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On the Contents of *Gracilinanus* Gardner and Creighton, 1989, with the Description of a Previously Unrecognized Clade of Small Didelphid Marsupials

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CONTENTS

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ABSTRACT

Five nominal species of small didelphid marsupials previously referred to *Gracilinanus* differ conspicuously from the type species (*G. microtarsus*) and from all of the other valid taxa that we recognize as members of that genus (*G. aceramarcae*, *G. agilis*, *G. dryas*, *G. emiliae*, *G. marica*). These anomalous forms can be distinguished morphologically from *Gracilinanus* (in the strict sense just defined) by lacking maxillary palatal vacuities, a secondary foramen ovale, and a rostral process of the premaxillae; in addition, P3 is taller than P2, and accessory cusps are often present on C1. A new genus, *Cryptonanus*, is described to contain these forms, all of which are provisionally recognized as valid species: *C. agricolai*, *C. chacoensis*, *C. guahybae*, *C. ignitus*, and *C. unduaviensis*. Separate and combined phylogenetic analyses of nonmolecular data and nuclear gene sequences suggest that *Cryptonanus* and *Gracilinanus* (sensu stricto) are reciprocally monophyletic and closely related, although they were not consistently recovered as sister taxa in any analysis. Available specimen records document that *Cryptonanus* is widely distributed in mostly unforested tropical, subtropical, and temperate biomes south of the Amazon River (from ca. 7°S in the Brazilian state of Ceará to ca. 34°S in the Argentinian province of Buenos Aires), but significant range extensions could be expected from pitfall trapping in extralimital savanna landscapes. Scant field data suggest that species of *Cryptonanus* may often be associated with wet or seasonally inundated grasslands, an unusual habitat for small didelphids.

INTRODUCTION

The small didelphid marsupials formerly classified as *Marmosa* (sensu Tate, 1933) include numerous superficially similar species distinguished from other confamilial taxa by their small size, dark circumocular masks, long prehensile tails, and lack of a pouch. Despite such resemblances, ‘‘marmosines’’ are now widely recognized as a polyphyletic group, some members of which may be more closely related to *Didelphis* and other large opossums than to *Marmosa* sensu stricto (see Kirsch and Palma, 1995; Patton et al., 1996; Jansa and Voss, 2000; Voss and Jansa, 2003). Although considerable progress has been made toward a monophyletic classification of these animals, the unrevised contents of several genera remain problematic.

Species of *Gracilinanus* are small (<50 g) arboreal or semiarboreal inhabitants of tropical and subtropical forests from Colombia to Paraguay and southeastern Brazil. As originally described by Gardner and Creighton (1989), *Gracilinanus* contained 17 nominal taxa, most of which had previously been referred by Tate (1933) to the ‘‘*Microtarsus* Group’’ of *Marmosa*; of these, 6 were recognized as valid species and 11 were treated as synonyms (table 1). Although Hershkovitz (1992) subsequently described three more species, Voss et al. (2001, 2004a) removed *kalinowskii* (one of Hershkovitz’s new species) and *formosa* (an alleged synonym of *G. agilis*) to new genera and remarked that *Gracilinanus* still included several forms that did not fit Gardner and Creighton’s original generic diagnosis.

Our attention was initially drawn to the taxonomic problems discussed below when we discovered that some museum specimens identified as *Gracilinanus agilis* have a secondary foramen ovale formed by an anteromedial process of the alisphenoid tympanic wing, whereas others do not. Similar variation had previously been noted by Hershkovitz (1992), who interpreted it as intraspecific polymorphism. However, the presence or absence of secondary foramina ovales formed by anteromedial bullar processes is a phylogenetically conservative character among didelphids—with a marked tendency to be constant within genera and even higher taxa (Voss and Jansa, 2003: character 45)—so we looked for correlated characters that might indicate the presence of two or more forms within the material that has traditionally been referred to *G. agilis*. To our surprise, such characters were not hard to find. Moreover, the same characters appeared to diagnose a group of species comprising a hitherto unrecognized clade.

In this paper we name that clade, which we provisionally rank as a new genus. After providing diagnostic comparisons and sum-

TABLE 1

Contents of *Gracilinanus* According to Recent Authors

Gardner and Creighton (1989)[a]	Hershkovitz (1992)	This report
G. aceramarcae *G. agilis* Synonyms: *beatrix* *blaseri* *buenavistae* *chacoensis*[b] *formosa*[c] *peruana* *rondoni* *unduaviensis*[b] *G. dryas* *G. emiliae* Synonyms: *agricolai*[b] *G. marica* *G. microtarsus* Synonyms: *guahybae*[b] *herhardti*	*G. aceramarcae* *G. agilis* Synonyms: *beatrix* *blaseri* *buenavistae* *chacoensis*[b] *formosa*[c] *peruana* *rondoni* *unduaviensis*[b] *G. dryas* *G. emiliae* Synonyms: *agricolai*[b] *G. kalinowskii* (new)[d] *G. longicaudus* (new) *G. marica* *G. microtarsus* Synonyms: *guahybae*[b] *herhardti* *G. perijae* (new)	*G. aceramarcae* *G. agilis* Synonyms: *beatrix* *buenavistae* *peruana* *G. dryas* *G. emiliae* Synonyms: *longicaudus*[e] *G. marica* Synonyms: *perijae*[f] *G. microtarsus* Incertae sedis[g] *blaseri* *herhardti* *rondoni*

[a] The classification also followed by Gardner (1993); see Gardner and Creighton (1989) for authors, dates, and original descriptions of all referred nominal taxa.

[b] Removed to a new genus in this report.

[c] Originally described as *muscula* Shamel, 1930; removed to *Chacodelphys* by Voss et al. (2004a).

[d] Removed to *Hyladelphys* by Voss et al. (2001).

[e] Apparently indistinguishable from *G. emiliae* (see Voss et al., 2001).

[f] Synonymized with *G. marica* by Gardner (2005).

[g] We are unable to evaluate the status of three nominal taxa referred to *Gracilinanus* by Gardner and Creighton (1989), Hershkovitz (1992), and Gardner (1993). Originally described under the binomens *Marmosa blaseri* Miranda-Ribeiro (1936: 373), *M. herhardti* Miranda-Ribeiro (1936: 382), and *Thylamys rondoni* Miranda-Ribeiro (1936: 387), these taxa are represented by type material in the Museu Nacional of Brazil (Langguth et al., 1997) that should be reexamined to determine their generic membership and alleged synonymies with older names.

marizing relevant nomenclatural issues, we analyze phylogenetic relationships among 43 didelphid terminal taxa based on morphological, karyotypic, and molecular characters. Although inconclusive in some respects, our results clearly indicate the phylogenetic distinctness of the new genus and underscore the need for additional character data to resolve still-problematic aspects of didelphid phylogeny.

MATERIALS AND METHODS

The specimens we examined and others cited in our text are preserved in the following collections (listed in order of their standard institutional abbreviations): AMNH, American Museum of Natural History (New York); BMNH, Natural History Museum (London); FMNH, Field Museum of Natural History (Chicago); MNRJ, Museu Nacional

(Rio de Janeiro); MSB, Museum of Southwestern Biology (Albuquerque); MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (Lima); MVZ, Museum of Vertebrate Zoology (Berkeley); MZUSP, Museu de Zoologia da Universidade de São Paulo (São Paulo); ROM, Royal Ontario Museum (Toronto); USNM, National Museum of Natural History (Washington, D.C.); ZMB, Museum für Naturkunde der Humboldt-Universität zu Berlin (Berlin); and ZMUC, Zoological Museum of the University of Copenhagen (Copenhagen). In addition, we examined seven uncataloged specimens identified only by field numbers: GD (= Guillermo D'Elia) 521 has already been returned to the Museo Nacional de Historia Natural del Paraguay (Asunción); IGP (= I.G. Phillips) 157 is temporarily being held at the USNM; and TK (= Tissue/Karyotype) 60201, 61053, 61074, 61103, and 65331 are at the Texas Tech University Museum (Lubbock).

We transcribed total length (nose to fleshy tail-tip, TL) and length of tail (basal flexure to fleshy tip, LT) from specimen tags or field notes, and we computed head-and-body length (HBL) by subtracting LT from TL. We also transcribed length of hind foot (heel to tip of longest claw, HF), length of ear (from notch, Ear), and weight from specimen tags or field notes; however, we sometimes remeasured HF on fluid specimens to check the accuracy of values recorded by the collector, and we used our value rather than the collector's whenever large discrepancies were found. All external measurements are reported to the nearest millimeter (mm), and all weights are reported to the nearest gram (g).

