PHYLOGENETIC RELATIONSHIPS AND CLASSIFICATION OF DIDELPHID MARSUPIALS, AN EXTANT RADIATION OF NEW WORLD METATHERIAN MAMMALS

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Representative opossums (top to bottom, not to the same scale): *Caluromys derbianus*, *Monodelphis brevicaudata*, *Marmosa robinsoni*, *Chironectes minimus*, *Metachirus nudicaudatus*.

CONTENTS

ABSTRACT

This report summarizes a decade of morphological and molecular research on the phylogenetic relationships of didelphid marsupials (opossums), a substantially intact radiation of New World metatherian mammals. We review the comparative morphology of Recent opossums, emphasizing those anatomical systems from which taxonomically useful information is available for the majority of living genera and species, namely the integument, cranium, and dentition. Morphological similarities and differences among didelphids and other plesiomorphic marsupials (caenolestids, microbiotheriids, dasyurids, and peramelids) are also described. These observations, representing evolved differences in diverse functional-morphological systems, together with karyotypic information gleaned from the literature, provide the basis for coding 129 phylogenetic characters that we scored for 44 ingroup and seven outgroup taxa.

Published information about the size, internal organization, chromosomal location, and physiological properties of five nuclear genes (BRCA1, DMP1, IRBP, RAG1, vWF) sequenced for this study suggest that these loci are unlinked, exist as single copies, are active in different tissues, and encode protein products with widely divergent functions. All of the sequenced fragments are long (>900 bp), free of ingroup alignment ambiguities, and translate to open reading frame. Nucleotide data from a total of 7320 aligned sites were obtained from 43 ingroup and seven outgroup taxa.

Separate parsimony, likelihood, and Bayesian analyses of these six data partitions (morphology + karyotypes, five genes) resulted in highly congruent estimates of didelphid phylogeny with few examples of conflict among strongly supported nodes. Analyses of concatenated sequences and combined (nonmolecular + sequence) datasets effectively summarize all of the common signal recovered from separate analyses: a completely resolved ingroup phylogeny with high support statistics at most nodes. Remaining problems (not conclusively resolved in this study) include the position of the ingroup root and the relationships of three genera (*Chacodelphys*, *Cryptonanus*, *Tlacuatzin*) within their respective suprageneric clades.

The history of didelphid classification is reviewed, and all previous systems are found to contain nonmonophyletic groups. A revised phylogenetic classification consistent with our analytic results includes the following higher taxa: Glironiinae (for *Glironia*), Caluromyinae (*Caluromys* and *Caluromysiops*), Hyladelphinae (*Hyladelphys*), Didelphinae (Marmosini, Metachirini, Didelphini, and Thylamyini), Marmosini (*Marmosa*, *Monodelphis*, and *Tlacuatzin*), Metachirini (*Metachirus*), Didelphini (*Chironectes*, *Didelphis*, *Lutreolina*, and *Philander*), and Thylamyini (*Chacodelphys*, *Cryptonanus*, *Gracilinanus*, *Lestodelphys*, *Marmosops*, and *Thylamys*). The probable relationships of several Neogene fossil genera are also discussed. To facilitate identifications, all Recent genera are redescribed, representative crania are illustrated, and a key is provided.

INTRODUCTION

They affirme that there are trees of suche byggenes, that xvi men ioyninge handes togyther and standinge in coompasse, can scarsely embrase sum of them. Emonge these trees is fownde that monstrous beaste with a snowte lyke a foxe, a tayle lyke a marmasette, eares lyke a batte, handes lyke a man, and feete lyke an ape, bearing her whelpes abowte with her in an owtwarde bellye much lyke vnto a great bagge or purse. — Richard Eden (1555), describing the first European encounter with a marsupial, by Vicente Yáñez Pinzón and his men on the coast of Brazil in the year 1500

The oldest known metatherian mammals occur in Cretaceous sediments of eastern Asia and western North America (Rougier et al., 1998; Luo et al., 2003; Kielan-Jaworowska et al., 2004), and other early metatherians are present in the Tertiary record of Europe and Africa (Crochet, 1980; Kurz, 2007; Hooker et al., 2008). The metatherian crown group Marsupialia, however, probably evolved in South America and subsequently dispersed across Antarctica to Australia and New Guinea (Muizon et al., 1997; Springer et al., 1997a; Rougier et al., 1998). Living marsupials comprise seven major groups, currently ranked as orders in the Linnaean hierarchy, each of which is endemic to either the New World or the Old World (table 1).

Although the extant New World marsupial fauna consists of three orders, two of these

TABLE 1
**Higher Classification and Geographic Distribution of
Recent Marsupials[a]**

	Genera	Species	Distribution[b]
DASYUROMORPHIA			
Dasyuridae	20	69	OW
Myrmecobiidae	1	1	OW
Thylacinidae	1	1	OW
DIDELPHIMORPHIA			
Didelphidae	18[c]	91[c]	NW
DIPROTODONTIA			
Acrobatidae	2	2	OW
Burramyidae	2	5	OW
Hypsiprymnodontidae	1	1	OW
Macropodidae	11	65	OW
Petauridea	3	11	OW
Phalangeridae	6	27	OW
Phascolarctidae	1	1	OW
Potoroidae	4	10	OW
Pseudocheiridae	6	17	OW
Tarsipedidae	1	1	OW
Vombatidae	2	3	OW
MICROBIOTHERIA			
Microbiotheriidae	1	1	NW
NOTORYCTEMORPHIA			
Notoryctidae	1	2	OW
PERAMELEMORPHIA			
Chaeropodidae	1	1	OW
Peramelidae	6	18	OW
Thylacomyidae	1	2	OW
PAUCITUBERCULATA			
Caenolestidae	3	6	NW

[a] Numbers of genera and species after Wilson and Reeder (2005) except as noted.

[b] NW = New World; OW = Old World (Sahul).

[c] After Gardner (2008).

are represented by a mere handful of living forms: Microbiotheria by a single genus and species (*Dromiciops gliroides*), and Paucituberculata by six species in three genera (*Caenolestes*, *Lestoros*, *Rhyncholestes*). Both groups inhabit wet-temperate Patagonian forests, but paucituberculates also occur in climatically similar montane habitats of the tropical Andes (Bublitz, 1987; Patterson and Gallardo, 1987; Albuja and Patterson, 1996; Hershkovitz, 1999; Lunde and Pacheco, 2003). Because microbiotherians and paucituberculates were more diverse and widely

distributed in the Tertiary than they are today (Marshall, 1980, 1982b; Bown and Fleagle, 1993; Goin, 1997; Goin and Candela, 2004), these orders are appropriately regarded as relictual elements in modern faunas.

Instead, the only substantially intact radiation of New World marsupials is represented by the family Didelphidae, commonly known as opossums, of which 91 Recent species in 18 genera are currently recognized (Gardner, 2008). Although didelphids were the first metatherians to be encountered by European explorers (Eden, 1555), the first to be described scientifically (Tyson, 1698), and the first to be classified by taxonomists (Linnaeus, 1758), zoological interest in opossums was soon eclipsed by the discovery of Australasian marsupials. Nevertheless, steady advances in didelphid taxonomy (mostly involving the description of new species) were made throughout the 19th and 20th centuries. Although this progress was periodically summarized by authors (e.g., Thomas, 1888; Winge, 1893; Cabrera, 1919, 1958), there is no modern monographic treatment of the family, and the current suprageneric classification (McKenna and Bell, 1997; Gardner, 2005, 2008) does not reflect current knowledge about opossum evolutionary relationships.

The history of didelphid phylogenetic research was reviewed by Jansa and Voss (2000), who analyzed DNA sequence data from the nuclear Interphotoreceptor Retinoid Binding Protein (IRBP) gene for 21 species. Subsequent reports were focused on analyses of morphological and karyotypic character data in combination with IRBP sequences for larger sets of species (Voss and Jansa, 2003; Voss et al., 2005), on phylogenetic problems associated with individual taxa (Voss et al., 2004a; Jansa and Voss, 2005), or on the evolutionary dynamics of newly sequenced nuclear loci (Jansa et al., 2006; Gruber et al., 2007). However, no comprehensive phylogenetic synthesis has yet been attempted, and much new morphological and molecular character data remain unanalyzed.

This monograph summarizes our collaborative research to date on didelphid phylogenetic relationships and concludes the first

phase of our ongoing evolutionary study of the family. Although we take this opportunity to review information that has previously been published elsewhere, many new results are reported herein. Among these, we describe morphological comparisons of didelphids with other plesiomorphic (polyprotodont) marsupial clades; we describe and illustrate integumental and craniodental traits not previously discussed in the literature; we report new sequence data from the Breast Cancer Activating 1 gene (BRCA1) and the von Willebrand Factor gene (vWF); we analyze didelphid phylogenetic relationships based on a new set of morphological and karyotypic characters together with sequence data from five protein-coding nuclear loci; we propose a new suprageneric classification consistent with our analytic results; and we provide morphological descriptions and cranial illustrations of all currently recognized genera to facilitate taxonomic identifications.

Materials and Methods

PHYLOGENETIC ASSUMPTIONS AND TAXON SAMPLING: Our phylogenetic analyses are based on the assumption of didelphid monophyly, which is strongly supported by a variety of nuclear-gene sequence datasets (e.g., Jansa and Voss, 2000; Amrine-Madsen et al., 2003; Meredith et al., 2008). Our ingroup terminals (table 2) consist of 44 species representing every currently recognized didelphid genus and subgenus, including all of the species previously analyzed by Jansa and Voss (2000, 2005), Voss and Jansa (2003), Voss et al. (2004a, 2005), Jansa et al. (2006), and Gruber et al. (2007). Altogether, this is by far the most taxon-dense and character-rich didelphid dataset ever analyzed.

The outgroups for this study include representatives of every extant ordinal-level clade that has ever been recovered within one or two nodes of Didelphidae in previous analyses of marsupial relationships, including caenolestids (Paucituberculata), dasyurids (Dasyuromorphia), *Dromiciops* (Microbiotheria), and peramelids (Peramelemorphia). We did not include *Notoryctes* (Notoryctemorphia) or diprotodontians because these taxa have never been considered close to didelphids, and because their highly derived morphologies raise many unresolved issues of homology that are beyond the scope of this study.

COMPARATIVE MORPHOLOGY: Our morphological comparisons are based on skins, skulls, and fluid-preserved specimens (appendix 1), which we examined for discretely varying traits that could be scored for most of the terminal taxa in our analysis. Additionally, we summarize information about other phenotypic characters that, although not suitable for phylogenetic analysis due to continuous variation (e.g., body size), provide taxonomically useful descriptors. Information about morphological character variation among nondidelphid marsupials is largely based on our scoring of outgroup terminal taxa, but we also include remarks on the morphology of other Old World marsupials where these seem relevant or interesting.

To provide a maximally user-friendly reference, our morphological observations are summarized in two different formats. First, we describe taxonomic comparisons using normal (nontelegraphic) prose in the body of the text. These accounts, organized organ-system-by-organ system, are accompanied as necessary by illustrations of representative specimens. Second, we summarize morphological descriptors taxon-by-taxon using telegraphic prose in the generic accounts of our classification. Although largely redundant with our data matrix (appendix 4), these generic descriptions are easier to use for taxonomic identifications, and they provide an opportunity to summarize relevant observations that were not encoded as characters.

Formal character descriptions (in appendix 3) are accompanied by technical details about coding procedures and ordering criteria. Our criteria for character choice were described at length by Voss and Jansa (2003), so they are not repeated here. The only noteworthy methodological change in this study concerns our coding of polymorphisms. As in our previous study, we ignored rare variants (on the assumption that all characters are polymorphic given sufficiently large samples) and coded only those polymorphisms represented by nearly equal frequencies of alternative states (e.g., when

TABLE 2
Marsupial Terminal Taxa Scored for Phylogenetic Analysis[a]

	Percent complete character data[b]		
	Nonmolecular	Molecular	Combined
INGROUP:			
Didelphidae			
Caluromys lanatus	99.2	100	100
Caluromys philander	99.2	100	100
Caluromysiops irrupta	93.7	16.5	17.8
Chacodelphys formosa	86.0	0	1.5
Chironectes minimus	99.2	99.8	99.8
Cryptonanus chacoensis	98.4	95.2	95.3
Cryptonanus unduaviensis	93.0	99.8	99.7
Didelphis albiventris	100	99.1	99.1
Didelphis marsupialis	100	99.1	99.1
Didelphis virginiana	100	100	100
Glironia venusta	93.0	100	99.9
Gracilinanus aceramarcae	93.0	99.8	99.7
Gracilinanus agilis	95.3	99.7	99.6
Gracilinanus emiliae	95.3	99.8	99.7
Gracilinanus microtarsus	95.3	95.1	95.1
Hyladelphys kalinowskii	95.3	100	99.9
Lestodelphys halli	97.6	30.4	31.6
Lutreolina crassicaudata	99.2	100	100
Marmosa (Marmosa) lepida	96.1	100	99.9
Marmosa (Marmosa) mexicana	99.2	98.8	98.8
Marmosa (Marmosa) murina	99.2	98.6	98.6
Marmosa (Marmosa) robinsoni	99.2	98.8	98.8
Marmosa (Marmosa) rubra	92.2	99.7	99.6
Marmosa (Micoureus) demerarae[c]	99.2	98.5	98.5
Marmosa (Micoureus) paraguayana[c]	96.1	95.7	95.7
Marmosa (Micoureus) regina[c]	99.2	100	100
Marmosops impavidus	98.4	98.0	98.0
Marmosops incanus	96.8	99.0	99.0
Marmosops noctivagus	98.4	100	100
Marmosops parvidens	95.3	98.8	98.7
Marmosops pinheiroi	95.3	99.7	99.6
Metachirus nudicaudatus	98.4	98.9	98.9
Monodelphis brevicaudata	97.7	100	100
Monodelphis emiliae	96.1	100	99.9
Monodelphis peruviana[d]	92.3	100	99.9
Monodelphis theresa	89.9	100	99.8
Philander frenatus	97.7	100	100
Philander mcilhennyi	100	99.2	99.2
Philander opossum	99.2	99.1	99.1
Thylamys macrurus	96.1	99.8	99.7
Thylamys pallidior	96.1	98.3	98.3
Thylamys pusillus	98.4	95.7	95.7
Thylamys venustus	96.1	99.5	99.4
Tlacuatzin canescens	99.2	97.5	97.5
OUTGROUPS:			
Caenolestidae			
Caenolestes fuliginosus	86.9	63.3	63.7
Rhyncholestes raphanurus	85.3	62.5	62.9

	Percent complete character data[b]		
	Nonmolecular	Molecular	Combined
Dasyuridae			
Murexia longicaudata	95.3	57.9	58.5
Sminthopsis crassicaudata	96.1	42.1	43.0
Microbiotheriidae			
Dromiciops gliroides	99.2	63.3	63.9
Peramelidae			
Echymipera kalubu	95.3	63.2	63.8
Perameles gunnii	93.0	63.3	63.8

[a] Nomenclature follows Wilson and Reeder (2005) and Gardner (2008) except as noted.

[b] Number of filled (total minus empty) cells in the corresponding row of each data matrix, divided by the total number of cells (N= 129, 7320, and 7449 for nonmolecular, molecular, and combined data, respectively) × 100. For the nonmolecular data, empty cells include those scored as missing ("?") and those scored as inapplicable ("-"). For the molecular data, only unsequenced base pairs were counted as missing ("?"); gaps ("-") were counted as filled data cells.

[c] *Micoureus* was formerly treated as a full genus.

[d] Formerly identified as *Monodelphis adusta* (e.g., by Jansa and Voss, 2000; Voss and Jansa, 2003), our material is referable to *M. peruviana*, a distinct species recently resurrected from synonymy by Solari (2007).

presence and absence were both commonly observed for a given taxon). However, whereas we formerly (Voss and Jansa, 2003) treated such polymorphism as a separate state intermediate to the two fixed conditions, with transformations to and from the polymorphic state weighted as half-steps (the "scaled" option discussed by Wiens, 2000), we here conform with the prevailing custom of coding polymorphisms as taxonomic ambiguities (e.g., as "0/1" for a binary character). This coding change has minimal impact on our results (only weakly supported relationships are affected, even in separate analyses of morphology) but it facilitates likelihood modeling of morphological character evolution (Lewis, 2001) in Bayesian analyses of our combined datasets (see below).

MOLECULAR SEQUENCING AND HOMOLOGY COMPARISONS: The laboratory procedures we used for DNA amplification and sequencing (including the names and locations of primers used in PCR reactions) have already been described for three of the protein-coding nuclear loci analyzed in this report: IRBP (Jansa and Voss, 2000), Dentin Matrix Protein 1 (DMP1; Jansa et al., 2006), and Recombination Activating 1 Gene (RAG1; Gruber et al., 2007). In addition, we sequenced two other protein-coding nuclear genes as described below.

We amplified 2.1 kb of BRCA1 exon 11 from genomic DNA in two fragments using the primers listed in table 3. The first fragment, comprising the upstream 1.2 kb of the exon, was amplified using primers F1 paired with R1218 or F47 paired with R1343. The second, downstream fragment (ca. 1 kb) was amplified with primers F1163 or F1163a paired with R2078 or R2151. These amplification products were then used in a second round of PCR to generate smaller pieces of suitable size for sequencing. For the upstream fragment, either F1 or F47 was paired with R743, and F593 was paired with either R1218 or R1343. For the downstream fragment, F1163 or F1163a was paired with R1780, and F1697 was paired with either R2078 or R2151. A single fragment of ca. 1 kb was amplified from vWF exon 28 using either F104 or F120 paired with R1141. This product was then used in a second round of PCR in which F1 or F47 was paired with either R665 or R742, and F557 was paired with R1141.

Initial amplifications using genomic DNA as template were performed as 20 μl reactions using Ampli-Taq Gold polymerase (Perkin-Elmer Corp.) and recommended concentrations of primers, nucleotides, buffer, and $MgCl_2$. These genomic amplifications were performed using a four-stage touch-

TABLE 3
Primers Used to Amplify and Sequence BRCA1 and vWF

Primer name	Sequence
BRCA1- F1	5′ TCATTACTGCCTGAGATCACCAG
BRCA1- F47	5′ TATTGCCTAACACAGACAGCAT
BRCA1- F593	5′ CAACAATATTGAAGACAAAATATTAGGAAA
BRCA1- F1163	5′ ATGARACWGAACTACWGATCGATAG
BRCA1- F1163a	5′ AATGAGACTGAACTACAGATCGAT
BRCA1- F1697	5′ TTWGATGRTTGTTCATCYRAAAACAC
BRCA1- R743	5′ TTGATGAAATCCTCAGGCTGYAGGT
BRCA1- R1218	5′ GAAGYCTTCTGCTGCGTCTGA
BRCA1- R1343	5′ CTAACATTTGATCACTATCAGTAG
BRCA1- R1780	5′ TAAATAYTGGGTRTCRAGTTCACT
BRCA1- R2078	5′ GAAATTTCCTGGTTGTTTCCAGCAA
BRCA1- R2151	5′ TCCTTTTGATYAGGAACTTGTGAAATT
VWF- F104	5′ GGTGTGATGGAGCGTTTACACATCTC
VWF- F120	5′ GACTTGGCYTTYCTSYTGGATGGCTC
VWF- F557	5′ CCTGGGCTACCTCTGTGACCTGGT
VWF- R655	5′ CTTCTAGCACAAACACCACATCCAGAACCA
VWF- R743	5′ CTCACATCCATYCGTTGCATCA
VWF- R1141	5′ ATCTCATCSGTRGCRGGATTGC

down protocol as described in Jansa and Voss (2000). Reamplification reactions were performed using Taq DNA polymerase (Promega Corp.) in 25 µl reactions for 30 PCR cycles. The resulting PCR products were sequenced in both directions using amplification primers and dye-terminator chemistry on an AB 3700 automated sequencer.

We searched the draft *Monodelphis domestica* genome using the BLAT (modified BLAST; Kent, 2002) algorithm to determine the copy number and chromosomal location of query sequences from *M. brevicaudata*. As reported on the Ensemble database (www.ensemble.org/index.html), the available reference genome (assembly MonDom5) was released on October 2006 and has a base coverage of approximately 7.3×.

ALIGNMENT AND PHYLOGENETIC ANALYSIS: We aligned DNA sequences with reference to translated amino-acid sequences using MacClade 4.08 (http://macclade.org). Aligned sequences were then analyzed phylogenetically using maximum parsimony (MP) as implemented by PAUP* ver. 4.0b10 (Swofford, 1998), maximum likelihood (ML) as implemented by GARLI ver. 0.95 (Zwickl, 2006), and Bayesian inference as implemented by MrBayes ver. 3.1.1 (Ronquist and Huelsenbeck, 2003). For MP

analyses, all molecular characters were treated as unordered and equally weighted, and all tree searches were heuristic with at least 10 replicates of random stepwise taxon addition followed by tree bisection-reconnection (TBR) branch swapping. To choose the best models of nucleotide substitution for ML and Bayesian analyses, we examined the fit of various models separately for each of our five gene partition (IRBP, vWF, BRCA1, DMP1, and first and second codon positions of RAG1) based on neighbor-joining trees of Jukes-Cantor-corrected distances using both hierarchical likelihood-ratio tests (hLRTs) and the Akaike Information Criterion (AIC) as implemented in ModelTest 3.7 (Posada and Crandall, 1998). Where the two approaches disagreed on model choice, we used the model selected by the AIC for reasons outlined by Posada and Buckley (2004). For both ML and Bayesian searches, the best-fit model was specified, but model parameter values were not fixed. For ML analyses, we conducted three independent runs of genetic-algorithm searches in GARLI, with random starting topologies and automatic termination after 10,000 generations with no improvement in log-likelihood scores. For Bayesian analysis of each gene partition, we conducted two independent runs of Metrop-

olis-coupled Markov-chain Monte Carlo (MCMCMC), each with one cold and three incrementally heated chains. For each run, we assumed uniform-interval priors for all parameters, except base composition, which assumed a Dirichlet prior. Runs were allowed to proceed for 5×10^6 generations, and trees were sampled every 100 generations. We evaluated the burn-in for each run, and pooled the post-burn-in trees to calculate estimated parameter distributions and posterior probabilities for each node. We assessed nodal support from MP and ML analyses using nonparametric bootstrapping (Felsenstein, 1985). Bootstrap values for the parsimony analyses (MPBS) were calculated in PAUP* from 1000 pseudoreplicated datasets, each of which was analyzed heuristically with 10 random-addition replicates with TBR branch swapping. Bootstrap values for the likelihood analysis (MLBS) were calculated in GARLI using genetic-algorithm searches of 1000 pseudoreplicated datasets, allowing model parameters to be estimated for each pseudoreplicate.

We analyzed the combined-gene dataset using ML as implemented in RAxML-VI-HPC (ver. 2.2.3; Stamatakis, 2006). We specified the GTRMIX model, which performs initial tree inference using a GTRCAT approximation, with final topology evaluation performed under a GTRGAMMA model. We allowed parameters to be estimated independently across the five gene partitions. To evaluate nodal support for this combined-gene, mixed-model analysis, we performed 1000 bootstrap replicates, again allowing model parameters to be estimated independently across the five genes. We also performed a Bayesian analysis of the combined-gene dataset, using the same MCMCMC settings given above. For this analysis, we specified the best-fit model for each gene, decoupled estimation of substitution parameters across the partitions, and allowed each gene to assume a separate rate.

We analyzed the nonmolecular (morphological + karyotypic) data alone and in combination with the molecular data using MP and Bayesian approaches. Due to the large number of suboptimal trees recovered from parsimony analysis of the nonmolecular dataset, we first performed 1000 random-taxon-addition replicates with TBR branch swapping, but saved only 10 trees per replicate. We then used this pool of 10,000 trees as the starting point for an unbounded heuristic search. Parsimony analysis of the combined (molecular + nonmolecular) dataset did not exhibit this problem; therefore, we analyzed the combined dataset using unbounded heuristic searches with 1000 replicates of random-taxon addition and TBR branch swapping. For Bayesian analysis of the morphological dataset alone, we specified the Mkv model (Lewis, 2001) with a Γ-distributed rate parameter and ascertainment bias corrected for omission of constant characters (lset coding = variable). For Bayesian analysis of the combined (molecular + nonmolecular) dataset, we specified this same model for the morphological data and applied the best-fit model to each of the five gene partitions. As above, we allowed parameters to be estimated independently across all partitions and used the same MCMCMC settings. To assess the impact of the large amount of missing data from *Chacodelphys*, we performed all analyses that included nonmolecular characters with and without this taxon.

ONLINE DATA ARCHIVES: All of the new molecular sequences produced for this study have been deposited in GenBank with accession numbers FJ159278–FJ159314 and FJ 159316–FJ159370 (for a complete list of GenBank accession numbers of all analyzed sequences, old and new, see table 9). All of our datasets, selected ML and Bayesian analyses, and associated trees have been deposited on TreeBase (http://www.treebase.org) with accession numbers S2164, M4107, and M4108. Our nonmolecular data matrix has also been deposited on MorphoBank (http://morphobank.geongrid.org) with accession number X600.

COMPARATIVE MORPHOLOGY

The literature on didelphid comparative morphology is widely scattered, and no adequate review of this topic has yet been published. Although the following accounts are far from comprehensive, they include most of the anatomical features that have been surveyed widely among extant genera and that provide relevant taxonomic infor-

mation.[1] In effect, such information comes from commonly available materials that can be examined without dissection or other special preparations. Therefore, microscopic features (e.g., those of the spermatozoa; Temple-Smith, 1987) and visceral characters (e.g., of the digestive tract; Santori et al., 2004) are not reviewed below, nor are osteological traits that require X-ray computed tomography, serial sectioning, or destructive methods for their study.

Size and External Features

Most opossums are externally unremarkable mammals with pointed muzzles, large rhinaria, well-developed vibrissae, prominent eyes, membranous ears, nonspinous pelage, subequal limbs, pentadactyl feet, and naked tails. In many of these respects they resemble other plesiomorphic marsupials (e.g., *Dromiciops* and dasyurids) as well as certain unspecialized placentals (e.g., solenodontids, rice tenrecs, gymnures, and tree shrews). Closer inspection, however, reveals numerous distinctive and phylogenetically informative details of didelphid external morphology.

SIZE: Didelphids are small to medium-sized mammals. The smallest Recent species is probably *Chacodelphys formosa*, the young adult holotype of which had a head-and-body length of 68 mm and probably weighed about 10 g (Voss et al., 2004a). By contrast, the largest living opossum, *Didelphis virginiana*, can measure almost 500 mm in head-and-body length and weigh more than 3000 g (Hamilton, 1958). Most didelphids, however, range in head-and-body length from about 100 to 300 mm and weigh between about 20 and 500 g (table 4). Although some authors have recognized "large", "medium", and "small" opossums, taxonomic assignments to discrete size categories are often arbitrary and sometimes misleading. For example, Reig et al. (1987: character 25) scored *Metachirus* as "large" and *Caluromys* as "medium" in their phylogenetic analysis, but linear measurements and weights that we compiled suggest that these taxa are indistinguishable in size. More taxonomically

comprehensive compilations of morphometric data will probably document a continuum of didelphid size distributions.

By comparison, Old World marsupials include some species that are smaller and others that are much larger than any didelphid. The smallest living Australian species, for example, is said to be *Planigale ingrami*, with an adult weight of only about 4 g, and the largest is *Macropus rufus*, males of which are said to weigh as much as 85 kg (Dawson et al., 1989). The extinct Pleistocene species *Diprotodon optatum*, however, may have weighed almost 2800 kg (Wroe et al., 2004).

RHINARIUM AND MOUTH: The rhinarium, a prominent pad of naked glandular skin surrounding the nostrils, is divided by a median crease or sulcus (sulcus medianus; Ade, 1999) that extends from between the nares to the upper lip in all examined didelphids. The part of the rhinarium that borders the upper lip (pars supralabialis) is broad, and its ventral margin is notched by one or two distinct grooves on each side of the median sulcus (fig. 1). Two ventrolateral grooves are present on each side in most examined taxa, but only a single groove is present in *Chironectes*, *Didelphis*, *Lestodelphys*, *Lutreolina*, *Metachirus*, *Monodelphis*, *Philander*, and *Thylamys pallidior*. Dasyurids and *Dromiciops* have rhinaria that are essentially similar in gross morphology to those of didelphids, with a pars supralabialis that makes broad contact with the upper lip; however, only a single ventrolateral groove is present in these taxa (Pocock, 1926: figs. 26–28). By contrast, the supralabial part of the rhinarium is reduced to a narrow philtrum in caenolestids and peramelids, such that the groove-bearing ventral rhinarial margin of other marsupials is effectively absent.

The mouth is large in all didelphids, with a posterior angle (angulis oris; Brown, 1971) that extends posteriorly to a point below the eye; the upper and lower oral margins are smooth or irregularly wrinkled and anatomically featureless. Most other marsupials have anatomically featureless oral margins like those of didelphids, but caenolestids are uniquely provided with reciprocating fleshy lappets of unknown function on the upper and lower lips (Osgood, 1921: pl. 2; Bublitz,

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[1] An important exception is postcranial skeletal morphology, the topic of an independent study (Flores, 2009).

TABLE 4
External Measurements (mm) and Weights (g) of Exemplar Didelphid Species[a]

	N[b]	Head and Body[c]	Tail[d]	Weight
Caluromys (Caluromys) philander[e]	7	261 (224–279)	390 (373–410)	330 (220–390)
Caluromys (Mallodelphys) lanatus[f]	8	278 (270–296)	422 (400–446)	412 (349–500)
Caluromysiops irrupta[g]	1	260	310	496
Chironectes minimus[h]	6	289 (276–307)	348 (316–362)	605 (520–700)
Cryptonanus unduaviensis[i]	8	105 (97–121)	122 (112–135)	25 (15–40)
Didelphis marsupialis[e]	9	419 (405–446)	434 (366–497)	1351 (1025–1700)
Glironia venusta[j]	2	194 (188–201)	208 (201–215)	130 (129–130)
Gracilinanus agilis[k]	11	98 (86–109)	137 (121–162)	25 (18–34)
Hyladelphys kalinowskii[e]	3	77 (76–78)	111 (107–113)	16 (13–18)
Lestodelphys halli[l]	1	132	88	76
Lutreolina crassicaudata[m]	11	295 (241–342)	283 (242–336)	530 (300–800)
Marmosa (Marmosa) murina[n]	13	133 (118–152)	173 (156–195)	51 (35–80)
Marmosa (Micoureus) regina[f]	41	180 (142–209)	262 (238–294)	118 (70–164)
Marmosops noctivagus[f]	16	138 (118–155)	183 (154–202)	51 (30–70)
Marmosops pinheiroi[e]	11	103 (94–121)	149 (137–156)	27 (21–33)
Metachirus nudicaudatus[e]	9	262 (249–287)	345 (326–370)	380 (260–480)
Monodelphis emiliae[f]	6	107 (97–113)	50 (45–53)	30 (20–38)
Philander opossum[e]	11	301 (264–346)	306 (280–333)	549 (380–695)
Thylamys karimii[o]	33	104 (78–129)	80 (69–106)	28 (16–43)
Thylamys macrurus[o]	6	112 (101–126)	144 (136–153)	39 (30–55)
Tlacuatzin canescens[p]	7	137 (126–149)	137 (131–145)	— (38–60)

[a] Tabulated statistics are the sample mean (rounded to the nearest whole unit) and the observed range (in parentheses) of measurements and weights recorded from dentally mature specimens; male and female data were combined to increase sample size despite apparent sexual dimorphism in some species. Most genera are represented by a single exemplar species, but several genera with recognized subgenera or that include taxa differing conspicuously in size or body:tail ratios are represented by additional species.

[b] Sample size.

[c] Obtained by subtracting length of tail from total length following the standard American protocol.

[d] Basal flexure to fleshy tip.

[e] French Guianan specimens measured by Voss et al. (2001).

[f] Measurements and weights from western Brazilian specimens (Patton et al., 2000).

[g] Measurements and weight of AMNH 208101; because this was a zoo specimen that may have been obese, the weight datum is suspect.

[h] From Paraguayan specimens (UMMZ 126289, 134022, 134023, 134025, 134559, 134560).

[i] From Bolivian specimens measured by Voss et al. (2005).

[j] Measurements and weight of MMD 607 (collected near Iquitos, Peru; to be deposited in the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima; M.M. Díaz, personal commun.) and INPA 5237 (collected near Mirassol d'Oeste, Mato Grosso, Brazil; Santos Filho et al., 2007).

[k] From Paraguayan specimens (UMMZ 124675, 126104, 133998–134006).

[l] Measurements and weight from MVZ 173727.

[m] From Paraguayan specimens (UMMZ 126109–126111, 126113, 134010, 134011, 134017–134021).

[n] From Surinamese specimens measured by Voss et al. (2001).

[o] From Carmignotto and Monfort (2006).

[p] External measurements from Oaxacan specimens unaccompanied by weight data (AMNH 3111/2433, 3111/2434, 3114/2437, 148969, 149104, 165651, 165653); range of weights from Zarza et al. (2003).

1987: fig. 4; Patterson and Gallardo, 1987: fig. 3).

FACIAL VIBRISSAE AND MARKINGS: Didelphid facial vibrissae are grouped into discrete tracts that are easily homologized with those described and illustrated by Pocock (1914), Lyne (1959), and Brown (1971), whose terminology is followed here. All of the taxa we examined (including representative species from every genus) exhibit well-developed mystacial, submental, interramal, superciliary (supraorbital), and genal vibrissae. La-
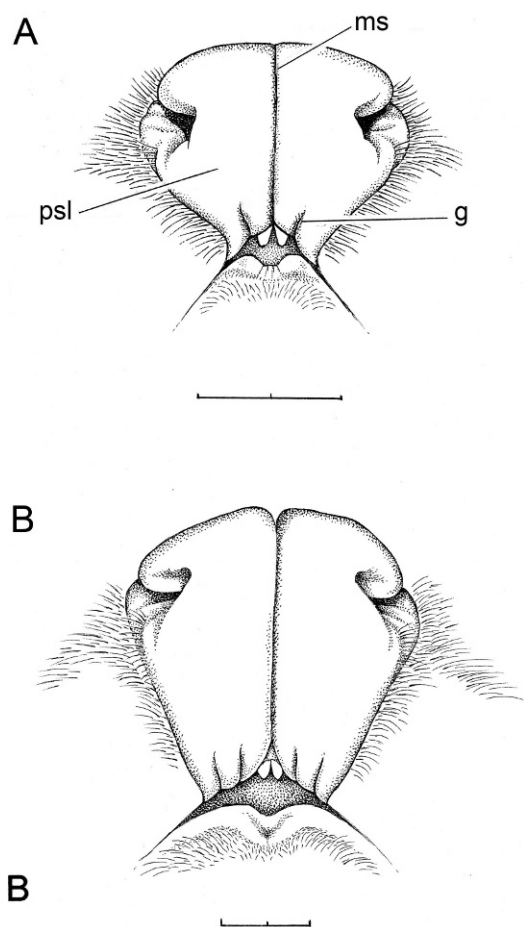
Fig. 1. Ventral view of rhinarium in *Thylamys pallidior* (**A**, UMMZ 156349) and *Marmosa robinsoni* (**B**, UMMZ 117236). Both species have a broad pars supralabialis (**psl**) that contacts the upper lip. Only a single groove (**g**) is present along the ventral margin of the pars supralabialis on each side of the median sulcus (**ms**) in *T. pallidior*, whereas two ventrolateral grooves are present in *M. robinsoni*. Scale bars = 2 mm.

beled illustrations of didelphid facial vibrissae are provided by Pocock (1914: fig. 1A) and Lyne (1959: fig. 2). Most other plesiomorphic marsupials closely resemble didelphids in cranial vibrissal traits, but caenolestids lack interramal vibrissae (Lyne, 1959).

Didelphids exhibit conspicuous taxonomic variation in facial markings (frontispiece; Voss and Jansa, 2003: fig. 3). In *Caluromys*, a median streak of dark fur, unconnected with any other dark marking, extends from the rostrum to the frontal region. In other didelphids, a chevron of dark coronal fur sometimes extends anteriorly between the ears and down the rostral midline, but the condition seen in *Caluromys* is distinctive and apparently nonhomologous. No nondidelphid marsupial that we examined has a dark midrostral stripe.

The fur surrounding the eye is not distinctively colored in *Caluromysiops*, *Lutreolina*, or *Monodelphis*, but most other didelphids have masklike markings. A circumocular mask or ring of dark (usually blackish) fur that contrasts sharply with the paler (usually brownish, whitish, or grayish) color of the crown and cheeks is present in *Glironia*, *Lestodelphys*, and ''marmosines'' (taxa formerly included in ''*Marmosa*'' sensu Tate, 1933). Species of *Caluromys* have essentially similar reddish-brown eye rings that contrast with grayish cheeks and crowns. A blackish mask is likewise present in all examined species of *Didelphis*, but this marking is inconspicuous in *D. marsupialis* and *D. virginiana*. A blackish mask is also present in *Metachirus*, *Chironectes*, and *Philander*, but the dark circumocular fur in these taxa is usually continuous with dark fur on the crown of the head. Among nondidelphid marsupials, dark circumocular masks are present in *Dromiciops*, some dasyurids (e.g., *Sminthopsis crassicaudata*), a few peramelemorphians (e.g., *Echymipera kalubu*), and some small arboreal diprotodontians (e.g., *Petaurus breviceps*); only one examined outgroup taxon, *Echymipera kalubu*, has a mask that is more or less continuous with dark coronal fur.

A distinct whitish supraocular spot is consistently present in species of *Metachirus* and *Philander*, resulting in the ''four-eyed'' marking by which these animals are commonly known. Most other didelphids lack pale supraocular markings. (An indistinct pale bar above each eye in *Chironectes* appears to be part of the unique transverse banding pattern in that taxon rather than a homologue of the condition seen in *Metachirus* and *Philander*.) We have not examined any nondidelphid marsupial with pale supraocular spots.

GULAR GLAND: As described by Tate (1933: 30), many didelphids have a cutaneous

gular (throat) gland, the presence of which is indicated on dried skins and fluid-preserved specimens by a bare median patch of skin; often, but not invariably, the surrounding fur is discolored. According to Barnes (1977: 390), this secretory region contains ''hypertrophied apocrine sudoriferous glands and sebaceous glands, both confined to the thickened dermis.'' External signs of glandular activity tend to be maximally developed in fully mature males (loc. cit.).

No unambiguously glandular throat patch was observed in any examined specimens of *Caluromys*, *Caluromysiops*, *Chironectes*, *Hyladelphys*, *Lutreolina*, *Philander*, or *Tlacuatzin*. By contrast, fully adult male specimens of *Cryptonanus*, *Gracilinanus*, *Lestodelphys*, and *Thylamys* usually exhibit well-developed gular glands. A gular gland is also present on the young adult male holotype (and only known skin) of *Chacodelphys formosa*. Other didelphid genera (*Marmosa*, *Marmosops*, and *Monodelphis*) include some species that consistently develop adult male gular glands and others that just as consistently show no trace of such organs (Voss and Jansa, 2003). Although adult male *Didelphis* often have discolored gular fur, no glandular skin is macroscopically distinguishable. Because we were not able to examine any fully adult male specimens of *Glironia*, the occurrence of gular glands in this taxon is unknown.

Gular (or sternal) glands that are macroscopically and histologically similar to those of didelphids are present in most dasyurids (Cooper et al., 2005), but other plesiomorphic outgroup taxa (e.g., caenolestids, peramelids, *Dromiciops*) seem to lack all external traces of glandular activity on the throat or chest.

BODY PELAGE: All didelphids have one or more tracts of postcranial vibrissae (Brown and Yalden, 1973), including ulnar-carpal vibrissae (at the wrist), medial antebrachial vibrissae (at or near the middle of the forearm), anconeal vibrissae (at the elbow), and/or calcaneal vibrissae (on the ankle). Lyne (1959) reported the occurrence of postcranial vibrissae in several didelphid species based on his examination of pouch young, whose sensory hair follicles are easily seen because they are not obscured by coat hairs. Unfortunately, postcranial vibrissae are much harder to observe on fully furred adult specimens, the only material commonly available for most species. We found ulnar-carpal and medial antebrachial vibrissae on most examined didelphids, whereas anconeal and calcaneal vibrissae were often inapparent.

All didelphids have soft (nonspinous) fur consisting of two or more distinct types of hairs whose density and morphology determine the appearance and texture of the coat. Some taxa (e.g., *Caluromys*) have somewhat woolly fur that does not lie flat or exhibit the glossy highlights typically seen in the pelts of many other taxa, but textural differences are hard to define by objective criteria that can be used for character-state definitions or taxonomic diagnoses. The only structural (nonpigmental) feature of didelphid body pelage that seems useful in this context is the presence of uniquely long, coarse guard hairs that project conspicuously from the underfur in species of *Didelphis*.

The dorsal body pelage of most didelphids is uniformly colored and unpatterned, usually some shade of brownish or grayish, but some taxa are distinctively marked (see illustrations in Eisenberg, 1989; Redford and Eisenberg, 1992; Pérez-Hernández et al., 1994; Reid, 1997; Eisenberg and Redford, 1999). Blackish transverse bars connected middorsally on a pale-grayish background, for example, characterize *Chironectes*; dark scapular stripes are unique to *Caluromysiops*; three longitudinal stripes are present in several species of *Monodelphis* (e.g., *M. theresa*); a grayish middorsum contrasting with reddish flanks is exhibited by other species in that genus (e.g., *M. brevicaudata*); and a grayish midbody contrasting with reddish head and rump is seen in others (e.g., *M. emiliae*). The subtle but consistently diagnostic ''tricolor'' shading of *Thylamys* and *Lestodelphys* was described by Tate (1933: 209):

> Instead of the usual bicolor system composed of a dorsal color, paling a little on the sides, which is replaced at a generally well-marked transition line by a distinct ventral color, the *elegans* group [= *Thylamys*] displays three distinct shades, separated from each other along each side by two lines of transition. The additional lines are subdorsal, running from a point at the center of

the frons [forehead] past the inner edge of each ear (not including it), and straight backward through scapulae and hips, where they again approach the median line of the body and merge with the tail. This pair of lines encloses the major part of the dorsal area of head and body, the color of the area being very dark brownish-gray or grayish fuscous. The fuscous area is pointed at front, projecting forward between the ears, and narrows again to a point as it merges with the dark color of the upper surface of the tail. The second [lateral] area, light gray in color, frequently tinged with buffy or yellowish, extends [on each side] between the dark dorsal region and the edge of the belly color at the normal transition line. Ventral color either buffy, grayish, or snowy white.

The hair bases of the dorsal fur are heavily pigmented, usually dark gray (or grayish), in most didelphids, but species of *Didelphis* uniquely exhibit white dorsal underfur.

The ventral pelage also exhibits noteworthy taxonomic variation among didelphids. In some species the ventral fur is "gray-based," a descriptor that applies when the individual hairs are grayish basally and abruptly paler (usually whitish, yellowish, or brownish) distally; the overall color of the ventral fur then depends on the degree to which the dark basal pigmentation shows through the paler superficial hue. In other species, the ventral fur is partially or entirely "self-colored," a descriptor that applies when the individual hairs have the same pigmentation (usually whitish) from root to tip. Because marked differences in the patterning of gray-based versus self-colored ventral pelage can occur among closely related (congeneric) species, such variation is often described and illustrated in the revisionary taxonomic literature (e.g., Patton et al., 2000: fig. 41). However, the existence of numerous intermediate conditions spanning the entire range of taxonomic variation in ventral color patterns (e.g., from entirely gray-based to completely self-white ventral fur) precludes meaningful phylogenetic scoring of this character.

Whereas most of the pelage colors (and color patterns) described above are preserved on museum skins that have been protected in dark cabinets from the bleaching effects of light, other colors that can be striking in life fade quickly after death. The ventral pelage

of live *Monodelphis emiliae*, for example, has been described as "bright glowing violaceous pink" (Emmons, 1997: 34), a lurid hue that is not retained in any examined museum specimens. What little is known about such fugitive pigments (some of which fluoresce under ultraviolet light) was summarized by Pine et al. (1985).

Most other marsupials have unremarkable body pelage that essentially resembles the common didelphid condition as described above, but postcranial vibrissae are reduced or absent in a few clades (Lyne, 1959) and peramelemorphians have stiff, dorsally grooved guard hairs (illustrated in cross section by Lyne and McMahon, 1951: figs. 51, 60) that impart a distinctively harsh, spinous texture to their fur. Most other marsupials also resemble didelphids in having unpatterned dorsal fur, although there are noteworthy examples of apparently convergent markings (e.g., those of *Dromiciops* somewhat resemble *Chironectes*'; Marshall, 1978b) and some strikingly divergent ones (e.g., the transverse sacral barring seen in *Perameles gunnii*; Lyne, 1951: pl. 1B). All examined outgroup taxa have dark dorsal underfur.

WRIST: The wrists of males and females are morphologically similar and externally featureless in most didelphids, but striking sexual dimorphism is present in certain small arboreal and scansorial forms (Lunde and Schutt, 1999). Grossly enlarged glabrous tubercles supported internally by carpal ossifications are exhibited by large adult males of *Cryptonanus*, *Gracilinanus*, *Marmosops*, *Tlacuatzin*, and some species of *Marmosa*. Two distinct kinds of tubercles can be distinguished, consisting of lateral ("ulnar") tubercles supported internally by the pisiform, and medial ("radial") tubercles supported by the prepollex (op. cit.). Although some intraspecific variation in the development of carpal tubercles has been documented, most of it can be attributed to ontogeny: tubercles are consistently present in the largest adult male specimens of species in which such structures occur, whereas they may be lacking in some smaller (presumably younger) conspecific males. Lunde and Schutt (1999) plausibly suggest that these structures function as clasping devices during copulation.
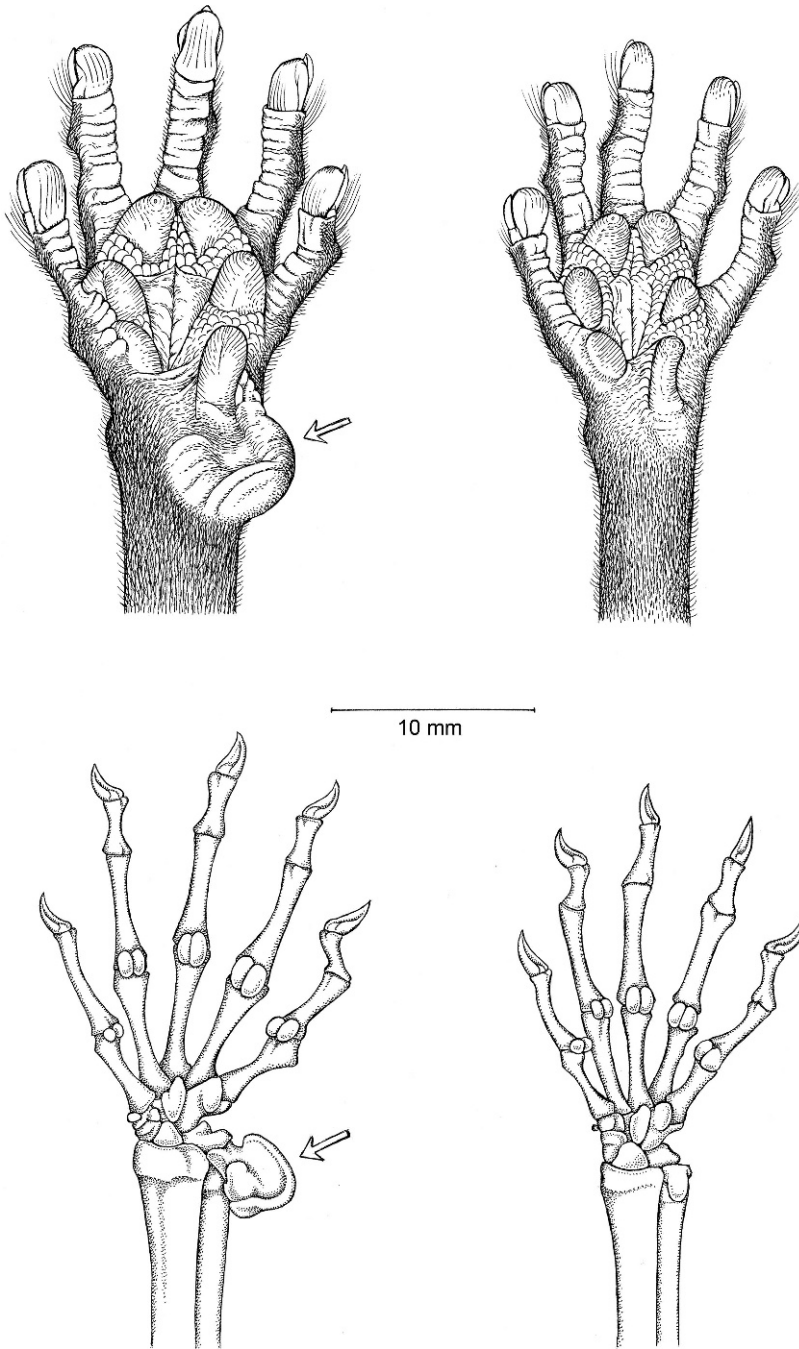
Fig. 2. Sexually dimorphic wrist morphology of *Marmosops pinheiroi*. Adult males (**left,** AMNH 267346) possess an externally obvious lateral carpal tubercle that is supported internally by an enlarged pisiform bone (arrows); females (**right,** AMNH 267342) do not exhibit this trait.

Lateral carpal tubercles (fig. 2) are more widespread than medial carpal tubercles, occurring in all taxa that exhibit any externally obvious sexual dimorphism in the wrist. We found these structures to be consistently present in large adult male specimens of *Cryptonanus*, *Gracilinanus*, *Marmosops*, *Tlacuatzin*, and most species of *Marmosa*. In addition, we observed medial carpal tubercles (Lunde and Schutt, 1999: fig. 3) in *Marmosa demerarae*, *M. mexicana*, *M. paraguayana*, *M. regina*, *M. robinsoni*, and *M. rubra*. Other didelphids appear to lack sexually dimorphic carpal tubercles,[2] but we were not able to determine whether or not such structures are present in *Chacodelphys* and *Glironia* because no fully adult male specimens of either genus are currently available for study.

The water opossum *Chironectes* has carpal tubercles that, uniquely, are neither sexually dimorphic nor ontogenetically variable. In this taxon, juveniles and adults of both sexes possess a large, fleshy process on the outside of the wrist, resembling a sixth finger, that is supported internally by the pisiform (Augustiny, 1942: fig. 16; Mondolfi and Medina, 1957: fig. 14; Oliver, 1976: fig. 1b).

No examined nondidelphid marsupial has carpal tubercles of any kind.

MANUS: The didelphid hand is provided with five well-developed clawed digits (fig. 3). When the digits are flexed, their tips converge toward the center of the palm, and it seems likely that at least the arboreal and scansorial forms—which tend to have relatively longer fingers than terrestrial taxa (Lemelin, 1999; Kirk et al., 2008)—are capable of manual prehension. In most didelphids, the manual digits are more or less evenly spaced, but in some arboreal taxa (e.g., *Caluromys*, *Caluromysiops*, *Marmosa*) the gap between dII and dIII is somewhat larger than the gaps separating other pairs of adjacent fingers, and it is possible that these taxa are incipiently schizodactylous (sensu Haines,

1958). The pollex (dI) of *Chironectes* is set off from the other manual digits by a wide gap and appears to be pseudo-opposable (sensu Napier, 1961); in fluid-preserved specimens it is often folded across the palm (Augustiny, 1942: fig. 16).

According to Tate (1947), the third and fourth digits of the didelphid manus are subequal and longer than the other fingers (fig. 3C), proportions that correspond to the paraxonic morphotype defined by Brown and Yalden (1973). Not all didelphids have paraxonic forefeet, however. Instead, many have a mesaxonic manus in which dIII is distinctly longer than the other fingers; taxa that exhibit this condition include *Chacodelphys*, *Chironectes*, *Didelphis*, *Lestodelphys*, *Lutreolina*, *Marmosops* (fig. 3B), *Metachirus*, *Monodelphis* (fig. 3A), *Philander*, and *Thylamys*. Yet another alternative condition is seen in *Caluromys* and *Caluromysiops*, in which dIV is slightly but distinctly longer than dIII (fig. 3D).

Many didelphids have small, weakly recurved manual claws that do not extend much (if at all) beyond the fleshy apical pad of each digit (fig. 3B, C), but some arboreal taxa such as *Caluromys* (fig. 3D) and others that are strictly terrestrial such as *Monodelphis* (fig. 3A) have large manual claws that extend well beyond the apical pads. The large manual claws of *Glironia* (not illustrated) are unusually deep, laterally compressed, and strongly recurved. Although illustrated taxonomic differences in claw length are striking, intermediate morphologies observed among other forms (e.g., *Hyladelphys*) make it difficult to recognize discrete character states for taxonomic analysis.

Like most other plantigrade mammals (Whipple, 1904; Brown and Yalden, 1973), didelphids usually have two well-developed metacarpal pads (thenar, hypothenar) and four interdigital pads on the hairless ventral (plantar or volar) surface of the manus. These six pads encircle a central palmar region that is either smooth or sparsely tubercular (as in most didelphids; see Hershkovitz, 1997: fig. 6A) or densely covered with small convex tubercles (as in *Chacodelphys*, *Lestodelphys*, and most species of *Thylamys*; see Carmignotto and Monfort, 2006: fig. 3C). In almost all species, the epidermis that covers

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[2] Prochel and Sánchez-Villagra (2003) reported that adult males of *Monodelphis domestica*, a species that lacks external evidence of sexual dimorphism in the wrist, nevertheless have significantly larger and more robust pisiforms than females. This condition could obviously be interpreted as a state intermediate to complete absence of sexual dimorphism in the wrist on the one hand and the very marked dimorphism exhibited by species with male carpal tubercles on the other.
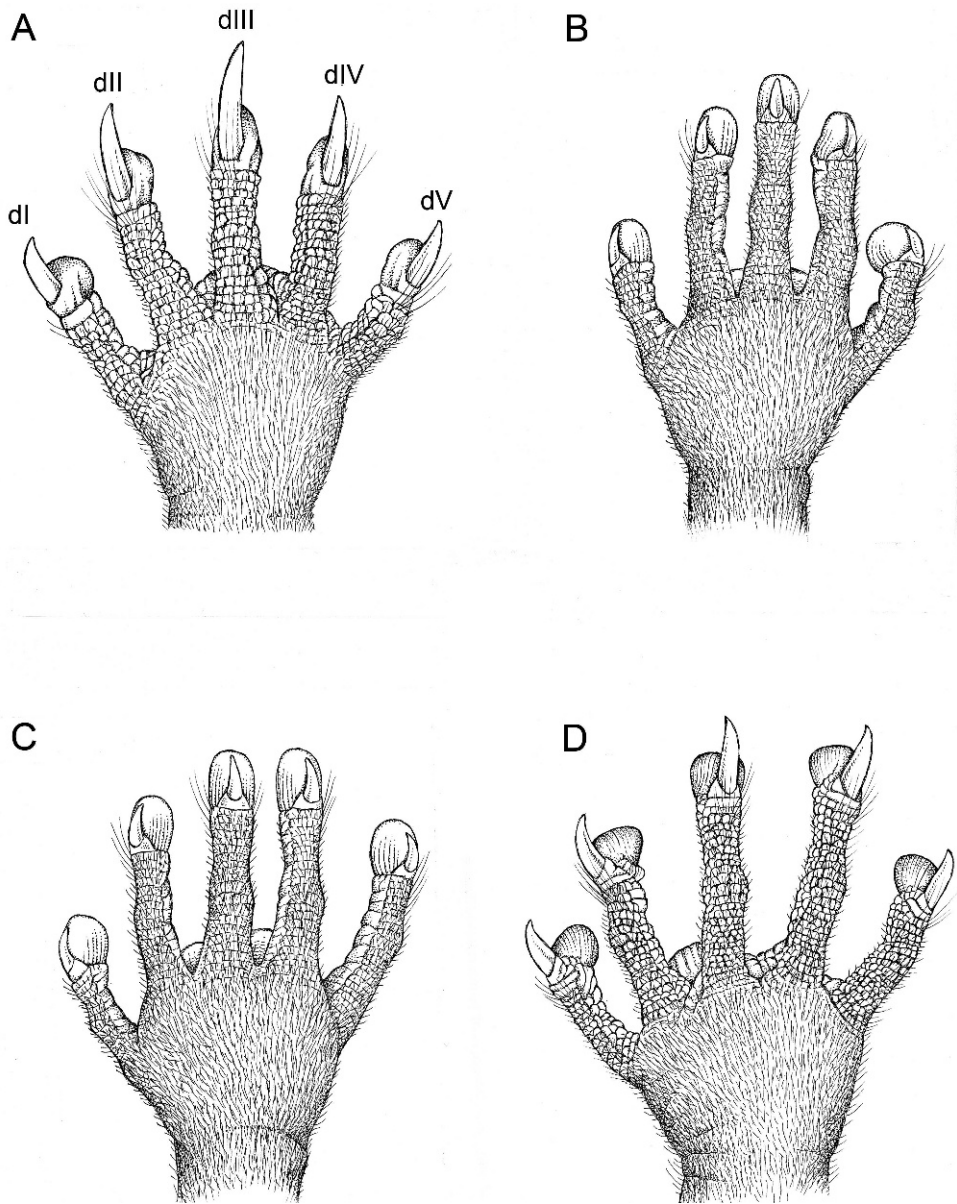
Fig. 3. Dorsal views of right forefeet of *Monodelphis brevicaudata* (**A,** AMNH 140466), *Marmosops incanus* (**B,** MVZ 197629), *Marmosa robinsoni* (**C,** AMNH 259983), and *Caluromys philander* (**D,** AMNH 7433) illustrating generic differences in claw size and digital proportions. *Monodelphis* and *Marmosops* both have mesaxonic forefeet in which the third digit (dIII) is longest, whereas *Marmosa* has a paraxonic forefoot in which dIII and dIV are subequal. In *Caluromys*, dIV is the longest manual digit.

the plantar pads is sharply differentiated from that of the surrounding plantar surface because it is provided with dermatoglyphs (friction or papillary ridges; Hamrick, 2001) resembling those on human fingertips. Plantar pads tend to be larger and to have more pronounced dermatoglyphs in arboreal opossums (e.g., *Caluromys*) than in terrestrial forms (e.g., *Monodelphis*), but a few didelphids exhibit qualitatively different morphologies.

The plantar pads of two Brazilian species of *Thylamys* (illustrated by Carmignotto and Monfort, 2006: figs. 3a, 3b) are fused together and fill the entire palmar region rather than encircling a central palmar surface as in other didelphids. Additionally, only the apices of the plantar pads are provided with dermatoglyphs in *T. velutinus*, whereas the pads of *T. karimii* lack dermatoglyphs completely. Instead, the plantar pads are mostly (*T. velutinus*) or entirely (*T. karimii*) covered with small convex tubercles like those that occur on the center of the palm in other species of *Thylamys*.

The ventral surface of the manus in the water opossum uniquely lacks any trace of plantar pads. Instead, the palm of *Chironectes* is essentially flat and densely covered with microscopically dentate tubercles whose fine structure was described and illustrated by Brinkmann (1911) and Hamrick (2001). Numerous smooth, hemisperical papillae (not mentioned by Hamrick, 2001), however, are scattered at regular intervals among the dentate tubercles and presumably have a different function (Brinkmann, 1911).

Among other plesiomorphic marsupials, dasyurids and *Dromiciops* most closely resemble didelphids in manual morphology, both taxa having five well-developed clawed digits. However, whereas dIII and dIV are subequal in *Dromiciops*, dIII is distinctly longer than dIV in dasyurids. By contrast, dI and dV are conspicuously reduced and nail bearing in caenolestids (Osgood, 1921: pl. 2, fig. 4), and the same digits are vestigial—lacking claws or nails—in perameleorphians (Lyne, 1951: fig. 11); of the remaining manual digits, dIII is distinctly the longest in both of these groups. Manual plantar pads are indistinct or absent in all examined perameleorphians but they are distinct in dasyurids, caenolestids, and *Dromiciops*. Whereas the plantar pads of *Dromiciops* and at least some dasyurids (e.g., *Murexia*) have dermatoglyphs, the plantar pads of other dasyurids (e.g., *Sminthopsis crassicaudata*) are tubercular, and those of caenolestids are smooth. The central palmar surface is essentially smooth (or irregularly creased) in caenolestids and *Dromiciops*, but it is densely tubercular in examined dasyurids and peramelids.
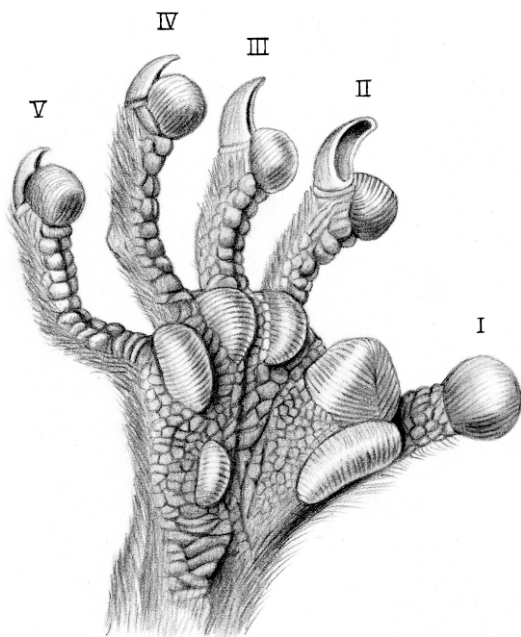

Fig. 4. Plantar view of right hind foot of *Gracilinanus marica* (redrawn from Boas, 1918: pl. 1, fig. 2). Pedal characters that distinguish didelphids from most other marsupials include eleuthrodactyly, a large opposable hallux (digit I), a grooming claw (Putzkralle) on digit II, and prominent dermatoglyph-bearing plantar pads.

PES: Most didelphids have an eleuthrodactylous hind foot with five well-developed digits that are all separate and freely movable (fig. 4). The only exception is *Chironectes*, whose pedal digits are bound together by webs of skin to form a paddlelike swimming organ (illustrated by Augustiny, 1942: Mondolfi and Medina, 1957; Oliver, 1976; Hershkovitz, 1997). Although Bensley (1903), Tate (1933), and Kirsch (1977b) suggested that some didelphids exhibit incipient fusion of dII and dIII, we have not observed any specimen with a hind foot that even remotely resembles the syndactylous condition seen in perameleorphians and diprotodontians.[3]

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[3] Weisbecker and Nilsson (2008) likewise concluded that didelphids do not exhibit incipient syndactyly. The illustration in Hall (1987: fig. 1n) that appears to show an incipiently syndactylous foot in "*Didelphis microtarsus*" (= *Gracilinanus microtarsus*) is a grotesque cartoon that does not accurately depict the pedal morphology of that species or any other opossum (for an anatomically accurate illustration of the hind foot of *Gracilinanus*, see fig. 4).

The didelphid hallux (dI) is well developed, set off at a wide angle from the other pedal digits, and fully opposable. As in other marsupials, the hallux is claw- and nailless in opossums. Although this digit tends to be maximally developed in arboreal forms, it is always long enough to contact the tips of the other digits when they are flexed, even in such strictly terrestrial taxa as *Lestodelphys*, *Lutreolina*, and *Monodelphis*.

The remaining pedal digits bear well-developed claws that are laterally compressed and dorsoventrally recurved like those of most other plantigrade mammals (Brown and Yalden, 1973). The claws on dIV and dV are more or less symmetrically crescentic, with an unguis that is equally extensive on the axial and abaxial surfaces, and a sub-unguis that is only exposed ventrally. Digit II, however, bears a strikingly asymmetrical grooming claw (Putzkralle; Boas, 1918) with an abaxially exposed subunguis and a rounded, spoon-shaped apex. The subunguis is sometimes also exposed abaxially on the claw of dIII, but the asymmetry is consistently less than that of the second digital claw, and the third claw never has a rounded tip.

In the strictly terrestrial opossums *Lestodelphys*, *Lutreolina*, and *Monodelphis*, the third pedal digit is longer than the adjacent second and fourth digits, and the hind foot is therefore mesaxonic (sensu Brown and Yalden, 1973). By contrast, dII, dIII, and dIV are subequal (none distinctly longer than the others) in *Didelphis albiventris* and *D. virginiana*. Among all other examined didelphid taxa (including *Didelphis marsupialis*), the second, third, and fourth pedal digits progressively increase in length, such that dIV is the longest toe opposing the hallux. It is noteworthy that the relative lengths of pedal digits do not strictly covary with those of the manual digits, as they might be expected to do if transformations of the pes and manus were functionally or developmentally determined by the same factors. For example, whereas dIV is the longest pedal digit in *Marmosops*, dIII is the longest manual digit in that genus.

In most didelphids (e.g., *Philander*; Hershkovitz, 1997: fig. 6B) the entire ventral surface of the hind foot is macroscopically naked from the apex of the heel to the tips of the toes. Under high magnification, a fine plantar pelage of very short hairs partially or completely covers the heel in some taxa (e.g., *Marmosops*), but intermediate conditions in other forms and variation among conspecific individuals suggest that such microscopic details are not a reliable basis for either phylogenetic analysis or taxonomic diagnosis. By contrast, a morphologically distinctive condition occurs in *Lestodelphys* and *Thylamys* (see Carmignotto and Monfort, 2006: fig. 3), whose heels are entirely covered by coarse (macroscopically visible) fur.

Most didelphids have six separate plantar pads like many other plantigrade mammals (Brown and Yalden, 1973), but several patterns of taxonomic variation are noteworthy: (1) The position normally occupied by the hypothenar (lateral tarsal) and fourth interdigital pads in most didelphids is occupied by a single elongate pad in *Caluromys*, *Caluromysiops*, and *Glironia*; although this large structure is plausibly interpreted as the result of fusion (hypothenar + interdigital 4), this scenario is complicated by the occasional presence (e.g., in AMNH 273038) of a small proximal metatarsal pad that might be a vestigial hypothenar. (2) The hypothenar is absent or variably present but clearly vestigial in *Monodelphis*, *Lutreolina*, *Philander*, and *Didelphis*. (3) The thenar (medial tarsal) and first interdigital pads are often in contact or indistinguishably fused among arboreal taxa (e.g., *Caluromys* and *Marmosa*), but a continuum of intermediate conditions precludes any unambiguous distinction between these morphologies and the separate conditions seen in terrestrial forms (e.g., *Monodelphis* and *Thylamys*). (4) Interdigital 2 is much larger than interdigital 3 in most arboreal/scansorial forms (e.g., *Marmosa*, *Marmosops*), but they are subequal in some terrestrial taxa (e.g., *Monodelphis* and *Lutreolina*).

The pedal plantar pads of most didelphids are provided with dermatoglyphs like those of the manual plantar pads. However, the dermatoglyph-bearing epithelium is much reduced in *Thylamys velutinus*, and in *T. karimii* the pedal plantar pads are entirely tubercular (lacking dermatoglyphs completely; Carmignotto and Monfort, 2006: fig. 3). As in so many other aspects of its appendic-

ular morphology, *Chironectes* is unique among didelphids in lacking any trace of pedal plantar pads.

The eleuthrodactylous hind foot of *Dromiciops* resembles the common didelphid morphotype in having a large opposable hallux, a grooming claw on dII, dIV > dIII, and dermatoglyph-bearing plantar pads (Hershkovitz, 1999: fig. 21). By contrast, the hind foot of peramelids is syndactylous (with fused dII and dIII; Hall, 1987; Weisbecker and Nilsson, 2008); the hallux is small and effectively nonopposable in caenolestids (Osgood, 1921: pl. 2, fig. 3), dasyurids (Thomas, 1888: pl. 23, fig. 8), and peramelids (Lyne, 1951: fig. 12); dIII and dIV are subequal in examined caenolestids and dasyurids, both of which groups also lack a grooming claw on dII; peramelids do not have distinct plantar pads; the plantar pads of caenolestids are smooth; and the plantar pads of some dasyurids are tubercular. The plantar epithelium of the heel is macroscopically naked in most of these outgroup taxa, but the underside of the heel is coarsely furred in some dasyurids (e.g., *Sminthopsis crassicaudata*).

POUCH AND MAMMAE: Based on our first-hand examination of parous adult female specimens, pouchlike enclosures for nursing young are unequivocally present or absent among didelphids. Although our sample sizes were always small, we observed no intraspecific variation in this aspect of female reproductive morphology, nor did we observe any intermediate condition between absence and presence of a pouch. Despite the fact that several distinctly different pouch configurations can be recognized among opossums, we provisionally recognize all pouches as homologous in the absence of a priori evidence to the contrary.

We found no trace of a pouch in suitable material (fluid-preserved specimens and carefully prepared skins) of parous adult female *Cryptonanus*, *Glironia*, *Gracilinanus*, *Hyladelphys*, *Lestodelphys*, *Marmosa*, *Marmosops*, *Metachirus*, *Monodelphis*, *Thylamys*, and *Tlacuatzin*. By contrast, well-developed pouches were consistently found to be present in suitably prepared parous adult females of *Caluromys*, *Chironectes*, *Didelphis*, and *Philander*. Although *Lutreolina* was described as pouchless by Thomas (1888),

Cabrera (1919), and Marshall (1978a), two fluid-preserved parous females that we examined (UMMZ 166634, USNM 536827) had pouches exactly resembling the morphology illustrated and described by Krieg (1924: fig. 11). *Caluromysiops* is said to have a pouch (Izor and Pine, 1987; Reig et al., 1987), but no explicit description or illustration of the female reproductive anatomy of this genus is available, nor were we able to examine suitably preserved parous female specimens. The presence or absence of a pouch remains undocumented for many opossums, notably *Chacodelphys*. Contradictory literature accounts of a pouch as present or absent in *Metachirus* were discussed by Voss and Jansa (2003).

The marsupium of *Caluromys philander* uniquely consists of deep lateral skin folds that enclose the nursing young and open in the midline (resembling the morphology that Tyndale-Biscoe and Renfree [1987: fig. 2.8] incorrectly attributed to didelphids in general). In *Caluromys lanatus*, *Didelphis*, and *Philander*, however, the lateral pockets are joined posteriorly, forming a more extensive enclosure that opens anteriorly (Enders, 1937: fig. 19). Yet another condition is exhibited by *Chironectes* and *Lutreolina*, in which the lateral pockets are connected anteriorly, forming a marsupium that opens posteriorly (Krieg, 1924: fig. 11A; Oliver, 1976: fig. 1B).

In all marsupials that possess a pouch the mammae are contained within it, but the mammae of pouchless taxa are variously distributed (Tate, 1933: fig. 3). In most pouchless didelphids (e.g., *Glironia*, *Marmosa*, *Metachirus*) the mammae are confined to a more or less circular inguinal/abdominal array that occupies the same anatomical position as the pouch in taxa that possess a marsupium. However, other pouchless opossums (e.g., *Cryptonanus guahybae*, *Marmosops incanus*) have bilaterally paired mammae that extend anteriorly well beyond the pouch region. Although most of these anterior teats are not actually located on the upper chest, they are usually referred to as ''pectoral'' or ''thoracic'' mammae (e.g., by Tate, 1933; Reig et al., 1987).

Most didelphids have, in addition to bilaterally paired mammae, an unpaired

median teat that occupies the ventral midline approximately in the center of the circular abdominal-inguinal array (fig. 5B). Mammary counts for didelphids are therefore usually odd-numbered, an allegedly diagnostic attribute previously noted by Bresslau (1920), Osgood (1921), and Tate (1933, 1947, 1948a). The only exceptions that we have encountered are *Caluromys lanatus*, *Glironia venusta*,[4] and *Hyladelphys kalinowskii* (fig. 5A), examined females of which have four mammae in two abdominal-inguinal pairs with no trace of a median teat. By convention, didelphid mammary complements are summarized by formulae representing the right-side (R), median (M), left-side (L), and total (T) teat counts in the format R–M–L = T. Thus, the mammary complement of the illustrated specimen of *Marmosops parvidens* could be written as 4–1–4 = 9, whereas that of *Hyladelphys kalinowskii* would be 2–0–2 = 4. Occasionally, lateral teats are unpaired, resulting in even-numbered totals for taxa that possess an unpaired median teat, but such anomalies are easily distinguished by formulae (e.g., 3–1–4 = 8 if the anteriormost right teat of AMNH 267344 were really missing in fig. 5B).

Among other plesiomorphic marsupials that we examined, a marsupium is absent only in caenolestids and some dasyurids (e.g., *Murexia*). The pouch of *Dromiciops* consists of lateral skin folds opening medially (Hershkovitz, 1999: fig. 14), whereas the pouches of other dasyurids are variously configured (Woolley, 1974), and those of peramelids open posteriorly. Most nondidelphid marsupials lack an unpaired median teat, and therefore normally have even-numbered mammary counts, but an unpaired median teat is said to be present in *Rhyncholestes* (e.g., by Osgood, 1924; Patterson and Gallardo, 1987).

CLOACA AND MALE GENITALIA: In most didelphids the openings of the urogenital and rectal ducts are inguinal, closely juxtaposed,
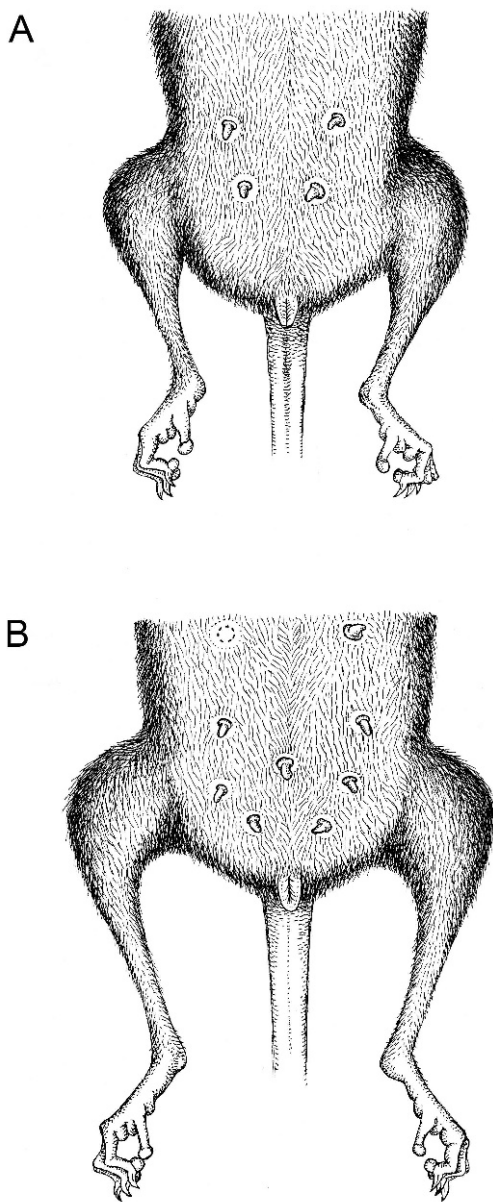
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[4] A parous adult female specimen with 2–0–2 = 4 mammae was recently collected near Iquitos, Peru, by M. Monica Díaz, whose observations confirm Marshall's (1978c) report of four teats based on an old museum skin (FMNH 41440). The Iquitos specimen (with field number MMD 607) will be deposited in the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (M.M. Díaz, personal commun.).

Fig. 5. Mammary morphology of adult female specimens of *Hyladelphys kalinowskii* (**A**, AMNH 267339) and *Marmosops parvidens* (**B**, AMNH 267344). Only two pairs of inguinal-abdominal teats are present in *H. kalinowskii*, which is unusual among didelphids in lacking an unpaired median teat; its mammary formula is 2–0–2 = 4. By contrast, the illustrated specimen of *M. parvidens* has four pairs of inguinal-abdominal teats plus an unpaired median teat (4–1–4 = 9).

and share a continuous mucosa. In life, both openings are normally recessed in a common sinus (cloaca), but this feature is obscured in male specimens with everted genitalia. *Chironectes* uniquely lacks a cloaca because the urogenital and rectal openings are widely separated by furred inguinal skin (Nogueira et al., 2004: fig. 1). Conflicting descriptions of didelphid cloacal morphology by Hershkovitz (1992a, 1992b) were discussed and refuted by Voss and Jansa (2003). All examined nondidelphid marsupials have an inguinal cloaca resembling the common didelphid condition, with the conspicuous exception of *Dromiciops*, in which the cloaca is basicaudal (Hershkovitz, 1999: fig. 12).

Descriptions of didelphid male genitalia (e.g., by Ribeiro and Nogueira, 1990; Martinelli and Nogueira, 1997; Nogueira et al., 1999a, 1999b; Nogueira and Castro, 2003) were recently reviewed and summarized by Nogueira et al. (2004), who tabulated morphological comparisons among 18 species in 12 genera. All examined opossums have a bifid penis (contra Hershkovitz, 1992b), but didelphid male genitalia exhibit conspicuous taxonomic variation in length, shape, disposition of the urethral grooves, presence/absence of diverticula, and other details. Unfortunately, the genitalic characters of many species remain unstudied, and we were unable to extend Nogueira et al.'s (2004) observations for this report.

TAIL: Most didelphids have a tail that is substantially longer than the combined length of the head and body, but some taxa are much shorter tailed (table 5). The known range of relative tail length in the family is bracketed on the one hand by *Gracilinanus emiliae*, an arboreal species with a tail that may be almost twice as long as the combined length of its head and body (Voss et al., 2005: table 2), and on the other by some terrestrial forms (e.g., *Monodelphis* spp.) with a tail that may be less than half as long as the head and body. However, arboreal taxa are not always longer tailed than terrestrial forms. Tree-dwelling *Glironia venusta*, for example, has a tail that is subequal in length to its head and body, whereas ground-dwelling *Metachirus nudicaudatus* is much longer tailed.

Body pelage (soft fur composed of ordinary coat hairs that are not associated with

TABLE 5
Relative Tail Length of Exemplar Species from 18 Didelphid Genera

	LT/HBL[a]
Caluromys (Caluromys) philander	1.49
Caluromys (Mallodelphys) lanatus	1.52
Caluromysiops irrupta	1.19
Chacodelphys formosa	0.81[b]
Chironectes minimus	1.20
Cryptonanus unduaviensis	1.16
Didelphis marsupialis	1.04
Glironia venusta	1.07
Gracilinanus agilis	1.40
Hyladelphys kalinowskii	1.44
Lestodelphys halli	0.67
Lutreolina crassicaudata	0.96
Marmosa (Marmosa) murina	1.30
Marmosa (Micoureus) regina	1.46
Marmosops noctivagus	1.33
Marmosops pinheiroi	1.45
Metachirus nudicaudatus	1.32
Monodelphis emiliae	0.47
Philander opossum	1.01
Thylamys karimii	0.77
Thylamys macrurus	1.29
Tlacuatzin canescens	1.00

[a] Length of tail (LT) divided by length of head and body (HBL), computed from mean values in table 4 except as noted.
[b] From external measurements of the holotype (Voss et al., 2004a).

epidermal scales) extends to a variable extent onto didelphid tails. Body fur extends onto the tail much farther dorsally than ventrally in *Glironia* (see da Silva and Langguth, 1989: fig. 1), *Caluromysiops*, and some species of *Caluromys* and *Monodelphis* (see Voss et al., 2001: fig. 29A). By contrast, body fur extends onto the tail dorsally and ventrally to about the same extent (from about one-sixth to about one-third the length of that organ) in *Caluromys philander*, *Chironectes*, *Didelphis*, *Lutreolina*, *Philander*, and some species of *Marmosa* (e.g., *M. paraguayana*). In most other didelphids, however, body fur does not extend more than a short distance, if at all, onto the tail base.

The exposed skin of didelphid tails is variously pigmented. Some species have uniformly pigmented (concolored) tails that are usually some shade of grayish or brownish, but pale markings are not uncommon.

Many species, for example, have parti-colored tails that are paler distally than basally. In most taxa with pale tail tips, the basal color is grayish or brownish and the transition is either gradual (the basal color fading to whitish distally; e.g., in *Marmosops ocellatus*) or irregularly mottled (e.g., as in *Caluromys derbianus*; frontispiece). However, in most specimens of *Chironectes* (frontispiece), *Didelphis*, *Lutreolina*, and *Philander*, the tail is blackish basally with an abruptly white tip. Dorsoventrally bicolored tails (which are grayish or brownish above and pale on the underside) represent another widespread pattern of didelphid caudal marking that is indistinct in some species but sharply defined in others. Different patterns of caudal markings often distinguish closely related species and can be used in combination with other external traits to identify congeneric taxa in the field (Voss et al., 2004b: table 4).

The epidermal scales that cover the unfurred nonprehensile surfaces of didelphid tails differ taxonomically in shape and arrangement (Tate, 1933: fig. 2). Square or rectangular caudal scales in unambiguously annular series occur in *Chacodelphys*, *Cryptonanus*, *Thylamys*, *Tlacuatzin*, and most species of *Gracilinanus*. Although individual cutaneous scales are indistinct in *Lestodelphys* and *Monodelphis*, the annular arrangement of caudal bristles in both taxa suggest that they also conform to the *Thylamys* pattern. By contrast, rhomboidal (diamond-shaped) or hexagonal scales in spiral series occur in *Caluromys*, *Caluromysiops*, *Chironectes*, *Didelphis*, *Lutreolina*, *Marmosops*, *Philander*, and most species of *Marmosa*. A few taxa, however, have caudal scales that appear to be morphologically intermediate between the annular and spiral morphotypes. In these taxa (e.g., *Hyladelphys*, *Metachirus*, *Marmosa mexicana*) the caudal scales are arrayed in annular series over the vertebral articulations and in more or less spiral series elsewhere. *Glironia* cannot be assigned to any of these caudal-scale patterns because the dorsal and lateral surfaces of its tail are covered by body fur and the entire ventral surface is modified for prehension (da Silva and Langguth, 1989: fig. 1).

