: character 30S; Pacheco, 2003: characters 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: character 84P). Rejected: continuous trait (and invariant: less than 59%).

4.2.5. Fusion of tibia-fibula: less than 30% (0); or between 31-36% (1); or between 37-41% (2) or greater than 42% (3). (Carleton, 1980: character 42). Rejected: metric character.

*4.2.6. Trochlear process of calcaneum at the same level as posterior articular facet, trochlear process broad and shelf-like (0); or gap between proximal edge of trochlear

process and posterior articular facet, process shorter and less shelf-like (1). (Carleton, 1980: character 40; Stepan, 1995: character 32S; Pacheco, 2003: characters 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). (Stepan, 1995: character 31S; Pacheco, 2003: characters 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 investiture (0); or one-half to three-quarters of body spiny (1); or less than one-half of body spiny (2); or body wholly denude of spines (3). (Carleton, 1980: character 52; Pacheco, 2003: character 133T). Rejected. Sigmodontomys alfari has only 4/5 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 have 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 extends no more than half the body (1); or deep, extends beyond half the length of body (2). (Pacheco, 2003: characters 105S and 134T; the coding follows the latter character; the former has only two states, absent or shallow X present). Rejected: continuous trait.

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

5.1.4. Dorsal lappets absent (0); or present (1). (Carleton, 1980: character 56).

Rejected: autapomorphy for Peromyscus.

5.1.5. Ventral lappets absent (0); or present (1). (Carleton, 1980: character 57).

Rejected: autapomorphy for Peromyscus.

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

5.1.7. Urinary meatus terminal, or nearly so (0); or subterminal (1). (Carleton, 1980: character 55; Pacheco, 2003: character 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: character 61). Rejected: invariant (absent).

5.1.9. Ventral shield absent (0); or present (1). (Carleton, 1980: character 62; Pacheco, 2003: character 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: character 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: character 136T). Rejected: invariant (same height).

5.1.13. Notch on midventral margin of crater rim absent (0); or present (1). (Pacheco, 2003: character 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: character 60; Steppan, 1995: characters 36S; Pacheco, 2003: character 107S; see also Voss, 1988: character 18). Included: #85.

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

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

5.2.4. Knob on dorsal surface of lateral mounds absent (0); or present (1). (Steppan, 1995: character 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: character 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: character 140T). Rejected: continuous trait.

5.2.8. Spines on lateral mounds absent (0); or present (1). (Pacheco, 2003: character 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: character 113S). Rejected: invariant (absent).

5.3.3. Urethral process spineless (0); or spiny (1). (modified from Carleton, 1980: character 58; Pacheco, 2003: character 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: character 59; Pacheco, 2003: characters 110S and 143T). Rejected: autapomorphy for Peromyscus.

5.4. Phallus - Ratios

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

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

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

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

Rejected: metric character.

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

5.4.6. Ratio of cartilaginous tip length / bacular length (Carleton, 1980: character 65; Steppan, 1995: character 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: character 68; Steppan, 1995: characters 37S and 97P; Pacheco, 2003: characters 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: characters 69 and 70; see also Pacheco, 2003: characters 116S and 145T). Included: #91.

*5.5.3. Anterior prostate glands present (0); or absent (1). (modified from Carleton, 1980: character 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: character 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: character 145T).

Rejected: continuous trait.

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5.5.6. Bulbo-urethral glands present, 'normal' size (0); or present, large (1); or present, 'huge' (2). (Carleton, 1980: character 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: character 74). Rejected: invariant (present, normal).

5.5.8. Ampullae of ductus deferens absent (0); or present (1). (Carleton, 1980: character 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: character 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: character 49; Voss, 1988: character 17; Voss, 1991: character 8; Voss, 1993: 24; Voss and Carleton, 1993: 25; Stepan, 1995: characters 38S and 98P; Voss et al., 2002: 18; Pacheco, 2003: characters 122S and 132T). Included: #98.