Craniodental measurements were taken with digital calipers and recorded to the nearest 0.01 mm, but values reported herein are rounded to the nearest 0.1 mm. The following dimensions were measured as illustrated by Voss et al. (2001, 2004b): condylobasal length (CBL), measured from the occipital condyles to the anteriormost point of the premaxillae; nasal breadth (NB), measured across the triple-point suture of the nasal, frontal, and maxillary bones on each side; least interorbital breadth (LIB), measured at the narrowest point across the frontals between the orbits, even when the *postorbital constriction* (between the temporal fossae) is narrower; zygomatic breadth (ZB), measured at the widest point across both zygomatic arches; palatal length (PL), measured from the anteriormost point of the premaxillae to the postpalatine torus, including the postpalatine spine (if present); palatal breadth (PB), measured across the labial margins of the fourth molar (M4) crowns, at or near the stylar A position; maxillary toothrow length (MTR), measured from the anterior margin of the canine (C1) to the posterior margin of the fourth molar (M4); length of molars (LM), measured from the anteriormost labial margin of M1 to the posteriormost point on M4; length of M1–M3 (M1–M3), measured from the anteriormost labial margin of M1 to the posteriormost point on M3.

Except as noted below, all measurements and qualitative character data were obtained from adult specimens as determined by dental criteria. Following Voss et al. (2001), a specimen was judged to be *juvenile* if dP3 is still in place, *subadult* if dP3 has been shed but P3 and/or M4 are still incompletely erupted, and *adult* if the permanent dentition is complete. Qualitative morphological characters were scored for phylogenetic analysis following procedures described by Voss and Jansa (2003), who also defined and illustrated most of the anatomical terminology used herein. The material that we examined to score morphological characters for taxa not included in previous phylogenetic analyses is listed in appendix 1. Karyotypic character data for three taxa whose phylogenetic relationships are newly analyzed in this report were taken from the literature: Palma (1995) reported the karyotype of *Thylamys macrurus*, Palma and Yates (1998) reported the karyotype of *T. pusillus*, and Carvalho et al. (2002) reported the karyotype of *Gracilinanus agilis*.

For all specimens newly sequenced in this study (appendix 2), DNA was extracted from heart, liver, or kidney tissue that had been frozen or preserved in ethanol in the field. Procedures for DNA extraction, sequencing, and alignment were described by Jansa and Voss (2000). Briefly, a region approximately 1.2 kb long of IRBP exon 1 was amplified from genomic DNA using primers A and D1. This product was used as a template in two subsequent PCR reactions, one using primer A paired with F and one using primers E1 and D1. The resulting PCR product was sequenced in both directions using amplification primers and dye terminator chemistry (BigDye Cycle Sequencing, Applied Biosystems Inc.). All sequences analyzed in this report have been deposited in GenBank with accession numbers AF257675–AF247710 (from Jansa and Voss, 2000), AY233765–AY233791 (from Voss and Jansa, 2003), and AY957486–AY957494 (from this project).

Phylogenetic analyses of nonmolecular characters, IRBP sequences, and combined-data (nonmolecular + IRBP) supermatrices were executed using heuristic search algorithms implemented by PAUP* 4.0b10 (Swofford, 1998) with all characters weighted equally. Whereas some multistate nonmolecular characters were treated as ordered transformation series (after Voss and Jansa, 2003), IRBP sequence characters were always treated as unordered. An initial search for each dataset employed 1000 replicates of random-taxon addition and TBR branch-swapping with only five trees saved per replicate. The resulting pool of minimal-length trees was then subjected to a second round of TBR branch swapping with no limit on the number of trees saved. We used the same nodal support algorithms and rooting conventions previously explained by Voss and Jansa (2003).

TAXONOMIC ACCOUNTS

Several nominal species of small didelphid marsupials hitherto referred to *Gracilinanus* differ conspicuously from the type species (*G. microtarsus*) and from all other species that we recognize as members of that genus (table 1). Because these anomalous forms exhibit no clearly recognizable pattern of derived similarities with other didelphid taxa, we provide a new generic name for them below. Alternative classificatory options, all of which would have undesirable consequences, are briefly considered in the Discussion.

Cryptonanus, new genus

Figures 1A, 1B, 2A, 3A

TYPE SPECIES: *Cryptonanus chacoensis* (Tate, 1931), originally described as a subspecies of *Marmosa agilis* (Burmeister, 1854).

CONTENTS: We refer five nominal taxa to *Cryptonanus*, including *chacoensis* Tate (1931), *guahybae* Tate (1931), *unduaviensis* Tate (1931), *agricolai* Moojen (1943), and *ignitus* Díaz et al. (2002). Despite the absence of unambiguously diagnostic characters in the small series we examined, it seems appropriate to accept provisionally the null hypothesis that all of these names represent valid species. However, in the event that *chacoensis*, *guahybae*, and *unduaviensis*—all named in the same publication (Tate, 1931) and therefore having equal priority—should prove to be conspecific, we select *chacoensis* to have precedence under Article 24.2 of the International Code of Zoological Nomenclature (ICZN, 1999).

MORPHOLOGICAL DIAGNOSIS: Species of *Cryptonanus* are small (15–40 g) didelphid marsupials that can be distinguished from other confamilial taxa by the following combination of qualitative morphological character states (see Voss and Jansa [2003] for character definitions and anatomical terminology).

Ventral margin of rhinarium with two shallow grooves on each side of median sulcus; eye narrowly surrounded by mask of dark fur contrasting in color with paler fur of cheeks and crown; pale spot above eye 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); manual digits III and IV subequal and longer than adjacent digits (II and V); manual claws shorter than fleshy digital pads; central palmar surface of manus sparsely tubercular (neither smooth nor densely covered with convex tubercles); lateral carpal tubercles present in adult males; pedal digit IV longer than adjacent digits III and V; plantar epithelium of pes naked from heel to toes; pouch absent; mammary complements differing among species, from 4–1–4 = 9 (without pectoral teats) to 7–1–7 = 15 (with pectoral teats); cloaca present; tail macroscopically naked but sparsely covered by short subequal hairs (three per caudal scale);

caudal integument more-or-less bicolored (dark above, paler below) in most specimens; caudal scales in distinctly annular series; caudal prehensile surface present (the ventral surface naked distally, with an apical pad bearing dermatoglyphs); tail not incrassate.

Rostral process of premaxillae absent; palatal process of premaxilla contacts C1 alveolus on each side; nasal tips extend anterior to I1; nasals conspicuously wider posteriorly than anteriorly; maxillary turbinals large and elaborately branched; supraorbital margins rounded, without beads or processes (except in a few very old specimens with incipient postorbital processes and temporal scars); distinct interorbital and postorbital constrictions usually present in juveniles and young adults; sagittal crest absent; parietal and alisphenoid in contact (no squamosal-frontal contact); petrosal laterally exposed in fenestra between parietal and squamosal; maxillopalatine fenestrae large; palatine fenestrae present; maxillary fenestrae absent; posterolateral palatal foramina not extending lingual to M4 protocones; posterior palate with prominent lateral corners, the internal choanae abruptly constricted behind; maxillary and alisphenoid not in contact on orbital floor; transverse canal foramen present; secondary foramen ovale absent (anteromedial process of alisphenoid tympanic wing incomplete or absent); ectotympanic suspension direct; fenestra cochleae laterally exposed; paroccipital process of exoccipital small, adnate to petrosal; dorsal margin of foramen magnum formed by supraoccipital and exoccipitals; triangular stapes perforated by large foramen; two mental foramina on lateral aspect of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal, slightly increasing in breadth from front to back (I2 ≤ I5); unworn C1 usually with one or two small accessory cusps (the posterior accessory cusp is more consistently distinct than the anterior cusp); P1 present, smaller than posterior premolars but not vestigial; P2 distinctly shorter than P3; P3 without anterior cutting edge; upper molars strongly dilambdodont and highly carnassialized, increasing in width (transverse dimension) from front to back (width M1 ≪ width M4); ectoflexus shallow or absent on M1, deeper on M2, and consistently deep on M3. Unworn lower incisors with distinct lingual cusp; c1 procumbent, usually with small posterior accessory cusp (often absent on even moderately worn teeth); p2 taller than p3; m3 hypoconid labially salient (level with labial apex of protoconid); hypoconulid twinned with entoconid; entoconid large, much taller than hypoconulid.

COMPARISONS WITH *GRACILINANUS*: Species of *Cryptonanus* and *Gracilinanus* are similar in size and external characters and might be indistinguishable in the field.[4] Although side-by-side comparisons of museum specimens suggest that species of *Gracilinanus* tend to have broader circumocular masks, larger ears, and longer mystacial vibrissae than species of *Cryptonanus*, these impressions are hard to document with measurements or illustrations. Species of *Gracilinanus* also appear to have relatively longer tails (on average) than species of *Cryptonanus*, but there is enough overlap in the data at hand (table 2) to suggest that this trait is not a reliable basis for generic identifications.