Three stiff, bristlelike hairs emerge from the posterior margin of each caudal scale in most didelphids, but four or more hairs usually emerge from each caudal scale in *Lutreolina* and *Philander*. Although individual cutaneous scales are hard to distinguish in *Monodelphis*, the caudal hairs of species that we examined usually emerge from the skin in triplets, so this genus appears to conform to the widespread didelphid condition. The number of hairs normally associated with each caudal scale is impossible to assess in *Glironia* (whose dorsal caudal surface is furry and whose ventral caudal surface is modified for prehension; see above and below) and *Lestodelphys* (on which no discrete clustering within rows of caudal hairs could be distinguished with confidence). The hairs that emerge from the posterior margin of each caudal scale are not grossly differentiated, varying in length but subequal in thickness, in most didelphids. However, in most species of *Marmosops* the middle hair of each caudal-scale triplet is conspicuously thicker than the lateral hairs, and it is often more darkly pigmented (Gardner and Creighton, 1989).

Although all didelphids are perhaps capable of caudal prehension to some extent, external morphological features associated with this behavior are variably developed in the family. The unfurred caudal surfaces of *Chacodelphys*, *Chironectes*, *Lestodelphys*, *Lutreolina*, *Metachirus*, and *Monodelphis* are covered with unmodified scales from base to tip (for illustrations of *Chironectes* and *Lutreolina*, see Hershkovitz, 1997: fig. 7). In taxa conforming to this morphology, the tail tip is sometimes provided with a smooth terminal button but never with a ventrally expanded apical pad bearing dermatoglyphs. The tails of all other didelphids are provided with a distal prehensile surface that may be smooth or covered by modified scales (conspicuously unlike those of the caudal dorsum) but is always transversely creased and glabrous; in taxa conforming to this morphology, the tail tip is invariably provided with a ventrally expanded pad bearing dermatoglyphs (for illustrations of *Didelphis* and *Philander*, see Hershkovitz, 1997: fig. 7). Some taxa additionally exhibit caudal modifications for basal prehension. Whereas the unfurred ventral surface of the tail base in most didelphids is covered by smooth flat

scales, each of which is soft and flexible (yielding easily to the tip of a probe on fluid-preserved material), the scales on the underside of the base of the tail are heavily cornified, forming hard raised tubercles in *Glironia* (see da Silva and Langguth, 1989: fig 1a), *Caluromysiops*, and some species of *Caluromys*.

The tail is a slender, muscular organ in most didelphids, but *Thylamys* and *Lestodelphys* have incrassate tails (Morton, 1980) in which fat is seasonally deposited. Incrassate tails can be recognized superficially by their characteristically swollen outline and soft texture in fresh and fluid-preserved material, and by their flattened, grease-stained appearance in most skins. When the external aspect of the tail leaves some room for doubt, the presence or absence of subcutaneous adipose tissue is easily determined by dissection. For example, a midventral incision that we made near the base of the tail of MZUSP 32097 provided unambiguous confirmation of Carmignotto and Monfort's (2006) statement that the tail of *Thylamys macrurus* is incrassate (contra Palma, 1997; Creighton and Gardner, 2008).

Among other marsupials, representative caenolestids, dasyurids, and peramelemorphians that we examined have nonprehensile tails that are uniformly pigmented, annularly scaled, and lack basal extensions of body pelage; most are slender, muscular organs, but those of *Rhyncholestes* and some dasyurids (e.g., *Sminthopsis crassicaudata*) are incrassate. The tail of *Dromiciops* is incrassate, annularly scaled, and distally prehensile, with a conspicuous extension of body pelage onto the basal 1/4 to 1/3 of the caudal dorsum.

Cranium and Mandible

The best general description of didelphid cranial morphology is Wible's (2003) account of the skull of *Monodelphis brevicaudata*, which includes a review of the literature on didelphid cranial ontogeny, myology, and other relevant topics. Whereas Wible's description is mostly limited to external cranial features, Rowe et al. (2005) provided a detailed description of internal structures of the nasal skeleton of a closely related species, *M. domestica*. Together, these publications provide detailed and abundantly illustrated accounts of the didelphid head skeleton as exemplified by two species in a single genus that is increasingly popular among biomedical researchers.

Other didelphids, however, differ from *Monodelphis* in numerous aspects of cranial morphology (Voss and Jansa, 2003), including some characters that remain undescribed in the literature. Additionally, the literature contains no comprehensive account of the cranial features by which didelphids as a group differ from other marsupials, although important comparative observations were made by Osgood (1921), Tate (1947, 1948b), Archer (1976a), Reig et al. (1987), Marshall et al. (1995), Wroe (1997), Muizon (1998), and Sánchez-Villagra and Wible (2002), among others. Following a brief consideration of overall cranial shape, the following accounts summarize relevant cranial comparisons in a roughly anterior to posterior sequence along the dorsolateral contours of the skull, starting with the rostrum and nasal cavity and proceeding to the orbital region and braincase. A second sequence describes ventral cranial features beginning with the palate and proceeding to the basicranium and occiput. The principal osteological features of the didelphid skull and mandible are illustrated in figures 6 and 7.

SHAPE VARIATION: Didelphids exhibit conspicuous variation in overall cranial shape that is illustrated in the taxonomic accounts below (figs. 37–54). Although some shape variation is obviously allometric (larger opossums tending to have relatively larger rostra and temporal fossae but relatively smaller orbits and braincases than smaller opossums), size-independent shape contrasts are also obvious. Thus, the rostrum is relatively short and broad in both *Hyladelphys* and *Lutreolina*, whereas the rostrum is relatively long and narrow in *Marmosops* and *Metachirus*.[5] A continuous taxonomic series of intermediate proportions makes any qual-

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[5] We quantified rostral proportions in exemplar skulls from taxa that were visually judged to represent morphological extremes in this respect. We measured rostral length (RL) from the anterior margin of one orbit to the tip of the ipsilateral nasal bone, and we measured skull size as condylobasal length (CBL). The values we obtained for the index (RL ÷ CBL) × 100 ranged from about 30% (in *Lutreolina*) to about 45% (in *Metachirus*).
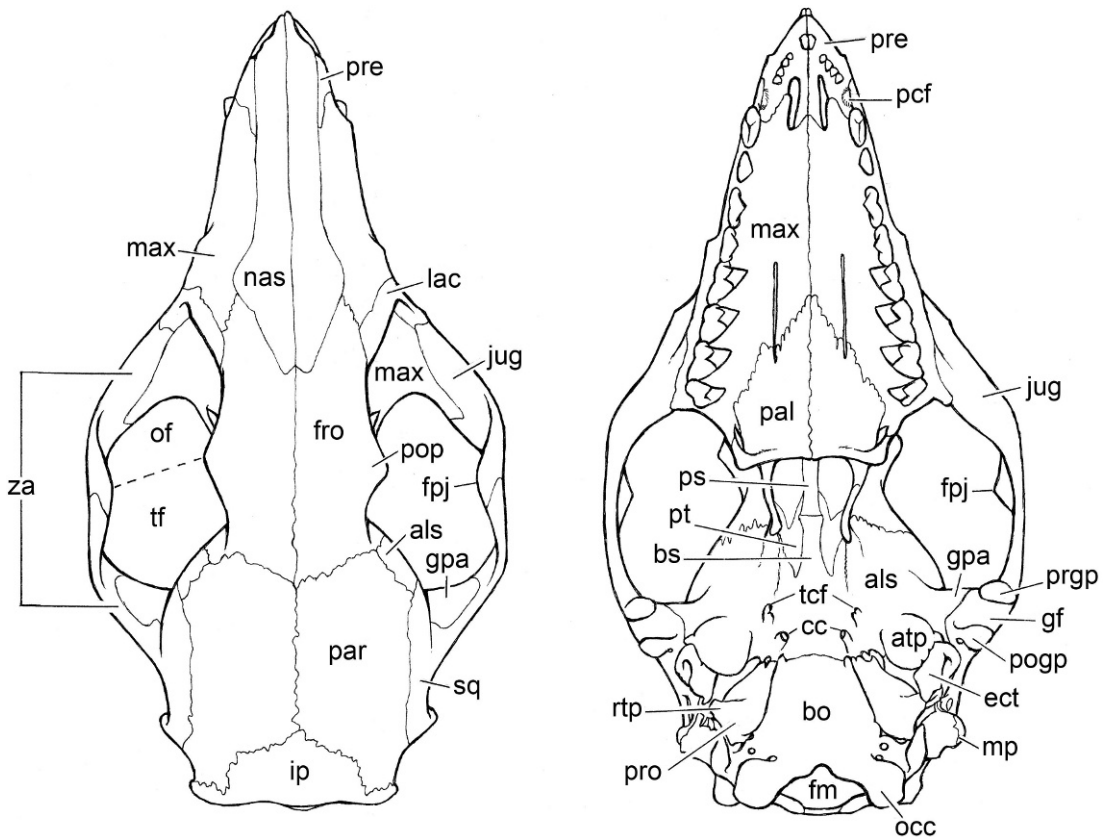
Fig. 6. Dorsal and ventral cranial views of *Marmosa murina* showing principal osteological features mentioned in the text. Abbreviations: **als,** alisphenoid; **atp,** alisphenoid tympanic process; **bo,** basioccipital; **bs,** basisphenoid; **cc,** carotid canal; **ect,** ectotympanic; **fm,** foramen magnum; **fpj,** frontal process of jugal; **fro,** frontal; **gf,** glenoid fossa; **gpa,** glenoid process of alisphenoid; **ip,** interparietal; **jug,** jugal; **lac,** lacrimal; **max,** maxillary; **mp,** mastoid process (of petrosal); **nas,** nasal; **occ,** occipital condyle (of exoccipital); **of,** orbital fossa; **pal,** palatine; **par,** parietal; **pcf,** paracanine fossa; **pogp,** postglenoid process (of squamosal); **pop,** postorbital process; **pre,** premaxillary; **prgp,** preglenoid process (of jugal); **pro,** promontorium (of petrosal); **ps,** presphenoid; **pt,** pterygoid; **rtp,** rostral tympanic process (of petrosal); **sq,** squamosal; **tcf,** transverse canal foramen; **tf,** temporal fossa; **za,** zygomatic arch.

itative coding of such variation an arbitrary exercise, but shape differences are visually conspicuous and are sometimes useful for diagnosing clades discovered by analyzing other data. The nascent literature on didelphid cranial morphometrics is not large, but it includes studies of intraspecific ontogenetic variation (Abdala et al., 2001; Flores et al., 2003), multivariate comparisons of conspecific species (e.g., Ventura et al., 1998, 2002; Cerqueira and Lemos, 2000), analyses of evolutionary rates (Lemos et al., 2001), geometric modeling of taxonomic variation (Astúa de Moraes et al., 2000), and prelim-

inary attempts to explain shape differences in functional terms (e.g., Medellín, 1991).

ROSTRUM: The premaxillae of many didelphids (*Caluromysiops, Chacodelphys, Chironectes, Cryptonanus, Didelphis, Glironia, Hyladelphys, Lestodelphys, Lutreolina, Metachirus, Monodelphis, Philander, Thylamys, Tlacuatzin*) are short, terminating abruptly in front of the incisors, and often lack a definitive suture between the left and right elements (fig. 8B). By contrast, in other didelphids the premaxillae are produced anteriorly as a more or less acutely pointed shelflike process that extends the bony
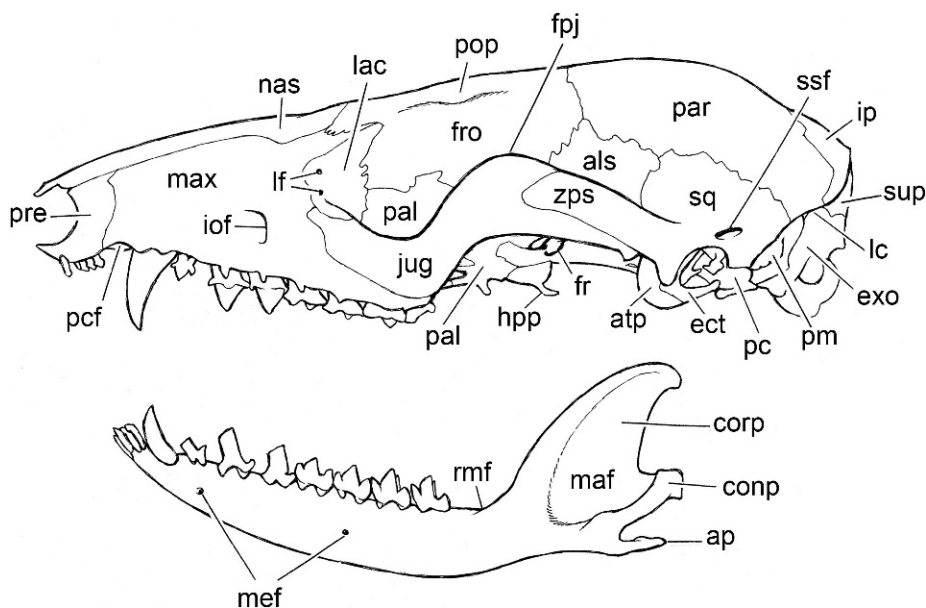
Fig. 7. Left lateral cranial and mandibular views of *Marmosa murina* showing principal osteological features mentioned in the text. Abbreviations: **als,** alisphenoid; **ap,** angular process; **atp,** alisphenoid tympanic process; **conp,** condylar process; **corp,** coronoid process; **ect,** ectotympanic; **exo,** exoccipital; **fpj,** frontal process of jugal; **fr,** foramen rotundum; **fro,** frontal; **hpp,** hamular process of pterygoid; **iof,** infraorbital foramen; **ip,** interparietal; **jug,** jugal; **lac,** lacrimal; **lc,** lambdoid crest; **lf,** lacrimal foramina; **maf,** masseteric fossa; **max,** maxillary; **mef,** mental foramina; **nas,** nasal; **pal,** palatine; **par,** parietal; **pc,** pars cochlearis (of petrosal); **pcf,** paracanine fossa; **pm,** pars mastoideus (of petrosal); **pop,** postorbital process; **pre,** premaxillary; **rmf,** retromolar fossa; **sq,** squamosal; **ssf,** subsquamosal foramen; **sup,** supraoccipital; **zps,** zygomatic process of squamosal.

rostrum beyond I1 and contains a distinct suture between the right and left bones (fig. 8A). Taxa that exhibit a well-developed premaxillary rostral process include *Caluromys*, *Gracilinanus*, *Marmosa*, and most examined species of *Marmosops*. Aspects of rostral process development that impact phylogenetic character scoring, including some discrepancies and ambiguities in the published literature on didelphid premaxillary morphology, were previously discussed by Voss and Jansa (2003: 22–23).

Didelphid nasal bones always extend anteriorly beyond the vertically oriented facial processes of the premaxillae to form a well-defined median apex, and they always extend posteriorly between the lacrimals. Despite such consistency, taxonomic differences in nasal length can be defined with respect to other anatomical landmarks. The tips of the nasal bones are produced anteriorly beyond I1 in most opossums, and the

nasal orifice is consequently not visible from a dorsal perspective (figs. 37–44, 49–54). In *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander*, however, the tips of the nasals do not extend so far anteriorly, and the nasal orifice is dorsally exposed (figs. 45–48).

The nasals are wider posteriorly than anteriorly in most didelphids, but they are not so wide posteriorly as to contact the lacrimals (except as rare, often unilateral, variants). The transition from the narrow anterior part of each nasal to the broader posterior part may be gradual or abrupt and usually occurs at or near the maxillary-frontal suture. By contrast with this widespread condition, a few taxa (*Chacodelphys*, *Thylamys*, *Marmosops incanus*) have uniformly narrow nasals with subparallel lateral margins (e.g., fig. 54). Due to the usual absence of nasolacrimal contact, the maxillae and frontals are normally in contact on both sides of the rostrum.
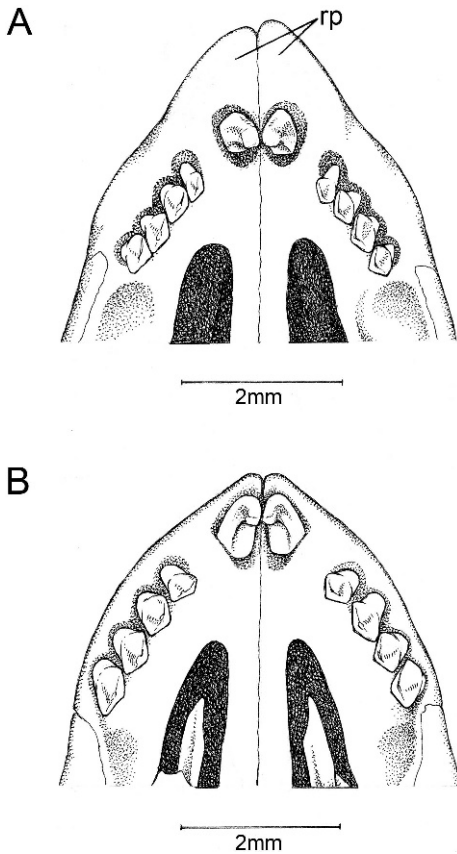
Fig. 8. Ventral view of rostrum in *Marmosa rubra* (**A**, MVZ 153280) and *Monodelphis brevicaudata* (**B**, AMNH 257203) illustrating taxonomic differences in premaxillary morphology. A broad, shelflike rostral process (**rp**) extends the suture between right and left bones well anterior to the incisors in *M. rubra*, but the premaxillae form only narrow alveolar rims anterior to I1 in *M. brevicaudata*, where the left and right bones are separated by a small tissue-filled gap (not a distinct suture).

Most of the lateral surface of the didelphid rostrum is formed by the maxilla, which is prominently perforated above P2 or P3 by the infraorbital foramen. The foramen is notably larger in *Chironectes* than in other didelphids, presumably to accommodate the hypertrophied infraorbital nerve that conducts trigeminal sensory fibers from the well-developed mystacial vibrissae of this semiaquatic taxon (Sánchez-Villagra and Asher, 2002). Aside from small nutrient foramina that may be variably present or absent in some taxa, there are no other lateral rostral openings in didelphids; in particular, no fenestra is ever present at or near the conjunction of the maxillary, nasal, and frontal bones.

Other marsupials exhibit a wide range of rostral morphologies. In all examined dasyuromorphians, for example, the nasals are very short and do not extend anteriorly beyond the facial processes of the premaxillae; rather than forming an acute apex, they are notched medially, and the incisive foramina (in the floor of the nasal orifice) are exposed to dorsal view (e.g., in *Dasyurus*; Flores et al., 2006: fig. 4B). In Recent peramelemorphians, the nasals do not extend posteriorly between the lacrimals (Freedman, 1967: fig. 2), whereas Recent caenolestids have a prominent fenestra on each side of the rostrum at or near the conjunction of the nasal, frontal, and maxillary bones (Thomas, 1895; Osgood, 1921: pl. 20, fig. 2). In a few Old World marsupials (e.g., *Lasiorhinus*, *Tarsipes*) the nasals contact the lacrimals (separating the maxillae from the frontals), whereas the premaxillae contact the frontals (separating the nasals from both the lacrimals and the maxillae) in dactylopsiline petaurids (Tate, 1948a). By contrast, many other marsupials (e.g., *Dromiciops*) essentially resemble didelphids in rostral morphology.

NASAL CAVITY: The complex morphology of the bony turbinals inside the didelphid nasal cavity is difficult to visualize without X-ray computed tomography, which has only been used to describe the endonasal skeleton of *Monodelphis domestica* (see Rowe et al., 2005). However, some turbinal structures are accessible to direct inspection. The maxilloturbinals, for example, are thin, dorsally scrolling sheets of bone that occupy the lower part of the didelphid nasal fossa, where they arise from the inner surface of the maxilla on each side. In most didelphids, the greater curvature of each maxilloturbinal scroll throws off secondary lamellae, which branch to form tertiary lamellae, some of which branch again to form an elaborate dendritic mass that fills much of the ventrolateral part of the nasal lumen. By contrast, the maxilloturbinals are simple, slender, unbranched (or sparsely ornamented) scrolls in all examined species of *Monodelphis*.

The morphology of the nasal cavity remains to be surveyed among other marsu-

pials. However, some peramelemorphians (e.g., *Echymipera*, *Perameles*) appear to have simple (unbranched) maxilloturbinals, whereas the maxilloturbinals of examined dasyurids (e.g., *Murexia*, *Sminthopsis*) and *Dromiciops* closely resemble the elaborately dendritic condition seen in most didelphids. A monographic study of marsupial endonasal features based on high-resolution X-ray computed tomography (Macrini and Voss, in preparation) will doubtless provide additional points of comparison among didelphids and other marsupial clades.

ZYGOMATIC ARCH: The bones comprising the zygomatic arch exhibit few variable features among didelphids. The maxillary-jugal suture is always more or less straight or irregularly crescentic, a frontal process of the jugal is invariably present, and the jugal-squamosal suture is always deeply inflected (typically <- or ⊂- shaped). Likewise, a faceted preglenoid process of the jugal and a well-developed postglenoid process of the squamosal are always present, and a distinct glenoid (entoglenoid) process of the alisphenoid consistently forms part of the posterior zygomatic root. Although the zygomatic arch tends to be more gracile, to have a more pronounced suborbital deflection, and to have a more distinct frontal process in small opossums (with relatively large eyes and weakly developed masticatory muscles; e.g., *Hyladelphys*; fig. 40) than in large opossums (with relatively smaller eyes but massive masticatory muscles; e.g., *Lutreolina*; fig. 47), most didelphids exhibit intermediate zygomatic morphologies.

Contrasting features of the zygomatic region among other marsupial groups include: (1) the deeply inflected maxillary-jugal suture of peramelemorphians, which divides the jugal into distinct anterodorsal and anteroventral processes flanking a well-developed nasolabial fossa (Filan, 1990); (2) the absence of a frontal process of the jugal in caenolestids and some peramelemorphians (Osgood, 1921); (3) the absence of a faceted preglenoid process of the jugal in several Old World clades (e.g., *Thylacinus* and macropodoids); (4) the absence of a distinct postglenoid process of the squamosal in *Hypsiprymnodon*, *Tarsipes*, and vombatids; and (5) the absence of a glenoid process of

the alisphenoid in *Myrmecobius* and many diprotodontians.

ORBITAL MOSAIC: The anteriormost part of the didelphid orbit is formed by the lacrimal, which is always prominently exposed in lateral view. The lacrimal is perforated by one or more lacrimal foramina that are sometimes concealed within the orbit (fig. 9A) but usually open laterally on or near the orbital margin (fig. 9B). Most didelphids normally have two lacrimal foramina on each side, but *Chironectes*, *Hyladelphys*, and some populations of *Didelphis virginiana* usually have just one lacrimal foramen, and many other didelphids that normally have two lacrimal foramina occasionally have a single foramen on one or both sides of the skull. The orbital margin formed by the lacrimal is smoothly rounded in all didelphids, none of which exhibits lacrimal tubercles (e.g., like those seen in macropodids; Wells and Tedford, 1995: fig. 9) or distinct crests (as in *Myrmecobius* and some peramelemorphians). Unlike the condition seen in some Old World marsupials with maxillary-frontal contact on the medial wall of the orbit (Flannery et al., 1987: fig. 3), the didelphid lacrimal is always in posteroventral contact with the palatine.[6]

The medial wall of the didelphid orbit is perforated by several openings, including the sphenopalatine foramen (always in the palatine bone), the ethmoid foramen (in the suture between the orbitosphenoid and frontal), the sphenorbital fissure (between the palatine, orbitosphenoid, alisphenoid, presphenoid, and sometimes the pterygoid), and the foramen rotundum (in the alisphenoid). The configuration of these orbital perforations in all examined taxa is essentially similar to that illustrated for *Monodelphis* by Wible (2003: fig. 4). In particular, the foramen rotundum is always exposed to lateral view behind the sphenorbital fissure, from which it is invariably separated by a bony partition.[7] Many

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[6] Note that elements of the didelphid orbital mosaic are incorrectly labeled in some published illustrations (e.g., Hershkovitz, 1992b [fig. 19], 1997 [fig. 12]), where the orbital process of the palatine that contacts the lacrimal is misidentified as the "sphenoid."

[7] According to Novacek (1986, 1993), the foramen rotundum is confluent with the sphenorbital fissure in didelphids, but these foramina are unambiguously separate openings in all of the material examined by us and by Wible (2003).
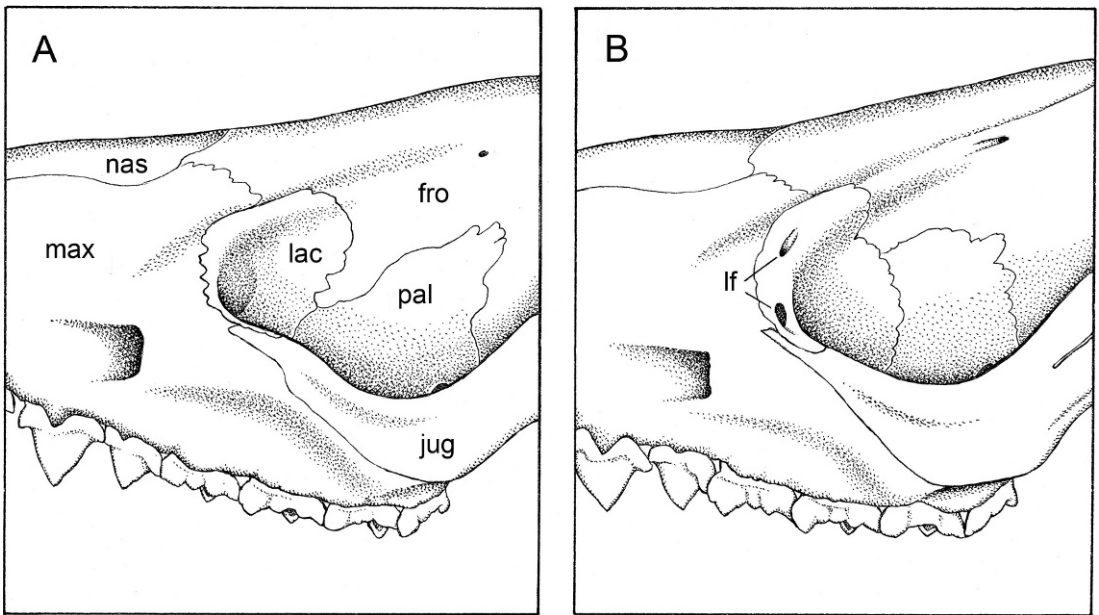
Fig. 9. Detail of the anterior orbital region in *Marmosops parvidens* (**A,** AMNH 267359) and *M. pinheiroi* (**B,** AMNH 267345). In *M. parvidens* the lacrimal foramina (**lf**) are concealed from lateral view inside the orbit, whereas the lacimal foramina are laterally exposed anterior to the orbit in *M. pinheiroi*. Other abbreviations: **fro,** frontal; **jug,** jugal; **lac,** lacrimal; **max,** maxillary; **nas,** nasal; **pal,** palatine.

other marsupials essentially resemble didelphids in these features, but some exhibit noteworthy differences. In *Dromiciops*, for example, the foramen rotundum is concealed from lateral view within a common vestibule that it shares with the sphenorbital fissure in the rear of the orbit (Giannini et al., 2004).

The maxillary and alisphenoid bones are usually separated by the palatine on the orbital floor of most didelphids (fig. 10A). By contrast, the maxillary and the alisphenoid are consistently in contact on the orbital floor of *Lutreolina* and *Monodelphis* (fig. 10B). The maxillary and alisphenoid are separated by the palatine in most nondidelphid marsupials, but the maxillary and alisphenoid broadly contact one another in all examined macropodoids (e.g., *Macropus*; Wells and Tedford, 1995: fig. 9A).

INTERORBITAL REGION: The morphology of the interorbital region is highly variable among didelphids. The frontals produce distinct postorbital processes in several genera, most of which are rather large opossums (e.g., *Caluromys*, *Philander*), but some of which are small (e.g., *Tlacuatzin*). In *Calur-* *omys*, *Caluromysiops*, *Glironia*, *Tlacuatzin*, and most species of *Marmosa* (fig. 11A) the postorbital processes are flattened and more or less triangular, but the postorbital processes of *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander* are often bluntly pyramidal or hornlike projections. Because frontal outgrowths tend to develop late in postweaning ontogeny (Abdala et al., 2001), postorbital processes are often absent in juvenile and subadult specimens of taxa that normally exhibit them when fully grown. The postorbital processes of *Glironia* uniquely consist of both frontal and parietal moieties (fig. 37).

Among didelphids that normally lack distinct postorbital processes (*Chacodelphys*, *Cryptonanus*, *Gracilinanus*, *Lestodelphys*, *Marmosops*, *Metachirus*, *Monodelphis*, *Thylamys*), the supraorbital margins of the frontals may be beaded (with a dorsally upturned edge) or more or less smooth and featureless. Taxa with supraorbital beads include some species of *Gracilinanus* (e.g., *G. emiliae*), *Hyladelphys*, some species of *Marmosops* (e.g., *M. noctivagus*; fig. 11B), *Marmosa rubra*, and *Metachirus*. By contrast,
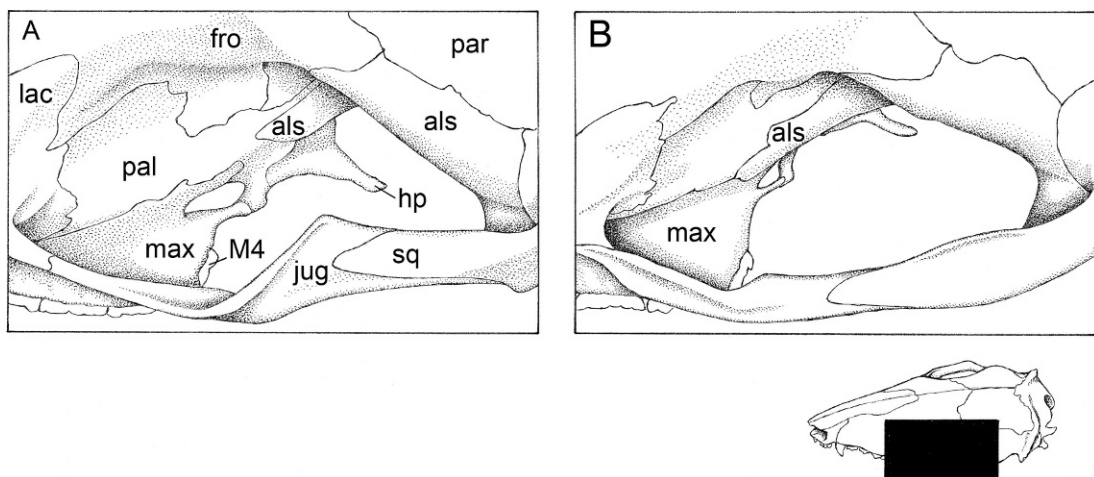
Fig. 10.   Oblique dorsolateral view of the left orbital floor in *Thylamys venustus* (**A**, AMNH 263562) and *Monodelphis peruviana* (**B**, AMNH 272695) illustrating taxonomic differences in sutural patterns. In *Thylamys* (and most other didelphids), the maxillary (**max**) and alisphenoid (**als**) bones are separated by the palatine (**pal**), but the alisphenoid extends anteriorly across the palatine to contact the maxillary in *Monodelphis*. Other osteological abbreviations: **fro**, frontal; **hp**, hamular process of pterygoid; **jug**, jugal; **lac**, lacrimal; **par**, parietal; **sq**, squamosal.

the supraorbital margins are consistently smooth and essentially featureless in most specimens of *Cryptonanus*, *Lestodelphys*, *Thylamys*, and other species of *Marmosops* and *Gracilinanus* (e.g., *G. agilis*; fig. 11C).

Distinct postorbital processes are consistently absent in many nondidelphid marsupial groups (e.g., caenolestids, peramelemorphians, macropodoids), but they are present in some dasyuromorphians (e.g., *Thylacinus*, *Sarcophilus*) and in a few diprotodontians (e.g., *Petaurus breviceps*, thylacoleonids). Other aspects of interorbital morphology are too variable among nondidelphid marsupial clades to describe succinctly here, but none appear to provide an unambiguous basis for phylogenetic inference or taxonomic diagnosis.

DORSOLATERAL BRAINCASE: The right and left frontals and parietals are separated by ontogenetically persistent median sutures in most didelphids (fig. 6), but the midfrontal suture is incomplete or absent in most juveniles and in all examined subadult and adult specimens of *Chironectes* (fig. 45), *Didelphis* (fig. 46), *Lutreolina* (fig. 47), and *Philander* (fig. 48). All examined juveniles and one young adult specimen (FMNH 84426) of *Caluromysiops* have complete mid-

frontal and midparietal sutures, but the right and left frontals and parietals are co-ossified in all of the remaining (fully adult) specimens of *Caluromysiops* that we examined. Most nondidelphid marsupials have ontogenetically persistent median sutures separating the braincase roofing bones, but the left and right frontals and parietals are co-ossified in all examined subadult and adult caenolestids (Osgood, 1924: figs. 1–3; Patterson and Gallardo, 1987: fig. 1). The midparietal suture is also fused in most examined postjuvenile peramelemorphians.

The scars that mark the dorsalmost origin of the temporalis muscle on each side of the braincase are widely separated, and no sagittal crest is developed in most didelphids. In large adult specimens of *Caluromys*, *Lestodelphys*, and *Monodelphis*, however, a small sagittal crest is sometimes developed over the interparietal or along the midparietal suture. By contrast, much larger sagittal crests that extend anteriorly onto the frontals—an unambiguously different condition—are consistently developed in adult specimens of *Caluromysiops*, *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander*. Sagittal crests are altogether absent in caenolestids,
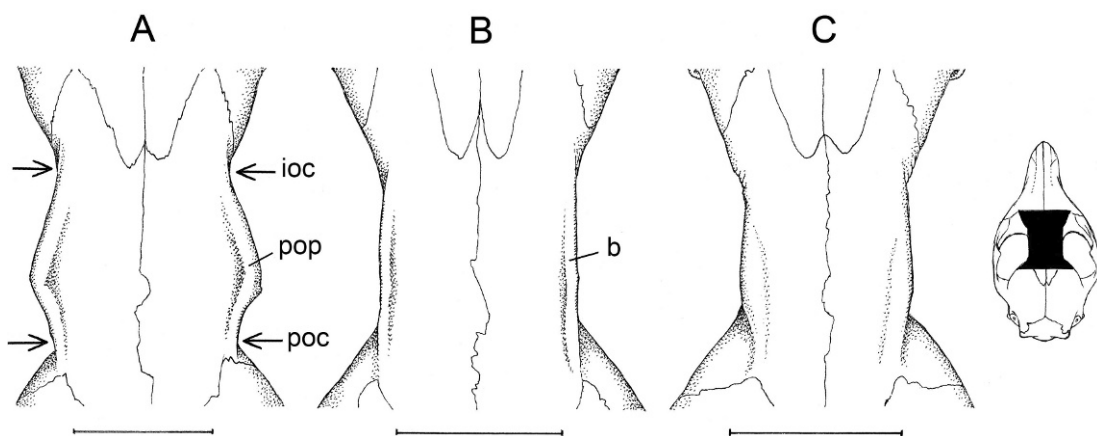
Fig. 11. Dorsal views of the interorbital region in *Marmosa murina* (**A**, AMNH 267368), *Marmosops noctivagus* (**B**, AMNH 262402), and *Gracilinanus agilis* (**C**, MVZ 197439) illustrating taxonomic differences in the development of processes and beads. Distinct postorbital processes (**pop**) are normally present in fully adult specimens of most *Marmosa* species, but they are usually absent in *Marmosops* and *Gracilinanus*. Supraorbital beads (**b**), consisting of upturned dorsally grooved ridges, are present in some but not all species of *Marmosops*. Other abbreviations: **ioc,** interorbital constriction; **poc,** postorbital constriction. Scale bars = 5 mm.

Dromiciops, and in most small-bodied Old World marsupials, but well-developed sagittal crests are present in adult specimens of some dasyuromorphians (*Dasyurus*, *Sarcophilus*, *Thylacinus*), some peramelemorphians (*Macrotis*), and some diprotodontians (e.g., phalangerids, †*Wakaleo*, †*Ekaltadeta*).

The taxonomic distribution of parietal-alisphenoid versus frontal-squamosal contact on the lateral braincase of metatherian mammals has often been discussed by authors (e.g., Archer, 1976a; Marshall et al., 1995; Muizon, 1998; Wroe et al., 1998), not all of whom have correctly reported the distribution of these alternative conditions among didelphids (Voss and Jansa, 2003). In fact, parietal-alisphenoid contact is exhibited by all didelphids with the unique exception of *Metachirus* (fig. 44). Among other marsupials, parietal-alisphenoid contact is also found in caenolestids (Osgood, 1921: pl. 20, fig. 2), most dasyuromorphians (e.g., *Dasycercus*; Jones, 1949: fig. 8), some fossil peramelemorphians (e.g., *Yarala*; Muirhead, 2000), and many diprotodontians, whereas squamosal-frontal contact is present in some dasyuromorphians (e.g., *Sminthopsis*; Archer, 1981: fig. 4), all Recent peramelemorphians, and a few diprotodontians (Wroe et al., 1998). *Dromiciops*, the only microbiotherian for which the lateral braincase morphology is known, also exhibits squamosal-frontal contact.[8]

In most didelphids (*Chironectes*, *Didelphis*, *Glironia*, *Lutreolina*, *Marmosa*, *Metachirus*, *Monodelphis*, *Philander*, and *Tlacuatzin*) the petrosal is only exposed on the occiput (behind the lambdoid crest) and on the ventral surface of the skull (between the exoccipital, basioccipital, and alisphenoid; see Wible, 1990: fig. 1). In taxa conforming to this morphology, there are no gaps among the bones that normally form the lateral surface of the braincase (squamosal, parietal, and interparietal; fig. 12A). By contrast, the petrosal capsule that encloses the paraflocculus and the semicircular canals (= pars mastoideus or pars canalicularis) is consistently exposed through a fenestra in the suture between the parietal and squamosal in *Chacodelphys*, *Cryptonanus*, *Gracilinanus*, *Thylamys*, and some species of *Marmosops* (fig. 12B). Both conditions—presence and absence of a fenestra in the squamosal-

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[8] Hershkovitz (1999: fig. 25) erroneously depicted the lateral braincase of *Dromiciops* with alisphenoid-parietal contact and with a large "orbitosphenoid" ossification wedged between the frontal, alisphenoid, and parietal bones. The correct morphology of lateral braincase elements in this taxon was illustrated by Giannini et al. (2004: fig. 2G).
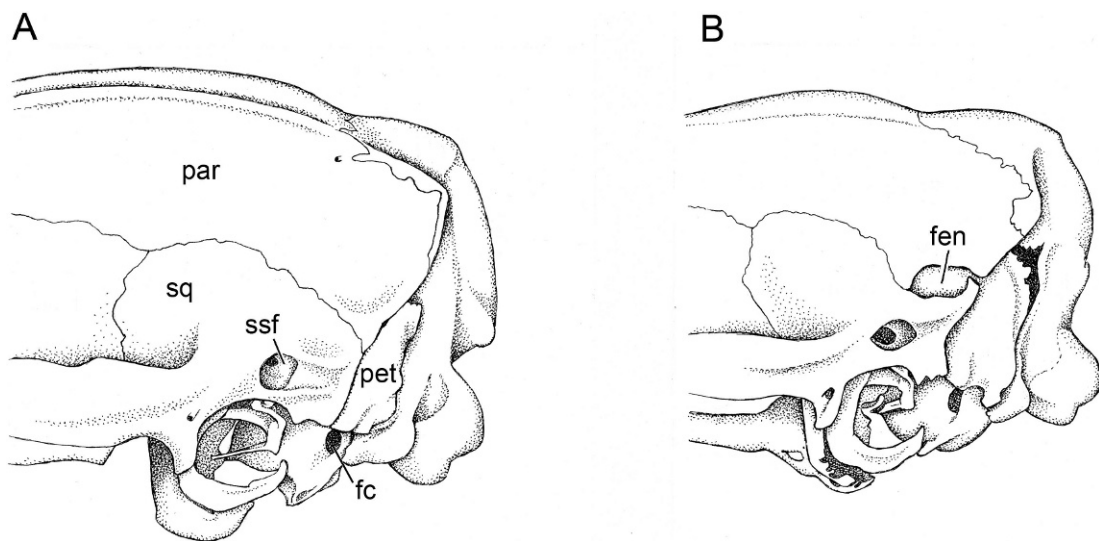
Fig. 12.   Lateral view of posterior braincase in *Marmosa murina* (**A,** AMNH 272816) and *Marmosops impavidus* (**B,** AMNH 272709), illustrating the presence of a fenestra (**fen**) that exposes the petrosal (**pet**) between the parietal (**par**) and squamosal (**sq**) in *Marmosops*. The petrosal is not laterally exposed by a fenestra in the parietal-squamosal suture of *Marmosa*. Other abbreviations: **fc,** fenestra cochleae; **ssf,** subsquamosal foramen.

parietal suture—occur as balanced polymorphisms (neither state clearly predominating) in *Lestodelphys*, *Marmosops incanus*, and *M. noctivagus*. No nondidelphid marsupial that we examined has a fenestrated squamosal-parietal suture.

INTERPARIETAL: Although some authors (e.g., Novacek, 1993) have stated that marsupials lack an interparietal bone, a large interparietal is unequivocally present in *Dromiciops* (see Giannini et al., 2004: fig. 3), many diprotodontians (e.g., *Tarsipes*; Parker, 1890: fig. 2), and some dasyuromorphians (e.g., *Myrmecobius*). In these taxa, the sutures that separate the interparietal from adjacent bones (supraoccipital and parietals) are clearly visible and ontogenetically persistent. In all of the taxa we examined with such distinctly sutured interparietals, the interparietal-supraoccipital boundary coincides closely with the transverse (lambdoid) crest that marks the dorsalmost insertion of the neck extensor musculature.

An interparietal is also unambiguously present in didelphids, all of which exhibit a large, unpaired, wedge-shaped or oblong element between the left and right parietals in the same position (anterior to the lamb-doid crest) as the sutured interparietals of other marsupials. The didelphid interparietal, however, is fused with the supraoccipital in all of the skulls we examined (including postweaning juveniles assignable to Gardner's [1973] age class 1), few of which show any trace of a suture.[9] Fortunately, developmental studies of didelphid pouch young are available to prove the existence of a distinct interparietal center of ossification. In *Didelphis* the interparietal first appears around day 8 postpartum (p) and fuses with the supra-orbital by day 28p (Nesslinger, 1956), whereas in *Monodelphis* these events occur on days 3p and 8p, respectively (Clark and Smith, 1993). By contrast, the didelphid interparietal never appears to fuse with the parietals, the sutures between them persisting even in the largest adult specimens we examined.

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[9] Vestiges of the interparietal-supraoccipital suture in juvenile specimens of *Monodelphis brevicaudata* were described by Wible (2003). What appears to be a well-defined suture between the interparietal and supraoccipital of *Didelphis albiventris* in an illustration published by Abdala et al. (2001: fig. 3) was intended to represent the hypothetical boundary between bones that were indistinguishably fused in all of the specimens examined by the authors of that report (D.A. Flores, personal commun.).
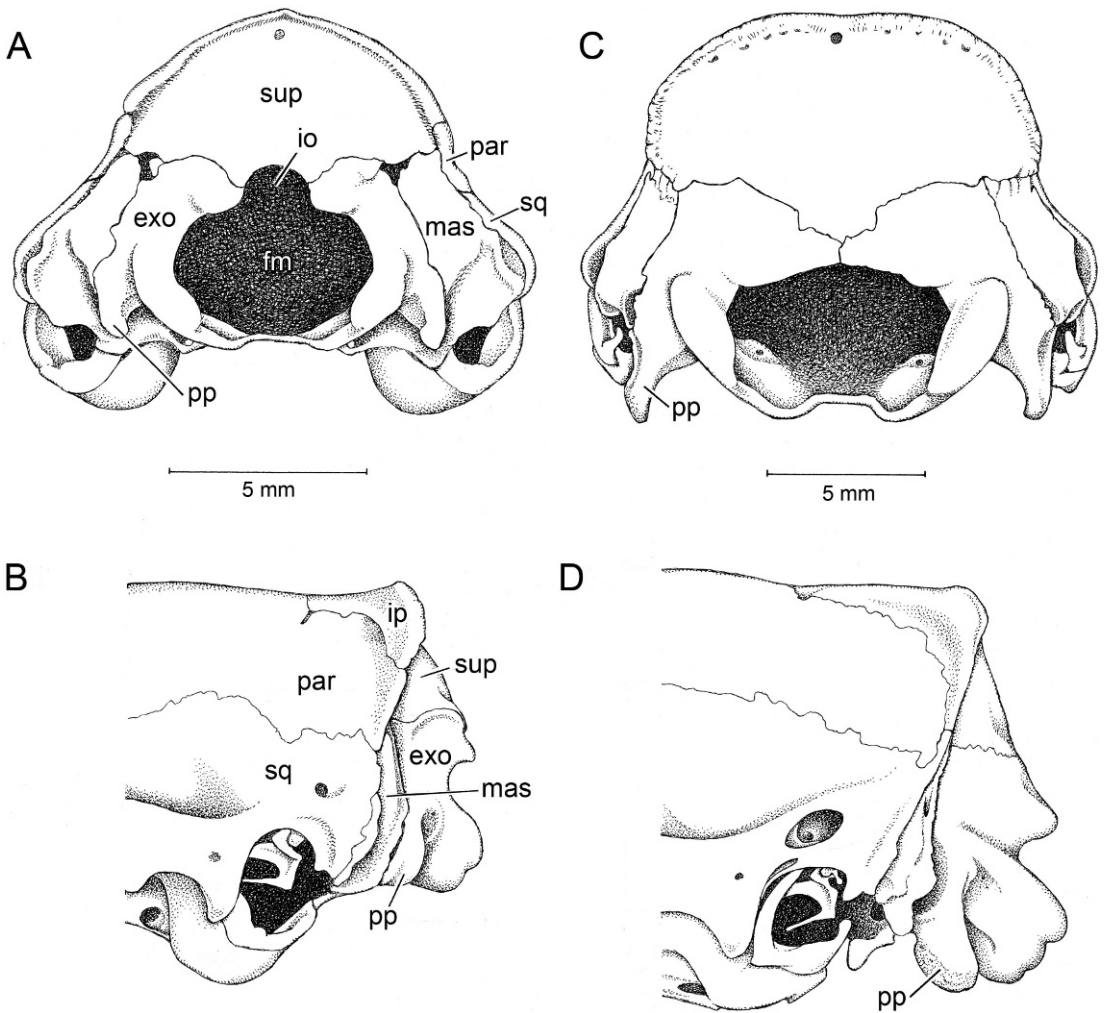
Fig. 13. Posterior and lateral views of the occipital region in *Lestodelphys halli* (**A, B,** UWZM 22422) and *Metachirus nudicaudatus* (**C, D,** AMNH 267009) illustrating taxonomic differences in several cranial characters discussed in the text, including alternative patterns of contact among the interparietal (**ip**), squamosal (**sq**), parietal (**par**), and mastoid (= pars mastoideus of petrosal, **mas**). Additionally, the incisura occipitalis (**io**), a distinct notch in the dorsal margin of the foramen magnum (**fm**), separates the right and left exoccipitals in *Lestodelphys*. By contrast, the incisura occipitalis is absent because medial processes of the right and left exoccipitals are in contact, excluding the supraoccipital from the dorsal margin of the foramen magnum in *Metachirus*. Another conspicuous taxonomic difference illustrated in these views concerns the paroccipital process (**pp**), which is a small, inconspicuous bony mass adnate to the mastoid in *Lestodelphys*. The paroccipital process of *Metachirus* is much larger and projects almost straight ventrally.

The didelphid condition (a large interparietal fused to the supraoccipital but not to the parietals) appears to be unique among marsupials. In young dasyurids, for example, the interparietal is small and separated by open sutures from neighboring bones, or it is absent; no examined dasyurid has a large median element fused to the supraoccipital that is suturally distinct from the parietals and wedged between their posterior borders. The interparietal appears to be completely missing in peramelemorphians, none of which show any trace of a bony element wedged between the parietals anterior to the
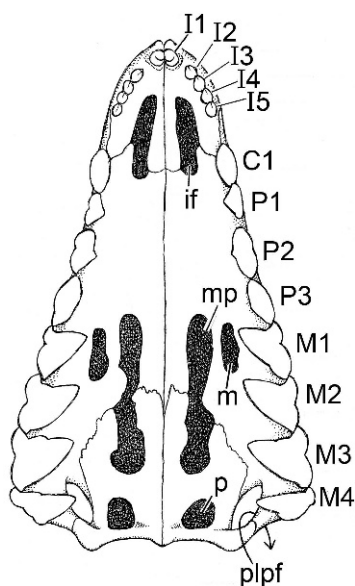
Fig. 14. Palatal morphology of *Thylamys venustus* (AMNH 261254) illustrating nomenclature for fenestrae, foramina, and other features described in the text. Dental loci (I1–M4) provide convenient landmarks for defining the size and position of palatal structures. Abbreviations: **if**, incisive foramen; **m**, maxillary fenestra; **mp**, maxillopalatine fenestra; **p**, palatine fenestra; **plpf**, posterolateral palatal foramen.

lambdoid crest, even as juveniles. The condition in caenolestids is uninterpretable because no sutures persist on the posterodorsal braincase of any examined specimen.

The didelphid interparietal participates in two alternative patterns of contact among bones of the posterior braincase and the occiput. In most opossums the interparietal does not contact the squamosal because the parietal is in contact with the mastoid (fig. 13A, B). However, in *Chironectes*, *Didelphis*, *Lutreolina*, *Philander*, and in one examined specimen of *Metachirus* (fig. 13C, D) the interparietal contacts the squamosal and prevents the parietal from contacting the mastoid. Two species of *Monodelphis* (*M. brevicaudata* and *M. emiliae*) exhibit both conditions with approximately equal frequency among the specimens we examined. Most examined nondidelphid marsupials exhibit parietal-mastoid contact, but acrobatids and *Tarsipes* exhibit broad interparietal-squamosal contact (Parker, 1890: fig. 2), and

phalangerids uniquely exhibit squamosal-exoccipital contact (Flannery et al., 1987: fig. 4C, D).

PALATE: The bony palate is variously perforated by foramina and fenestrae that exhibit considerable variation in occurrence, size, and position among marsupials. Unfortunately, inconsistent terminology has long inhibited clear communication about taxonomic differences. The nomenclature for palatal perforations adopted herein is illustrated in figure 14 and compared with other terminology in table 6.

The incisive foramina are prominent slots in the anterior palate that transmit the nasopalatine ducts (Sánchez-Villagra, 2001a) together with nerves and blood vessels that remain to be identified in marsupials (Wible, 2003). In didelphids, these openings extend from the upper incisor arcade posteriorly to or between the canines. Although didelphid incisive foramina are always bordered posteriorly and posterolaterally by the maxillary bones, their dividing septum is formed primarily by the premaxillae. By contrast, the enormously elongated incisive foramina of caenolestids extend posteriorly between the premolar rows (opposite P1 or P2), and the posterior part of the dividing septum is formed by the maxillae (Osgood, 1921: pl. 20). The long incisive foramina of peramelemorphians do not extend behind C1, but the posterior part of their dividing septum is likewise formed by the maxillae. Most other marsupials (e.g., dasyuromorphians and *Dromiciops*) have incisive foramina that essentially resemble those of didelphids, with the conspicuous exception of some diprotodontians (e.g., *Macropus*; Wells and Tedford, 1995: fig. 9E) in which these openings are completely contained by the premaxillae.

Among Recent didelphids, only *Caluromys* and *Caluromysiops* consistently lack well-formed maxillopalatine fenestrae (figs. 38, 39). Although small perforations in the maxillary-palatine sutures occur in most examined specimens of both genera, these are obviously vascular openings (perhaps homologous with the major palatine foramina of placental mammals) that do not resemble the nonvascular fenestrae of other didelphids. *Glironia* is sometimes said to lack palatal fenestrae (e.g., by Archer, 1982; Reig

2009 VOSS AND JANSA: DIDELPHID MARSUPIALS 37

TABLE 6
Terminology for Marsupial Palatal Foramina and Fenestrae

This report	Other names
incisive foramen	anterior palatal foramen (Tate, 1933), anterior palatine vacuity (Osgood, 1921), palatine fissure (Rowe et al., 2005), premaxillary vacuity (Archer, 1976a, 1981)
maxillary fenestra	mesolateral fenestra (Creighton, 1984)
maxillopalatine fenestra	major palatine foramen (Wible, 2003), maxillary vacuity (Archer, 1976a, 1981), maxillopalatine or mesolateral vacuity (Hershkovitz, 1992b, 1997), palatine fenestra (Clemens et al., 1989), palatine foramen (Novacek, 1993), posterior palatine vacuity (Osgood, 1921)
palatine fenestra	palatine vacuity (Archer, 1976a, 1981), posteromedial fenestra (Creighton, 1984), posteromedial or palatine vacuity (Hershkovitz, 1992b, 1997)
posterolateral palatal foramen	lateral posterior palatal foramen (Tate, 1933), minor palatine foramen (Wible, 2003), palatine canal (Clemens et al., 1989), posterolateral fenestra (Creighton, 1984), postero-lateral foramen (Osgood, 1921), postero-lateral palatine foramen (Archer, 1976a), postpalatine foramen (Marshall et al., 1995; Muizon, 1998)

et al., 1987), but distinct maxillopalatine openings are present in most adult specimens that we examined (e.g., INPA 2570; fig. 37). When present, the left and right maxillopalatine fenestrae of didelphids are invariably separated by a broad median septum, and they never extend posteriorly behind the molar rows. Maxillopalatine fenestrae are very widely distributed among other marsupials, but they are absent in a few taxa (e.g., *Myrmecobius*, *Dactylopsila*, *Phascolarctos*). Among nondidelphid marsupials that possess these openings, the right and left fenestrae are often confluent because no median septum is developed (as in *Rhyncholestes* and *Perameles gunnii*), or they may extend posteriorly well behind the molar rows (as in acrobatids and some burramyids).

Many didelphids have, in addition to maxillopalatine fenestrae, separate openings in the posterior palate that are entirely contained within the palatine bones. Palatine fenestrae are consistently present in adult specimens of *Cryptonanus*, *Didelphis*, *Gracilinanus*, *Lutreolina*, *Philander*, *Thylamys*, some species of *Marmosa*, and some species of *Marmosops* (e.g., *M. creightoni*; fig. 52). Presence is also the modal condition for other taxa (e.g., *Lestodelphys*) in which individuals without palatine perforations are uncommon variants (Martin, 2005). By contrast, palatine fenestrae are consistently absent in *Caluromys*, *Caluromysiops*, *Chironectes*, *Glironia*, *Hyladelphys*, *Metachirus*, *Monodelphis*, some

species of *Marmosops* (e.g., *M. pinheiroi*; fig. 53), and most species of *Marmosa*. The single intact skull of *Chacodelphys* has palatine fenestrae, but these are incompletely separated from the maxillopalatine openings; the normal morphology for this taxon remains to be determined. Palatine vacuities are less widely distributed than maxillopalatine openings among other marsupials, but they occur in some dasyurids (e.g., *Sminthopsis*; Archer, 1981: fig. 5A), some peramelemorphians (e.g., *Isoodon*; Lyne and Mort, 1981: fig. 9), and a few diprotodontians (e.g., *Phascolarctos*, *Vombatus*).

Most didelphids with fenestrated palates have only maxillopalatine or maxillopalatine and palatine openings. A few species, however, have additional fenestrae that are located in the maxillary bone between the maxillopalatine fenestra and the toothrow (at the level of M1 or M2) on each side of the palate. Maxillary fenestrae are normally present in *Chacodelphys*, *Gracilinanus*, many species of *Thylamys* (e.g., *T. pusillus*), and in *Tlacuatzin canescens*. Most other didelphids lack maxillary vacuities except as rare (usually unilateral) variants. These palatal openings are not known to occur in nondidelphid marsupials.

The posterolateral palatal foramen perforates the maxillary-palatine suture behind M4 or posterolingual to M4 on each side of the skull in most metatherians. According to Archer (1976a), this foramen transmits the
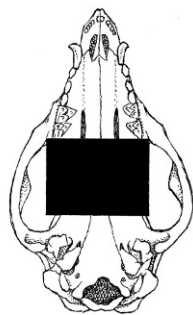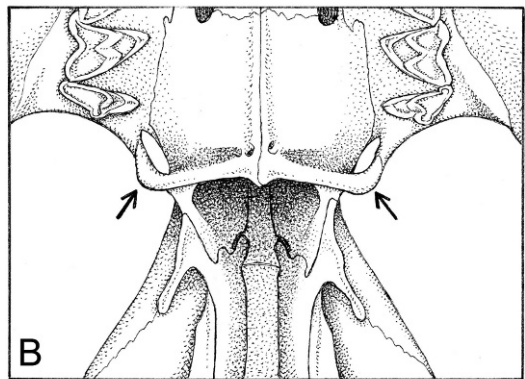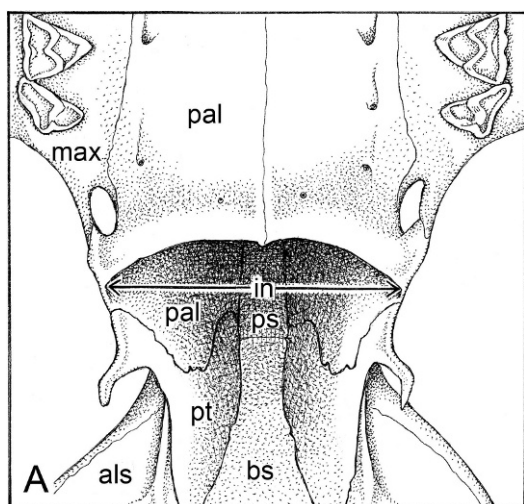
Fig. 15.   Ventral midcranial view of *Caluromys philander* (**A**, AMNH 267002) and *Marmosa demerarae* (**B**, AMNH 266428) illustrating taxonomic differences in palatal morphology. In caluromyines the posterior palate slopes gently ventrally, and the palatal margin is arched (concave posteriorly) without strongly projecting lateral corners; the internal nares (or choanae, **in**) are very broad. In didelphines, however, the posterior palate is abruptly inflected ventrally

minor palatine artery from the maxillary artery to the ventral surface of the palate. In didelphids, caenolestids, *Dromiciops*, peramelemorphians, and stem metatherians, this foramen is completely surrounded by bone, but the foramen is incomplete or absent in many dasyurids (e.g., *Murexia* and *Sminthopsis*) because the maxillary and palatine processes that form the posterior border of this opening in other taxa fail to ossify (Wroe, 1997). In most didelphids the posterolateral palatal foramina are small and located behind the fourth upper molar, but these openings are conspicuously larger and extend lingual to the protocone of M4 on each side of the skull in *Thylamys* (fig. 54) and most specimens of *Lestodelphys* (fig. 51).

Two alternative morphologies of the posterior palate can be recognized among didelphids. In *Caluromys*, *Caluromysiops*, and *Glironia*, the posterior palate slopes ventrally without any abrupt inflection, the caudal palatal margin is usually broadly arched, and prominent lateral corners are not developed; behind the palate, the choanae are not strongly constricted (fig.15A). By contrast, the posterior palate of most other didelphids is abruptly inflected ventrally, and the caudal palatal margin is more or less straight with prominent lateral corners; behind the palate, the choanae are strongly constricted (fig. 15B). Most nondidelphid marsupials have posterior palates that do not conform strictly to either of these morphotypes, but they more closely resemble those of *Caluromys* in lacking well-developed lateral corners.

NASOPHARYNGEAL AND MESOPTERYGOID REGION: The roof of the nasopharyngeal passageway (or meatus; Rowe et al., 2005) is formed by the vomer, the palatines, and the presphenoid, of which only the palatines and the presphenoid are usually exposed to ventral view. Usually concealed inside the nasopharyngeal passageway, the vomer is deeply divided by the presphenoid into paired

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and the palatal margin is more or less straight with projecting lateral corners (arrows in lower panel); the internal nares are narrow. Other abbreviations: **als,** alisphenoid; **bs,** basisphenoid; **max,** maxillary; **pal,** palatine; **ps,** presphenoid; **pt,** pterygoid.

lateral processes that only occasionally extend posteriorly into the mesopterygoid fossa to contact the pterygoids (e.g., in *Caluromysiops*; fig. 39). Most other marsupials, however, exhibit different configurations of the nasopharyngeal roofing bones. In particular, the vomer is undivided and extends caudally to underlie the presphenoid (concealing most or all of it from ventral view) in caenolestids, dasyurids, peramelemorphians, and *Dromiciops*.

The left and right pterygoid bones are widely separated by the presphenoid and the basisphenoid in didelphids. In other marsupials, the vomer may also extend between the left and right pterygoids, but in *Dromiciops* the pterygoids are in midline contact, underlying the presphenoid and concealing its suture with the basisphenoid from ventral view; the conjoined pterygoids of *Dromiciops* form a strong sagittal keel, which is continuous with that formed anteriorly by the vomer and posteriorly by the basisphenoid.[10]

BASICRANIAL FORAMINA: A foramen that transmits the venous transverse canal perforates the alisphenoid anterolateral to the carotid canal in most didelphids (Sánchez-Villagra, 2001b; Sánchez-Villagra and Wible, 2002). *Caluromys* and *Caluromysiops*, however, consistently lack a transverse canal foramen (Archer, 1976a; Sánchez-Villagra and Wible, 2002; Voss and Jansa, 2003). According to Kirsch and Archer (1982: character 24), the ''transverse canal'' is absent in *Metachirus nudicaudatus* and *Philander opossum*, but most of the specimens we examined of both taxa had a transverse canal foramen on each side of the skull. The transverse canal foramen is normally present in most other marsupials (e.g., caenolestids, dasyurids, peramelemorphians, and *Dromiciops*), although its reduction or absence in a few taxa (e.g., *Planigale*, *Tarsipes*) has been noted by authors (Archer, 1976a; Aplin, 1990; Sánchez-Villagra and Wible, 2002).

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[10] The obviously autapomorphic midventral basicranial keel of *Dromiciops* is usually described as formed by the presphenoid and the basisphenoid (e.g., by Hershkovitz, 1999; Giannini et al., 2004), but the presphenoid does not participate in forming this structure in any specimen that we examined. Note that the presphenoid is incorrectly labeled as the vomer in some illustrated ventral views of the didelphid skull (e.g., Novacek, 1993: fig. 9.4B).

The openings through which the mandibular division of the trigeminal nerve (V^3) exits the skull have been variously named by systematists. Following Gaudin et al. (1996), we use the term ''foramen ovale'' for the primary orifice through which V^3 exits the endocranial lumen of the adult skull. In most didelphids, the foramen ovale is bordered by the alisphenoid and the petrosal (fig. 16A), but the foramen is sometimes contained entirely within the alisphenoid, and both conditions can be seen on opposite sides of the same skull (Gaudin et al., 1996: fig. 6). Because it is often difficult to determine the position of this opening with respect to relevant endocranial sutures, however, we did not score the position of the foramen ovale per se. Instead, secondary enclosures of V^3 by outgrowths of the alisphenoid tympanic process provide a more accessible basis for taxonomic comparisons. Two different (apparently nonhomologous) conditions of secondary nerve enclosure occur among didelphids.

In juveniles and adults of *Gracilinanus*, *Lestodelphys*, *Marmosops*, *Metachirus*, and *Thylamys*, the extracranial course of V^3 is enclosed by an alisphenoid process or strut that arises from the anteromedial surface of the bulla and extends anteriorly, medially, and dorsally to span the transverse canal foramen. In the smaller species with this condition (e.g., *Marmosops pinheiroi*; fig. 16B) the extracranial course of V^3 remains unenclosed between this process and the primary foramen ovale, but in larger species (e.g., *Marmosops noctivagus*) a sheet of bone produced from the posterior edge of the process extends caudally to form a more or less complete canal late in postnatal life.

An alternative pattern of secondary foramen and canal formation is seen in *Caluromysiops*, *Chironectes*, *Didelphis*, *Lutreolina*, *Philander*, and some species of *Monodelphis* (e.g., *M. theresa*). In these taxa, V^3 is broadly enclosed by an alisphenoid lamina (fig. 16C) that extends along the posteromedial bullar surface, but there is no anteromedial process spanning the transverse canal foramen. Many juvenile specimens of some taxa scored with this condition (e.g., *Didelphis*) do not have a fully enclosed secondary foramen and canal, but they usually show some laminar devel-

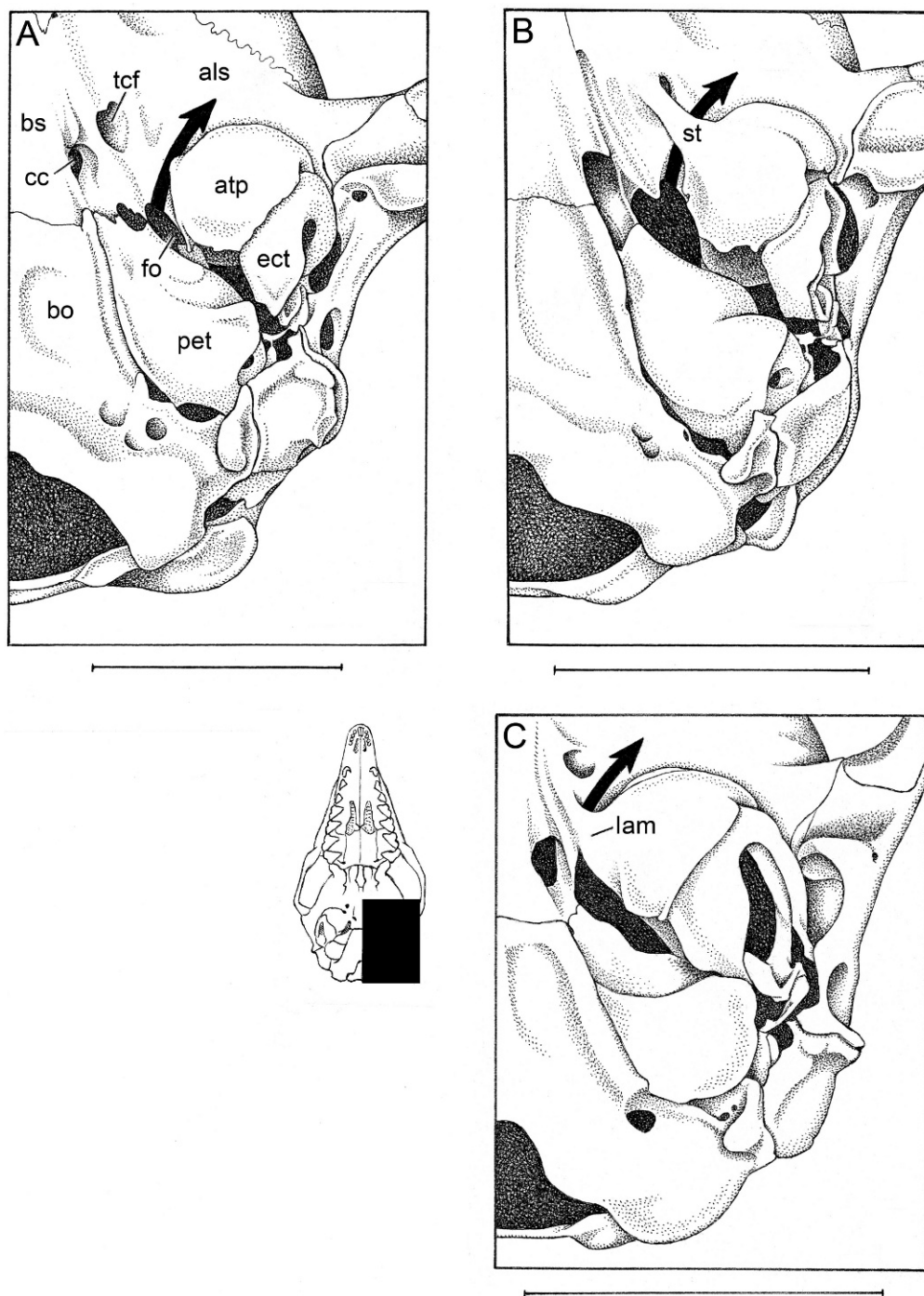Fig. 16.   Ventral view of left ear region in *Marmosa murina* (**A**, AMNH 267368), *Marmosops pinheiroi* (**B**, AMNH 267346), and *Monodelphis theresa* (**C**, MVZ 182775) illustrating taxonomic differences in secondary foramen ovale formation. In *Marmosa*, the mandibular branch of the trigeminal nerve (V^3, reconstructed course shown by heavy arrow) emerges from the endocranial lumen via the foramen ovale

opment; subadults and young adults show progressively more complete enclosure; and old adults (large specimens with heavily worn teeth) usually have completely enclosed foramina and canals (Abdala et al., 2001). All other didelphid taxa (*Caluromys*, *Chacodelphys*, *Cryptonanuns*, *Glironia*, *Hyladelphys*, *Marmosa*, *Tlacuatzin*, and most species of *Monodelphis*) lack secondary enclosures of the mandibular nerve except as rare (usually unilateral) variants.

Although many nondidelphid marsupials (e.g., caenolestids, *Dromiciops*, most dasyuromorphians) have only a primary foramen ovale, secondary foramina ovales are also widely distributed. Unfortunately, these traits remain to be widely surveyed, and inconsistent terminology (discussed by Gaudin et al., 1996) makes it difficult to interpret some published descriptions of marsupial basicrania. Although other developmental mechanisms have obviously been responsible for secondary enclosures of the mandibular nerve in some taxa (e.g., *Phascolarctos*), putative homologues of both didelphid patterns of secondary foramen formation can be recognized among certain Old World marsupials. At least some specimens of *Thylacinus*, for example, have a secondary foramen formed by an anteromedial bullar strut that spans the transverse canal foramen, whereas the secondary foramen ovale of Recent peramelemorphians (e.g., *Echymipera*, *Perameles*) is formed by a broad medial bullar lamina.

EAR REGION: All didelphids have an osteologically well-defined middle ear cavity or hypotympanic sinus (sensu van der Klaauw, 1931: 19). A cup-shaped tympanic process (or "wing") of the alisphenoid invariably forms the anterior part of the floor of the middle ear, but this structure exhibits significant taxonomic variation in size. The alisphenoid tympanic process is large and extends far enough posteriorly to closely approximate or contact the rostral tympanic process of the petrosal in *Caluromys* and *Caluromysiops* (see Reig et al., 1987: fig. 44B, D). In other opossums, a distinct gap separates the alisphenoid tympanic process from the rostral tympanic process of the petrosal, such that at least part of the floor of the middle ear is membranous (e.g., in *Marmosa* and *Monodelphis*; Reig et al., 1987: fig. 41B, D). In *Lestodelphys* and *Thylamys* a rather indistinct medial process of the ectotympanic makes a small contribution to the floor of the middle ear, partially filling in the gap between the tympanic processes of the alisphenoid and petrosal (Reig et al., 1987: fig. 42B, D). The roof of the hypotympanic sinus in all Recent didelphids is almost exclusively formed by the alisphenoid, with the petrosal making only a small, often negligible, contribution. The didelphid squamosal does not participate in forming any part of the floor or roof of the middle ear cavity.

Caenolestids, dasyurids, peramelemorphians, and *Dromiciops* resemble didelphids in that the alisphenoid forms most of the anterior part of the floor of the middle ear. However, whereas caenolestids and some peramelemorphians (e.g., *Echymipera*) have a small alisphenoid tympanic process that does not contact the rostral tympanic process of the petrosal, the alisphenoid tympanic process is large and broadly contacts the petrosal in dasyurids, *Dromiciops*, and other peramelemorphians (e.g., *Perameles*). The hypotympanic sinus roof of dasyurids and

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(fo), which is bordered by the alisphenoid (als) and the petrosal (pet); the extracranial course of the nerve is unenclosed in this taxon. In *Marmosops*, however, the extracranial course of V^3 is partially enclosed by a bony strut (st) that extends from the anteromedial surface of the alisphenoid tympanic process (atp) across the transverse canal foramen (tcf); the nerve then emerges from a so-called secondary foramen ovale. Another kind of secondary enclosure is seen in *Monodelphis*, where the nerve emerges from a secondary foramen ovale formed by a medial lamina (lam) of the alisphenoid tympanic process. Other abbreviations: bs, basisphenoid; bo, basioccipital; cc, carotid canal; ect, ectotympanic. Scale bars = 5 mm.

Dromiciops is almost exclusively formed by the alisphenoid (as in didelphids), but a broad petrosal shelf forms part of the sinus roof in caenolestids and some peramelemorphians. Diprotodontians exhibit a very wide range of bullar morphologies (reviewed by Aplin, 1990), many of which include substantial squamosal participation.

The epitympanic recess of didelphids is a shallow concavity in the ventral surface of the petrosal pars canalicularis that encloses the mallear-incudal articulation (Wible, 2003: fig. 7D).[11] Although this morphology is widespread among other marsupials, a few (e.g., *Macrotis*, *Perameles*) have an enormously inflated epitympanic recess that vaults high above the ossicles, leaving the mallear-incudal joint effectively unenclosed by bone.

The promontorium of the petrosal pars cochlearis is not marked by any vascular grooves in didelphids. Instead, the most conspicuous feature of this otherwise smooth, bulbous structure is the rostral tympanic process (sensu MacPhee, 1981; Wible, 1990). The rostral tympanic process is small, more or less conical, and perhaps serves only to anchor the posterior (ventral) limb of the ectotympanic annulus in some opossums (e.g., *Glironia*), but it is anteroposteriorly expanded, dorsally concave, and substantially contributes to the ventral enclosure of the middle ear in others (e.g., *Marmosa*; Reig et al., 1987: figs. 38–42). In *Caluromys* and *Caluromysiops*, the rostral tympanic process extends along the entire length of the promontorium from the fenestra cochleae to the anterior pole (Sánchez-Villagra and Wible, 2002). The rostral tympanic process of caenolestids and most peramelemorphians is small and more or less conical, but dasyurids, some peramelemorphians (e.g., *Macrotis*), and *Dromiciops* have an anteroposteriorly extensive and dorsally

concave process that forms a substantial part of the bullar floor in these taxa.

In most didelphids, the fenestra cochleae is exposed in lateral or ventrolateral view as illustrated for *Didelphis* by Wible (1990: fig. 1). In others (e.g., *Caluromys*, *Caluromysiops*, *Lestodelphys*, *Marmosa rubra*, *Monodelphis emiliae*, and *Thylamys*), the fenestra cochleae is concealed within a chamber or sinus formed by a laminar outgrowth of the pars canalicularis that approximates or contacts the rostral tympanic process of the pars cochlearis. This lamina, which appears to be homologous with the caudal tympanic process of MacPhee (1981), is invariably fused posteroventrally with the paroccipital process of the exoccipital, which also throws forward a small "tympanic" outgrowth. The resulting auditory chamber—corresponding to the "periotic hypotympanic sinus" of Archer (1976a) and the "post-promontorial tympanic sinus" of Wible (1990)—is always small and uninflated in opossums.

The fenestra cochleae is also exposed in caenolestids and some peramelemorphians (e.g., *Echymipera*), in which tympanic processes of the petrosal are either small or absent. In other peramelemorphians (e.g., *Perameles*) and in dasyurids, however, the fenestra cochleae is concealed within a postpromontorial sinus formed by the seamless fusion of the rostral and caudal tympanic processes; in these forms (as in *Caluromys* and other didelphids with similar petrosal features), the sinus is small and uninflated. The fenestra cochleae of *Dromiciops* is enclosed in an inflated (bubblelike) postpromontorial sinus that, although strikingly unlike the smaller sinuses of other plesiomorphic marsupials, is also assumed to have resulted from fusion of caudal and rostral tympanic processes (Sánchez-Villagra and Wible, 2002: fig. 11).

No other bone (besides the alisphenoid, ectotympanic, and petrosal) participates in auditory sinus formation among Recent didelphids, which have only one or two hypotympanic cavities as described above. Caenolestids and *Dromiciops* are similar to didelphids in this respect, but Recent dasyuromorphians and some peramelemorphians (e.g., *Macrotis* and *Perameles*) have a well-developed epitympanic sinus formed by the

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[11] Because the illustrations in Wible (1990) are so useful in other respects, it is important to note that the epitympanic recess is mislabeled in two views of the tympanic surface of the petrosal of *Didelphis virginiana*. As noted by Muizon (1998: 90), the concavity so labeled in Wible's figure 4A and 4C is really the posterior part of the hypotympanic sinus roof; the true epitympanic recess is a smaller depression posterolateral to the hypotympanic sinus roof and separated from it by a low ridge, the petrosal crest.
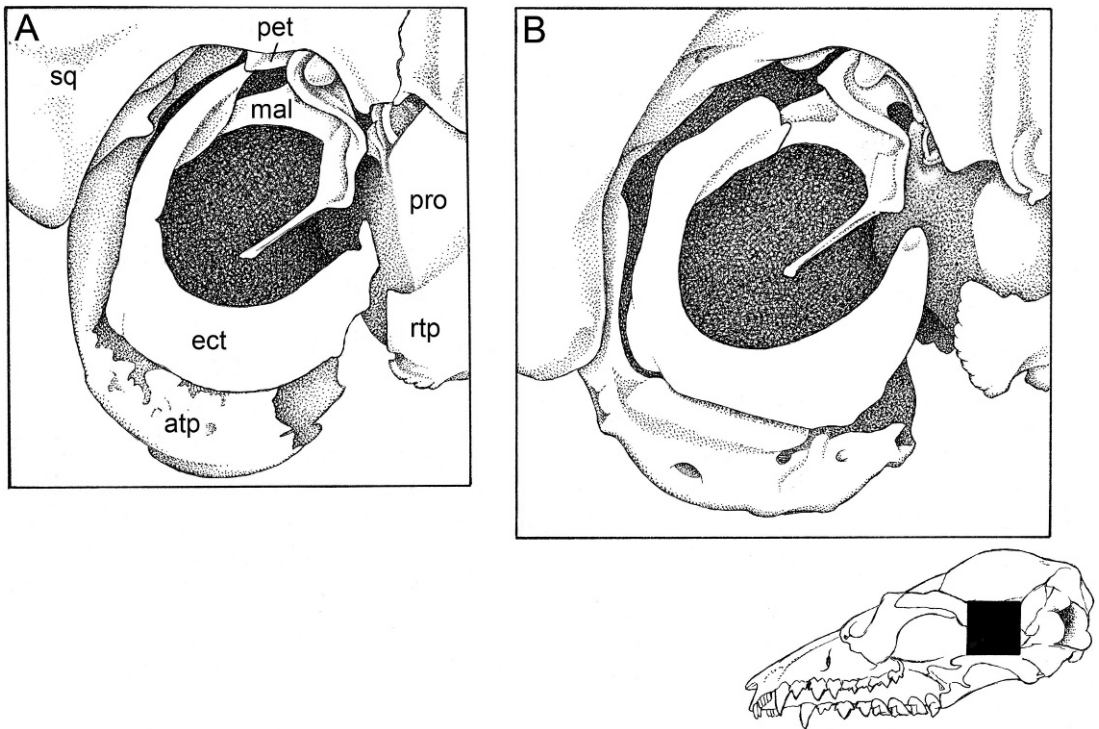
Fig. 17. Oblique ventrolateral view of left ear region in *Marmosops impavidus* (**A,** MUSM 13284) and *Philander mcilhennyi* (**B,** MUSM 13299) illustrating taxonomic differences in ectotympanic suspension. Whereas the ectotympanic (**ect**) is suspended from the skull by attachments both to the petrosal (**pet**) and to the malleus (**mal**) in *Marmosops*, the ectotympanic of *Philander* is suspended only from the malleus (there is no attachment to the petrosal). Other abbreviations: **atp,** alisphenoid tympanic process; **pro,** promontorium (of petrosal); **rtp,** rostral tympanic process (of petrosal); **sq,** squamosal.

squamosal. This structure is a cup-shaped cavity that, in all skulls retaining vestiges of auditory soft tissues, appears to be covered by the membrana Shrapnelli (pars flaccida of the tympanic membrane). Archer (1976a: 304) remarked that, "[i]n some didelphids (e.g., *Metachirus*) there is a depression in the squamosal which is clearly the homologue of this sinus," but nothing resembling the squamosal epitympanic sinus of dasyurids occurs in any living opossum.