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

5.6.3. Gastric epithelium hemiglandular (0); or discoglandular (1). (modified from Carleton, 1980: character 46; see also Voss, 1988: character 16; Stepan, 1995: characters 39S and 40S; Voss et al., 2002: 16; Pacheco, 2003: characters 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: character 20; Voss and Carleton, 1993: character 24). Included: #99.

5.6.5. Sulcus on greater curvature of stomach absent (0); or present (1). (Carleton, 1980: character 48; Pacheco, 2003: character 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: character 50). Not observed.

5.6.7. Caecum moderately long, simple internally (0); or short, simple sac (1); or long, elaborate infolding (2). (Carleton, 1980: character 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: character 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: character 45; Pacheco, 2003: 129T). Not observed.

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

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

APPENDIX 4. CHARACTER TRANSFORMATIONS IN MORPHOLOGICAL TREE

Character transformations in morphological tree with polymorphisms analyzed as composites. Legend: a: character numbers; b: consistency index; c: optimization method (A = ACCTRAN, D = DELTRAN, U = unambiguous optimization).

Node	Taxon content	Char ^a	CI ^b	Opt ^c	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	anapophysis absent on TL17
		96	0.50	A	0=>1	compact ampullary glands
2	1 – <u>Thomasomys</u>	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 – <u>Delomys</u>	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 hind foot digits
		31	0.17	U	0=>1	incisive foramina reach M1
		32	0.17	U	1=>2	long palate
		68	0.14	U	0=>1	M3 without posteroloph

6	Clade A + Clade C	36	0.19	A	0=>1	reduced sphenopalatine vacuities
		58	0.12	A	0=>2	M1 with undivided anterocone
		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
7	Clade A	29	0.10	A	1=>0	zygomatic plate at same level as M1 alveolus
		80	0.11	D	0=>1	anapophysis absent on TL17
		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
8	<u>Zygodontomys</u>	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
		22	0.18	U	3=>4	strongly cuneate interorbit with overhanging crests
		31	0.17	U	1=>0	incisive foramina do not reach 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
9	Clade C	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
		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
10	<u>Neacomys</u>	29	0.10	D	1=>0	zygomatic plate at same level as M1 alveolus
		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)
11	<u>Neacomys minutus</u> + <u>N. spinosus</u>	94	1.00	A	0=>1	preputial glands do not extend to the ventral flexure of the penis
		37	0.13	U	1=>0	primitive carotid circulation

		45	0.11	D	1=>2	developed capsular process of lower incisor alveolus
12	26 – <u>Neacomys</u>	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	<u>Microryzomys</u> + <u>Oryzomys</u> <u>balneator</u>	28	0.33	U	1=>0	narrow zygomatic plate
		32	0.17	U	2=>1	medium palate
		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	<u>Oligoryzomys</u>	35	0.33	U	1=>0	flat parapterygoid
		36	0.19	U	1=>0	large sphenopalatine vacuities
		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	<u>Oligoryzomys</u> <u>nigripes</u> + <u>Ol.</u> <u>fulvescens</u>	90	0.50	U	1=>2	preputial glands absent
		81	0.33	D	1=>2	hemal arches with spinous posterior border
16	<u>Oligoryzomys</u> <u>flavescens</u> + <u>Ol.</u> <u>fornesi</u> + <u>Ol.</u> <u>stramineus</u>	69	0.09	U	0=>1	M3 without hypoflexus (or diminutive)
17	<u>Oligoryzomys</u> <u>flavescens</u> + <u>Ol.</u> <u>fornesi</u>	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	<u>Oryzomys</u> <u>megacephalus</u> + <u>O. talamancae</u> + <u>Handleyomys</u> + <u>O. albigularis</u> + <u>O. levipes</u>	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
20	<u>Oryzomys</u> <u>talamancae</u> + <u>Handleyomys</u> + <u>O. albigularis</u> + <u>O. levipes</u>	22	0.18	A	3=>1	amphoral interorbit with square edges
		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	anapophysis present on TL17