Visual cranial comparisons (figs. 1, 2) suggest that *Cryptonanus* specimens have relatively shorter rostrums and smaller orbits than specimens of *Gracilinanus*, but such proportions are ontogenetically variable and available samples are too small for statistically compelling morphometric analyses. Fortunately, several discrete characters provide a less subjective basis for taxonomic diagnosis (table 3). A secondary foramen ovale (formed by an anteromedial process of the alisphenoid tympanic wing; Voss and Jansa, 2003: character 45, fig. 8) is uniformly present in our material of five species of *Gracilinanus*, including *G. aceramarcae*, *G. dryas*, *G. emiliae*, *G. marica*, and *G. microtarsus*. By contrast, a secondary foramen ovale is consistently absent in examined specimens of *Cryptonanus chacoensis*, *C. guahybae*, *C. ignitus*, and *C. unduaviensis*.

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[4] Three species of *Cryptonanus* that usually have self-whitish or self-buffy ventral fur (*C. agricolai*, *C. chacoensis*, and *C. unduaviensis*) occur sympatrically with *Gracilinanus agilis*, which usually has distinctly gray-based ventral fur. Allopatric congeners, however, are differently marked. *Cryptonanus guahybae*, for example, has gray-based ventral fur, and some species of *Gracilinanus* (e.g., *G. emiliae*) have self-whitish ventral fur.

TABLE 2

Relative Tail Length (LT/HBL) among Species of *Gracilinanus* and *Cryptonanus*

	N[a]	Mean[b]	Observed range
Gracilinanus			
aceramarcae[c]	3	1.50	1.50–1.52
agilis[d]	6	1.40	1.34–1.45
dryas[e]	6	1.49	1.20–1.68
emiliae[f]	1	1.96	1.96
marica[g]	5	1.35	1.32–1.38
microtarsus[h]	3	1.33	1.25–1.38
Cryptonanus			
agricolai[i]	3	1.22	1.17–1.27
chacoensis[j]	4	1.25	1.04–1.32
guahybae[k]	1	[1.23]	[1.23]
ignitus[l]	1	[1.10]	[1.10]
unduaviensis[m]	9	1.21	1.01–1.40

[a] Sample size (males and females combined); except as noted, only data from adult specimens measured in the field following the standard American protocol (see Materials and Methods) were used to compute ratios.

[b] The mean ratio (LT/HBL), not the ratio of means.

[c] LSU 17897, MVZ 171411, UMMZ 156004.

[d] MVZ 197437–197442.

[e] USNM 372924–372926, 385017, 385018, 418517.

[f] MUSM 15292. All other specimens of this exceedingly rare species are either subadults or were measured by the British method (body length and tail length measured separately). Ratios computed from subadults and/or British measurements ($N = 5$) have a mean of 1.81 and an observed range of 1.71–1.89.

[g] USNM 280881, 280884, 370045–370047.

[h] FMNH 94294, 94295; MVZ 197436.

[i] MNRJ 36215, 36216, 36305.

[j] GD 521; UMMZ 126105, 137143; USNM 236329.

[k] BMNH 82.9.30.42, a fluid-preserved specimen with extracted skull, unaccompanied by field measurements. Although we measured this specimen in preservative, we cannot vouch for the accuracy of the results as approximations of the missing field data.

[l] AMNH 167852, apparently measured by the British method.

[m] AMNH 72563, 209150, 209152, 209154, 209156; MSB 57000, 58508, 70752; USNM 364718.

Polymorphisms were observed in only two species. Of 38 specimens of *G. agilis* scored for this character, a secondary foramen ovale was observed in 37 specimens; the unique exception is UMMZ 126104 (from the Paraguayan department of Cordillera), a typical specimen of *G. agilis* in all respects but its lack of anteromedial bullar processes. The other polymorphic species is *C. agricolai,* of which two examined adult specimens (ZMUC 151, 154) have a secondary foramen ovale and six others (BMNH 93.4.16.4; MN 1494, 36305, 36215; ZMUC 152, 160) do not; a single juvenile (MN 36526, not scored for table 3) also exhibits a secondary foramen ovale, and one adult with damaged bullae (MN 36216, likewise not scored) has broken anteromedial processes on each bulla that may have formed a secondary foramen ovale in life.

Maxillary fenestrae (nonvascular perforations of the maxillary palate between the maxillopalatine fenestrae and M1 or M2; Voss and Jansa, 2003: character 40, fig. 5) appear to be consistently present in most species of *Gracilinanus* (e.g., *G. aceramarcae, G. agilis, G. dryas, G. marica,* and *G. microtarsus*), but they are small and individually variable—sometimes absent unilaterally or bilaterally—in *G. emiliae*. By contrast, these openings are uniformly absent in our material of three *Cryptonanus* species (*C. chacoensis, C. guahybae,* and *C. ignitus*), and they are absent in most examined specimens of two others (*C. agricolai* and *C. unduaviensis*). The exceptions include the paratype of *C. agricolai* (MNRJ 1494), which has a small (0.5 mm) maxillary vacuity on each side of the palate opposite M1; the paratype of *C. unduaviensis* (AMNH 72565), which has a somewhat larger opening on the right side of the palate; and another specimen of *C. unduaviensis* (AMNH 209156), which has very small (<0.5 mm) openings on both sides of the palate.

The relative heights of the second and third upper premolars (fig. 4) provide the most consistent basis for generic diagnosis because intraspecific variation is minimal. However, relative premolar heights cannot be scored from old adults with heavily worn teeth, so sample sizes tend to be smaller for this character than for the two previously discussed. Nevertheless, in all examined specimens of *Gracilinanus* that preserve the apices of these teeth, P2 and P3 are subequal in height (in most species, P2 and P3 are equally tall, but P2 is often slightly taller than P3 in our samples of *G. aceramarcae, G. emiliae,* and *G. microtarsus*). By contrast, P2 is distinctly shorter than P3 in all examined

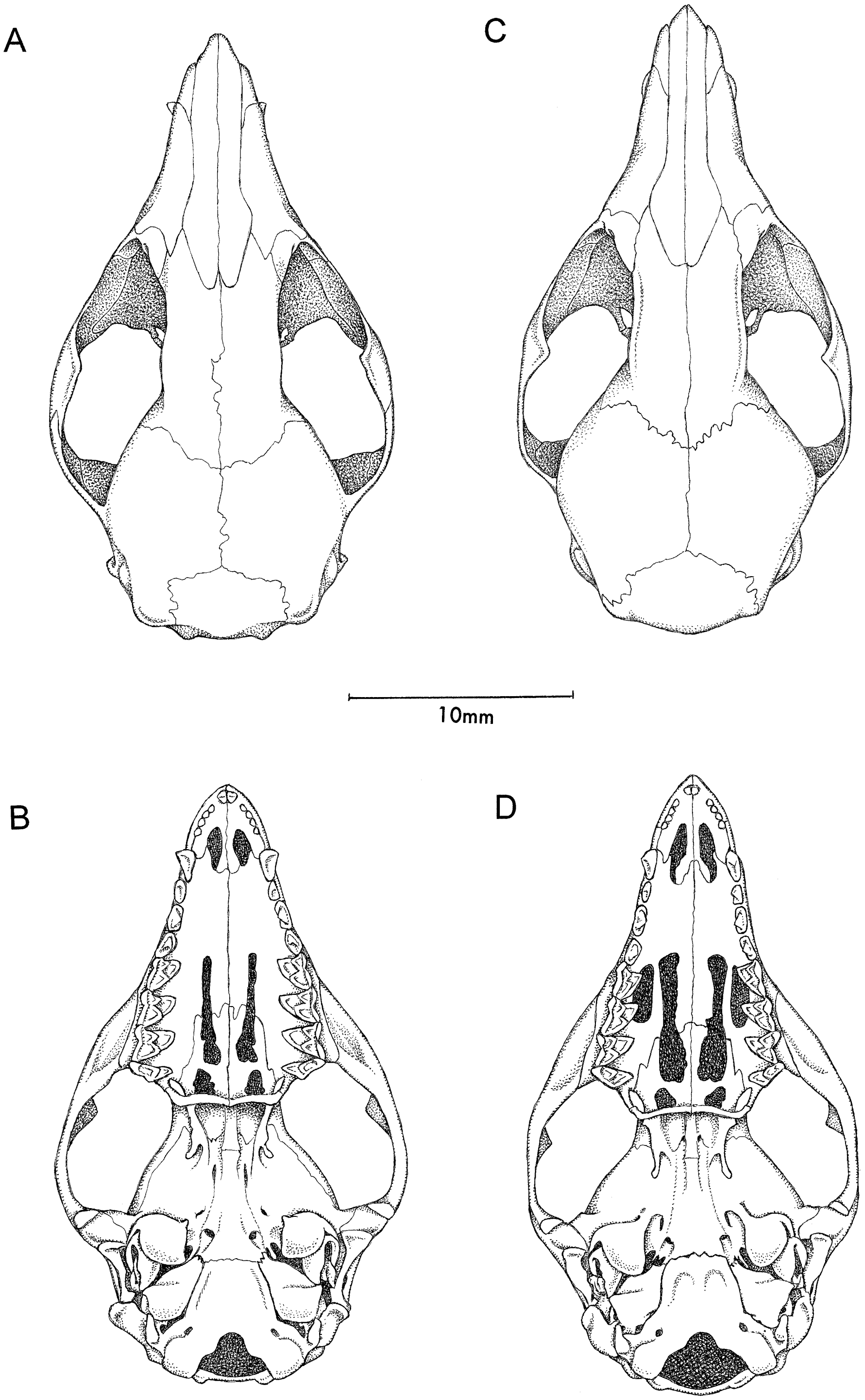

Fig. 1. Dorsal and ventral cranial views of *Cryptonanus unduaviensis* (**A, B,** AMNH 209152) and *Gracilinanus agilis* (**C, D,** MVZ 197437) illustrating generic differences discussed in the text.