ECTOTYMPANIC AND OSSICLES: Although didelphids were described by van der Klaauw (1931: 26) as having a completely free ectotympanic, two distinct patterns of ectotympanic attachment can be recognized in the family. In most didelphids the anterior limb (or crus) of the ectotympanic annulus is directly connected to the skull near the point where the squamosal, alisphenoid, and petrosal are juxtaposed behind the postglenoid process. Where the connection can be seen clearly (dried remnants of soft tissues frequently obscure this feature), the actual attachment seems to be to the petrosal (fig. 17A). In six genera (*Caluromys*, *Caluromysiops*, *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander*), however, the anterior limb of the ectotympanic is not directly attached to the skull, and the suspension is indirect, via the anterior (tympanic) process of the malleus (fig. 17B). In all didelphids with an indirect dorsal connection between the ectotympanic and the skull, the tympanic annulus is more or less ringlike because the posterior (ventral) limb is not expanded to form part of the floor of the middle ear cavity. By contrast, in some taxa with direct ectotympanic suspension, the

posterior limb tends to be dorsoventrally flattened and laterally expanded, forming part of the floor of the external ear canal to a greater or lesser extent.[12] The anterior and posterior limbs of the didelphid ectotympanic are always widely separated by a broad posterodorsal gap, the incisura tympanica.

Caenolestids, dasyurids, most peramelemorphians, and *Dromiciops* essentially resemble didelphids in most aspects of ectotympanic morphology. The anterior limb is suspended loosely but directly from the basicranium, and it is separated from the posterior limb by a broad posterodorsal incisura tympanica. However, whereas the ectotympanic annulus in didelphids, caenolestids, dasyurids, and peramelemorphians is prominently exposed on the lateral aspect of the bulla, the ectotympanic is uniquely concealed from lateral view within the auditory bulla of *Dromiciops* (see Segall, 1969a: fig. 3, 1969b: fig. 4). The ectotympanics of Recent diprotodontians differ strikingly from those of didelphids and other marsupials, principally by forming tubelike extensions of the ear canal, by ankylosis or fusion with neighboring bones, and by dorsal migration and narrowing or closure of the incisura tympanica (Aplin, 1990).

The outermost auditory ossicles of didelphids conform to a pattern that is widespread among other plesiomorphic marsupials. In particular, the malleus invariably has a long, sharply inflected neck, a small orbicular apophysis, a well-developed lamina, and a manubrium that is approximately parallel to the anterior (tympanic or gracile) process; the body of the incus is distinctly differentiated from the long and short processes of that bone (Segall, 1969b: figs. 7, 9; Henson, 1974: fig. 20A). Although taxonomic differences in

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[12] We were previously incorrect in describing the expansion of the posterior limb of the ectotympanic as "medial" in taxa with direct suspension (Voss and Jansa, 2003: 30). As noted by Wible (2003: 165), the expansion of the posterior limb of the ectotympanic in *Monodelphis* is lateral to the sulcus tympanicus, and therefore contributes to the floor of the external ear canal (acoustic meatus) rather than to the bullar floor. This is also true of most other didelphids with direct ectotympanic suspension. Only in *Chacodelphys*, *Cryptonanus*, *Gracilinanus*, *Lestodelphys*, *Thylamys*, and some species of *Marmosa* does the ectotympanic also make a small bullar contribution.

certain details of didelphid mallear and incudal structure were noted by Sánchez-Villagra et al. (2002) and Schmelzle et al. (2005), we did not attempt the requisite dissections to assess the phylogenetic distribution of the features they described. The didelphid stapes, however, exhibits striking morphological variation that can be determined without dissection.

Despite some intraspecific variation noted by Gaudin et al. (1996), most didelphids normally exhibit one or the other of two different stapedial morphotypes defined by Novacek and Wyss (1986). Most didelphids (e.g., *Philander*; Novacek and Wyss, 1986: fig. 5F) have a more or less triangular or stirrup-shaped, bicrurate stapes that is perforated by a large stapedial (obturator or intercrural) foramen. Other didelphids have a columelliform (or columnar) stapes that is imperforate (or microperforate: with a foramen whose maximum diameter is less than the width of a surrounding crus; Gaudin et al., 1996). Taxa with columelliform stapes include *Caluromysiops*, *Lestodelphys*, and several species of *Monodelphis* (e.g., *M. peruviana*, *M. theresa*).

The ossicular morphology of nondidelphid marsupials exhibits significant taxonomic variation. Whereas the mallei of caenolestids, dasyurids, and peramelemorphians essentially resemble those of didelphids in the features described above, the malleus of *Dromiciops* has a short, uninflected neck, no lamina, and a manubrium that forms an open angle with the anterior process (Segall, 1969a, 1969b). The stapes of *Dromiciops* is bicrurate (with a large foramen, like didelphids), but the stapes of caenolestids, dasyurids, and peramelemorphians are columelliform and imperforate (Novacek and Wyss, 1986; Schmelzle et al., 2005). *Notoryctes* and phalangeriform diprotodontians have ossicles that are strikingly unlike those of didelphids and other plesiomorphic marsupials (Segall, 1970; Sánchez-Villagra and Nummela, 2001).

OCCIPUT: Fusion of the supraoccipital with the interparietal is common to all didelphids and occurs very early in postnatal life as has already been discussed, so the dorsal part of the lambdoid crest is not associated with any visible sutures, nor does it develop sesamoids for the insertion of

nuchal muscles (as in peramelemorphians, see below). The crest itself is only weakly developed in juveniles and in adult specimens of the smaller forms, but it is prominent in fully adult specimens of all of the larger opossums. The mastoid (pars mastoideus of the petrosal) is always prominently exposed on the lateral occiput, where it is bordered by the supraoccipital, exoccipital, squamosal, and sometimes the parietal. All didelphids have a well-developed mastoid process at the ventrolateral corner of the occiput that is sometimes provided with a sesamoid.

The dorsal margin of the foramen magnum is formed by the exoccipitals and the supraoccipital in most didelphids (fig. 13A). In taxa that conform to this morphology, the foramen has a distinct middorsal emargination, the incisura occipitalis, that separates the left and right exoccipitals. By contrast, medial processes of the left and right exoccipitals are joined at the midline above the foramen magnum—excluding the supraoccipital from the dorsal margin of the foramen and occluding the incisura (fig. 13C)—in adult specimens of *Didelphis*, *Lutreolina*, *Metachirus*, and *Philander*. Juvenile (and some subadult) specimens of these genera, however, resemble other didelphids in their occipital morphology, such that both conditions (presence and absence of a supraoccipital margin) can be observed in ontogenetic series of conspecific skulls (Abdala et al., 2001: fig. 3). The medial processes of the exoccipitals are closely approximated in *Chironectes*, but in all of the specimens we examined the supraoccipital still forms part of the dorsal margin of the foramen magnum (contra Sánchez-Villagra and Wible, 2002), and the incisura occipitalis persists as a narrow middorsal notch.

The paroccipital process of the exoccipital is inconspicuous in most didelphids, consisting of a low, rounded or subtriangular bony mass for muscle attachment that is broadly adnate to the petrosal; the indistinct apex of the process in taxa that conform to this widespread condition is directed posteroventrally (fig. 13A, B). By contrast, in *Chironectes*, *Didelphis*, *Lutreolina*, *Metachirus*, and *Philander* the paroccipital process is much larger, more erect, and points almost straight ventrally in most examined specimens (fig. 13C, D).

Among other plesiomorphic marsupials, dasyurids are essentially similar to didelphids in most occipital features, but mastoid processes are indistinct in caenolestids, and *Dromiciops* lacks paroccipital processes. Peramelemorphians differ from all other marsupials in having unique osseous structures that are sutured between the parietals and the supraoccipital on each side of the skull. Commonly illustrated but seldom labeled or described by authors, these are the lambdoid sesamoids of Filan (1990), who hypothesized that they function as force multipliers for M. rectus capitis dorsalis and other head extensors. Another occipital feature that might be unique to peramelemorphians is a sesamoid that is probably associated with the origin of the posterior belly of the digastric; this small bone occupies the apex of the paroccipital process in some peramelemorphians (e.g., *Perameles*), but it attaches to the otherwise smooth ventrolateral corner of the exoccipital in taxa that lack a paroccipital process (e.g., *Microperoryctes*).

MANDIBLE: The didelphid mandible consists of an anteroposteriorly elongate horizontal ramus that contains the dental alveoli, an ascending ramus with well-developed coronoid and condylar processes, and a posteroventral angular process. The mandibular symphysis is never fused, and the retromolar space (between m4 and the base of the coronoid process) is either imperforate or pierced by tiny nutrient foramina of inconstant number and position. The masseteric fossa (a prominent concavity for the insertion of the eponymous muscle on the posterolateral surface of the jaw) is always imperforate, and its posteroventral border is defined by a distinct shelf. The articular condyle is transversely elongate and more or less semicylindrical. Although substantial variation in mandibular shape is apparent from the drawings that accompany our systematic accounts (figs. 37–54), other features are more readily characterized for taxonomic diagnoses and phylogenetic inference.

Most didelphids have two mental foramina that perforate the lateral surface of the horizontal ramus, of which the more anterior is usually larger and located below p1 or p2, and the more posterior is usually smaller and located below p3 or m1. *Chironectes*, howev-

er, has only a single mental foramen, which is very large and occupies the same position as the anterior foramen in those taxa with two lateral mandibular perforations.

Alternative states of the form and orientation of the marsupial angular process were defined by Sánchez-Villagra and Smith (1997), but we are unable to consistently recognize the distinction between the "rod-like" and "intermediate" conditions they scored for didelphid exemplars. Instead, the common didelphid condition seems more appropriately characterized as "acute and strongly inflected" (Voss and Jansa, 2003: 34). *Caluromys* and *Caluromysiops* are the only didelphids with bluntly rounded and weakly inflected mandibular angles.

Most other plesiomorphic marsupials have mandibles that grossly resemble the common didelphid morphotype, but *Dromiciops* has only one mental foramen and some peramelemorphians (e.g., *Perameles gunnii*) often have three mental foramina. Additionally, *Caenolestes* has a small foramen in the retromolar space that Sánchez-Villagra et al. (2000) called the retrodental canal (after Hoffstetter and Villaroel, 1974), and it has a small masseteric foramen near the ventral margin of the masseteric fossa (Osgood, 1921), the lumen of which communicates with that of the much larger mandibular foramen on the medial surface of the jaw.

Dentition

All didelphids normally have 50 teeth that most authors now recognize as including I1–5, C1, P1–3, and M1–4 in the upper dentition and i1–4, c1, p1–3, and m1–4 in the lower dentition. As in other metatherians, only the third upper and lower premolars have deciduous precursors (Flower, 1867; Luckett, 1993; Luo et al., 2004; van Nievelt and Smith, 2005a, 2005b). Despite this prevailing consensus, marsupial tooth homologies have long been controversial, with the result that several alternative systems have been used to identify didelphid dental loci (table 7).

As far as we have been able to determine without dissections or X-rays (i.e., from external inspection of teeth in situ, and from the alveoli of specimens with loose teeth), all didelphids have single-rooted incisors and canines, double-rooted premolars and lower molars, and three-rooted upper molars; apparently, dP3 always has three roots and dp3 has two. Most of the following remarks therefore concern crown morphologies, which afford greater scope for taxonomic comparisons.

UPPER INCISORS: The didelphid first upper incisor (I1) is a more or less styliform, somewhat procumbent, hypsodont tooth that is conspicuously unlike I2–I5, from which it is always separated by a small diastema. Although taxonomic variation among opossums in I1 hypsodonty and diastema formation has been suggested by authors (e.g., Takahashi, 1974; Archer, 1976b; Creighton, 1984; Wroe et al., 2000), diagnostically useful differences are more easily recognized among the posterior teeth of this series.

The crowns of I2–I5 in most didelphids are approximately symmetrical, labiolingually compressed rhomboids with subequal anterior (mesial) and posterior (distal) cutting edges that converge to form a sharp central apex; usually, a distinct anterior angle (mesiostyle) and a posterior angle (distostyle) can be seen on unworn teeth (fig. 18A). This is the morphology that Takahashi (1974: 414) termed "premolariform", as exemplified by *Monodelphis*, *Marmosa*, and *Metachirus* in her study. In many taxa with posterior upper incisors of this type, the tooth crowns increase in length (anteroposterior or mesiodistal dimension) from front to back, such that I2 appears visibly smaller than I5 in labial view. This tendency is very pronounced in some taxa with premolariform incisors (e.g., *Marmosops*, *Metachirus*) but seems to grade imperceptibly (via intermediate morphologies) to the essentially uniform toothrows of other taxa (e.g., *Lestodelphys*, *Tlacuatzin*) in which I2 and I5 are subequal in crown length.

An alternative morphology, in which the crowns of I2–I5 are conspicuously asymmetrical, with much longer anterior (mesial) than posterior (distal) cutting edges, occurs in *Caluromys*, *Caluromysiops*, *Didelphis*, *Glironia*, *Hyladelphys*, *Lutreolina*, and *Philander*. On unworn teeth of these taxa, the anterior angle (mesiostyle) is more frequently distinct than is the posterior angle (distostyle), which is often entirely lacking on I5 (fig. 18B). This is the morphology that Takahashi (1974) labeled "incisiform," which she recorded for

TABLE 7
Alternative Hypotheses of Marsupial Tooth Homologies

This study[a]	Thomas (1887)[b]	Archer (1984)[c]	Hershkovitz (1992b)[d]	Luckett (1993)[e]	Goin (1997)[f]
P1	P1	P1	P1	dP1	P1
P2	P3	P2	P2	dP2	P2
dP3	dP4	M1	M1	dP3	M0
P3	P4	P3	P3	P3	P3
M1	M1	M2	M2	M1	M1
M2	M2	M3	M3	M2	M2
M3	M3	M4	M4	M3	M3
M4	M4	M5	M5	M4	M4
i1	i1	i1	i2	i1	i2
i2	i2	i2	i3	i2	i3
i3	i3	i3	i4	i3	i4
i4	—	—	i5	i4	i5
p1	p1	p1	p1	dp1	p1
p2	p3	p2	p2	dp2	p2
dp3	dp4	m1	m1	dp3	m0
p3	p4	p3	p3	p3	p3
m1	m1	m2	m2	m1	m1
m2	m2	m3	m3	m2	m2
m3	m3	m4	m4	m3	m3
m4	m4	m5	m5	m4	m4

[a] The system adopted here was used by Tate (1933) and is currently followed by most metatherian researchers (e.g., Marshall et al., 1995; Rougier et al., 1998; Wroe et al., 2000; Voss and Jansa, 2003). Note that there is no substantive inconsistency in the literature regarding the identification of I1–I5, C1, or c1. In order to focus these comparisons on real differences in assumptions about dental homologies, semantically equivalent notations used by authors (e.g., I_2 for i2, pm^3 for P3) have been modified as necessary to conform with our usage.

[b] Also Thomas (1888), who assumed that marsupials primitively had four premolars, of which the second was lost.

[c] Based on the assumption that the replaced teeth are M1/m1 (Archer, 1978), this is the nomenclature followed throughout most of the marsupial literature for the next 10 years (e.g., Reig et al., 1987).

[d] Based on the assumption that marsupials primitively had five lower incisors, of which the first was lost (Hershkovitz, 1982). Note that whereas Hershkovitz (1992b) accepted Archer's (1984) system of postcanine homologies, Hershkovitz (1997, 1999) did not.

[e] The only difference between Luckett's (1993) notation and ours concerns his designation of the anterior premolars as first-generation (formerly deciduous) teeth. Although we do not dispute his interpretation of the developmental data at hand, we think it confusing to use deciduous notation for unreplaced teeth.

[f] Goin's (1997) system was based on Hershkovitz's (1982) theory that the ancestral first lower incisor of marsupials is missing in living taxa, and on Archer's (1978) conjecture that replaced teeth in the upper and lower dentition are molars; by designating these as M0/m0, Goin intended to preserved traditional notation for the permanent molariform teeth.

Chironectes in addition to *Caluromys* and other taxa in her study. However, the unworn juvenile dentitions of *Chironectes* that we examined have approximately symmetrical, rhomboidal crowns. There is a tendency (more marked in *Glironia* than in other genera of this category) for I2–I5 to decrease in crown length from front to back, such that I2 is sometimes visibly larger than I5 in labial view. Aspects of didelphid upper incisor morphology reported by authors whose observations we have not been able to replicate were discussed by Voss and Jansa (2003: 35).

Most peramelemorphians and *Dromiciops* resemble didelphids in having five upper incisors, but I5 is missing in dasyurids, caenolestids, *Echymipera*, and *Rhyncho-meles*.[13] The first upper incisor is styliform

[13] Following Thomas (1887), we assume that upper teeth are lost from (or added to) the posterior (distal) end of the incisor row. Although there appears to be no developmental data to support this notion, we observed that I5 is small and occupies a separate alveolus from I2–I4 (whose alveoli are usually at least partially confluent) in some taxa with five upper incisors (e.g., *Glironia*, *Hyladelphys*), and that the loss of such a tooth would simply enlarge an already existing diastema between the incisors and C1 rather than opening a fresh gap in the dental arcade.
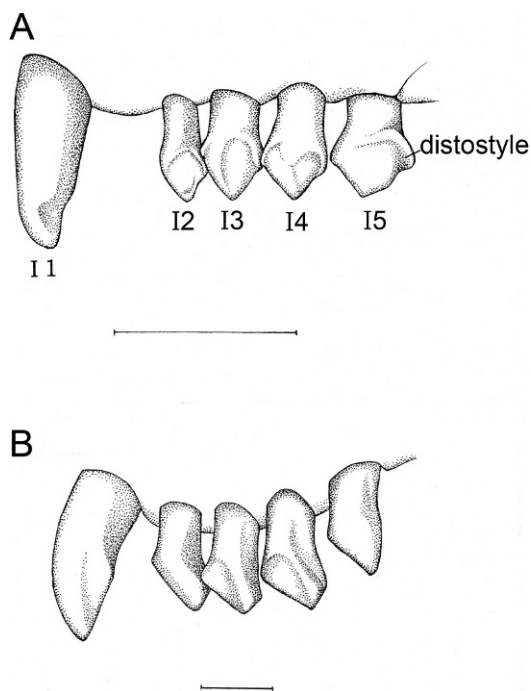
Fig. 18. Unworn premaxillary dentitions of *Marmosops pinheiroi* (**A,** AMNH 267341) and *Lutreolina crassicaudata* (**B,** AMNH 210422) illustrating taxonomic differences in the shape of the incisor crowns. In *Marmosops* and many other small didelphines, the crowns of I2–I4 are symmetrically rhomboidal, with subequal anterior (mesial) and posterior (distal) cutting edges that converge to form a sharp central apex; a distinct posterior corner (distostyle) is always present on I5. By contrast, in *Lutreolina* (and certain other taxa), the crowns of I2–I4 are conspicuously asymmetrical, with longer anterior than posterior cutting edges; a distinct distostyle is usually absent on I5. Scale bars = 1 mm.

in most of these taxa, but I1 is a laterally compressed, distinctly chisellike tooth in caenolestids, and it is a labiolingually compressed, flat-crowned tooth in peramelemorphians. The unworn posterior incisors have approximately rhomboidal crowns with subequal anterior and posterior cutting edges that converge to a sharp apex in most dasyurids and in *Dromiciops*, but I2–4 in caenolestids have strikingly asymmetrical crowns (appropriately described as "hatchet-shaped" by Osgood, 1921: 117), the posterior margins of which are deeply

notched in *Rhyncholestes* (see Osgood, 1924: figs. 3b, c; Bublitz, 1987: fig. 13). In peramelemorphians, I2–4 are flat crowned (like I1), but I5 (when present) is caniniform. All of the upper incisors are single rooted in dasyurids, caenolestids, *Dromiciops*, and many peramelemorphians, but I5 is double rooted in *Perameles gunnii*.

UPPER CANINE: The didelphid upper canine (C1) is invariably separated from the posteriormost upper incisor by a wide diastema that may or may not contain a distinct paracanine fossa for the reception of the lower canine. In most didelphids, C1 occupies the premaxillary-maxillary suture, despite the fact that the maxilla always extends anterolaterally beyond this tooth, sometimes reaching the alveolus of I5; therefore, the premaxilla only contacts the C1 alveolus medially (fig. 14). In *Caluromys* and *Caluromysiops*, however, the upper canine alveolus is entirely contained within the maxilla (figs. 38, 39).

The upper canine is a simple unicuspid tooth in most didelphids, but some species (e.g., *Gracilinanus emiliae*; Voss et al., 2001: fig. 12A) have a small posterior accessory cusp, and others (e.g., *Marmosops pinheiroi*; fig. 53) have both anterior and posterior accessory cusps. Some care is needed in determining canine crown morphology, however, because accessory cusps are sometimes obliterated by wear (as inferred from their absence in old adults of species that uniformly exhibit such structures as juveniles and subadults). Alternatively, a false posterior accessory cusp is sometimes formed when the trailing edge of C1 is notched by occlusion with p1. Unlike other teeth whose size does not increase ontogenetically after the crown is fully erupted, didelphid canines often appear much larger in older adults than in younger animals because the root is continuously extruded from the alveolus throughout life.

Most other marsupials have single-rooted unicuspid upper canines like those of didelphids, but accessory cusps are present in some peramelids (e.g., *Echymipera*) and dasyurids (e.g., *Antechinomys*; Archer, 1976b). Additionally, the canine is double rooted and provided with accessory cusps in female *Caenolestes* and *Rhyncholestes* and in
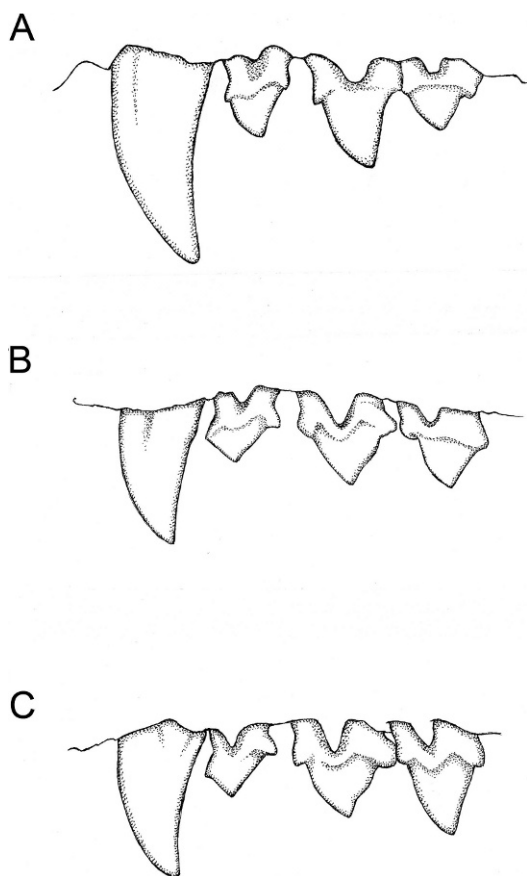
Fig. 19. Lateral views of left C1–P3 in *Hyladelphys kalinowskii* (**A,** AMNH 267338), *Gracilinanus agilis* (**B,** AMNH 134005), and *Thylamys pusillus* (**C,** AMNH 275445) illustrating taxonomic differences in the relative heights of P2 and P3 (toothrows are not drawn to the same scale).

both sexes of *Lestoros*, whereas male *Caenolestes* and *Rhyncholestes* have single-rooted unicuspid teeth (Osgood, 1924; Bublitz, 1987). The position of C1 with respect to the maxillary-premaxillary suture has not been widely surveyed in Marsupialia, but the upper canine alveolus is entirely contained by the maxilla in *Dromiciops*, some peramelemorphians (e.g., *Echymipera*, *Perameles*), and some dasyuromorphians (*Murexia*, *Sminthopsis*). In several diprotodontian clades, C1 is absent.

UPPER PREMOLARS: The didelphid first upper premolar (P1) is usually in contact with or very close to C1, but a diastema is often present between P1 and P2. The gap

between P1 and P2 tends to be individually and ontogenetically variable, however, and a continuous range of intermediates exist between taxa in which it is usually absent (e.g., *Lestodelphys*; fig. 51) and those in which it is normally present (e.g., *Philander*; fig. 48). By contrast, no diastema is ever present between P2 and P3, the crowns of which are in contact or closely approximated in all examined opossum dentitions.

Although consistently smaller than the posterior premolars, P1 in most didelphids is at least half the height or width of P2, which it essentially resembles in having a large, laterally compressed, more or less triangular central cusp that is usually flanked by smaller anterior and posterior accessory cusps. By contrast, P1 is a much smaller (apparently vestigial) tooth that lacks distinct occlusal features in *Caluromys* (fig. 38) and *Caluromysiops* (fig. 39). In a few specimens of the latter genus (e.g., AMNH 244364), P1 is missing.

The second and third upper premolars are always large and well-developed teeth. Each is surrounded by a broad basal cingulum in *Caluromys* and *Caluromysiops*, but the basal cingulum of P2 and/or P3 is often incomplete or indistinct in other didelphids. The second upper premolar is distinctly taller than P3 in *Caluromys*, *Caluromysiops*, and *Hyladelphys* (fig. 19A), but P3 is distinctly taller than P2 in *Chironectes*, *Cryptonanus*, *Didelphis*, *Lestodelphys*, *Lutreolina*, *Monodelphis*, *Philander*, and *Thylamys* (fig. 19C). By contrast, P2 and P3 are about the same height in *Chacodelphys*,[14] *Glironia*, *Gracilinanus* (fig. 19B), *Marmosa*, *Marmosops*, and *Metachirus*.

When unworn, P3 is provided with sharp anterior and posterior cutting edges—each of which extends from the cingulum to the apex of the tooth—in *Caluromys*, *Caluromysiops*, *Glironia*, and *Hyladelphys*. In all other didelphids, however, the anterior margin of

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[14] Although we (Voss et al., 2004a) previously reported that P2 is taller than P3 in *Chacodelphys* based on our examination of the holotype of *C. formosa* (USNM 236330), subsequently collected material (Teta et al., 2006) includes five individuals in which P2 and P3 are subequal in height. We reexamined USNM 236330 and concluded that, although the crown of P3 was completely exposed above the alveolus, it had not yet attained its definitive adult position in the toothrow of this young adult specimen.

the tooth is rounded, and only the posterior cutting edge is well developed. Small anterior blades are variably present near the base of P3 in *Chironectes* and *Philander*, but the apex of the tooth is always rounded anteriorly as in the other taxa with single-bladed P3s.

Most other plesiomorphic marsupials have three upper premolars, but some dasyurids (e.g., *Dasyurus*) have only two. In addition to the usual diastema between P1 and P2, some adult dasyurids (e.g., *Murexia*) and all adult peramelemorphians have a diastema between P2 and P3. The third upper premolar (P3) is taller than P2 in caenolestids, *Dromiciops*, and some dasyurids (e.g., *Murexia*, *Sminthopsis*), but P2 is taller than P3 in other dasyurids (e.g., *Myoictis*). An anterior cutting edge is apparently absent from P3 in all nondidelphid marsupials.

UPPER MILK PREMOLAR: Although the deciduous upper premolar (dP3) of didelphids has consistently been described as large and molariform (Flower, 1867; Thomas, 1888; Bensley, 1903; Tate, 1948b; Archer, 1976b), there is noteworthy taxonomic variation in the morphology of this tooth. In most opossums dP3 is, indeed, a sizable tooth: its crown area ranges from about 42% to 96% of the crown area of M1, the tooth immediately behind it (Voss et al., 2001: table 5). An obviously functional element of the upper toothrow, dP3 occludes with both the deciduous lower premolar (dp3) and with m1. *Hyladelphys*, however, has a very small upper milk premolar (<10% of the crown area of M1; op. cit.) that appears to be functionally vestigial because it does not occlude with any lower tooth.

Although molariform, the didelphid upper milk premolar does not always match the teeth behind it in all occlusal details. In most specimens, the paracone of dP3 is located on the labial margin of the crown, and the stylar shelf is correspondingly incomplete, whereas the paracone is lingual to a continuous stylar shelf on all didelphid molars (see below). Among those didelphids whose milk premolars we examined, only *Caluromys* has a dP3 in which the paracone is usually lingual to a continuous stylar shelf.

The morphology of milk premolars remains to be widely surveyed in Marsupialia, but of those taxa that we examined, only

Dromiciops has a large, molariform dP3 resembling the common didelphid condition (Marshall, 1982b: fig. 17; Hershkovitz, 1999: fig. 32). By contrast, dP3 is much smaller, more or less vestigial, and structurally simplified in caenolestids, dasyurids, and peramelemorphians (Tate, 1948a; Archer, 1976b; Luckett and Hong, 2000).

UPPER MOLARS: Didelphid upper molars conform to the basic tribosphenic bauplan (Simpson, 1936) in having three principal cusps—paracone, protocone, and metacone—connected by the usual crests in a more or less triangular array (fig. 20). A broad stylar shelf and an anterolabial cingulum are invariably present; the centrocrista (postparacrista + premetacrista) and the ectoloph (preparacrista + centrocrista + postmetacrista) are uninterupted by gaps; the para- and metaconules are indistinct or absent;[15] and there is no posterolingual talon. In addition, most didelphids have several (usually five or six) small cusps on the stylar shelf, for which most authors employ alphabetical labels (after Bensley, 1906; Simpson, 1929; Clemens, 1966). Of these, stylar cusp B (labial to the paracone) is more consistently recognizable than the others, but a stylar cusp in the D position (labial to the metacone) is often subequal to it in size.

Didelphids differ conspicuously in the relative width (transverse or labial-lingual dimension) of successive molars within toothrows. In some taxa, the anterior molars tend to be wide in proportion to more posterior teeth, but in others the posterior molars are relatively wider (fig. 21). The ratio obtained by dividing the width of M4 by the width of M1 (M4/M1; table 8) conveniently indexes this size-independent shape variation and ranges from a minimal value of 0.83 (in

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[15] The literature is inconsistent on this point, with some authors claiming to have observed significant taxonomic variation among Recent didelphids in the occurrence of conules (see Voss and Jansa, 2003: appendix 4). Indeed, careful examination of unworn teeth usually reveals a tiny enameled chevron on the postprotocrista that is presumably homologous with the metaconule of stem metatherians; corresponding structures on the preprotocrista, presumably vestigial paraconules, are much less frequently observed. The fact that conules have been scored as present and absent in the same taxon (e.g., *Didelphis*) by different authors (e.g., Reig et al. [1987] versus Wroe et al. [2000]) sufficiently illustrates the ambiguous interpretation of such indistinct features.
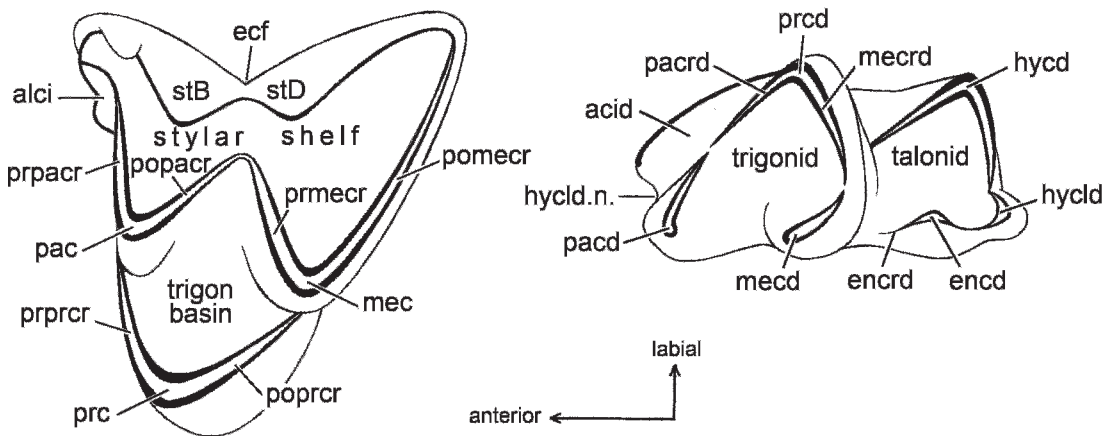
Fig. 20. Occlusal views of left upper and right lower didelphid molars illustrating features of crown morphology discussed in the text. Abbreviations: **acid,** anterior cingulid; **alci,** anterolabial cingulum; **ecf,** ectoflexus; **encd,** entoconid; **encrd,** entocristid; **hycd,** hypoconid; **hycld,** hypoconulid; **hycld.n.,** hypoconulid notch; **mec,** metacone; **mecd,** metaconid; **mecrd,** metacristid; **pac,** paracone; **pacd,** paraconid; **pacrd,** paracristid; **pomecr,** postmetacrista; **popacr,** postparacrista; **poprcr,** postprotocrista; **prc,** protocone; **prcd,** protoconid; **prmecr,** premetacrista; **prpacr,** preparacrista; **prprcr,** preprotocrista; **stB,** stylar cusp B; **stD,** stylar cusp D.

Caluromysiops) to a maximal value of 1.76 (in *Lutreolina*). Morphometric comparisons of dental measurements (Voss and Jansa, 2003: fig. 12) and visual inspections of toothrows suggest that this index is correlated with a pattern of molar occlusal transformation that has been described in the literature as "carnassialization" (Reig and Simpson, 1972: 534) or as "an emphasis on postvallum-prevalid shear" (Muizon and Lange-Badré, 1997). These tendencies are redundantly described by numerous dental ratios that have been coded as independent characters in previous phylogenetic studies (for an extended discussion, see Voss and Jansa, 2003).

In effect, didelphids with relatively wide anterior molars have dentitions that can be described as not or only weakly carnassialized, whereas those with relatively wide posterior molars have strongly carnassialized teeth. Although the endpoints of this morphocline are strikingly different, the essentially continuous distribution of intermediate morphologies renders any attempt to make qualitative distinctions based on molar proportions an arbitrary exercise. We therefore employ "not carnassialized," "weakly carnassialized," "moderately carnassialized," and "strongly carnassialized" as heuristic

descriptors of a visually compelling but phylogenetically intractable aspect of didelphid dental variation.[16]

The ectoflexus is a V-shaped labial indentation of the stylar shelf that is either present or absent on tribosphenic marsupial molars. Among didelphids, *Caluromys* and *Caluromysiops* are the only taxa that lack any trace of an ectoflexus (e.g., figs. 21A, B). In most other opossums, a distinct ectoflexus is present on M3, on M2 and M3, or (rarely) on M1–M3. When ectoflexi are present on multiple teeth, they invariably increase in depth from anterior to posterior.

The shape of the centrocrista (postparacrista + premetacrista) and the descriptive nomenclature associated with its alternative states have been a source of some confusion among marsupial researchers. Traditionally, taxa with a ∧-shaped (labially inflected) centrocrista have been described as "dilambdodont" because the ectoloph (preparacrista + centrocrista + postmetacrista) is then W-shaped (like two inverted lambdas), whereas taxa with a straight (uninflected) centrocrista

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[16] We were not so circumspect in earlier phylogenetic analyses, where computed ratios were used to define qualitative states (e.g., Voss and Jansa, 2003: character 57), but measurements from additional taxa (including outgroups not analyzed by us in 2003) have blurred distinctions that once seemed clear.
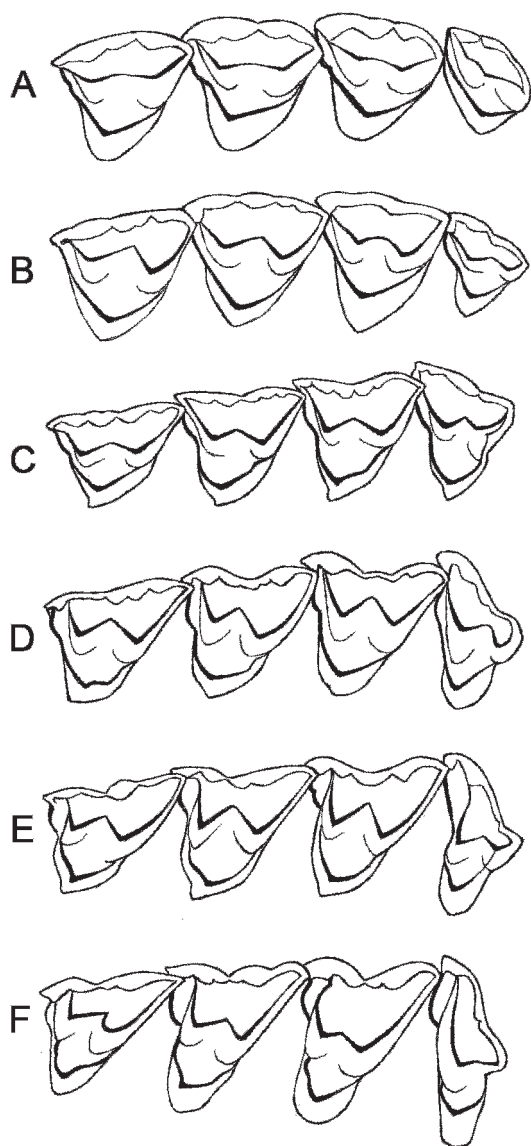
Fig. 21. Occlusal views of left upper molar rows illustrating taxonomic differences in relative widths of teeth (not drawn to the same scale). **A,** *Caluromysiops irrupta* (FMNH 84426); **B,** *Caluromys philander* (AMNH 267334); **C,** *Glironia venusta* (AMNH 71395); **D,** *Marmosa regina* (MVZ 190333); **E,** *Marmosops impavidus* (MUSM 13284); **F,** *Lestodelphys halli* (MMNH 15708).

have usually been called "predilambdodont" (e.g., by Reig et al., 1987). Unfortunately, neither descriptor applies unambiguously to some didelphids (Goin, 1997), and certain taxa have been coded with contradictory

character states in different phylogenetic datasets (e.g., *Didelphis*; see Reig et al., 1987 [character 1]; Wroe et al., 2000 [character 10]; Wible et al., 2001 [character 31]). Our observations agree with Johanson's (1996), that the shape (linearity versus labial inflection) of this crest is correlated with its occlusal relief (apical height above the trigon basin), and we recognize an intermediate condition for taxa that do not conform with either traditionally recognized morphotype.

Among didelphids, only *Caluromysiops* has a truly linear centrocrista on M1–M3. In this taxon, the apex of the centrocrista is essentially level with the floor of the trigon basin, clearly conforming to the predilambdodont condition defined by Johanson (1996). By contrast, the centrocrista is strongly inflected labially (buccally)—and therefore distinctly ∧-shaped—in *Chacodelphys*, *Cryptonanus*, *Gracilinanus*, *Lestodelphys*, *Marmosa*, *Marmosops*, *Metachirus*, *Monodelphis*, *Thylamys*, and *Tlacuatzin*. The apex of the crest is elevated well above the trigon floor in these taxa, which are unambiguously dilambdodont sensu Johanson (1996). The intermediate condition occurs in the seven remaining genera (*Caluromys*, *Chironectes*, *Didelphis*, *Glironia*, *Hyladelphys*, *Lutreolina*, *Philander*) in which the centrocrista has a weak labial inflection with a slightly elevated apex; these taxa can appropriately be described as weakly dilambdodont.

In many didelphids—*Caluromys*, *Caluromysiops*, *Glironia*, *Gracilinanus*, *Hyladelphys*, *Marmosa*, *Tlacuatzin*, and some species of *Cryptonanus* and *Marmosops*—the preprotocrista passes labially around the base of the paracone to join with the anterolabial cingulum. This results in the formation of a continuous shelf along the anterior margin of the tooth (fig. 21A–D), and taxa possessing this feature are sometimes said to have a "complete" anterior cingulum (Archer, 1976b: 3) or to exhibit "double rank prevallum-postvallid shearing" (Cifelli, 1993: 213). In the alternative morphology—exhibited by *Chacodelphys*, *Chironectes*, *Didelphis*, *Lestodelphys*, *Lutreolina*, *Metachirus*, *Monodelphis*, *Philander*, *Thylamys*, and other species of *Cryptonanus* and *Marmosops*—the preprotocrista extends only to a point at or

TABLE 8
Upper Molar Measurements and Proportions[a]

	N[b]	Widths (mm)[c]				Ratio (M4/M1)
		M1	M2	M3	M4	
Caluromys lanatus	5	2.87	3.09	3.01	2.44	0.85
Caluromys philander	5	2.52	2.84	2.90	2.37	0.94
Caluromysiops irrupta	5	2.99	3.21	3.06	2.48	0.83
Chacodelphys formosa	2	1.23	1.64	1.84	1.88	1.53
Chironectes minimus	5	4.04	4.69	5.33	5.34	1.32
Cryptonanus chacoensis	4	1.30	1.71	1.89	1.85	1.42
Cryptonanus unduaviensis	5	1.39	1.79	2.01	2.02	1.45
Didelphis albiventris	1	4.04	5.01	5.60	5.47	1.35
Didelphis marsupialis	3	4.73	5.50	6.04	6.02	1.27
Didelphis virginiana	5	4.59	5.50	6.54	6.99	1.52
Glironia venusta	4	1.92	2.36	2.56	2.47	1.29
Gracilinanus aceramarcae	4	1.20	1.51	1.64	1.69	1.41
Gracilinanus agilis	5	1.28	1.66	1.87	1.89	1.48
Gracilinanus emiliae	3	1.14	1.49	1.67	1.65	1.45
Gracilinanus microtarsus	4	1.30	1.66	1.84	1.86	1.43
Hyladelphys kalinowskii	5	0.96	1.14	1.26	1.21	1.26
Lestodelphys halli	5	1.80	2.40	2.73	2.97	1.65
Lutreolina crassicaudata	4	2.76	3.36	4.15	4.85	1.76
Marmosa (Marmosa) lepida	5	1.33	1.69	1.90	1.96	1.47
Marmosa (Marmosa) mexicana	5	1.44	1.82	2.08	2.26	1.57
Marmosa (Marmosa) murina	5	1.46	1.78	2.08	2.18	1.49
Marmosa (Marmosa) robinsoni	5	1.71	2.10	2.36	2.53	1.48
Marmosa (Marmosa) rubra	5	1.61	2.05	2.33	2.57	1.60
Marmosa (Micoureus) demerarae	5	1.98	2.51	2.82	2.81	1.42
Marmosa (Micoureus) paraguayana	3	2.11	2.65	3.01	3.06	1.45
Marmosa (Micoureus) regina	5	2.18	2.77	3.12	3.17	1.45
Marmosops impavidus	5	1.58	2.00	2.30	2.46	1.56
Marmosops incanus	4	1.74	2.18	2.42	2.69	1.55
Marmosops noctivagus	5	1.83	2.31	2.67	2.82	1.54
Marmosops parvidens	5	1.34	1.67	1.91	1.90	1.42
Marmosops pinheiroi	5	1.33	1.68	1.92	2.04	1.53
Metachirus nudicaudatus	5	2.84	3.29	3.69	3.62	1.27
Monodelphis brevicaudata	5	2.08	2.46	2.64	2.90	1.39
Monodelphis emiliae	5	1.85	2.21	2.34	2.57	1.39
Monodelphis peruviana	5	1.57	1.87	2.05	2.15	1.37
Monodelphis theresa	2	1.36	1.67	1.84	2.11	1.55
Philander frenatus	3	2.77	3.32	3.92	4.17	1.51
Philander mcilhennyi	3	3.53	4.15	4.71	4.99	1.41
Philander opossum	4	3.18	3.74	4.30	4.55	1.43
Thylamys macrurus	5	1.55	2.05	2.32	2.37	1.53
Thylamys pallidior	5	1.31	1.74	2.04	2.12	1.62
Thylamys pusillus	5	1.34	1.72	1.96	2.05	1.53
Thylamys venustus	5	1.37	1.78	2.00	2.10	1.53
Tlacuatzin canescens	5	1.54	1.98	2.28	2.33	1.51

[a] Teeth were measured with digital calipers while viewed under low magnification to ensure that the caliper jaws were consistently placed.

[b] Sample size.

[c] Molar width was measured from the stylar shelf (at or near the "A" position) to the lingual apex of the protocone. Tabulated values are sample means.

near the base of the paracone; the anterolabial cingulum does not converge toward the preprotocrista in these taxa, but passes obliquely dorsally such that the two crests are discontinuous on the anterior surface of the tooth crown (fig. 21E, F). Voss and Jansa (2003: 39) discussed several inconsistencies in the published literature concerning the distribution of these traits among didelphids.

The postprotocrista also exhibits noteworthy variation among didelphids. In most genera, this crest decreases in height and width as it passes posterolabially around the base of the metacone before merging with the posterior surface of the tooth crown, leaving a distinct groove or gap in the posterior wall of the trigon basin. By contrast, the postprotocrista connects directly with the base of the metacone, such that the posterior wall of the trigon basin has no gap or groove, in *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander*; instead, the unworn postprotocrista of these taxa exhibits a distinct carnassial notch near the base of the metacone.

Dasyurids and *Dromiciops* have tribosphenic upper molars that differ from those of didelphids in only minor details. Indeed, some dasyurids and didelphids are indistinguishable in published matrices of upper molar characters (e.g., Archer, 1976b: table 1), although there is a tendency for stylar cusp D to be larger than stylar cusp B when both structures are present in the former group (Wroe, 1997), and a few dasyurids (e.g., *Sarcophilus*) are conspicuously divergent in other upper molar traits. The upper molars of *Dromiciops* differ from those of most didelphids by having a linear centrocrista, indistinct stylar cusps, and a stylar shelf that is conspicuously reduced in width labial to the paracone on M1.[17]

The upper molars of Recent peramelemorphians differ from those of didelphids in several respects, most notably by having a discontinuous centrocrista: instead of forming a ∧-shaped (labially inflected) crest with an apex that is lingual to the stylar shelf, the postparacrista and the premetacrista of modern peramelemorphians terminate on the labial margin of the tooth, where they are separated by a small gap (Muirhead and Filan [1995] referred to this trait as the result of the centrocrista "breaching" the ectoloph). Additionally, all modern peramelemophians have a large posterolingual cusp on M1–M3; in most genera (e.g., *Echymipera*, *Perameles*) this is a hypertrophied metaconule, but in *Macrotis* it is the metacone (Archer, 1976b). Another peramelemorphian trait is that the preparacrista of M1 is a tall crest that passes posterolabially to a large stylar cusp at or near the C position (Archer, 1976b). The anterolabial cingulum is present in some peramelemorphians (e.g., *Echymipera*) but not in others (e.g., *Perameles*).

On caenolestid molars the principal labial cusps are hypertrophied stylar elements in the B and D positions (Osgood, 1921; Marshall, 1987; Goin and Candela, 2004; Goin et al., 2007). In both *Caenolestes* and *Rhyncholestes*, the paracone is absent (or indistinguishably fused with stylar cusp B). The metacone is also absent in *Rhyncholestes* but, although fused to the lingual aspect of stylar cusp D, the metacone is still clearly recognizable in *Caenolestes*. Given this interpretation of caenolestid cusp homologies, it follows that a low crest along the labial base of the tooth crowns in both genera is a neomorphic cingulum rather than a vestigial stylar shelf. The first two caenolestid upper molars also have a well-developed posterolingual cusp that has been interpreted either as a hypertrophied metaconule (Marshall, 1987; Goin and Candela, 2004; Goin et al., 2007) or as a neomorphic outgrowth of the postprotocingulum (Hunter and Jernvall, 1995). Another distinctive trait of the upper molars of Recent caenolestids is the complete absence of an anterolabial cingulum.

UPPER DENTAL ERUPTION SEQUENCES: As described by Tribe (1990), P3 is the last upper tooth to erupt in most didelphids. By contrast, P3 erupts before M4, which is the

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[17] These distinctive features are not apparent in some published illustrations of the dentition of *Dromiciops*, notably Marshall's (1982b) figure 16b, where an occlusal view of the upper teeth of FMNH 22671 shows ∧-shaped centrocristae and an unreduced stylar shelf on M1. However, in another illustration (based on FMNH 22673; op. cit.: fig. 17b), M1 is correctly shown with a reduced stylar shelf labial to the paracone, and with a linear centrocrista. We borrowed FMNH 22671 to determine whether this specimen is unusual in any way and found that it is not: the paracone of M1 is almost on the labial margin of the tooth, and the centrocristae of M1–M3 are linear; therefore, Marshall's figure 16b is inaccurate.

last upper tooth to emerge in *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander*. In a few didelphids (e.g., *Metachirus nudicaudatus*, *Monodelphis brevicaudata*), M4 and P3 appear to erupt simultaneously. Molar eruption sequences have not been widely surveyed among other marsupials, but P3 seems to be the last upper tooth to erupt in most nondidelphid clades, with the exception of *Dromiciops* and caenolestids, in which M4 is usually last (Hershkovitz, 1999; Luckett and Hong, 2000).

LOWER INCISORS: The four lower incisors of didelphids are subequal in size and essentially similar in coronal shape, but the alveolus of i2 is always ''staggered'' (displaced lingually and dorsally relative to the alveoli of i1, i3, and i4), and the root of this tooth is correspondingly supported by a prominent labial buttress of alveolar bone (Hershkovitz, 1982, 1995). The unworn lower incisor crowns of most didelphids have a distinct lingual cusp or heel (fig. 22, top) that is indistinct or absent in *Chironectes*, *Didelphis*, *Lutreolina* (fig. 22, bottom), and *Philander*. This character has the same taxonomic distribution among didelphids as Takahashi's (1974) distinction between the ''subrectangular'' teeth of *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander* on the one hand, and the ''suboval'' lower incisors of *Caluromys*, *Marmosa*, *Metachirus*, and *Monodelphis* on the other, but we are unable to appreciate the basis for her shape descriptors. No didelphid has a lobed or indented cutting edge on any of the lower incisor crowns.

Among other marsupials, *Dromiciops* resembles didelphids in having four lower incisors, whereas dasyurids and peramelemorphians have only three. The missing tooth in dasyurids and peramelemorphians is presumably i4, because there is only one tooth behind staggered-and-buttressed i2, and because it seems more likely that teeth should be lost from the end of the incisor series than from intermediate loci. In all of these polyprotodont groups, the lower incisors are short-crowned nonprocumbent teeth that differ from those of didelphids in only minor details.

The unworn lower incisors of most dasyurids (e.g., *Murexia*, *Sminthopsis*) have a distinct lingual cusp or heel, but this structure is lacking in at least some of the larger carnivorous forms (e.g., *Dasyurus*). A distinctive feature of unworn i3 in dasyurids is the consistent presence of a small posterior lobe on the cutting edge of the tooth.[18] As implied by Bensley (1903: 113), this structure appears to be homologous with the much larger posterior lobe of i3 seen in peramelemorphians. All peramelemorphian lower incisors lack a lingual cusp or heel, but i1 and i2 are otherwise unremarkable in this group. The lower incisor dentition of *Dromiciops* is similar to that of didelphids except for the fact that i2 is neither staggered nor buttressed in microbiotherians (Hershkovitz, 1999: figs. 5A, 29E).

The anteriormost lower incisor of caenolestids is a long-crowned procumbent (gliriform) tooth that most authors (e.g., Ride, 1962; Marshall, 1980; Sánchez-Villagra, 2001b) assume to be either i1 or i2. Whichever it is, at least two of the four single-rooted unicuspids that normally occur between the gliriform tooth and the anteriormost undisputed premolar must also be incisors.[19] None of the lower incisors of *Caenolestes* or *Rhyncholestes* has a staggered alveolus.

LOWER CANINE: The lower canine is an erect unicuspid tooth that is conspicuously differentiated from the incisors and premolars in all of the larger didelphids (*Caluromys*, *Caluromysiops*, *Chironectes*, *Didelphis*, *Lutreolina*, *Philander*), and in some of the smaller forms as well (*Glironia*, *Hyladelphys*,

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[18] This is the ''posterobuccal'' lobe of Archer (1976b: 6) who stated that it is present in only a few dasyurids. However, it is immediately recognizable in juvenile specimens of all the dasyurids we examined. Ontogenetically persistent in some taxa, it is soon obliterated with wear in others and may be indistinguishable in adults.

[19] Like others who have pondered caenolestid antemolar tooth homologies (e.g., Thomas, 1895; Ride, 1962; Marshall, 1980), we assume that no more than one lower canine and three lower premolars are normally present. Because the presence of two lower premolars (each with two roots; Osgood, 1921) is undisputed, only one of the problematic unicuspids could belong to this series. Hershkovitz (1982) implied that none of the lower incisor alveoli of caenolestids are staggered, but he later (Hershkovitz, 1995) stated that Recent caenolestids have a staggered i2 (''i3''). In all of the specimens of *Caenolestes* and *Rhyncholestes* that we examined, however, the four unicuspids behind the gliriform tooth have colinear alveoli; there is no suggestion of lingual displacement at the second locus.
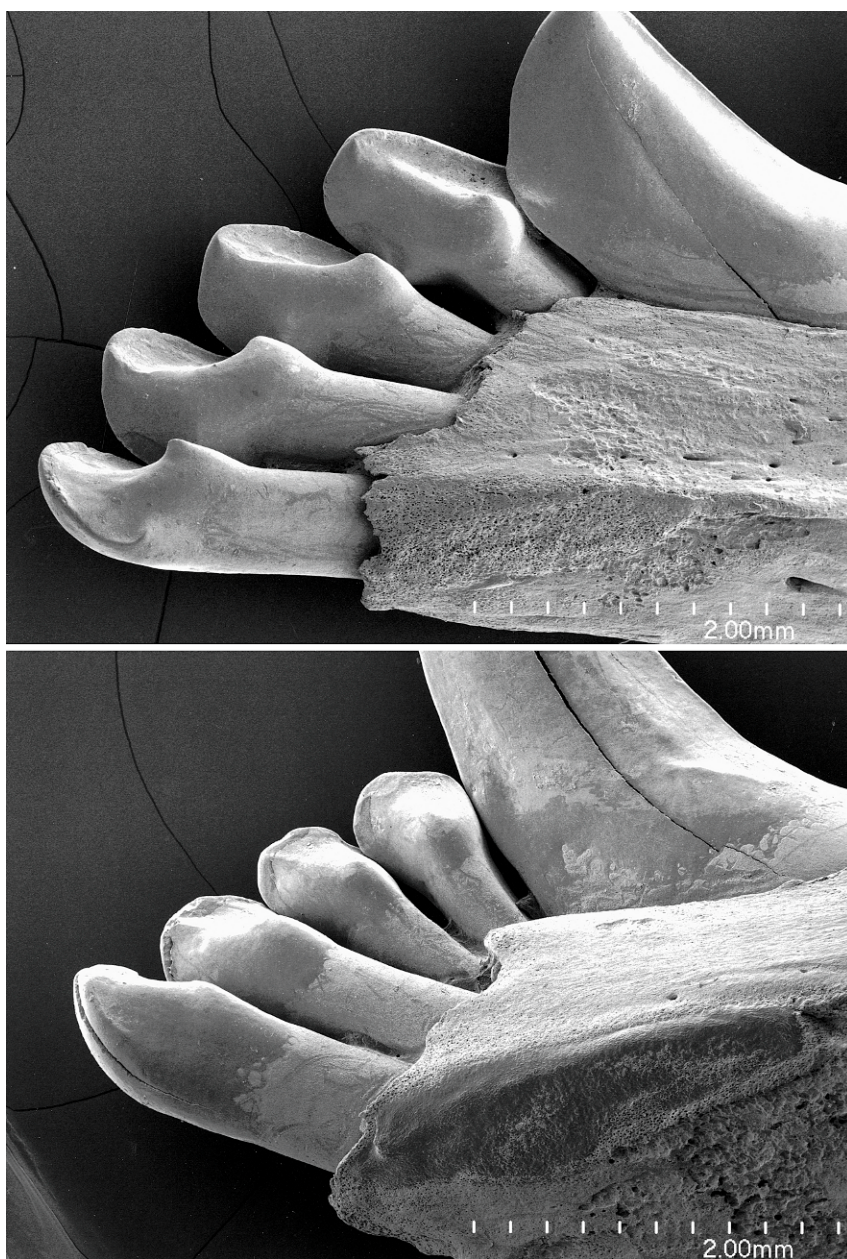
Fig. 22.   Lingual views of lower incisors. **Top,** *Metachirus nudicaudatus* (AMNH 266452) with distinct posterior accessory cusps on i1–i4. **Bottom,** *Lutreolina crassicaudata* (AMNH 210424) without distinct posterior accessory cusps on i1–i4.

Lestodelphys, Monodelphis, Tlacuatzin). In all of these taxa, the unworn crown of c1 tapers to a sharp apical point (fig. 23A). By contrast, the lower canine is procumbent and tends to become premolariform in other small didelphids. Premolarization of c1 includes the development of a flattened anterior blade (rather than a sharp tip) and a posterior cingulum that sometimes produces a distinct accessory cusp. Whereas these
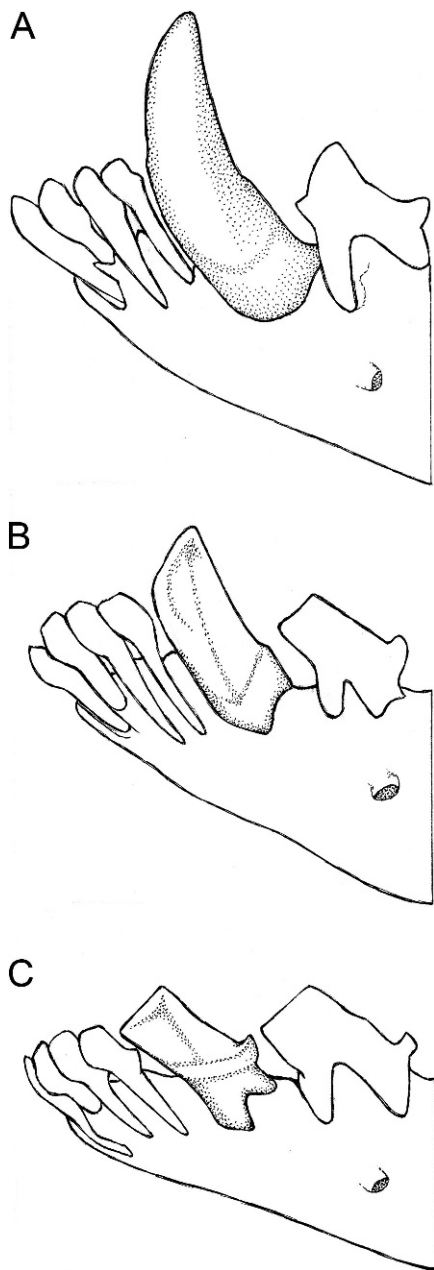
Fig. 23. Labial views of unworn anterior mandibular dentitions illustrating taxonomic differences in lower canine (c1) morphology. **A,** *Lestodelphys halli* (MMNH 17171) with erect, acutely pointed, and simple c1. **B,** *Marmosa mexicana* (AMNH 17136) with semiprocumbent and flat-crowned but simple c1. **C,** *Marmosops pinheiroi* (AMNH 267342) with fully premolariform c1 (procumbent and flat crowned with posterior accessory cusp).

tendencies are minimally indicated on the unworn teeth of *Chacodelphys* and *Metachirus* (which are flattened along their anterior margin but have no posterior cingulum), they are increasingly apparent in *Cryptonanus*, *Gracilinanus*, *Marmosa* (fig. 23B), and *Thylamys*. Premolarization of the lower canine is maximally developed in the smaller species of *Marmosops* (e.g., *M. parvidens* and *M. pinheiroi*), where c1 and p1–3 form a series of four strikingly similar teeth (fig. 23C). Generally speaking, taxa with well-developed accessory cusps on the upper canine also have a well-developed posterior accessory cusp on c1, so variation in these occluding teeth is at least partially correlated.

Large dasyurids (e.g., *Dasyurus*) have erect, unicuspid lower canines, but many small dasyurids (e.g., *Sminthopsis*) have procumbent, premolariform teeth. The lower canines are small and blunt in peramelemorphians. In *Dromiciops*, c1 is procumbent and more or less premolariform (Marshall, 1982b: fig. 14).

LOWER PREMOLARS: Didelphid lower premolars are unremarkable teeth, each having a single dominant cusp and a well-developed distal cingulum that often produces a posterior accessory cusp. Small diastemata are sometimes present between p1 and c1, between p1 and p2, and (rarely) between p2 and p3. The lower first premolar (p1) is vestigial and occlusally featureless in *Caluromys* and *Caluromysiops*, but it is well developed in all of the other genera.

The second lower premolar is distinctly taller than p3 in most didelphids, but p2 and p3 are subequal in *Marmosops incanus* and most examined species of *Monodelphis* and *Thylamys*. In *Lestodelphys* and in certain other species of *Monodelphis* (e.g., *M. emiliae*), however, p3 is distinctly taller than p2.

Most other plesiomorphic marsupials have three lower premolars that are essentially similar to those of didelphids, although some dasyurids (e.g., *Dasyurus*) have only two. Among the taxa we examined, p3 is taller than p2 in caenolestids, *Dromiciops* (see Marshall, 1982b: fig. 14), some dasyurids (e.g., *Murexia*), and some peramelemorphians (e.g., *Echymipera*), but p2 and p3 are subequal in height or p2 is the taller tooth in other dasyurids (e.g., *Sminthopsis*) and peramelemorphians (e.g., *Macrotis*).
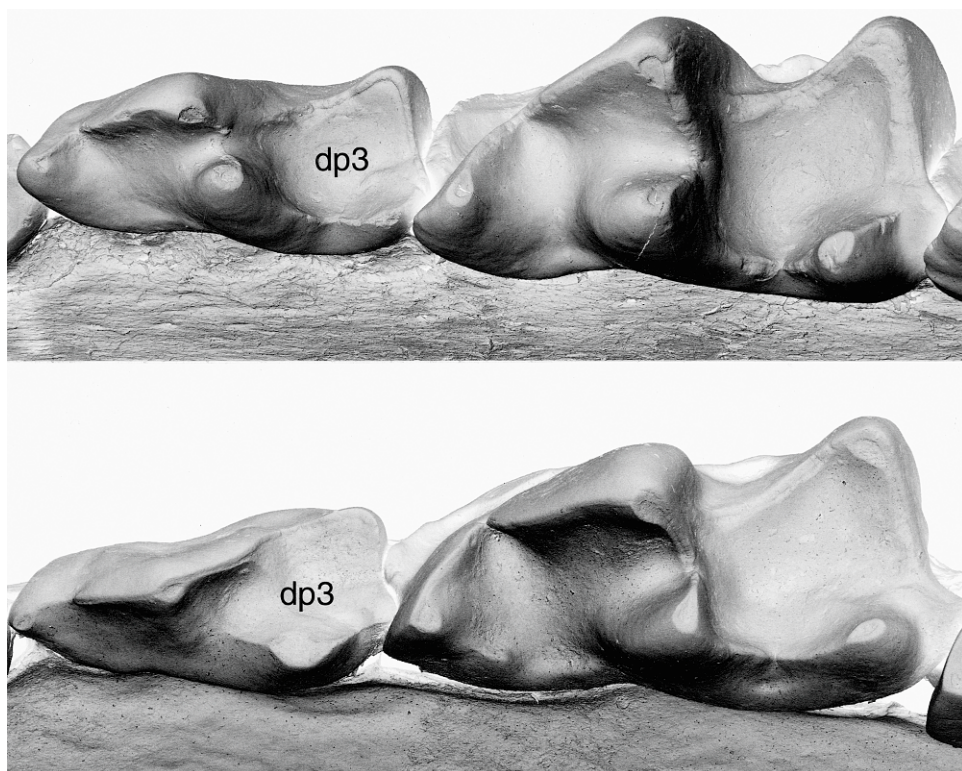
Fig. 24.   Occlusal views of right dp3 and m1 illustrating taxonomic differences in trigonid morphology of the deciduous tooth. **Top,** *Marmosops impavidus* (MUSM 13286) with a complete (tricuspid) dp3 trigonid. **Bottom,** *Marmosa murina* (MUSM 15297) with an incomplete (bicuspid) dp3 trigonid.

LOWER MILK PREMOLAR: Taxonomically significant variation among didelphids in the size and shape of dp3 was reported by Voss et al. (2001: table 5). Many didelphids (*Caluromys lanatus*, *Caluromysiops*, *Chironectes*, *Cryptonanus chacoensis*, *Didelphis*, *Lutreolina*, *Marmosops*, *Metachirus*, *Monodelphis emiliae*, *Philander*) have a fully molariform dp3 in which the trigonid is represented by its normal complement of three cusps (paraconid, protoconid, metaconid) in a more or less triangular configuration (fig. 24, top). A fully molariform dp3 is also the modal condition for *Monodelphis brevicaudata*, in which seven of nine specimens examined with intact milk dentitions had complete trigonids. By contrast, dp3 is only partially molariform in *Cryptonanus unduaviensis*, *Gracilinanus agilis*, *Lestodelphys*, *Marmosa*, and *Thylamys*, which have incomplete, blade-like trigonids bearing only one or two distinct cusps (fig. 24, bottom). Although just the protoco-

nid of dp3 is usually distinct in our material of *Caluromys philander*, the trigonid of this taxon is triangular in occlusal outline and more closely resembles the fully molariform condition than the blade-like uni- or bicuspid alternative. Among other plesiomorphic marsupials that we examined, only *Dromiciops* has a large and fully molariform dp3, whereas dasyurids and peramelemorphians have small, structurally simplified and obviously vestigial lower milk premolars.

LOWER MOLARS: Didelphid lower molars conform to the usual tribosphenic pattern and are readily described using standard nomenclature (fig. 20). The trigonid moiety of each tooth invariably consists of three distinct cusps (paraconid, protoconid, and metaconid) that are connected by two tall and deeply notched crests (paracristid and metacristid); three additional cusps (hypoconid, entoconid, and hypoconulid) surround the talonid basin. A well-developed anterior

cingulid (precingulid) is always present, but a posterior cingulid (postcingulid) is just as consistently absent.[20] The anterior cingulid never extends all the way to the base of the paraconid because it abuts on the hypoconulid of the preceding tooth (dp3 in the case of m1), resulting in a prominent concavity in the anterolingual occlusal outline (the "hypoconulid notch" of Archer, 1976b). The entocristid is a short crest that approximately parallels the lingual margin of the tooth.

Didelphid lower molars exhibit taxonomic shape variation that is correlated with carnassialization as previously described for the upper teeth. Thus, taxa with uncarnassialized molars have relatively small trigonids and large talonids, whereas opossums with highly carnassialized molars have relatively large trigonids and small talonids. Trigonid enlargement is invariably accompanied by an increase in occlusal relief, the protoconid and metacristid in particular tending to become very tall in the most carnassialized forms (e.g., *Lestodelphys* and *Lutreolina*). The width gradient previously noted for the upper molars is also seen in the lowers, m2 being the widest tooth in uncarnassialized dentitions whereas m3 or m4 is widest in progressively more carnassialized forms. As for the upper teeth, the highly divergent endpoints of this conspicuous gradient of dental shape variation are connected by an almost continuous taxonomic series of morphological intermediates.

Only a few lower molar traits that vary among didelphids seem useful for the purposes of taxon diagnoses and phylogenetic analysis. Among these, the labial prominence of the hypoconid tends to vary along the toothrow, so we standardized comparisons at the third molar locus. In most opossums, the hypoconid is labially salient (projecting beyond the protoconid or level with it) on m3, but the hypoconid is lingual to the protoconid in *Chacodelphys*, *Lestodelphys*, *Lutreolina*, and *Monodelphis*.

Most didelphids have a well-developed entoconid that is about as tall as the hypoconid and much exceeds the adjacent hypoconulid in height and breadth on m1–m3 (fig. 25, top). In *Chacodelphys* and *Monodelphis*, however, the entoconid is very small, never more than subequal to the hypoconulid, and often smaller than that cusp (fig. 25, bottom); it becomes indistinct or is obliterated by wear in most adult specimens. Discrepant observations in the literature about didelphid entoconid size variation were discussed by Voss and Jansa (2003).

In most didelphids, the hypoconulid is much closer to the entoconid than it is to the hypoconid, and is said to be "twinned" with the former cusp. Although twinning of the hypoconulid and entoconid is often stated (or implied) to be universally present among tribosphenic marsupials (e.g., by Clemens, 1979; Kielan-Jaworowska et al., 2004), it is not. The hypoconulid and entoconid are not closely approximated in *Caluromysiops*, and in some specimens (e.g., FMNH 121522) the hypoconulid is at the center of the posterior talonid margin, equidistant to the hypoconid and the entoconid.

Most other plesiomorphic marsupials have lower molars that resemble those of didelphids in common tribosphenic features, but several differences are noteworthy. Dasyurids, for example, have a well-developed posterior cingulid on m1–m3, the anterior cingulid of peramelemorphian lower molars lacks a hypoconulid notch, the anterior cingulid is vestigial in *Dromiciops* (which lacks a hypoconulid notch on m1), and an entocristid is absent in some dasyurids (e.g., *Sminthopsis*) and peramelemorphians (e.g., *Perameles*).

As they are in so many other character complexes, caenolestids are the most divergent basal marsupials in lower molar morphology. In both *Caenolestes* and *Rhyncholestes* the paracristid is unnotched and decreases gradually in height from the apex of the protoconid to the anterolingual corner of the tooth; the paraconid is therefore indistinct. Whereas the paracristid runs in an uninterrupted arc from the protoconid to the anterolingual corner of the tooth on m1, the paracristid on m2 and m3 abuts the hypoconulid of the preceding tooth (m1 and m2, respectively), at which point it is abruptly deflected posterolingually. The only distinct trigonid cusp on m4 is the metaconid, from

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[20] A posterior cingulid ("postcingulum") was illustrated by Goin and Candela (2004: fig. 2B) on a diagram representing the occlusal features of a "didelphimorphian opossum," but no living didelphimorphian has such a structure.
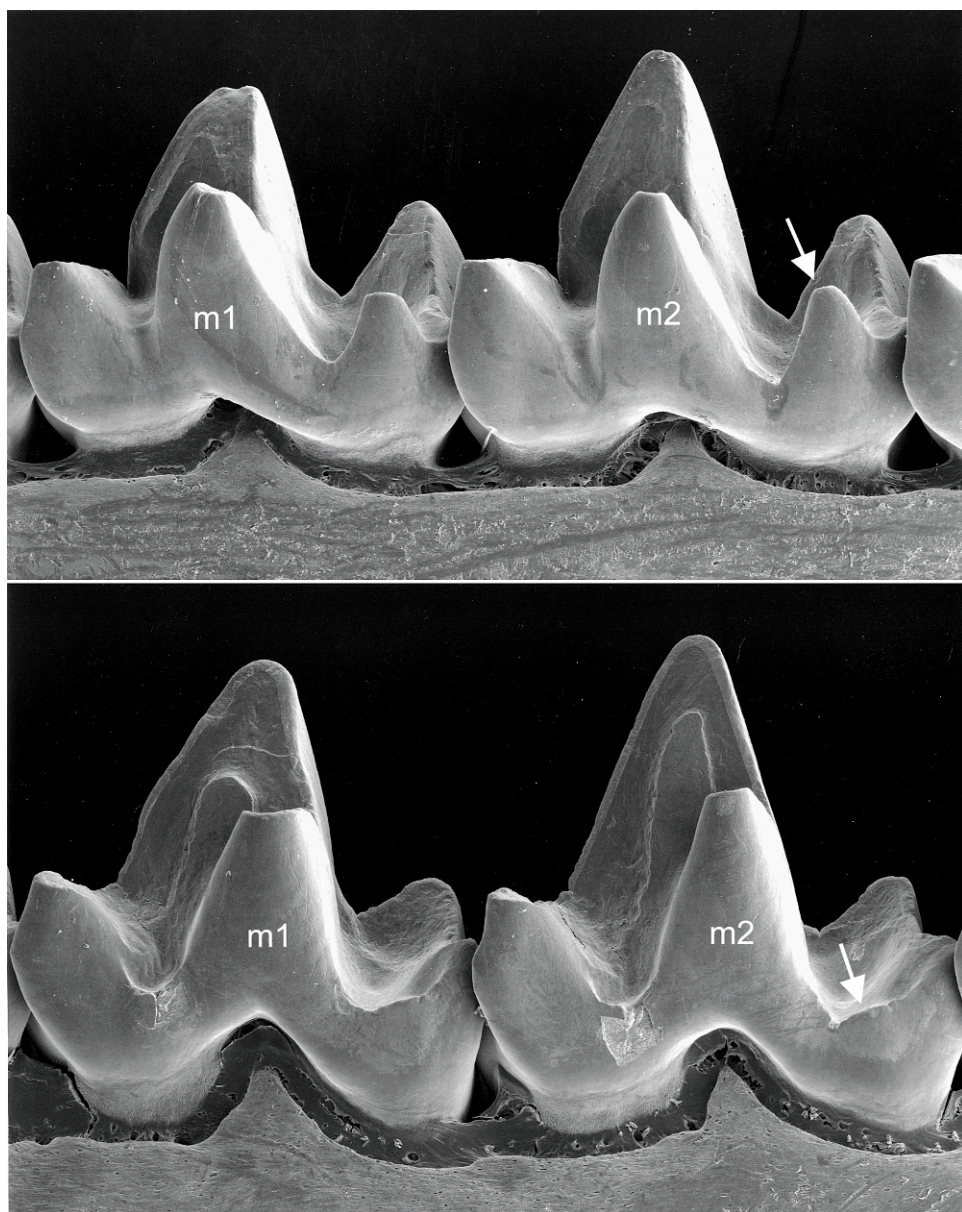
Fig. 25. Lingual views of right m2 and m3 illustrating taxonomic differences in entoconid size. **Top,** *Thylamys pallidior* (AMNH 262405) with a large entoconid (arrow). **Bottom,** *Monodelphis peruviana* (AMNH 272781) with an indistinct entoconid (arrow).

which a diminutive crest (comprising a vestigial metacristid and part of the paracristid) curves anterolabially to abut the hypoconulid of m3. The entocristid on m1–m3 is a long crest that is deflected labially, away from the lingual margin of the tooth, and terminates deep inside the talonid basin.

Summary

The morphological observations described above provide evidence of taxonomic differences in many phenotypic attributes suitable for phylogenetic analysis, including unambiguously distinguishable aspects of pelage

color and structure; sexually dimorphic skin glands and carpal tubercles; manual and pedal digital proportions; the presence, absence, and morphology of cutaneous shelters for nursing young; caudal modifications for prehensility and fat storage; the sizes and shapes of cranial bones and bony processes; the presence, absence, and ontogenetic persistence of cranial sutures; the number and occurrence of cranial foramina and fenestrae; auditory morphology; and the sizes, shapes and eruption sequences of teeth. Because the relevant literature on mammalian functional morphology is too extensive to review effectively in this report, we can only assert that such taxonomic differences are likely to reflect adaptations for such diverse functions as concealment, locomotion, reproduction, sense perception, and food reduction. Anatomical trait variation (together with published information about karyotypic differences that are not reviewed above) is formally described as qualitative characters in appendix 3, where we also explain the criteria used to score individual specimens and discuss the justification for ordering multistate transformation series. The resulting data are summarized in appendix 4.

GENE SEQUENCES

Of the many genes that have been sequenced to date from one or more didelphid marsupials (including the entire genome of *Monodelphis domestica*; Mikkelsen et al., 2007), only a few have been sequenced from enough taxa to be useful for phylogenetic inference. Below we summarize information about five protein-coding nuclear loci from which long (>900 bp) nucleotide sequences have now been obtained from numerous species representing almost all of the currently recognized genera (table 9). The following accounts describe the size, internal organization, and chromosomal location of each gene, as well as the tissues in which it is known to be active and the physiological activity of its translated protein product. We also provide a brief synopsis of previous analyses based on each gene in mammalian phylogenetic research before describing the sequence characteristics of the fragments we amplified from didelphids and other marsupials.

Breast Cancer Activating 1 Gene

The human BRCA1 gene consists of 22 coding exons distributed over ca. 100 kb of genomic DNA on the long arm of chromosome 17 (Miki et al., 1994). The gene is expressed in numerous tissues, but it is especially active in epithelial cells undergoing high levels of proliferation and differentiation (Miki et al., 1994; Casey, 1997). BRCA1 is a tumor suppressor gene whose unmutated product is a large (1863 amino acids) nuclear-cytoplasmic-shuttling phosphoprotein of unknown structure but with apparently essential roles in transcriptional regulation and DNA repair, among other intracellular functions (Rodríguez and Henderson, 2000; Dimitrov et al., 2001; Venkitaraman, 2001).

Nucleotide sequence data from BRCA1 exon 11 have been analyzed in several mammalian phylogenetic studies, usually in concatenated datasets with other genes (e.g., Adkins et al., 2001; Madsen et al., 2001; Delsuc et al., 2002; Douady et al., 2002; Raterman et al., 2006). Homology comparisons of the 2163 bp fragment that we amplified and sequenced for this study are consistent with the presence of a single full-length copy in *Monodelphis domestica*, where the gene appears to be located on chromosome 2. BRCA1 sequence data are available from 48 terminals in our analyses, including 41 didelphids (*Caluromysiops* and *Lestodelphys* were not sequenced) and all 7 nondidelphid outgroups. All of the marsupial sequences that we obtained and others that we downloaded from GenBank translate to open reading frame. Twenty independent insertion-deletion events (indels) ranging in length from 3 to 39 bp were required to align didelphid BRCA1 sequences; of these, 9 were unique to single taxa and 11 were shared by two or more taxa.

Dentin Matrix Protein 1

The human DMP1 gene (originally known as AG1; George et al., 1993) consists of six exons spanning about 14 kb of genomic DNA on the long arm of chromosome 4 (Hirst et al., 1997). DMP1 is an acidic calcium-binding secreted phosphoprotein of about 513 amino acids, most of which are

TABLE 9
GenBank Accession Numbers for Molecular Sequences Analyzed in This Report[a]

	BRCA1	DMP1	IRBP	RAG1	vWF
Didelphidae					
Caluromys lanatus	FJ159278	DQ083120	AF257690	DQ865883	FJ159328
Caluromys philander	FJ159279	DQ083121	AY233766	DQ865884	FJ159329
Caluromysiops irrupta	N/A	N/A	AF257675	N/A	N/A
Chironectes minimus	FJ159280	DQ083122	AF257679	DQ865885	FJ159330
Cryptonanus chacoensis	FJ159281	DQ083123	AY957494	DQ865886	FJ159331
Cryptonanus unduaviensis	FJ159282	DQ083124	AY957492	DQ865887	FJ159332
Didelphis albiventris	FJ159283	DQ083125	AF257683	DQ865888	FJ159333
Didelphis marsupialis	FJ159284	DQ083126	AF257703	DQ865889	FJ159334
Didelphis virginiana	FJ159285	DQ083127	AF257678	DQ865890	FJ159335
Glironia venusta	FJ159286	DQ083128	AF257688	DQ865891	FJ159336
Gracilinanus aceramarcae	FJ159287	DQ083129	AY957488	DQ865892	FJ159337
Gracilinanus agilis	FJ159288	DQ083130	AY957487	DQ865893	FJ159338
Gracilinanus emiliae	FJ159289	DQ083131	AY957486	DQ865894	FJ159339
Gracilinanus microtarsus	FJ159290	DQ083132	AF257687	DQ865895	FJ159340
Hyladelphys kalinowski	FJ159291	DQ112326	DQ112324	DQ865923	FJ159341
Lestodelphys halli	N/A	DQ083133	AF257710	N/A	N/A
Lutreolina crassicaudata	FJ159292	DQ083134	AF257685	DQ865896	FJ159342
Marmosa demerarae[b]	FJ159304	DQ083146	AF257693	DQ865908	FJ159354
Marmosa lepida	FJ159293	DQ083135	AY233769	DQ865897	FJ159343
Marmosa mexicana	FJ159294	DQ083136	AY233770	DQ865898	FJ159344
Marmosa murina	FJ159295	DQ083137	AF257709	DQ865899	FJ159345
Marmosa paraguayana[b]	FJ159305	DQ083147	AY233778	DQ865909	FJ159355
Marmosa regina[b]	FJ159306	DQ083148	AY233780	DQ865910	FJ159356
Marmosa robinsoni	FJ159296	DQ083138	AY233774	DQ865900	FJ159346
Marmosa rubra	FJ159297	DQ083139	AY233776	DQ865901	FJ159347
Marmosops impavidus	FJ159298	DQ083140	AF257695	DQ865902	FJ159348
Marmosops incanus	FJ159299	DQ083141	AY233785	DQ865903	FJ159349
Marmosops noctivagus	FJ159300	DQ083142	AF257704	DQ865904	FJ159350
Marmosops parvidens	FJ159301	DQ083143	AF257680	DQ865905	FJ159351
Marmosops pinheiroi	FJ159302	DQ083144	AF257677	DQ865906	FJ159352
Metachirus nudicaudatus	FJ159303	DQ083145	AF257707	DQ865907	FJ159353
Monodelphis brevicaudata	FJ159307	DQ083150	AY233782	DQ865912	FJ159357
Monodelphis emiliae	FJ159308	DQ083151	AF257692	DQ865913	FJ159358
Monodelphis peruviana[c]	FJ159309	DQ083149	AF257694	DQ865911	FJ159359
Monodelphis theresa	FJ159310	DQ083152	AY233783	DQ865914	FJ159360
Philander frenatus	FJ159312	DQ083153	AY233787	DQ865915	FJ159362
Philander mcilhennyi	FJ159313	DQ083154	AF257706	DQ865916	FJ159363
Philander opossum	FJ159314	DQ083155	AY233789	DQ865917	FJ159364
Thylamys macrurus	FJ159317	DQ083156	AY957491	DQ865918	FJ159366
Thylamys pallidior	FJ159318	DQ083157	AF257689	DQ865919	FJ159367
Thylamys pusillus	FJ159319	DQ083158	AY957489	DQ865920	FJ159368
Thylamys venustus	FJ159320	DQ083159	AY233791	DQ865921	FJ159369
Tlacuatzin canescens	FJ159321	DQ083160	AY233768	DQ865922	FJ159370
Caenolestidae					
Caenolestes fuliginosus	AF355794	N/A	FJ159322	AY243384	AY243403
Rhyncholestes raphanurus	AY243454	N/A	AY243440	AY243399	FJ159365
Dasyuridae					
Murexia longicaudata	FJ159311	N/A	FJ159325	N/A	FJ159361
Sminthopsis crassicaudata	FJ159316	N/A	FJ159327	N/A	AY243413

TABLE 9
(*Continued*)

	BRCA1	DMP1	IRBP	RAG1	vWF
Microbiotheriidae					
Dromiciops gliroides	AY243446	N/A	FJ159323	AY243389	AY243407
Peramelidae					
Echymipera kalubu	AF355796	N/A	FJ159324	AY243386	AY243405
Perameles gunnii	AY243450	N/A	FJ159326	AY243394	AY243411

[a] See table 2 for taxonomic conventions. N/A = not available (see text).