21	<u>Handleyomys</u> + <u>Oryzomys</u> <u>albigularis</u> + <u>O.</u> <u>levipes</u>	90	0.50	A	1=>2	preputial glands absent
		57	0.20	D	0=>2	flexi deeply interpenetrating on M1
		50	0.25	U	0=>1	m1 with 3 roots
22	<u>Oryzomys</u> <u>albigularis</u> + <u>O.</u> <u>levipes</u>	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
		32	0.17	U	2=>1	medium palate
23	<u>Oryzomys</u> <u>yunganus</u> + 24	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
		11	0.12	U	1=>2	tail strongly bicolored
24	25 + 27	36	0.19	U	1=>2	completely ossified sphenopalatine
		66	0.17	A	0=>1	M2 with labial and lingual fosseti at mesoflexus position
		57	0.20	D	0=>1	flexi meet at midline on M1
25	<u>nitidus</u> group	37	0.13	U	1=>0	primitive carotid circulation
		43	0.17	U	1=>0	completely ossified mastoid
		50	0.25	U	0=>1	m1 with 3 roots
26	<u>Oryzomys lamia</u> + <u>O. russatus</u>	80	0.11	A	1=>0	anapophysis present on TL17
		45	0.11	U	0=>2	developed capsular process of lower incisor alveolus
27	<u>Oryzomys</u> <u>hammondi</u> + <u>Oecomys</u>	72	0.17	U	1=>0	m1 without ectolophid
		11	0.12	U	2=>0	tail unicolored
		25	0.20	U	0=>1	parietal with deep lateral expansion
28	<u>Oecomys</u>	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 fossete at mesoflexus position
		5	0.40	U	1=>0	pes with extremely developed interdigital pads
		22	0.18	U	3=>4	strongly cuneate interorbit with overhanging crests
29	28 - <u>Oecomys</u> <u>catherinae</u>	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	0.10	U	1=>0	zygomatic plate at same level as M1 alveolus
30	<u>Oecomys bicolor</u> + <u>Oe. trinitatis</u>	14	0.20	A	0=>1	totally white ventral hairs
		43	0.17	A	0=>1	mastoid with large fenestra
		21	0.13	U	0=>1	lacrimal articulates mainly with maxillary
31	<u>Oecomys</u> <u>concolor</u> + <u>Oe.</u> <u>mamora</u>	45	0.11	U	1=>2	developed capsular process of lower incisor alveolus
		80	0.11	D	0=>1	anapophysis absent on TL17
		15	0.11	U	0=>1	subtle countershading

32	Clade D*	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
		25	0.20	U	0=>1	parietal with deep lateral expansion
		34	0.33	U	2=>3	complex posterolateral palatal pits
33	32 – <u>Oryzomys polius</u>	37	0.13	U	1=>2	derived carotid circulation 2
		80	0.11	A	1=>0	anapophysis present on TL17
		81	0.33	A	1=>2	hemal arches with spinous posterior border
		36	0.19	D	1=>0	large sphenopalatine vacuities
		45	0.11	U	0=>2	developed capsular process of lower incisor alveolus
34	33 - <u>Oryzomys angouya</u>	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 fosseti at mesoflexus position
		81	0.33	D	1=>2	hemal arches with spinous posterior border
35	<u>Oryzomys subflavus</u> + 36	7	0.33	U	0=>1	ungual tufts absent on D1, developed in remaining hind foot digits
		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
36	37 + 39	40	0.38	A	0=>2	vestigial subsquamosal fenestra
		29	0.10	U	1=>0	zygomatic plate at same level as M1 alveolus
		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 fosseti at mesoflexus position
37	<u>O. chapmani</u> + <u>O. alfaroi</u> + <u>O. rostratus</u>	51	0.20	U	0=>1	m2 with 3 roots
		80	0.11	U	0=>1	anapophysis absent on TL17
		11	0.12	A	1=>2	tail strongly bicolored
		40	0.38	A	2=>0	subsquamosal fenestra present
		32	0.17	D	1=>2	long palate
38	<u>O. alfaroi</u> + <u>O. rostratus</u>	31	0.17	U	0=>1	incisive foramina 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
39	<u>Oryzomys sensu stricto</u> + 41	6	0.13	A	1=>0	pes with smooth plantar surface
		25	0.20	A	1=>0	parietal without lateral expansion
		37	0.13	U	2=>0	primitive carotid circulation
		45	0.11	U	2=>1	reduced capsular process of lower incisor alveolus
		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 hind foot 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
40	<u>Oryzomys sensu stricto</u>	86	0.25	A	1=>0	long central bacular digit
		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
41	<u>Pseudoryzomys</u> + <u>Lundomys</u> + <u>Holochilus</u>	86	0.25	D	1=>0	long central bacular digit
		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
42	<u>Holochilus</u> + <u>Lundomys</u>	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
		3	0.33	U	0=>1	ungual tufts absent on forefeet digits
		7	0.33	U	2=>3	ungual tufts absent on hind foot 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 tooth row
		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	anapophysis present on TL17
		11	0.12	A	2=>0	tail unicolored
43	<u>Holochilus</u>	11	0.12	D	1=>0	tail unicolored
		86	0.25	D	1=>0	long central bacular digit
		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 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