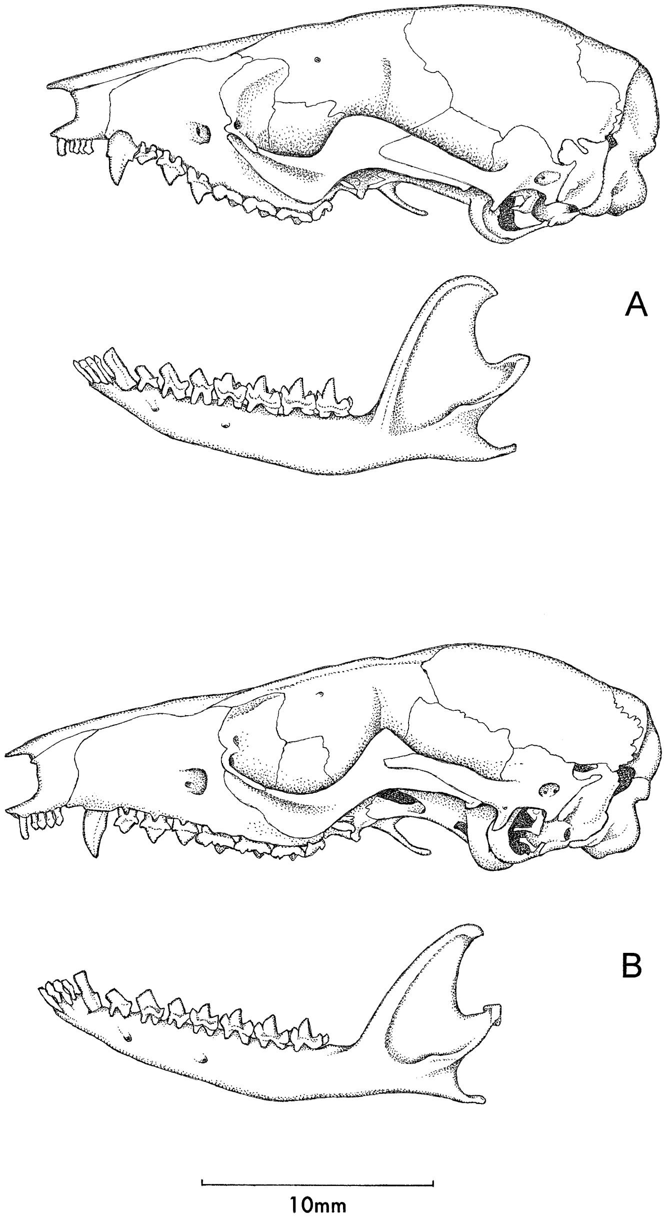

Fig. 2. Lateral cranial and mandibular views of *Cryptonanus unduaviensis* (**A,** AMNH 209152) and *Gracilinanus agilis* (**B,** MVZ 197437) illustrating generic differences discussed in the text.

specimens of *Cryptonanus* with suitably preserved (unworn or lightly worn) dentitions.

A character whose diagnostic potential we did not recognize until late in this project, and for which we have correspondingly less information, is the rostral process of the premaxillae (Voss and Jansa, 2003: character 29, fig. 4). This bony projection, which extends the suture between left and right premaxillae anterior to I1, is sometimes damaged during specimen preparation, and it is often obscured by dried skin or connective tissue on incompletely cleaned skulls. Among the specimens that we were able to score for this feature (table 3), a rostral process was consistently present in *Gracilinanus aceramar-*

TABLE 3

Craniodental Trait Frequencies in Species of *Gracilinanus* and *Cryptonanus*[a]

	2° foramen ovale		Maxillary palatal fenestrae			Height of premolars		Rostral process		C1 accessory cusps	
			Bilaterally present	Unilaterally present	Bilaterally absent						
	Present	Absent				P2≈P3	P2<P3	Present	Absent	Present	Absent
Gracilinanus											
aceramarcae[b]	4	0	4	0	0	4	0	4	0	0	4
agilis[c]	37	1	38	0	0	34	0	15	0	1	19
dryas[d]	7	0	7	0	0	7	0	6	0	0	5
emiliae[e]	7	0	3	1	2	5	0	3	0	6	0
marica[f]	12	0	12	0	0	11	0	8	0	0	10
microtarsus[g]	9	0	9	0	0	8	0	4	0	0	8
Cryptonanus											
agricolai[h]	2	6	1	0	9	0	10	—	—	10	0
chacoensis[i]	0	8	0	0	7	0	7	0	6	5	2
guahybae[j]	0	2	0	0	2	0	2	0	1	2	0
ignitus[k]	0	1[l]	0	0	1	0	1	0	1	—	—
unduaviensis[m]	0	16	1	1	12	0	12	0	9	8	4

[a] Table entries are numbers of specimens. Not all specimens could be scored for every character.

[b] Specimens examined: AMNH 72568 (holotype of *aceramarcae*); LSU 17897; MVZ 171411; UMMZ 156004.

[c] Specimens examined: AMNH 133217, 133221, 133225, 133227, 133229, 133230, 133233, 133234, 133236, 133238, 202651, 202652, 209157; BMNH 3.2.3.39, 3.4.7.22, 3.4.7.23, 4.1.5.46, 4.1.5.47, 11.4.25.24 (holotype of *beatrix*), 26.12.4.91 (holotype of *buenavistae*), 27.11.1.268 (holotype of *peruanus*), 28.2.9.93; MVZ 197437–197442; UMMZ 124675, 126104, 133998–134006.

[d] Specimens examined: BMNH 98.5.15.2 (holotype of *dryas*); USNM 372924–372926, 385017, 385018, 418517.

[e] Specimens examined: AMNH 203363, 267006; BMNH 9.3.9.10 (holotype of *emiliae*); FMNH 87924 (holotype of *longicaudus*); MUSM 15292; RMNH 18231; ROM 35466.

[f] Specimens examined: AMNH 21319, 21324, 21329, 21331, 21332, 24321, 24325, 24326, 206763; BMNH 98.5.15.1 (holotype of *marica*); USNM 280881 (holotype of *perijae*), 280884.

[g] Specimens examined: FMNH 22438, 26575, 92958, 94294, 94295; MVZ 182055, 182057, 197436, 197587.

[h] Specimens examined: BMNH 93.4.16.4; MNRJ 1494, 36215, 36216, 36305, 36526; ZMUC 151, 152, 154, 160. Specimens were not scored for presence or absence of a rostral process, the significance of which was not appreciated at the time.

[i] Specimens examined: AMNH 167851, 185270; BMNH 4.1.5.48 (holotype of *chacoensis*), 5.8.1.8; UMMZ 126105, 134552, 137143; USNM 236329.

[j] Specimens examined: BMNH 82.9.30.42; USNM 236677.

[k] Specimens examined: AMNH 167852 (holotype of *ignitus*).

[l] Díaz et al. (2002) suggested that the anteromedial process of the alisphenoid tympanic wing was "apparently present but lost during preparation" of the holotype of *ignitus*, but we examined AMNH 167852 under high magnification and found no sign of breakage.

[m] AMNH 72563 (holotype of *unduaviensis*), 72565, 209150–209156, 262401; FMNH 114658, 114664, 114665; MSB 57000, 58508, 70752.

cae, G. agilis, G. dryas, G. emiliae, G. marica, and *G. microtarsus*.[5] No distinct rostral process was observed in *Cryptonanus chacoensis, C. guahybae, C. ignitus,* or *C. unduaviensis*. The expression of this character remains to be determined in *C. agricolai*, examples of which are not at hand at the time of writing.