[b] As *Micoureus* in GenBank.

[c] Formerly *Monodelphis adusta*.

encoded by exon 6 (Hirst et al., 1997). The protein is assumed to have some role in tissue mineralization based on its chemical properties and presence in the extracellular matrix of dentine and bone (Butler and Ritchie, 1995; Feng et al., 2003). However, mRNA transcripts and the protein itself have also been detected in a wide range of soft tissues, where the gene presumably has other functions (Terasawa et al., 2004).

Nucleotide sequence data from DMP1 exon 6 have been analyzed in several previous studies of mammalian intraordinal relationships (e.g., Van Den Bussche et al., 2003; Reeder and Bradley, 2004; Jansa et al., 2006). Homology comparisons of the 1176 bp fragment that we amplified and sequenced for this study are consistent with the presence of a single full-length copy in *Monodelphis domestica*, where the gene appears to be located on chromosome 5. We obtained DMP1 sequences from 42 didelphids (none is available from *Caluromysiops*). Fourteen indels ranging in length from 3 to 18 bp are required to align didelphid DMP1 sequences, including 6 that are unique to single taxa and 8 that are shared by two or more taxa. Unfortunately, didelphid DMP1 sequences cannot be aligned unambiguously with sequences from nondidelphid marsupials, so no outgroups are available to root phylogenetic analyses of this gene (Jansa and Voss, 2005; Jansa et al., 2006).

Interphotoreceptor Retinoid Binding Protein

The human IRBP gene (also known as the Retinol Binding Protein 3 gene, RBP3) consists of four exons spanning about 9.5 kb of genomic DNA on the long arm of chromosome 10 (Liou et al., 1989; Fong et al., 1990; Pepperberg et al., 1993). The gene product is a large (1230 amino acids) secreted glycolipoprotein that is primarily found in the extracellular matrix between the retinal pigment epithelium (RPE) and the neural retina of the eye; the protein apparently functions as a two-way carrier of retinoid between the rod photoreceptors and the RPE, and therefore plays a critical role in visual pigment regeneration (Pepperberg et al., 1993).

Nucleotide sequences from IRBP exon 1 were among the first molecular character data to provide convincing support for mammalian superordinal relationships (Stanhope et al., 1992, 1996; Springer et al., 1997b), and they have also been analyzed in several subsequent studies focused on lower-level relationships (e.g., Jansa and Voss, 2000; Mercer and Roth, 2003; Weksler, 2003; Jansa and Weksler, 2004). The 1158 bp fragment that we amplified and sequenced from didelphids is homologous with a single full-length copy in *Monodelphis domestica*, where the gene is apparently located on chromosome 1. IRBP sequences are available from 43 didelphid terminal taxa (including *Caluromysiops* and *Lestodelphys*) and 7 nondidelphid outgroups. No indels are required to align didelphid IRBP sequences, all of which translate to open reading frame (Jansa and Voss, 2000, 2005; Voss and Jansa, 2003).

Recombination Activating 1 Gene

The human RAG1 gene contains a single uninterrupted exon of 3.1 kb located on the short arm of chromosome 11 adjacent to the

RAG2 locus; the gene product is a large DNA-binding protein of 1043 amino acids (Schatz et al., 1989; Oettinger et al., 1990, 1992). Recombination activating genes are expressed only in the nucleus of developing B and T lymphocytes, where the RAG1 and RAG2 proteins act synergistically to make double-stranded breaks at specific recognition sequences, initiating recombination of variable (V), diversity (D), and joining (J) gene segments; completion of the V(D)J rearrangement process yields functional immunoglobulin and T-cell receptor proteins, an essential step in the development of a mature immune system (Gellert, 2002).

Nucleotide sequence data from RAG1 have previously been analyzed in several vertebrate phylogenetic studies (e.g., Groth and Barrowclough, 1999; Barker et al., 2002; Baker et al., 2004; Gruber et al., 2007). The 2790 bp fragment that we amplified and sequenced for this study is homologous with a single full-length copy in *Monodelphis domestica*, where the gene is apparently located on chromosome 5. Although RAG1 occupies the same chromosome as DMP1, the considerable distance that separates these loci ($>2 \times 10^8$ bp) suggests that they belong to different linkage groups. We obtained full-length RAG1 sequences from 41 didelphids (excluding *Caluromysiops* and *Lestodelphys*), and we downloaded shorter (543 bp) outgroup sequences from Genbank. Ingroup and outgroup sequences all translate to open reading frame. Only two indels (of 6 bp each) were required to align didelphid RAG1 sequences; one indel is unique to *Metachirus nudicaudatus*, whereas the other is shared by *Marmosops parvidens* and *M. pinheiroi*.

von Willebrand Factor

The human vWF gene consists of 52 exons spanning 178 kb of genomic DNA on the short arm of chromosome 12 (Mancuso et al., 1989). The gene is normally active only in vascular endothelium and in bone-marrow megakaryocytes (Ruggieri and Zimmerman, 1987). The mature (post-translationally processed) gene product is a large (2050 amino acids) glycoprotein that is assembled into multimers of various sizes; these multimers are either secreted into the plasma or into the subendothelial matrix (by endothelial cells), or they are packaged into the μ granules of platelets (by megakaryocytes). Multimeric vWF mediates adhesion of platelets to exposed subendothelium following vascular injury, and it serves as the plasma chaperone of blood factor VIII, an important regulatory protein in the coagulatory cascade (Ruggieri and Zimmerman, 1987; Ginsburg and Bowie, 1992; Sadler, 1998).

Nucleotide sequence data from exon 28 of the von Willebrand factor gene have been analyzed in many previous mammalian phylogenetic studies (e.g., Porter et al., 1996; Huchon et al., 1999; Neumann et al., 2006). The 963 bp fragment that we amplified and sequenced for this study is homologous with a single full-length copy in *Monodelphis domestica*, where the gene is apparently located on chromosome 8. We obtained vWF sequences from 41 didelphids (excluding *Caluromysiops* and *Lestodelphys*) and seven outgroup taxa, all of which translate to open reading frame. Only three indels (two of 3 bp and one of 6 bp) are required to align didelphid vWF sequences; all three indels are unique to single taxa.

Summary, Sequence Characteristics, and Model Fitting

Available information suggests that the five nuclear genes sequenced for this study exist as single full-length copies in the only didelphid genome currently available for inspection, that they are unlinked (on separate chromosomes or very widely separated), that they are active in different tissues, and that their translated protein products have widely differing functions (table 10). Therefore, it is reasonable to expect that taxonomic patterns of nucleotide substitution at these loci provide substantially independent evidence of phylogenetic relationships. Additionally, the coding sequences we obtained appear to be fully functional (all translate to open reading frame), and none exhibits alignment ambiguities among our ingroup taxa. Other sequence characteristics that might affect the utility of these genes for phylogenetic analysis are considered below.

Base-compositional heterogeneity, as indicated by significant taxonomic variation in

TABLE 10
Biological Properties of Genetic Loci Sequenced for This Study[a]

	Gene		Protein product	
	Location[b]	Active in	Location	Primary function
BRCA1	chr 2	many tissues	nucleus & cytoplasm	tumor suppression
DMP1	chr 5	dentine & bone	extracellular	mineralization
IRBP	chr 1	retina	extracellular	photoreception
RAG1	chr 5	developing B & T lymphocytes	nucleus	immune response
vWF	chr 8	endothelium & megakaryocytes	extracellular	blood clotting

[a] As indicated primarily by research on humans and other placental taxa (see references cited in text).

[b] Chromosome number in *Monodelphis domestica* genome.

GC (versus AT) content, is now widely recognized as a potential problem for phylogenetic inference (see literature reviewed by Gruber et al., 2007). Of the five genes analyzed herein, BRCA1 and DMP1 exhibit the lowest overall GC content (fig. 26). For BRCA1, GC content at all codon positions is remarkably consistent across taxa. However, GC content at third codon positions (GC_3) of DMP1 is substantially higher in two taxa (*Hyladelphys* and *Tlacuatzin*) than it is in other didelphids (Jansa and Voss, 2005). As reported elsewhere, third codon positions of RAG1 are so highly variable in GC content among didelphids that plausible phylogenetic results cannot be recovered from datasets that include these positions (Gruber et al., 2007); therefore, only first and second codon positions of RAG1 are analyzed below. The GC content of vWF is most similar to that of RAG1, but vWF does not exhibit the exceptionally high taxonomic variation in GC_3 seen in the latter gene. Compared to the other loci, IRBP has relatively high GC content at all codon positions, with one taxon (*Cryptonanus chacoensis*) exhibiting elevated GC content at first and second codon positions.

Additional sequence characteristics can be effectively summarized in the context of model fitting (Posada and Crandall, 1998). The best-fitting model of nucleotide substitution for each gene is either a general-time-reversible (GTR) model or a modification thereof (TVMef) that assumes equal base frequencies and equal transition rates (table 11). In addition, the best-fitting model for each gene includes among-site rate heterogeneity as approximated by a gamma distribu-

tion (Γ), and a proportion of invariant sites (p_{inv}) applies to three genes. Fitted base-compositional parameters (πA, πC, πG, πT) for GTR-modeled loci are relatively even for IRBP, slightly skewed towards A for the RAG1 partition, strongly skewed towards A for BRCA1, and strongly biased towards A and G for DMP1. All five genes exhibit higher rates of transitions than transversions; in addition, first and second positions of RAG1 exhibit a relatively high rate of A-to-C transversions. The degree of among-site rate heterogeneity was lowest for BRCA1 (α =1.48), and highest for the RAG1 partition (α = 0.41).

PHYLOGENETIC RELATIONSHIPS

The six data partitions recognized herein (nonmolecular characters plus nucleotide sequences from five loci) were analyzed separately and in combination to explore relevant patterns of support for monophyletic groups. To assess the sensitivity of our results to missing data and to different analytic methods, we conducted MP and Bayesian analyses of the nonmolecular data with and without *Chacodelphys* (4 analyses); MP, ML, and Bayesian analyses of each single-gene dataset (15 analyses); MP, ML, and Bayesian analyses of a concatenated-gene dataset (3 analyses); and MP, ML, and Bayesian analyses of a combined (nonmolecular + molecular) dataset with and without *Chacodelphys* (6 analyses). Given the complexity of these results (a total of 28 separate analyses), the following accounts are focused on issues of generic monophyly and on higher-level (intergeneric) relationships among
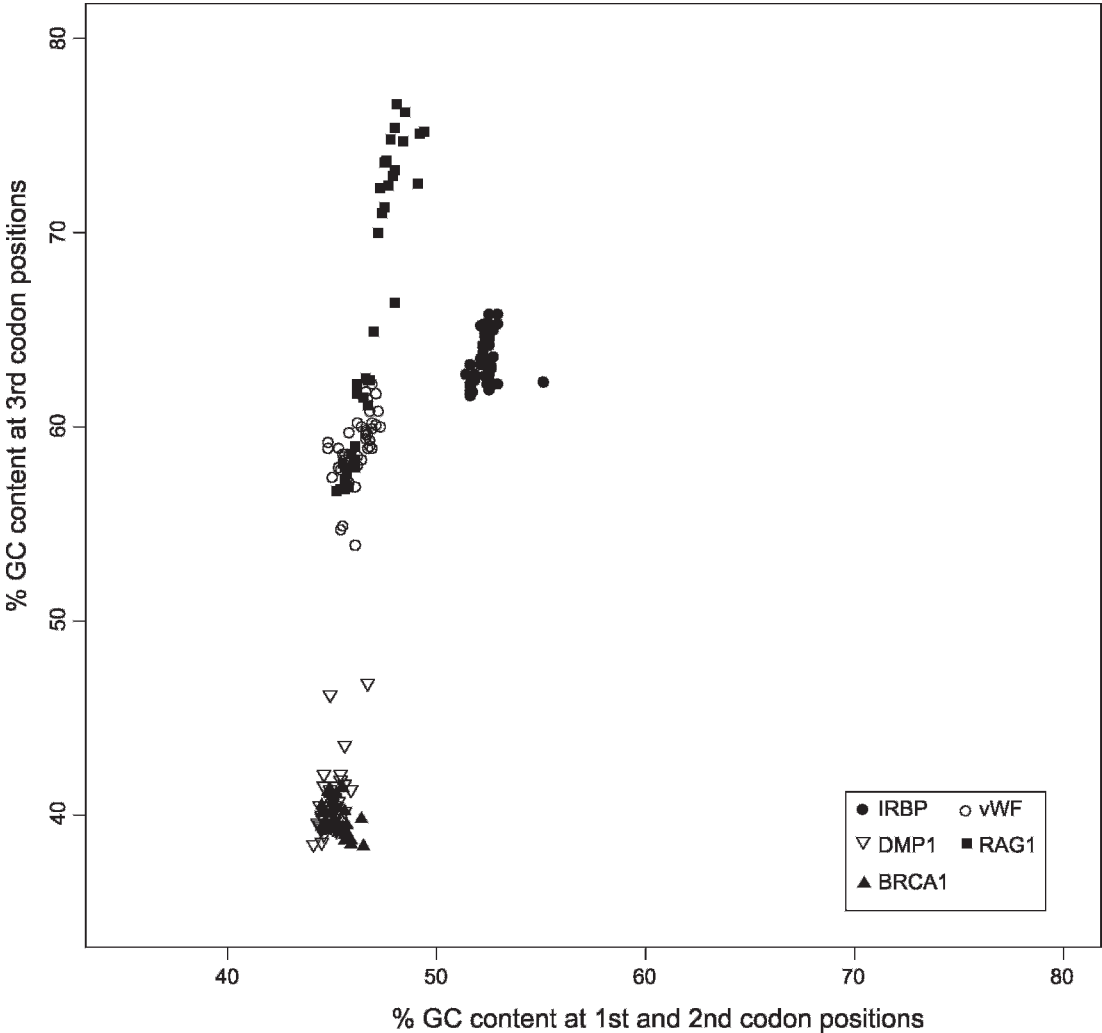
Fig. 26.   Scatterplot of percent GC content among didelphid sequences at first and second codon positions versus percent GC content at third codon positions for the five genes included in this study.

didelphid terminal taxa.[21] To simplify comparisons of support values among the many (>1000) ingroup nodes recovered by these analyses, we restrict our attention to bootstrap frequencies (from MP and ML analyses) and Bayesian posterior probabilities, both of which have respectable statistical pedigrees (Felsenstein, 1985; Efron et al., 1996; Huelsenbeck et al., 2002) despite their imperfect relationship to type I error rates (Erixon et al., 2003; Alfaro and Holder, 2006).

Analyses of Nonmolecular Data

Despite the large amount of missing data from *Chacodelphys* (table 2), including this taxon in a parsimony analysis of our nonmolecular (morphological + karyotypic) characters resulted in fewer equally parsimonious trees (with a correspondingly better-resolved strict consensus) than we obtained from a parsimony analysis with *Chacodelphys* excluded (table 12). Among other notewor-

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[21] Marsupial interordinal relationships and relationships among congeneric didelphid species will be treated in subsequent reports.

TABLE 11
Results of Maximum-likelihood Model Fitting with Single-gene Datasets

	BRCA1	vWF	IRBP	DMP1	RAG1[a]
Model	GTR + Γ	TVMef + I + Γ	GTR + I + Γ	GTR + Γ	GTR + I + Γ
Parameter estimates:					
πA	0.37	0.25	0.25	0.37	0.31
πC	0.19	0.25	0.26	0.18	0.23
πG	0.21	0.25	0.27	0.26	0.24
πT	0.23	0.25	0.22	0.18	0.22
rAC	0.91	2.03	1.96	1.12	3.03
rAG	4.75	7.01	5.88	2.64	4.59
rAT	0.76	1.26	1.46	0.39	0.77
rCG	1.05	1.07	1.13	0.77	1.73
rCT	5.52	7.01	7.43	6.74	7.22
α	1.48	0.83	0.81	0.69	0.41
p_{inv}	0.00	0.19	0.32	0.00	0.52
Ln-likelihood[b]	−15078.42	−6648.62	−6817.82	−5943.66	−6343.58

[a] First and second codon positions only.

[b] Of best tree.

thy features of this topology (fig. 27), didelphid monophyly is only weakly supported, as are most patterns of intergeneric relationships. In fact, only six genera and intergeneric clades are strongly supported (with bootstrap values >75%) by parsimony analysis of these data: (1) a group containing *Lestodelphys* and *Thylamys*; (2) a group that includes *Caluromys* and *Caluromysiops*; (3) the genus *Didelphis*; (4) a group that includes *Lutreolina*, *Philander*, and *Didelphis*; (5) a group that includes the latter three genera plus *Chironectes*; and (6) the genus *Monodelphis*.

However, several other groups (e.g., the genus *Thylamys*, the genus *Marmosops*, the genus *Caluromys*, the genus *Philander*, and *Philander* + *Didelphis*) receive moderate bootstrap support.

Bayesian analysis of these nonmolecular data (implementing the Mkv model of Lewis, 2001) provides strong support (posterior probabilities >95%) for most of the same clades that are strongly supported by parsimony, with the notable exception of (4) among those listed above. In addition, there is strong Bayesian support for the monophy-

TABLE 12
Results of Parsimony Analyses of Datasets with Nonmolecular Characters

	Nonmolecular data[a]		Combined data[b]	
	w/ *Chacodelphys*	w/o *Chacodelphys*	w/ *Chacodelphys*	w/o *Chacodelphys*
Ingroup taxa	44	43	44	43
Outgroup taxa	7	7	7	7
Total characters	129	129	7449	7449
Informative characters	114	114	2073	2073
Minimum-length trees	1068	21,803	12	12
Length of best trees	362	356	5960	5954
Consistency Index	0.508	0.517	0.638	0.639
Retention Index	0.788	0.793	0.777	0.777
Resolved nodes (%)[c]	37 (77.1)	27 (57.4)	44 (91.7)	43 (91.5)

[a] Morphological and karyotypic characters.

[b] Nonmolecular data plus concatenated sequences from five loci.

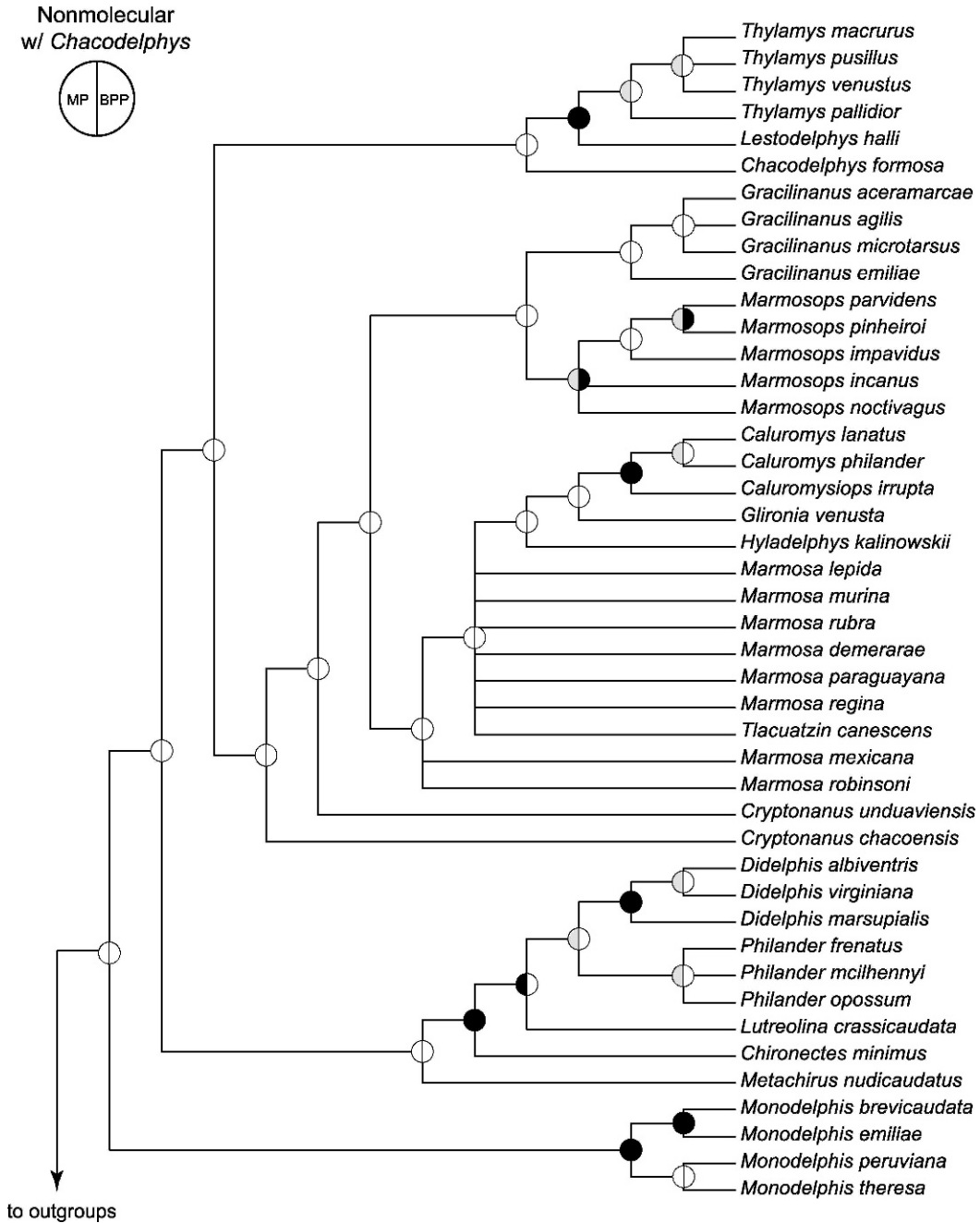[c] In strict consensus of minimum-length trees.

Fig. 27.   The strict consensus of 1068 minimum-length trees resulting from parsimony analysis of the nonmolecular (morphological + karyotypic) dataset with *Chacodelphys* included. Divided circles at each resolved node indicate support from parsimony bootstrap and Bayesian analyses. For parsimony bootstrap analysis (MP), white indicates bootstrap frequencies ≤50%, grey indicates bootstrap frequencies between 50% and 75%, and black indicates bootstrap frequencies ≥75%. For the Bayesian analysis (BPP), white indicates posterior probabilities <0.95, whereas black indicates posterior probabilities ≥0.95.

ly of *Marmosops* (only moderately supported by parsimony). However, Bayesian support is weak for several nodes with moderate parsimony bootstrap support, including the genus *Thylamys*, the genus *Caluromys*, and the genus *Philander*.

Most of the obvious differences between these results and our previously published analyses of didelphid morphological character data are attributable to rooting. Whereas we previously (Voss and Jansa, 2003; Voss et al., 2004a; Jansa and Voss, 2005) rooted our estimates of didelphine relationships using *Caluromys*, *Caluromysiops*, and *Glironia* as outgroups, these analyses are rooted using nondidelphid marsupial outgroups. Considered as an undirected network, the ingroup topology of figure 27 is almost identical to that obtained by Jansa and Voss (2005: fig. 1C) for the same set of didelphid terminal taxa.

Single-gene Analyses

Maximum-likelihood topologies with superimposed summaries of nodal statistics from three analyses (MP, ML, and Bayesian) of each single-gene dataset (figs. 28–32) illustrate similarities and differences in clade support among the five loci we sequenced. Because our analytic results for IRBP and DMP1 have already been published (Jansa and Voss, 2005), only summary comments are warranted here. Briefly, the monophyly of all genera represented by two or more terminal taxa is strongly supported by both of these genes (figs. 28, 29) with the exception of *Gracilinanus* (weakly to moderately supported by IRBP, not recovered as monophyletic by DMP1), *Thylamys* (only weakly supported by Bayesian analysis of DMP1), and *Didelphis* (inconsistently recovered as monophyletic by analyses of IRBP). On the assumption that the DMP1 tree (lacking outgroup terminals) is appropriately rooted within a node or two of *Glironia*, several patterns of intergeneric relationships are also supported by both genes, including the nested clades (*Metachirus* (*Chironectes* (*Lutreolina* (*Didelphis* + *Philander*)))); a group that includes *Lestodelphys* and *Thylamys*; a group that includes *Cryptonanus*, *Gracilinanus*, and *Lestodelphys* + *Thylamys*; a group that

includes the latter four genera plus *Marmosops*; and a group that includes *Marmosa*, *Monodelphis*, and *Tlacuatzin*. As reported elsewhere (Jansa and Voss, 2005), there are no examples of hard incongruence to be found in comparing analytic results between IRBP and DMP1 because all conflicting nodes (e.g., those resolving the position of *Hyladelphys*) have weak support from one or both genes.

Analyses of first and second codon positions of RAG1 (fig. 30) support the monophyly of most polytypic didelphid genera (except *Caluromys*, *Didelphis*, and *Philander*), but some genera recovered as monophyletic groups (e.g., *Thylamys*, *Marmosops*, and *Monodelphis*) do not receive consistently strong support. Many of the same intergeneric relationships supported by IRBP and DMP1 were also recovered, notably including the branching patterns among *Metachirus*, *Chironectes*, *Lutreolina*, and *Philander* + *Didelphis*. Additionally, *Marmosops* was recovered as the sister group to a clade that includes *Cryptonanus*, *Gracilinanus*, and *Thylamys*. Unfortunately, the uncertain position of the root (probably an artifact of incomplete outgroup sequences; see above) is reflected in the lack of strong support for any basal relationships in this topology.

Analyses of sequence data from BRCA1 produced the most compelling single-gene estimate of didelphid relationships recovered to date, with strikingly consistent high nodal support values and an almost completely resolved consensus topology (fig. 31). Among other salient features, every polytypic opossum genus with the exception of *Didelphis* was recovered with strong support, as were almost all of the higher-level clades recovered with strong support by any analysis of other single-gene datasets (the only exceptions are groups that include *Lestodelphys* and *Caluromysiops*, taxa from which BRCA1 sequences are not available). Three of these merit particular attention. One is "clade H" of Jansa and Voss (2000), which unites the *Thylamys* cluster with *Metachirus* and the large opossums with 22 chromosomes (*Chironectes*, *Lutreolina*, *Philander*, and *Didelphis*). Another is the subfamily Didelphinae of traditional usage (excluding *Hyladelphys*, *Caluromys*, and *Glironia*), and
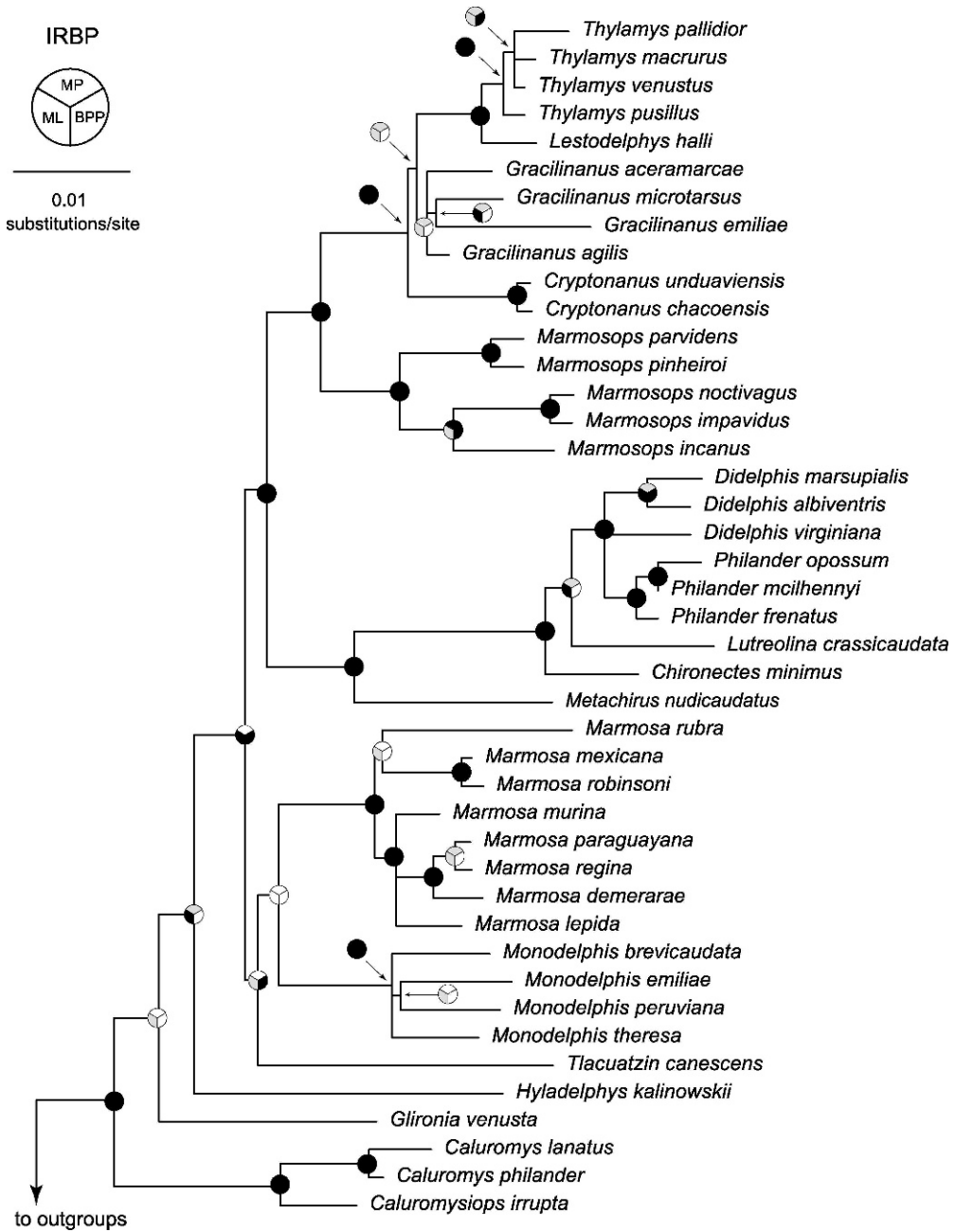
Fig. 28.   The tree resulting from maximum-likelihood analysis of the IRBP dataset under its best-fitting model (GTR + I + Γ, ln-likelihood = −6817.82; table 11). Support statistics from a parsimony bootstrap analysis, a maximum-likelihood bootstrap analysis, and a Bayesian analysis are indicated at each resolved node. For the parsimony and maximum-likelihood analyses (MP and ML, respectively), white indicates bootstrap frequencies ≤50%, grey indicates bootstrap frequencies between 50% and 75%, and black indicates bootstrap frequencies ≥75%. For the Bayesian analysis (BPP), white indicates posterior probabilities <0.95, whereas black indicates posterior probabilities ≥0.95.
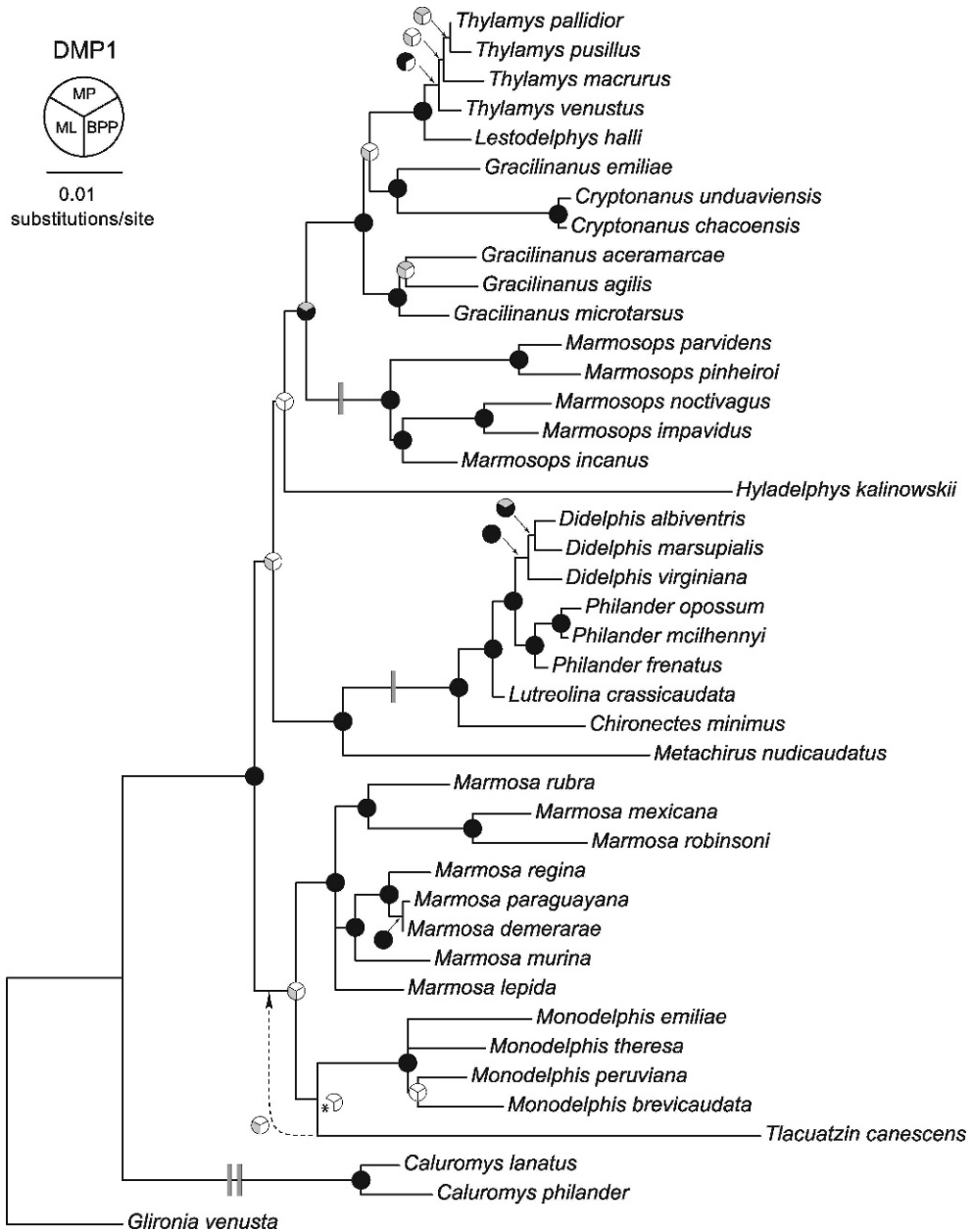
Fig. 29.   The tree resulting from maximum-likelihood analysis of the DMP1 dataset under its best-fitting model (GTR + Γ, ln-likelihood = –5943.66; table 11). Four of the five deletion events that optimize as synapomorphies on this topology are indicated with vertical gray bars; the fifth (not shown) is shared by *Marmosa regina*, *M. paraguayana*, *M. demerarae*, *M. murina*, and *M. lepida*, but this clade is subtended by a zero-length branch. Because alignable DMP1 sequences are not available from outgroup taxa (see text), this tree is rooted with *Glironia*. Conventions for indicating nodal support are described in the caption to figure 28. The broken arrow indicates the alternative position of *Tlacuatzin* recovered by ML bootstrap analysis (the position for this taxon recovered by ML analysis of the original data was not supported by bootstrapping).
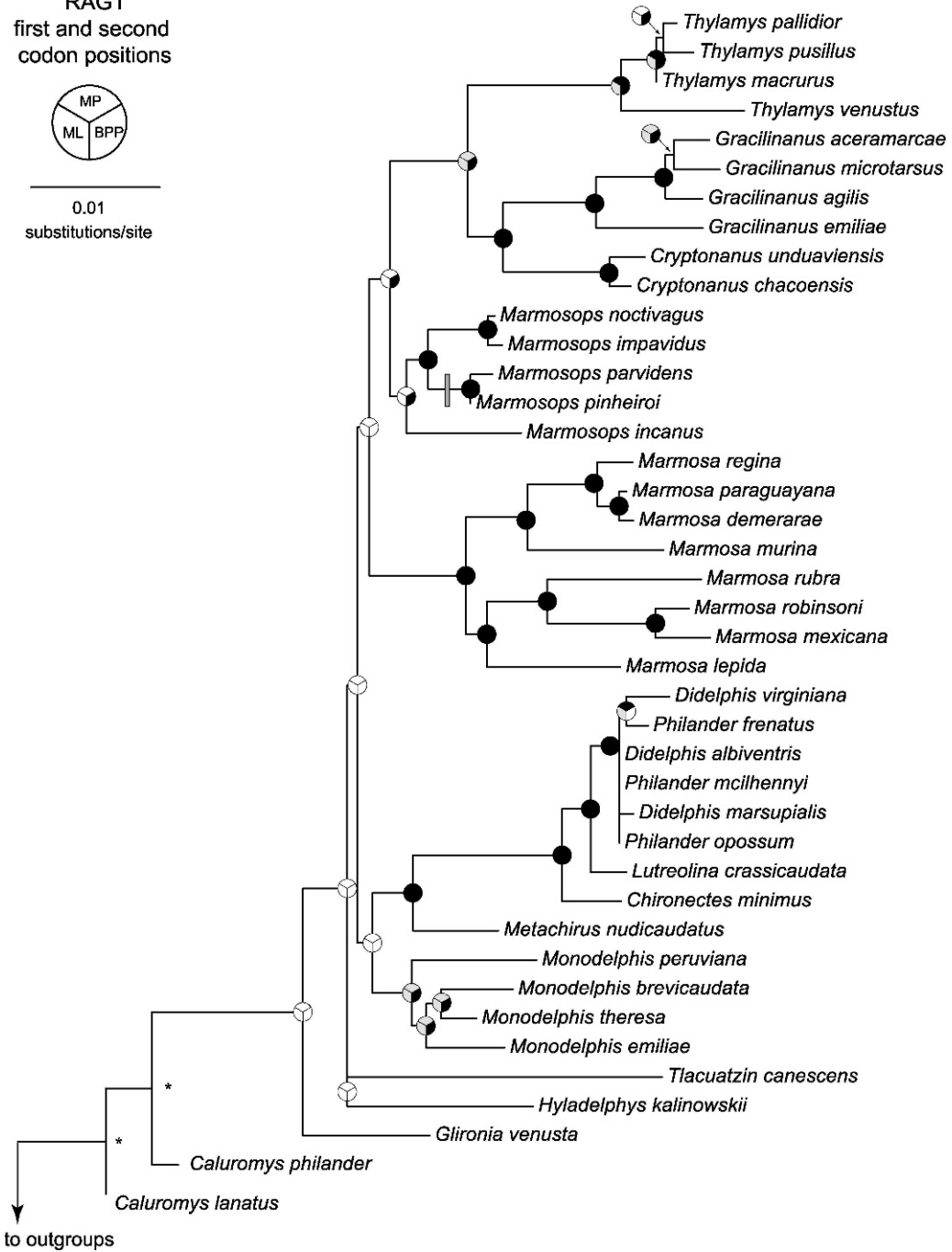
Fig. 30.   The tree resulting from maximum-likelihood analysis of first and second codon positions of RAG1 under its best-fitting model (GTR + I + Γ, ln-likelihood = −6343.58; table 11). The single synapomorphic deletion event in this gene is indicated with a vertical gray bar. Conventions for indicating nodal support are described in the caption to figure 28. Asterisks indicate nodes resolved by ML analysis of the original data that lack bootstrap support.
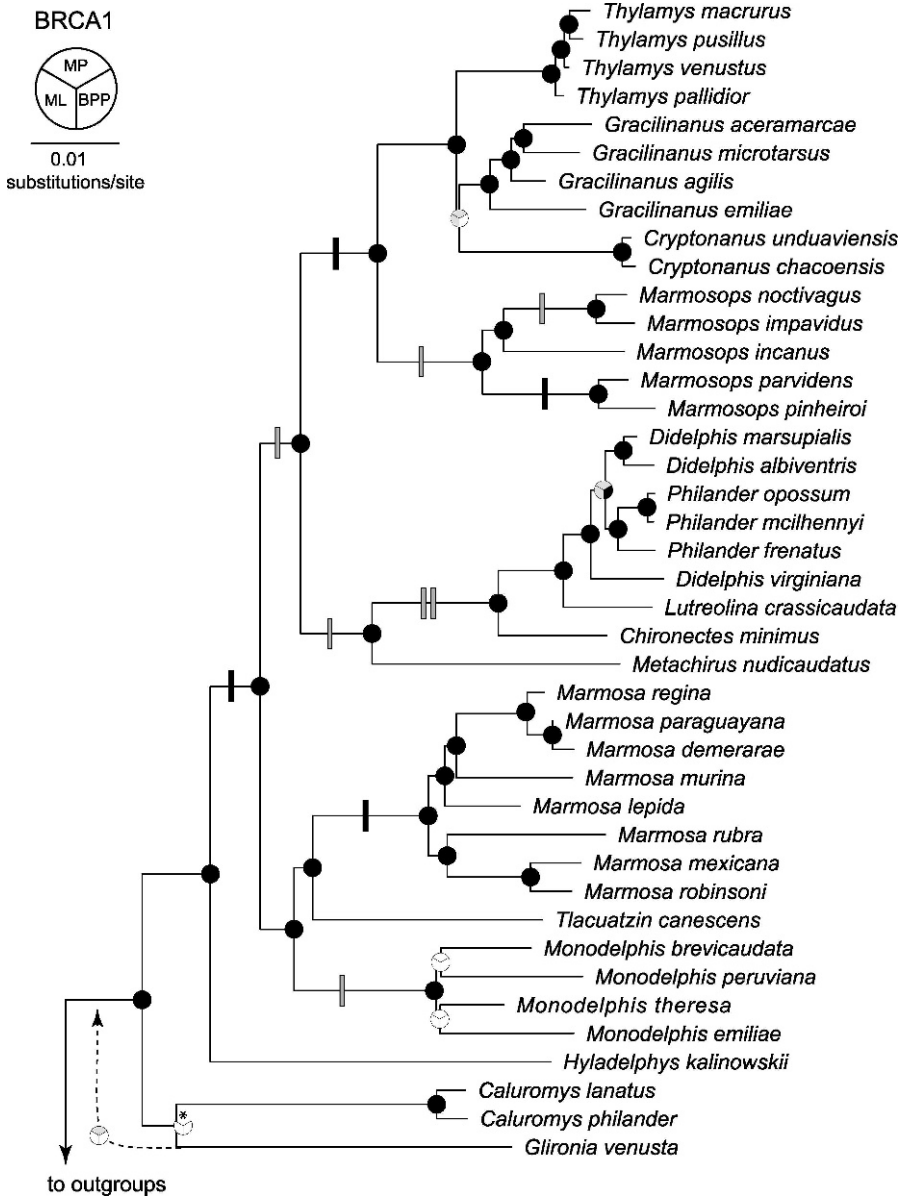
Fig. 31. The tree resulting from maximum-likelihood analysis of the BRCA1 dataset under its best-fitting model (GTR + Γ, ln-likelihood = −15078.42; table 11). Vertical bars indicate unique and unreversed synapomorphic insertions (black) or deletions (gray) in this gene. Conventions for indicating nodal support are described in the caption to figure 28. The broken arrow indicates the alternative position of *Glironia* recovered by parsimony analysis.

the third is *Hyladelphys* + Didelphinae. A novel result (uniquely recovered with strong support by BRCA1 but not strongly contradicted by any other gene) is the sister-group relationship between *Marmosa* and *Tlacuatzin*. In effect, the only relevant intergeneric

nodes not convincingly resolved by BRCA1 are the one that clusters *Cryptonanus* with *Gracilinanus* (recovered with only weak to moderate support by MP, ML, and Bayesian analyses) and the position of the ingroup root. The latter was placed between *Glironia*
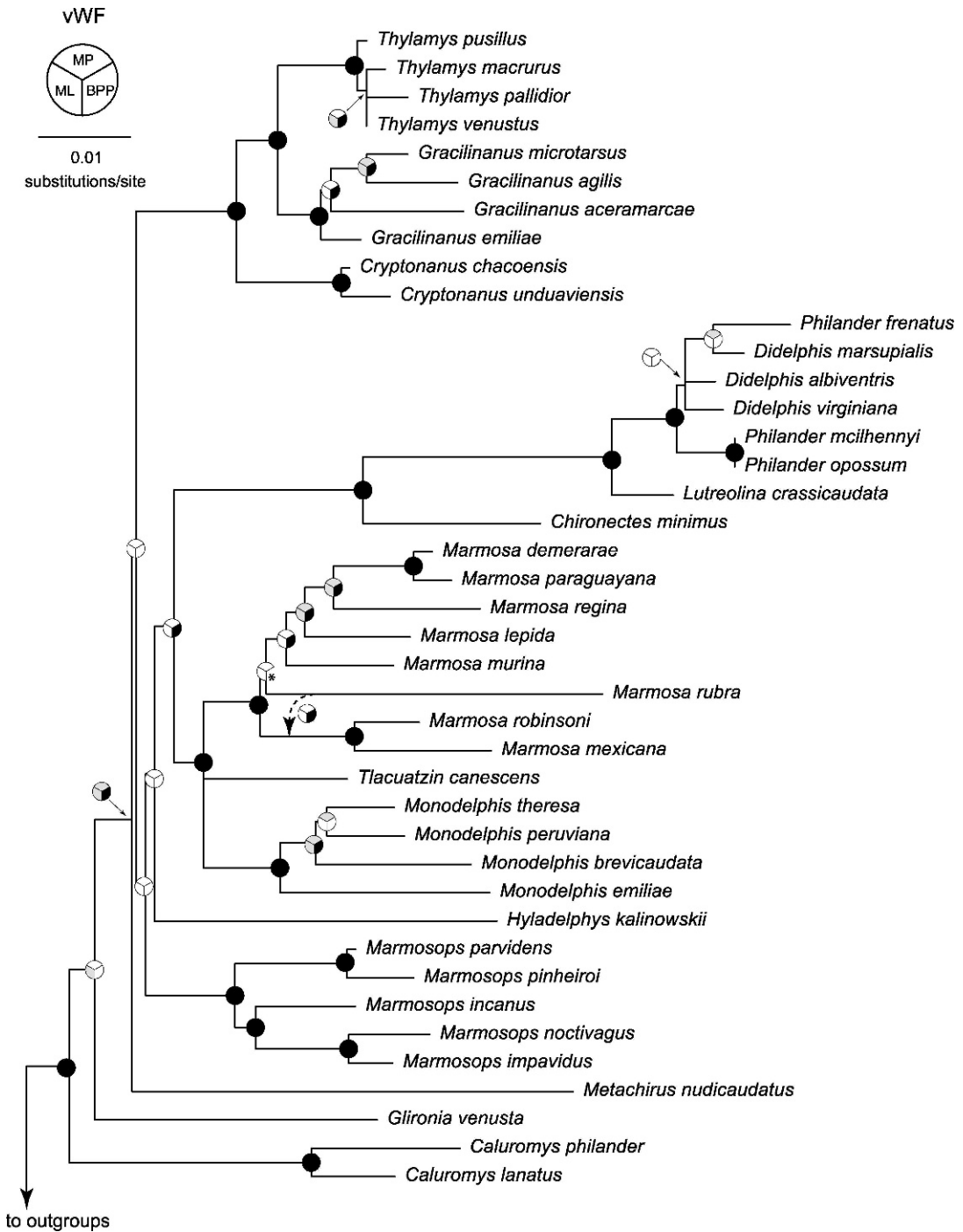
Fig. 32.   The tree resulting from maximum-likelihood analysis of the vWF dataset under its best-fitting model (TVMef + I + Γ, ln-likelihood = −6648.62; table 11). Conventions for indicating nodal support are described in the caption to figure 28. The broken arrow indicates the alternative position of *Marmosa rubra* supported by Bayesian analysis.

TABLE 13
Results of Parsimony Analyses of Six Molecular Datasets

	BRCA1	vWF	IRBP	DMP1	RAG1[a]	Concatenated
Ingroup taxa	41	41	43	42	41	43
Outgroup taxa	7	7	7	0	5	7
Aligned sites	2163	963	1158	1176	1860	7320
Variable sites[b]	753	324	267	444	315	2103
% variable sites[b]	34.8	33.6	23.1	37.8	16.9	28.7
Informative sites[b]	443	202	161	246	210	1262
Minimum-length trees	8	60	121	30	717	8
Length of best trees	2297	967	947	735	584	5583
Consistency Index	0.67	0.60	0.64	0.72	0.66	0.65
Retention Index	0.80	0.75	0.77	0.81	0.80	0.78
Resolved nodes (%)	43 (92.5)	40 (87.0)	38 (79.2)	34 (85.0)	15 (34.1)	45 (92.8)

[a] First and second codon positions only.

[b] Among ingroup taxa.

[c] Among ingroup taxa in strict consensus of minimum-length trees.

and *Caluromys* with moderate support from MP, but it was placed between *Caluromys* + *Glironia* and other didelphids with weak support in ML and Bayesian analyses.

Analyses of sequence data from vWF (fig. 32) strongly support the monophyly of all polytypic didelphid genera except *Didelphis* and *Philander*. In addition, they strongly support some of the same intergeneric clades common to our other single-gene results, including (*Chironectes* (*Lutreolina* (*Philander* + *Didelphis*))); a group that includes *Thylamys*, *Gracilinanus*, and *Cryptonanus*; and another that includes *Marmosa*, *Monodelphis*, and *Tlacuatzin*. A novel result—not strongly supported by any other gene and strongly contradicted by our RAG1 results— is a sister-group relationship between *Gracilinanus* and *Thylamys*. No other intergeneric clades are consistently strongly supported by parsimony, likelihood, or Bayesian analyses of vWF sequence data; indeed, most are weakly supported by two or more analyses.

In summary, most didelphid genera were recovered as monophyletic groups with strong nodal support values from most genes (table 14). Support statistics suggest that the most problematic genera are *Didelphis* (recovered as monophyletic with strong support only by analyses of DMP1), *Philander* (inconsistently recovered as monophyletic by analyses of RAG1 and vWF), and *Gracilinanus* (not recovered as monophyletic

by analyses of DMP1). Although *Caluromys* was not recovered as monophyletic by analyses of RAG1 sequences, this result is plausibly attributable to the unstable position of the ingroup root.

Several patterns of intergeneric relationships were also consistently recovered, usually with strong support. These include the nested clades (*Chironectes* (*Lutreolina* (*Didelphis* + *Philander*))) and a group comprised of *Thylamys*, *Gracilinanus*, and *Cryptonanus*. In addition, both loci (IRBP, DMP1) from which sequence data were available for *Lestodelphys* support a sister-group relationship between that genus and *Thylamys*. Lastly, all of the recovered single-gene trees are consistent with our assumption of didelphid monophyly.

With a single exception, no pattern of intergeneric relationships strongly supported by any analysis of these genes was strongly contradicted by another. Examples of relationships strongly supported by some analyses and not strongly contradicted by any other include the sister-group relationship of *Marmosops* to *Thylamys* + *Gracilinanus* + *Cryptonanus*; the sister-group relationship of *Metachirus* to the large opossums with 22 chromosomes; a group that includes *Marmosa*, *Monodelphis*, and *Tlacuatzin*; the group *Marmosa* + *Tlacuatzin*; the subfamily Didelphinae; and the clade *Hyladelphys* + Didelphinae. In effect, the only example of

TABLE 14
Support for Generic Monophyly from Single-gene Datasets[a]

	IRBP	DMP1	RAG1	BRCA1	vWF
Caluromys	**	**	NR	**	**
Cryptonanus	**	**	**	**	**
Didelphis	NR	**	NR	NR	NR
Gracilinanus	R	NR	**	**	**
Marmosa	**	**	**	**	**
Marmosops	**	**	*	**	**
Monodelphis	**	**	*	**	**
Philander	**	**	NR	**	NR
Thylamys	**	*	*	**	**

[a] Key: ** = strong support from all analyses (MP, ML, Bayesian); * = strong support from at least one analysis; R = recovered without strong support; NR = not recovered.

hard incongruence among patterns of intergeneric relationships supported individually by these loci concerns the relationships of *Cryptonanus*. This obviously problematic taxon was recovered with strong nodal support either as the sister group of *Gracilinanus emiliae* (in all analyses of DMP1), or as the sister group of *Gracilinanus* (in all analyses of RAG1), or as the sister group of *Thylamys* + *Gracilinanus* (in all analyses of vWF).

Analyses of Concatenated Genes

Maximum parsimony, maximum likelihood, and Bayesian analyses of concatenated sequence data from all five genes (7320 bp) resulted in well-resolved and strikingly similar trees with high support values at most nodes (fig. 33). Among other analytic similarities, all polytypic genera were recovered as monophyletic groups, as were all of the higher-level clades common to two or more of the single-gene analyses discussed above. However, three intergeneric nodes remain weakly or inconsistently supported.

The first of these concerns the position of the ingroup root. Whereas maximum parsimony weakly supports placing the root between *Glironia* and other didelphids (which were recovered as a monophyletic group with a bootstrap frequency of 74%), maximum likelihood places the root between (*Glironia* (*Caluromys* + *Caluromysiops*)) and *Hyladelphys* + Didelphinae; however, likelihood bootstrap support for the former group is weak (<50%). Bayesian posterior probabilities for three alternative placements of the

ingroup root (fig. 34A, B, C) suggest that the parsimony and likelihood solutions are almost equiprobable but slightly favor the latter.

The second equivocal node concerns the relationships of *Marmosa*, *Tlacuatzin*, and *Monodelphis*. Although *Marmosa* and *Tlacuatzin* were recovered as sister taxa, support for this clade was uniformly weak. Bayesian posterior probabilities for all possible resolutions of this node (fig. 34D, E, F), however, suggest a somewhat clearer ranking than was obtained for alternative placements of the ingroup root.

The third problematic issue concerns relationships among *Gracilinanus*, *Cryptonanus*, and *Thylamys* + *Lestodelphys*. Here, parsimony provides moderate bootstrap support (58%) for grouping *Gracilinanus* with *Cryptonanus* as does likelihood (70%). Although Bayesian support for *Gracilinanus* + *Cryptonanus* is weak, posterior probabilities clearly favor this clade over other phylogenetic alternatives (fig. 34G, H, I).

Analyses of Combined Datasets

Maximum parsimony and Bayesian analyses of the combined (nonmolecular + molecular) data without *Chacodelphys* recover the same higher-level topologies that were obtained from analyses of the concatenated-gene data, with only a few noteworthy changes in nodal support (fig. 35). For example, parsimony bootstrap support for the monophyly of *Didelphis* increases slightly when nonmolecular character data are added
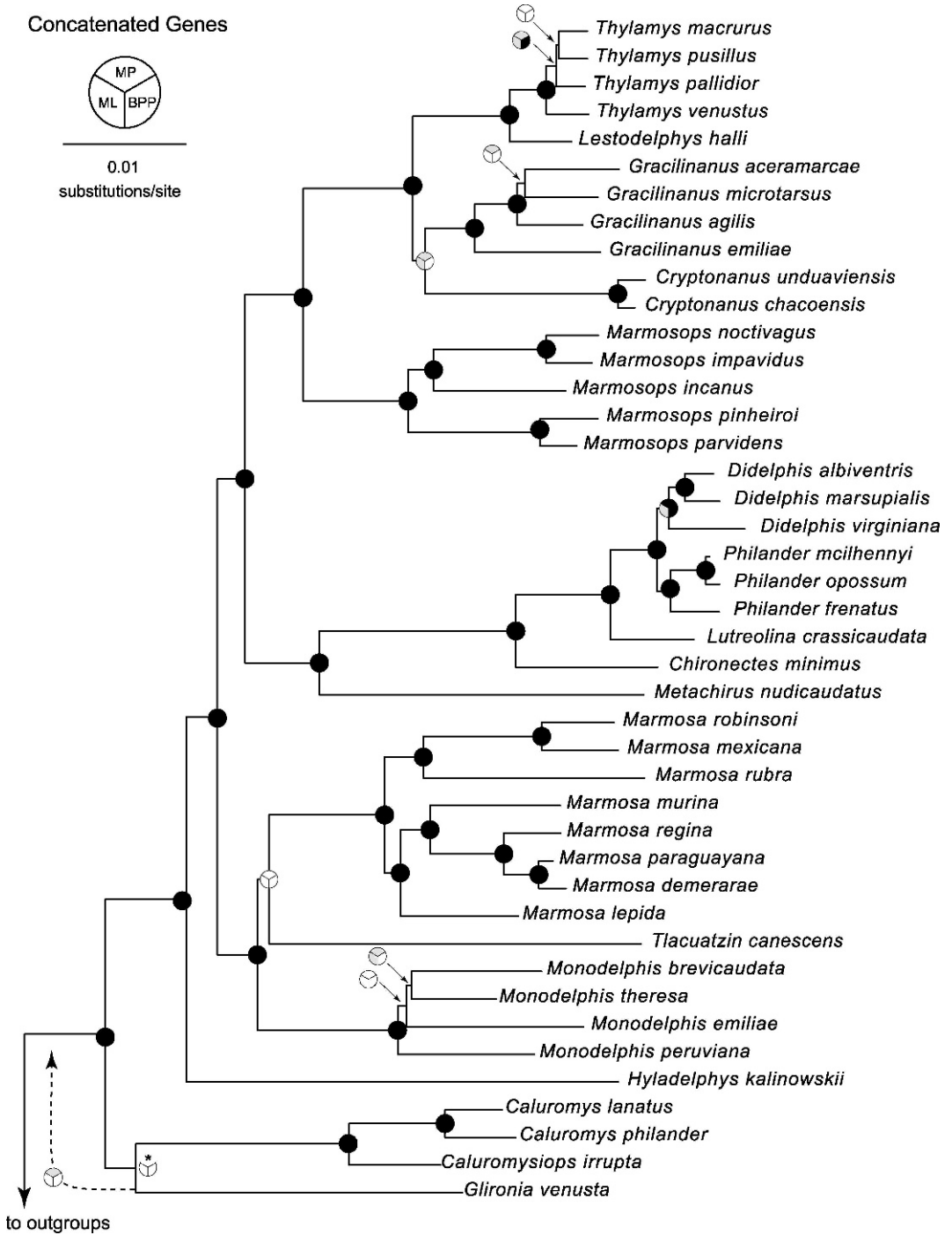
Fig. 33. The tree resulting from a mixed-model maximum-likelihood analysis of the concatenated (five-gene) dataset. Conventions for indicating nodal support are described in the caption to figure 28. The broken arrow indicates the alternative position of *Glironia* recovered by parsimony analysis.
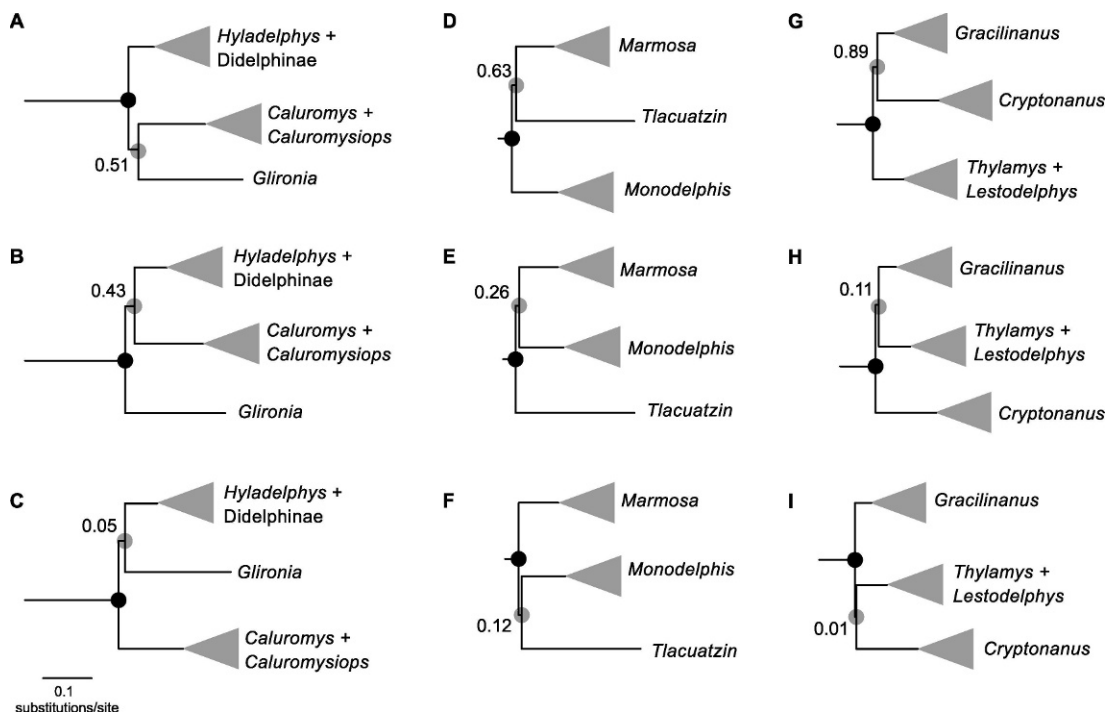
Fig. 34. Alternative resolutions for three patterns of intergeneric relationships that exhibit nodal posterior probabilities <0.95 in the Bayesian analysis of the concatenated five-gene dataset (see fig. 33). **A, B, C,** alternative relationships among *Glironia*, *Hyladelphys* + Didelphinae, and *Caluromys* + *Caluromysiops*; **D, E, F,** alternative relationships among *Tlacuatzin*, *Marmosa*, and *Monodelphis*; **G, H, I,** alternative relationships among *Cryptonanus*, *Thylamys* + *Lestodelphys*, and *Gracilinanus*. Black and grey circles at nodes indicate posterior probabilities ≥0.95 or <0.95, respectively. Branch lengths are shown at the same scale across all trees.

(from 80% to 93%), as does the Bayesian posterior probability for placing the ingroup root between (*Glironia* (*Caluromys* + *Caluromysiops*)) and other didelphids (from 0.51 to 0.87). Similarly, adding nonmolecular characters marginally improves the Bayesian posterior probability for *Marmosa* + *Tlacuatzin* (from 0.63 to 0.83).

By contrast, including *Chacodelphys* in a combined-data parsimony analysis dramatically erodes bootstrap support for five intergeneric nodes (fig. 36). In fact, the strict consensus of 12 minimum-length trees (not shown) places *Chacodelphys* as the sister group of *Monodelphis* with weak (MPBS = 49%) support. Bayesian analysis, however, strongly supports the membership of *Chacodelphys* in a clade that also includes *Gracilinanus*, *Cryptonanus*, and *Thylamys* + *Lestodelphys*, and posterior probabilities for other

nodes are substantially unaffected by taxon addition.

Discussion

Analyses of our combined dataset (excluding *Chacodelphys*; fig. 35) effectively summarize all of the shared phylogenetic signal that we have found to date in morphology, karyotypes, and five unlinked protein-coding nuclear genes. Additional support is provided by 16 parsimony-informative indels (figs. 29, 30, 31) that were not coded as phylogenetic characters but which optimize as synapomorphies on this topology. Lastly, this tree is congruent with the results of independent phylogenetic analyses based on sequence data from intron 1 of the nuclear transthyretin (TTR) gene and the mitochondrial 12S rDNA gene (Steiner et al., 2005). To the best

Fig. 35.   The 50% majority-rule consensus of post-burnin trees resulting from a mixed-model Bayesian analysis of the combined (nonmolecular + molecular) dataset without *Chacodelphys*. Conventions for indicating nodal support are described in the caption to figure 28. The broken arrow indicates the alternative position of *Glironia* recovered by parsimony analysis.
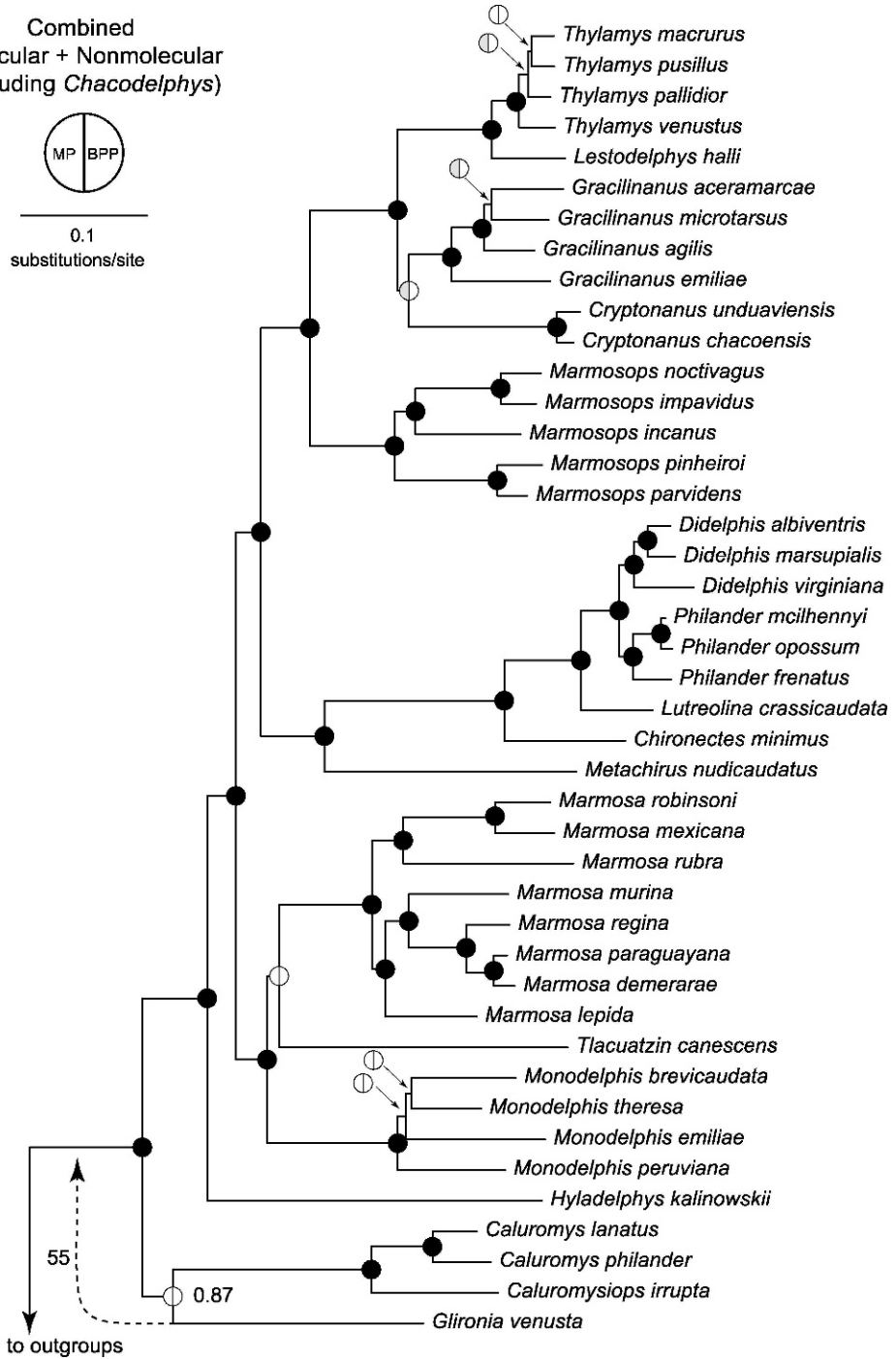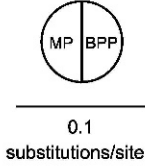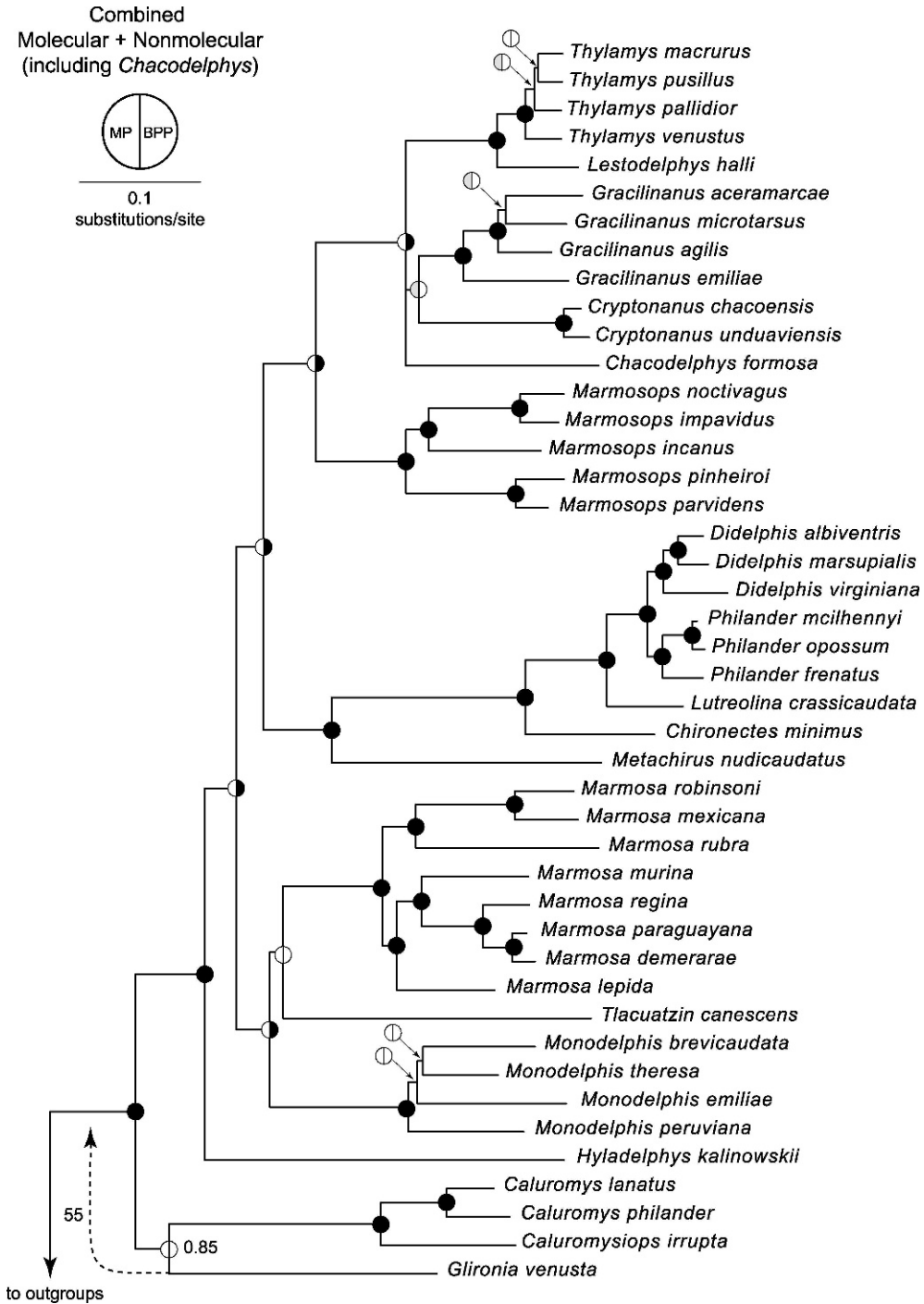
Fig. 36.   The 50% majority-rule consensus of post-burnin trees resulting from a mixed-model Bayesian analysis of the combined (nonmolecular + molecular) dataset including *Chacodelphys*. Conventions for indicating nodal support are described in the caption to figure 28. The broken arrow indicates the alternative position of *Glironia* recovered by parsimony analysis.

of our knowledge, no strongly conflicting valid results have been obtained in any other published phylogenetic analysis of molecular or morphological character data.[22] Although this tree is fully resolved with high support values at most nodes, several outstanding problems merit comment.

As we have previously noted elsewhere, *Chacodelphys* exhibits conflicting patterns of derived morphological similarities with *Thylamys + Lestodelphys* on the one hand and with *Monodelphis* on the other (Voss et al., 2004a). Weak parsimony support for nodes along the phylogenetic path between *Thylamys + Lestodelphys* and *Monodelphis* in the combined-data analysis that includes *Chacodelphys* (fig. 36) presumably reflects such character conflict, although it is noteworthy that Bayesian support for the same nodes is unaffected by taxon addition. Although we are convinced that *Chacodelphys* is closely related to *Lestodelphys* and *Thylamys* by a host of phenotypic resemblances too indefinite to code as characters but too numerous to ignore, a compelling analytic solution to this vexing problem is unlikely to be forthcoming until at least some of the missing molecular data for *Chacodelphys* can be obtained from fresh material.

However, even substantial amounts of sequence data are clearly not enough to resolve other phylogenetic uncertainties. Indeed, it is not a little frustrating that, with >7000 bp of protein-coding nuclear sequence in hand, the relationships of *Glironia*, *Cryptonanus*, and *Tlacuatzin* should still be problematic. *Glironia* is of special concern, because the two plausible phylogenetic resolutions for this genus (fig. 34A, B) determine the root of the didelphid radiation. The alternative phylogenetic resolutions of *Cryptonanus* and *Tlacuatzin* within their respective groups do not seem like comparably weighty issues, but each could affect ecobehavioral character optimizations of significant evolu-

tionary interest. Phenotypically, *Cryptonanus* is certainly more similar to *Gracilinanus* than it is to *Thylamys* or *Lestodelphys*, whereas *Tlacuatzin* is undeniably more similar to *Marmosa* than it is to *Monodelphis*. The positions of these genera in our combined-data trees are therefore plausible despite the absence of compelling parsimony or Bayesian support.

Although it might seem best to wait until these few remaining issues are convincingly resolved before proposing a formal classification, there is no guarantee that additional data will soon be forthcoming or useful. In the meantime, other relationships that are strongly supported by our results merit nomenclatural recognition, and the contents of some taxa currently recognized as valid need to be revised on the basis of our analytic results. As documented below, no previous classification is consistent with what is now confidently known about didelphid phylogenetic relationships.

CLASSIFICATION

Most essays on marsupial classification (e.g., Simpson, 1945; Kirsch, 1977a; Marshall, 1981; Aplin and Archer, 1987; Archer and Kirsch, 2006) are uninformative about the historical development of opossum systematics. To be sure, the chronological and bibliographic details of didelphid taxonomy are of limited interest, so the following paragraphs mention only a few milestones on the long road to the currently accepted classification. Because most of the technical information about how and why names were formerly applied to taxa was recently summarized by Gardner (2008), this brief narrative is primarily intended to serve as an introduction to the revised phylogenetic system that we propose.

Linnaeus (1758) described only five species of marsupials, all of which were didelphids. Although the four Linnaean species currently recognized as valid (*marsupialis*, *philander*, *opossum*, and *murina*) are now referred to different genera, the great Swede placed all of them in the genus *Didelphis*. New generic names for opossums proliferated over subsequent decades of the 18th and 19th centuries (table 15), but no consistent binomial usage had emerged prior to Thomas's (1888) land-

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[22] DNA-DNA hybridization results showing *Gracilinanus* nested within *Marmosops* (Kirsch and Palma, 1995; Kirsch et al., 1997) were based on taxonomic misidentifications (Voss and Jansa, 2003: 57). Analyses of 12S gene sequences by Palma and Spotorno (1999) recovered *Metachirus* and *Marmosops* as sister taxa, but this grouping was not found in subsequent analyses of 12S sequence data (Steiner et al., 2005) for reasons that remain unexplained.

TABLE 15
Chronological List of Available Generic Names for Recent Didelphids
(Boldface indicates taxa recognized as valid genera in this report.)

	Type species[a]	Current status (if not valid)
Didelphis Linnaeus, 1758	*Didelphis marsupialis* Linnaeus, 1758[b]	
Philander Brisson, 1762	*Didelphis opossum* Linnaeus, 1758[c]	
Chironectes Illiger, 1811	*Lutra minima* Zimmerman, 1780[d]	
Memina G. Fischer, 1814	*Lutra minima* Zimmermann, 1780[d]	synonym of *Chironectes* Illiger, 1811
Opossum Schmid, 1818	*Didelphis marsupialis* Linnaeus, 1758[e]	synonym of *Didelphis* Linnaeus, 1758
Sarigua Muirhead, 1819	*Didelphis marsupialis* Linnaeus, 1758[f]	synonym of *Didelphis* Linnaeus, 1758
Marmosa Gray, 1821	*Didelphis murina* Linnaeus, 1758[d]	
Monodelphis Burnett, 1830	*Didelphis brachyuros* Schreber, 1777[g]	
Asagis Gloger, 1841	*Didelphis murina* Linnaeus, 1758[b]	synonym of *Marmosa* Gray, 1821
Micoureus Lesson, 1842	*Didelphis cinerea* Temminck, 1824[b]	subgenus of *Marmosa* Gray, 1821
Peramys Lesson, 1842	*Didelphis brachyuros* Schreber, 1777[b]	synonym of *Monodelphis* Burnett, 1830
Thylamys Gray, 1843	*Didelphis elegans* Waterhouse, 1839[d]	
Grymaeomys Burmeister, 1854	*Didelphis murina* Linnaeus, 1758[b]	synonym of *Marmosa* Gray, 1821
Metachirus Burmeister, 1854	*Didelphis nudicaudata* E. Geoffroy, 1803[h]	
Microdelphys Burmeister, 1856	*Didelphis tristriata* Olfers, 1818[b]	synonym of *Monodelphis* Burnett, 1830
Cuica Liais, 1872	*Didelphis murina* Linnaeus, 1758[i]	synonym of *Marmosa* Gray, 1821
Gamba Liais, 1872	*Didelphis palmata* Daudin, 1799[i]	synonym of *Chironectes* Illiger, 1811
Caluromys J.A. Allen, 1900	*Didelphis philander* Linnaeus, 1758[i]	
Lutreolina Thomas, 1910	*Didelphis crassicaudata* Desmarest, 1804[d]	
Glironia Thomas, 1912	*Glironia venusta* Thomas, 1912[j]	
Leucodidelphis Ihering, 1914	*Didelphis paraguayensis* J.A. Allen, 1902[j]	synonym of *Didelphis* Linnaeus, 1758
Marmosops Matschie, 1916	*Didelphis incana* Lund, 1840[j]	
Metachirops Matschie, 1916	*Didelphis quica* Temminck, 1824[j]	synonym of *Philander* Brisson, 1762
Monodelphiops Matschie, 1916	*Microdelphys sorex* Hensel, 1872[j]	synonym of *Monodelphis* Burnett, 1830
Holothylax Cabrera, 1919	*Didelphis opossum* Linnaeus, 1758[j]	synonym of *Philander* Brisson, 1762
Minuania Cabrera, 1919	*Didelphis dimidiata* Wagner, 1847[j]	synonym of *Monodelphis* Burnett, 1830
Mallodelphys Thomas, 1920	*Didelphis laniger* Desmarest, 1820[j]	subgenus of *Caluromys* J.A. Allen, 1900
Lestodelphys Tate, 1934	*Notodelphys halli* Thomas, 1921[j]	
Caluromysiops Sanborn, 1951	*Caluromysiops irrupta* Sanborn, 1851[j]	
Stegomarmosa Pine, 1972	*Marmosa* (*Stegomarmosa*) *andersoni* Pine, 1972[d]	synonym of *Marmosa* Gray, 1821
Gracilinanus Gardner & Creighton, 1989	*Didelphis microtarsus* Wagner, 1842[j]	
Grayium Kretzoi & Kretzoi, 2000	*Didelphis murina* Linnaeus, 1758[k]	synonym of *Marmosa* Gray, 1821
Hyladelphys Voss et al., 2001	*Gracilinanus kalinowskii* Hershkovitz, 1992[j]	
Tlacuatzin Voss & Jansa, 2003	*Didelphis* (*Micoureus*) *canescens* J.A. Allen, 1893[j]	
Chacodelphys Voss et al., 2004	*Marmosa formosa* Shamel, 1930[j]	
Cryptonanus Voss et al., 2005	*Marmosa agilis chacoensis* Tate, 1931[j]	

[a] For simplicity we have emended all nomenclaturally irrelevant mistakes made by authors, such as incorrect spellings (e.g., ''*Didelphys*'' for *Didelphis*) and misattributed authorship and dates for nominal species otherwise eligible for type fixation (ICZN, 1999: Article 67).

[b] Subsequently designated by Thomas (1888) who, however, sometimes used senior synonyms to denote originally included nominal species (e.g., *brevicaudata* Erxleben for *brachyuros* Schreber as the type species of *Peramys* Lesson).