		53	1.00	U	0=>1	procingulum
		54	1.00	U	0=>1	incisors with labial bevel
		57	0.20	U	1=>2	molars hypsodont
		58	0.12	U	1=>2	flexi deeply interpenetrating on M1
		63	0.50	U	0=>1	M1 with undivided anterocone
		64	0.20	U	0=>1	median mure not connect to protocone on M1
		19	0.14	A	1=>0	M2 without protoflexus
						nasals reach anterior to maxillary-frontal suture
		67	0.33	A	1=>0	M3 with mesoloph
		87	0.25	A	0=>1	basal 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	<u>Nesoryzomys</u> + <u>Oryzomys</u> <u>xanthaeolus</u> + <u>Amphinectomys</u> + <u>Nectomys</u> + <u>Sigmodontomys</u> + <u>Melanomys</u>	21	0.13	U	0=>1	lacrima 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	<u>Nesoryzomys</u>	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 - <u>Nesoryzomys</u>	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 - <u>Oryzomys</u> <u>xanthaeolus</u>	31	0.17	U	0=>1	incisive foramina reach M1
		36	0.19	U	0=>1	reduced sphenopalatine vacuities
		52	0.20	U	0=>1	orthodont incisors
		7	0.33	A	1=>2	ungual tufts absent on D1, sparse in remaining hind foot digits
		11	0.12	A	1=>0	tail unicolored

48	<u>Melanomys</u> + <u>Sigmodontomys</u> + <u>Nectomys</u>	58	0.12	A	0=>2	M1 with undivided anterocone
		20	0.22	D	1=>2	premaxillaries anterior to terminus of nasal
		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 hind foot digits
		11	0.12	D	1=>0	tail unicolored
49	<u>Sigmodontomys</u> + <u>Nectomys</u>	15	0.11	D	0=>1	subtle countershading
		58	0.12	D	0=>2	M1 with undivided anterocone
		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
50	<u>Sigmodontomys</u> <u>alfari</u> + <u>Nectomys</u>	29	0.10	A	1=>0	zygomatic plate at same level as M1 alveolus
		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
		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
51	<u>Nectomys</u>	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 THE COMBINED TREE

Character transformations in the combined tree with polymorphisms analyzed as composites. Legend: a: character numbers; b: consistency index; c: optimization method (A = ACCTRAN, D = DELTRAN, U = unambiguous optimization).