The only other character that merits discussion in this context is the presence or absence of accessory cusps on the upper canine (fig. 3). As previously noted by Voss and Jansa (2003: character 53), this trait must be scored from unworn dentitions because accessory cusps are often absent in old adults of species that consistently exhibit such structures in youth, and because a false pos-

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[5] We note that there are some taxonomic differences in the expression of this character in *Gracilinanus*, with *G. aceramarcae* having the longest rostral processes and *G. agilis* the shortest among the congeneric taxa we examined.

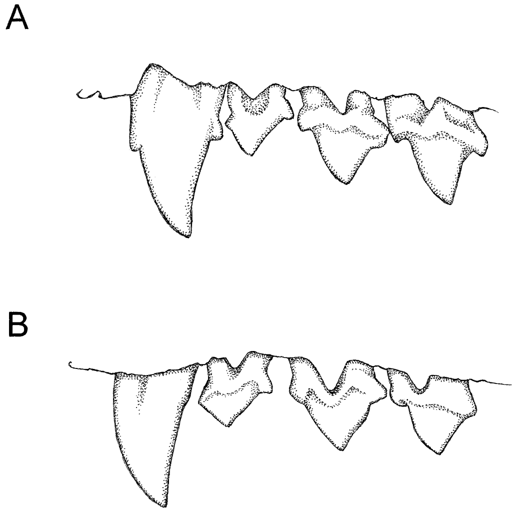

Fig. 3. Labial views of C1–P3 in *Cryptonanus chacoensis* (**A,** UMMZ 126105) and *Gracilinanus agilis* (**B,** UMMZ 134005) illustrating generic differences in the occurrence of accessory canine cusps and in the relative heights of P2 versus P3 (see text).

terior accessory cusp is sometimes formed when C1 is notched by occlusion with p1. Based on our examination of specimens with minimally worn dentitions, the upper canine is usually a simple (unicuspid) tooth in most species of *Gracilinanus*, whereas one or two distinct accessory cusps are usually present in species of *Cryptonanus* (table 3). The most conspicuous exception to this taxonomic trend is *G. emiliae* (see Voss et al., 2001: fig. 12), in which a distinct posterior accessory cusp is invariably present.

OTHER COMPARISONS: Morphological comparisons with other didelphid genera that appear to be closely related to *Cryptonanus* and *Gracilinanus* are summarized in table 4.

ETYMOLOGY: From the Greek words *kruptos* (hidden) and *nanos* (dwarf), as appropriate for small animals whose taxonomic identity has long been concealed by synonymy.

Cryptonanus agricolai (Moojen, 1943)

Grymaeomys pusillus: Winge, 1893: 27 (part). A misidentification based on a composite series of ZMUC specimens representing the present species and an unidentified species of *Gracilinanus* (see below); not *pusillus* Desmarest, 1804, a valid species of *Thylamys*.

Marmosa agilis agilis: Tate, 1933: 195 (part). Another misidentification based on the same series of ZMUC specimens; not *agilis* Burmeister, 1854, a valid species of *Gracilinanus*.

Marmosa agricolai Moojen, 1943: 2. Original description based on the holotype (by original designation: MNRJ 1495) and one paratype, both collected at Crato, Ceará, Brazil.

Marmosa (*Thylamys*) *agricolai*: Cabrera, 1958: 28. New name combination.

Thylamys agricolai: Reig et al., 1985: 340. New name combination implied by raising *Thylamys* (sensu Kirsch and Calaby, 1977) to generic rank.

Gracilinanus emiliae: Gardner and Creighton, 1989: 6 (part). New generic assignment and synonymy, based on alleged conspecificity with *G. emiliae* (Thomas, 1909).

IDENTIFICATION AND DISTRIBUTION: Specimens that we refer to this taxon are from the Caatinga and Cerrado biomes of east-central Brazil. By comparison with other forms of *Cryptonanus*, most specimens of *C. agricolai* have self-whitish ventral fur (the ventral fur is gray-based buffy in *guahybae*), small molars (4.9–5.4 mm versus >5.4 mm in most specimens of *unduaviensis*), and a complete anterior cingulum on M3 (versus M3 anterior cingulum usually incomplete in *chacoensis*). The unique exception to this provisional diagnosis is BMNH 93.4.16.4, a Reinhardt specimen from Lagoa Santa, which has gray-based ventral fur. It is also noteworthy that a larger proportion of examined specimens of *C. agricolai* exhibit a secondary foramen ovale than do our samples of other species (table 3). We have not seen any fluid-preserved parous adult females, so the mammary complement of this species is unknown. External and craniodental measurements of representative specimens examined are provided in table 5.

REMARKS: This species was synonymized with *Gracilinanus emiliae* by Gardner and Creighton (1989), but Voss et al. (2001: 29) disagreed and suggested that the type of *agricolai* needed to be reexamined to determine its true relationships. Although we have not seen the holotype, we were able to borrow the paratype (MNRJ 1494), which agrees in all relevant details with Moojen's (1943) description and illustration.

Carvalho et al. (2002) described the chromosomes of this species (which they identi-

TABLE 4

Morphological Comparisons among *Cryptonanus* and Other Closely Related Didelphine Taxa[a]

Chacodelphys	*Cryptonanus*	*Gracilinanus*	*Lestodelphys*	*Marmosops*	*Thylamys*
Dorsal body pelage uniformly colored, unpatterned.	*Dorsal body pelage* uniformly colored, unpatterned.	*Dorsal body pelage* uniformly colored, unpatterned.	*Dorsal body pelage* abruptly darker middorsally than on flanks.	*Dorsal body pelage* uniformly colored, unpatterned.	*Dorsal body pelage* abruptly darker middorsally than on flanks.
Manus mesaxonic (dIII longest).	*Manus* paraxonic (dIII and dIV subequal in length).	*Manus* paraxonic (dIII and dIV subequal in length).	*Manus* mesaxonic (dIII longest).	*Manus* mesaxonic (dIII longest).	*Manus* mesaxonic (dIII longest).
Central palmar surface of manus densely tuberculate.	*Central palmar surface of manus* sparsely tuberculate.	*Central palmar surface of manus* smooth.	*Central palmar surface of manus* densely tuberculate.	*Central palmar surface of manus* smooth.	*Central palmar surface of manus* densely tuberculate.
Lateral carpal tubercles undetermined.	*Lateral carpal tubercles* present in adult males.	*Lateral carpal tubercles* present in adult males.	*Lateral carpal tubercles* absent in both sexes.	*Lateral carpal tubercles* present in adult males.	*Lateral carpal tubercles* absent in both sexes.
Plantar epithelium of tarsus naked.	*Plantar epithelium of tarsus* naked.	*Plantar epithelium of tarsus* naked.	*Plantar epithelium of tarsus* densely furred.	*Plantar epithelium of tarsus* naked.	*Plantar epithelium of tarsus* densely furred.
Caudal scales in annular series.	*Caudal scales* in annular series.	*Caudal scales* usually in annular series.	*Caudal scales* in annular series.	*Caudal scales* in spiral series.	*Caudal scales* in annular series.
Ventral surface of tail-tip hairy, not modified for prehension.	*Ventral surface of tail-tip* naked, modified for prehension.	*Ventral surface of tail-tip* naked, modified for prehension.	*Ventral surface of tail-tip* hairy, not modified for prehension.	*Ventral surface of tail-tip* naked, modified for prehension.	*Ventral surface of tail-tip* naked, modified for prehension.
Caudal incrassation absent.	*Caudal incrassation* absent.	*Caudal incrassation* absent.	*Caudal incrassation* present.	*Caudal incrassation* absent.	*Caudal incrassation* present.
Rostral process of premaxillae absent.	*Rostral process of premaxillae* absent.	*Rostral process of premaxillae* present.	*Rostral process of premaxillae* absent.	*Rostral process of premaxillae* present.	*Rostral process of premaxillae* absent.
Nasals uniformly narrow, with subparallel lateral margins.	*Nasals* conspicuously widened posteriorly.	*Nasals* conspicuously widened posteriorly.	*Nasals* conspicuously widened posteriorly.	*Nasals* widened posteriorly in some species, narrow in others.	*Nasals* uniformly narrow, with subparallel lateral margins.
Maxillary palatal fenestrae present.	*Maxillary palatal fenestrae* usually absent.	*Maxillary palatal fenestrae* usually present.	*Maxillary palatal fenestrae* absent.	*Maxillary palatal fenestrae* absent.	*Maxillary palatal fenestrae* present in some species, absent in others.