[c] By plenary action of the International Commission on Zoological Nomenclature (ICZN, 1998).

[d] By monotypy.

[e] Subsequently designated by Brown (2004).

[f] Subsequently designated by Cerqueira and Tribe (2008).

[g] Subsequently designated by Matschie (1916).

[h] Subsequently designated by Thomas (1888); see Hershkovitz (1976).

[i] Subsequently designated by Hershkovitz (1949), but authorship and dates misattributed by him are emended herein.

[j] By original designation.

[k] *Grayium* was proposed as a replacement name for *Marmosa* Gray, 1821, on the mistaken assumption that the latter was preoccupied by *Marmosa* Rafinesque, 1815, a nomen nudum (Creighton and Gardner, 2008b).

TABLE 16
Classifications of Recent Opossums, 1888–1958[a]

Thomas (1888)	Matschie (1916)	Cabrera (1919)	Simpson (1945)	Cabrera (1958)
Didelphidae	Didelphidae	Didelphidae	Didelphidae	Didelphidae
Didelphis	*Didelphis*	*Dromiciops*	*Philander*	*Caluromys*
Didelphis[b]	*Didelphis*[b]	*Glironia*	*Monodelphis*	*Caluromysiops*
Metachirus[b]	*Metachirops*[b]	*Philander*	*Dromiciops*	*Glironia*
Philander[b]	*Metachirus*[b]	*Marmosa*	*Glironia*	*Dromiciops*
Micoureus[b]	*Peramys*[b]	*Marmosa*[b]	*Notodelphis*[c]	*Monodelphis*
Peramys[b]	*Micoureus*[b]	*Thylamys*[b]	*Marmosa*	*Monodelphis*[b]
Chironectes	*Caluromys*[b]	*Peramys*	*Metachirops*	*Minuania*[b]
	Marmosa[b]	*Minuania*	*Metachirus*	*Lestodelphys*
	Grymaeomys[b]	*Lutreolina*	*Lutreolina*	*Marmosa*
	Marmosops[b]	*Metachirus*	*Didelphis*	*Marmosa*[b]
	Thylamys[b]	*Holothylax*	*Chironectes*	*Thylamys*[b]
	Dromiciops[b]	*Didelphis*		*Philander*
	Glironia[b]	*Chironectes*		*Metachirus*
	Monodelphis[b]			*Lutreolina*
	Monodelphiops[b]			*Didelphis*
	Microdelphys[b]			*Chironectes*
	[*Chironectes*]			

[a] Incorrect spellings (e.g., ''*Didelphys*'' for *Didelphis*; Thomas, 1888) have been changed to conform with current usage throughout, but the sequence of names in each classification has been preserved as originally published. Note that some names (e.g., *Philander*) were used by early taxonomists for species that are now placed in other genera (see text).

[b] Ranked as subgenera.

[c] Not an available name. *Notodelphys* Thomas, 1921, originally proposed for the taxon now known as *Lestodelphys*, is preoccupied by *Notodelphys* Allman, 1847, a copepod (Tate, 1934).

mark catalog of the marsupials in the British Museum of Natural History.

By comparison with Old World marsupials, didelphids appeared to Thomas (1888: 315) to be ''an exceedingly homogeneous [family], its members presenting a very small range of differentiation.'' Accordingly, he recognized only *Didelphis* and *Chironectes* as full genera, but several other taxa were ranked as subgenera of *Didelphis* (table 16). These included *Metachirus* (containing species now referred to *Metachirus*, *Philander*, and *Lutreolina*), *Philander* (for *Caluromys*), *Micoureus* (containing species now referred to *Marmosa*, *Marmosops*, *Thylamys*, and *Gracilinanus*), and *Peramys* (for *Monodelphis*).

Although knowledge of didelphid diversity increased rapidly in the years following Thomas's classification, Matschie (1916) persisted in referring all nonaquatic opossums to the genus *Didelphis*. However, Matschie recognized more subgenera of *Didelphis* than Thomas did, resurrecting old names or describing new ones to suit his needs. *Dromiciops* (described as a didelphid by

Thomas, 1894) was also included. Matschie's taxonomy is noteworthy for his early recognition that the so-called ''murine'' opossums (pouchless mouse- and rat-sized species with circumocular masks and long tails) that Thomas (1888) had lumped together in *Micoureus* actually represent several distinct groups, and for treating those groups as coordinate taxa.

Cabrera's (1919) classification was not the first to reject Linnaeus's inclusive concept of *Didelphis*, but it was influential in establishing modern binomial usage. His taxonomy included 11 genera, only one of which contained subgenera. Like Thomas (1888) and Matschie (1916), Cabrera made no use of subfamilies, tribes, or other suprageneric categories to indicate relationships among living opossums. Unlike Matschie, Cabrera grouped all of the ''murine'' opossums together, using *Marmosa* as the name for the taxon that Thomas called *Micoureus*.

Simpson (1945) recognized several subfamilies of didelphids, but he placed all of the living opossums (plus *Dromiciops*) in the

subfamily Didelphinae, and he did not use tribal nomenclature to indicate relationships among them. In effect, his treatment of Recent didelphids amounted to no more than an alphabetic list of generic names, conveying even less information about inferred relationships than the classifications of his predecessors.

Cabrera's (1958) checklist of South American mammals was one of the last attempts to classify Recent opossum diversity by traditional (prephylogenetic) criteria, and it remained more or less unchallenged until the advent of molecular systematics in the mid-1970s. Despite the fact that at least some contemporaneous researchers (e.g., Reig, 1955) recognized suprageneric groups among living opossumlike marsupials, Cabrera did not. Instead, only his taxonomic sequence and his use of subgenera for *Monodelphis* and *Marmosa* hint at inferred patterns of relationships. Most of the generic names that Cabrera recognized as valid are still used in the same sense today, with the conspicuous exception of *Marmosa*: whereas the nominotypical subgenus contained (in addition to *Marmosa* sensu stricto) species now referred to *Marmosops*, the subgenus *Thylamys* contained (in addition to *Thylamys* sensu stricto) species now referred to *Chacodelphys*, *Cryptonanus*, and *Gracilinanus*.

Reig et al. (1985) provided the first classification of opossumlike marsupials based on an explicitly phylogenetic analysis (subsequently published by Reig et al., 1987), and their classification was also the first to incorporate results from molecular and cytogenetic research (Kirsch, 1977b; Reig et al., 1977). Not surprisingly, this classification (table 17) departed from its predecessors in several respects. Among them, *Dromiciops* was once and for all removed to a separate family, "caluromyines" and didelphines were distinguished as separate subfamilies, and several tribes of the latter were recognized: all of the large opossums with a diploid number ($2n$) of 22 chromosomes were referred to the Didelphini, all of the smaller taxa with $2n = 14$–18 chromosomes were referred to the Marmosini (thus implying a close relationship between *Monodelphis* and the "murine" opossums), and a monotypic tribe was created for *Metachirus*.

The classification proposed by Hershkovitz (1992b) was not supported by any phylogenetic analysis, nor were phylogenetic criteria cited to support any of its novel features, including the recognition of four groups of Recent opossums as separate families (Marmosidae, Caluromyidae, Glironiidae, Didelphidae). Taxonomic rank aside, these taxa represent significant departures from previous classifications by grouping *Metachirus* with *Monodelphis* and the "murine" opossums, by the absence of any formal relationship between this group (Marmosidae) and the large opossums with 22 chromosomes (Didelphidae), and by the separation of *Glironia* on the one hand from *Caluromys* and *Caluromysiops* on the other. Also unlike other classifications, four "murine" genera (*Gracilinanus*, *Marmosops*, *Marmosa*, *Micoureus*) were associated in a single taxon (Marmosinae) that excluded *Thylamys* and *Lestodelphys*.

Kirsch and Palma (1995) formalized the results of their DNA-DNA hybridization experiments in a classification that, for the first time, associated *Metachirus* (as a monotypic tribe) with the large $2n = 22$ opossums (Didelphini), associated *Monodelphis* with *Marmosa* and *Micoureus*, and recognized the other "murine" opossums (*Gracilinanus*, *Lestodelphys*, *Marmosops*, *Thylamys*) as forming a separate clade. All of these taxa were referred to the family Didelphidae, whereas *Glironia*, *Caluromys*, and *Caluromysiops* were referred to the Caluromyidae.

McKenna and Bell's (1997) classification of Recent opossums followed Reig et al. (1985), but they used the name Monodelphini for the group that those authors called Marmosini. This was the system subsequently adopted by Gardner (2005, 2008) who lumped all of the old "murine" genera together with several new taxa in the tribe Monodelphini. No subordinate taxa (within Monodelphini) were recognized by these authors to indicate relationships among the many genera assigned to this group.

A Revised Phylogenetic System

As reviewed above, all previous classifications of Recent opossums contain nonmonophyletic groups. Examples include "Marmo-

TABLE 17
Classifications of Recent Opossums, 1985–2008

Reig et al. (1985)[a]	Hershkovitz (1992b)[b]	Kirsch and Palma (1995)	Gardner (2008)[c]
Didelphidae	Marmosidae	Didelphidae	Didelphidae
Didelphinae	Marmosinae	Didelphinae	Caluromyinae
Didelphini	*Gracilinanus*	Didelphini	*Caluromys*
Chironectes	*Marmosops*	*Didelphis*	*Caluromysiops*
Didelphis	*Marmosa*	*Philander*	*Glironia*
Lutreolina	*Micoureus*	*Lutreolina*	Didelphinae
Philander	Thylamyinae	*Chironectes*	Didelphini
Marmosini	*Thylamys*	Metachirini	*Chironectes*
Lestodelphys	Lestodelphyinae	*Metachirus*	*Didelphis*
Marmosa	*Lestodelphys*	Thylamyinae	*Lutreolina*
Micoureus	Metachirinae	Thylamyini	*Philander*
Monodelphis	*Metachirus*	*Thylamys*	Metachirini
Thylamys	Monodelphinae	*Lestodelphys*	*Metachirus*
Metachirini	*Monodelphis*	Marmosopsini	Monodelphini
Metachirus	Caluromyidae	*Marmosops*	*Chacodelphys*
Caluromyinae	Caluromyinae	*Gracilinanus*	*Cryptonanus*
Caluromys	*Caluromys*	Marmosinae	*Gracilinanus*
Caluromysiops	Caluromyiopsinae	Marmosini	*Hyladelphys*
Glironia	*Caluromysiops*	*Marmosa*	*Lestodelphys*
	Glironiidae	*Micoureus*	*Marmosa*
	Glironia	Monodelphini	*Marmosops*
	Didelphidae	*Monodelphis*	*Micoureus*
	Philander	Caluromyidae	*Monodelphis*
	Didelphis	Caluromyinae	*Thylamys*
	Chironectes	*Caluromys*	
	Lutreolina	*Caluromysiops*	
		Glironiinae	
		Glironia	

[a] This is also the classification of Reig et al. (1987) and Marshall et al. (1990).

[b] The classification of Hershkovitz (1992a) differs from this one in minor details. Hershkovitz (1997) proposed that *Lutreolina* and *Chironectes* each be placed in monotypic subfamilies of Didelphidae.

[c] Gardner's (2008) suprageneric classification and nomenclature followed McKenna and Bell (1997) but included subsequently described genera.

sini'' sensu Reig et al. (1985), ''Marmosidae'' sensu Hershkovitz (1992b); ''Marmosopsini'' sensu Kirsh and Palma (1995), and ''Monodelphini'' sensu Gardner (2005, 2008). Therefore, a revised phylogenetic system is needed.

The classification suggested below is based on the following principles: (1) taxa should be demonstrably monophyletic; (2) binomial nomenclature should remain as stable as possible consistent with the requirement of monophyly; (3) it is not necessary to name every node in a cladogram; (4) if future discoveries can be reasonably anticipated, taxa should be named so that these can be incorporated with minimal disruption; and (5) usage should be consistent with the International Code of Zoological Nomencla-

ture. Points (1) and (2) should be familiar to most readers and, we trust, are not controversial. Point (3) might be disputed by those who feel that cladograms should be completely described by classifications, but the mnemonic value of names is lost if they proliferate beyond reasonable need, the hierarchical ordering implied by the consistent use of familiar suffixes (e.g., -idae, -inae, -ini) is compromised if many clade names with unfamiliar endings are interpolated, and naming weakly supported clades that might disappear when new character data or taxa are added to future analyses is not in the interest of nomenclatural stability. Point (4) refers to long branches, which can be interpreted as artifacts of extinction or

incomplete taxon sampling (Horovitz, 1999); this notion provides some justification for naming monotypic higher taxa to accommodate future discoveries of new forms. Point (5) acknowledges the necessity for widely accepted rules to govern the use of technical names.

Because detailed generic synonymies have recently been published by Gardner (2008), we do not provide them here. However, a chronological list of available names with information about type species and current status (table 15) contains most of the information needed to understand current binomial usage. Under the indented heading ''Contents'' we list all of the valid lower-level taxa included by each higher-level taxon; for example, the genera referred to a tribe, or the species referred to a genus. In lists of congeneric species, those currently regarded as valid are in boldface, followed by an alphabetic list of available junior synonyms in parentheses; however, names of doubtful application (e.g., *brasiliensis* Liais, 1872, which might be a junior synonym of more than one currently recognized species of *Didelphis*; see Cerqueira and Tribe, 2008) are not included.

Under ''Diagnosis'' we list unique combinations of traits that distinguish members of suprageneric taxa from other marsupials, whether or not such traits are unambiguously assignable by parsimony as relevant synapomorphies (listed in appendix 5). Under ''Morphological description'' (for genera) we list all phenotypic descriptors that apply to included species; traits of particular importance for identification are indicated by italics. Ranges of metrical traits (e.g., 170–210 mm) are approximations that match or slightly exceed known minimal and maximal adult values that we believe to be reliable based on published and unpublished sources. Except as noted otherwise, all descriptions of cranial traits are based on adult specimens, and all dental descriptions are based on unworn teeth.

Under ''Remarks'' we discuss evidence for monophyly and other issues that relate to taxon recognition and rank. Although ranks are biologically arbitrary, they affect spelling and information retrieval in the prevailing Linnaean system, and they are regulated by widely accepted rules of biological nomenclature. The lack of species-level revisionary studies for most genera is also discussed under this heading.

Family Didelphidae Gray, 1821

CONTENTS: Glironiinae, Caluromyinae, Hyladelphinae, and Didelphinae.

DIAGNOSIS: Didelphids can be distinguished unambiguously from other marsupials by their soft (nonspinous) body pelage; five subequal claw-bearing manual digits; five separate pedal digits (loosely connected by webbing in *Chironectes*), of which the hallux (dI) is large and opposable and the second (dII) bears an asymmetrical grooming claw; inguinal cloaca; prehensile tail (secondarily lacking external evidence of prehensility in some taxa); long nasal bones (extending anteriorly beyond the facial processes of the premaxillae and posteriorly between the lacrimals); unfenestrated rostrum; uninflected maxillary-jugal suture; distinct foramen rotundum (not confluent or sharing a common vestibule with the sphenorbital fissure); alisphenoid-parietal contact (except in *Metachirus*); large interparietal fused to the supraoccipital; complete posterolateral palatal foramina; deeply divided vomer that does not conceal the presphenoid or extend posteriorly into the mesopterygoid fossa; lack of midline contact between the left and right pterygoids; unkeeled basisphenoid; well-developed tympanic process of the alisphenoid; well-developed rostral tympanic process of the petrosal; lack of a squamosal epitympanic sinus; laterally exposed ectotympanic; unspecialized malleus (with long sharply inflected neck, small orbicular apophysis, and well-developed lamina); distinct mastoid and paroccipital processes; unreduced dental complement of 50 teeth; nongliriform incisors; large milk premolars (except in *Hyladelphys*); tribosphenic upper molars, each with a continuous stylar shelf, uninterrupted centrocrista, and reduced or absent para- and metaconules; and tribosphenic lower molars, each with a well-developed anterior cingulid (notched for the hypoconulid of the preceding tooth), notched paracristids, and without any trace of a posterior cingulid.

Didelphids have often been compared with dasyurids, but the literature contains no adequate statement of the many characters that distinguish these superficially similar yet highly divergent clades. Among the external and craniodental features treated in this report, dasyurids consistently differ from didelphids by their small, nonopposable hallux; lack of a grooming claw on pedal digit II; a nonprehensile tail (provided with a terminal tuft of hairs that is never present in opossums); anteriorly truncated and medially notched nasals; a small interparietal that, when present in juvenile skulls, is suturally distinct from the supraoccipital; incomplete posterolateral palatal foramina; an undivided vomer that extends posteriorly to underlie the presphenoid within the mesopterygoid fossa; well-developed squamosal epitympanic sinuses; four upper and three lower incisors; a distinct posterior lobe on the unworn cutting edge of i3; vestigial milk premolars; and a distinct posterior cingulid on the lower molars.

Originally described as a didelphid by Thomas (1894) and long maintained in that family by subsequent authors (e.g., Simpson, 1945), *Dromiciops* differs from opossums by its basicaudal cloaca; a foramen rotundum recessed in a common vestibule with the sphenorbital fissure; frontal-squamosal contact; a large interparietal that is suturally distinct from the supraoccipital; an undivided vomer that underlies the presphenoid within the mesopterygoid fossa; left and right pterygoid bones that contact one another in the midline; keeled basisphenoid; a concealed ectotympanic; a specialized malleus (with a short uninflected neck, no orbicular apophysis, and no lamina); lack of a paroccipital process; a discontinuous stylar shelf on M1; an unstaggered i2 alveolus; and a vestigial anterior cingulid on the lower molars (of which m1 lacks a hypoconulid notch).

Caenolestids, peramelids, and other marsupials are sufficiently distinct from opossums that explicit comparisons would be pointless here. Some stem metatherians (e.g., herpetotheriids) that are strikingly similar to didelphids in most respects (including ear morphology; Gabbert, 1998) differ from didelphids by having a distinct posterior cingulid on the lower molars in addition to the diagnostic endocranial and postcranial features described by Sánchez-Villagra et al. (2007).[23]

REMARKS: A wide range of fossil taxa have at one time or another been regarded as didelphids (e.g., by Simpson, 1935, 1945; Clemens, 1979; Marshall, 1981; McKenna and Bell, 1997), but phylogenetic analyses suggest that most of the extinct forms once thought to be closely related to Recent opossums (e.g., †*Alphadon*, †*Andinodelphys*, †*Glasbius*, †*Herpetotherium*, †*Jaskhadelphys*, †*Pediomys*) are stem metatherians and not members of the crown group Marsupialia (Rougier et al., 1998; Wible et al., 2001; Luo et al., 2003; Sánchez-Villagra et al., 2007). Herein we explicitly restrict Didelphidae to living didelphimorphians, their most recent common ancestor, and all of its descendants.

Even more restrictive concepts of Didelphidae have been proposed, but none is widely accepted. Hershkovitz (1992b), for example, used Didelphidae to include just the large opossums with $2n = 22$ chromosomes (*Chironectes*, *Didelphis*, *Lutreolina*, *Philander*), whereas Kirsch and Palma (1995) excluded *Glironia*, *Caluromys*, and *Caluromysiops* from the family. Because Didelphidae in any of these applications (ours, Hershkovitz's, or Kirsch and Palma's) is monophyletic, the choice among them must be justified by other criteria. In our view, the name Didelphidae and its colloquial equivalent (''didelphids'') are so deeply entrenched in the literature as referring to all Recent opossums that more restrictive applications would serve no adequate compensatory purpose.

Although didelphid monophyly is impressively supported by nucleotide sequence data

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[23] As noted above, the posterior cingulid is absent in didelphids, caenolestids, microbiotherians, and peramelids, so it optimizes as an unambiguous marsupial synapomorphy on all metatherian topologies in which these groups are recovered as basal clades (e.g., Meredith et al. 2008). Because most Cretaceous and early Tertiary metatherians are known only from teeth, this trait provides a potentially useful criterion for distinguishing stem taxa from members of the crown clade. For example, several of the Paleocene Brazilian fossils classified as didelphids by Marshall (1987) are described by that author as having posterior cingulids and might plausibly be regarded on that basis as stem metatherians. By contrast, Marsupialia (in the crown-group sense) does not seem to be diagnosable by any upper molar trait.

(e.g., Jansa and Voss, 2000; Amrine-Madsen et al., 2003; Meredith et al., 2008), unambiguous morphological synapomorphies of the family remain to be confidently identified. Because our analyses did not include any nonmarsupial outgroup, the position of the marsupial root node was not determined, and the phylogenetic interpretation of character-state transformations on the branch separating didelphids from nondidelphid marsupials is correspondingly equivocal. If, as most recent analyses suggest, didelphids are the basalmost branch of Marsupialia (Nilsson et al., 2004; Amrine-Madsen et al., 2003; Horovitz and Sánchez-Villagra, 2003; Asher et al., 2004; Sánchez-Villagra et al., 2007; Meredith et al., 2008; Beck, 2008), then such transformations might be didelphid synapomorphies, or they could be synapomorphies of the unnamed clade that includes caenolestids and Australidelphia.

Comparisons with stem metatherians that are believed to be close outgroups to Marsupialia, including †Mayulestes (see Muizon, 1998), †Pucadelphys (see Marshall et al., 1995), and †Herpetotherium (see Gabbert, 1998; Sánchez-Villagra et al., 2007) suggest that most of the craniodental traits by which didelphids differ from other marsupials are plesiomorphic, but one exception merits comment. Bone homologies on the posterodorsal braincase have received little attention in the literature, but they appear to be phylogenetically informative at many taxonomic levels within Metatheria. In particular, the presence of a large undivided interparietal bone that is wedged between the parietals anteriorly and fused to the supraoccipital posteriorly may be a didelphid synapomorphy. According to Muizon (1998: 38, fig. 6), paired interparietal ossifications are fused to the parietals in †Mayulestes, but the basis for this interpretation (which has no analog among living metatherians) is not explained, and it seems equally possible that the interparietal(s) is(are) absent in this taxon. In †Pucadelphys, paired interparietals ("postparietals") are suturally distinct from the parietals and from the supraoccipital (Marshall et al., 1995: 50, fig. 12). The occiput of †Herpetotherium has not previously been described, but in a well-preserved specimen that we examined (127684 in the AMNH

vertebrate paleontology catalog) there is no bone wedged between the parietals and the supraoccipital, which share a suture just behind the lambdoid crest. Therefore, the available evidence suggests that the didelphid condition is unique.

Other alleged morphological synapomorphies of didelphids include features of the spermatozoa (Temple-Smith, 1987), postcranial skeleton (Horovitz and Sánchez-Villagra, 2003), and petrosal (Ladevèze, 2007). However, the phylogenetic interpretation of such traits is compromised by sparse ingroup sampling. Spermatozooa, for example, have not been studied from many genera (e.g., Caluromysiops, Glironia, Hyladelphys, Lutreolina, Marmosops, Thylamys), and published phylogenetic analyses of postcranial and petrosal characters have not included basal didelphids (analyzed didelphid terminal taxa in both of the osteological studies cited above belong to the subfamily Didelphinae). Hopefully, future studies will help fill in many of these taxonomic gaps and contribute to a better assessment of anatomical character support for didelphid monophyly.

Only Recent didelphids are formally classified and described below, but several South American Neogene genera represented by well-preserved cranial material (†Hyperdidelphys, †Thylatheridium, †Thylophorops) are clearly members of the didelphimorph crown clade. Pending a phylogenetic analysis of their relationships with living forms, we follow current paleontological judgments of taxonomic affinity in suggesting where these fossils belong. By contrast, most other fossil didelphids are only represented by dental fragments from which few characters can be scored, and their relationships to extant taxa are correspondingly ambiguous.

Subfamily Glironiinae, new

CONTENTS: Glironia.

DIAGNOSIS: Members of this clade differ from other didelphids by the extension of soft fur along the dorsal surface of the tail from base to tip (the dorsal surface of the tail is macroscopically naked distally in other opossums), by strongly recurved and laterally compressed manual claws (manual claws are much less strongly recurved and laterally

compressed in other opossums), and by postorbital processes that are formed by the frontals and parietals (postorbital processes are absent or are formed only by the frontals in other opossums).

REMARKS: The name Glironiidae as used by Hershkovitz (1992a, 1992b, 1999) was a nomen nudum because it was not accompanied by a statement of diagnostic characters (ICZN, 1999: Article 13). To our knowledge, no family-group name based on *Glironia* is technically available from any other publication.

Glironia Thomas, 1912
Figure 37

CONTENTS: *venusta* Thomas, 1912 (including *aequatorialis* Anthony, 1926; and *criniger* Anthony, 1926).

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body probably ca. 170–210 mm; adult weight probably ca. 100–200 g (measurements from the only two adult specimens known to have been measured by the American method and accompanied by weight data are in table 4). Rhinarium with two ventrolateral grooves on each side of median sulcus; dark circumocular mask present; pale supraocular spot absent; dark midrostral stripe absent; throat gland unknown (no suitably preserved adult male specimens have been examined for this feature). Dorsal body pelage unpatterned, brownish; dorsal underfur gray; dorsal guard hairs short and inconspicuous; ventral fur grayish or gray-based whitish, with or without self-whitish pectoral markings. Manus paraxonic (dIII = dIV); *manual claws strongly recurved, laterally compressed, and much longer than fleshy apical pads of digits*; dermatoglyph-bearing manual plantar pads present; central palmar epithelium smooth; carpal tubercles absent. Pes unwebbed; dIV longer than other pedal digits; plantar surface of heel naked. Pouch absent; mammae 2–0–2 = 4, all abdominal/inguinal; cloaca present. Tail about as long as combined length of head and body or a little longer, slender and muscular (not incrassate), and *densely furred from base to tip except along ventral midline*; naked ventral caudal surface modified for prehension *with raised tubercles near base* and apical pad bearing dermatoglyphs.

Premaxillary rostral process absent. Nasals long, extending anteriorly beyond I1 (concealing nasal orifice from dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. Lacrimal foramina concealed within anterior orbital margin or exposed laterally, usually two on each side. Orbits very large; supraorbital crests well developed; flattened triangular postorbital processes present, *formed by both frontal and parietal bones*. Left and right frontals and parietals separated by persistent median sutures. Parietal contacts alisphenoid on lateral braincase (no frontal-squamosal contact). Sagittal crest absent. Petrosal not laterally exposed through fenestra in parietal-squamosal suture (fenestra absent). Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae usually present, but small; palatine fenestrae absent; maxillary fenestrae absent; posterolateral palatal foramina small, not extending anteriorly between M4 protocones; posterior palatal morphology *Caluromys*-like (without prominent lateral corners, the choanae not constricted behind). Maxillary and alisphenoid not in contact on floor of orbit (separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process smoothly globular, without anteromedial process or posteromedial lamina enclosing extracranial course of mandibular nerve (secondary foramen ovale absent), and not in contact with rostral tympanic process of petrosal. Anterior limb of ectotympanic suspended directly from basicranium. Stapes triangular with large obturator foramen. Fenestra cochleae exposed, not concealed by rostral and caudal tympanic processes of petrosal. Paroccipital process small, adnate to petrosal. Dorsal margin of foramen magnum bordered by exoccipitals and supraoccipital, incisura occipitalis present.

Two mental foramina present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 asymmetrical (''incisiform''), with longer anterior than posterior cutting edges; I5 separated from I4 by small diastema in some specimens (e.g.,
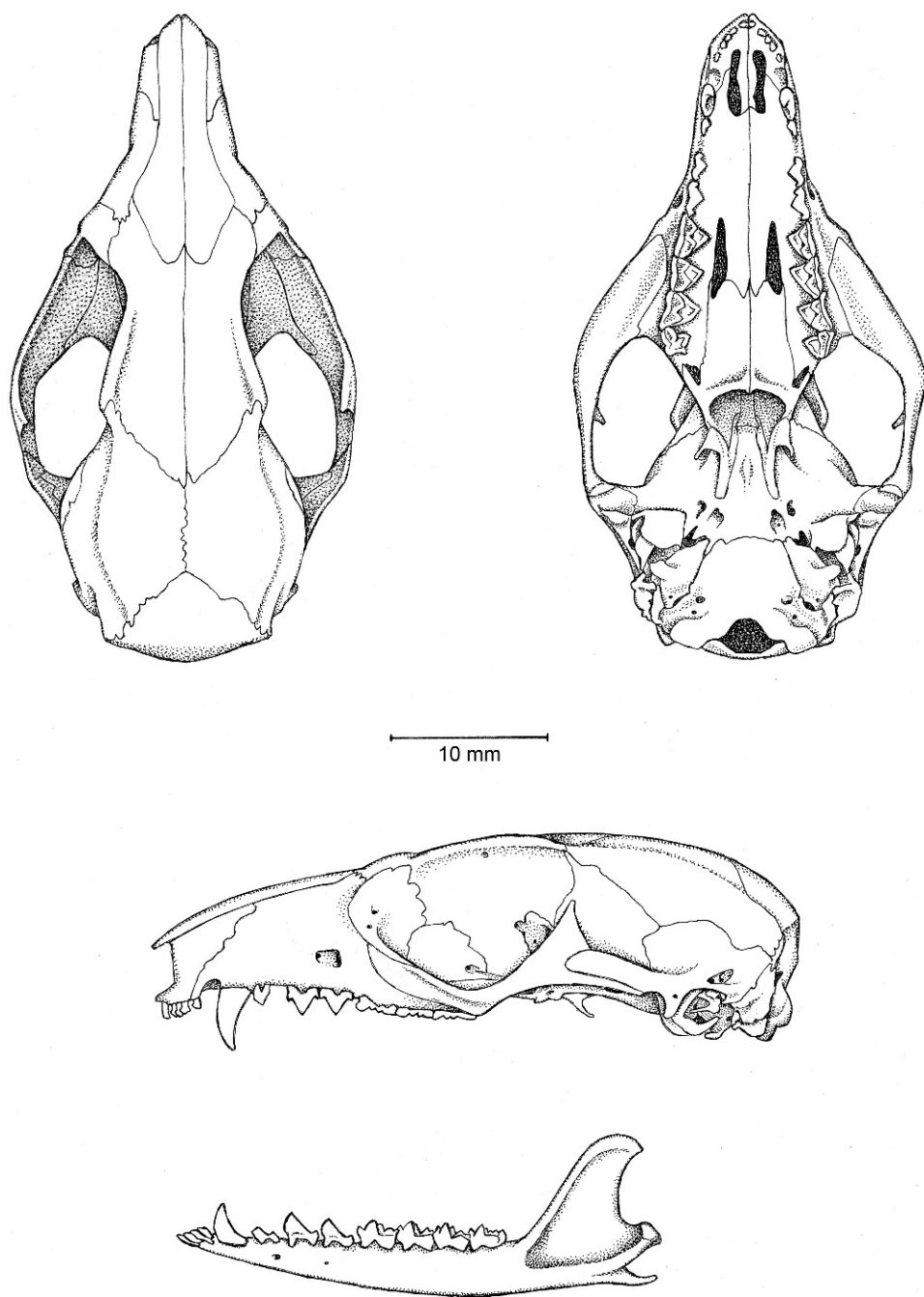
10 mm

Fig. 37. *Glironia venusta* (based primarily on INPA 2570, a subadult male from the Rio Urucú, Amazonas, Brazil). Because p3 is incompletely erupted on INPA 2570, the morphology and adult position of this tooth was reconstructed from other specimens. The postorbital processes become more pronounced with age.

INPA 2570) but not others (e.g., FMNH 41440). Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple, without accessory cusps. First upper premolar (P1) present, smaller than more posterior premolars but well formed and not vestigial; second and third upper premolars (P2 and P3) subequal in height; P3 with both anterior and posterior cutting edges. Molars weakly carnassialized (postmetacristae longer than postprotocristae); relative widths M1 < M2 < M3 > M4; centrocrista weakly inflected labially on M1–M3; ectoflexus absent or indistinct on M1 and M2, distinct but usually shallow on M3; anterolabial cingulum continuous with preprotocrista (complete anterior cingulum present) on M3; postprotocrista without carnassial notch. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. Lower canine (c1) erect, acutely pointed, and simple (without a posterior accessory cusp). Second lower premolar (p2) taller than p3; morphology of lower milk premolar (dp3) unknown (no juvenile specimens examined). Hypoconid labially salient on m3; hypoconulids twinned with entoconids on m1–m3; entoconids much taller than hypoconulids on m1–m3.

DISTRIBUTION: *Glironia* is currently known from fewer than two dozen specimens collected at widely scattered localities between 300 and 1000 m above sea level in Brazil (Amazonas, Mato Grosso, Pará, Rodônia), eastern Ecuador, eastern Peru, and eastern Bolivia (Díaz and Willig, 2004; Santos-Filho et al., 2007; Barkley, 2008). Although the genus probably also occurs in southeastern Colombia, no specimens are known to have been collected there (Díaz and Willig, 2004). Most records accompanied by definite habitat information are from primary or secondary Amazonian rainforest, but a single specimen was recently reported from the upper Paraguay Basin (Santos-Filho et al., 2007), and several Bolivian records are from dry forest (Tarifa and Anderson, 1997; Emmons, 1998).

REMARKS: Only the type species of *Glironia* is currently recognized as valid, but it seems probable that additional taxa are represented among the material now preserved in museum collections.

Subfamily Caluromyinae Reig et al., 1987

CONTENTS: *Caluromys* and *Caluromysiops*.

DIAGNOSIS: Caluromyines can be distinguished from other confamilial taxa by their long fourth manual digit (dIII is the longest manual digit, or dIII and dIV are subequal in all other didelphids); a completely ossified palate (maxillopalatine and sometimes additional palatal fenestrae are consistently present in most other didelphids); lack of a transverse canal foramen (transverse canal foramina are almost invariably present in all other didelphids); an alisphenoid tympanic process that contacts or closely approximates the rostral tympanic process of the petrosal (the alisphenoid tympanic process and the rostral tympanic process of the petrosal are widely separated in other didelphids); an indirectly suspended anterior limb of the ectotympanic (the anterior limb of the ectotympanic is directly suspended from the skull in most other didelphids); a fenestra cochleae that is concealed in a sinus formed by the rostral and caudal tympanic processes of the petrosal (the fenestra cochleae is exposed in most other didelphids); a blunt and weakly inflected angular process (the mandibular angle is acute and strongly inflected in all other didelphids); an upper canine alveolus that is completely contained by the maxilla (C1 occupies the premaxillary-maxillary suture in all other didelphids); a vestigial or absent first upper premolar (P1 is present and nonvestigial in all other didelphids); a tall second upper premolar that much exceeds P3 in height (P2 is either subequal to or smaller than P3 in most other didelphids); and lack of an ectoflexus on all of the upper molars (a distinct ectoflexus is present, at least on M3, in all other didelphids).

REMARKS: Caluromyine monophyly is strongly supported by morphological characters (appendix 5) and IRBP gene sequences (fig. 28), and this clade is recovered with strong support in analyses of concatenated genes (fig. 33) and total evidence (nonmolecular + molecular characters; figs. 35, 36) despite the overall incompleteness of our data from *Caluromysiops* (table 2). Two deletions at the DMP1 locus that currently optimize as synapomorphies of *Caluromys* (fig. 29) might prove to be caluromyine

synapomorphies when this gene is eventually sequenced for *Caluromysiops*. Although most recent authors (e.g., Reig et al., 1985, 1987; Kirsch and Palma, 1995; McKenna and Bell, 1997; Gardner, 2005, 2008) have included *Glironia* in the Caluromyinae (or Caluromyidae), that genus appears to represent an ancient lineage of basal didelphids that may not be closely related to *Caluromys* + *Caluromysiops* (see Jansa and Voss, 2000; this report, above). The authorship of family-group names based on *Caluromys* is often attributed to Kirsch (1977b), but no such name in that work fulfills the technical criteria for nomenclatural availability (ICZN, 1999: Article 13). Apparently, the first explicit statement of characters purported to differentiate this taxon from other opossums appeared in Reig et al. (1987: 72).

Caluromys J.A. Allen, 1900
Figure 38

CONTENTS: ***derbianus*** Waterhouse, 1841 (including *antioquiae* Matschie, 1917; *aztecus* Thomas, 1913; *canus* Matschie, 1917; *centralis* Hollister, 1914; *fervidus* Thomas, 1913; *guayanus* Thomas, 1899; *nauticus* Thomas, 1913; *pallidus* Thomas, 1899; *pictus* Thomas, 1913; *pulcher* Matschie, 1917; *pyrrhus* Thomas, 1901; and *senex* Thomas, 1913); ***lanatus*** Olfers, 1818 (including *bartletti* Matschie, 1917; *cahyensis* Matschie, 1917; *cicur* Bangs, 1898; *hemiurus* Miranda-Ribeiro, 1936; *jivaro* Thomas, 1913; *juninensis* Matschie, 1917; *lanigera* Desmarest, 1820; *meridensis* Matschie, 1917; *modesta* Miranda-Ribeiro, 1936; *nattereri* Matschie, 1917; *ochropus* Wagner, 1842; *ornatus* Tschudi, 1845; and *vitalinus* Miranda-Ribeiro, 1936); and ***philander*** Linnaeus, 1758 (including *affinis* Wagner, 1842; *cajopolin* Müller, 1776; *cayopollin* Schreber, 1777; *cayopollin* Kerr, 1792; *dichurus* Wagner, 1842; *flavescens* Brongniart, 1792; *leucurus* Thomas, 1904; *trinitatis* Thomas, 1894; and *venezuelae* Thomas, 1903).

These taxa are currently allocated to two subgenera, *Caluromys* J.A. Allen, 1900 (containing only *C. philander*), and *Mallodelphys* Thomas, 1920 (containing *C. derbianus* and *C. lanatus*), that can be distinguished unambiguously by the traits noted below.

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body ca. 210–300 mm; adult weight ca. 190–500 g. Rhinarium with two ventrolateral grooves on each side of median sulcus; dark circumocular mask present; pale supraocular spot absent; dark midrostral stripe present; throat gland absent. Dorsal pelage unpatterned, grayish or reddish brown, or indistinctly mottled with same colors; dorsal underfur grayish; dorsal guard hairs short and inconspicuous; ventral fur gray based or self-colored. Manual digit IV longer than other manual digits; manual claws longer than fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar epithelium smooth or sparsely tuberculate; carpal tubercles absent. Pedal digits unwebbed; pedal digit IV longer than other pedal digits; plantar surface of heel naked. Pouch present, consisting of separate lateral skin folds opening medially (subgenus *Caluromys*) or a deep pocket opening anteriorly (subgenus *Mallodelphys*); known mammary formulae apparently 2–0–2 = 4 (in *C. lanatus*) and 3–1–3 = 7 (in *C. philander*); cloaca present. Tail much longer than combined length of head and body, slender and muscular (not incrassate); body fur extends onto tail base to the same extent dorsally as ventrally (subgenus *Caluromys*) or much further dorsally than ventrally (subgenus *Mallodelphys*); naked caudal integument dark (grayish or brownish) basally and whitish distally with mottled transition; caudal scales in spiral series, each scale with three subequal bristlelike hairs emerging from distal margin (the central hair of each caudal-scale triplet longer than the lateral hairs but not grossly swollen or petiolate); naked ventral caudal surface modified for prehension, with raised tubercles near base (*Mallodelphys* only) and apical pad bearing dermatoglyphs.

Premaxillary rostral process present. Nasals long, extending anteriorly above I1 (concealing nasal orifice from dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. Lacrimal foramina exposed to lateral view at or near anterior orbital margin, usually two on each side. Large, flattened, triangular postorbital processes of frontals present. Left and right frontals and parietals separated by persistent
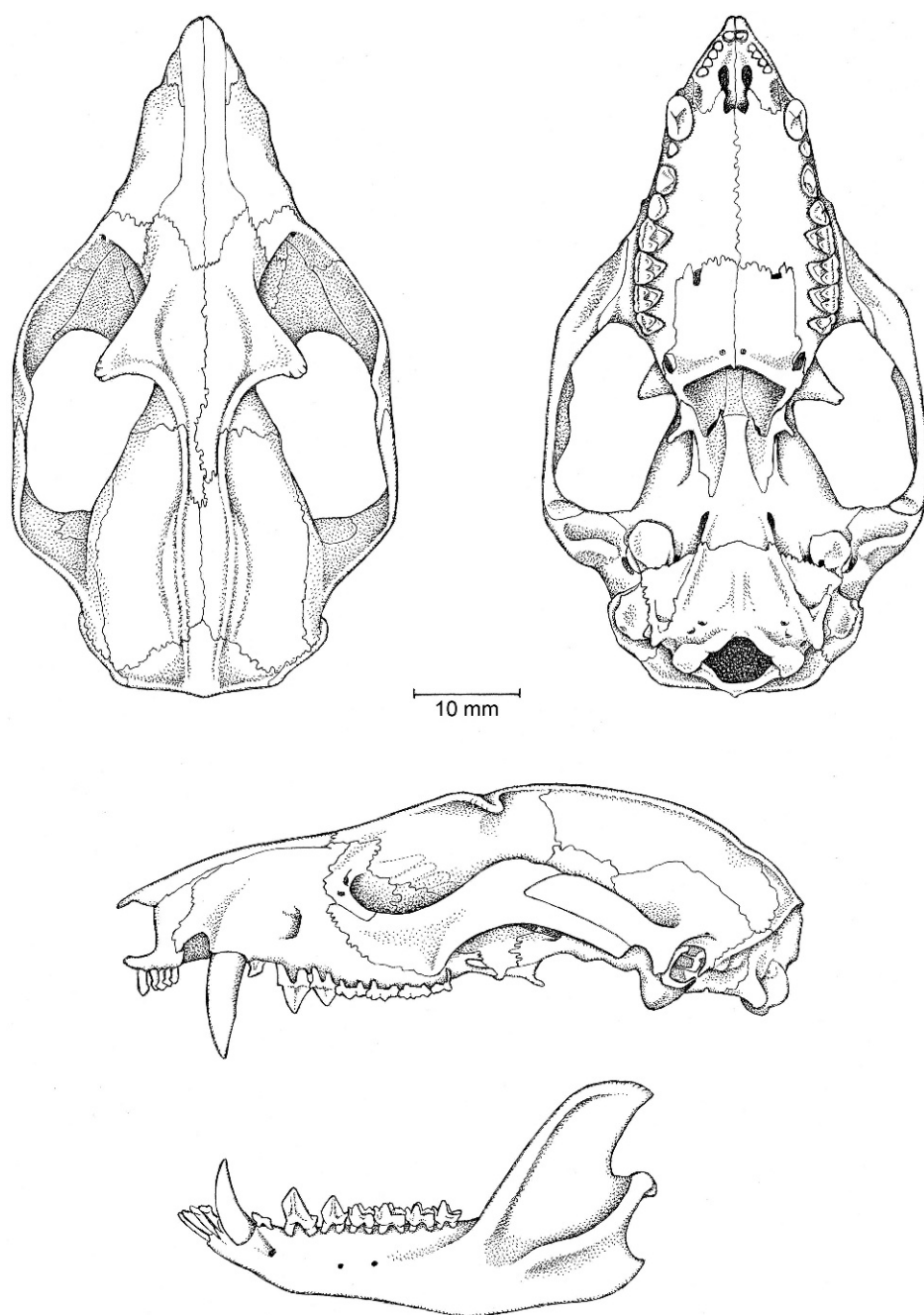
Fig. 38.   *Caluromys philander* (based on AMNH 266409, an adult male from Paracou, French Guiana).

median sutures. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest weakly developed on interparietal and/or along midparietal suture (not extending anteriorly to frontals) in some large adult specimens. Petrosal not laterally exposed through fenestra in parietal-squamosal suture (fenestra absent). Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae usually absent (small fenestrae, never extending anteriorly beyond M1 or posteriorly beyond M2, are uni- or bilaterally present in occasional specimens); palatine and maxillary fenestrae absent; posterolateral palatal foramina small, not extending anteriorly between M4 protocones; posterior palate gently sloping ventrally, usually with arched caudal margin and without prominent posterolateral corners (the choanae unconstricted behind). Maxillary and alisphenoid not in contact on floor of orbit (separated by palatine). Transverse canal foramen absent. Alisphenoid tympanic process more or less conical (acutely pointed ventrally), usually without posteromedial lamina enclosing extracranial course of mandibular nerve (secondary foramen ovale absent),[24] and contacting or closely approximating rostral tympanic process of petrosal. Anterior limb of ectotympanic indirectly suspended from basicranium (by malleus). Stapes triangular with large obturator foramen (in subgenus *Caluromys*) or subtriangular with small but patent foramen (in subgenus *Mallodelphys*). Fenestra cochleae concealed in sinus formed by rostral and caudal tympanic processes of petrosal. Paroccipital process small, rounded and subtriangular, adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina usually present on lateral surface of each hemimandible; angular process blunt and weakly inflected.

Unworn crowns of I2–I5 asymmetrical ("incisiform"), with much longer anterior than posterior cutting edges. Upper canine (C1) alveolus contained entirely in maxillary bone; C1 simple, without accessory cusps. First upper premolar (P1) minute, vestigial, and lacking any consistent occlusal features; second upper premolar (P2) much taller than P3; P3 with both anterior and posterior cutting edges; upper milk premolar (dP3) large and molariform. Molars not carnassialized (postprotocristae and postmetacristae are subequal in subgenus *Mallodelphys*) or weakly carnassialized (postmetacristae are

slightly longer than postprotocristae in subgenus *Caluromys*); relative widths usually M1 < M2 > M3 > M4 (subgenus *Mallodelphys*) or M1 < M2 < M3 > M4 (subgenus *Caluromys*); centrocrista weakly inflected labially on M1–M3; ectoflexus consistently absent on all upper molars; anterolabial cingulum continuous with preprotocrista (complete anterior cingulum present) on M3; postprotocrista without carnassial notch. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. Lower canine (c1) erect, acutely pointed, and simple (without a posterior accessory cusp). Second upper premolar (p2) much taller than p3; lower milk premolar (dp3) trigonid with or without paraconid (when present, the paraconid is small and often indistinct). Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid much taller than hypoconulid on m1–m3.

DISTRIBUTION: *Caluromys* occurs from the Mexican state of Veracruz southward throughout most of the forested regions of Central and South America (including Trinidad) to eastern Bolivia, eastern Paraguay, and northeastern Argentina (Hall, 1981; Gardner, 2008). Most specimens of *C. lanatus* and *C. philander* (e.g., those reported by Handley, 1976; Anderson, 1997) are from lowland or lower montane rainforest; however, *C. philander* has also been observed in dry forest (Emmons, 1998), and *C. derbianus* ranges from sea level to over 2000 m and occurs in both rainforest and dry forest (Handley, 1966; Bucher and Hoffmann, 1980; Sánchez et al., 2004).

REMARKS: Generic monophyly (vis-à-vis *Caluromysiops*) is supported by IRBP sequence data (fig. 28), by the presence of a distinct midrostral stripe, and by the presence of a small but distinct rostral process of the premaxillae (the latter two traits optimize as unambiguous generic synapomorphies; appendix 5).

The genus *Caluromys* has never been revised, and there is substantial divergence in morphology and/or cytochrome *b* sequences among some allegedly conspecific populations (Voss et al., 2001; Patton and Costa, 2003). Indeed, no revisionary study has documented the conspecific status of the

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[24] We examined one old adult male (MVZ 190249) with a secondary foramen ovale formed by a posteromedial lamina.

many subjective synonyms listed above for either *C. philander* or *C. lanatus*. It is an open question as to whether the subgenera *Caluromys* and *Mallodelphys* will prove to be reciprocally monophyletic or not in future phylogenetic analyses based on denser taxon sampling.

Caluromysiops Sanborn, 1951
Figure 39

CONTENTS: ***irrupta*** Sanborn, 1951.

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body probably ca. 250–300 mm (Izor and Pine, 1987); adult weight probably ca. 300–500 g. Rhinarium with two ventrolateral grooves on each side of median sulcus; *fur of head uniformly pale, without any marking* (dark circumocular mask, supraocular spots, and midrostral stripes absent); throat gland absent. *Dorsal pelage pale overall but prominently marked by paired blackish stripes extending from forelimbs to shoulders and thence posteriorly as narrowing parallel bands to rump*; dorsal underfur dark (apparently grayish but discolored with age in all examined specimens); dorsal guard hairs short; ventral fur variously colored (gray-based buffy in some specimens, self-buffy in others). Manual digit IV longer than other manual digits; manual claws longer than fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar epithelium smooth; carpal tubercles absent. Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel usually naked. Pouch said to be present (Izor and Pine, 1987) but morphological details unknown; mammary formula unknown; cloaca present. Tail longer than combined length of head and body, slender and muscular (not incrassate); *densely covered with body fur from base almost to tip except along ventral midline and posterolaterally*; posterolateral caudal scales in spiral series, each scale with three subequal bristlelike hairs emerging from distal margin; naked ventral surface modified for prehension *with raised tubercles near base*, and apical pad bearing dermatoglyphs.

Premaxillary rostral process absent. Nasals long, extending anteriorly above I1 (conceal-ing nasal orifice from dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. One or two lacrimal foramina exposed on each side on or near anterior orbital margin. Large flattened, triangular postorbital processes of frontals present, continuous with supraorbital crests. Left and right frontals and parietals co-ossified in most adult specimens (median sutures incomplete or obliterated). Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). *Sagittal crest present*, *prominently developed on parietals and extending onto frontals in most adult specimens.* Petrosal not laterally exposed through fenestra in parietal-squamosal suture (fenestra absent). Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine, palatine, and maxillary fenestrae absent (palate completely ossified); posterolateral palatal foramina small, not extending anteriorly between M4 protocones; posterior palatal morphology conforms to *Caluromys* morphotype (without strongly developed lateral corners, the choanae unconstricted behind). Maxillary and alisphenoid widely separated by palatine on floor of orbit. Transverse canal foramen absent. Alisphenoid tympanic process smoothly globular, apparently always with posteromedial lamina enclosing extracranial course of mandibular nerve (secondary foramen ovale present), and extending posteriorly to contact or closely approximate rostral tympanic process of petrosal. Anterior limb of ectotympanic indirectly suspended from basicranium (by malleus). Stapes usually columellar and imperforate (rarely microperforate). Fenestra cochleae usually concealed in sinus formed by rostral and caudal tympanic processes of petrosal (but not in USNM 397626, possibly due to pathology or postmortem damage). Paroccipital process small, adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina usually present on lateral surface of each hemimandible; angular process obtuse, weakly inflected.

Unworn crowns of I2–I5 asymmetrical (''incisiform''), with longer anterior than
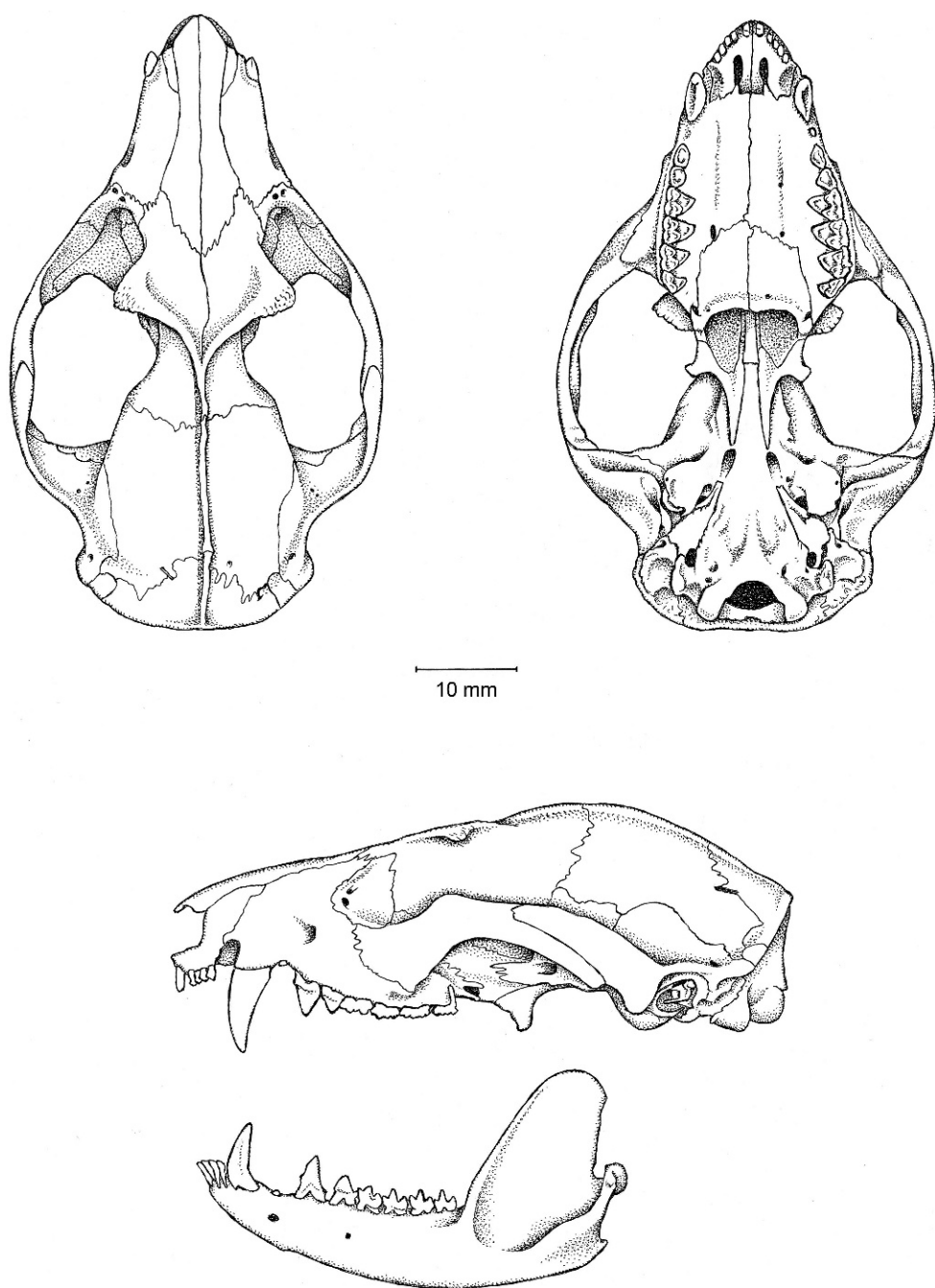
10 mm

Fig. 39.   *Caluromysiops irrupta* (a composite illustration based on several imperfect adult specimens, mostly from zoos: AMNH 208101, 244364; USNM 397626; FMNH 84426).

posterior cutting edges. Upper canine (C1) alveolus contained entirely within maxillary bone; C1 simple (without accessory cusps), and very large in adult specimens. First upper premolar (P1) absent or minute and vestigial; second upper premolar (P2) much taller than P3; P3 with both anterior and posterior cutting edges; upper milk premolar (dP3) large and molariform. Molars not carnassialized (postmetacristae subequal to postprotocristae); relative widths M1 < M2 > M3 > M4; *centrocrista straight (uninflected) on M1–M3*; ectoflexus absent on all upper molars; anterolabial cingulum continuous with preprotocrista (complete anterior cingulum present) on M3; postprotocrista without carnassial notch. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. Lower canine (c1) erect, acutely pointed, and simple (without a posterior accessory cusp). Second lower premolar (p2) much taller than p3; lower milk premolar (dp3) large and nonvestigial, but paraconid not well developed (trigonid incomplete). Hypoconid labially salient on m3; *hypoconulid not twinned with entoconid on any lower molar*; entoconid much taller than hypoconulid on m1–m3.

DISTRIBUTION: *Caluromysiops* is currently known from just seven localities in the rainforested Amazonian lowlands of southeastern Colombia, eastern Peru and western Brazil (Emmons, 2008).

REMARKS: Various authors (e.g., Cabrera, 1958; Simpson, 1972; Izor and Pine, 1987) have questioned whether it is useful to separate *Caluromysiops* from *Caluromys*, but none explicitly considered the suite of trenchant morphological characters that distinguish these taxa. Among other features, *Caluromysiops* differs from *Caluromys* by its lack of a circumocular mask and dark midrostral stripe, presence of dark scapular stripes, shorter tail (table 5), absence of a premaxillary rostral process, co-ossified frontals, presence of a well-developed sagittal crest, presence of a secondary foramen ovale, globular (versus conical) alisphenoid bullae, columelliform stapes, linear centrocrista, and untwinned hypoconulid. Although there is no cladistic problem with combining these taxa under a single generic name, maintaining current binomial usage is likewise unobjectionable and serves to separate the monophyletic cluster of species currently known as *Caluromys* from its long-branched sister taxon.

Subfamily Hyladelphinae, new

CONTENTS: *Hyladelphys*.

DIAGNOSIS: Members of this clade uniquely differ from other didelphids by their vestigial milk dentition (dP3/dp3 are large, more or less molariform teeth in other opossums; Voss et al., 2001: table 5). Additional contrasts among hyladelphines and members of other didelphid subfamilies were tabulated by Jansa and Voss (2005: table 2).

REMARKS: Given the phylogenetic results at hand, a monotypic suprageneric taxon for *Hyladelphys* could either be ranked as a subfamily (as it is here) or as a tribe (if the genus were referred to the Didelphinae). Although the issue of rank is not biologically meaningful, the former option serves to emphasize the intermediate position of this odd little opossum between basal didelphids (*Glironia* and caluromyines) and the speciose radiation of lineages that are more closely related to *Didelphis*. The branch leading to *Hyladelphys* is very long in most molecular reconstructions of didelphid anagenesis (e.g., fig. 33), suggesting an ancient history of independent evolution accompanied by extinction of transitional forms; the same conclusion is suggested by its uniquely reduced milk dentition and by characters of the postcranial skeleton (Flores, 2009). In effect, excluding *Hyladelphys* from Didelphinae simplifies the diagnosis of the latter clade and provides a new higher taxon to accommodate fossil relatives of the former, should any be discovered.

Hyladelphys Voss et al., 2001
Figure 40

CONTENTS: **kalinowskii** Hershkovitz, 1992.

MORPHOLOGICAL DESCRIPTION: Combined adult length of head and body ca. 75–95 mm; adult weight ca. 10–20 g. Rhinarium with two ventrolateral grooves on each side of median sulcus; dark circumocular mask
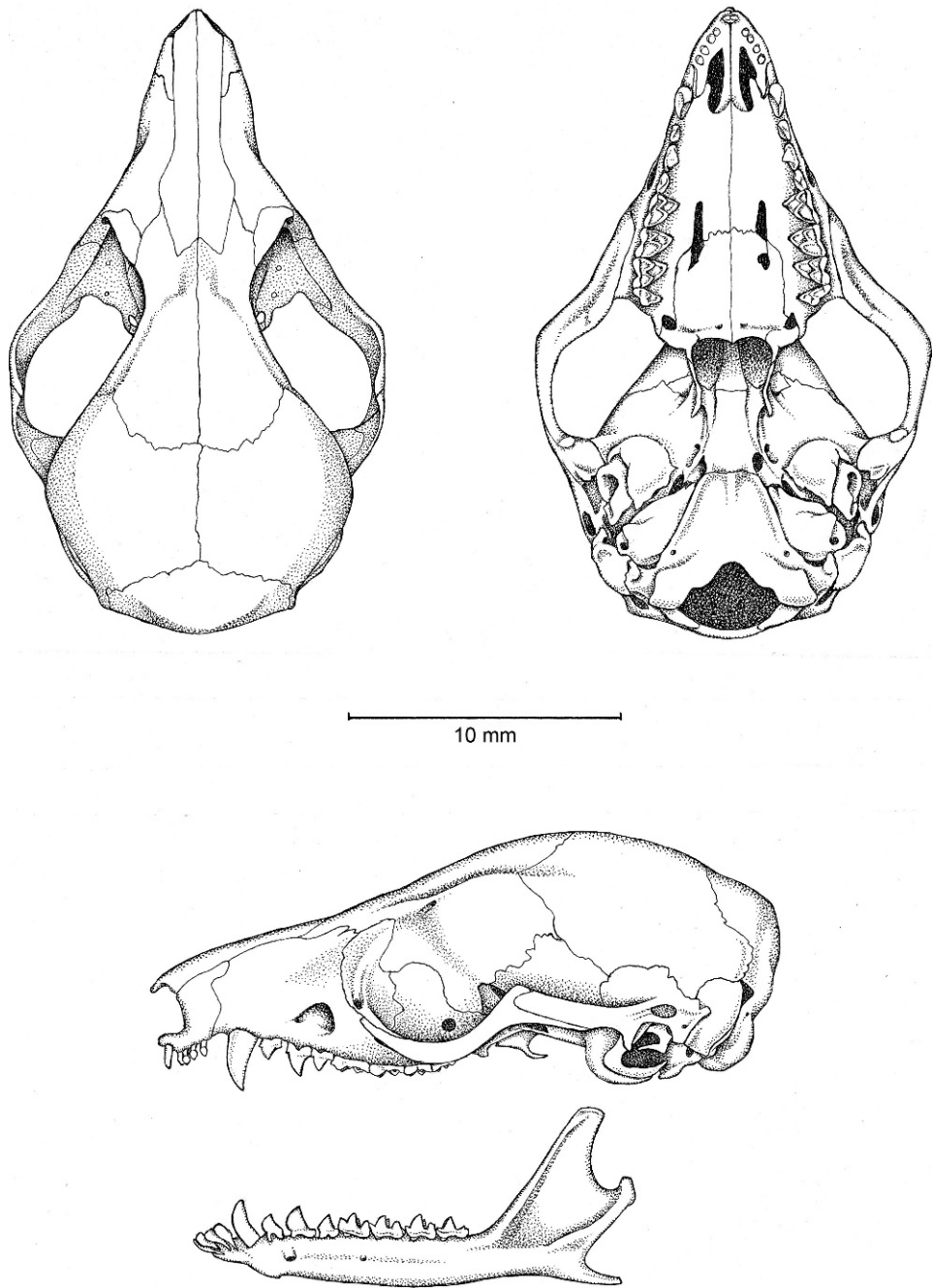
Fig. 40. *Hyladelphys kalinowskii* (based on AMNH 267338, an adult male from Paracou, French Guiana).

present, extending posteriorly from mystacial region to base of ear on each side of face; pale supraocular spot absent; dark midrostral stripe absent; throat gland absent. Dorsal pelage unpatterned reddish-brown with dark-gray hair bases; dorsal guard hairs short and inconspicuous; ventral fur self-white. Manus paraxonic (dIII = dIV); manual claws relatively large, strongly recurved, and slightly longer than fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar epithelium smooth or sparsely tubercular; carpal tubercles absent. Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel naked. Pouch absent; mammae 2–0–2 = 4, all abdominal-inguinal; cloaca present. Tail much longer than combined length of head and body, slender and muscular (not incrassate), and apparently naked (without a conspicuously furred base); *caudal scales in both annular and spiral series*, each scale with three subequal bristle-like hairs emerging from distal margin; ventral caudal surface modified for prehension distally, with apical pad bearing dermatoglyphs.

Premaxillary rostral process absent. Nasals long, extending anteriorly above I1 (concealing most of nasal orifice from dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. Lacrimal foramina exposed laterally on or near anterior orbital margin, one or two on each side. *Orbits very large*; *interorbital region strongly convergent anteriorly*, *with beaded dorsolateral margins*; postorbital processes absent. Left and right frontals and parietals separated by persistent median sutures. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest absent. Petrosal not exposed laterally through fenestra in parietal-squamosal suture (fenestra absent). Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae present; palatine and maxillary fenestrae absent; posterolateral palatal foramina small, not extending anteriorly between M4 protocones. Posterior palatal morphology more *Didelphis*-like than *Caluromys*-like (with moderately well-developed posterolateral corners, the internal choanae distinctly constricted behind). Max-illary and alisphenoid bones not in contact on floor of orbit (widely separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process smoothly globular, without anteromedial process or posteromedial lamina (secondary foramen ovale absent), and not in contact with rostral tympanic process of petrosal. Anterior limb of ectotympanic suspended directly from basicranium. Stapes triangular with large obturator foramen. Fenestra cochleae exposed, not concealed by rostral and caudal tympanic processes of petrosal. Paroccipital process small and adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present.

One or two mental foramina present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 asymmetrical (''incisiform''), with much longer anterior than posterior cutting edges. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple, without accessory cusps. First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; second upper premolar (P2) much taller than P3; P3 with both anterior and posterior cutting edges; *milk premolar (dP3) very small*, *vestigial*, *and lacking distinct occlusal features*. Upper molars not strongly carnassialized (postmetacristae only slightly longer than postprotocristae); relative widths M1 < M2 < M3 > M4; centrocrista weakly inflected labially on M1–M3; ectoflexus indistinct on M1, shallow on M2, distinct on M3; anterolabial cingulum continuous with preprotocrista (complete anterior cingulum present) on M3; postprotocrista without carnassial notch. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. Lower canine (c1) erect, acutely pointed, and simple (without a posterior accessory cusp). Second lower premolar (p2) taller than p3; *lower milk premolar (dp3) small*, *vestigial*, *and lacking distinct occlusal features*. Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid taller than hypoconulid on m1–m3.

DISTRIBUTION: Currently known from fewer than a dozen specimens, *Hyladelphys* has been reported from just nine localities in the rainforested lowlands of eastern Peru, central Amazonian Brazil, southern Guyana, and French Guiana (Astúa, 2007). Extrapolating from these scanty data is obviously problematic, but it would not be surprising to find this elusive taxon anywhere in Amazonia.

REMARKS: High levels of molecular divergence between sequenced specimens of *Hyladelphys* from French Guiana and Peru, together with geographic variation in morphological characters, suggest that additional species remain to be described in this genus (Jansa and Voss, 2005).

Subfamily Didelphinae Gray, 1821

CONTENTS: Marmosini, Metachirini, Didelphini, and Thylamyini.

DIAGNOSIS: Members of this clade uniquely differ from other didelphids by lacking an anterior cutting edge on P3 (the third upper premolar is double bladed in all basal didelphids). In addition, Didelphinae differs from Glironiinae by having a caudal dorsum that is macroscopically naked, at least near the tip; an unpaired median teat; well-developed posterolateral palatal corners; and postorbital processes that (when present) are formed only by the frontals. Didelphinae additionally differs from Caluromyinae by having a shorter fourth manual digit (dIII is subequal to or longer than dIV), an incompletely ossified palate (maxillopalatine and sometimes other fenestrae are invariably present), transverse canal foramina, a wide gap between the alisphenoid tympanic process and the rostral tympanic process of the petrosal, an acute and strongly inflected mandibular angle, an upper canine alveolus that lies within the premaxillary-maxillary suture, a nonvestigial P1, a larger P3 (subequal to or taller than P2), and a distinct ectoflexus on M3. Didelphinae additionally differs from Hyladelphinae by having an unpaired median teat, nonvestigial milk teeth, and a larger P3 (subequal to or taller than P2).

REMARKS: The monophyly of Didelphinae is strongly supported by all analyses of BRCA1 sequences (fig. 31), concatenated sequence data from five genes (fig. 33), and combined (nonmolecular + molecular) data when *Chacodelphys* is excluded (fig. 35). Subfamilial monophyly is also supported by a uniquely shared insertion (not coded for phylogenetic analysis) at the BRCA1 locus (fig. 31). However, only two morphological traits optimize as unambiguous synapomorphies of Didelphinae: an unpaired median teat and a strongly labially inflected centrocrista (subsequently reversed in Didelphini; appendix 5). In addition to genera referred to the tribes named above, the genus †*Hyperdidelphys* (here unassigned to tribe) clearly belongs to this subfamily based on characters described and illustrated by Goin and Pardiñas (1996) and others subsequently scored for phylogenetic analysis by D.A. Flores and the senior author.

Tribe Marmosini Hershkovitz, 1992

CONTENTS: *Marmosa*, *Monodelphis*, †*Thylatheridium*, and *Tlacuatzin*.

DIAGNOSIS: Marmosines can be distinguished from other members of the subfamily Didelphinae by lacking a pouch (present in all Didelphini), by lacking an anteromedial bullar process spanning the transverse canal foramen (present in Metachirini and most Thylamyini), by lacking a fenestra in the squamosal-parietal suture (present in most Thylamyini), and by having the supraoccipital form part of the dorsal margin of the foramen magnum (absent in adult Metachirini and most adult Didelphini).

REMARKS: The monophyly of Marmosini as construed herein is strongly supported by all analyses of BRCA1 (fig. 31), vWF (fig. 32), concatenated sequence data from five genes (fig. 33), and our combined (nonmolecular + molecular) dataset excluding *Chacodelphys* (fig. 35). However, no morphological trait optimizes as an unambiguous synapomorphy of this molecularly robust clade. Instead, all of the diagnostic features listed above appear to be plesiomorphic within the subfamily Didelphinae.

Although the name Marmosini was used by Reig et al. (1985, 1987) it was not accompanied by an explicit statement of taxonomically differentiating characters. To

the best of our knowledge, the first family-group name based on *Marmosa* is technically available from Hershkovitz (1992b). An alternative name for this clade is Monodel-phini, which McKenna and Bell (1997) attributed to Talice et al. (1961). However, Talice et al. did not mention any characters purported to differentiate Monodelphini from other didelphids, so their name is unavailable (ICZN, 1999: Article 13). To the best of our knowledge, the first family-group name based on *Monodelphis* is also available from Hershkovitz (1992b). As first revisors in the sense of the Code (ICZN, 1999: Article 24), we select Marmosini Hershkovitz, 1992, to have precedence over Monodelphini Hershkovitz, 1992.

Our reluctance to recognize any subtribal distinction between *Marmosa* and *Monodelphis* is based on the uncertain position of *Tlacuatzin*, which is not convincingly resolved despite the large amount of data at hand (>2000 parsimony-informative characters; table 12). In the event that a sister-group relationship between *Marmosa* and *Tlacuatzin* (weakly indicated by supermatrix analyses; figs. 33–36) were strongly supported by some future dataset, it would then make sense to recognize one subtribe (e.g., Marmosina) for those taxa and another (Monodelphina) for *Monodelphis* and †*Thylatheridium*. Although it seems indisputable that *Monodelphis* and †*Thylatheridium* are closely related (Goin and Rey, 1997), we note that this hypothesis has yet to be tested analytically, nor is it certainly known whether or not these taxa are reciprocally monophyletic.[25]

Marmosa Gray, 1821
Figure 41

CONTENTS: We recognize two subgenera, *Marmosa* Gray, 1821, and *Micoureus* Lesson, 1842 (see Remarks, below).

The subgenus *Marmosa* contains **andersoni** Pine, 1972; **lepida** Thomas, 1888 (including

grandis Tate, 1931); **mexicana** Merriam, 1897 (including *mayensis* Osgood, 1913; *savannarum* Goldman, 1917; and *zeledoni* Goldman, 1917); **murina** Linnaeus, 1758 (including *bombascarae* Anthony, 1922; *chloe* Thomas, 1907; *dorsigera* Linnaeus, 1758; *duidae* Tate, 1931; *guianensis* Kerr, 1792; *klagesi* J.A. Allen, 1900; *macrotarsus* Wagner, 1842; *madeirensis* Cabrera,. 1913; *maranii* Thomas, 1924; *meridionalis* Miranda-Ribeiro, 1936; *moreirae* Miranda-Ribeiro, 1936; *muscula* Cabanis, 1848; *parata* Thomas, 1911; *roraimae* Tate, 1931; *tobagi* Thomas, 1911; and *waterhousei* Tomes, 1860); **quichua** Thomas, 1899 (including *musicola* Osgood, 1913); **robinsoni** Bangs, 1898 (including *casta* Thomas, 1911; *chapmani* J.A. Allen, 1900; *fulviventer* Bangs, 1901; *grenadae* Thomas, 1911; *isthmica* Goldman, 1912; *luridavolta* Goodwin, 1961; *mimetra* Thomas, 1921; *mitis* Bangs, 1898; *nesaea* Thomas, 1911; *pallidiventris* Osgood, 1912; *ruatanica* Goldman, 1911; and *simonsi* Thomas, 1899); **rubra** Tate, 1931; **tyleriana** Tate, 1931 (including *phelpsi* Tate, 1939); and **xerophila** Handley and Gordon, 1979.

The subgenus *Micoureus* contains **alstoni** J.A. Allen, 1900 (including *nicaraguae* Thomas, 1905); **constantiae** Thomas, 1904 (including *budini* Thomas, 1920); **demerarae** Thomas, 1905 (including *areniticola* Tate, 1931; *domina* Thomas, 1920; *esmeraldae* Tate, 1931; *limae* Thomas, 1920; and *meridae* Tate, 1931); **paraguayana** Tate, 1931 (including *cinerea* Temminck, 1824 [preoccupied]); **phaea** Thomas, 1899 (including *perplexa* Anthony, 1922); and **regina** Thomas, 1898 (including *germana* Thomas, 1904; *mapiriensis* Tate, 1931; *parda* Tate, 1931; *rapposa* Thomas, 1899; and *rutteri* Thomas, 1924).

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body ca. 100–210 mm; adult weight ca. 20–170 g. Rhinarium with two ventrolateral grooves on each side of median sulcus; dark circumocular mask present; pale supraocular spot absent; dark midrostral stripe absent; throat gland absent in some species (e.g., *M. murina*) but present in adult males of other species (e.g., *M. mexicana*). Dorsal pelage unpatterned, superficially brownish, reddish, or grayish, but dorsal hair bases always dark gray; dorsal guard hairs short and inconspicuous;

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[25] In fact, it has been suggested that they are not: "Considero que *Thylatheridium* es un género derivado, en el Plioceno inferior, de una de las especies de *Monodelphis* que, ante posibilidades ecológicas favorables, aceleró su ritmo evolutivo, apartándose rápidamente de sus congéneres de evolución lenta …" (Reig, 1958: 90).
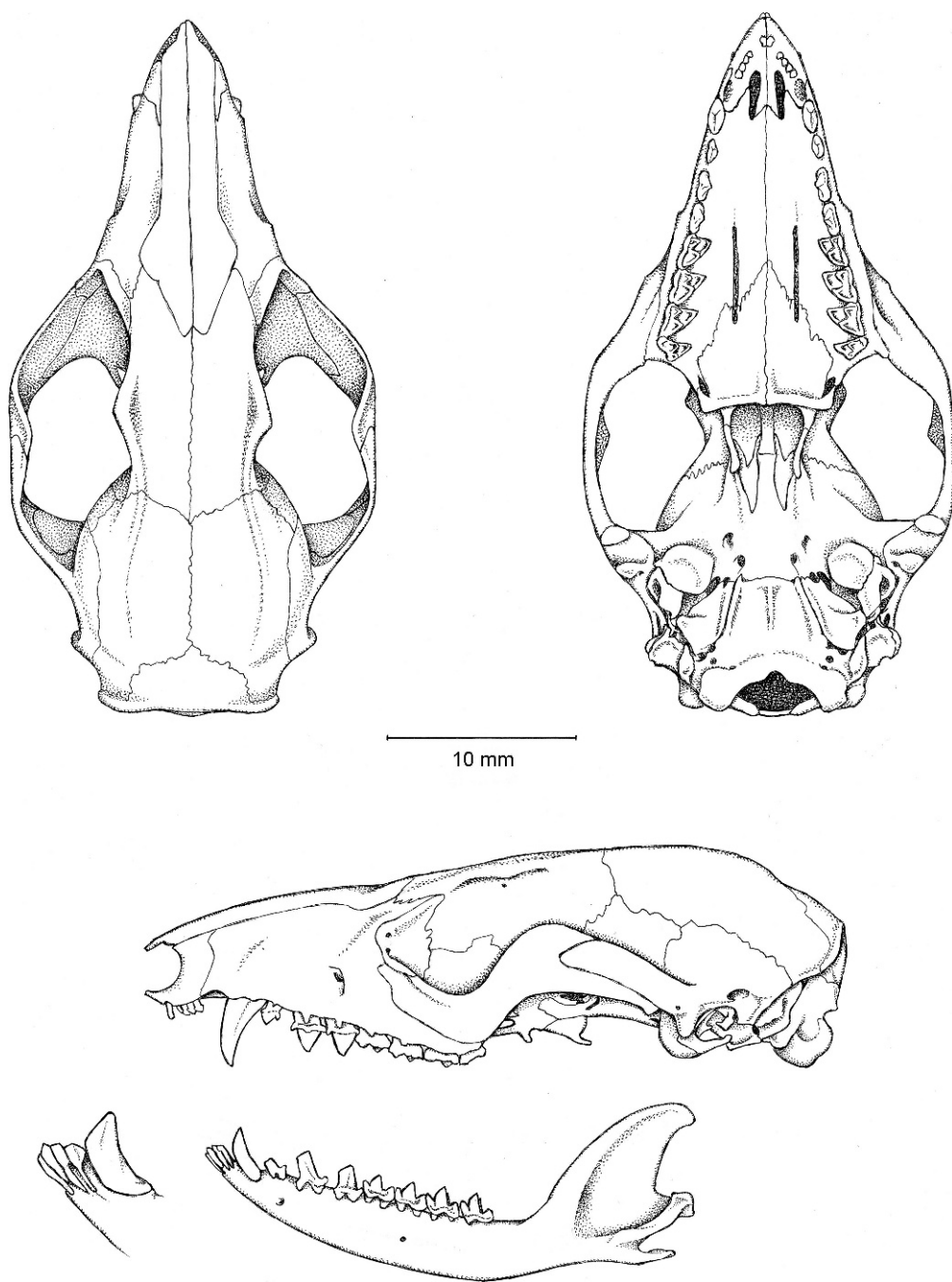
10 mm

Fig. 41.   *Marmosa murina* (based on AMNH 267368, an adult of unknown sex from Paracou, French Guiana). The inset shows the morphology of the unworn lower canine (with flattened apical blade; based on AMNH 266416, a young adult female from the same locality).

ventral fur superficially whitish, yellowish, or orange, wholly or partly gray based (apparently never completely self-colored). Manus paraxonic (dIII = dIV); manual claws about as long as or slightly longer than fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar epithelium smooth or sparsely covered with flattened tubercles (never densely tuberculate); carpal tubercles completely absent in some species (e.g., *M. murina*), or only lateral carpal tubercles present in adult males (e.g., in *M. lepida*), or both medial and lateral carpal tubercles present in adult males (e.g., in *M. robinsoni*). Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel macroscopically naked, but all or part of heel covered with microscopic hairs in some species (e.g., *M. rubra*). Pouch absent; mammae 3–1–3 = 7 (e.g., in *M. lepida*) to 7–1–7 = 15 (in *M. mexicana*), all abdominal-inguinal; cloaca present. Tail always substantially longer than combined length of head and body; slender and muscular (not incrassate); without a conspicuously furred base in some species (e.g., *M. murina*) or tail base conspicuously furred to about the same extent dorsally as ventrally (e.g., in *M. paraguayana*); naked caudal integument unicolored (all dark) in most species but mottled distally with white spots and/or white tipped in others (e.g., *M. paraguayana*); caudal scales in spiral series (e.g., in *M. murina*) or in both spiral and annular series (e.g., in *M. mexicana*), each scale usually with three subequal bristlelike hairs emerging from distal margin; ventral caudal surface always modified for prehension distally, with apical pad bearing dermatoglyphs.

Premaxillary rostral process present in most species (absent in *M. xerophila*). Nasals long, extending anteriorly beyond I1 (concealing nasal orifice in dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. Lacrimal foramina usually two on each side, exposed to lateral view on or near anterior orbital margin. Supraorbital margins with distinct beads or prominent crests; *flattened, triangular postorbital processes usually present in fully mature adults* but substantially larger in some species than in others (absent or indistinct in *M. rubra*).

Left and right frontals and parietals separated by persistent median sutures. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest never developed. Petrosal usually not exposed laterally through fenestra in parietal-squamosal suture (fenestra absent).[26] Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae present; palatine fenestrae absent in most species (but consistently present in some; e.g., *M. mexicana*); maxillary fenestrae absent; posterolateral palatal foramina small, never extending anteriorly between M4 protocones; posterior palatal morphology conforms to *Didelphis* morphotype (with well-developed lateral corners, the choanae constricted behind). Maxillary and alisphenoid not in contact on floor of orbit (separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process smoothly globular, without anteromedial process or posteromedial lamina enclosing the maxillary nerve (secondary foramen ovale usually absent),[27] and not in contact with rostral tympanic process of petrosal. Anterior limb of ectotympanic suspended directly from basicranium. Stapes usually triangular, with large obturator foramen (microperforate and imperforate stapes occur as rare variants in several species). Fenestra cochleae exposed in most species, but fenestra concealed in sinus formed by caudal and rostral tympanic processes of petrosal in *M. rubra*. Paroccipital process small, rounded, adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina usually present on lateral surface of each hemimandible (one foramen or three foramina occur as rare,

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[26] We observed a fenestra between the squamosal and parietal on just two skulls, both of which are examples of *Marmosa lepida*. This trait occurs bilaterally on MNHN 1998-306 (from French Guiana) and unilaterally on MVZ 155245 (from Peru). All of the other six specimens of *M. lepida* that we examined for this character resemble other *Marmosa* spp. in lacking these openings.