Node	Taxon content	Char ^a	CI ^b	Opt ^c	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	anapophysis absent on TL17
		96	0.50	A	0=>1	compact ampullary glands
2	1 – <u>Thomasomys</u>	1	0.50	U	1=>2	Eight 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
3	2 – <u>Delomys</u>	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
		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
4	Oryzomyini	35	0.33	D	0=>1	excavated parapterygoid
		80	0.13	D	0=>1	anapophysis absent on TL17
		7	0.30	U	0=>1	ungual tufts absent on D1, developed in remaining hind foot digits
		31	0.17	U	0=>1	incisive foramina 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
5	4 – <u>Oryzomys hammondi</u>	98	0.50	D	0=>1	Gall bladder absent
		32	0.17	U	1=>2	long palate

6	Clade A	34	0.38	U	1=>2	simple posterolateral palatal pits
		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
		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
7	<u>Zygodontomys</u>	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
		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 do not reach 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
8	5 – Clade A	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
		64	0.25	U	1=>0	M2 with protoflexus
		43	0.14	A	0=>1	mastoid with large fenestra
9	Clade B	30	0.22	D	0=>1	jugal reduced, constricted centrally
		81	0.40	D	0=>1	hemal arches present on CA2-3
		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
10	<u>nitidus</u> group	72	0.14	A	0=>1	m1 with ectolophid
		36	0.16	D	1=>2	completely ossified sphenopalatine
		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	anapophysis present on TL17
11	<u>Oryzomys lamia</u> + <u>O. russatus</u>	66	0.17	A	0=>1	M2 with labial and lingual fosseti at mesoflexus position
		45	0.11	U	1=>2	developed capsular process of lower incisor alveolus
		72	0.14	U	1=>0	m1 without ectolophid
		61	0.22	D	1=>0	enamel bridge connection between paracone and protocone at posteriormost end of

12	13 + 18	49	0.14	A	0=>1	protocone on M1
		61	0.22	D	1=>0	M1 with labial root enamel bridge connection between paracone and protocone at posteriormost end of protocone on M1
13	<u>Oecomys</u>	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
14	13 - <u>Oecomys catherinae</u>	68	0.14	U	1=>0	M3 with posteroloph
		49	0.14	D	0=>1	M1 with labial root
		29	0.09	U	1=>0	zygomatic plate at same level as M1 alveolus
		14	0.20	A	0=>1	totally white ventral hairs
		21	0.13	U	0=>1	lacrimal articulates mainly with maxillary
15	<u>Oecomys bicolor</u> + <u>Oe. trinitatis</u>	45	0.11	U	1=>2	developed capsular process of lower incisor alveolus
						subtle countershading
16	<u>Oecomys mamorae</u> + <u>Oe. concolor</u>	15	0.13	U	0=>1	
		37	0.13	U	0=>2	derived carotid circulation 2
17	18 + 21	14	0.20	D	0=>1	totally white ventral hairs
		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	<u>Handleyomys</u> + <u>O. chapmani</u> + <u>O. alfaroi</u> + <u>O. rostratus</u>	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 fosseti 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
19	<u>O. chapmani</u> + <u>O. alfaroi</u> + <u>O. rostratus</u>	49	0.14	D	0=>1	M1 with labial root
		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
20	<u>Oryzomys chapmani</u> + <u>O. rostratus</u>	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
		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
21	22 + 23	34	0.38	D	2=>3	complex posterolateral palatal pits
		11	0.13	U	0=>1	tail slightly bicolored
		96	0.50	U	1=>0	ampullary glands forming tufts of tubules
22	<u>Oryzomys</u> <u>megacephalus</u> + <u>O. yunganus</u>	49	0.14	A	1=>0	M1 without labial root
		37	0.13	U	0=>1	derived carotid circulation 1
		45	0.11	U	1=>0	capsular process of lower incisor alveolus absent
23	<u>O. talamancae</u> + <u>Oryzomys levipes</u> + <u>O. albigularis</u>	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	anapophysis present on TL17
24	<u>Oryzomys levipes</u> + <u>O. albigularis</u>	34	0.38	A	2=>3	complex posterolateral palatal pits
		90	0.45	A	1=>2	preputial glands absent
		22	0.17	U	3=>1	amphoral interorbit with square edges
25	Clade C + Clade D	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
26	Clade C	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
27	<u>Neacomys</u>	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
28	<u>Neacomys</u> <u>minutus</u> + <u>N. musseri</u>	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
29	26 - <u>Neacomys</u>	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
30		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
		13	0.50	U	0=>1	spiny pelage
31		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)
32		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
		99	0.17	A	0=>1	extended gastric glandular epithelium
33		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	<u>Microryzomys</u> + <u>Oryzomys</u> <u>balneator</u>	28	0.29	U	1=>0	narrow zygomatic plate
		32	0.17	U	2=>1	medium palate
		70	0.50	U	1=>2	m1 with anteromedian flexid
		99	0.17	U	0=>1	extended gastric glandular epithelium
31	<u>Oligoryzomys</u>	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	<u>Oligoryzomys</u> <u>nigripes</u> + <u>Ol.</u> <u>stramineus</u>	none				
33	<u>Oligoryzomys</u> <u>flavescens</u> + <u>Ol.</u> <u>fornesi</u>	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 do not reach 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 – <u>Oryzomys</u> <u>polius</u>	49	0.14	U	0=>1	M1 with labial root
		66	0.17	U	0=>1	M2 with labial and lingual fosseti 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 hind foot 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
		50	0.18	D	1=>2	m1 with 4 roots