TABLE 4
(*Continued*)

Chacodelphys	*Cryptonanus*	*Gracilinanus*	*Lestodelphys*	*Marmosops*	*Thylamys*
Posterolateral palatal foramina small, posterior to M4 protocones.	*Posterolateral palatal foramina* small, posterior to M4 protocones.	*Posterolateral palatal foramina* small, posterior to M4 protocones.	*Posterolateral palatal foramina* very large, usually extending lingual to M4 protocones.	*Posterolateral palatal foramina* small, posterior to M4 protocones.	*Posterolateral palatal foramina* very large, extending lingual to M4 protocones in most species.
Secondary foramen ovale absent.	*Secondary foramen ovale* usually absent.	*Secondary foramen ovale* usually present.	*Secondary foramen ovale* present.	*Secondary foramen ovale* present.	*Secondary foramen ovale* present.
Fenestra cochleae laterally exposed.	*Fenestra cochleae* laterally exposed.	*Fenestra cochleae* laterally exposed.	*Fenestra cochleae* concealed in a bony sinus.	*Fenestra cochleae* laterally exposed.	*Fenestra cochleae* concealed in a bony sinus.
Upper canine simple, without accessory cusps.	*Upper canine* usually with one or two small accessory cusps.	*Upper canine* simple, without accessory cusps (except *G. emiliae*).	*Upper canine* simple, without accessory cusps.	*Upper canine* simple in some species, with small accessory cusps in others.	*Upper canine* simple, without accessory cusps.
Second upper premolar taller than P3.	*Second upper premolar* shorter than P3.	*Second upper premolar* subequal to P3.	*Second upper premolar* shorter than P3.	*Second upper premolar* subequal to P3.	*Second upper premolar* shorter than P3.
M3 anterior cingulum incomplete.	*M3 anterior cingulum* complete in some species, incomplete in others.	*M3 anterior cingulum* complete.	*M3 anterior cingulum* incomplete.	*M3 anterior cingulum* complete in some species, incomplete in others.	*M3 anterior cingulum* incomplete.

[a] All tabulated morphological comparisons are based on characters defined by Voss and Jansa (2003) as follows: *dorsal body pelage* (op. cit.: character 7), *manus* (op. cit.: character 10), *central palmar surface of manus* (op. cit.: character 11), *lateral carpal tubercles* (op. cit.: character 12), *plantar epithelium of tarsus* (op. cit.: character 16), *caudal scales* (op. cit.: character 23), *ventral surface of tail tip* (op. cit.: character 25), *caudal incrassation* (op. cit.: character 28), *rostral process of premaxillae* (op cit: character 29), *nasals* (op. cit.: character 33), *maxillary palatal fenestrae* (op. cit.: character 40), *posterolateral palatal foramina* (op. cit.: character 41), *secondary foramen ovale* (op. cit.: character 45), *fenestra cochleae* (op. cit.: character 47), *upper canine* (op. cit.: character 53), *second upper premolar* (op. cit.: character 55), *M3 anterior cinguulum* (op. cit.: character 60).

TABLE 5

External and Craniodental Measurements (mm) and Weights (g) of *Cryptonanus agricolai*

(All referred specimens are from Brazil.)

	Ceará		Goiás		Minas Gerais			
	MNRJ 1494[a]	MNRJ 1495[b]	MNRJ 36215	MNRJ 36305	ZMUC 151	ZMUC 154	ZMUC 152	ZMUC 160
Sex	male	male	male	male	female	female	male	male
HBL	82[c]	82[c]	87	89	—	—	—	—
LT	105[c]	105[c]	106	104	—	—	—	—
HF	12[c]	15[c]	12	13	—	—	—	—
Ear	—	—	17	15	—	—	—	—
CBL	24.2	—	24.6	25.1	26.3	23.1	25.3	26.8
NB	2.8	—	3.1	3.4	2.9	2.9	3.0	3.2
LIB	4.1	4.0[c]	4.0	4.1	4.4	4.2	4.4	4.8
ZB	13.6	13.2[c]	13.1	13.6	14.7	12.8	13.3	15.5
PL	12.9	—	13.2	13.4	14.4	12.8	13.8	14.6
PB	7.7	—	7.3	7.8	8.3	7.4	7.6	8.4
MTR	9.3	—	9.3	9.6	9.9	9.3	9.5	10.2
LM	5.0	—	4.9	5.1	5.2	5.3	5.0	5.4
M1–M3	4.3	—	4.2	4.6	4.5	4.6	4.4	4.6
Weight	—	—	—	18	—	—	—	—

[a] Paratype.

[b] Holotype.

[c] Measurements from Moojen (1943).

fied as *Gracilinanus emiliae*) based on 13 specimens from Goiás. According to their cytogenetic analysis, the karyotype consists of 14 diploid chromosomes, of which 6 pairs are biarmed autosomes ($2n = 14$, FN = 24); the X chromosome is metacentric or acrocentric (polymorphism in this trait was noted), the Y is acrocentric, and the nucleolar organizing region is on the short arm of chromosome 6.

The Lagoa Santa material that Winge (1893) reported as *Grymaeomys pusillus* is composite. Whereas three ZMUC specimens so identified in Winge's distinctive handwriting (ZMUC 149, 151, 160) are *Cryptonanus agricolai*, another (ZMUC 225) is an unidentified species of *Gracilinanus*.[6] Winge's published illustration (1893: pl. II, fig. 4), however, clearly shows the principal diagnostic traits of *Cryptonanus* (premolar proportions, absence of maxillary palatal fenestrae, and absence of a secondary foramen ovale). Tate (1933) examined many of the ZMUC specimens listed below and misidentified them as *Marmosa agilis agilis*.

SPECIMENS EXAMINED: **Brazil**—*Ceará*, Crato (MNRJ 1494); *Goiás*, 20 km NW Colinas do Sul (MNRJ 36305, 36526), Serra Negra region (MNRJ 36215, 36216); *Minas Gerais*, Lagoa Santa (BMNH 93.4.16.4; ZMUC 149–152, 154, 155, 157, 160).

Cryptonanus chacoensis (Tate, 1931)

Marmosa agilis chacoensis Tate, 1931: 10. Original description based on the holotype (by original designation: BMNH 4.1.5.48) collected at Sapucay, Paraguay, and five paratypes.

Marmosa (*Thylamys*) *agilis agilis*: Cabrera, 1958: 27 (part). New name combination and synonymy based on alleged identity with the nominotypical form of *M.* (*T.*) *agilis* (Burmeister, 1854).

Gracilinanus agilis: Gardner and Creighton, 1989: 5 (part). New name combination.

IDENTIFICATION AND DISTRIBUTION: We are using this name for specimens of *Crypto-*

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[6] ZMUC 225, a skin and partial skull from Lund's original collection (number L.16), is either *Gracilinanus agilis* or *G. microtarsus*—morphologically similar and occasionally sympatric species whose diagnostic differences were not known to RSV at the time he examined this specimen in Copenhagen. Tate (1933: 191) examined ZMUC 225 and referred it to *G. microtarsus*, but this identification should be reconfirmed using the criteria suggested by Costa et al. (2003).

nanus with self-colored ventral fur (versus ventral fur gray-based in *C. guahybae*), 4–1–4 = 9 abdominal-inguinal mammae (versus 7–1–7 = 15 mammae, of which the anteriormost two or three pairs are pectoral in *C. guahybae*), small molars (LM = 4.9–5.4 mm, versus mostly >5.4 mm in *C. unduaviensis*), and an incomplete anterior cingulum on M3 (versus M3 anterior cingulum narrow but complete in other forms). Specimens that we examined with these traits are from Paraguay and northern Argentina (Chaco and Jujuy). If correctly identified, the specimens reported by Massoia and Fornes (1972) also document the occurrence of this species in the Argentinian provinces of Buenos Aires, Entre Ríos, Formosa, and Misiones.[7] External and craniodental measurements of representative specimens examined are provided in table 6.

REMARKS: Tate (1933) reported BMNH specimens of both *Marmosa agilis agilis* and *M. a. chacoensis* from Sapucay, Paraguay, but he did not appear to recognize the paradox of sympatric subspecies at this locality, nor did he provide any unambiguous morphological criterion for distinguishing them. Cabrera (1958) thought that two such doubtfully distinct taxa were unlikely to occur together and synonymized them under the former trinomen, apparently without having examined the material in question. In fact, the BMNH specimens from Sapucay were correctly identified by Tate and exhibit all of the diagnostic features of the genera to which we now refer them. Although taken at the same locality, the Sapucay specimens of *Gracilinanus agilis* and *Cryptonanus chacoensis* were not collected simultaneously, and it is possible that they were found in different local habitats.[8]

Anderson (1997) reported four specimens of ‘‘*Gracilinanus agilis chacoensis*’’ from three Bolivian localities. Based on a card file in the AMNH Department of Mammalogy archives that provides the museum catalog numbers of the specimens Anderson examined, we determined that his record of *chacoensis* from Chuquisaca was based on MSB 63275, an unidentified species of *Marmosops* (see Voss et al., 2004b). Unfortunately, we have not been able to examine the other material that Anderson reported as *chacoensis*, most of which was returned to Bolivia.