[27] Two out of 12 examined specimens of *Marmosa regina* have secondary foramina ovales formed by posteromedial bullar laminae: this trait occurs bilaterally on MVZ 190326 and unilaterally on MVZ 190328.

usually unilateral variants in some species); angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal (''premolariform''), with subequal anterior and posterior cutting edges, and increasing in length (mesiodistal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple (without accessory cusps in most species) or with posterior accessory cusp only (in *M. lepida*). First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; second and third upper premolars (P2 and P3) subequal in height; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars moderately carnassialized (postmetacristae are visibly longer than postprotocristae); relative widths usually M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus indistinct or absent on M1, shallow but usually distinct on M2, and consistently deep on M3; anterolabial cingulum continuous with preprotocrista (complete anterior cingulum present) on M3. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. *Unworn lower canine (c1) usually semiprocumbent, with flattened bladelike apex, with or without distinct posterior accessory cusp*. Second lower premolar (p2) taller than p3; lower milk premolar (dp3) trigonid incomplete (bicuspid). Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid much taller than hypoconulid on m1–m3.

DISTRIBUTION: Species of *Marmosa* collectively range from the Mexican state of Tamaulipas southward throughout most of Central and tropical South America to Bolivia, Paraguay, and northern Argentina (Hall, 1981; Creighton and Gardner, 2008b; Gardner and Creighton, 2008b). Although most species inhabit lowland rainforests, a few are restricted to dry habitats (e.g., *M. xerophila*; Handley and Gordon, 1979) and some species of the subgenus *Micoureus* occur in montane rainforest at elevations in excess of 2000 m (e.g., *M. mapiriensis* sensu Tate, 1933: 76).

REMARKS: The monophyly of *Marmosa* (including *Micoureus*) is supported by sequence data from five genes analyzed separately (figs. 28–32), in tandem (fig. 33), and in combination with nonmolecular characters (figs. 35, 36); generic monophyly is also supported by a uniquely shared insertion at the BRCA1 locus (fig. 31). Only a single morphological character, the possession of a rostral process of the premaxillae, optimizes as an unambiguous generic synapomorphy (appendix 5), but even this weak phenotypic evidence is compromised by the absence of a rostral process in *M. xerophila*, a species that we did not score for this study.

No published phylogenetic analysis supports the reciprocal monophyly of *Marmosa* and *Micoureus*, both of which have been treated as valid genera by recent authors (e.g., Gardner, 2005; Creighton and Gardner, 2008b; Gardner and Creighton, 2008b). Instead, species of *Micoureus* have consistently been recovered as nested within a paraphyletic group of *Marmosa* species (Kirsch and Palma, 1995; Voss and Jansa, 2003; Jansa and Voss, 2005; Steiner et al., 2005; Jansa et al., 2006; Gruber et al., 2007). Obviously, there are several alternative taxonomic solutions to this problem.

One solution would be to treat *Micoureus* as a junior synonym of *Marmosa* without recognizing any subgenera of the latter. Another would be to recognize *Micoureus* as a subgenus of *Marmosa* and to name new subgenera for other monophyletic clusters of *Marmosa* species. A third would be to recognize *Micoureus* as a genus and to describe new genera as needed to make *Marmosa* monophyletic. Unfortunately, the first option would result in the loss of a useful name (*Micoureus*, see below), whereas the second and third options are not currently workable because many species of *Marmosa* have not been included in any phylogenetic analysis, and their relationships are correspondingly obscure. Our interim solution is to move the currently intractable problem of paraphyly from the generic to the subgeneric level. Although taxonomic rank is biologically arbitrary, it affects binomial usage, which should be conformable with phylogenetic relationships insofar as these are known. In effect, because the use of generic names is obligatory under the current Linnaean system, it is crucial that genera be monophyletic.

The monophyly of *Micoureus* has been supported in every sequencing study to date that has included two or more exemplar species (e.g., Patton et al., 1996; Voss and Jansa, 2003; this study), and it may often be appropriate to indicate this fact in contradistinction to the paraphyly of the subgenus *Marmosa*. Where appropriate, this can be achieved using double quotes for the latter, as for the species *Marmosa* (''*Marmosa*'') *lepida* as contrasted with *Marmosa* (*Micoureus*) *demerarae*. Predictably, the subgeneric classification of *Marmosa* will be refined as future studies based on denser taxon sampling yield increasingly resolved estimates of relationships within this speciose group.

Most of the species herein referred to *Marmosa* have not been revised since Tate (1933), and some currently recognized synonymies are the result of uncritical lumping by subsequent authors (e.g., Hershkovitz, 1951; Cabrera, 1958). Recent analyses of both mtDNA sequence data (e.g., by Patton et al., 2000; Patton and Costa, 2003) and morphological characters (Rossi, 2005) suggest that several nominal taxa currently listed as synonyms (e.g., of *M. demerarae*, *M. murina*, and *M. robinsoni*) are probably valid species. Therefore, significant changes to the species-level taxonomy of *Marmosa* should be expected soon.

Monodelphis Burnett, 1830
Figure 42

CONTENTS: ***adusta*** Thomas, 1897 (including *melanops* Goldman, 1912); ***americana*** Müller, 1776 (including *brasiliensis* Erxleben, 1777; *brasiliensis* Daudin, 1802; *trilineata* Lund, 1840; and *tristriata* Illiger, 1815); ***brevicaudata*** Erxleben, 1777 (including *brachyuros* Schreber, 1777; *dorsalis* J.A. Allen, 1904; *hunteri* Waterhouse, 1841; *orinoci* Thomas, 1899; *sebae* Gray, 1827; *surinamensis* Zimmermann, 1780; *touan* Bechstein, 1800; *touan* Shaw, 1800; *touan* Daudin, 1802; and *tricolor* E. Geoffroy, 1803); ***dimidiata*** Wagner, 1847 (including *fosteri* Thomas, 1924); ***domestica*** Wagner, 1842 (including *concolor* Gervais, 1856); ***emiliae*** Thomas, 1912; ***glirina*** Wagner, 1842; ***handleyi*** Solari, 2007; ***iheringi*** Thomas, 1888; ***kunsi*** Pine, 1975; ***maraxina*** Thomas, 1923; ***osgoodi*** Doutt, 1938; ***palliolata*** Osgood, 1914; ***peruviana*** Osgood, 1913; ***reigi*** Lew and Pérez-Hernández, 2004; ***ronaldi*** Solari, 2004; ***rubida*** Thomas, 1899; ***scalops*** Thomas, 1888; ***sorex*** Hensel, 1872 (including *henseli* Thomas, 1888; *itatiayae* Miranda-Ribeiro, 1936; *lundi* Matschie, 1916; and *paulensis* Vieira, 1950); ***theresa*** Thomas, 1921; ***umbristriatus*** Miranda-Ribeiro, 1936; and ***unistriatus*** Wagner, 1842.

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body ca. 70–200 mm; adult weight ca. 15–150 g. *Rhinarium with one ventrolateral groove on each side of median sulcus*; *dark circumocular mask absent*; pale supraocular spot absent; dark midrostral stripe absent; throat gland present in adult males of most species but possibly absent in some (e.g., *M. theresa*). Dorsal pelage coloration highly variable, but dorsal hair bases always dark gray; dorsal guard hairs short and inconspicuous; ventral fur self-colored or gray based, highly variable in surface pigmentation. *Manus mesaxonic (dIII > dIV)*; *manual claws very long, extending well beyond fleshy apical pads of digits*; dermatoglyph-bearing manual plantar pads present, but pads small and dermatoglyphs sometimes indistinct; central palmar epithelium smooth or sparsely tuberculate; carpal tubercles absent in both sexes. Pedal digits unwebbed; *pedal digit III longer than digit IV*; plantar surface of heel naked. Pouch absent; mammae 4–1–4 = 9 (all abdominal-inguinal; e.g., in *M. brevicaudata*) to 13–1–13 = 27 (including pectoral teats; e.g., in *M. sorex*); cloaca present. *Tail much shorter than combined length of head and body*; thick but muscular, not incrassate; tail conspicuously furred at base to about the same extent dorsally as ventrally (e.g., in *M. emiliae*), or caudal fur extends farther dorsally than ventrally (e.g., *M. brevicaudata*), or tail base unfurred (e.g., *M. peruviana*); *unfurred caudal surfaces covered with macroscopic bristlelike hairs, not naked-appearing*; *caudal scales often inapparent but always in annular series*; relationship between caudal scales and hairs usually obscure, but subequal hairs usually arranged in triplets; *ventral caudal surface not modified for prehension*.

Premaxillary rostral process absent. Nasals long, extending anteriorly beyond I1 (con-
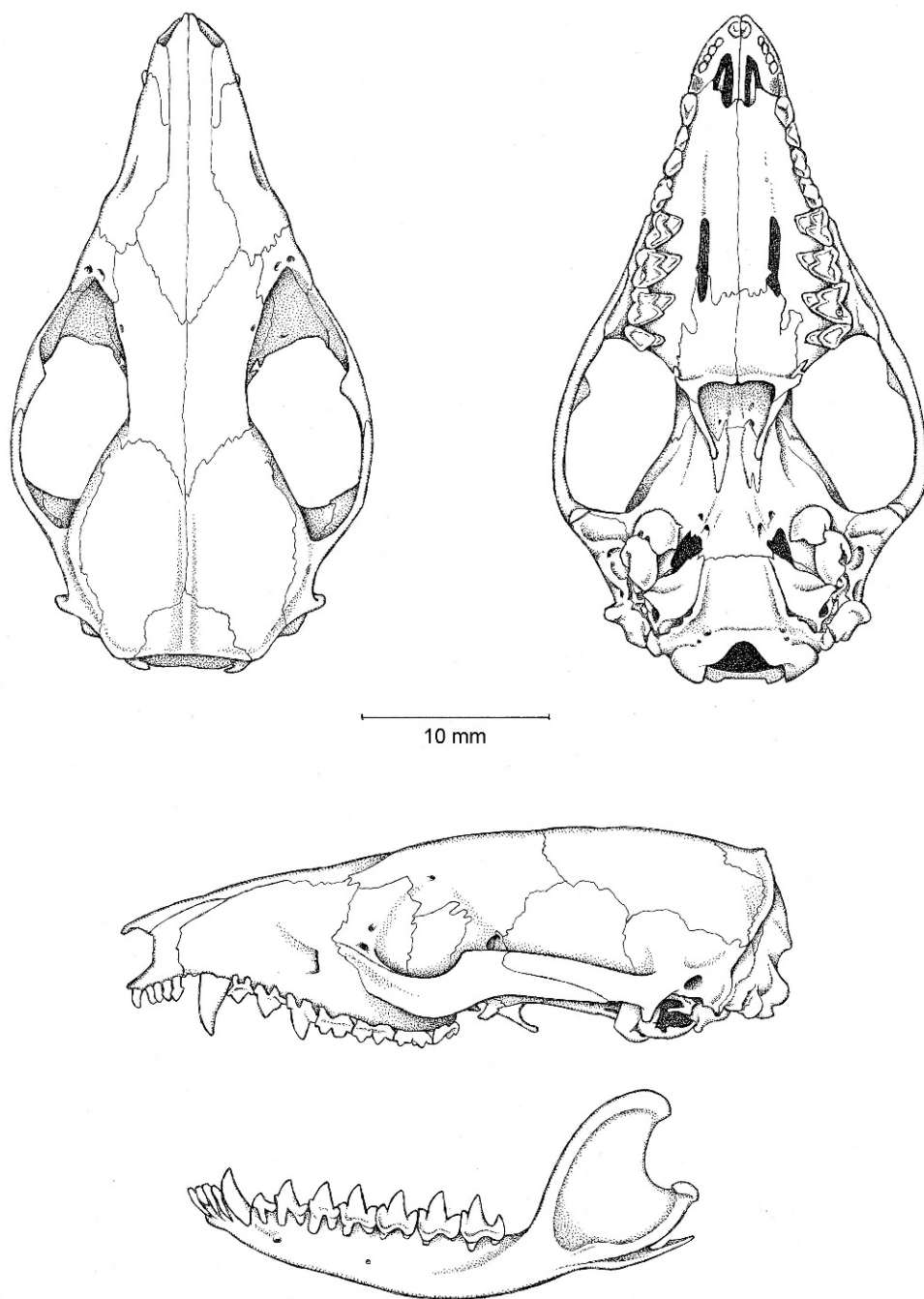
Fig. 42.   *Monodelphis brevicaudata* (based on AMNH 257203, an adult female from San Ignacio de Yuruaní, Bolívar, Venezuela).

cealing nasal orifice from dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture. *Maxillary turbinals (viewed through the nasal orifice) simple or sparsely ornamented scrolls, not elaborately branched.* Lacrimal foramina (usually two on each side) prominently exposed on orbital margin or on face anterior to orbit. Orbits small, interorbital region more or less parallel sided (usually without conspicuous constrictions); supraorbital margins smoothly rounded, without beads or distinct postorbital processes (but blunt, indistinct processes occasionally developed in large specimens of some species; e.g., *M. emiliae*). Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest absent (e.g., in *M. theresa*) or small (usually not extending to frontals; e.g., in *M. brevicaudata*). Petrosal not exposed laterally through fenestra in parietal-squamosal suture (fenestra absent). Parietal-mastoid contact usually present (interparietal seldom contacts squamosal).

Maxillopalatine fenestrae present; palatine fenestrae usually absent; maxillary fenestrae absent; posterolateral palatal foramina small, not extending anteriorly between M4 protocones; posterior palatal morphology conforms to *Didelphis* morphotype (with moderately well-developed lateral corners, the choanae somewhat constricted behind). *Maxillary and alisphenoid in contact on floor of orbit (not separated by palatine).* Transverse canal foramen present. Alisphenoid tympanic process smoothly globular; posteromedial lamina forming secondary foramen ovale present in some species (e.g., *M. theresa*) or lamina and secondary foramen ovale absent (e.g., in *M. brevicaudata*). Anterior limb of ectotympanic suspended directly from basicranium. Stapes triangular with large obturator foramen (e.g., in *M. brevicaudata*), or columellar and microperforate or imperforate (e.g., in *M. peruviana*). Fenestra cochleae exposed in most species, but fenestra concealed in sinus formed by rostral and caudal tympanic processes of petrosal in *M. emiliae*. Paroccipital process small, rounded, and adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal ("premolariform"), with subequal anterior and posterior cutting edges, and usually increasing in length (mesiodistal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 usually simple (without accessory cusps), but small posterior accessory cusp sometimes present (e.g., in *M. peruviana*). First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; *third upper premolar (P3) taller than P2*; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars highly carnassialized (postmetacristae much longer than postprotocristae); relative widths consistently M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus shallow on M1, deeper on M2, and consistently deep on M3; *anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3*. Last upper tooth to erupt is P3 in some species (e.g., *M. peruviana*), or P3 and M4 erupt simultaneously (e.g., in *M. brevicaudata*).

Lower incisors (i1–i4) with distinct lingual cusps. *Second lower premolar (p2) subequal in height to p3* (e.g., in *M. brevicaudata*), *or p3 taller than p2* (e.g., in *M. emiliae*); lower milk premolar (dp3) trigonid usually complete (tricuspid). *Hypoconid lingual to protoconid (not labially salient) on m3*; hypoconulid twinned with entoconid on m1–m3; *entoconid subequal to or smaller than hypoconulid on m1–m3*.

DISTRIBUTION: Species of *Monodelphis* occur in lowland and montane rain forests and dry forests from eastern Panama throughout most of tropical and subtropical South America to about 37°S in eastern Argentina (see range maps in Pine and Handley, 2008); recorded elevations range from sea level to at least 2500 m (on the eastern slopes of the tropical Andes). The apparent absence of *Monodelphis* from the trans-Andean lowlands of western South America is noteworthy, but this is possibly an artifact of inadequate collecting; a representative of the *M. adusta* complex is rumored to occur along the Pacific littoral

of Colombia and northern Ecuador (Solari, 2007), but no specimen-based records have yet been published from that region.

REMARKS: The monophyly of *Monodelphis* vis-à-vis other Recent didelphids is convincingly supported by 10 nonmolecular characters (appendix 5); by a uniquely shared and unreversed deletion at the BRCA1 locus (fig. 31); and by sequence data from five genes analyzed separately (figs. 28–32), together (fig. 33), and in combination with morphology and karyotypes (figs. 35, 36).

Tlacuatzin Voss and Jansa, 2003
Figure 43

CONTENTS: **canescens** J.A. Allen, 1893 (including *gaumeri* Osgood, 1913; *insularis* Merriam, 1908; *oaxacae* Merriam, 1897; and *sinaloae* J.A. Allen, 1898).

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body ca. 110–160 mm; adult weight ca. 30–70 g. Rhinarium with two ventrolateral grooves on each side of median sulcus; dark circumocular mask present; pale supraocular spot absent; dark midrostral stripe absent; throat gland absent. Dorsal pelage unpatterned, usually pale gray or grayish brown; dorsal underfur gray; dorsal guard hairs short and inconspicuous; ventral fur self-whitish, -cream, or -buffy. Manus paraxonic (dIII = dIV); manual claws about as long as fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar epithelium sparsely tuberculate; adult males with well-developed lateral carpal tubercles but not medial carpal tubercles. Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel naked. Pouch absent; mammae 4–1–4 = 9 or 5–1–5 = 11, all abdominal-inguinal; cloaca present. Tail about as long as combined length of head and body, slender and muscular (not incrassate); body pelage present on basal 1/10 or less of tail; naked caudal integument uniformly grayish or faintly bicolored (darker dorsally than ventrally), occasionally parti-colored (with a whitish tip); caudal scales in annular series, each scale with three subequal bristle-like hairs emerging from distal margin; ventral caudal surface modified for prehension distally, with apical pad bearing dermatoglyphs.

Premaxillary rostral process absent. Nasals long, extending anteriorly beyond I1 (concealing nasal orifice from dorsal view), and usually widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. Lacrimal foramina visible in lateral view at or near anterior orbital margin, usually two on each side. Flattened, triangular postorbital processes well developed in fully adult specimens. Left and right frontals and parietals separated by persistent median sutures. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact. Sagittal crest absent. Petrosal not exposed laterally through fenestra in parietal-squamosal suture (fenestra absent). Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae present; palatine fenestrae absent; *maxillary fenestrae present, usually opposite M2, sometimes partially confluent with maxillopalatine openings*; posterolateral palatal foramina small, not extending anteriorly between M4 protocones; posterior palatal morphology conforms to *Didelphis* morphotype (with well-developed lateral corners, the choanae constricted behind). Maxillary and alisphenoid not in contact on floor of orbit (separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process smoothly globular, without anteromedial process or posteromedial lamina enclosing extracranial course of mandibular nerve (secondary foramen ovale absent), and not in contact with rostral tympanic process of squamosal. Anterior limb of ectotympanic directly suspended from basicranium. *Stapes usually subtriangular and microperforate or imperforate* (rarely triangular with a large obturator foramen). Fenestra cochleae exposed, not concealed by rostral and caudal tympanic processes of petrosal. Paroccipital process of exoccipital small, rounded, adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal ("premolariform"), with subequal anterior and posterior cutting edges,
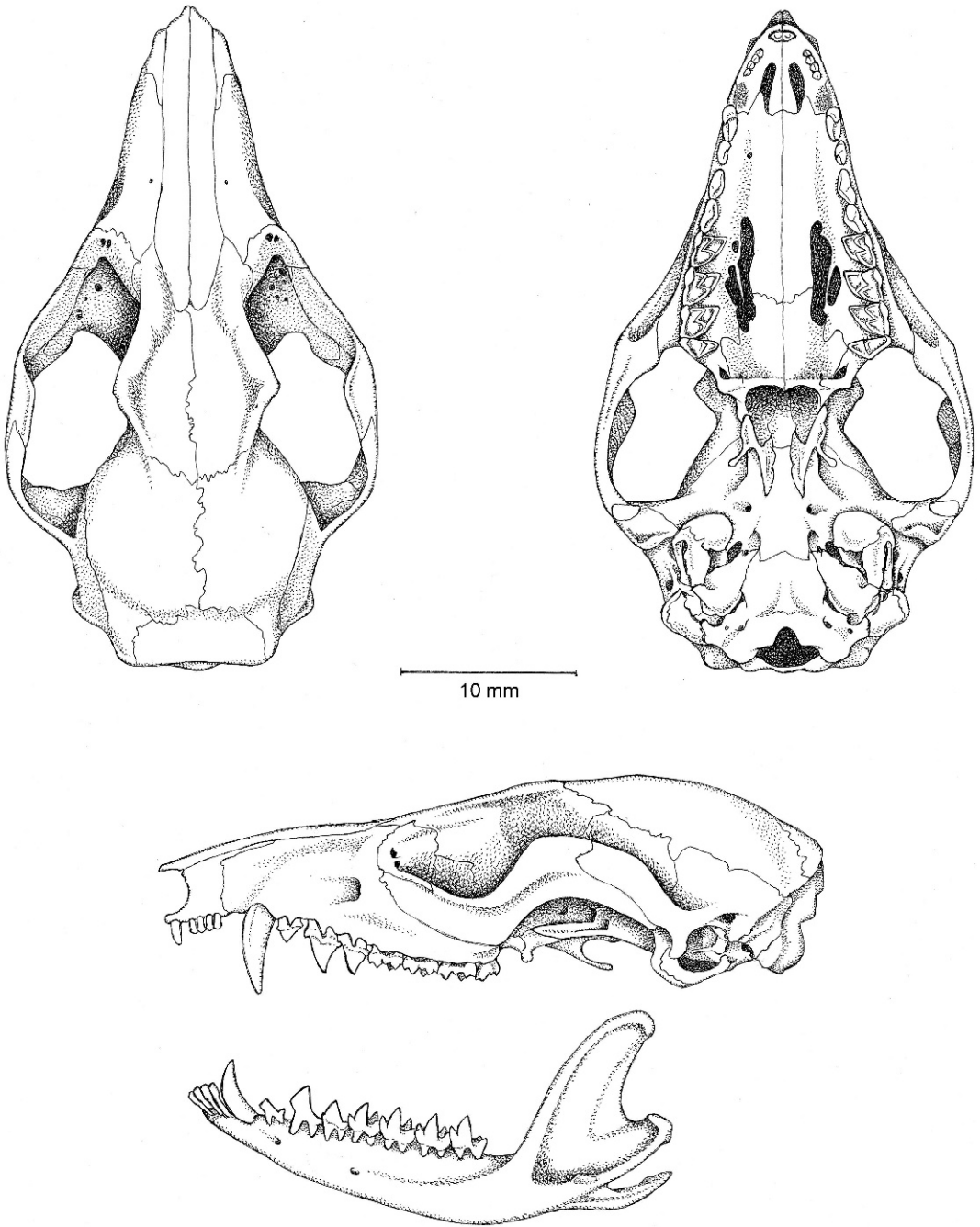
Fig. 43. *Tlacuatzin canescens* (based on primarily on USNM 511261, an adult female from Rancho Sapotito, Nayarit, Mexico; some dental details were reconstructed from USNM 125659, an adult male from Los Reyes, Michoacan, Mexico).

and subequal in length (mesiodistal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple, without accessory cusps. First upper premolar (P1) present, smaller than posterior premolars but well formed and not vestigial; second and third upper premolars (P2 and P3) subequal in height; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars moderately carnassialized (postmetacristae longer than postprotocristae); relative widths usually M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus usually absent on M1, shallow on M2, deep and distinct on M3; anterolabial cingulum continuous with preprotocrista (complete anterior cingulum present) on M3; postprotocrista without carnassial notch. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. Lower canine (c1) erect, acutely pointed, and simple (without a posterior accessory cusp). Second lower premolar (p2) taller than p3; lower milk premolar (dp3) with incomplete (usually bicuspid) trigonid. Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid taller than hypoconulid on m1–m2, usually subequal in height to hypoconulid on m3.

DISTRIBUTION: *Tlacuatzin* is apparently endemic to Mexico, where it occurs in tropical dry forests from Sonora southward (principally along the Pacific littoral and adjacent slopes of the coastal cordilleras) to Oaxaca and Chiapas; isolated populations also occur in the northern part of the Yucatan Peninsula and on the Tres Marías Islands (Hall, 1981; Wilson, 1991; Reid, 1997; Zarza et al., 2003).

Tribe Metachirini Hershkovitz, 1992

CONTENTS: *Metachirus*.
DIAGNOSIS: Metachirini is uniquely distinguished from other members of the subfamily Didelphinae (indeed, from all other didelphids) by contact between the frontal and squamosal on the lateral surface of the braincase.
REMARKS: Although *Metachirus* could logically be referred to the Didelphini, a new name would then be needed for the clade now awkwardly referred to in the literature as the "large $2n = 22$ opossums" (*Chironectes, Didelphis, Lutreolina, Philander*). Because many morphological characters unambiguously diagnose the latter group, whereas only a few diagnose the group that includes the large $2n = 22$ opossums plus *Metachirus* (see appendix 5), the present arrangement seems preferable. Additionally, because the branch leading to *Metachirus* is a long one (e.g., in fig. 33), we expect that fossils will eventually be found to occupy it, and that such discoveries will minimally disrupt the suprageneric nomenclature if a tribe is already available to accommodate them.

The name Metachirini was credited by Gardner and Dagosto (2008) to Reig et al. (1985), but no family-group name based on *Metachirus* fulfills the technical criteria for availability (ICZN, 1999: Article 13) prior to Hershkovitz (1992b), who effectively diagnosed Metachirinae in a key. By the Principle of Coordination (ICZN, 1999: Article 36), Metachirini is available with the same authorship and date.

Metachirus Burmeister, 1854
Figure 44

CONTENTS: **nudicaudatus** E. Geoffroy, 1803 (including *antioquiae* J.A. Allen, 1916; *colombianus* J.A. Allen, 1900; *bolivianus* J.A. Allen, 1901; *dentaneus* Goldman, 1912; *imbutus* Thomas, 1923; *infuscus* Thomas, 1923; *modestus* Thomas, 1923; *myosuros* Temminck, 1824; *personatus* Miranda-Ribeiro, 1936; *phaeurus* Thomas, 1901; and *tschudii* J.A. Allen, 1900).

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body ca. 250–300 mm; adult weight ca. 250–500 g. Rhinarium with one ventrolateral groove on each side of median sulcus; dark circumocular mask present, continuous with dark coronal fur; *pale supraocular spot present*; dark midrostral stripe absent; throat gland present in adult males. Dorsal pelage unpatterned, usually some shade of grayish or reddish brown; dorsal underfur gray; dorsal guard hairs short and inconspicuous; ventral fur self-whitish, -cream, or -buffy. Manus mesaxonic (dIII > dIV); manual claws shorter
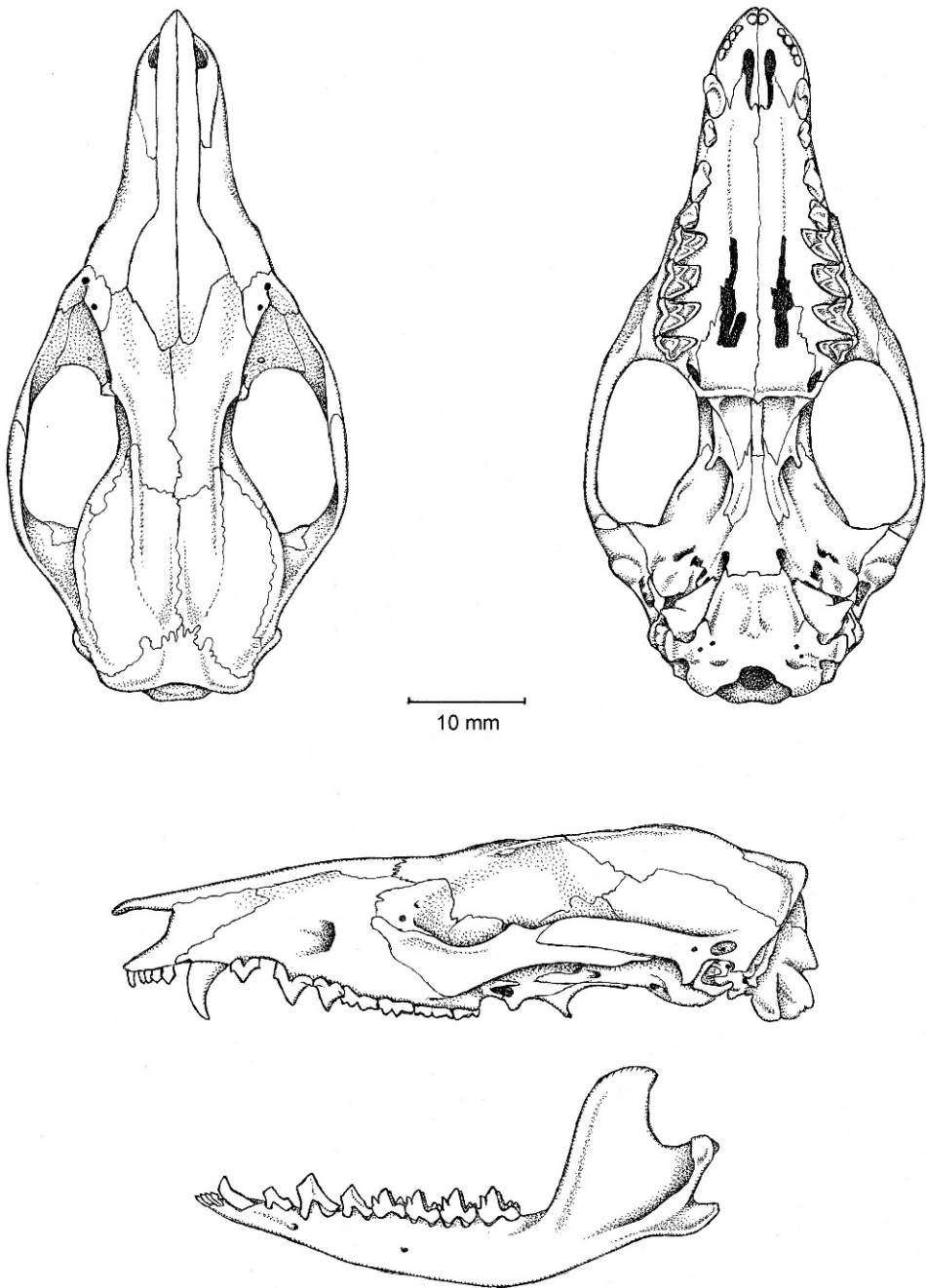
Fig. 44. *Metachirus nudicaudatus* (based on AMNH 267009, an adult male from Paracou, French Guiana).

than fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar epithelium smooth or sparsely tuberculate; carpal tubercles absent. Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel naked. Pouch absent; mammae 4–1–4 = 9, all abdominal-inguinal; cloaca present. Tail longer than

combined length of head and body, slender and muscular (not incrassate), unfurred except at base; naked caudal integument bicolored basally (brownish or grayish dorsally, paler ventrally), gradually becoming all pale distally; caudal scales in both annular and spiral series (neither pattern predominating), each scale with three subequal bristlelike hairs emerging from distal margin; ventral caudal surface not externally modified for prehension.

Premaxillary rostral process absent. Nasals long, extending anteriorly above or beyond I1 (concealing nasal orifice from dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. Two lacrimal foramina laterally exposed on each side on or just anterior to orbital margin. *Interorbital region very broad, with distinctly beaded supraorbital margins*; postorbital processes absent. Left and right frontals and parietals separated by persistent median sutures. *Frontal and squamosal in contact on lateral braincase (no parietal-alisphenoid contact).* Sagittal crest absent or weakly developed just anterior to occiput. Petrosal not exposed laterally through fenestra in parietal-squamosal suture (fenestra absent). Parietal-mastoid contact normally present (interparietal usually does not contact squamosal).

Maxillopalatine fenestrae present; palatine and maxillary fenestrae absent; posterolateral palatal foramina small, not extending anteriorly between M4 protocones; posterior palatal morphology conforms to *Didelphis* morphotype (with well-developed lateral corners, the choanae constricted behind). Maxillary and alisphenoid usually not in contact on floor of orbit (separated by palatine in most examined specimens). Transverse canal foramen present. Alisphenoid tympanic process laterally compressed (not globular), with anteromedial process enclosing extracranial course of mandibular nerve (secondary foramen ovale present), and not in contact with rostral tympanic process of petrosal. Anterior limb of ectotympanic suspended directly from basicranium. Stapes triangular with large obturator foramen. Fenestra cochleae usually exposed, not or incompletely concealed by rostral and caudal tympanic processes of petrosal. Paroccipital process large, erect, projecting ventrally (not adnate to petrosal). Dorsal margin of foramen magnum bordered by exoccipitals only, incisura occipitalis absent.

Two mental foramina present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal (''premolariform''), with subequal anterior and posterior cutting edges, and increasing in length (mesiodistal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple, without accessory cusps. First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; second and third upper premolars (P2 and P3) subequal in height; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars highly carnassialized (postmetacristae much longer than postprotocristae); relative widths M1 < M2 < M3 > M4 or M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus usually shallow on M1 and M2 but distinct on M3; anterolabial cingulum and preprotocrista usually discontinuous (anterior cingulum usually incomplete)[28] on M3; postprotocrista without carnassial notch. *Third upper premolar (P3) and M4 erupt simultaneously.*

Lower incisors (i1–i4) with distinct lingual cusps. Lower canine (c1) procumbent, with flattened bladelike anterior margin, but usually without a distinct posterior accessory cusp. Second lower premolar (p2) taller than p3; lower milk premolar (dp3) trigonid complete (tricuspid). Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid much taller than hypoconulid on m1–m3.

DISTRIBUTION: *Metachirus* is widely distributed in humid lowland and lower montane forests (usually below 2000 m) from Chiapas, Mexico (Medellín et al., 1992) to northern Argentina (Flores et al., 2007). Published distribution maps (e.g., Reid,

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[28] Because this character is normally quite constant within species, it is noteworthy that one specimen from Paracou, French Guiana (AMNH 266451), has a complete anterior cingulum whereas others from the same locality (e.g., AMNH 267362) have an incomplete anterior cingulum.

1997; Gardner and Dagosto, 2008) indicate several range disjunctions, but some of these may be artifacts of inadequate collecting effort in suitable habitats.

REMARKS: Although only a single species of *Metachirus* is currently regarded as valid, recent mtDNA sequencing studies have revealed deep molecular divergence (>10% at the mitochondrial cytochrome *b* locus; Patton et al., 2000; Patton and Costa, 2003) among supposedly conspecific geographic populations, and it seems likely that several of the names currently listed as junior synonyms of *M. nudicaudatus* will be resurrected as valid species by future revisionary studies.

Tribe Didelphini Gray, 1821

CONTENTS: *Chironectes*, *Didelphis*, *Lutreolina*, *Philander*, and †*Thylophorops*.

DIAGNOSIS: Members of the tribe Didelphini differ from all other members of the subfamily Didelphinae by their possession of a well-developed pouch, black-and-white marked tail, nasal tips that do not extend above I1, co-ossified frontals, well-developed sagittal crest, ectotympanic suspension via the malleus only, delayed eruption of M4, and lower incisors without a distinct lingual cusp.

REMARKS: The monophyly of Didelphini is strongly supported by most phylogenetic analyses published to date (e.g., Kirsch and Palma, 1995; Kirsch et al., 1997; Jansa and Voss, 2000, 2005; Voss and Jansa, 2003, this report; Steiner et al., 2005; Jansa et al., 2006; Gruber et al., 2007). The only exceptions appear to be primitive parsimony (''Wagner'') trees, unaccompanied by support statistics, that were based largely on dental characters (e.g., Reig et al., 1987: figs. 64–67). All of the diagnostic morphological features listed above, together with several other craniodental and karyotypic traits, optimize as unambiguous tribal synapomorphies (appendix 5). The monophyly of Didelphini is additionally supported by a uniquely shared deletion at the DMP1 locus (fig. 29), and by two uniquely shared deletions at the BRCA1 locus (fig. 31).

Chironectes Illiger, 1811
Figure 45

CONTENTS: **minimus** Zimmermann, 1780 (including *argyrodytes* Dickey, 1928; *bres-*

slaui Pohle, 1927; *cayennensis* Turton, 1800; *guianensis* Kerr, 1792; *gujanensis* Link, 1795; *langsdorffi* Boitard, 1845; *palmata* Daudin, 1802; *panamensis* Goldman, 1914; *paraguensis* Kerr, 1792; *sarcovienna* Shaw, 1800; *variegatus* Olfers, 1818; and *yapock* Desmarest, 1820).

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body ca. 250–320 mm; adult weight ca. 510–790 g. Rhinarium with one ventrolateral groove on each side of median sulcus; dark circumocular mask present, continuous with dark coronal fur (the whole top of the head except for an indistinct pale bar over each eye is blackish); pale supraocular spot absent; dark midrostral stripe absent; throat gland absent. *Dorsal pelage pale silvery gray with blackish transverse bars connected by blackish middorsal stripe* (when fresh; old museum skins become brownish or reddish with age); dorsal underfur pale gray; dorsal guard hairs short; ventral fur self-white. Manus mesaxonic (dIII >dIV); manual claws shorter than fleshy apical pads of digits; *dermatoglyph-bearing manual plantar pads absent (plantar epithelium uniformly and very densely covered with minutely denticulate tubercles among which are scattered at regular intervals many smooth, hemispherical papillae)*; *large, fleshy carpal tubercle supported internally by pisiform present in both sexes. Pedal digits webbed from base to terminal phalanges*; dIV longer than other pedal digits; plantar surface of heel naked. Pouch present, opening posteriorly; mammae 2–1–2 = 5; *cloaca absent* (urogenital and rectal openings widely separated by furred skin). Tail longer than combined length of head and body, thick and muscular (not incrassate); body fur extends onto basal one-sixth or less of tail, to about the same extent dorsally as ventrally; naked caudal integument (beyond furry base) blackish with abruptly whitish tip (rarely all blackish); caudal scales in spiral series, each dorsal scale usually with three subequal bristlelike hairs emerging from distal margin (ventral scales often have 4–5 hairs each); ventral caudal surface not externally modified for prehension.

Premaxillary rostral process absent. Nasals short, not extending anteriorly above I1 (exposing nasal orifice in dorsal view), and
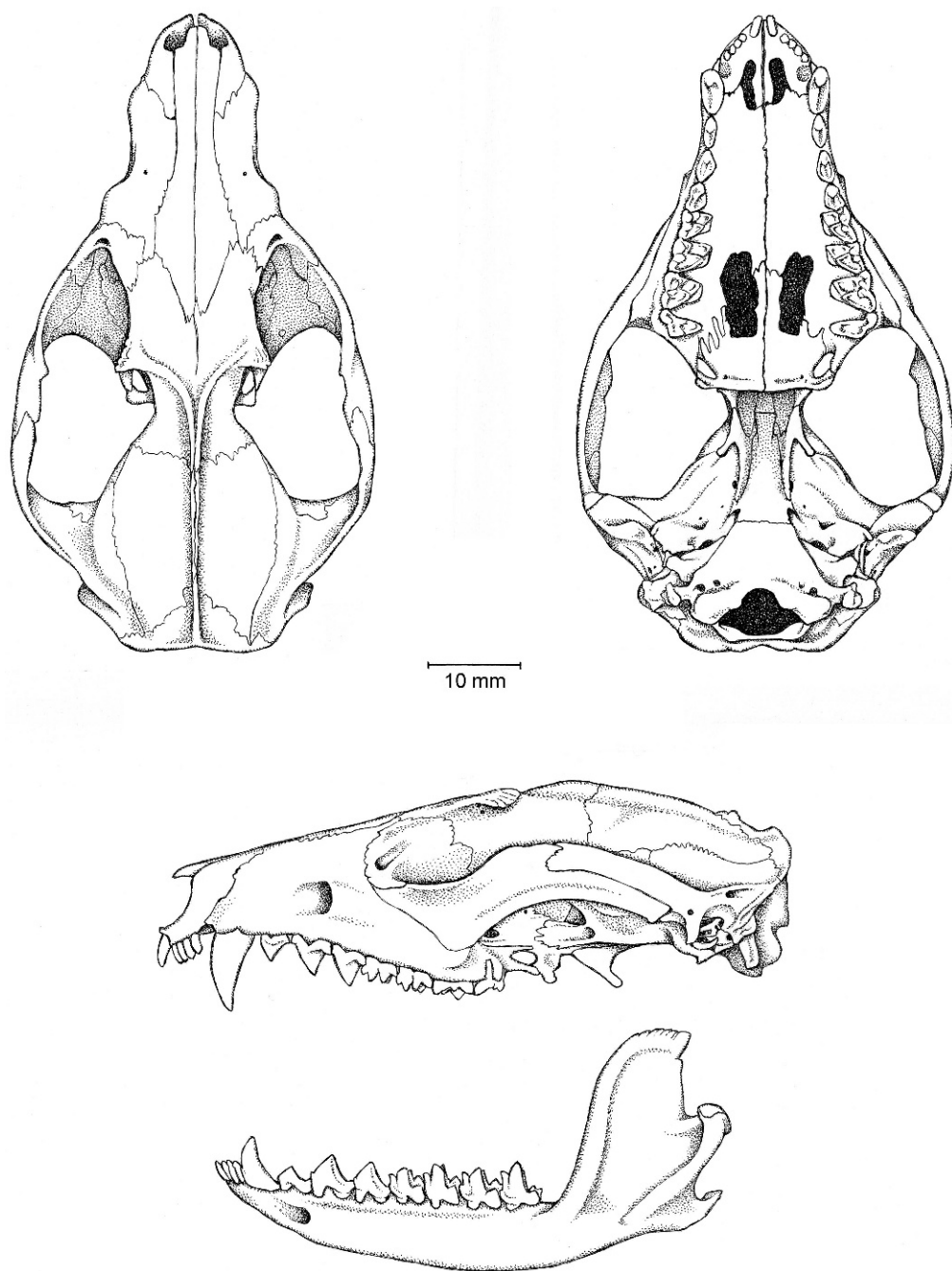
Fig. 45. *Chironectes minimus* (based on AMNH 96759, an adult male from Ilha do Taiuna, Pará, Brazil).

conspicuously widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. *One lacrimal foramen usually present on each side* just outside anterior orbital margin. Blunt, hornlike postorbital frontal processes present in adults. Right and left frontals co-ossified, midfrontal suture incomplete or absent; left and right parietals separated by persistent midparietal suture. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest present, well developed on parietals, and extending anteriorly onto frontals. Petrosal not laterally exposed through fenestra in parietal-squamosal suture (fenestra absent). Parietal-mastoid contact absent (interparietal narrowly contacts squamosal).

Maxillopalatine fenestrae present; palatine and maxillary fenestrae absent; posterolateral palatal foramina not extending anteriorly between M4 protocones; posterior palatal morphology conforms to *Didelphis* morphotype (with well-developed lateral corners, the choanae constricted behind). Maxillary and alisphenoid usually not in contact on floor of orbit (uni- or bilateral contacts were observed as rare variants). Transverse canal foramen present. Alisphenoid tympanic process small and uninflated, usually with medial lamina enclosing extracranial course of mandibular nerve (secondary foramen ovale usually present), and not in contact with rostral tympanic process of petrosal. Anterior limb of ectotympanic suspended indirectly from basicranium (by malleus). Stapes triangular, with large obturator foramen. Fenestra cochleae exposed, not concealed by rostral and caudal tympanic processes of petrosal. Paroccipital process large and erect, not adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present but narrow.

One mental foramen present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal (''premolariform''), with subequal anterior and posterior cutting edges, and subequal in length (mesiodistal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture;

C1 simple, without accessory cusps. First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; third upper premolar (P3) taller than P2; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Upper molars highly carnassialized (postmetacristae much longer than postprotocristae); relative widths M1 < M2 < M3 > M4 or M1 < M2 < M3 < M4; centrocrista only weakly inflected labially on M1–M3; ectoflexus shallow but distinct on M1 and M2, deepest on M3; anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3; postprotocrista with carnassial notch. Last upper tooth to erupt is M4.

Lower incisors (i1–i4) without distinct lingual cusps. Lower canine (c1) erect, acutely pointed, and simple (without a posterior accessory cusp). Second lower premolar (p2) taller than p3; lower milk premolar (dp3) large and molariform with a complete (tricuspid) trigonid; hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid much taller than hypoconulid on m1–m3.

DISTRIBUTION: *Chironectes* occurs along streams in moist lowland and lower montane forests (the highest elevational record appears to be about 1900 m; Handley, 1976) from the Mexican state of Oaxaca throughout most of Central America and tropical South America to northeastern Argentina (Misiones) and Uruguay (González and Fregueiro, 1998). As mapped by Marshall (1978d), the geographic range of this genus is strikingly disjunct, but collecting localities subsequently reported by Anderson (1997), Linares (1998), and Brown (2004) have closed many distributional gaps. As mapped by Stein and Patton (2008a), *Chironectes* appears to be absent from central Amazonia, but an unvouchered record from the lower Tapajos (George et al., 1988) suggests that this hiatus may be an artifact of inadequate collecting. Although water opossums are known to inhabit gallery-forested streams in the Cerrado (Mares et al., 1989), there are no published records from the Caatinga and Chaco.

REMARKS: Given the very broad geographic distribution of this unrevised genus, it

seems probable that at least some of the many putative synonyms of *Chironectes minimus* will be found to represent valid taxa in future analyses of morphological and/or molecular data.

Didelphis Linnaeus, 1758
Figure 46

CONTENTS: ***albiventris*** Lund, 1840 (including *bonariensis* Marelli, 1930; *dennleri* Marelli, 1930; *lechei* Ihering, 1892; *leucotis* Wagner, 1847; *paraguayensis* J.A. Allen, 1902; *poecilotis* Wagner, 1842; and *poecilonota* Schinz, 1844); ***aurita*** Wied-Neuweid, 1826 (including *koseritzi* Ihering, 1892; *longipilis* Miranda-Ribeiro, 1935; and *melanoidis* Miranda-Ribeiro, 1935); ***imperfecta*** Mondolfi and Pérez-Hernández, 1984; ***marsupialis*** Linnaeus, 1758 (including *battyi* Thomas, 1902; *cancrivora* Gmelin, 1788; *caucae* J.A. Allen, 1900; *colombica* J.A. Allen, 1900; *etensis* J.A. Allen, 1902; *insularis* J.A. Allen, 1902; *karkinophaga* Zimmermann, 1780; *particeps* Goldman, 1917; *richmondi* J.A. Allen, 1901; and *tabascensis* J.A. Allen, 1901); ***pernigra*** J.A. Allen, 1900 (including *andina* J.A. Allen, 1902; and *meridensis* J.A. Allen, 1902); and ***virginiana*** Kerr, 1792 (including *boreoamericana* J.A. Allen, 1902; *breviceps* Bennett, 1833; *californica* Bennett, 1833; *cozumelae* Merriam, 1901; *illinensium* Link, 1795; *pigra* Bangs, 1898; *pilosissima* Link, 1795; *pruinosa* Wagner, 1843; *texensis* J.A. Allen, 1901; *woapink* Barton, 1806; and *yucatanensis* J.A. Allen, 1901).

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body 310–495 mm; adult weight 600–5100 g. Rhinarium with one ventrolateral groove on each side of median sulcus; dark circumocular mask indistinct in some species (*D. aurita*, *D. marsupialis*, *D. virginiana*) but distinct in others (*D. albiventris*, *D. imperfecta*, *D. pernigra*); pale supraocular spot absent; dark midrostral stripe absent; throat gland absent. Dorsal pelage unpatterned; *dorsal underfur white*; *dorsal guard hairs long*, *coarse and conspicuous*, *giving the pelage a distinctively shaggy appearance*; ventral fur pale (usually whitish) tipped with black. Manus mesaxonic (dIII > dIV); manual claws usually longer than fleshy apical pads of digits; dermato-

glyph-bearing manual plantar pads present; central palmar epithelium smooth or sparsely tuberculate; carpal tubercles absent. Pedal digits unwebbed; dIV slightly longer than other pedal digits in some species (e.g., *D. marsupialis*) or dII, dIII, and dIV subequal (e.g., in *D. albiventris* and *D. virginiana*); plantar surface of heel naked. Pouch well developed, opening anteriorly; mammae normally 3–1–3 = 7 to 6–1–6 = 13 or more[29]; cloaca present. Tail slightly longer than combined length of head and body, slender and muscular (not incrassate); basal 1/6 to 1/4 densely furred (covered with body pelage); naked caudal integument blackish proximally and abruptly whitish distally; caudal scales in spiral series, each scale usually with three subequal bristlelike hairs emerging from distal margin; ventral caudal surface variably modified for prehension distally (prehensile modifications are more strongly developed in *D. auritus* and *D. marsupialis* than in the other species), but dermatoglyph-bearing apical pad consistently present.

Premaxillary rostral process absent. Nasals short, not produced anteriorly above I1 (exposing nasal orifice in dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. Lacrimal foramina one or two on each side, exposed laterally on orbital margin or on face just anterior to orbit. Postorbital processes bluntly pyramidal, maximally developed in old adults. Left and right frontals co-ossified (midfrontal suture incomplete or absent), but left and right parietals separated by persistent midparietal suture. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest large, well developed, and extending onto frontals. Petrosal not exposed laterally through fenestra in squamosal-parietal suture (fenestra absent). Parietal-mastoid contact absent (interparietal narrowly contacts squamosal).

Maxillopalatine and palatine fenestrae present; maxillary fenestrae absent; posterolateral palatal foramina not extending anteriorly lingual to M4 protocones; posterior

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[29] Occasional records of *Didelphis virginiana* with up to 17 pouch young (cited by Hamilton, 1958) suggest that teat counts in this species may sometimes exceed 6–1–6 = 13.
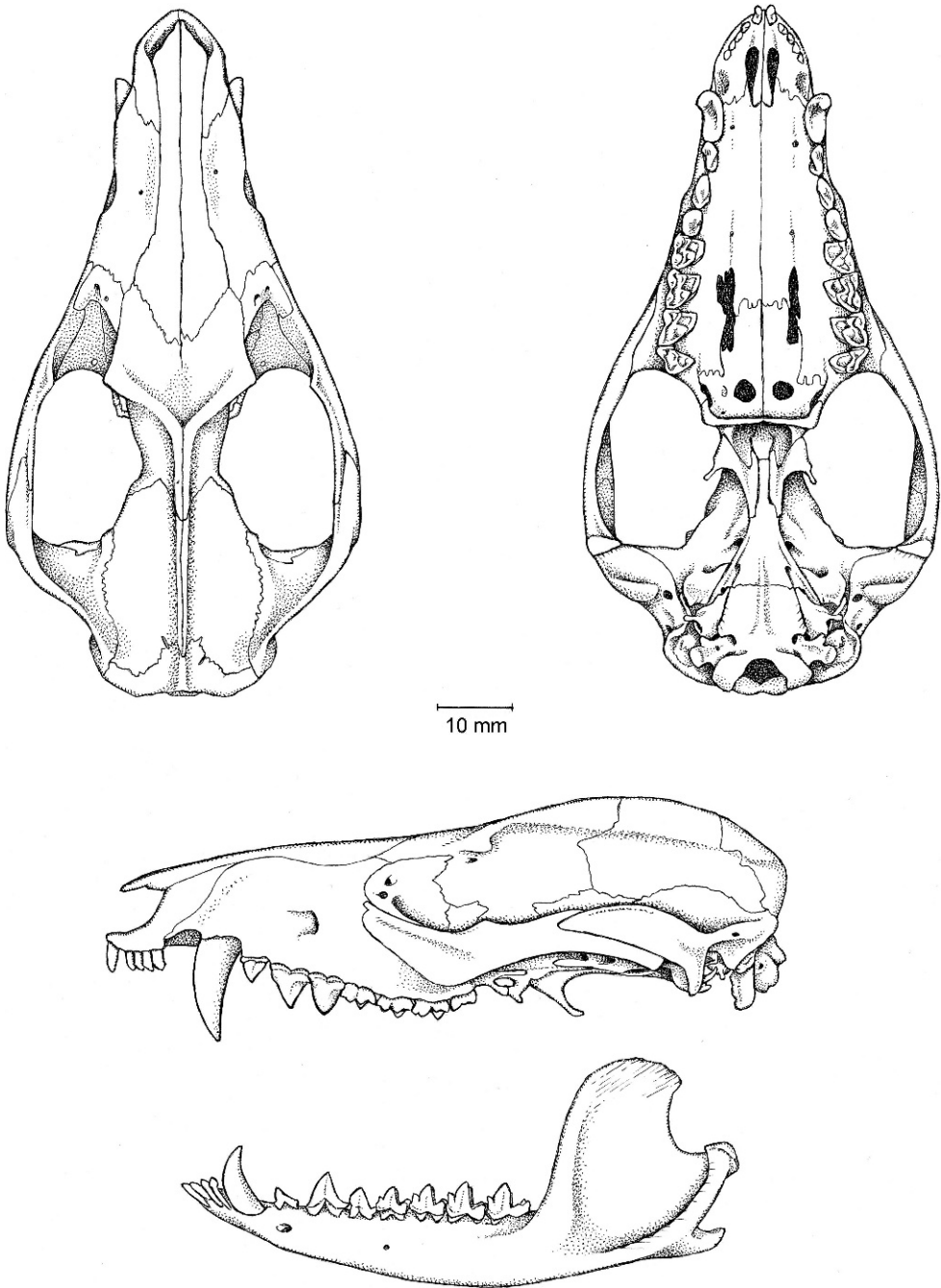
Fig. 46. *Didelphis marsupialis* (based on AMNH 266459, an adult male from Paracou, French Guiana).

palate with prominent lateral corners, the choanae abruptly constricted behind. Maxillary and alisphenoid not in contact (separated by palatine) on floor of orbit. Transverse

canal foramen present. Alisphenoid tympanic process small and uninflated, usually with posteromedial lamina enclosing extracranial course of mandibular nerve (secondary fora-

men ovale usually present), and not in contact with rostral tympanic process of petrosal. Anterior limb of ectotympanic suspended indirectly from basicranium (by malleus). Stapes usually triangular with large obturator foramen but sometimes columellar and imperforate (varies within species). Fenestra cochleae exposed, not concealed by rostral and caudal tympanic processes of petrosal. Paroccipital process large, erect (not adnate to petrosal) and projecting ventrally. Dorsal margin of foramen magnum bordered by exoccipitals only, incisura occipitalis absent.

Two mental foramina usually present on lateral surface of each hemimandible (one foramen is present unilaterally in a single examined specimen of *D. albiventris*); mandibular angular process acute and strongly inflected medially.

Unworn crowns of I2–I5 asymmetrical (''incisiform''), with much longer anterior than posterior cutting edges. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple, without accessory cusps. First upper premolar (P1) smaller than posterior premolars, but well-formed and not vestigial; third upper premolar (P3) taller than second (P2); P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars highly carnassialized (postmetacristae conspicuously longer than postprotocristae); relative widths M1 < M2 < M3 > M4 or M3 < M4; centrocrista only weakly inflected labially on M1–M3; ectoflexus shallow, indistinct, or absent on M1 and M2, but consistently deep and distinct on M3; anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3; postprotocrista with carnassial notch. Last upper tooth to erupt is M4.

Lower incisors (i1–i4) without distinct lingual cusps. Second lower premolar (p2) much taller than p3; lower milk premolar (dp3) with complete (tricuspid) trigonid. Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid much taller than hypoconulid on m1–m3.

DISTRIBUTION: *Didelphis* is a quintessentially eurytopic genus that ranges from southern Canada throughout most of North America (except the Rockies, the northern Great Plains, the Great Basin, the arid southwest, north-central Mexico, and Baja California; Hall, 1981), all of Central America, and most of South America (to about 40°S latitude in central Argentina; Flores et al., 2007). South American collection records (mapped by Cerqueira and Tribe, 2008) represent almost every non-desert tropical and subtropical biome on the continent.

REMARKS: Despite contradictory or ambiguous phylogenetic results from most sequenced loci analyzed separately (table 14), the monophyly of *Didelphis* is strongly supported by parsimony and Bayesian analyses of morphology (fig. 27), a concatenated five-gene dataset (fig. 33), and combined (nonmolecular + molecular) supermatrices (figs. 35, 36). Revisionary studies of the genus *Didelphis* in its modern sense were initiated by Allen (1901, 1902) and continued by Krumbiegel (1941), Gardner (1973), Cerqueira (1985), and Lemos and Cerqueira (2002). Useful summaries of morphological characters that distinguish *Didelphis* species in local faunas are provided by Mondolfi and Pérez-Hernández (1984), Catzeflis et al. (1997), Cerqueira and Lemos (2000), Flores and Abdala (2001), and Ventura et al. (2002). Analyses of mitochondrial DNA sequence variation within and among South American species were reported by Patton et al. (2000) and Patton and Costa (2003).

Lutreolina Thomas, 1910
Figure 47

CONTENTS: **crassicaudata** Desmarest, 1804 (including *crassicaudis* Olfers, 1818; *bonaria* Thomas, 1923; *ferruginea* Larrañaga, 1923; *lutrilla* Thomas, 1923; *macroura* Desmoulins, 1824; *paranalis* Thomas, 1923; *travassosi* Mirando-Ribeiro, 1936; and *turneri* Günther, 1879).

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body ca. 240–345 mm; adult weight ca. 300–800 g). Rhinarium with one ventrolateral groove on each side of median sulcus; *head entirely pale and unmarked* (dark circumocular mask, pale supraocular spots, and dark midrostral stripe absent); throat gland absent. Dorsal pelage unpatterned, usually some shade of yellowish
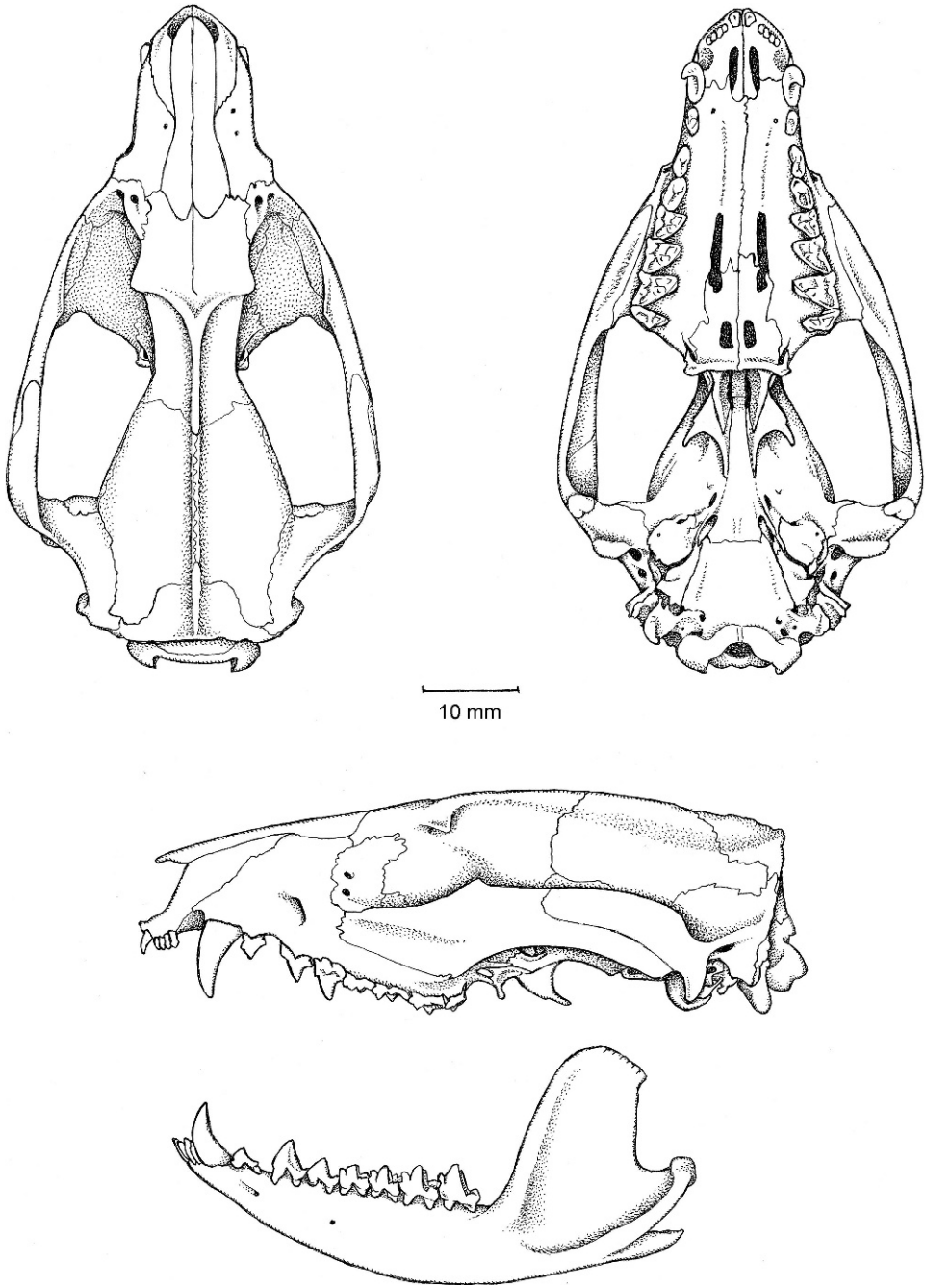
10 mm

Fig. 47. *Lutreolina crassicaudata* (based AMNH 254513, an adult female from Punta Lara, Buenos Aires, Argentina).

brown with grayish hair bases; dorsal guard hairs short and inconspicuous; ventral fur gray based or self-buffy. Manus mesaxonic (dIII > dIV); *manual claws much longer than fleshy apical pads of digits*; dermatoglyph-bearing manual plantar pads present; central palmar epithelium more or less smooth; carpal tubercles absent. Pedal digits un-webbed; *dIII longer than other pedal digits*; plantar surface of heel naked. Pouch present, opening posteriorly; mammae 4–1–4 = 9 to 5–1–5 = 11; cloaca present. *Tail usually slightly shorter than combined length of head and body*, thicker than in other large opossums but muscular, not incrassate; furred to about the same extent dorsally and ventrally for basal one-third to one-half; naked caudal integument blackish proximally but abruptly whitish near tail tip; caudal scales in spiral series, each scale usually with four or five subequal bristlelike hairs emerging from distal margin; ventral caudal surface not externally modified for prehension.

Premaxillary rostral process absent. Nasals short, not extending anteriorly above I1 (exposing nasal orifice in dorsal view), and widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. Lacrimal foramina two on each side, exposed laterally on orbital margin or on face just anterior to orbit. Short, blunt, hornlike postorbital processes usually present in large adult specimens. Left and right frontals co-ossified (midfrontal suture incomplete or absent), but left and right parietals separated by persistent midparietal suture. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest present, well developed on parietals and extending anteriorly onto frontals. Petrosal not laterally exposed through fenestra in squamosal-parietal suture (fenestra absent). Parietal-mastoid contact absent (interparietal narrowly contacts squamosal).

Maxillopalatine and palatine fenestrae present; maxillary fenestrae absent; postero-lateral palatal foramina not extending anteriorly between M4 protocones; posterior palatal morphology conforming to *Didelphis* morphotype (with well-developed lateral corners, the choanae abruptly constricted behind). *Maxillary and alisphenoid in contact (overlying palatine) on floor of orbit*. Trans-verse canal foramen present. Alisphenoid tympanic process small and usually rounded (somewhat more inflated than in *Chironectes* or *Didelphis*), with broad lamina enclosing extracranial course of mandibular nerve (secondary foramen ovale present), and not in contact with rostral tympanic process of petrosal. Anterior limb of ectotympanic suspended indirectly from braincase (by malleus). Stapes triangular with large obturator foramen; fenestra cochleae exposed (not enclosed by bony laminae). Paroccipital process large, erect, directed posteroventrally. Dorsal margin of foramen magnum bordered by exoccipitals only, incisura occipitalis absent.

Two mental foramina present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 asymmetrical ("incisiform"), with much longer anterior than posterior cutting edges. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple, without accessory cusps. First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; third upper premolar (P3) taller than P2; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Upper molars highly carnassialized (postmetacristae conspicuously longer than postprotocristae); relative widths M1 < M2 < M3 < M4; centrocrista only weakly inflected labially on M1–M3; ectoflexus usually distinct only on M3; anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3; post-protocrista with carnassial notch. Last upper tooth to erupt is M4.

Lower incisors (i1–i4) without distinct lingual cusps. Lower canine (c1) erect, acutely pointed, and simple (without a posterior accessory cusp). Second lower premolar (p2) taller than p3; lower milk premolar (dp3) large and molariform with complete (tricuspid) trigonid. *Hypoconid lingual to protoconid (not labially salient) on m3*; hypoconulid twinned with entoconid on m1–m3; entoconid taller than hypoconulid on m1 and m2, but sometimes subequal in height to hypoconulid on m3.

DISTRIBUTION: The known distribution of *Lutreolina* consists of two disjunct regions of

nonforest vegetation in South America (Stein and Patton, 2008b). Specimens traditionally referred to the subspecies *L. crassicaudata turneri* are from widely scattered localities in the savanna lowlands (below 900 m) in eastern Colombia and central Venezuela, and from the isolated but adjacent savannas of southern Venezuela and northern Guyana (Voss, 1991: 91); although specimens of this form are currently unknown from Surinam and French Guiana, they could be expected to occur in the as yet poorly surveyed coastal savannas of either (or both) countries and in the adjacent Brazilian state of Amapá. Southern South American specimens (representing several nominal taxa in addition to the nominotypical subspecies *L. c. crassicaudata*) are much more commonly collected in a wide range of tropical, subtropical, and temperate habitats in Paraguay, Uruguay, eastern Bolivia, southern Brazil, and northern Argentina (Flores et al., 2007; Stein and Patton, 2008b).

REMARKS: Although several morphologically diagnosed subspecies of *Lutreolina* have been treated as valid by authors (e.g., Thomas, 1923; Ximénez, 1967; Graipel et al., 1996; Stein and Patton, 2008b), no published analysis of molecular variation has tested the implicit assumption that only a single species occurs across the vast range of South American landscapes from which specimens have been collected.

Philander Brisson, 1762
Figure 48

CONTENTS: ***andersoni*** Osgood, 1913 (including *nigratus* Thomas, 1923); ***deltae*** Lew et al., 2006; ***frenatus*** Olfers, 1818 (including *azaricus* Thomas, 1923; *quica* Temminck, 1824; and *superciliaris* Olfers, 1818); ***mcilhennyi*** Gardner and Patton, 1972; ***mondolfii*** Lew et al., 2006; ***olrogi*** Flores et al., 2008; and ***opossum*** Linnaeus, 1758 (including *canus* Osgood, 1913; *crucialis* Thomas, 1923; *fuscogriseus* J.A. Allen, 1900; *grisescens* J.A. Allen, 1901; *melantho* Thomas, 1923; *melanurus* Thomas, 1899; *pallidus* J.A. Allen, 1901; and *virginianus* Tiedemann, 1808).

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body ca. 250–350 mm; adult weight ca. 280–700 g. Rhinar-

ium with one ventrolateral groove on each side of median sulcus; *dark circumocular mask present, usually continuous with dark coronal fur* (the coronal fur is not dark in some examined specimens of *P. frenatus*); *pale supraocular spot present*; dark midrostral stripe absent; throat gland absent. Dorsal pelage unpatterned grayish or blackish, or with grayish flanks and black middorsal stripe; dorsal underfur gray; dorsal guard hairs usually short (longer middorsally than along flanks in *P. mcilhennyi*); ventral fur variously pigmented, usually gray-based buffy or cream, or entirely grayish (variable within and among examined taxa). Manus mesaxonic (dIII > dIV); manual claws about as long as fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar epithelium smooth or sparsely tuberculate; carpal tubercles absent. Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel naked. Pouch present, opening anteriorly; mammae usually 2–1–2 = 5 or 3–1–3 = 7; cloaca present. Tail longer than combined length of head and body, slender and muscular (not incrassate); furred dorsally and ventrally to about the same extent for basal one-fifth; naked caudal integument blackish proximally and abruptly whitish distally; caudal scales in spiral series, each scale with 4–6 bristle-like hairs emerging from distal margin; ventral caudal surface modified for prehension distally, with apical pad bearing dermatoglyphs.

Premaxillary rostral process absent. Nasals short, not extending anteriorly above I1 (exposing nasal orifice in dorsal view), and widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. Lacrimal foramina usually two on each side, exposed laterally on orbital margin or on face just anterior to orbit. Interorbital region smoothly rounded, without supraorbital beads or crests; short, blunt, hornlike postorbital processes usually present in large adult specimens. Left and right frontals co-ossified (midfrontal suture incomplete or absent), but left and right parietals separated by persistent midparietal suture. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest present, well developed on
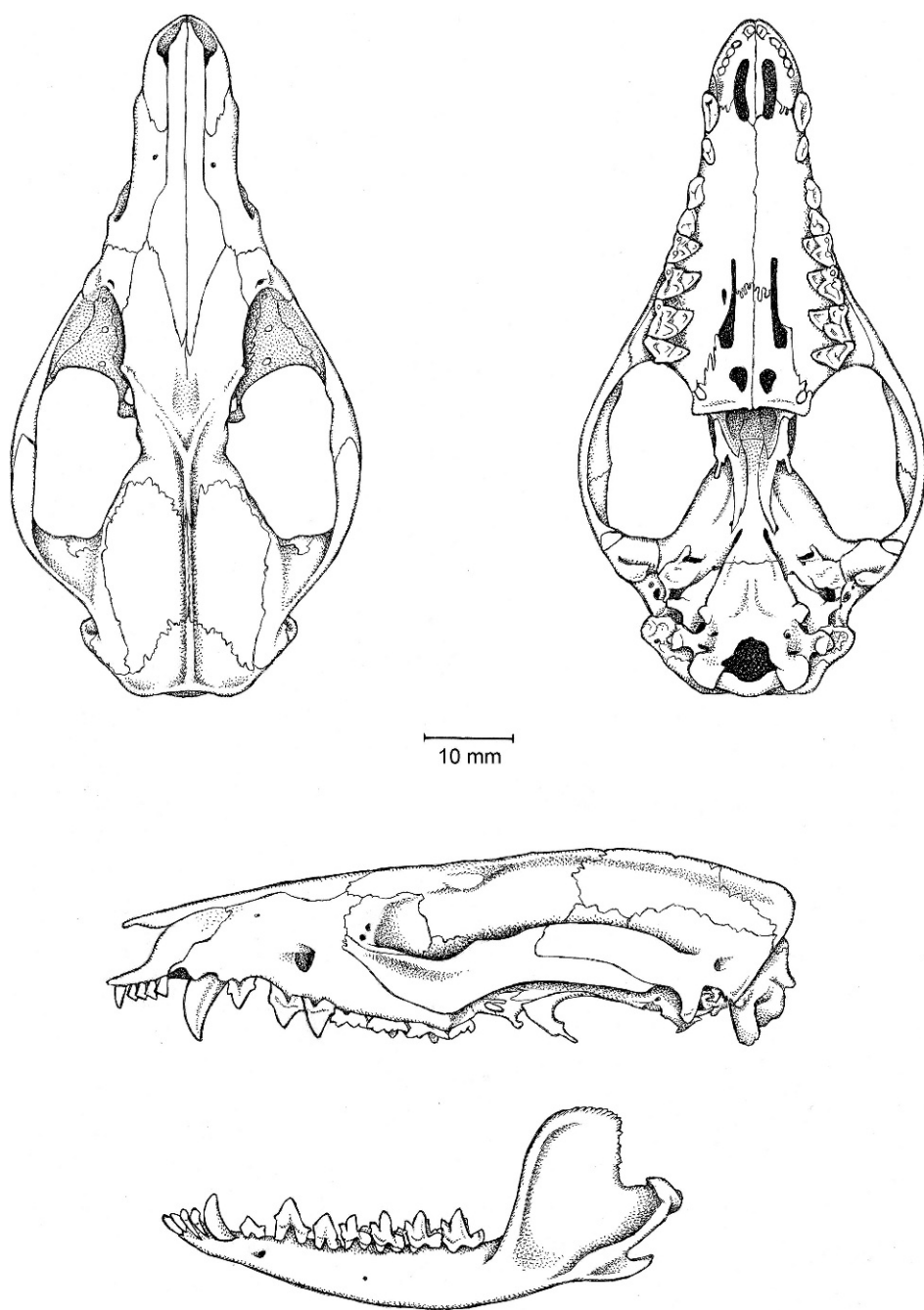
Fig. 48.   *Philander opossum* (based primarily on AMNH 266387, an adult female from Paracou, French Guiana; minor details were reconstructed from AMNH 266386 and 266994).

parietals and extending anteriorly onto frontals. Petrosal not exposed laterally through fenestra in squamosal-parietal suture (fenestra absent). Parietal-mastoid contact absent (interparietal narrowly contacts squamosal).

Maxillopalatine and palatine fenestrae present; maxillary fenestrae absent; posterolateral palatal foramina small, not extending anteriorly between M4 protocones; posterior palatal morphology conforming to *Didelphis* morphotype (with prominent lateral corners, the choanae constricted behind). Maxillary and alisphenoid usually separated by palatine on floor of orbit (maxillary-alisphenoid contact occurs unilaterally or bilaterally in a few specimens). Transverse canal foramen usually present. Alisphenoid tympanic process small and uninflated, usually with broad lamina enclosing extracranial course of mandibular nerve (secondary foramen ovale present), and not contacting rostral tympanic process of petrosal. Anterior limb of ectotympanic indirectly suspended from basicranium (by malleus). Stapes usually triangular with large obturator foramen. Fenestra cochleae exposed (not concealed by rostral and caudal tympanic processes of petrosal). Paroccipital process large, erect, directed posteroventrally. Dorsal margin of foramen magnum bordered by exoccipitals only, incisura occipitalis absent.

Two mental foramina present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 asymmetrical ("incisiform"), with much longer anterior than posterior cutting edges. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple, without accessory cusps. First upper premolar (P1) smaller than posterior premolars but well-formed and not vestigial; third upper premolar (P3) taller than P2; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars highly carnassialized (postmetacristae conspicuously longer than postprotocristae; relative widths M1 < M2 < M3 < M4; centrocrista only weakly inflected labially on M1–M3; ectoflexus usually distinct only on M3; anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3; postprotocrista with

carnassial notch. Last upper tooth to erupt is M4.

Lower incisors (i1–i4) without distinct lingual cusps. Lower canine (c1) erect, acutely pointed, and simple (without a posterior accessory cusp). Second lower premolar (p2) much taller than p3; lower milk premolar (dp3) large and molariform with complete (tricuspid) trigonid. Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid much taller than hypoconulid on m1–m3.

DISTRIBUTION: Species of *Philander* occur in lowland and lower montane moist forests (to 1600 m; Reid, 1997) from the Mexican state of Tamaulipas southward throughout most of Central America (Hall, 1981) and tropical South America (Patton and da Silva, 2008) to northern Argentina (Chaco, Formosa, and Misiones; Flores et al., 2007). Collecting localities mapped by Anderson (1997), Linares (1998), and Brown (2004) suggest that *Philander* is largely absent from intervening arid, semiarid, or treeless landscapes (e.g., the Chaco, Cerrado, Caatinga, and Llanos), with a few exceptions that may have been taken in gallery forests.

REMARKS: Although inconsistently supported by our separate nuclear-gene analyses (table 14) and by Patton et al.'s (1996) analyses of sequence data from the mitochondrial cytochrome *b* locus, the monophyly of *Philander* is moderately well supported by nonmolecular characters (fig. 27) and it is strongly supported by our analyses of concatenated genes and combined datasets (figs. 33, 35, 36). The current species-level classification given above largely follows Patton and da Silva (1997), who analyzed mtDNA haplotype diversity among 42 Central and South American specimens that they interpreted as representing six valid taxa (*andersoni, canus, frenatus, fuscogriseus, mcilhennyi, opossum*); three unsequenced taxa (*azarica, melanurus, pallidus*) were also recognized as valid on the basis of morphological traits. Whereas *andersoni, frenatus,* and *mcilhennyi* were recovered as monophyletic haplotype groups that Patton and da Silva recognized as monotypic species, their concept of *opossum* included several subspecies (*azarica, canus, fuscogriseus, melanurus, pallida*) and was not recovered as a clade. Based

on their phylogenetic analysis (op. cit.: fig. 2), it would be logical to recognize *fuscogriseus* and *canus* as valid species, but the authors reasonably cautioned against facile taxonomic decisions based on the results of analyzing a single maternally inherited gene. Indeed, the genus clearly requires a more comprehensive revisionary treatment, with particular attention devoted to obtaining analyzable character data from hitherto unrepresented taxa (notably *azarica*, *crucialis*, *grisescens*, *melanurus*, and *pallidus*). Our placement of *azarica* in the synonymy of *P. frenatus* uncritically follows Gardner (2005), who also allocated nominal taxa not treated by Patton and da Silva (1997) to the synonymy of *P. opossum*. Although an alternative species-level classification of *Philander* proposed by Hershkovitz (1997) was not based on any explicit analysis of specimen data, it raised several issues not adequately treated by other authors and drew attention to the possible existence of undescribed taxa. New species described by Lew et al. (2006) and Flores et al. (2008) contribute additional taxonomic complexities and underscore the need for critical revisionary work on this difficult genus.

The tiresome nomenclatural controversy regarding the use of *Philander* Tiedemann, 1808, versus *Metachirops* Matschie, 1916, as the correct generic name for the gray four-eyed opossums (Pine, 1973; Hershkovitz, 1976; Gardner, 1981) was made moot by a recent ruling of the International Commission on Zoological Nomenclature (ICZN, 1998) that definitively established the availability of *Philander* from Brisson (1762).

Tribe Thylamyini Hershkovitz, 1992

CONTENTS: *Chacodelphys*, *Cryptonanus*, *Gracilinanus*, *Lestodelphys*, *Marmosops*, and *Thylamys*.

DIAGNOSIS: Members of the tribe Thylamyini differ from all other didelphids by having a fenestra in the parietal-squamosal suture through which the petrosal is visible on the lateral surface of the braincase. Additionally, most thylamyines (*Chacodelphys* and *Cryptonanus* are exceptions) differ from otherwise similar marmosines by having a secondary foramen ovale formed by an anteromedial bullar process that spans the transverse canal foramen.

REMARKS: The monophyly of Thylamyini (without *Chacodelphys*, from which sequence data are unavailable) is strongly supported by parsimony, likelihood, and Bayesian analyses of IRBP (fig. 28) and BRCA1 (fig. 31); by likelihood and Bayesian analyses of DMP1 (fig. 29); and by Bayesian analysis of RAG1 (fig. 30). It is also strongly supported by all analyses of a concatenated five-gene dataset (fig. 33), and by Bayesian analysis of a combined (nonmolecular + molecular) dataset that includes *Chacodelphys*. The presence of a fenestra in the parietal-squamosal suture (appendix 5) and a uniquely derived insertion at the BRCA1 locus (fig. 31) both optimize as thylamyine synapomorphies.

Apparently, the earliest family-group name based on *Thylamys* is technically available from Hershkovitz (1992b), who erroneously attributed authorship of Thylamyinae to Reig et al. (1987).

Chacodelphys Voss et al., 2004

CONTENTS: ***formosa*** Shamel, 1930 (including *muscula* Shamel, 1930).

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body 68 mm (external measurements are only available from the young adult holotype); adult weight unknown but probably ca. 10 g. Rhinarial morphology unknown (no fluid-preserved specimens have been examined); dark circumocular mask present but narrow and inconspicuous; pale supraocular spot absent; dark midrostral stripe absent; gular gland present. Dorsal fur unpatterned, brownish, somewhat darker middorsally than along flanks, but pelage not distinctly tricolored; dorsal underfur gray based; dorsal guard hairs short and inconspicuous; ventral fur gray-based buffy. Manus mesaxonic (dIII > dIV); manual claws shorter than fleshy apical pads of digits; manual plantar pads present, but presence/absence of dermatoglyphs unknown; *central palmar surface of manus densely covered with small convex tubercles*; occurrence of carpal tubercles unknown. Pedal digits unwebbed; dIV slightly longer than other pedal digits; plantar surface of

heel naked. Mammary formula, morphology of pouch (if any), and presence/absence of cloaca unknown. Tail shorter than combined length of head and body, slender and muscular (not incrassate); body pelage not extending onto tail base; tail densely covered with short hairs and distinctly bicolored (dark above, pale below); caudal scales arranged in annular series, each scale with three subequal bristlelike hairs emerging from distal margin; *ventral caudal surface not externally modified for prehension.*

Rostral process of premaxillae absent. Nasals long, extending anteriorly beyond I1 (concealing nasal orifice from dorsal view), *with subparallel lateral margins (not widened posteriorly)*. Maxillary turbinals large and elaborately branched. Two lacrimal foramina laterally exposed on each side just anterior to orbital margin. Supraorbital margins smoothly rounded, without beads or processes; strongly marked interorbital and postorbital constrictions present. Right and left frontals and parietals separated by persistent median sutures. Parietal and alisphenoid bones in contact (no squamosal-frontal contact). Sagittal crest absent. Petrosal exposed laterally though fenestra in parietal-squamosal suture. Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae present and very large; palatine fenestrae present but incompletely separated from maxillopalatine openings; maxillary fenestrae very small but bilaterally present near M1/M2 commissure; posterolateral palatal foramina small, not extending lingual to M4 protocones; posterior palate conforms to *Didelphis* morphotype (with prominent lateral corners, the internal choanae abruptly constricted behind). Maxillary and alisphenoid not in contact on orbital floor (separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process probably smoothly globular (broken in both examined specimens), without anteromedial process or posteromedial lamina enclosing extracranial course of mandibular nerve (secondary foramen ovale absent), and probably not contacting rostral tympanic process of petrosal. Anterior limb of ectotympanic directly suspended from basicranium. Stapes triangular, perforated by large obturator foramen. Fenestra cochleae exposed, not concealed by rostral and caudal tympanic processes of petrosal. Paroccipital process small, adnate to petrosal. Dorsal margin of foramen magnum formed by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal (''premolariform''), with subequal anterior and posterior cutting edges, and increasing in length (mesiodistal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple, without accessory cusps. First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; second and third upper premolars (P2 and P3) subequal in height (see footnote 14, above); P3 with posterior cutting edge only; upper milk premolar (dP3) morphology unknown (no juvenile specimens examined). Upper molars highly carnassialized (postmetacristae conspicuously longer than postprotocristae); relative widths M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus absent on M1, very shallow on M2, distinct only on M3; anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3; postprotocrista without carnassial notch. Last upper tooth to erupt is probably P3.