37	<u>Oryzomys sensu stricto</u>	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	<u>Pseudoryzomys + Lundomys + Holochilus</u>	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 mesoloph
		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	<u>Holochilus + Lundomys</u>	3	0.33	U	0=>1	ungual tufts absent on forefeet digits
		7	0.30	U	2=>3	ungual tufts absent on hind foot 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 tooth row
		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
40	<u>Holochilus</u>	77	0.33	U	1=>2	m3 without posteroflexid
		80	0.13	U	1=>0	anapophysis present on TL17
		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 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	0.14	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 connect 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	<u>Oryzomys angouya</u> + <u>O. subflavus</u> + <u>Nesoryzomys</u> + <u>O. xanthaeolus</u> + <u>Amphinectomys</u> + <u>Nectomys</u> + <u>Sigmodontomys</u> + <u>Melanomys</u>	11	0.13	U	2=>1	tail slightly bicolored
		80	0.13	U	1=>0	anapophysis present on TL17
		32	0.17	D	2=>1	medium palate
42	<u>Oryzomys subflavus</u> + <u>Nesoryzomys</u> + <u>O. xanthaeolus</u> + <u>Amphinectomys</u> + <u>Nectomys</u> + <u>Sigmodontomys</u> + <u>Melanomys</u>	40	0.43	U	0=>2	vestigial subsquamosal fenestra
		86	0.25	U	0=>1	slim central bacular digit
		43	0.14	A	1=>0	completely ossified mastoid
		50	0.18	D	1=>2	m1 with 4 roots
		87	0.20	D	1=>0	bacular mounds not covered by rim of nonspinous tissue
43	42 - <u>Oryzomys subflavus</u>	46	0.20	U	0=>1	single-crest anterior masseteric ridges
		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	lacrima articulates mainly with maxillary
		43	0.14	D	1=>0	completely ossified mastoid
44	<u>Nesoryzomys</u>	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 - <u>Nesoryzomys</u>	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

		69	0.09	U	0=>1	cingulum on M1
		19	0.11	A	0=>1	M3 without hypoflexus (or diminutive)
		20	0.22	A	1=>2	nasals reach posterior to maxillary-frontal suture
		22	0.17	D	3=>4	premaxillaries anterior to terminus of nasal
						strongly cuneate interorbit with overhanging crests
46	45 – <u>Oryzomys xantheolus</u>	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 hind foot digits
		11	0.13	U	1=>0	tail unicolored
		31	0.17	U	0=>1	incisive foramina 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	<u>Amphinectomys</u> + <u>Nectomys</u>	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	<u>Nectomys</u>	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	<u>Sigmodontomys</u> + <u>Melanomys</u>	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	<u>Melanomys</u> + <u>Sigmodontomys</u> <u>aphrastus</u>	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	anapophysis absent on TL17
		19	0.11	D	0=>1	nasals reach posterior to maxillary-frontal suture

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CHAPTER 1

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