SPECIMENS EXAMINED: **Argentina**—*Chaco*, Las Palmas (USNM 236329); *Jujuy*, Santa Barbara (AMNH 185270), Yuto (AMNH 167851). **Paraguay**—*Alto Paraguay*, Estancia Doña Julia (TK 61053, 61072, 61074, 61103); *Caazapá*, Estancia Dos Marias (GD 521); *Canendiyú*, 13.3 km N Curuguaty by road (UMMZ 137143); *Chaco*, Palmar de las Islas (TK 65331); *Concepción*, Concepción (BMNH 11.11.19.23), Río Aquidaban at Paso Horqueta (UMMZ 134552); *Cordillera*, 1.6 km by road S Tobatí (UMMZ 126105); *Paraguarí*, Sapucay (BMNH 4.1.5.48, 5.8.1.8); *Presidente Hayes*, Estancia La Victoria (TK 60201).

Cryptonanus guahybae (Tate, 1931)

Marmosa microtarsus guahybae Tate, 1931: 10. Original description based on the holotype (by original designation: ZMB 4306) collected on the island of Guahiba near Porto Alegre, Rio Grande do Sul, Brazil, and eight paratypes.

Marmosa (*Thylamys*) *microtarsus guahybae*: Cabrera, 1958: 31. New name combination.

Gracilinanus microtarsus: Gardner and Creighton, 1989: 6 (part). New name combination.

IDENTIFICATION AND DISTRIBUTION: Based on Tate’s (1931, 1933) accounts and our examination of two paratypes, *Cryptonanus*

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[7] Massoia and Fornes (1972) did not describe any of the diagnostic traits of *Cryptonanus*, but their cranial illustration seems to indicate that maxillary vacuities and a secondary foramen ovale are absent, and their cranial measurements (e.g., zygomatic breath and least interorbital breadth) broadly overlap our measurements of *C. chacoensis*. On the other hand, the illustrated dentition lacks accessory canine cusps (usually present in *C. chacoensis*), and P2 seems to be subequal in height to P3. Because their report provides unique information about the distribution and natural history of *C. chacoensis* in northeastern Argentina, the specimens they collected should be reexamined to confirm this identification.

[8] Five specimens of *Gracilinanus agilis* (BMNH 3.2.3.39, 3.4.7.22, 3.4.7.23, 4.1.5.46, 4.1.5.47) were collected at Sapucay by William Foster between 7 September 1902 and 13 May 1903, whereas two Sapucay specimens of *Cryptonanus chacoensis* (BMNH 4.1.5.48, 5.8.1.8) were taken by the same collector on 10 August and 11 September 1903. The separate calendar intervals represented by these dates suggest that Foster might have shifted his collecting activities near Sapucay during the intervening three-month period, but we are not aware of any documentary evidence to support or refute this conjecture.

TABLE 6

External and Craniodental Measurements (mm) and Weights (g) of *Cryptonanus chacoensis*

	Argentina		Paraguay					
	Chaco	Jujuy	Cordillera	Concepción	Pres. Hayes	Canendiyú	Paraguarí	
	USNM 236329[a]	AMNH 167851	UMMZ 126105	UMMZ 134552	[TTU] TK60201	UMMZ 137143	BMNH 4.1.5.48[b]	BMNH 5.8.1.8[a]
Sex	male	female	female	female	female	male	male	male
HBL	82	90[d]	84	—	88	89	100[d]	96[d]
LT	108	95[d]	111	—	109	117	126[d]	115[d]
HF	14	14[d]	15	—	15	15	16[d]	16[d]
Ear	14[c]	18[d]	17	—	16	18	17[d]	18[d]
CBL	24.0	24.0	24.7	23.7	23.5	24.7	—	24.7
NB	2.8	3.0	2.9	2.9	2.3	3.2	3.3	3.0
LIB	4.2	4.3	4.3	4.3	4.0	4.6	4.6	4.6
ZB	13.2	13.8	—	13.6	13.2	14.1	14.4	13.9
PL	13.4	13.2	13.3	12.8	12.6	13.7	—	13.7
PB	7.8	7.7	7.8	7.6	7.6	7.7	7.7	7.8
MTR	9.7	9.2	9.8	9.6	9.3	9.7	10.0	9.8
LM	5.2	4.9	5.2	5.3	5.2	5.4	5.3	5.2
M1–M3	4.5	4.3	4.6	4.6	4.6	4.7	4.6	4.6
Weight	—	16	16	—	14	16	—	—

[a] Paratype of *chacoensis.*

[b] Holotype of *chacoensis.*

[c] Measured from crown.

[d] Measurement method unknown, but probably not following the standard American protocol.

guahybae is a distinctively reddish form with gray- based buffy underparts that differs conspicuously in coloration from other congeneric taxa (all of which have duller, usually brownish or grayish-brown dorsal fur and much paler, usually self-whitish ventral fur). Although overlapping broadly with *C. agricolai* and *C. chacoensis* in all measured dimensions (tables 5–7), *C. guahybae* has a geographically discrete distribution (all referred specimens are from Rio Grande do Sul), and other trenchant differences may emerge from side-by-side comparisons of fresh material. In particular, mammary counts may be diagnostic. In the material we examined, one fluid-preserved female specimen of *C. guahybae* (BMNH 82.9.30.42) has 7–1–7 = 15 mammae, of which the anteriormost three pairs are "pectoral" (arranged in parallel series anterior to the circular array of abdominal/inguinal teats; see Tate, 1933: fig. 3), whereas a fluid-preserved female specimen of *C. chacoensis* (UMMZ 134552) has 4–1–4 = 9 mammae, all of which are abdominal/inguinal.

SPECIMENS EXAMINED: **Brazil**—*Rio Grande do Sul,* São Lourenço (USNM 236677), Taquara (BMNH 82.9.30.42).

Cryptonanus ignitus (Díaz, Flores, and Barquez, 2002)

Gracilinanus ignitus Díaz, Flores, and Barquez, 2002: 825. Original description based on the holotype (by original designation: AMNH 167852) collected at Yuto, Departamento Ledesma, Provincia Jujuy, Argentina.

IDENTIFICATION: The holotype and only known specimen of *Cryptonanus ignitus* (AMNH 167852), collected in the northwestern Argentinian province of Jujuy, is an unusually large animal (table 8) with several qualitative traits that set it apart from most other congeneric material that we have examined. In particular, the ventral fur is self-orange ("clay colored" sensu Díaz et al., 2002) from chin to anus with a prominent mid-pectoral blaze of self-white hairs. In addition, the zygomatic arches are unusually wide and robust, and the postorbital process of the jugal is massively developed. Other unusual features include prominent temporal

TABLE 7
External and Craniodental Measurements (mm) of *Cryptonanus guahybae*
(Both specimens are paratypes from Rio Grande do Sul, Brazil.)

	BMNH 82.9.30.42	USNM 236677
Sex	female	unknown
HBL	[92][a]	—
LT	[113][a]	—
HF	[15][a]	—
Ear	[16][a]	—
CBL	27.0	25.5
NB	3.1	3.0
LIB	5.0	4.7
ZB	15.2	14.4
PL	14.9	13.8
PB	8.4	7.7
MTR	10.1	9.7
LM	5.3	5.2
M1–M3	4.7	4.5

[a] Measured on fluid-preserved specimen from which skull had been extracted.

scars that extend posteriorly from the postorbital region along the dorsolateral contour of the relatively small braincase to merge with well-developed lambdoidal crests near the dorsal apex of the occiput. The upper canines are very long, and the palatine fenestrae consist of two small holes on each side of the palate rather than the single large hole seen in most congeneric specimens.

Despite this impressive list of distinctive attributes, however, we note that AMNH 167852 is a very old adult male (as indicated by its heavily worn molars and fused basioccipital/basisphenoid suture) and that some of its peculiar features are age-correlated in other didelphid taxa. Large ontogenetic series of most opossums, for example, show a tendency for older animals to have better-developed temporal scars, lambdoidal crests, and more massive zygomatic arches, but relatively smaller braincases than younger conspecifics (e.g., Tate, 1933; Abdala et al., 2001; Flores et al., 2003). In addition, the canine fangs of old adult male didelphids are often extruded from their alveoli to a much greater extent than in conspecific females and younger males.

The holotype of *Cryptonanus ignitus* was collected sympatrically with *C. chacoensis* (represented in our material by AMNH 167851, a subadult female), and the latter species has also been taken elsewhere in Jujuy (e.g., AMNH 185270). Given the ontogenetic interpretation of some traits exhibited by the holotype of *ignitus*, the hypothesis that this specimen is just an elderly example of *chacoensis* merits consideration. Indeed, although the holotype of *ignitus* is larger than any specimens herein referred to *chacoensis* in most measurements, ontogenetically invariant dimensions of the molar dentition (LM, M1–M3) are similar in both forms (tables 6, 8).