Lower incisors (i1–i4) with distinct lingual cusps. Lower canine (c1) semiprocumbent, with flattened bladelike apex, but simple (without a distinct posterior accessory cusp). Second lower premolar (p2) taller than p3; lower milk premolar (dp3) morphology unknown (no juvenile specimens examined). *Hypoconid lingual to protoconid (not labially salient) on m3*; hypoconulid twinned with entoconid on m1–m3; *entoconid very small*, subequal in height to hypoconulid on m1–m3.

DISTRIBUTION: *Chacodelphys* is currently known from just five localities in the Argentinian provinces of Chaco and Formosa (between 25–27° S latitude and 58–60° W longitude; Teta et al., 2006). However, because the humid savanna habitats that occur at these sites resemble those found

elsewhere in northern Argentina, eastern Bolivia, western Paraguay, and southwestern Brazil, it would be reasonable to expect that the genus is more widely distributed.

REMARKS: In the absence of undamaged cranial material, we are unable to provide an illustration for this genus. However, photographs of two imperfect skulls were published by Voss et al. (2004a: fig. 2) and Teta et al. (2006: fig. 2).

The problematic relationships of this genus were discussed at length by Voss et al. (2004a) and seem unlikely to be resolved definitively in the absence of nuclear gene sequence data. As discussed above, the tribal membership of *Chacodelphys* is most compellingly supported by Bayesian analysis of a dataset that combines nonmolecular characters with nuclear-gene sequence data (fig. 36), but it is consistent with subjective assessments of similarity based on integumental and craniodental traits (e.g., by Tate, 1933). Although separate analyses of nonmolecular character data suggest that this genus may be more closely related to *Thylamys* and *Lestodelphys* than to other thylamyines (fig. 27), it seems premature to formalize such weakly supported results by subtribal nomenclature.

Cryptonanus Voss et al., 2005
Figure 49

CONTENTS: *agricolai* Moojen, 1943; *chacoensis* Tate, 1931; *guahybae* Tate, 1931; *ignitus* Díaz et al., 2002; and *unduaviensis* Tate, 1931.

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body ca. 80–120 mm; adult weight ca. 15–40 g. Ventral margin of rhinarium with two shallow grooves on each side of median sulcus; dark circumocular mask present; pale supraocular spot absent; dark midrostral stripe absent; gular gland present in adult males. Dorsal body pelage unpatterned, usually grayish or reddish brown; dorsal fur gray based; dorsal guard hairs very short and inconspicuous; ventral fur gray based or self-colored (varying among species). Manus paraxonic (dIII = dIV); manual claws shorter than fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar surface

of manus sparsely tubercular (neither smooth nor densely covered with convex tubercles); lateral carpal tubercles present in adult males. Pedal digits unwebbed; dIV longer than other pedal digits; plantar epithelium of heel naked. Pouch absent; mammae 4–1–4 = 9 (all abdominal-inguinal) to 7–1–7 = 15 (with pectoral teats); cloaca present. Tail longer than combined length of head and body, slender and muscular (not incrassate); body pelage not extending more than a few mm onto tail base; unfurred caudal integument more or less bicolored (dark above, paler below) in most specimens; caudal scales in distinctly annular series, each scale with three subequal bristlelike hairs emerging from distal margin; ventral caudal surface modified for prehension distally, with apical pad bearing dermatoglyphs.

Rostral process of premaxillae absent. Nasals long, extending anteriorly beyond I1 (concealing nasal orifice from dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture. Maxillary turbinals large and elaborately branched. Two lacrimal foramina laterally exposed on each side on or just anterior to orbital margin. Supraorbital margins rounded, without beads or processes (a few old individuals have incipient postorbital processes); distinct interorbital and postorbital constrictions usually present in juveniles and young adults. Left and right frontals and parietals separated by persistent median sutures. Parietal and alisphenoid in contact on lateral braincase (no squamosal-frontal contact). Sagittal crest absent. Petrosal laterally exposed through fenestra in parietal-squamosal suture. Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae large; palatine fenestrae present; maxillary fenestrae absent; posterolateral palatal foramina small, not extending lingual to M4 protocones; posterior palate conforms to *Didelphis* morphotype (with prominent lateral corners, the internal choanae abruptly constricted behind). Maxillary and alisphenoid not in contact on orbital floor (separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process smoothly globular, without anteromedial process or posteromedial lamina enclosing extracranial course of mandib-
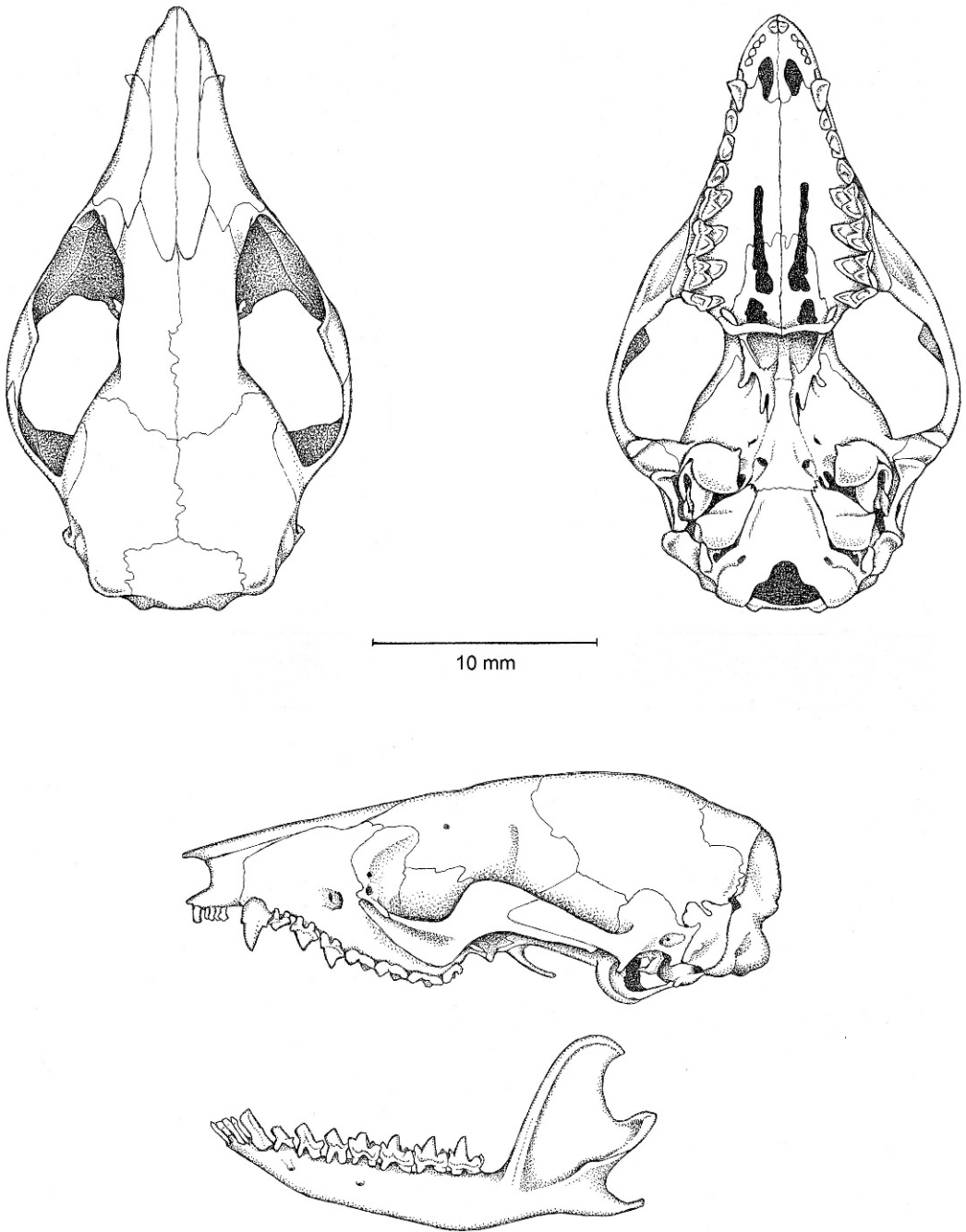
10 mm

Fig. 49. *Cryptonanus unduaviensis* (based on AMNH 209152, an adult female from the Río Baures, Beni, Bolivia).

ular nerve (secondary foramen ovale absent), and not contacting rostral tympanic process of petrosal. Anterior limb of ectotympanic directly suspended from basicranium. Stapes triangular, perforated by large obturator foramen. Fenestra cochleae exposed, not concealed by rostral and caudal tympanic processes of petrosal. Paroccipital process small, adnate to petrosal. Dorsal margin of foramen magnum formed by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal (''premolariform''), with subequal anterior and posterior cutting edges, slightly increasing in length (mesiodistal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 usually with one or two small accessory cusps (the posterior accessory cusp is more consistently distinct than the anterior cusp). First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; third upper premolar (P3) taller than P2; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Upper molars strongly carnassialized (postmetacristae conspicuously longer than postprotocristae); relative widths M1 < M2 < M3 > M4 or M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus shallow or absent on M1, deeper on M2, and consistently deep on M3; anterolabial cingulum continuous with preprotocrista (complete anterior cingulum present) on M3 in some species (e.g., *C. unduaviensis*) but anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3 in others (e.g., *C. chacoensis*); postprotocrista without carnassial notch. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. Lower canine (c1) procumbent, with flattened bladelike apex, usually with small posterior accessory cusp (but often absent on even moderately worn teeth). Second lower premolar (p2) taller than p3; lower milk premolar (dp3) with complete trigonid (tricuspid in in *C. chacoensis*) or with incomplete trigonid (bicuspid in *C. unduaviensis*). Hypoconid labially salient (level with labial apex of protoconid) on m3; hypoconulid twinned with entoconid on m1–m3; entoconid much taller than hypoconulid on m1–m3.

DISTRIBUTION: *Cryptonanus* is known from mostly unforested tropical and subtropical biomes south of the Amazon River and east of the Andes, including the Caatinga, Cerrado, Chaco, and northern Pampas; collection localities mapped by Voss et al. (2005) and D'Elía and Martínez (2006) are from Paraguay, Uruguay, eastern Bolivia, northern Argentina, and eastern Brazil.

REMARKS: Our species-level taxonomy of *Cryptonanus* follows Voss et al. (2005) who, however, cautioned that this arrangement is provisional and unsupported by rigorous tests of species limits. In particular, the genetic distinctness of *C. agricolai*, *C. chacoensis*, *C. ignitus*, and *C. unduaviensis* is not overwhelmingly indicated by available morphological data and merits careful evaluation. Molecular sequence comparisons would be an especially welcome supplement to the scant phenotypic evidence at hand.

Gracilinanus Gardner and Creighton, 1989
Figure 50

CONTENTS: **aceramarcae** Tate, 1931; **agilis** Burmeister, 1854 (including *beatrix* Thomas, 1910; *buenavistae* Tate, 1931; and *peruana* Tate, 1931); **dryas** Thomas, 1898; **emiliae** Thomas, 1909 (including *longicaudus* Hershkovitz, 1992); **marica** Thomas, 1898 (including *perijae* Hershkovitz, 1992); and **microtarsus** Wagner (1842).

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body ca. 75–130 mm; adult weight ca. 10–50 g. Rhinarium with two ventrolateral grooves on each side of median sulcus; dark circumocular mask present; pale supraocular spot absent; dark midrostral stripe absent; throat gland present in adult males. Dorsal pelage unpatterned reddish or grayish brown with dark-gray hair bases; dorsal guard hairs short and inconspicuous; ventral fur mostly gray-based buff or orange (e.g., in *G. microtarsus*), but self-white in some species (e.g., *G. emiliae*). Manus paraxonic (dIII = dIV); manual claws small, not extending beyond fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads
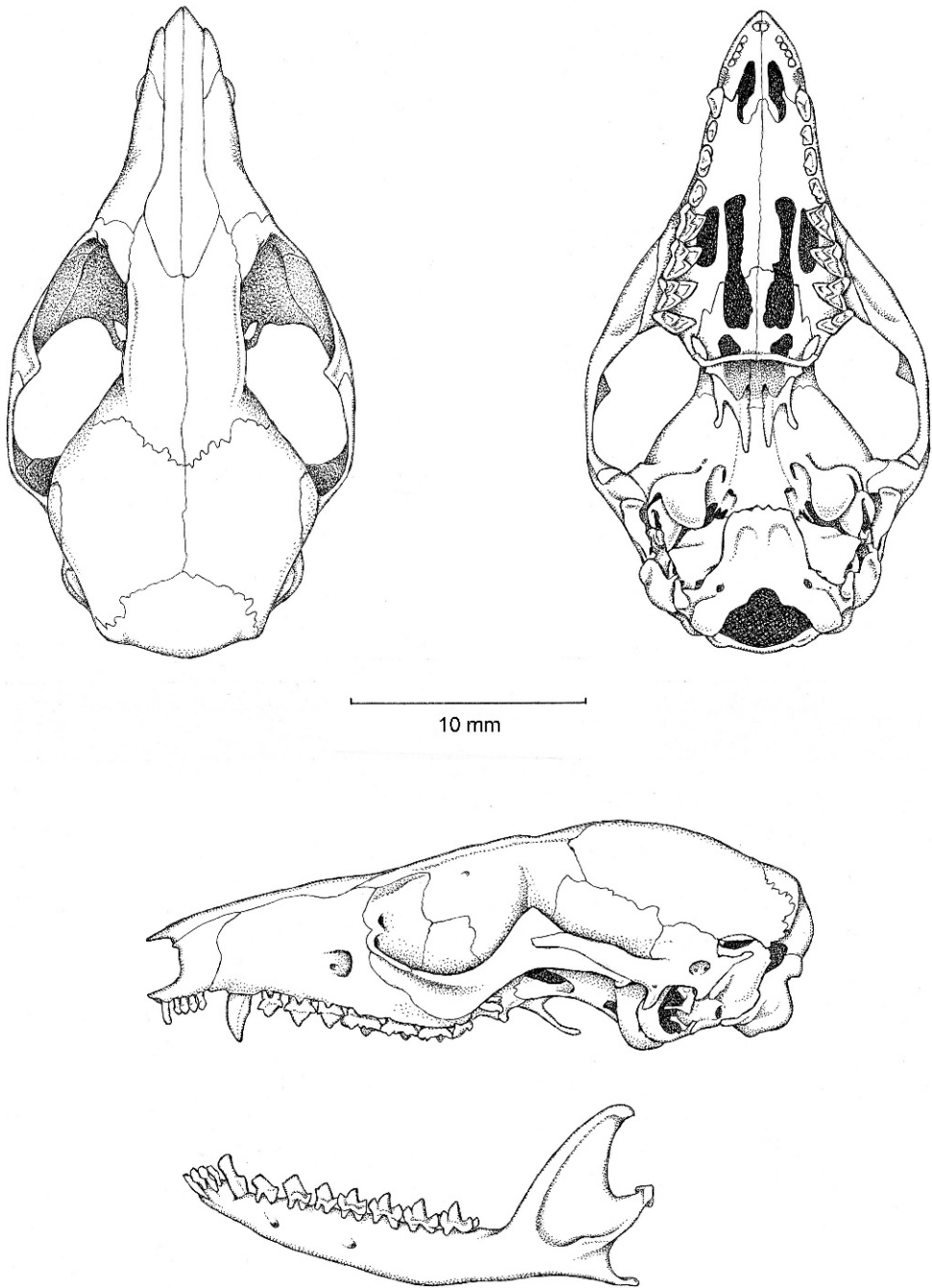
10 mm

Fig. 50.   *Gracilinanus agilis* (based on MVZ 197437, an adult male from Mato do Vasco, Minas Gerais, Brazil).

present; central palmar epithelium smooth or sparsely tuberculate; lateral carpal tubercles present in fully adult males, but medial carpal tubercles absent in both sexes. Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel naked. Pouch absent; mammary formula (unknown for most species) 3–1–3 = 7 to 4–1–4 = 9; cloaca present. Tail much longer than combined length of head and body, slender and muscular (not incrassate), and macroscopically naked (furred only near base); naked caudal integument usually unicolored (dark) but sometimes indistinctly bicolored (dark above, paler below) at base; caudal scales in annular series (most species) or annular and spiral series (*G. emiliae*), each scale with three subequal bristlelike hairs emerging from distal margin; ventral caudal surface modified for prehension distally (with naked median groove and apical pad bearing dermatoglyphs).

Premaxillary rostral process present. Nasals long, extending anteriorly beyond I1 (concealing nasal orifice from dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture. Maxillary turbinals elaborately branched. Two lacrimal foramina present on each side but usually inconspicuous in lateral view (partially concealed within anterior orbital margin). Interorbital region more or less parallel-sided, without well-developed constrictions; supraorbital margins smoothly rounded in most species (e.g., *G. dryas*) or with well-developed beads (in *G. emiliae*); postorbital processes usually absent except in large adult specimens of *G. microtarsus*. Left and right frontals and parietals separated by persistent median sutures. Parietal and alisphenoid in contact on lateral braincase (no squamosal-frontal contact). Sagittal crest absent. Petrosal laterally exposed through fenestra in parietal-squamosal suture. Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae present; palatine fenestrae present; maxillary fenestrae present in most species (but very small and occasionally absent uni- or bilaterally in *G. emiliae*); posterolateral palatal foramina small, not extending lingual to M4 protocones; posterior palatal morphology conforms to *Didelphis* morphotype (with well-developed lateral cor-

ners, the choanae constricted behind). Maxillary and alisphenoid not in contact on floor of orbit (separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process flask shaped or globular (not laterally compressed and without a well-developed ventral process), almost always with anteromedial strut enclosing extracranial course of mandibular nerve (secondary foramen ovale usually present), and not contacting rostral tympanic process of petrosal. Anterior limb of ectotympanic directly suspended from basicranium. Stapes triangular, with large obturator foramen. Fenestra cochleae usually exposed (partially concealed by caudal tympanic process of petrosal in some specimens of *G. aceramarcae* and *G. microtarsus*). Paroccipital process small, rounded, and adnate to petrosal. Dorsal margin of foramen magnum bordered by exoccipitals and supraoccipital, incisura occipitalis present.

Two mental foramina present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal ("premolariform"), with subequal anterior and posterior cutting edges, increasing in length (mesiodistal dimension) from I2 to I5 (e.g., in *G. microtarsus*), or I2–I5 crowns subequal in length (e.g., in *G. emiliae*). Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple, without accessory cusps except in *G. emiliae* (which consistently has a posterior accessory cusp). First upper premolar (P1) smaller than posterior premolars but well-formed and not vestigial; second and third upper premolars (P2 and P3) subequal in height; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars carnassialized (postmetacristae longer than postprotocristae); relative widths M1 < M2 < M3 > M4 or M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus indistinct or absent on M1 and M2 but consistently distinct on M3; anterolabial cingulum continuous with preprotocrista (complete anterior cingulum present) on M3; postprotocrista without carnassial notch. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. Second lower premolar (p2) taller than

p3; lower milk premolar (dp3) trigonid incomplete (unicuspid in the few specimens we were able to score for this trait). Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid taller than hypoconulid on m1–m3.

DISTRIBUTION: Species of *Gracilinanus* occur in tropical and subtropical moist forests in lowland and montane landscapes (to at least 3350 m; Voss et al., 2004b: table 12) from northern Venezuela to Bolivia, Paraguay, southeastern Brazil, northeastern Argentina, and northern Uruguay (D'Elía and Martínez, 2006; Teta et al., 2007; Creighton and Gardner, 2008a). Apparently, only one Argentinian record and two Uruguayan records of *Gracilinanus* are valid, the remaining published localities for this genus from both countries having been based on specimens of *Cryptonanus* (see Voss et al., 2005; D'Elía and Martínez, 2006; Teta et al., 2007). *Gracilinanus* is said not to occur in central Amazonia (Patton and Costa, 2003), but the species to be expected there (*G. emiliae*) is difficult to collect and this distributional hiatus is perhaps an artifact of inadequate faunal sampling.[30]

REMARKS: The contents of this genus have changed significantly in the years since it was first described by Gardner and Creighton (1989), principally by removal of distantly related forms to new genera (see Voss et al., 2005: table 1). With the exception of *Gracilinanus microtarsus* and *G. agilis*, species of this genus are not common in museum collections, and geographic distributions remain poorly documented. In addition, current species concepts will doubtless change as more information becomes available. For example, molecular data (summarized by Costa et al., 2003) suggest the presence of an undescribed, morphologically cryptic species among the material currently identified as *G. microtarsus*; the geographic distribution of material currently identified as *G. emiliae* is improbably broad; and some specimens from northern Colombia and eastern Peru do

not resemble any currently recognized taxa. Therefore, the species-level diversity of *Gracilinanus* seems certain to increase with future revisionary research.

The monophyly of *Gracilinanus* in its currently restricted sense is strongly supported by parsimony, likelihood, and Bayesian analyses of RAG1 (fig. 30), BRCA1 (fig. 31), vWF (fig. 32), concatenated sequence data from five genes (fig. 33), and combined datasets that include both nonmolecular and molecular characters (figs. 35, 36); it is also moderately supported by parsimony and likelihood analyses of IRBP (fig. 28). We have no plausible explanation as to why analyses of DMP1 strongly support the conflicting hypothesis that *G. emiliae* is the sister taxon of *Cryptonanus* (fig. 29). Although *Gracilinanus* is recovered as a clade by parsimony analysis of nonmolecular data (fig. 27), only two morphological traits optimize as unambiguous generic synapomorphies (appendix 5).

Lestodelphys Tate, 1934
Figure 51

CONTENTS: **halli** Thomas, 1921.

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body probably ca. 120–160 mm; adult weight probably ca. 60–100 g (very few reliably measured specimens accompanied by weights are available). *Rhinarium with one ventrolateral groove on each side of median sulcus*; dark circumocular mask present; pale supraocular spot absent; dark midrostral stripe absent; throat gland present in adult males. Dorsal pelage tricolored (distinctly darker middorsally than on flanks); dorsal underfur dark gray; dorsal guard hairs short and inconspicuous; ventral fur self-white from chin to anus. Manus mesaxonic (dIII > dIV); *manual claws much longer than fleshy apical pads of digits*; dermatoglyph-bearing manual plantar pads present; central palmar epithelium densely tuberculate; carpal tubercles absent. Pedal digits unwebbed; *dIII longer than other pedal digits*; *plantar surface of heel coarsely furred*. Pouch absent; *mammae 8–1–8 = 17 or 9–1–9 = 19, of which the anteriormost teats are "pectoral"*; cloaca present. *Tail shorter than combined length of head and body, incrassate,*

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[30] All of the central Amazonian records of *Gracilinanus emiliae* mapped by Hershkovitz (1992b: fig. 1) and Brown (2004: fig. 20) are either based on misidentified material or specimens that have yet to be examined for reliably diagnostic traits (Voss et al., 2001: 29–30).
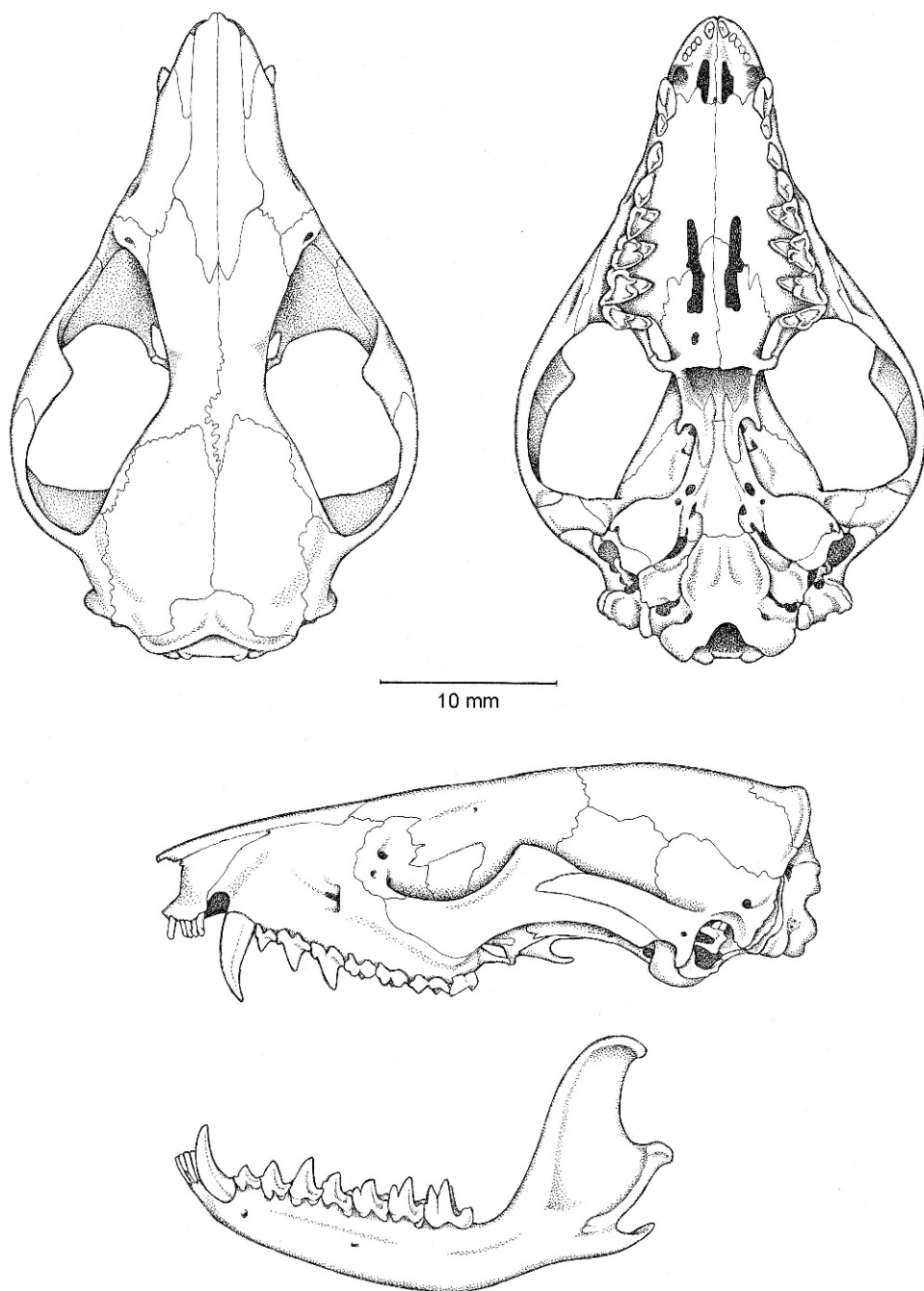
10 mm

Fig. 51. *Lestodelphys halli* (based on UWZM 22422, an adult male from Clemente Onelli, Río Negro, Argentina; and MVZ 173727, an adult male from Lihuel-Calel, La Pampa, Argentina).

and unfurred except at base; caudal integument bicolored (dark above, distinctly paler below); tail scales difficult to distinguish but apparently in annular series; caudal hairs all subequal in length and thickness; *ventral caudal surface not modified for prehension*.

Premaxillary rostral process absent. Nasals long, extending anterior to I1 (concealing nasal orifice in dorsal view), and conspicuously widened posteriorly near premaxillary-maxillary suture. Maxillary turbinals elaborately branched. Two lacrimal foramina present on each side, exposed in lateral view anterior to orbital margin. Supraorbital margins smoothly rounded, without beads or crests; postorbital frontal processes usually absent (indistinct processes are occasionally developed in old adult males). Left and right frontals and parietals separated by persistent median sutures. Parietal and alisphenoid bones in contact on lateral surface of braincase (no frontal-squamosal contact). Sagittal crest usually absent but weakly developed along midparietal suture (not extending anteriorly to frontals) in some large specimens.[31] Petrosal exposed through fenestra in parietal-squamosal suture in some individuals but not in others. Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae present but sometimes quite small; palatine fenestrae variable but usually present (Martin, 2005: fig. 2); maxillary fenestrae absent; *posterolateral palatal foramina very long*, *usually extending anteriorly lingual to M4 protocones*; posterior palatal morphology conforms to *Didelphis* morphotype (with strongly produced posterolateral corners, the choanae constricted behind). Maxillary and alisphenoid not in contact (separated by palatine) on floor of orbit. Transverse canal foramen present. Alisphenoid tympanic process smoothly globular, with well-developed anteromedial process enclosing extracranial course of mandibular nerve (secondary foramen ovale present), and not contacting rostral tympanic process of petrosal. Anterior limb of ectotympanic directly suspended from basicranium. *Stapes usually columelli-form and microperforate or imperforate. Fenestra cochleae concealed in sinus formed by rostral and caudal tympanic processes of petrosal.* Paroccipital process small, rounded, and adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina usually present on lateral surface of each hemimandible (three foramina are present unilaterally on two specimens examined); angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal ("premolariform"), with subequal anterior and posterior cutting edges, slightly increasing in length (mesiodistal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 simple, without accessory cusps. First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; *third upper premolar (P3) taller than P2*; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars strongly carnassialized (postmetacristae much longer than postprotocrista); relative widths M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus shallow or absent on M1, consistently present and distinct on M2, consistently deep on M3; anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3; postprotocrista without carnassial notch. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. Lower canine (c1) erect, acutely pointed, and simple (without a posterior accessory cusp). *Third lower premolar (p3) taller than p2*; lower milk premolar (dp3) large, but trigonid incomplete (uni- or bicuspid). *Hypoconid lingual to protoconid (not labially salient) on m3*; hypoconulid twinned with entoconid on m1–m3; entoconid taller than hypoconulid on m1–m3.

DISTRIBUTION: Most known specimens of *Lestodelphys* have been collected in semidesert shrubland and steppe habitats in Patagonian Argentina between 41° and 47°S latitude, but there are two outlying records from the Monte desert (between 32° and 38°S) that may represent a relictual population (Sauthier et al., 2007); all reported elevations

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[31] Among the specimens we examined, a small sagittal crest is best developed in UWZM 22422.

associated with collected specimens are less than 1000 m above sea level (Birney et al., 1996; Martin, 2003). As noted by Flores et al. (2007), the distribution of *Lestodelphys* extends further south than that of any other living marsupial.

Marmosops Matschie, 1916
Figures 52, 53

CONTENTS: *bishopi* Pine, 1981; *cracens* Handley and Gordon, 1979; *creightoni* Voss et al., 2004; *fuscatus* Thomas, 1896 (including *carri* J.A. Allen and Chapman, 1897; and *perfuscus* Thomas, 1924); *handleyi* Pine, 1981; *impavidus* Tschudi, 1845 (including *caucae* Thomas, 1900; *celicae* Anthony, 1922; *madescens* Osgood, 1913; *oroensis* Anthony, 1922; *sobrinus* Thomas, 1913; and *ucayalensis* Tate, 1931); *incanus* Lund, 1840 (including *bahiensis* Tate, 1931; and *scapulatus* Burmeister, 1856); *invictus* Goldman, 1912; *juninensis* Tate, 1931; *neblina* Gardner, 1990; *noctivagus* Tschudi, 1844 (including *albiventris* Tate, 1931; *collega* Thomas, 1920; *dorothea* Thomas, 1911; *keaysi* J.A. Allen, 1900; *leucastrus* Thomas, 1927; *lugendus* Thomas, 1927; *neglectus* Osgood, 1915; *politus* Cabrera, 1913; *purui* Miller, 1913; *stollei* Miranda-Ribeiro, 1936; and *yungasensis* Tate, 1931); *ocellatus* Tate, 1931; *parvidens* Tate, 1931; *paulensis* Tate, 1931; and *pinheiroi* Pine, 1981 (including *woodalli* Pine, 1981).

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body ca. 90–195 mm; adult weight ca. 20–140 g. Rhinarium with two ventrolateral grooves on each side of median sulcus; dark circumocular mask present; pale supraocular spot absent; dark midrostral stripe absent; throat gland consistently present in adult males of some species (e.g., *M. incanus*, *M. noctivagus*) but apparently absent in others (e.g., *M. impavidus*, *M. parvidens*). Dorsal pelage unpatterned, usually some shade of dull grayish brown, but distinctly reddish or grayish in some species; dorsal hair bases always dark gray; dorsal guard hairs short and inconspicuous; ventral fur self-colored (whitish, buffy, or brown) or entirely or partially gray based. Manus mesaxonic (dIII > dIV); manual claws small, shorter than fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar epithelium smooth or sparsely tuberculate; lateral carpal tubercles externally conspicuous on wrists of large adult males; medial carpal tubercles absent in both sexes. Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel macroscopically naked (a microscopic pelage of very short hairs, not coarse fur, is usually present). Pouch absent; mammae varying among examined species from 3–1–3 = 7 to 7–1–7 = 15, anteriormost pairs "pectoral" when mammae ≥11; cloaca present. Tail longer than combined length of head and body, slender and muscular (not incrassate), and macroscopically naked (without a conspicuously furred base); naked caudal integument uniformly dark (usually grayish), bicolored (dark above, pale below), or parti-colored (dark distally, paler distally); caudal scales in spiral series, each scale with three bristlelike hairs emerging from caudal margin; median hair of each caudal-scale triplet usually much thicker and darker than lateral hairs; ventral caudal surface modified for prehension distally (with naked median groove and apical pad bearing dermatoglyphs).

Premaxillary rostral process long and well developed in some species (e.g., *M. parvidens*, *M. pinheiroi*) but short in others (e.g., *M. noctivagus*) and apparently absent in some (*M. incanus*). Nasals long, extending anteriorly beyond I1 (concealing nasal orifice in dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture except in *M. incanus* (which has narrow, more or less parallel-sided nasals). Maxillary turbinals (viewed through nasal orifice) elaborately branched. Lacrimal foramina, usually two on each side, concealed from lateral view inside orbit (e.g., in *M. parvidens*) or exposed on orbital margin (e.g., in *M. pinheiroi*). Interorbital region without abrupt constrictions; supraorbital margins rounded in some species (e.g., *M. parvidens*), beaded in others (e.g., *M. noctivagus*); postorbital processes usually absent except in old males of some species (e.g., *M. impavidus*[32]). Left and right frontals and parietals separated by persistent median sutures. Parietal and alisphenoid in

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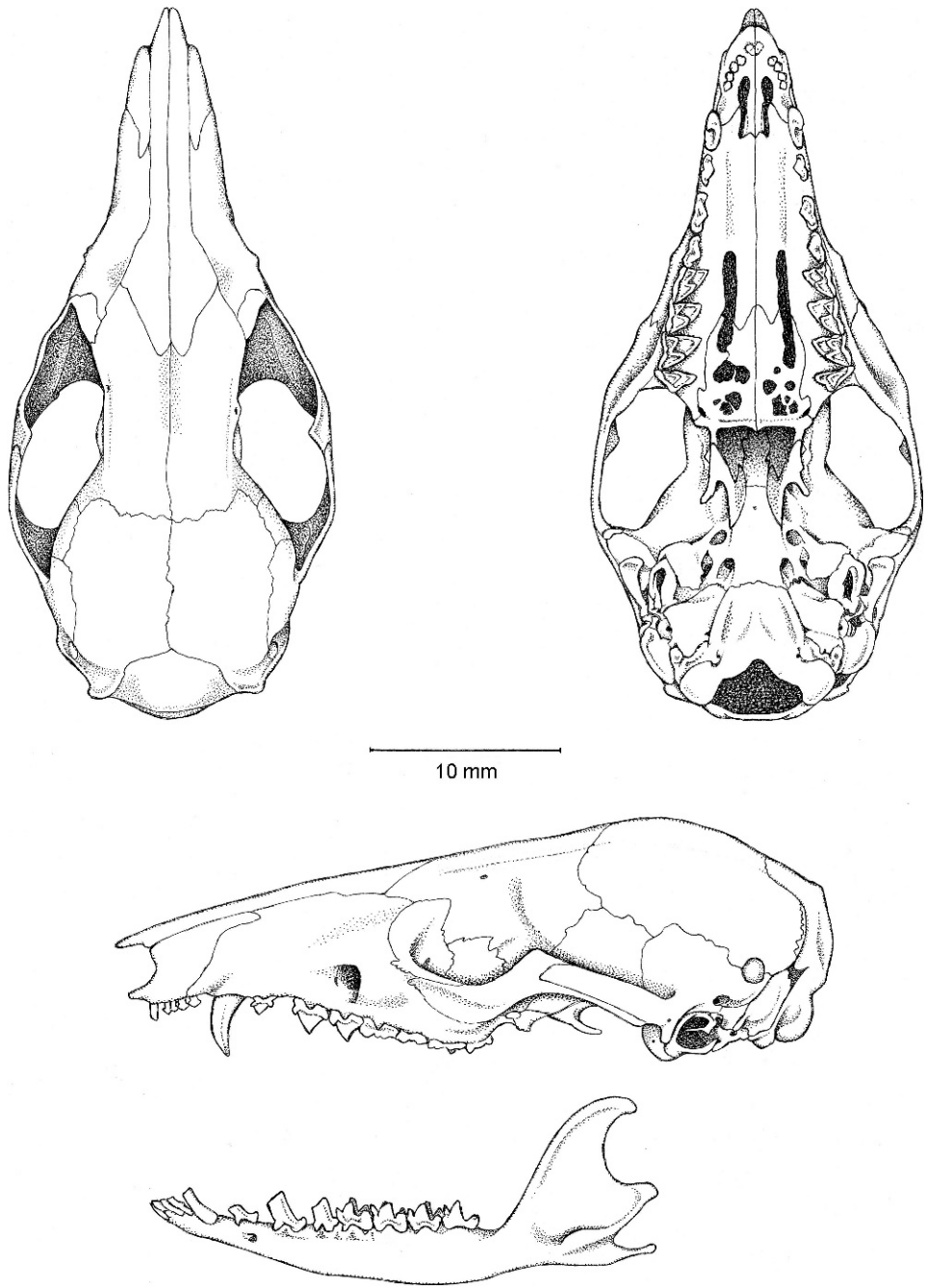[32] Postorbital processes in this species are best developed in AMNH 272760.

10 mm

Fig. 52. *Marmosops creightoni* (based on CBF 6552 and UMMZ 155999, adult males from the valley of the Río Zongo, La Paz, Bolivia).
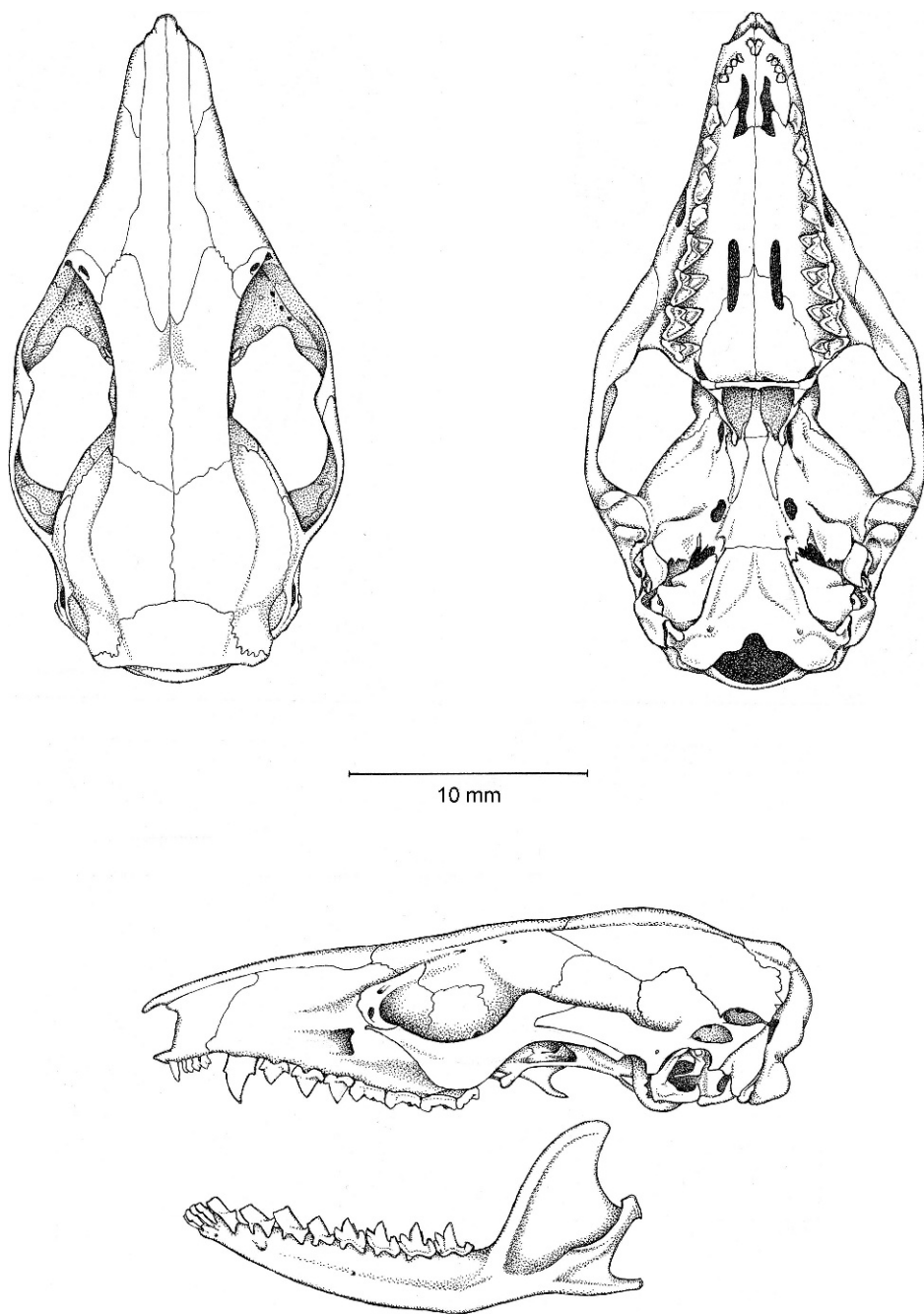
Fig. 53. *Marmosops pinheiroi* (based on AMNH 267345, a young adult male from Paracou, French Guiana), a small species that differs from *M. creightoni* (fig. 52) in several trenchant craniodental features including laterally exposed lacrimal foramina, absence of palatine vacuities, and presence of accessory cusps on C1.

contact on lateral braincase (no frontal-squamosal contact). Sagittal crest absent. Petrosal consistently exposed laterally through fenestra in parietal-squamosal suture in most species (fenestra polymorphically absent in *M. incanus* and *M. noctivagus*). Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae present; palatine fenestrae present in some species (e.g., *M. creightoni*; fig. 52), but absent in others (e.g., *M. pinheiroi*; fig. 53); maxillary fenestrae absent; posterolateral palatal foramina small, not extending anteriorly lingual to M4 protocones; posterior palatal morphology conforms to *Didelphis* morphotype (with prominent lateral corners, the choanae constricted behind). Maxillary and alisphenoid not in contact on floor of orbit (separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process small, often bluntly conical or laterally compressed (never smoothly globular), always with a well-developed anteromedial process enclosing the extracranial course of mandibular nerve (secondary foramen ovale present), and not contacting rostral tympanic process of petrosal. Anterior limb of ectotympanic directly suspended from basicranium. Stapes triangular, with large obturator foramen. Fenestra cochleae exposed, not concealed by rostral and caudal tympanic processes of petrosal. Paroccipital process small, rounded, and adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina usually present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal (''premolariform''), with subequal anterior and posterior cutting edges, increasing in length (mesiodistal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 without accessory cusps in some species (e.g., *M. creightoni*; fig. 52), or with posterior accessory cusp (e.g., *M. juninensis*), or with anterior and posterior accessory cusps (e.g., *M. pinheiroi*; fig 53). First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; second and third upper premolars (P2 and P3) subequal in height; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars strongly carnassialized (postmetacristae much longer than postprotocristae); relative widths usually M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus shallow or indistinct on M1, shallow but usually distinct on M2, and consistently deep on M3; anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3 in some species (e.g., *M. noctivagus*) but anterolabial cingulum continuous with preprotocrista (anterior cingulum complete) in others (e.g., *M. parvidens*); postprotocrista without carnassial notch. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. Second lower premolar (p2) subequal in height to p3 in some species (e.g., *M. incanus*) but distinctly taller than p3 in others (e.g., *M. impavidus*); lower milk premolar (dp3) trigonid complete. Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid usually taller than hypoconulid on m1–m3.

DISTRIBUTION: Species of *Marmosops* occur in tropical lowland and montane moist forests from central Panama southward along the Andes and throughout Amazonia to eastern Bolivia and southeastern Brazil (see maps in Gardner and Creighton, 2008a). The genus is apparently unknown from Paraguay, Argentina, and Uruguay. See Mustrangi and Patton (1997) for verified specimen records based on modern revisionary research in southeastern Brazil, Patton et al. (2000) for the same in western Amazonia, Voss et al. (2001) for northeastern Amazonia, and Voss et al. (2004b) for Bolivia. Many other published geographic data purporting to represent records of *Marmosops* species (e.g., Anderson, 1997; Brown, 2004) are based on misidentified material (Voss et al., 2004b).

REMARKS: The monophyly of *Marmosops* is uniformly strongly supported by parsimony, likelihood, and Bayesian analyses of IRBP (fig. 28), DMP1 (fig. 29), BRCA1 (fig. 31), vWF (fig. 32), and concatenated sequence data from five genes (fig. 33). The genus is also recovered with strong support by parsimony and Bayesian analyses of

combined datasets that include nonmolecular and molecular characters (figs. 35, 36), and by Bayesian analyses of nonmolecular characters (fig. 27) and RAG1 sequences (fig. 30). Spirally arranged caudal scales, the petiolate morphology of the central hair in each caudal-scale triplet, the presence of a rostral process of the premaxillae, and unique deletions at the DMP1 and BRCA1 loci optimize as unambiguous generic synapomorphies (appendix 5; figs. 29, 31). As noted elsewhere, Kirsch and Palma's (1995) suggestion that *Marmosops* is paraphyletic was based on misidentified voucher material (Voss and Jansa, 2003: 57).

Discrepancies between our species-level synonymies for *Marmosops* and those in Gardner (2005) are explained by Voss et al. (2004b). Few of the currently recognized species have received critical revisionary attention, and it seems likely that several widespread taxa (e.g., *M. fuscatus*, *M. noctivagus*, and *M. impavidus*) will prove to be composite. For regional revisions of *Marmosops* see Mustrangi and Patton (1997), Patton et al. (2000), and Voss et al. (2001, 2004b).

Thylamys Gray, 1843
Figure 54

CONTENTS: ***cinderella*** Thomas, 1902 (including *sponsorius* Thomas, 1921); ***elegans*** Waterhouse, 1839 (including *coquimbensis* Tate, 1931; and *soricinus* Philippi, 1894); ***karimii*** Petter, 1968; ***macrurus*** Olfers, 1818 (including *griseus* Desmarest, 1827); ***pallidior*** Thomas, 1902; ***pusillus*** Desmarest, 1804 (including *bruchi* Thomas, 1921; *citellus* Thomas, 1912; *nanus* Olfers, 1818; and *verax* Thomas, 1921); ***tatei*** Handley, 1957; ***velutinus*** Wagner, 1842 (including *pimelurus* Reinhardt, 1851); and ***venustus*** Thomas, 1902 (including *janetta* Thomas, 1926).

MORPHOLOGICAL DESCRIPTION: Combined length of adult head and body ca. 75–140 mm; adult weight ca. 10–65 g. Rhinarium with two ventrolateral grooves on each side of median sulcus in most examined species (but *T. pallidior* has only a single ventrolateral groove on each side); dark circumocular mask present; pale supraocular spot absent; dark midrostral stripe absent; throat gland present in fully adult males, and apparently also in adult females of some species (Carmignotto and Monfort, 2006). *Dorsal pelage usually grayish and distinctly darker middorsally than laterally ("tricolored"),* but dorsal fur brownish and without conspicuous patterning in *T. karimii* and *T. velutinus* (Carmignotto and Monfort, 2006); dorsal hair bases dark gray; dorsal guard hairs short and inconspicuous; ventral fur self-white in some species (e.g., *T. pusillus*), wholly or partly gray-based whitish or yellowish in others (e.g., *T. venustus*). Manus mesaxonic (dIII > dIV); manual claws about as long as fleshy apical pads in most species (but claws extend well beyond apical pads in *T. karimii* and *T. velutinus*; Carmignotto and Monfort, 2006); dermatoglyph-bearing manual plantar pads present in most species; central palmar epithelium densely covered with small convex tubercles; carpal tubercles absent in both sexes. Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel coarsely furred. Pouch absent; mammae varying among species from 4–1–4 = 9 (in *T. karimii*; Carmignotto and Monfort, 2006) to 7–1–7 = 15 (in *T. elegans*; Tate, 1933), including "pectoral" teats (when the total number of mammae ≥ 11); cloaca present. Tail longer than combined length of head and body in most species (except in *T. karimii* and *T. velutinus*; Carmignotto and Monfort, 2006); *apparently always incrassate* (but quantity of stored fat may vary seasonally); furred only at base (to about the same extent dorsally as ventrally); unfurred caudal integument bicolored (dark above, pale below) in most species and parti-colored in some (*T. macrurus* has an all-white tail tip); tail scales in annular series, each scale with three subequal bristlelike hairs emerging from distal margin; ventral caudal surface modified for prehension distally (with naked median groove and apical pad bearing dermatoglyphs) in most species, but ventral prehensile surface reduced or absent in *T. karimii* and *T. velutinus* (Carmignotto and Monfort, 2006).

Premaxillary rostral process absent. Nasals long, extending anteriorly above or beyond I1 (concealing nasal orifice in dorsal view), and *uniformly narrow (with subparallel lateral margins) in most specimens.* Maxillary turbinals elaborately branched. Two lacrimal
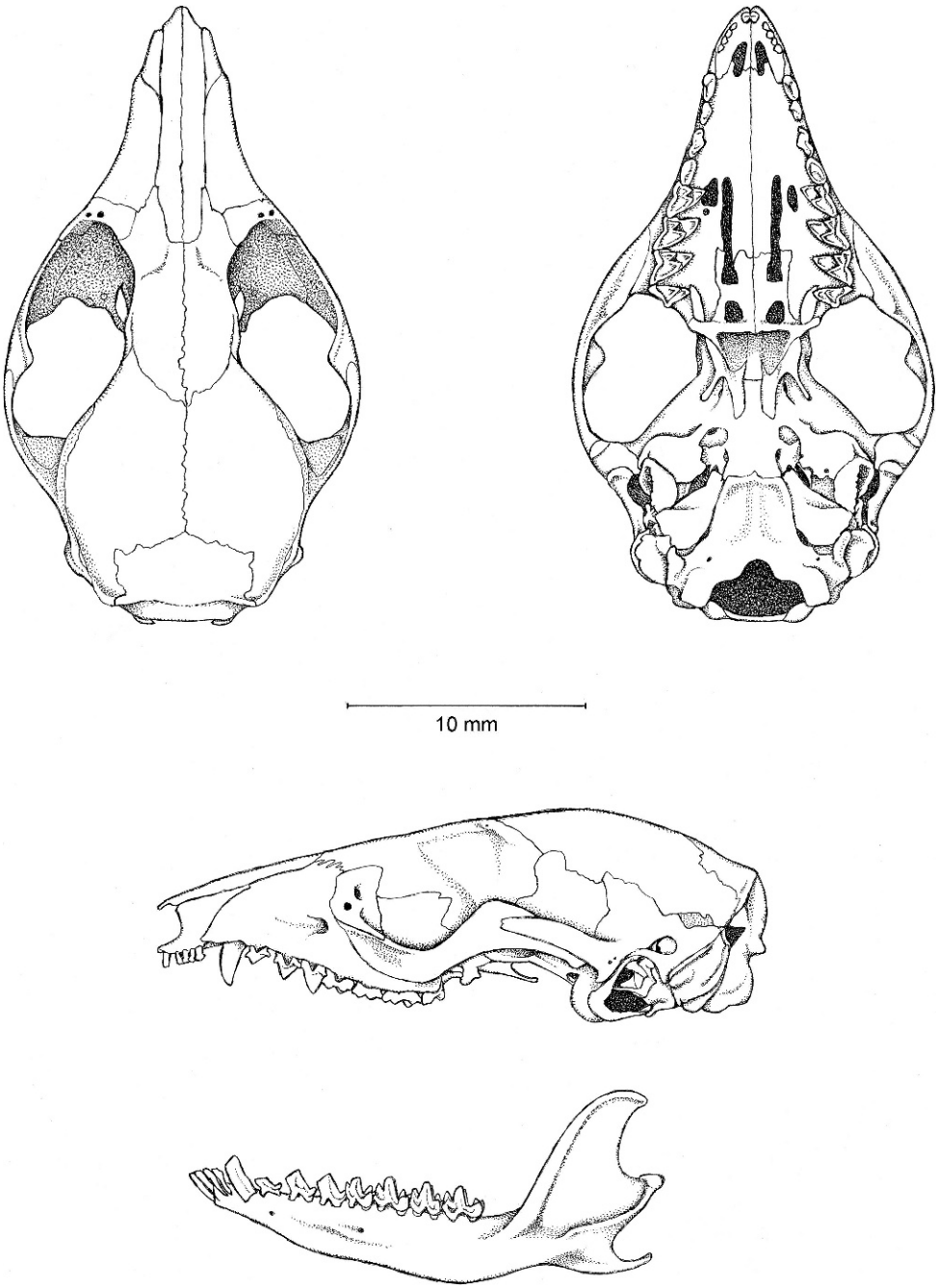
10 mm

Fig. 54.　*Thylamys pusillus* (based on AMNH 275442, an adult female, and 275445, an adult male, both from Estancia Bolívar, Tarija, Bolivia).

foramina present on each side, exposed to lateral view on anterior orbital margin in most species, but usually concealed inside orbit in others (e.g., *T. tatei*). Interorbital and postorbital constrictions often distinct; supraorbital margins rounded in some species (e.g., *T. pallidior*), squared or beaded in others; postorbital processes usually absent or indistinct but occasionally present in old adults of some species (e.g., *T. macrurus*). Left and right frontals and parietals separated by persistent median sutures. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest absent. Petrosal almost always exposed laterally through fenestra in parietal-squamosal suture. Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae present; palatine fenestrae present; maxillary fenestrae present in some species (e.g., *T. pusillus*) but absent in others (e.g., *T. pallidior*); *posterolateral palatal foramina very large*, *extending anteriorly between M4 protocones*; posterior palatal morphology conforms to *Didelphis* morphotype (with prominent lateral corners, the choanae constricted behind). Maxillary and alisphenoid not in contact on floor of orbit (separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process smoothly globular, with anteromedial process enclosing extracranial course of mandibular nerve (secondary foramen ovale present), and not contacting rostral tympanic process of petrosal. Anterior limb of ectotympanic directly suspended from basicranium. Stapes triangular, with large obturator foramen. *Fenestra cochleae concealed in sinus formed by rostral and caudal tympanic processes of petrosal*. Paroccipital process small, rounded, adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal ("premolariform"), with subequal anterior and posterior cutting edges, increasing in length (mesiodistal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 without accessory cusps in all examined species (but see Carmignotto and Monfort, 2006).[33] First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; third upper premolar (P3) taller than P2; P3 with posterior cutting edge only; upper milk premolar (dP3) large, molariform, and nonvestigial. Molars strongly carnassialized (postmetacristae much longer than postprotocristae); relative widths usually M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus absent or indistinct on M1, usually present but shallow on M2, consistently deep and distinct on M3; anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3; postprotocrista without carnassial notch. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. *Second and third upper premolars (p2 and p3) subequal in height*; lower milk premolar (dp3) trigonid usually incomplete (bicuspid). Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid much taller than hypoconulid on m1–m3.

DISTRIBUTION: Species of *Thylamys* collectively range from north-central Peru (Ancash) southward along the Andes and Pacific coastal lowlands to central Chile; in the unforested landscapes south of Amazonia, the genus extends eastward across Bolivia (Anderson, 1997), Paraguay, and Argentina (Flores et al., 2007) to Uruguay (González et al., 2000) and eastern Brazil (Bahia, Pernambuco, and Piauí; Carmignotto and Monfort, 2006). Recorded elevations range from near sea level to at least 3800 m (Solari, 2003).

REMARKS: The monophyly of *Thylamys* is strongly supported by parsimony, likelihood, and Bayesian analyses of IRBP (fig. 28), BRCA1 (fig. 31), vWF (fig. 32), and concatenated sequence data from five genes (fig. 33). Strong support for this clade is also

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[33] Although several Brazilian species of *Thylamys* were scored as polymorphic for presence of posterior accessory canine cusps by Carmignotto and Monfort (2006: table 4), the increasing frequencies that they observed in older age classes suggest that C1 in these taxa is notched by occlusion with p1 in their material, and that the structure in question is not homologous with the posterior accessory cusp scored from specimens with unworn dentitions by Voss and Jansa (2003: character 53).

provided by parsimony and likelihood analyses of DMP1 (fig. 29) and by parsimony and Bayesian analyses of RAG1 (fig. 30) and combined datasets that include both nonmolecular and molecular characters (figs. 35, 36). The monophyly of *Thylamys* is also recovered with moderate support by parsimony analysis of nonmolecular characters (fig. 27), but only one morphological trait (uniformly narrow nasals; see appendix 5) optimizes as an unambiguous generic synapomorphy.

We tentatively recognize *bruchi* as a synonym of *Thylamys pusillus* following Voss et al. (in press), who explain why the former name does not belong in the synonymy of *T. pallidior* (contra Creighton and Gardner, 2008c), and we refer *sponsorius* to the synonymy of *T. cinderella* following Braun et al., (2005). The names *pulchellus* Cabrera, 1934, and *fenestrae* Marelli, 1932, might be synonyms of *T. pusillus* and *T. pallidior*, respectively, but we have not seen the holotypes and published information about these nominal taxa is insufficient to support any definite conclusions about them. Many other species-level issues in this genus remain problematic despite much recent taxonomic work (e.g., Palma et al., 2002; Solari, 2003; Braun et al., 2005; Carmignotto and Monfort, 2006).

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APPENDIX 1

Morphological Specimens Examined

The specimens from which morphological character data were scored for phylogenetic analysis are listed below. These include the skins, skulls, and fluid-preserved material previously examined by Voss and Jansa (2003), Voss et al. (2004a, 2005), and Jansa and Voss (2005), together with additional material newly examined for this report. Except as noted, all examined specimens (including vouchers for sequenced tissues; see appendix 2) are preserved in collections identified by the following institutional acronyms: AMNH, American Museum of Natural History (New York); AMS, Australian Museum (Sydney); ANWC, Australian National Wildlife Collection (Canberra); BMNH, Natural History Museum (London); CM, Carnegie Museum of Natural History (Pittsburgh); CNP, Centro Nacional Patagónico (Puerto Madryn); FMNH, Field Museum of Natural History (Chicago); INPA, Instituto Nacional de Pesquizas da Amazônia (Manaus); KU, University of Kansas Museum of Natural History (Lawrence); MCZ, Museum of Comparative Zoology at Harvard University (Cambridge); MMNH, Bell Museum of Natural History (University of Minnesota, St. Paul); MNHN, Muséum National d'Histoire Naturelle (Paris); MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima); MVZ, Museum of Vertebrate Zoology (University of California, Berkeley); ROM, Royal Ontario Museum (Toronto); SAM, South Australian Museum (Adelaide); TTU, Museum of Texas Tech University (Lubbock); UMMZ, University of Michigan Museum of Zoology (Ann Arbor); UMSNH, Universidad Michoacana de San Nicolas de Hidalgo (Morelia); USNM, National Museum of Natural History (Washington, DC); UWZM, University of Wisconsin Zoological Museum (Madison); V-, voucher collection of F. Catzeflis, Université de Montpellier (Montpellier).

Caenolestidae

Caenolestes fuliginosus—Skins: UMMZ 155572, 155580. Adult skulls: FMNH 70847; UMMZ 127107–127109, 127156, 155575, 155581. Subadult skulls: FMNH 70858, 70859, 92299. Juvenile skulls: none. Fluid specimens: AMNH 248261, 248271.

Rhyncholestes raphanurus—Skins: FMNH 50071, 124002. Adult skulls: FMNH 127468, 127474, 129824, 129827, 129828, 129834, 135035. Subadult skulls: none. Juvenile skulls: none. Fluid specimens: FMNH 129825.

Dasyuridae

Murexia longicaudata—Skins: AMNH 105022, 108558. Adult skulls: AMNH 101971–101973, 108554, 108555, 108557, 108558. Subadult skulls: none. Juvenile skulls: AMNH 101970. Fluid specimens: AMNH 196649.

Sminthopsis crassicaudata—Skins: none. Adult skulls: SAM 8254, 19819, 12332, 12333. Subadult skulls: SAM 8441. Juvenile skulls: SAM 11536. Fluid specimens: AMNH 160413 (parous female), 160416.

Didelphidae

Caluromys lanatus—Skins: MUSM 15290, 15291; MVZ 190248, 190249. Adult skulls: AMNH 230001, 273038, 273059; MVZ 190249, 190251. Subadult skulls: MUSM 15291. Juvenile skulls: AMNH 75913; MUSM 15290; MVZ 190248. Fluid specimens: AMNH 273038, 273059; MVZ 191185 (parous female).

Caluromys philander—Skins: AMNH 266408, 266409, 267001. Adult skulls: AMNH 266409, 267002, 267335–267337. Subadult skulls: AMNH 266408, 267332. Juvenile skulls: AMNH 96629, 96652, 267330, 267333, 267334. Fluid specimens: AMNH 266402 (parous female), 266408.

Caluromysiops irrupta—Skins: AMNH 208101; FMNH 68336; USNM 396061, 397626. Adult skulls: AMNH 208101, 244364; FMNH 60698, 84426; USNM 396061, 397626. Subadult skulls: none. Juvenile skulls: FMNH 68336, 121522. Fluid specimens: FMNH 60154, 60398.

Chacodelphys formosa—Skins: USNM 236330. Adult skulls: CNP 639, USNM 236330, plus several uncataloged cranial fragments recovered from owl pellets. Subadult skulls: none. Juvenile skulls: none. Fluid specimens: none.

Chironectes minimus—Skins: AMNH 164494, 264571, 264572, 266477, 266478. Adult skulls: AMNH 33027, 37483, 47190, 62365, 72020, 96759, 96760, 97319, 129704, 164494, 182939, 212909, 264572. Subadult skulls: AMNH 34197. Juvenile skulls: AMNH 16072, 126979, 127563, 128994, 264573, 266478. Fluid specimens: AMNH 24411, 150033, 266479; UMMZ 134560 (parous female).

Cryptonanus chacoensis—Skins: AMNH 167851, UMMZ 126105, USNM 236329. Adult skulls: UMMZ 126105, 134552, 137143; USNM 236329. Subadult skulls: AMNH 167851. Juvenile skulls: BMNH 11.11.19.23. Fluid specimens: UMMZ 134552 (parous female).

Cryptonanus unduaviensis—Skins: AMNH 209150, 209153, 209154; FMNH 114658, 114665. Adult skulls: AMNH 209150, 209152–209155; FMNH 114658. Subadult skulls: AMNH 262401, FMNH 114664. Juvenile skulls: FMNH 114667. Fluid specimens: AMNH 247754, MSB 70752.

Didelphis albiventris—Skins: AMNH 66779, 132897, 132898, 132906, 248304, 248305. Adult skulls: AMNH 132905, 132942, 248303, 248304. Subadult skulls: AMNH 66779, 132929. Juvenile skulls: AMNH 132894, 238007. Fluid specimens: AMNH 202706; UMMZ 134565–134567.

Didelphis marsupialis—Skins: AMNH 209177, 247654, 266457, 266462. Adult skulls: AMNH 266457, 266459, 266468, 266471, 266474. Subadult skulls: AMNH 266460, 266472. Juvenile skulls: AMNH 266464, 266466, 266470, 266473, 266475, 267367. Fluid specimens: AMNH 210445, 272836.

Didelphis virginiana—Skins: AMNH 90322, 139915, 146632, 180141, 180142. Adult skulls: AMNH 217749, 217762, 217772, 217775, 217786, 219223, 219224, 219231, 219234, 219235. Subadult skulls: AMNH 217750, 217782, 219868. Juvenile skulls: AMNH 217780, 217790, 219869, 219878, 240517. Fluid specimens: UMMZ 103462 (parous female), 110758, 114837 (parous female).

Glironia venusta—Skins: AMNH 71394, 71395; FMNH 41440. Adult skulls: AMNH 71394, 71395; FMNH 41440. Subadult skulls: INPA 2570. Juvenile skulls: none. Fluid specimens: INPA 2570.

Gracilinanus aceramarcae—Skins: AMNH 72568, LSU 17897, MVZ 171411. Adult skulls: AMNH 72568, LSU 17897, MVZ 171411, UMMZ 156004, 156005. Subadult skulls: none. Juvenile skulls: none. Fluid specimens: UMMZ 156004, 156005.

Gracilinanus agilis—Skins: MVZ 197437–197441. Adult skulls: MVZ 197437–197441. Subadult skulls: none. Juvenile skulls: AMNH 133224. Fluid specimens: MVZ 197649, 197651, 197652, 197655.

Gracilinanus emiliae—Skins: AMNH 203363, BMNH 9.3.9.10. Adult skulls: AMNH 203363, MUSM 15292, ROM 35466. Subadult skulls: AMNH 267006. Juvenile skulls: ROM 33807, USNM 385066. Fluid specimens: AMNH 267006, MUSM 15292 (parous adult female), ROM 35465 (parous adult female).

Gracilinanus microtarsus—Skins: FMNH 92958, 94294, 94295; MVZ 182055, 197436. Adult skulls: FMNH 94294, 94295; MVZ 197436. Subadult skulls: FMNH 92958; MVZ 182055–182057. Juvenile skulls: none. Fluid specimens: MVZ 182054.

Hyladelphys kalinowskii—Skins: FMNH 89991. Adult skulls: AMNH 267003, 267338, 267339; FMNH 65754, 89991; ROM 34271. Subadult skulls: none. Juvenile skulls: MUSM 11031, and an uncataloged specimen (field number V-1791) to be deposited at the MNHN. Fluid specimens: AMNH 267338, 267339 (parous adult female).

Lestodelphys halli—Skins: BMNH 28.12.11.207; MMNH 15708, 17171; MVZ 173727; UWZM 22422. Adult skulls: BMNH 28.12.11.207; MVZ 160109, 171069, 171070, 179180, 179182, 173727; UWZM 22422. Subadult skulls: MMNH 15708. Juvenile skulls: MMNH 17171; MVZ 17193. Fluid specimens: none.

Lutreolina crassicaudata—Skins: AMNH 133249, 133250, 143886. Adult skulls: AMNH 133249, 139825, 210420, 254512, 254513. Subadult skulls: AMNH 133255, 210419. Juvenile skulls: AMNH 210421, 210423, 210424. Fluid specimens: AMNH

202727, 235546; UMMZ 166634 (parous female); USNM 536827 (parous female).

Marmosa (Marmosa) lepida—Skins: AMNH 67279, 182937; MNHN 1998.306; MVZ 154750. Adult skulls: AMNH 78001, 98656, 273186; KU 135118; MNHN 1998.306; MVZ 154750, 155245; USNM 461468. Subadult skulls: MNHN 1982.653; MVZ 154752. Juvenile skulls: FMNH 140824. Fluid specimens: AMNH 273186; KU 135118; MVZ 155245.

Marmosa (Marmosa) mexicana—Skins: AMNH 12454/10763, 243700; ROM 95795, 96090, 99776. Adult skulls: AMNH 189209, 189484, 265851; ROM 96090, 99608. Subadult skulls: AMNH 17136, 213754. Juvenile skulls: AMNH 189483, 189485. Fluid specimens: AMNH 265851 (parous female).

Marmosa (Marmosa) murina—Skins: AMNH 273178; MUSM 15296. Adult skulls: AMNH 272816, 273062, 273063, 273140, 273178, 273188; MUSM 15293. Subadult skulls: AMNH 272870; MUSM 13283, 15294. Juvenile skulls: MUSM 15295, 15297. Fluid specimens: AMNH 268214, 272816, 273063, 273140; MUSM 15293.

Marmosa (Marmosa) robinsoni—Skins: AMNH 36725, 36728, 37890, 147759. Adult skulls: USNM 456812, 456815, 456821, 456826, 456833. Subadult skulls: USNM 456825. Juvenile skulls: USNM 456813, 456814, 456817, 456820, 456848. Fluid specimens: UMMZ 117236, 117237.

Marmosa (Marmosa) rubra—Skins: AMNH 71950, 71952, 71974; MVZ 153280, 153282, 153283, 154765. Adult skulls: MVZ 153280, 153282, 153283, 154765. Subadult skulls: none. Juvenile skulls: AMNH 68128, 68129; MVZ 154759. Fluid specimens: none.

Marmosa (Micoureus) demerarae—Skins: AMNH 266427, 266428, 267370, 267818. Adult skulls: AMNH 266427, 266428, 266431, 266432, 267370, 267371. Subadult skulls: AMNH 266433, 267369. Juvenile skulls: AMNH 266429, 266430, 266434. Fluid specimens: AMNH 266427, 266428, 266432 (parous female).

Marmosa (Micoureus) paraguayana—Skins: MVZ 182063, 182064; UMMZ 165664. Adult skulls: MVZ 182063–182065; UMMZ 165664. Subadult skulls: none. Juvenile skulls: none. Fluid specimens: MVZ 182065; UMMZ 134551.

Marmosa (Micoureus) regina—Skins: AMNH 273164; MUSM 11063, 15316; MVZ 190323, 190332. Adult skulls: MVZ 190323, 190325, 190331, 190332. Subadult skulls: MVZ 190333. Juvenile skulls: MVZ 190324, 190328. Fluid specimens: MVZ 191201 (parous female).

Marmosops impavidus—Skins: AMNH 272760; MUSM 15298, 15299. Adult skulls: AMNH 272709, 272760, 273151; MUSM 13284, 15299, 15300. Subadult skulls: AMNH 273050. Juvenile skulls: MUSM 13285, 13286, 15306, 15307. Fluid specimens: AMNH 272709 (parous female), 273151; MUSM 13284, 15300.

Marmosops incanus—Skins: MVZ 182061, 182768, 182769; UMMZ 165662, 165663. Adult skulls: MVZ 182061, 182768–182770; UMMZ 165662, 165663. Subadult skulls: UMMZ 165661. Juvenile

skulls: none. Fluid specimens: MVZ 182771, 197629.

Marmosops noctivagus—Skins: AMNH 272775, 273131; MUSM 15305. Adult skulls: AMNH 272775, 272782, 272809, 273051; MUSM 13288. Subadult skulls: MUSM 15301, 15303. Juvenile skulls: AMNH 272704, 272715; MUSM 13289–13292. Fluid specimens: AMNH 272782 (parous female), 272809, 273034, 273051 (parous female); MUSM 13288.

Marmosops parvidens—Skins: AMNH 266426, 267817. Adult skulls: AMNH 266421, 267344, 267347, 267353, 267359, 267361. Subadult skulls: AMNH 266422, 266425, 267817. Juvenile skulls: AMNH 266426, 267350, 267355. Fluid specimens: AMNH 267344 (parous female), 267348, 267353, 267359, 267361.

Marmosops pinheiroi—Skins: AMNH 266423, 267007, 267352. Adult skulls: AMNH 267340, 267342, 267345, 267346, 267349, 267352, 267357. Subadult skulls: AMNH 267007, 267356. Juvenile skulls: AMNH 266424, 267008, 267351, 267354. Fluid specimens: AMNH 267342 (parous female), 267345, 267346, 267356 (parous female), 267357.

Metachirus nudicaudatus—Skins: AMNH 266450, 267009, 267010. Adult skulls: AMNH 266435–266437, 266440, 266449, 266450, 267009, 267010. Subadult skulls: AMNH 266439, 267362. Juvenile skulls: AMNH 266451–266453, 267364. Fluid specimens: AMNH 255815, 261283, 261285; USNM 461138, 577756 (parous female).

Monodelphis brevicaudata—Skins: AMNH 36317, 48133, 75830, 75831. Adult skulls: AMNH 257203; USNM 393438, 393439, 393441, 461435, 578009. Subadult skulls: AMNH 268061; USNM 393426, 393431. Juvenile skulls: AMNH 16953, 267744; USNM 392046, 392049, 393429, 393432, 393434, 393440, 393442, 543303, 568009. Fluid specimens: AMNH 140465, 140466, 244469.

Monodelphis emiliae—Skins: AMNH 268221; MUSM 13298; MVZ 190334; USNM 461883, 461884. Adult skulls: AMNH 268221; MUSM 13298; MVZ 190334; USNM 461883, 461884, 579574. Subadult skulls: MVZ 190335. Juvenile skulls: AMNH 95816. Fluid specimens: AMNH 95816; USNM 579574.

Monodelphis peruviana—Skins: AMNH 272695; MUSM 13297; USNM 582782, 588019. Adult skulls: AMNH 272695; MUSM 7157, 11654, 13297; USNM 582782, 588019. Subadult skulls: AMNH 272781. Juvenile skulls: none. Fluid specimens: AMNH 272781; MUSM 15318.

Monodelphis theresa—Skins: FMNH 25738; MVZ 182775. Adult skulls: FMNH 25739; MVZ 182775, 182776. Subadult skulls: none. Juvenile skulls: none. Fluid specimens: FMNH 25739; MVZ 182776.

Philander frenatus—Skins: MVZ 182066, 182067, 183246, 183247. Adult skulls: MVZ 182066, 182067, 183246. Subadult skulls: none. Juvenile skulls: none. Fluid specimens: MVZ 182068 (parous female).

Philander mcilhennyi—Skins: AMNH 272818, 273054, 273089; MUSM 13299. Adult skulls: AMNH 272818, 273040, 273054, 273055, 273089; MUSM

13299. Subadult skulls: MVZ 190336, 190338. Juvenile skulls: AMNH 273039; MUSM 15319–15321, 15323. Fluid specimens: MUSM 15319; MVZ 191202 (parous female), 191203 (parous female).

Philander opossum—Skins: AMNH 266995, 266996, 266998, 267014. Adult skulls: AMNH 266379, 266381, 266386, 266387, 267014, 267328. Subadult skulls: AMNH 266389, 266994. Juvenile skulls: AMNH 266394, 266395, 266398, 266400, 266997. Fluid specimens: AMNH 266380, 266390.

Thylamys macrurus—Skins: MSB 70700, MZUSP 32094–32096, UMMZ 125243. Adult skulls: BMNH 3.4.7.21, MSB 70700, MZUSP 32094–32096, UMMZ 125243. Subadult skulls: BMNH 99.11.17.1. Juvenile skulls: none. Fluid specimens: MZUSP 32097.

Thylamys pallidior—Skins: AMNH 262406–262408; FMNH 54255, 162495. Adult skulls: AMNH 262406–262408; FMNH 54255, 162495. Subadult skulls: AMNH 262405. Juvenile skulls: FMNH 51004–51006. Fluid specimens: UMMZ 156015.

Thylamys pusillus—Skins: AMNH 275440, 275442; MSB 67016. Adult skulls: AMNH 246444, 246448, 275440, 275442, 275445, 275446; MSB 67016, 87105. Subadult skulls: AMNH 246449; UMMZ 155837, 155840. Juvenile skulls: AMNH 246452; UMMZ 155838, 155839, 155841. Fluid specimens: UMMZ 156026, 156029, 156030, 156032 (parous adult female).

Thylamys venustus—Skins: AMNH 263558, 263562; FMNH 162505. Adult skulls: AMNH 263558, 263561, 263562; FMNH 162505. Subadult skulls: AMNH 262400, 263555, 263557. Juvenile skulls: AMNH 263559, 263560. Fluid specimens: AMNH 261250, 261251.

Tlacuatzin canescens—Skins: AMNH 24896, 149104, 172128, 185769. Adult skulls: AMNH 24894, 148969, 148970; USNM 70767, 73320, 125659, 125925. Subadult skulls: AMNH 185770, 213753; USNM 37134, 70241, 96754, 508354. Juvenile skulls: AMNH 145237; USNM 70239, 70242. Fluid specimens: AMNH 144638, 165653; USNM 9514.

Microbiotheriidae

Dromiciops gliroides—Skins: AMNH 92147, 97746; FMNH 127450. Adult skulls: FMNH 50075, 127440, 127453, 127460, 127464, 129804, 129807. Subadult skulls: FMNH 127437, 127438, 127447. Juvenile skulls: FMNH 22673, 22675, 127445, 127465. Fluid specimens: AMNH 238022; FMNH 127439 (parous female), 127456.

Peramelidae

Echymipera kalubu—Skins: AMNH 190970, 190976, 221664. Adult skulls: AMNH 190970, 190973, 190984, 190986, 192168, 236834. Subadult skulls: AMNH 221663. Juvenile skulls: AMNH 190977, 190978, 221654, 221662. Fluid specimens: AMNH 152838, 192693, 192694.

Perameles gunnii—Skins: none. Adult skulls: MVZ 127059, 127070–127073, 127099, 127100, 132246, 132248. Subadult skulls: none. Juvenile skulls: MVZ 127060. Fluid specimens: MVZ 127057 (parous female), 127062.

APPENDIX 2

Specimens Sequenced for Nuclear Genes

Nuclear gene sequences were obtained from the following specimens, listed alphabetically by family, genus, and species. The institutional catalog number of each voucher specimen is listed first (in parentheses), followed by a tissue identifier (if any, in square brackets). See appendix 1 for institutional abbreviations.

Caenolestidae

Caenolestes fuliginosus: Ecuador, Bolívar, 4 km E Cruz de Lizo (MSB 70587 [NK 27708]).

Rhyncholestes raphanurus: Chile, Osorno, La Picada (Universidad Austral de Chile, unvouchered [LG 420]).

Dasyuridae

Murexia longicaudata: Papua New Guinea, Morobe, Mt. Missim (ANWC M29669 [''female 3'']); Papua New Guinea, Southern Highlands Province, Bobole (AMS M18453 [ABTC 45110]).

Sminthopsis crassicaudata: Australia, New South Wales, Remington Station (ANWC M16816); Australia, South Australia, Ngarkat Conservation Park (SAM M20207 [ABTC 27560]).

Didelphidae

Caluromys lanatus: Ecuador, Napo, Parque Nacional Yasuní (ROM 104570).

Caluromys philander: French Guiana, Les Nouragues (V-823 [T-1754], V-960 [T-2020]).

Caluromysiops irrupta: New York Zoological Society (AMNH 244364).

Chironectes minimus: Guyana, Barima-Waini, Waikerebi (ROM 98855 [FN 31677]).

Cryptonanus chacoensis: Paraguay, Caazapá, Estancia Dos Marias (uncataloged specimen returned to Paraguay [GD 521]).

Cryptonanus unduaviensis: Bolivia, Pando, Independencia (AMNH 262401 [NK 14234]); Bolivia, Santa Cruz, Santiago de Chiquitos (AMNH 260032 [NK 12313]).

Didelphis albiventris: Paraguay, Canendiyu, 13.3 km N Curuguaty (UMMZ 134041 [GKC 783]); Paraguay, Presidente Hayes, 24 km NW Villa Hayes (UMMZ 134058 [GKC 816]).

Didelphis marsupialis: Peru, Loreto, Río Gálvez (AMNH 272836 [RSV 2357], MUSM 13282 [RSV 2273]).

Didelphis virginiana: Mexico, Yucatán, 1.5 km N Labna (ROM 96483 [FN 30300]).

Glironia venusta: Brazil, Amazonas, alto Rio Urucu (INPA 2570 [MNFS 75]).

Gracilinanus aceramarcae: Peru, Cusco, Cordillera Vilcabamba (MUSM 13002 [LHE 1342]).

Gracilinanus agilis: Brazil, Minas Gerais, Mata do Vasco, 12 km W Nova Ponte (MVZ 197438 [LPC 363], MVZ 197439 [LPC 364]).

Gracilinanus emiliae: Peru, Loreto, Río Gálvez, Nuevo San Juan (MUSM 15292 [DWF 413]).

Gracilinanus microtarsus: Brazil, São Paulo, Fazenda Intervales (MVZ 182055 [MAM 38], MVZ 182056 [MAM 49]).

Hyladelphys kalinowskii: French Guiana, Route de Kaw, 30 km SE Cayenne (MNHN, uncataloged [T4385]).

Lestodelphys halli: Argentina, Río Negro, 10 km by road E Clementi Onelli (UWZ 22422 [Kirsch lab extract 775]).

Lutreolina crassicaudata: Paraguay, Misiones, 2 km NE Ayolas (UMMZ 134018 [GKC 848], UMMZ 134019 [GKC 849]).

Marmosa (Marmosa) lepida: Guyana, Potaro-Siparuni, Iwokrama Reserve (ROM 107034 [F 38809]); Peru, Amazonas, Huampami on Río Cenepa (MVZ 155245 [FC 4928, JLP7844]).

Marmosa (Marmosa) mexicana: Guatemala, El Petén, Biotopo Cerro Cahui, El Ramate (ROM 99608 [FN 32277]); Guatemala, El Progreso, Río Uyús, 5 km E San Cristóbal, Acasaguascatlán (ROM 99776 [FN 34135]).

Marmosa (Marmosa) murina: Peru, Loreto, Río Gálvez (AMNH 272816 [RSV 2303], AMNH 272870 [RSV 2413]); Surinam, Para, Zanderij (CM 68346 [TK 17359], 68353 [TK 17387]).

Marmosa (Marmosa) robinsoni: Panama, Darién, Cana (TTU 39117 [TK 22552], 39118 [TK 22555]).

Marmosa (Marmosa) rubra: Peru, Amazonas, 0.5 mi W Huampami on Río Cenepa (MVZ 153280 [JLP 6930]).

Marmosa (Micoureus) demerarae: Peru, Loreto, Río Gálvez (AMNH 272667 [RSV 2029], MUSM 13294 [RSV 2085]).

Marmosa (Micoureus) paraguayana: Brazil, São Paulo, Fazenda Intervales, Capão Bonito (MVZ 182064 [MAM 46], 182065 [MAM 47]).

Marmosa (Micoureus) regina: Brazil, Amazonas, Igarapé Nova Empresa, left bank Rio Juruá (MVZ 190323 [JLP 15435]); Brazil, Acre, Igarapé Porongaba, right bank Rio Juruá (MVZ 190332 [MNFS 1232]).

Marmosops impavidus: Peru, Loreto, Río Gálvez (AMNH 272760 [RSV 2202], MUSM 13284 [RSV 2114]).

Marmosops incanus: Brazil, Minas Gerais, Estação Biológica de Caratinga, Fazenda Montes Claros, 54 km E Caratinga (MVZ 182768 [MAM 201], 182769 [MAM 202]).

Marmosops noctivagus: Ecuador, Napo, Parque Nacional Yasuní (ROM 105316 [F 37644]); Peru, Loreto, Río Gálvez (AMNH 272775 [RSV 2225], AMNH 272782 [RSV 2242], AMNH 272809 [RSV 2294], MUSM 13289 [RSV 2224], MUSM 13292 [RSV 2131]).

Marmosops parvidens: Guyana, Upper Takutu-Upper Essequibo, Karanambo (ROM 97938 [FN 33439]).

Marmosops pinheiroi: Guyana, Potaro-Siparuni, Iwokrama Reserve (ROM 108920 [F 43900]).

Metachirus nudicaudatus: Peru, Loreto, Río Gálvez (AMNH 272780 [RSV 2236], MUSM 13293 [RSV 2329]).

Monodelphis brevicaudata: Surinam, Saramacca, Raleigh Falls (CM 63511 [TK 10244]); Surinam, Nickerie, Kayserberg Airstrip (CM 68359 [TK 17069]).

Monodelphis emiliae: Peru, Loreto, Río Gálvez (MUSM 13298 [RSV 2083]).

Monodelphis peruvianus (= *M.* "*adusta*" of previous reports; see Solari, 2007): Peru, Loreto, Río Gálvez (AMNH 272695 [RSV 2086]).

Monodelphis theresa: Brazil, São Paulo, Ilha de Sebastião, Parque Estadual Ilhabela (MVZ 182776 [MAM 160]).

Philander frenatus: Brazil, São Paulo, Fazenda Intervales, Capão Bonito (MVZ 182066 [MAM 41], 182067 [MAM 64]).

Philander mcilhennyi: Peru, Loreto, Río Gálvez (AMNH 272818 [RSV 2310], MUSM 13299 [RSV 2153]).

Philander opossum: Surinam, Para, Zanderij (CM 68365 [TK 17015]); Surinam, Suriname, Plantation Clevia, 8 km NE Paramaribo (CM 76743 [TK 17524]).

Thylamys macrurus: Paraguay, Concepción, 7 km NE Concepción (MSB 70700 [NK 27536].

Thylamys pallidior: Bolivia, Tarija, roadside above Cieneguillas (FMNH 162495 [NBH 76-97]).

Thylamys pusillus: Bolivia, Tarija, Estancia Bolívar (MSB 67016 [NK 25139]).

Thylamys venustus: Bolivia, Tarija, Chuquiaca (FMNH 162505 [BDP 3345]); Bolivia, Tarija, ca. 10 km by road W Narváez (FMNH 162507 [BDP 3309]).

Tlacuatzin canescens: Mexico, Jalisco, 6 km SE Chamela (TTU 37700 [TK 11826]); Mexico, Michoacan, 1 km E Playa Azul (UMSNH 2993 [TK 45085]).

Microbiotheriidae

Dromiciops gliroides: Argentina, Neuquen, near Estancia Paso Coihue (MVZ 184914 [JLP 16545]).

Peramelidae

Echymipera kalubu: Papua New Guinea, Western Highlands, Trauna Valley (MVZ 138476 [FC 868]).

Perameles gunni: Australia, Tasmania, Ridgley (SAM, unvouchered [ABTC 66105]).

APPENDIX 3

Nonmolecular Character Descriptions

EXTERNAL MORPHOLOGY

Character 1: *Pars supralabialis of rhinarium broad (0); or reduced to a narrow philtrum (1).* See text for a discussion of this character and its taxonomic distribution.

Character 2: *Rhinarium with two ventrolateral grooves flanking the median sulcus (0); or with a single ventrolateral groove on each side (1).* Information about the distribution of these traits among didelphid terminal taxa was summarized by Voss and Jansa (2003: character 1). See text for comments about traits expressed by outgroup taxa. This character was scored as inapplicable ("-") for taxa with a very narrow pars supralabialis (see above).

Character 3: *Reciprocating lateral fleshy outgrowths of upper and lower oral margins absent (0); or present (1).* See text for a discussion of this character and its taxonomic distribution.

Character 4: *Interramal vibrissae present (0); or absent (1).* See text for a discussion of this character and its taxonomic distribution.

Character 5: *Dark midrostral stripe absent (0); or present (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 2). See text for comments about traits expressed by outgroup taxa.

Character 6: *Fur surrounding eye not distinctively colored (0); or eye surrounded by mask of dark fur (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 3). See text for comments about traits expressed by outgroup taxa.

Character 7: *Circumocular mask contrasts with coloration of cheeks and crown (0); or dark fur around eye continuous with dark coronal fur (1).* This character was modified from Voss and Jansa's (2003) character 4 by eliminating an intermediate condition for polymorphism, which was recoded as 0/1 for this analysis. See text for comments about traits expressed by outgroup taxa.

Character 8: *Conspicuous pale spot above each eye absent (0); or present (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 5). See text for comments about traits expressed by outgroup taxa.

Character 9: *Gular gland absent (0); or present (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 6). See text for comments about traits expressed by outgroup taxa.

Character 10: *Dorsal body pelage more or less uniformly colored, unpatterned (0); or marked by dark transverse bars connected middorsally (1); or marked by paired scapular stripes (2); or marked by one median and two lateral stripes (3); or grayish middorsum contrasting with reddish or yellowish flanks (4); or grayish midbody (including flanks) contrasting with reddish head and rump (5); or "tricolored" (6); or with transverse sacral bars (7).* Scoring criteria and information about the distribution of states 0–6 among didelphid terminal taxa were provided by Voss and Jansa (2003: character 7). See text for comments about traits expressed by outgroup taxa. In the absence of any compelling evidence for intermediacy among these alternative conditions, this character was treated as unordered in all of our analyses.

Character 11: *Dorsal underfur dark (0); or white (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 8). See text for comments about traits expressed by outgroup taxa.

Character 12: *Dorsal pelage hairs not grossly dissimilar in length or coarseness (0); or dorsal pelage with guard hairs conspicuously longer and coarser than underfur (1); or dorsal pelage with stiff, dorsally*

grooved guard hairs (2). Scoring criteria and information about the distribution of states 0 and 1 among didelphid terminal taxa were provided by Voss and Jansa (2003: character 9). See text for comments about traits expressed by outgroup taxa. In the absence of any compelling evidence for intermediacy among these alternative conditions, this character was treated as unordered in all of our analyses.

Character 13: *Externally conspicuous lateral carpal tubercles absent in both sexes (0); or large adult males with a prominent lateral carpal tubercle supported internally by the pisiform (1); or both sexes with a finger-like fleshy tubercle supported internally by the pisiform (2)*. This character is modified from Voss and Jansa's (2003: character 12) interpretation of pisiform-supported tubercular structures by including a third state for the unique condition seen in *Chironectes*. See text for comments about traits expressed by outgroup taxa. In the absence of any compelling evidence for intermediacy among these alternative conditions, this character was treated as unordered in all of our analyses.

Character 14: *Externally conspicuous medial carpal tubercles absent in both sexes (0); or large adult males with a prominent medial tubercle supported internally by the prepollex (1)*. Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 13). See text for comments about traits expressed by outgroup taxa.

Character 15: *First manual digit (dI) large and claw-bearing (0); or small and nail-bearing (1); or vestigial and lacking an unguis entirely (2)*. See text for a discussion of this character and its taxonomic distribution. Because state 1 can be plausibly interpreted as intermediate to states 0 and 2 in each case, both characters were treated as ordered $(0 \leftrightarrow 1 \leftrightarrow 2)$ in all of our analyses.

Character 16: *Fifth manual digit (dV) large and claw-bearing (0); or small and nail-bearing (1); or vestigial and without an unguis of any kind (2)*. See text for a discussion of this character and its taxonomic distribution. Although functional reduction in manual digits I and V covary among marsupials and might be coded together as a single character on the assumption that the transformations in question are developmentally or functionally dependent, dI and dV exhibit independent patterns of variation among placental mammals, suggesting that such changes are not necessarily linked. (All rodents, for example, have a reduced and clawless dI, whereas dV is typically large and claw-bearing.) Because state 1 can be plausibly interpreted as intermediate to states 0 and 2 in each case, both characters were treated as ordered $(0 \leftrightarrow 1 \leftrightarrow 2)$ in all of our analyses.

Character 17: *Manual digit III longer than other manual digits (0); or dIII and dIV subequal and longer than other manual digits (1); or dIV longer than other manual digits (2)*. Scoring criteria and information about the distribution and ordering $(0 \leftrightarrow 1 \leftrightarrow 2)$ of these traits among didelphid terminal taxa were provided by Voss and Jansa

(2003: character 10). See text for comments about traits expressed by outgroup taxa.

Character 18: *Manus with well-developed plantar pads (0); or manus without distinct plantar pads (1)*. See text for a discussion of this character and its taxonomic distribution.

Character 19: *Plantar pads of manus provided with dermatoglyphs (0); or manual plantar pads smooth (1); or plantar pads tuberculate (2)*. See text for a discussion of this character and its taxonomic distribution. This character was scored as inapplicable ("-") for taxa lacking plantar pads (*Chironectes* and peramelids, see text). In the absence of any compelling evidence for intermediacy among these alternative conditions, this character was treated as unordered in all of our analyses.

Character 20: *Central palmar surface of manus smooth, or sparsely provided with large flattened tubercles (0); or densely covered with small convex tubercles (1); or entire plantar surface of manus sandpapery, covered with microscopically dentate tubercles (2)*. Scoring criteria and information about the distribution of these unordered traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 11). See text for comments about traits expressed by outgroup taxa.

Character 21: *Hallux large and opposable (0); or very small and effectively nonopposable (1)*. See text for a discussion of this character and its taxonomic distribution.

Character 22: *Pedal digit III distinctly longer than digit IV (0); or pedal digits III and IV subequal (1); or pedal IV distinctly longer than III (2)*. Scoring criteria and information about the distribution and ordering $(0 \leftrightarrow 1 \leftrightarrow 2)$ of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 14). See text for comments about traits expressed by outgroup taxa.

Character 23: *Pedal digits free (0); or all pedal digits bound together by extensive fleshy webs (1); or pedal digits II and III fused (2)*. This character differs from Voss and Jansa's (2003) character 15 by including a separate state for the syndactylous hind feet of peramelids. In the absence of any compelling evidence for intermediacy among these alternative conditions, we treated this character as unordered in all of our analyses.

Character 24: *Claws on pedal digits II–V all alike (0); or claw on pedal digit II asymmetrically modified for grooming (1); or claws of pedal digits II and III asymmetrically and reciprocally modified for grooming (2)*. See text for a discussion of this character and its taxonomic distribution. Although state 2 is said to be correlated with syndactyly (Hall, 1987), some syndactylous marsupials (e.g., *Phascolarctos, Vombatus*) do not have grooming claws (Putzkrallen) on dII and dIII, an observation that implies some degree of independence between claw function and digital fusion. In the absence of any compelling evidence for intermediacy among these alternative conditions, we treated this character as unordered in all of our analyses.

Character 25: *Plantar epithelium of tarsus macroscopically naked (0); or densely covered with coarse fur (1)*. Scoring criteria and information about the

distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 16). See text for comments about traits expressed by outgroup taxa.

Character 26: *Pouch absent (0); or present (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 17). See text for comments about traits expressed by outgroup taxa.

Character 27: *Pouch consists of separate lateral skin folds opening medially (0); or lateral folds connected posteriorly, pouch opening anteriorly (1); or lateral folds connected anteriorly, pouch opening posteriorly (2); or folds connected anteriorly and posteriorly, pouch opening by a central orifice (3).* Scoring criteria and information about the distribution of states 0–2 among didelphid terminal taxa were provided by Voss and Jansa (2003: character 18). See text for comments about traits expressed by outgroup taxa. In the absence of any compelling evidence for intermediacy among these alternative conditions, we treated this character as unordered in all of our analyses.

Character 28: *Mammae all abdominal/inguinal, more or less confined to pouch region (0); or extending anteriorly beyond pouch region to thoracic region (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 19). See text for comments about traits expressed by outgroup taxa.

Character 29: *Unpaired median teat absent (0); or present (1).* See text for a discussion of this character and its taxonomic distribution. Our scoring of *Rhyncholestes* was based on literature cited in the text. In the absence of suitably preserved parous female specimens or relevant published descriptions of mammary counts, we scored 11 didelphid terminals as missing ("?") for this character.

Character 30: *Urogenital and rectal openings are inguinal (0); or basicaudal (1).* See text for a discussion of this character and its taxonomic distribution.

Character 31: *Urogenital and rectal openings closely juxtaposed, and sharing a common mucosa (0); or urogenital and rectal openings widely separated by furred skin (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 20). See text for comments about traits expressed by outgroup taxa.

Character 32: *Body pelage extends onto tail conspicuously farther dorsally than ventrally (0); or body pelage extends onto dorsal and ventral surfaces of tail to about the same extent (1); or body pelage does not extend appreciably onto tail (2).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 21). See text for comments about traits expressed by outgroup taxa. In the absence of any compelling

evidence for intermediacy among these alternative conditions, this character was treated as unordered in all of our analyses.

Character 33: *Caudal integument uniformly pigmented or indistinctly or irregularly marked (0); or blackish basally and abruptly whitish distally (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 22). No examined outgroup taxon exhibits state 1.

Character 34: *Tail scales in predominantly annular series (0); or in annular and spiral series (1); or in predominantly spiral series (2).* Scoring criteria and information about the distribution and ordering $(0 \leftrightarrow 1 \leftrightarrow 2)$ of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 23). All examined outgroup taxa have annular caudal scale rows.

Character 35: *Unfurred ventral surface of tail base covered with smooth scales (0); or provided with raised tubercles (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 24). No examined outgroup taxon has raised tubercles on the ventral surface of the tail base.

Character 36: *Ventral surface of tail tip covered by unmodified hair-bearing scales (0); or ventral surface of tail tip modified for prehension (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 25). See text for comments about traits expressed by outgroup taxa.

Character 37: *Caudal scales bearing three hairs each (0); or more than three hairs each (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 26). Despite the fact that annular scale rows could be distinguished in all examined outgroup taxa, individual scales were seldom clearly distinguishable within rows, so the number of hairs per scale could not be counted. The exceptions were *Caenolestes* (which usually has three hairs per scale; state 0) and *Dromiciops* (which usually has four or more hairs per scale; state 1).

Character 38: *Tail hairs emerging from each scale not grossly differentiated, varying in length but subequal in thickness (0); or central hair much thicker than lateral hairs (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 27). Adjacent caudal hairs were similar in gross morphology (state 0) in all examined outgroups.

Character 39: *Tail not incrassate (0); or incrassate (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 28). See text for comments about traits expressed by outgroup taxa.

CRANIUM AND MANDIBLE

Character 40: *Premaxillae not produced anteriorly beyond alveolar margin of I1 (0); or forming a distinct, shelf-like rostral process anterior to I1 (1).* Scoring criteria and information about the distribution of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 29). Among our outgroups, only *Caenolestes*, *Dromiciops*, and *Perameles* exhibit state 1.

Character 41: *Nasals produced anteriorly above or beyond I1, obscuring nasal orifice in dorsal view (0); or nasals posterior to I1, exposing nasal orifice dorsally (1); or nasals posterior to premaxillary facial processes, exposing incisive foramina in dorsal view (2).* Scoring criteria and information about the distribution of states 0 and 1 among didelphid terminal taxa were provided by Voss and Jansa (2003: character 32). See text for comments about traits expressed by outgroup taxa. Because state 1 is obviously intermediate to states 0 and 2, this character was treated as ordered (0 ↔ 1 ↔ 2) in all of our analyses.

Character 42: *Nasals extend posteriorly between lacrimals (0); or truncated anterior to lacrimals (1).* Among the taxa examined for this study, nasals that are truncated anterior to the lacrimals (state 1) are peculiar to peramelemorphians (see text).

Character 43: *Nasals conspicuously wider posteriorly than anteriorly (0); or nasals uniformly narrow, their lateral margins subparallel (1).* Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 33). Among our outgroups, only *Echymipera* and *Perameles* exhibit state 1.

Character 44: *Antorbital fenestra between nasal, frontal, and maxillary bones on each side of rostrum absent (0); or present (1).* See text for a discussion of this character and its taxonomic distribution.

Character 45: *Maxilloturbinals large and elaborately branched (0); or small and unbranched (1).* Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 31). See text for comments about traits expressed by outgroup taxa.

Character 46: *Maxillary-jugal suture straight, crescentic, or irregular (0); or suture deeply bifid, dividing jugal into dorsal and ventral processes flanking antorbital fossa (1).* See text for a discussion of this character and its taxonomic distribution.

Character 47: *Distinct frontal process of jugal absent (0); or present (1).* See text for a discussion of this character and its taxonomic distribution.

Character 48: *Lacrimal margin of orbit smoothly rounded (0); or forming a distinct crest (1).* See text for a discussion of this character and its taxonomic distribution.

Character 49: *One lacrimal foramen usually present (0); or two lacrimal foramina usually present (1).* See text for a discussion of this character and its taxonomic distribution.

Character 50: *Foramen rotundum laterally exposed behind sphenorbital fissure (0); or foramen rotundum concealed from lateral view, partly or wholly confluent with sphenorbital fissure in rear of orbit (1).* See text for a discussion of this character and its taxonomic distribution.

Character 51: *Maxillary and alisphenoid separate (0); or in contact on orbital floor (1).* Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 43). See text for comments about traits expressed by outgroup taxa.

Character 52: *Postorbital processes absent or indistinct (0); or present (1).* This character was modified from Voss and Jansa's (2003) character 34 by eliminating our former distinction between "flattened" and "not flattened" postorbital processes, which are not consistently distinguishable among nondidelphid marsupials. See text for comments about traits expressed by outgroup taxa.

Character 53: *Postorbital processes formed by frontals only (0); or by frontals and parietals (1).* In the context of this study, state 1 is an autapomorphy of *Glironia* (see text).

Character 54: *Left and right frontals separated by ontogenetically persistent median suture (0); or left and right frontals partially or completely co-ossified in adults (1).* See text for a discussion of this character and its taxonomic distribution.

Character 55: *Left and right parietals separated by ontogenetically persistent median suture (0); or left and right parietals partially or completely co-ossified in adults (1).* See text for a discussion of this character and its taxonomic distribution.

Character 56: *Parietal and alisphenoid in contact on lateral aspect of braincase (0); or frontal and squamosal in contact (1).* Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 36). See text for comments about traits expressed by outgroup taxa.

Character 57: *Scars of M. temporalis origin on braincase not joined middorsally to form sagittal crest (0); or sagittal crest small, not extending to frontals (1); or sagittal crest large and extending to frontals (2).* Descriptions of character states and an account of their taxonomic distribution among didelphid terminals were provided by Voss and Jansa (2003: character 35), but an intermediate state between absence of a sagittal crest and presence of a large crest extending to the frontals is recognized here. See text for comments about traits expressed by outgroup taxa. Because state 1 is obviously intermediate to states 0 and 2, this character was treated as ordered (0 ↔ 1 ↔ 2) in all of our analyses.

Character 58: *Fenestra in squamosal-parietal suture absent (0); or present (1).* This character is modified from its original formulation (Voss and Jansa, 2003: character 37) by eliminating an intermediate state for polymorphisms, which were recoded as 0/1 for this analysis. See text for comments about traits expressed by outgroup taxa.

Character 59: *Interparietal absent (0); or present (1).* See text for a discussion of this character and its taxonomic distribution.

Character 60: *Interparietal and supraoccipital separated by an open suture, at least in juvenile specimens (0); or interparietal-supraoccipital suture fused in juveniles and adults (1).* See text for a discussion of this character, which was scored as inapplicable ("-") for taxa lacking an interparietal, and as missing ("?") for taxa in which it is not known whether an interparietal is present or absent (see above).

Character 61: *Parietal-mastoid contact present (0); or absent (1).* See text for a discussion of this character and its taxonomic distribution.

Character 62: *"Accessory" fenestrae absent (0); or present (1).* These nonvascular openings (first apparently named by Lyne and Mort, 1981: 124) perforate the maxillary palate at the level of P1 and/or P2, occupying a position in between the incisive foramina and the maxillopalatine fenestrae. In the context of this study, state 1 is an autapomorphy of *Perameles*.

Character 63: *Maxillopalatine fenestrae absent (0); or present (1).* This character was modified from its original formulation (Voss and Jansa, 2003: character 38) by eliminating an intermediate state for polymorphism, which was recoded as 0/1 for this analysis. See text for comments about traits expressed by outgroup taxa.

Character 64: *Left and right maxillopalatine fenestrae separated by a median septum (0); or confluent, septum absent (1).* See text for a discussion of this character and its taxonomic distribution.

Character 65: *Palatine fenestrae absent (0); or present (1).* Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 39). See text for comments about traits expressed by outgroup taxa.

Character 66: *Maxillary fenestrae absent (0); or present (1).* Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 40). See text for comments about traits expressed by outgroup taxa.

Character 67: *Posterolateral palatal foramina present, with complete bony margins (0); or absent, bony margins incomplete, represented by open notches in posterolateral palate (1).* See text for a discussion of this character and its taxonomic distribution.

Character 68: *Posterolateral palatal foramina posterior to fourth molars (0); or extending lingual to M4 protocones (1).* Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 41). See text for comments about traits expressed by outgroup taxa. Although posterolateral palatal foramina are coded as absent in dasyurids, their position behind the M4 protocones in those taxa is indicated by the open notches mentioned in the preceding character description.

Character 69: *Posterior palate without distinct lateral corners, the choanae unconstricted behind (0); or posterior palate with distinct lateral corners, choanae constricted (1).* Descriptions of the states of this character have been slightly reworded from their original phrasing in Voss and Jansa (2003: character 42), where the distribution of these traits was described for didelphid terminals. See text for comments about traits expressed by outgroup taxa.

Character 70: *Presphenoid exposed in roof of nasopharyngeal orifice above posterior palatal margin (0); or presphenoid concealed by vomer above posterior palatal margin (1).* See text for a discussion of this character and its taxonomic distribution.

Character 71: *Left and right pterygoids separate (0); or in midline contact and forming a sagittal keel (1).* See text for a discussion of this character and its taxonomic distribution.

Character 72: *Transverse canal foramen absent (0); or present (1).* Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 44). See text for comments about traits expressed by outgroup taxa.

Character 73: *Extracranial course of mandibular nerve not enclosed by bone (0); or consistently enclosed by anteromedial strut of alisphenoid bulla (1); or usually enclosed by posteromedial bullar lamina (2).* Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 45). See text for comments about traits expressed by outgroup taxa. In the absence of any compelling evidence for intermediacy among these alternative conditions, this character was treated as unordered in all of our analyses.

Character 74: *Alisphenoid tympanic process and rostral tympanic process of petrosal separated by a distinct gap (0); or in contact (1).* See text for a discussion of this character and its taxonomic distribution.

Character 75: *Epitympanic recess small, snugly enclosing the mallear-incudal joint (0); or inflated, arching high above mallear-incudal joint (1).* See text for a discussion of this character and its taxonomic distribution.

Character 76: *Rostral and caudal tympanic processes of petrosal separated by a distinct gap (0); or in contact and separated by a suture (1); or indistinguishably fused (2).* States 0 and 1 of this character represent the same pattern of ingroup variation that Voss and Jansa (2003: character 47) described in terms of concealment of the fenestra cochleae. See text for comments about traits expressed by outgroup taxa. Because state 1 is plausibly intermediate to states 0 and 2, this character was treated as ordered $(0 \leftrightarrow 1 \leftrightarrow 2)$ in all of our analyses.

Character 77: *Squamosal epitympanic sinus absent (0); or present (1).* See text for a discussion of this character and its taxonomic distribution.

Character 78: *Anterior limb of ectotympanic directly attached to skull (0); or indirectly attached via malleus (1).* Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 46). See text for comments about traits expressed by outgroup taxa.

Character 79: *Ectotympanic laterally exposed (0); or concealed from lateral view inside bulla (1).* See text

for a discussion of this character and its taxonomic distribution.

Character 80: *Malleus with long and sharply inflected neck, well-developed lamina, and manubrium parallel to anterior process (0); or with short and uninflected neck, no lamina, and manubrium not parallel to anterior process (1).* See text for a discussion of this character and its taxonomic distribution.

Character 81: *Stapes triangular and bicrurate, perforated by a large foramen (0); or stapes columelliform and microperforate or imperforate (1).* See text for a discussion of this character and its taxonomic distribution. Although Schmelzle et al. (2005: character 12) scored *Didelphis marsupialis* as having a columelliform stapes, most of the specimens of *D. marsupialis* that we examined have a triangular stapes with a large foramen.

Character 82: *Lambdoid sesamoids absent (0); or present (1).* See text for a discussion of this character and its taxonomic distribution.

Character 83: *Dorsal margin of foramen magnum formed by exoccipitals and supraoccipital, incisura occipitalis present (0); or by exoccipitals only, incisura occipitalis absent (1).* Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 49). See text for explanation of reworded state descriptions and for comments about traits expressed by outgroup taxa.

Character 84: *Paroccipital process absent (0); small and broadly adnate to the petrosal (1); or large, erect and usually directed ventrally (2).* This character differs from Voss and Jansa's (2003) character 48 by including a new state (0) for absence of the paroccipital process in *Dromiciops*. See text for comments about traits expressed by other outgroup taxa. Because state 1 is plausibly intermediate to states 0 and 2, this character was treated as ordered (0 ↔ 1 ↔ 2) in all of our analyses.

Character 85: *Mandible usually with one mental foramen (0); or with two mental foramina (1); or with three mental foramina (2).* This character differs from Voss and Jansa's (2003) character 50 by including a new state for the three mental foramina of *Perameles gunni*. See Jansa and Voss (2005) for a discussion of polymorphism in *Hyladelphys*, and the text of this report for information about outgroup variation. Because state 1 is plausibly intermediate to states 0 and 2, this character was treated as ordered (0 ↔ 1 ↔ 2) in all of our analyses.

Character 86: *Angular process acute and strongly inflected (0); or obtuse and weakly inflected (1).* Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 51). See text for explanation of reworded state descriptions and for comments about traits expressed by outgroup taxa.

Character 87: *Retromolar fossa imperforate (0); or pierced by retrodental canal (1).* See text for a discussion of this character and its taxonomic distribution.

Character 88: *Masseteric foramen absent (0); or present (1).* See text for a discussion of this character and its taxonomic distribution.

UPPER DENTITION

Character 89: *First upper incisor styliform or chisellike (0); or I1 mesiodistally expanded and flat-crowned (1).* See text for a discussion of this character and its taxonomic distribution.

Character 90: *Second through fourth upper incisors with approximately symmetrical, rhomboidal crowns bearing subequal anterior and posterior cutting edges (0); or I2–I4 conspicuously asymmetrical, with much longer anterior than posterior cutting edges (1); or I2–I4 hatchet-shaped (2); or I2–I4 flat-crowned (3).* See text for a discussion of this character and its taxonomic distribution. In the absence of any compelling evidence for intermediacy among these alternative conditions, this character was treated as unordered in all of our analyses.

Character 91: *Fifth upper incisor present (0); or I5 absent (1).* See text for a discussion of this character and its taxonomic distribution.

Character 92: *Fifth upper incisor similar to I4 (0); or I5 caniniform and double-rooted (1).* See text for a discussion of this character and its taxonomic distribution. This character was scored as inapplicable ("-") for taxa lacking I5.

Character 93: *Upper canine alveolus occupies premaxillary-maxillary suture (0); or C1 alveolus contained entirely in maxillary bone (1).* This character is rephrased from Voss and Jansa (2003: character 30), who misleadingly described the same taxonomic variation in terms of the presence or absence of a premaxillary palatal process. See text for comments about traits expressed by outgroup taxa.

Character 94: *Upper canine simple, without distinct accessory cusps (0); or with distinct posterior accessory cusp (1); or with distinct anterior and posterior accessory cusps (2); or with distinct anterior accessory cusp (3).* This character is restructured from Voss and Jansa's (2003) character 53, which treated states 0, 1, and 2 as stages of an ordered transformation series. The discovery of another condition (state 3) among the outgroup taxa of this study introduced another hypothetically intermediate condition between the absence of any accessory cusps and the presence of both anterior and posterior accessory cusps. Although this could be accommodated by a step matrix, we have also observed dentitions with indistinct anterior *and* posterior accessory cusps, suggesting that transitions between states 0 and 2 need not involve states 1 or 3 as intermediate stages. Therefore, we now treat this character as unordered. We scored sexual dimorphism in canine morphology in caenolestids as polymorphisms (0/3 for *Caenolestes*, 0/2 for *Rhyncholestes*; see text).

Character 95: *First upper premolar (P1) large, at least one-half the height or width of P2 (0); or vestigial, less than one-third the height or width of P2, or absent (1).* Scoring criteria and information about

the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 54). See text for comments about traits expressed by outgroup taxa.

Character 96: *P2 distinctly taller than P3 (0); or P2 and P3 subequal in height (1); or P3 distinctly taller than P2 (2)*. Scoring criteria and information about the distribution and ordering $(0 \leftrightarrow 1 \leftrightarrow 2)$ of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 55). See text for comments about traits expressed by outgroup taxa.

Character 97: *Third upper premolar (P3) with well-developed anterior and posterior cutting edges (0); or only posterior cutting edge well developed (1)*. Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 56). See text for comments about traits expressed by outgroup taxa.

Character 98: *Deciduous third premolar (dP3) large and molariform, occluding with dp3 and m1 (0); or smaller, lacking a distinct protocone, and occluding only with m1 (1); or very small, nonoccluding, and structurally simplified (2)*. See text for a discussion of this character and its taxonomic distribution. Because state 1 is plausibly intermediate to states 0 and 2, we treated this character as ordered $(0 \leftrightarrow 1 \leftrightarrow 2)$ in all of our analyses.

Character 99: *Stylar shelf present (0); or absent (1)*. See text for a discussion of this character and its taxonomic distribution.

Character 100: *Neomorphic labial cingulum absent (0); or present (1)*. See text for a discussion of this character and its taxonomic distribution.

Character 101: *Upper molars without a distinct ectoflexus on any tooth (0); or distinct ectoflexus present on one or more teeth (1)*. Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 59). See text for comments about traits expressed by outgroup taxa. This character was coded as inapplicable ("-") for taxa lacking a stylar shelf (see above).

Character 102: *Anterolabial cingulum present (0); or absent (1)*. See text for a discussion of this character and its taxonomic distribution.

Character 103: *Preparacrista of M1 passes anterolabially or labially to stylar shelf (0); or M1 preparacrista passes posterolabially to stylar shelf (1)*. See text for a discussion of this character and its taxonomic distribution.

Character 104: *Centrocrista of M1–M3 linear, its apex almost level with floor of trigon basin (0); or weakly $\wedge$-shaped, its apex distinctly elevated above floor of trigon basin (1); or strongly $\wedge$-shaped, its apex high above floor of trigon basin (2); or discontinuous (3)*. Scoring criteria and information about the distribution of traits 0–2 among didelphid terminals were provided by Voss and Jansa (2003: character 58). Only peramelemorphian outgroups exhibit state 3 (see text). Although Wroe et al. (2000) and Wroe and Musser (2001) analyzed the shape of the centrocrista and whether or not it is discontinuous as separate characters, the obvious interme-

diacy of states 1 and 2 with respect to 0 and 3 suggest that these traits be scored as elements of a single ordered transformation series $(0 \leftrightarrow 1 \leftrightarrow 2 \leftrightarrow 3)$. This character was scored as inapplicable ("-") for caenolestids, which lack postparacristae and premetacristae due to fusion of the paracone and metacone with stylar cusps B and D, respectively (see text).

Character 105: *Preprotocrista and anterolabial cingulum joined to form a continuous shelf along anterior margin of M3 (0); or crista and cingulum separate, not forming a continuous shelf (1)*. Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 60). *Murexia*, *Dromiciops*, and *Echymipera* exhibit state 0, whereas *Sminthopsis* exhibits state 1. This character was scored as inapplicable ("-") for caenolestids and *Perameles*, which lack an anterolabial cingulum.

Character 106: *Postprotocrista unnotched (0); or with a distinct carnassial notch (1)*. See text for a discussion of this character and its taxonomic distribution among didelphid terminals. No examined outgroup taxon has a similarly notched postprotocrista.

Character 107: *Upper molar posterolingual cusp absent (0); or present (1)*. See text for a discussion of this character and its taxonomic distribution.

Character 108: *Third premolar is last upper tooth to erupt (0); or M4 and P3 erupt simultaneously (1); or M4 is last upper tooth to erupt (2)*. Scoring criteria and information about the distribution and ordering $(0 \leftrightarrow 1 \leftrightarrow 2)$ of these traits among didelphid terminal taxa were provided by Voss and Jansa (2003: character 61). Suitable subadult specimens were not available to determine eruption sequences for several species, for which this character was coded as missing ("?"). Our scoring of *Rhyncholestes* was based on Luckett and Hong's (2000) observation of a subadult specimen that we did not examine.

LOWER DENTITION

Character 109: *Lower incisors with distinct lingual cusp (0); or lower incisors without distinct lingual cusps (1)*. Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 62). See text for comments about traits expressed by outgroup taxa.

Character 110: *Anteriormost lower incisor small and short-crowned (0); or large, long-crowned, and conspicuously procumbent (1)*. See text for a discussion of this character and its taxonomic distribution.

Character 111: *Second lower incisor (i2) with staggered alveolus (0); or I2 alveolus not staggered (1)*. See text for a discussion of this character and its taxonomic distribution. This character was scored as missing ("?") for caenolestids, for which lower incisor homologies are unknown.

Character 112: *Cutting edge of unworn i3 not bilobed (0); or distinctly bilobed (1)*. See text for a discussion of this character and its taxonomic distribution. This character was scored as missing ("?") for caenolestids, for which lower incisor homologies are unknown.

Character 113: *Fourth lower incisor (i4) present (0); or absent (1)*. See text for a discussion of this character and its taxonomic distribution. This character was scored as missing ("?") for caenolestids, for which lower incisor homologies are unknown.

Character 114: *Second lower premolar distinctly taller than p3 (0); or p2 and p3 subequal in height (1); or p3 distinctly taller than p2 (2)*. Scoring criteria and information about the distribution and ordering $(0 \leftrightarrow 1 \leftrightarrow 2)$ of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 63). See text for comments about traits expressed by outgroup taxa.

Character 115: *Deciduous lower third premolar (dp3) large and occlusally functional, with tricuspid (complete) trigonid (0); or dp3 smaller but still occlusally functional, with unicuspid or bicuspid (incomplete) trigonid (1); or dp3 vestigial, usually lacking distinct occlusal features (2)*. See text for a discussion of this character and its taxonomic distribution. In the absence of juvenile specimens, this character was scored as missing ("?") for several taxa. Because state 1 is plausibly intermediate to states 0 and 2, we treated this character as ordered $(0 \leftrightarrow 1 \leftrightarrow 2)$ in all of our analyses.

Character 116: *Hypoconulid notch in anterior cingulum of m2–m4 present (0); or absent (1)*. See text for a discussion of this character and its taxonomic distribution.

Character 117: *Paracristid of m1 deeply notched (0); or unnotched (1)*. See text for a discussion of this character and its taxonomic distribution.

Character 118: *Paracristid of m2 extends from protoconid to paraconid without deflection (0); or m2 paracristid abruptly deflected posterolingually by hypoconulid of m1 (1)*. See text for a discussion of this character and its taxonomic distribution.

Character 119: *Trigonid of m4 complete (0); or only metaconid distinct on m4 trigonid (1)*. See text for a discussion of this character and its taxonomic distribution.

Character 120: *Lower third molar hypoconid labially salient (0); or m3 hypoconid lingual to salient protoconid (1)*. Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 65). Caenolestids, *Dromiciops*, and peramelid outgroups have salient hypoconids, but the hypoconid is lingual to the protoconid in *Murexia* and *Sminthopsis*.

Character 121: *Entoconid large and well developed on m1–m3 (0); or very small or indistinct (1)*. Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 66). All examined ougroup taxa exhibit state 0.

Character 122: *Entocristid absent or indistinct (0); or present (1)*. A distinct entocristid is present in all examined taxa except *Sminthopsis* and *Perameles*.

Character 123: *Entocristid a short crest parallel to lingual margin of tooth (0); or entocristid long and labially deflected into talonid basin (1)*. See text for a discussion of this character and its taxonomic distribution. This character was coded as inapplicable ("-") in taxa lacking an entocristid (above).

Character 124: *Hypoconulid at or near posterolingual margin of talonid, "twinned" with entoconid on m1–m3 (0); or at midline of tooth, approximately equidistant to hypoconid and entoconid, not "twinned" with the latter cusp (1)*. Scoring criteria and information about the distribution of these traits among didelphid terminals were provided by Voss and Jansa (2003: character 67). All examined ougroup taxa exhibit state 0.

Character 125: *Lower molars without a posterior cingulid (0); or posterior cingulid present (1)*. See text for a discussion of this character and its taxonomic distribution.

KARYOTYPES

Character 126: *Robertsonian equivalents {acr1 + acr5, met1} present as a single metacentric chromosome (0); or as two acrocentric chromosomes (1)*. Most marsupials, including all of the outgroups in this analysis, have a diploid number $(2n)$ of 14 chromosomes (Sharman, 1973; Hayman, 1977, 1990; Reig et al., 1977), and this is also the most widespread number among didelphids (table 18). By contrast, *Glironia* and *Monodelphis* have diploid counts of 18 chromosomes, whereas *Chironectes*, *Didelphis*, *Lutreolina*, *Philander*, and *Tlacuatzin* have $2n = 22$. Morphometric comparisons and G-banding studies indicate that each of these diploid groupings are homogeneous in the sense that different taxa with the same diploid number have chromosomes with essentially similar relative sizes, shapes (arm ratios), and banding patterns (Reig et al., 1977; Rofe and Hayman, 1985; Svartman and Vianna-Morgante, 1999). By implication, a shared history of Robertsonian changes (centric fissions or centric fusions) could account for the taxonomic membership of each diploid category.

A minimum of four centric fission/fusion events is required to account for the difference in diploid number between karyotypes with 14 chromosomes and those with 22 chromosomes. Based on arm homologies suggested by G-banding patterns, the following Robertsonian transformations involving eight acrocentric (acr) autosomes in the $2n = 22$ karyotype and four metacentric (met) autosomes in the $2n = 14$ karyotype are indicated (chromosomes are numbered from small to large within each karyotype): acr1 + acr5 $\leftrightarrow$ met1, acr2 + acr8 $\leftrightarrow$ met2, acr3 + acr10 $\leftrightarrow$ met3, and acr6 + acr9 $\leftrightarrow$ met4 (Svartman and Vianna-Morgante, 1999). The $2n = 18$ karyotype is intermediate because it has only two metacentric autosomes, of which the larger can be homologized with acr2 + acr8 of the $2n = 22$ karyotype and with met2 of the $2n = 14$

TABLE 18
Exemplar Didelphid Karyotypes

Taxon	$2n$[a]	References
Caluromys lanatus	14	Reig et al. (1977), Palma and Yates (1996), Patton et al. (2000)
Caluromys philander	14	Reig et al. (1977)
Chironectes minimus	22	Reig et al. (1977), Palma and Yates (1996)
Cryptonanus chacoensis[b]	14	Wainberg et al. (1979)
Didelphis albiventris	22	Reig et al. (1977), Palma and Yates (1996)
Didelphis marsupialis	22	Gardner (1973), Reig et al. (1977), Palma and Yates (1996), Patton et al. (2000)
Didelphis virginiana	22	Gardner (1973), Reig et al. (1977)
Glironia venusta	18	Fantin and da Silva (in press)
Gracilinanus agilis	14	Carvalho et al. (2002)
Gracilinanus microtarsus	14	Wainberg et al. (1979), Carvalho et al. (2002)
Lestodelphys halli	14	Birney et al. (1996)
Lutreolina crassicaudata	22	Reig et al. (1977), Palma and Yates (1996)
Marmosa (Micoureus) demerarae[c]	14	Reig et al. (1977), Palma and Yates (1996), Patton et al (2000)
Marmosa (Marmosa) mexicana	14	Biggers et al. (1965)
Marmosa (Marmosa) murina	14	Reig et al. (1977)
Marmosa (Micoureus) paraguayana[d]	14	Carvalho et al. (2002)
Marmosa (Micoureus) regina	14	Patton et al. (2000)
Marmosa (Marmosa) robinsoni	14	Reig et al. (1977)
Marmosops impavidus	14	Patton et al. (2000)
Marmosops incanus	14	Carvalho et al. (2002)
Marmosops noctivagus	14	Palma and Yates (1996), Patton et al. (2000)
Metachirus nudicaudatus	14	Reig et al. (1977), Palma and Yates (1996), Patton et al. (2000)
Monodelphis brevicaudata[e]	18	Carvalho et al. (2002)
Monodelphis emiliae	18	Patton et al. (2000)
Philander frenatus	22	Carvalho et al. (2002)
Philander mcilhennyi	22	Reig et al. (1977), Patton et al. (2000)
Philander opossum	22	Reig et al. (1977)
Thylamys macrurus	14	Palma (1995)
Thylamys pallidior	14	Palma and Yates (1996)
Thylamys pusillus	14	Palma and Yates (1998)
Thylamys venustus[f]	14	Palma and Yates (1996)
Tlacuatzin canescens	22	Engstrom and Gardner (1988)

[a] Diploid number.

[b] Identified as ''*Marmosa agilis chacoensis*'' by Wainberg et al. (1979).

[c] Identified as ''*Marmosa cinerea*'' by Reig et al. (1977), and as ''*Micoureus cinereus*'' by Palma and Yates (1996).

[d] The specimens of ''*Micoureus demerarae*'' that Carvalho et al. (2002) karyotyped from Rio Grande do Sul are referable to this taxon.

[e] Some karyotyped specimens previously identified in the literature as *Monodelphis brevicaudata* (sensu lato) may represent other species. Based on known geographic ranges (Voss et al., 2001), the Venezuelan karyotypes described by Reig et al. (1977) were probably obtained from *M. palliolata*, whereas the Bolivian karyotypes described by Palma and Yates (1996) were probably obtained from *M. glirina*.

[f] Karyotyped Bolivian material identified as *Thylamys elegans* by Palma and Yates (1996) was reidentified as *T. venustus* by Palma and Yates (1998).

karyotype, whereas the smaller metacentric can be homologized with acr6 + acr9 of the $2n = 22$ karyotype and with met4 of the $2n = 14$ karyotype (op. cit.). As explained by Voss and Jansa (2003: 42–44; see also Dobigny et al., 2004), these transformational homologies are appropriately coded as separate characters, one for each set of Robertsonian equivalents—for example, {acr2 +

acr8, met2}—which can exist in two states: fused (metacentric) or fissioned (acrocentric).

Character 127: *Robertsonian equivalents {acr2 + acr8, met2} present as a single metacentric chromosome (0); or as two acrocentric chromosomes (1).*

Character 128: *Robertsonian equivalents {acr3 + acr10, met3} present as a single metacentric chromosome (0); or as two acrocentric chromosomes (1).*

Character 129: *Robertsonian equivalents {acr6 + acr9, met4} present as a single metacentric chromosome (0); or as two acrocentric chromosomes (1).*

APPENDIX 4

Nonmolecular Data Matrix

The nonmolecular data analyzed in this report is reproduced below. Missing data are indicated as ''?'' and inapplicable characters are indicated as ''-''. Parentheses enclose observed polymorphisms. An electronic version of these data (in Nexus format) can be downloaded from Morpho-Bank (http://morphobank.geongrid.org) with accession number X600.

Caluromys lanatus: 00001 10000 00000 02000 02010 11000 00021 10001 00000 01010 01000 01011 000-0 00000 00010 10100 00011 10(01)01 00101 00000 00010 00000 00000 00000 01001 0000

Caluromys philander: 00001 10000 00000 02000 02010 10010 01020 10001 00000 01010 01000 01011 000-0 00000 00010 10100 00011 10001 00101 00000 00010 00000 00000 00000 01001 0000

Caluromysiops irrupta: 00000 0-002 00000 02000 02010 1?0?0 00021 10000 00000 010(01)0 01011 02011 000-0 00000 00210 10100 10011 10001 00101 00000 00000 00000 00000 00000 01011 ????

Chacodelphys formosa: ??000 10010 00??0 000?1 02010 ????0 ?2000 00000 00100 01010 00-00 00111 00101 10010 01000 00000 00011 00000 00000 01?00 10021 00?00 0000? 00001 11001 ????

Chironectes minimus: 01000 11001 00200 001-2 02110 12010 11120 00000 10000 01000 01010 02011 10100 00010 01200 00100 00020 00000 00000 21000 10011 10210 00000 00000 01001 1111

Cryptonanus chacoensis: 00000 10010 00100 01000 02010 0-010 02000 10000 00000 01010 00-00 00111 00101 00010 01000 00000 00011 00000 00010 21000 10021 00000 00000 00000 01001 0000

Cryptonanus unduaviensis: 00000 10010 00100 01000 02010 ????0 02000 10000 00000 01010 00-00 00111 00101 00010 01000 00000 00011 00000 00020 21000 10020 00000 00001 00000 01001 ????

Didelphis albiventris: 01000 10000 11000 00000 01010 11010 01120 10000 10000 01010 01010 02011 10101 00010 01200 00100 00121 00001 00000 21000 10011 10210 00000 00000 01001 1111

Didelphis marsupialis: 01000 10000 11000 00000 02010 11010 01120 10000 10000 01010 01010 02011 10101 00010 01200 00100 00121 00001 00000 21000 10011 10210 00000 00000 01001 1111

Didelphis virginiana: 01000 10000 11000 00000 01010 11010 01120 10000 10000 01010 01010 02011 10101 00010 01200 00100 00121 00001 00000 21000 10011 10210 00000 00000 01001 1111

Glironia venusta: 00000 100?0 00??0 01000 02010 0-000 000-1 1??00 00000 01010 01100 00011 00(01)00 00000 01000 00000 00011 00001 00000 10?00 10010 00000 0000? 00000 01001 0101

Gracilinanus aceramarcae: 00000 10010 00100 01000 02010 0-010 02000 10001 00000 01010 00-00 00111 00101 10010 01100 00000 00011 00000 00000 11?00 10020 00?00 0000? 00000 01001 ????

Gracilinanus agilis: 00000 10010 00100 01000 02010 ????0 02000 10001 00000 01010 00-00 00111 00101 10010 01100 00000 00011 00000 00000 11000 10020 00?00 00001 00000 01001 0000

Gracilinanus emiliae: 00000 10010 00100 01000 02010 0-010 02010 10001 00000 01010 00-00 00111 00101 10010 01100 00000 00011 00000 00010 11000 10020 00000 00001 00000 01001 ????

Gracilinanus microtarsus: 00000 10010 00100 01000 02010 ????0 02000 10001 00000 01010 01000 00111 00101 10010 01100 00000 00011 00000 00000 11?00 10020 00000 0000? 00000 01001 0000

Hyladelphys kalinowskii: 00000 10000 00000 01000 02010 0-000 02010 10000 00000 01000 00-00 00011 00100 00010 01000 00000 0001(01) 00001 00000 00200 10010 00000 00002 00000 01001 ????

Lestodelphys halli: 01000 10016 00000 00001 00011 0-110 02000 0?010 00000 01010 00-00 01(01)11 00101 00110 01100 10000 10011 00000 00000 21000 10021 00000 00021 00001 01001 0000

Lutreolina crassicaudata: 01000 0-000 00000 00000 00010 12010 01120 01000 10000 01010 11010 02011 10101 00010 01200 00100 00121 00001 00000 21000 10011 10210 00000 00001 01001 1111

Marmosa (Marmosa) lepida: 00000 10000 00100 01000 02010 0-010 02020 10001 00000 01010 01000 00011 00100 00010 01000 00000 00011 00000 00010 11000 10020 00000 00001 00000 01001 ????

Marmosa (Marmosa) mexicana: 00000 10010 00110 01000 02010 0-010 02010 10001 00000 01010 01000 00011 00101 00010 01000 00000 00011 00000 00000 11000 10020 00000 00001 00000 01001 0000

Marmosa (Marmosa) murina: 00000 10000 00000 01000 02010 0-010 02020 10001 00000 01010 01000 00011 00100 00010 01000 00000 00011 00000 00000 11000 10020 00000 00001 00000 01001 0000

Marmosa (Marmosa) robinsoni: 00000 10010 00110 01000 02010 0-010 02010 10001 00000 01010 01000 00011 00100 00010 01000 00000 00011 00000 00000 11000 10020 00000 00001 00000 01001 0000

Marmosa (Marmosa) rubra: ??000 10000 00110 01000 02010 0-0?0 ?2020 10001 00000 01010 00-00 00011 00100 00010 01000 10000 00011 00000 00000 11000 10020 00000 00001 01001 ????

Marmosa (Micoureus) demerarae: 00000 10000 00110 01000 02010 0-010 02020 10001 00000 01010 01000 00011 00100 00010 01000 00000 00011 00000 00000 11000 10020 00000 00001 00000 01001 0000

Marmosa (Micoureus) paraguayana: 00000 10000 00110 01000 02010 0-0?0 01020 10001 00000 01010 01000 00011 00100 00010 01000 00000 00011 00000 00000 11?00 10020 00?00 0000? 00000 01001 0000

Marmosa (Micoureus) regina: 00000 10000 00110 01000 02010 0-010 02020 10001 00000 01010 01000 00011 00100 00010 01000 00000 00011 00000 00000 11000 10020 00000 00001 00000 01001 0000

Marmosops impavidus: 00000 10000 00100 00000 02010 0-010 02020 10101 00000 01010 00-00

00111 00101 00010 01100 00000 00011 00000 00000 11000 10021 00000 00000 00000 01001 0000

Marmosops incanus: 00000 10010 00100 00000 02010 0-110 02020 1010? 00100 01010 00-00 00(01)11 00101 00010 01100 00000 00011 00000 00000 11000 10021 00000 0001? 00000 01001 0000

Marmosops noctivagus: 00000 10010 00100 00000 02010 0-010 02020 10101 00000 01010 00-00 00(01)11 00101 00010 01100 00000 00011 00000 00000 11000 10021 00000 00000 00000 01001 0000

Marmosops parvidens: 00000 10000 00100 00000 02010 0-010 02020 10101 00000 01010 00-00 00111 00100 00010 01100 00000 00011 00000 00020 11000 10020 00000 00000 00000 01001 ????

Marmosops pinheiroi: 00000 10000 00100 00000 02010 0-010 02020 10101 00000 01010 00-00 00111 00100 00010 01100 00000 00011 00000 00020 11000 10021 00000 00000 00000 01001 ????

Metachirus nudicaudatus: 01000 11110 00000 00000 02010 0-010 02010 00000 00000 01010 00-00 10011 00100 00010 01100 00000 00121 00000 00000 11000 10021 00100 00000 00000 01001 0000

Monodelphis brevicaudata: 01000 0-014 00000 00000 00010 0-010 00000 00000 00001 01010 10-00 01011 (01)0100 0(01)010 01000 00000 00011 00000 00000 21000 10021 00100 00010 00001 11001 0101

Monodelphis emiliae: 01000 0-015 00000 00000 00010 0-0?0 00000 00000 00001 01010 10-00 01011 (01)0100 00010 01000 10000 (01)0011 00000 00000 21000 10021 00?00 00020 00001 11001 0101

Monodelphis peruviana: 01000 0-010 00000 00000 00010 0-0?0 02000 00000 00001 01010 10-00 00011 10100 00010 01000 00000 10011 00000 00000 21?00 10021 00000 0001? 00001 11001 ????

Monodelphis theresa: 01000 0-003 00000 00000 00010 ????0 02000 00000 00001 01010 10-00 00011 00100 00010 01200 00000 10011 00000 00000 21?00 10021 00?00 0001? 00001 11001 ????

Philander frenatus: 01000 1(01)100 00000 00000 02010 11010 01120 11000 10000 010(01)0 01010 02011 10101 00010 01200 00100 00121 00001 00000 21?00 10011 10?10 0000? 00000 01001 1111

Philander mcilhennyi: 01000 11100 00000 00000 02010 11010 01120 11000 10000 01010 01010 02011 10101 00010 01200 00100 00121 00001 00000 21000 10011 10210 00000 00000 01001 1111

Philander opossum: 01000 11100 00000 00000 02010 110?0 01120 11000 10000 01010 01010 02011 10101 00010 01200 00100 00121 00001 00000 21000 10011 10210 00000 00000 01001 1111

Thylamys macrurus: 00000 10016 00000 00001 02011 0-1?0 02000 10010 00100 01010 00-00 00111 00101 10110 01100 10000 00011 00000 00000 21?00 10021 00000 0001? 00000 01001 0000

Thylamys pallidior: 01000 10016 00000 00001 02011 ????0 02000 10010 00100 01010 00-00 00111 00101 10110 01100 10000 00011 00000 00000 21000 10021 00000 00011 00000 01001 0000

Thylamys pusillus: 00000 10016 00000 00001 02011 0-110 02000 10010 00100 01010 00-00 00111 00101 10110 01100 10000 00011 00000 00000 21000 10021 00000 0001(01) 00000 01001 0000

Thylamys venustus: 00000 10016 00000 00001 02011 ????0 02000 10010 00100 01010 00-00 00111 00101

10110 01100 10000 00011 00000 00000 21000 10021 00000 00011 00000 01001 0000

Tlacuatzin canescens: 00000 10000 00100 01000 02010 0-010 02000 10000 00000 01010 01000 00011 00100 10010 01000 00000 00011 10000 00000 11000 10020 00000 00001 00000 01001 1111

Caenolestes fuliginosus: 1-110 0-000 00001 10010 11000 0-000 02000 00001 0001? 00000 00-11 000?? ?0100 00001 01000 00000 10011 01102 1-0(03)0 21?11 -1--- 01211 ???22 01110 01101 0000

Rhyncholestes raphanurus: 1-110 0-000 00001 10010 11000 0-010 02000 0?010 0001? 00000 00-11 000?? ?0110 00001 01000 00000 10011 00(01)02 1-0(02)0 21?11 -1--- 01211 ???2? 01110 01101 0000

Murexia longicaudata: 01000 0-010 00000 00001 11000 0-000 02000 0?000 20000 01000 00-0(01) 01010 00100 01001 01010 21000 10011 00000 1-100 21200 10020 00?00 01122 00001 01000 0000

Sminthopsis crassicaudata: 01000 10010 00000 00021 11001 13000 02000 0?010 20000 01000 00-00 1000- 00101 01001 01010 21000 10011 00000 1-100 21100 10021 00000 01112 00001 00-00 0000

Dromiciops gliroides: 01000 10001 00000 01000 02010 10001 00000 11011 00000 01011 00-00 10010 00100 00011 11010 20011 00000 00000 00100 21000 10000 00200 10020 00000 01001 0000

Echymipera kalubu: 1-000 11000 02002 201-1 12220 12000 02000 0?000 11101 10000 00-01 1000- 00100 00001 01200 00000 11011 00013 1-130 21200 10130 01010 01122 10000 01001 0000

Perameles gunnii: 1-000 0-007 02002 201-1 12220 12000 02000 0?001 01101 10100 00-01 1000- 01111 00001 01211 01000 11012 00013 01100 21200 1113- 01?10 01112 10000 00-01 0000

APPENDIX 5

Nonmolecular Apomorphy List

Here we list all of the unambiguous changes (those identically located on the tree under both ACCTRAN and DELTRAN optimizations; Swofford and Maddison, 1987) reconstructed by parsimony on our best-supported ingroup topology (without *Chacodelphys*, fig. 35). In effect, these morphological and karyotypic transformations summarize phenotypic character support for our classification, although it should be noted that we do not formally recognize all of the nodes in this tree as taxa.

Internal Branches

Caluromyinae + *Glironia*

Character 32. Body pelage on tail: none→longer dorsally than ventrally.

Character 35. Base of tail: not prehensile→prehensile.

Character 52. Postorbital process 1: absent→present.

Caluromyinae

Character 17. Manual digits III and IV: III = IV→IV longest.

Character 26. Pouch 1: absent→present.

Character 57. Sagittal crest: absent→small.

Character 72. Transverse canal foramen: present→absent.

Character 74. Alisphenoid tympanic process: no contact with RTP→contacts RTP.

Character 76. RTP-CTP contact: absent (gap)→sutured.

Character 78. Ectotympanic suspension: from skull→from malleus only.

Character 86. Angular process: acute-strongly inflected→obtuse-weakly inflected.

Character 93. C1 alveolus: in premaxillary-maxillary suture→in maxillary only.

Character 95. P1 size: large→vestigial or absent.

Character 96. Height P2, P3: subequal→P2 taller.

Character 101. Ectoflexus on M1–M3: present→absent.

Caluromys

Character 5. Midrostral stripe: absent→present.

Character 40. Rostral process of premaxillae: absent→present.

Hyladelphinae + Didelphinae

Character 69. Posterolateral palatal corners: absent or indistinct→present.

Didelphinae

Character 29. Unpaired median teat: absent→present.

Character 104. Centrocrista: weakly ∧-shaped→strongly ∧-shaped.

Didelphini + Metachirini + Thylamyini

Character 73. Secondary foramen ovale: absent→formed by anteromedial strut.

Didelphini + Metachirini

Character 2. Rhinarium: with 2 grooves→with 1 groove.

Character 7. Mask: like *Marmosa*→like *Metachirus*.

Character 36. Tail tip: prehensile→not prehensile.

Character 84. Paroccipital process: small, adnate to petrosal→large and erect.

Character 108. Upper molar eruption: P3 last→M4 and P3 together.

Didelphini

Character 26. Pouch: absent→present.

Character 32. Body pelage on tail: none→subequal.

Character 33. Caudal coloration: uniform or variable→black-and-white.

Character 34. Caudal scales: intermediate→spiral.

Character 41. Nasal tips: above or anterior to I1→posterior to I1.

Character 52. Postorbital processes: absent→present.

Character 54. Frontals: separate→fused.

Character 57. Sagittal crest: absent→large.

Character 61. Parietal-mastoid contact: present→absent.

Character 73. Secondary foramen ovale: formed by anteromedial strut→formed by lamina.

Character 78. Ectotympanic suspension: from skull→from malleus only.

Character 96. Height P2, P3: subequal→P3 taller.

Character 104. Centrocrista: strongly ∧-shaped→weakly ∧-shaped.

Character 106. Postprotocrista: unnotched→notched.

Character 108. Upper molar eruption: M4 and P3 together→M4 last.

Character 109. Lower incisors: with lingual cusp→without lingual cusp.

Character 126. RES {a1+ a5, m1}: metacentric→acrocentric.

Character 127. RES {a2+a8, m2}: metacentric→acrocentric.

Character 128. RES {a3+a10, m3}: metacentric→acrocentric.

Character 129. RES {a6+a9, m4}: metacentric→acrocentric.

Didelphis + Philander + Lutreolina

Character 65. Palatine fenestrae: absent→present.

Character 90. Shape I2-I4 crowns: symmetrical rhomboids→asymmetrical.

Didelphis + Philander

Character 27. Pouch: opens posteriorly→opens anteriorly.

Character 36. Tail tip: not prehensile→prehensile.

Didelphis

Character 7. Mask: like *Metachirus*→like *Marmosa*.

Character 11. Dorsal underfur: dark→white.

Character 12. Dorsal guard hairs: short→long.

Didelphis albiventris + D. marsupialis

No unambiguous changes.

Philander

Character 8. Spot above eye: absent→present.

Philander mcilhennyi + Philander opossum

No unambiguous changes.

Thylamyini

Character 58. Fenestra in parietal-squamosal suture: absent→present.

Cryptonanus + Gracilinanus + Lestodelphys + Thylamys

Character 34. Caudal scales: intermediate→annular.

Cryptonanus + Gracilinanus

Character 17. Manual digits III and IV: III longest→III = IV.

Cryptonanus

Character 73. Secondary foramen ovale: formed by anteromedial strut→absent.

Gracilinanus

Character 40. Rostral process of premaxillae: absent→present.

Character 66. Maxillary fenestrae: absent→present.

Gracilinanus aceramarcae + G. microtarsus + G. agilis

No unambiguous changes.

Gracilinanus aceramarcae + G. microtarsus

No unambiguous changes.

Lestodelphys + Thylamys

Character 10. Dorsal fur markings: unpatterned→tricolored.

Character 20. Central palmar surface: smooth→densely tubercular.

Character 25. Ventral tarsal surface: naked→furred.

Character 28. Mammary position: abdominal-inguinal→pectoral.

Character 39. Tail incrassate: no→yes.

Character 68. Posterolateral palatal foramina: behind M4 protocones→lingual to M4 protocones.

Character 76. RTP-CTP contact: absent (gap)→sutured.

Character 114. Height p2, p3: p2 taller→subequal.

Thylamys

Character 43. Nasal width: wider posteriorly→uniformly narrow.

Thylamys macrurus + T. pusillus + T. pallidior (branch 22)
No unambiguous changes

Thylamys macrurus + T. pusillus
No unambiguous changes

Marmosops
Character 34. Caudal scales: intermediate→spiral.
Character 38. Caudal hairs: all hairs alike→middle hair thickest.
Character 40. Rostral process of premaxillae: absent→present.

Marmosops impavidus + M. noctivagus + M. incanus
No unambiguous changes.

Marmosops impavidus + M. noctivagus
No unambiguous changes.

Marmosops parvidens + M. pinheiroi
Character 94. Upper canine: simple→anterior and posterior accessory cusps present.

Marmosini
No unambiguous changes.

Marmosa + Tlacuatzin
Character 13. Lateral carpal tubercles: absent→present in adult males.
Character 52. Postorbital process: absent→present.

Marmosa
Character 40. Rostral process of premaxillae: absent→present.

Marmosa lepida + M. murina + subgenus Micoureus
No unambiguous changes.

Marmosa murina + subgenus Micoureus
No unambiguous changes.

Subgenus *Micoureus*
Character 14. Medial carpal tubercles: absent→present in adult males.

Marmosa demerarae + M. paraguayana
No unambiguous changes.

Marmosa mexicana + M. robinsoni + M. rubra
Character 14. Medial carpal tubercles: absent→present in adult males.

Marmosa mexicana + M. robinsoni
Character 9. Gular gland: absent→present.

Monodelphis
Character 2. Rhinarium: with 2 grooves→with 1 groove.
Character 6. Mask: present→absent.
Character 22. Pedal digits III and IV: IV longest→III longest.
Character 36. Tail tip: prehensile→not prehensile.
Character 45. Maxilloturbinals: elaborately branched→simple scrolls.
Character 51. Maxillary and alisphenoid: separate→in contact.
Character 96. Height P2, P3: subequal→P3 taller.
Character 114. Height p2, p3: p2 taller→subequal.
Character 120. m3 hypoconid position: labially salient→lingual to protoconid.
Character 121. Entoconid size: taller than hypoconulid→small or indistinct.

Monodelphis brevicaudata + M. theresa + M. emiliae
No unambiguous changes.

Monodelphis brevicaudata + M. theresa
No unambiguous changes.

Terminal Branches

Caluromys lanatus:
No unambiguous changes.

Caluromys philander:
Character 29. Unpaired median teat: absent→present.
Character 32. Body pelage on tail: longer dorsally→subequal.
Character 35. Base of tail: with ventral tubercles→smooth ventrally.

Caluromysiops irrupta:
Character 6. Mask: present→absent.
Character 10. Dorsal fur markings: unpatterned→scapular stripes.
Character 54. Frontals: separate→fused.
Character 55. Parietals: separate→fused.
Character 57. Sagittal crest: small→large.
Character 73. Secondary foramen ovale: absent→formed by lamina.
Character 81. Stapes: bicrurate→columelliform.
Character 104. Centrocrista: weakly ∧-shaped→linear.
Character 124. Hypoconulid: twinned with entoconid→in midline.

Glironia venusta:
Character 53. Postorbital processes: frontal only→frontal and parietal.
Character 127. RES {a2+a8, m2}: metacentric→acrocentric.
Character 129. RES {a6+a9, m4}: metacentric→acrocentric.

Chironectes minimus:
Character 10. Dorsal fur markings: unpatterned→like *Chironectes*.
Character 13. Lateral carpal tubercles: absent→present in both sexes.
Character 18. Manual plantar pads: present→absent.
Character 20. Central palmar surface: smooth→sandpapery.
Character 23. Pedal morphology: eleuthrodactylous→webbed.
Character 31. Cloaca: present→absent.
Character 49. Lacrimal foramina: two→one.
Character 85. Mental foramina: two→one.

Didelphis albiventris:
No unambiguous changes.

Didelphis marsupialis:
No unambiguous changes.

Didelphis virginiana:
Character 49. Lacrimal foramina: two→one.

Philander frenatus:
No unambiguous changes.

Philander mcilhennyi:
No unambiguous changes.

Philander opossum:
No unambiguous changes.

Lutreolina crassicaudata:
Character 6. Mask: present→absent.
Character 22. Pedal digits III and IV: subequal or IV longest→III longest.
Character 51. Maxillary and alisphenoid: separate→in contact.
Character 120. m3 hypoconid position: labially salient→lingual to protoconid.

Metachirus nudicaudatus:
Character 8. Spot above eye: absent→present.
Character 56. Parietal and alisphenoid: in contact→separated.

Cryptonanus chacoensis:

Character 115. dp3 trigonid: uni- or bicuspid→tricuspid.

Cryptonanus unduaviensis:
No unambiguous changes.
Gracilinanus aceramarcae:
No unambiguous changes.
Gracilinanus microtarsus:
Character 52. Postorbital process: absent→present.
Gracilinanus agilis:
No unambiguous changes.
Gracilinanus emiliae:
Character 34. Caudal scales: annular→intermediate.
Lestodelphys halli:
Character 2. Rhinarium: with 2 grooves→with 1 groove.
Character 22. Pedal digits III and IV: IV longest→III longest.
Character 36. Tail tip: prehensile→not prehensile.
Character 57. Sagittal crest: absent→small.
Character 81. Stapes: bicrurate→columelliform.
Character 114. Height p2, p3: subequal→p3 taller.
Character 120. m3 hypoconid position: labially salient→lingual to protoconid.
Thylamys macrurus:
No unambiguous changes.
Thylamys pusillus:
No unambiguous changes.
Thylamys pallidior:
Character 2. Rhinarium: with 2 grooves→with 1 groove.
Thylamys venustus:
No unambiguous changes.
Marmosops impavidus:
No unambiguous changes.
Marmosops noctivagus:
No unambiguous changes.
Marmosops incanus:
Character 28. Mammary position: abdominal-inguinal→pectoral.
Character 43. Nasal width: wider posteriorly→uniformly narrow.
Character 114. Height p2, p3: p2 taller→subequal.
Marmosops parvidens:
Character 105. Preprotocrista: stops at paracone→meets anterolabial cingulum.
Marmosops pinheiroi:
No unambiguous changes.
Marmosa lepida:
Character 94. Upper canine: simple→posterior accessory cusp present.
Marmosa murina:
Character 13. Lateral carpal tubercles: present in adult males→absent.
Marmosa demerarae:
No unambiguous changes.
Marmosa paraguayana:
Character 32. Body pelage on tail: none→subequal.
Marmosa regina:
No unambiguous changes.
Marmosa mexicana:
Character 65. Palatine fenestrae: absent→present.
Marmosa robinsoni:
No unambiguous changes.
Marmosa rubra:
Character 52. Postorbital process: present→absent.

Character 76. RTP-CTP contact: absent (gap)→sutured.
Tlacuatzin canescens:
Character 66. Maxillary fenestrae: absent→present.
Character 126. RES {a1+ a5, m1}: metacentric→acrocentric.
Character 128. RES {a3+a10, m3}: metacentric→acrocentric.
Monodelphis brevicaudata:
No unambiguous changes.
Monodelphis theresa:
Character 9. Gular gland: present→absent.
Character 73. Secondary foramen ovale: absent→formed by lamina.
Monodelphis emiliae:
Character 76. RTP-CTP contact: absent (gap)→sutured.
Character 114. Height p2, p3: subequal→p3 taller.
Monodelphis peruviana:
Character 61. Parietal-mastoid contact: present→absent
Hyladelphys kalinowskii:
Character 96. Height P2, P3: subequal→P2 taller.
Character 98. Upper milk premolar: large & molariform→vestigial.

APPENDIX 6

Key to the Didelphid Genera

This key is intended for use on adult specimens (with completely erupted permanent dentitions). Juveniles (with dP3/dp3) and subadults (lacking dP3/dp3, but with incompletely erupted third premolars and/or fourth molars) may not key out accurately if they lack traits seen in conspecific adults (e.g., large size, postorbital processes, secondary foramina ovales, contact between left and right exoccipitals; Abdala et al., 2001). Although the following couplets are based, insofar as possible, on characters with unambiguously distinguishable alternative states, key results should always be checked by comparing specimens character-by-character against generic descriptions and cranial illustrations (figs. 37–54). Couplet 10, the only step in our key based on a single character, is obviously problematic if an atypical specimen is in hand. Users would be well advised, if an unsatisfactory result is obtained at any subsequent step, to follow the alternative sequence on the hypothesis that the species in question is polymorphic.

External and craniodental measurements used to index size in this key are defined and abbreviated as follows: Head-and-

Body Length (HBL) is obtained by subtracting length of tail from total length (Hall, 1981); Condylo-Basal Length (CBL) is measured from the occipital condyles to the anteriormost point of the premaxillae (Voss et al., 2004b: fig. 2); and Length of Molars (LM) is measured from the anteriormost labial margin of M1 to the posteriormost point on M4 (Voss et al., 2004b: fig. 2).

1a. Plantar surface of manus without distinct plantar pads; finger-like fleshy process on lateral surface of wrist (resembling a sixth finger) present in both sexes; hind foot conspicuously webbed; dorsal pelage gray boldly marked by transverse bars of black fur; single lacrimal foramen usually present on each side; each hemimandible usually with a single mental foramen . . . . . . *Chironectes*

1b. Plantar surface of manus with distinct plantar pads; no finger-like fleshy process on wrist; hind foot not webbed; dorsal pelage variously pigmented, sometimes with contrasting longitudinal stripes, but never boldly marked with transverse blackish bars on a gray background; two lacrimal foramina usually present on each side; each hemimandible usually with two mental foramina 2

2a. Dorsal surface of tail covered by long, soft fur from base to tip; postorbital processes present, formed by frontals and parietals . . . . *Glironia*

2b. Dorsal surface of tail macroscopically naked for at least one or two centimeters from tip; postorbital processes absent or, if present, formed only by frontals 3

3a. Large (HBL >245 mm, weight >260 g, CBL >55 mm, LM >11 mm); with or without pale supraocular spots; manual digit III longer than manual digit IV; dorsal margin of foramen magnum formed by right and left exoccipitals only (incisura occipitalis absent). 4

3b. Size small or large; never with pale supraocular spots; manual digit III longer than, subequal to, or shorter than digit IV; dorsal margin of foramen magnum formed by supraoccipital in addition to exoccipitals (incisura occipitalis present) 7

4a. Pale supraocular spots present; naked skin of tail brownish or grayish basally, fading to whitish distally; postorbital processes absent; right and left frontals separated by persistent median suture; sagittal crest absent; palatine fenestrae absent; secondary foramen ovale present, formed by anteromedial bullar process spanning transverse canal foramen; frontal contacts squamosal (no alisphenoid-parietal contact) . . . . *Metachirus*

4b. Pale supraocular spots present or absent; naked skin of tail blackish basally, becoming abruptly whitish distally (occasional specimens have all-black tails); postorbital processes usually present; right and left frontals fused (median suture incomplete); sagittal crest well developed, extending to frontals; palatine fenestrae present; secondary foramen ovale usually present, but formed by medial lamina that does not span the transverse canal foramen; alisphenoid contacts parietal (no frontal-squamosal contact) 5

5a. Pale supraocular spots present . . . *Philander*

5b. Pale supraocular spots absent. 6

6a. Dorsal pelage grayish or blackish (never brownish); dorsal underfur white; dorsal guard hairs very long (pelage has a shaggy appearance); maxillary and alisphenoid separated by palatine on orbital floor. . . . . *Didelphis*

6b. Dorsal pelage brownish or yellowish-brown; dorsal underfur gray; dorsal guard hairs short; maxillary and alisphenoid in contact on orbital floor. . . . . *Lutreolina*

7a. Manual digit IV slightly longer than digit III; postorbital processes well developed; palate not perforated by any large fenestrae; transverse canal foramen absent; alisphenoid tympanic process contacts or closely approximates rostral tympanic process of petrosal; ectotympanic annulus suspended from malleus; C1 alveolus contained in maxilla; P1 vestigial or absent; width of M4 less than width of M1. 8

7b. Length of manual digit IV subequal to or less than length of digit III; postorbital processes present or absent; palate perforated by at least one set of paired fenestrae; transverse canal foramen present (sometimes small and hard to see on incompletely cleaned skulls); alisphenoid tympanic process and rostral tympanic process of petrosal separated by wide gap; ectotympanic suspended directly from basicranium; P1 smaller than posterior premolars, but well-formed and nonvestigial; C1 alveolus in premaxillary-maxillary suture; width of M4 greater than width of M1. . . 9

8a. Circumocular mask and dark midrostral stripe present; dorsal body pelage without dark scapular markings; premaxillary rostral process present; right and left frontals separated by persistent median suture; sagittal crest absent (or weakly developed over interparietal); secondary foramen ovale absent; centrocrista weakly inflected labially;

hypoconulid twinned with entoconid. . . . .
. . . . *Caluromys*

8b. Pelage of head uniformly pale, without any dark markings; dark scapular stripes present; premaxillary rostral process absent; right and left frontals fused (median suture incomplete); sagittal crest well developed, extending anteriorly to frontals; secondary foramen ovale present; centrocrista linear, uninflected; hypoconulid not twinned with entoconid. . . . . *Caluromysiops*

9a. Circumocular mask absent; tail shorter than combined length of head and body, without prehensile modifications; postorbital processes absent or indistinct; premaxillary rostral process absent; palatine and maxillary fenestrae usually absent; maxillary and alisphenoid in contact on orbital floor; secondary foramen ovale absent or formed by medial bullar lamina that does not span transverse canal foramen; entoconid subequal to or smaller than hypoconulid on m1–m3 (absent or indistinct in worn dentitions) . . . . *Monodelphis*

9b. Dark circumocular mask present (but narrow and inconspicuous in some taxa); tail longer or shorter than combined length of head and body, with or without prehensile modifications; distinct postorbital processes present or absent; premaxillary rostral process present or absent; palatine and maxillary fenestrae present or absent; maxillary and alisphenoid separated by palatine on orbital floor; secondary foramen ovale absent or formed by anteromedial bullar process spanning transverse canal foramen; entoconid taller than hypoconulid on m1–m3 (except in *Chacodelphys*) 10

10a. Secondary foramen ovale usually present, formed by anteromedial bullar process spanning transverse canal foramen 11

10b. Secondary foramen ovale usually absent . .
. . . . 14

11a. Manual digits III and IV subequal in length; tail always longer than combined length of head and body; premaxillary rostral process present; maxillary fenestrae usually present (occasionally absent in one species); P2 and P3 subequal in height . . . . *Gracilinanus*

11b. Manual digit III longer than digit IV; tail longer or shorter than head-and-body; premaxillary rostral process present or absent; maxillary fenestrae absent or, if present, then P3 taller than P2 12

12a. Tail longer than combined length of head and body, with scales in spiral series, never incrassate; premaxillary rostral process present (but short in a few species); maxillary

fenestrae absent; fenestra cochleae exposed; P2 and P3 subequal in height. . . *Marmosops*

12b. Tail longer or shorter than head-and-body, with scales (when distinct) in annular series, incrassate (at least seasonally); premaxillary rostral process absent; maxillary fenestrae present or absent; fenestra cochleae concealed in a sinus formed by rostral and caudal tympanic processes of petrosal; P3 taller than P2 13

13a. Manual claws long, extending well beyond fleshy apical pads of digits; pedal digit III longer than digit IV; tail shorter than combined length of head and body; ventral surface of tail tip not modified for prehension; nasals conspicuously wider posteriorly than anteriorly; maxillary fenestrae absent; stapes columelliform and imperforate or microperforate; p3 taller than p2; hypoconid lingual to protocone on m3, not labially salient . . . . *Lestodelphys*

13b. Manual claws short, not extending much, if at all, beyond fleshy apical pads of digits; pedal digit IV longer than digit III; tail longer or shorter than combined length of head-and-body; ventral surface of tail tip modified for prehension in most species; nasals uniformly narrow (not much wider posteriorly than anteriorly), with subparallel lateral margins; maxillary fenestrae present or absent; stapes triangular with large obturator foramen; p2 and p3 subequal in height; hypoconid labially salient on m3, not lingual to protoconid. . . . . *Thylamys*

14a. Manual digit III longer than manual digit IV; tail shorter than combined length of head and body; nasals narrow, with subparallel lateral margins; maxillary fenestrae present; hypoconid not labially salient on m3 (lingual to protoconid). . . . . *Chacodelphys*

14b. Manual digits III and IV subequal in length; tail longer than head-and-body; nasals distinctly wider posteriorly than anteriorly; maxillary fenestrae absent (except in *Tlacuatzin*); hypoconid labially salient on m3 (not lingual to protoconid) 15

15a. Tail scales in annular series; rostral process of premaxillae absent; palatine fenestrae present; petrosal exposed on posterolateral surface of braincase through fenestra in parietal-squamosal suture; unworn C1 usually with small accessory cusps; P3 taller than P2 . . . . *Cryptonanus*

15b. Tail scales in annual or spiral series; rostral process of premaxillae present or absent; palatine fenestrae present or absent; petrosal not exposed through fenestra in parietal-squamosal suture (fenestra absent); C1 with-

out accessory cusps; P2 and P3 subequal in height or P2 taller than P3 16

16a. Very small (HBL <95 mm; weight <20 g; CBL <25 mm; LM <5 mm); mammae 2–0–2=4; rostral process of premaxillae absent; postorbital processes absent; palatine fenestrae absent; unworn crowns of I2–I5 asymmetrical (incisiform), with much longer anterior than posterior cutting edges; P2 much taller than P3; lower canine (c1) an erect, recurved-conical tooth, not premolarized . . . . *Hyladelphys*

16b. Larger; mammae 3–1–3=7 to 7–1–7=15; rostral process of premaxillae present or absent; postorbital processes usually present (indistinct in some young adults but absent in adults of at least one species); palatine fenestrae present or absent; unworn crowns of I2–I5 symmetrically rhomboidal, with subequal anterior and posterior cutting edges; P2 and P3 subequal in height; unworn c1 usually procumbent and somewhat premolariform 17

17a. Caudal scales in spiral series, at least in part (the caudal scale arrangement in some species is partly spiral and partly annular); rostral process of premaxillae usually present; maxillary fenestrae absent; crown of I2 visibly shorter (mesiodistal dimension) than crown of I5; unworn c1 procumbent and more or less premolariform. . . . . *Marmosa*

17b. Caudal scales in unambiguously annular series; rostral process of premaxillae absent; maxillary fenestrae present (sometimes confluent with maxillopalatine openings); crowns of I2–I5 subequal in length; c1 erect and recurved-conical, not premolarized . . . . *Tlacuatzin*