Díaz et al. (2002) did not explicitly compare *iginitus* with *chacoensis* because they regarded the latter form as conspecific with *Gracilinanus agilis* following then-current usage. Our side-by-side comparisons of AMNH 167852 with representative material of *chacoensis* do not reveal any consistent craniodental differences that cannot plausibly be attributed to age. However, the ventral pelage coloration of *ignitus* is unmatched by any specimens of *chacoensis* that we have yet examined, and on that basis we prefer to retain *Cryptonanus ignitus* as a valid binomen pending the results of ongoing fieldwork to obtain additional specimens (R.M. Barquez, personal commun.).

SPECIMENS EXAMINED: **Argentina**—*Jujuy*, Yuto (AMNH 167852).

Cryptonanus unduaviensis (Tate, 1931)

Marmosa unduaviensis Tate, 1931: 11. Original description based on the holotype (by original designation: AMNH 72563) and one paratype, both collected at Pitiguaya, Río Unduavi, La Paz, Bolivia.

Marmosa (*Thylamys*) *unduaviensis*: Cabrera, 1958: 33. New name combination.

Thylamys unduaviensis: Reig et al., 1985: 342. New name combination implied by raising *Thylamys* (sensu Kirsch and Calaby, 1977) to generic rank.

Gracilinanus agilis: Gardner and Creighton, 1989: 5 (part). New name combination and synonymy based on alleged conspecificity with *G. agilis* (Burmeister, 1854).

IDENTIFICATION AND DISTRIBUTION: Specimens that we refer to *Cryptonanus unduaviensis* are all from eastern Bolivia. These are

TABLE 8
External and Craniodental Measurements (mm) and Weight (g) of *Cryptonanus ignitus*

	AMNH 167852[a]
Sex	male
HBL	105
LT	115
HF	15
Ear	17
CBL	27.0
NB	3.8
LIB	4.8
ZB	15.6
PL	15.3
PB	8.4
MTR	10.1
LM	5.0
M1–M3	4.2
Weight	30

[a] The holotype and only known specimen.

among the largest specimens of the genus (table 9), with an average molar toothrow length that substantially exceeds than that of any other congeneric species sample (table 10). The anterior cingulum of M3 is narrow but complete (versus usually incomplete in *C. chacoensis*), and the ventral fur is either self-colored or indistinctly gray-based (versus distinctly gray-based buffy in *C. guahybae*). We have not examined any suitably preserved parous adult females, so the mammary complement of *C. unduaviensis* is unknown.

The material at hand is somewhat variable in coloration, possibly due to geographic variation, individual variation, and/or preservational artifacts that we are currently unable to distinguish as such. The dorsal fur is dull grayish-brown in the holotype and most other specimens, but a few skins collected by the Middle American Research Unit (MARU) of the National Institutes of Health (perhaps treated with borax or some other preservative) are distinctly reddish (e.g., FMNH 114658). The ventral pelage is indistinctly gray-based in some specimens, but most have self-colored whitish venters; the MARU-collected specimens mentioned earlier, however, have self-orange ventral fur. No craniodental variation appears to be correlated with any of this pelage variation, which does not appear to be taxonomically significant.

REMARKS: The series of Bolivian specimens from San Joaquín that Hershkovitz (1992: 35–36) referred to *Gracilinanus agilis* is composite. Among the 30 specimens that we were able to locate in the FMNH, four were *Cryptonanus unduaviensis* and 26 were *G. agilis*. Although some of the phenotypic variation that Hershkovitz remarked in the San Joaquín series is doubtless attributable to this heterogeneity, our taxonomic assignments do not agree in all cases with his observations about morphological anomalies in this material.[9]

Of the seven specimens identified as "*Gracilinanus agilis unduaviensis*" that Anderson (1997) reported from Bolivia, two (AMNH 72563, 72565) represent Tate's (1931) type series. Of the remainder, we were only able to examine three (UMMZ 155829, 156006, 156007), all of which are examples of *Marmosops noctivagus* as previously explained elsewhere (Voss et al., 2004b). Instead, most of the Bolivian material that we refer to *Cryptonanus unduaviensis* was identified by Anderson (1997) as *Gracilinanus agilis buenavistae* (e.g., AMNH 209150–209156, 260031, 260032, 262401).

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[9] Among other sources of confusion in attempting to reconcile our identifications with Hershkovitz's (1992) text, he referred to 39 specimens of *Gracilinanus agilis* from San Joaquín in a discussion of bullar variation (p. 23), but subsequently recorded having examined only 32 specimens from that locality (p. 36). We were able to find only 30 specimens from San Joaquín with this identification in the FMNH, of which the following are referrable to *G. agilis* in our usage of that binomen: 114652, 114654–114657, 114659–114663, 114666, 114668, 114669, 114671–114680, and 114682–114684. Consistent with our taxonomic assignments, Hershkovitz (p. 23) reported the absence of anteromedial bullar processes in FMNH 114658 (a specimen of *Cryptonanus unduaviensis*), but he also stated that these processes were absent in 114654 (a specimen of *G. agilis*). Because all of the *G. agilis* that we examined from San Joaquín have anteromedial bullar processes, the latter specimen may have been 114664 (*C. unduaviensis*). Hershkovitz's other remarks (p. 35) about individual differences in size, pelage color, premolar proportions, and other characters within the San Joaquín series are impossible to associate with particular specimens, but it is clear that he did not distinguish intraspecific from higher-taxonomic variation in this material.

TABLE 9

External and Craniodental Measurements (mm) and Weights (g) of *Cryptonanus unduaviensis*

(All tabulated measurements are from Bolivian specimens.)

	Beni				La Paz	Pando	Santa Cruz	
	AMNH 209156	MSB 70752	AMNH 209154	FMNH 114658	AMNH 72563[a]	MSB 57000	IGP 157	MSB 58508
Sex	female	female	male	male	male	male	male	male
HBL	97	111	106	110	102	105	121[b]	86
LT	112	112	132	115	120	133	135	120
HF	17	16	17	15	17	19	18	17
Ear	—	14	16	17	—	17	18	14
CBL	25.6	26.9	28.2	—	—	28.3	30.0	25.9
NB	3.5	3.7	4.2	3.5	3.3	4.2	4.4	3.3
LIB	4.7	4.6	5.2	4.9	—	5.0	5.3	4.8
ZB	14.2	15.3	15.0	—	—	16.3	17.6	14.7
PL	14.1	14.6	15.7	14.8	—	15.5	16.2	14.2
PB	8.2	8.3	8.1	8.6	—	8.3	9.6	8.4
MTR	10.3	10.5	10.9	10.7	10.9	10.7	11.0	10.5
LM	5.6	5.6	5.7	5.8	5.7	5.6	5.7	5.7
M1–M3	4.8	4.8	5.0	5.1	4.9	4.8	4.9	4.9
Weight	18	21	24	28	—	26	40	15

[a] Holotype.

[b] Not measured according to standard American protocol.

SPECIMENS EXAMINED: **Bolivia**—*Beni*, Boca del Río Baures (AMNH 209152, 209153), Campo Alegre (MSB 70752), Magdalena (USNM 460732), Pampa de Meio (AMNH 209150, 209151, 209154–209156), Puerto Caballo (AMNH 210396), San Joaquín (FMNH 114658, 114664, 114665, 114667; USNM 364718); *La Paz*, Pitiguaya (AMNH 72563, 72565); *Pando*, Independencia (AMNH 262401, MSB 57000); *Santa Cruz*, 2 km S Caranda (MSB 58508), El Refugio (IGP 157), Estancia Cachuela Esperanza (AMNH 260031), Santiago de Chiquitos (AMNH 260032).

PHYLOGENETIC ANALYSES

We analyzed nonmolecular (morphological and karyotypic) characters and nuclear gene sequences to assess the relationships of *Cryptonanus* with other didelphid taxa previously analyzed using the same data (Voss and Jansa, 2003; Voss et al., 2004a). A total of seven terminal taxa are newly analyzed in this report, including *C. chacoensis* and *C. unduaviensis*, three species of *Gracilinanus* (*G. aceramarcae*, *G. agilis*, and *G. emiliae*), and two species of *Thylamys* (*T. macrurus* and *T. pusillus*). The three species of *Gracilinanus* were added to test the monophyly of that genus (represented in previous analyses only by *G. microtarsus*), and the two species of *Thylamys* were added to improve our sampling of a speciose and possibly closely related clade (previously represented only by *T. venustus* and *T. pallidior*). Percent completeness for the new taxa is generally high (table 11) with the exception of *C. chacoensis*, from which only a partial IRBP sequence could be obtained. Relevant descriptive statistics for each of the analyses described below are provided in table 12.

A heuristic parsimony analysis of nonmolecular (morphological and karyotypic) characters discovered 1080 equally most-parsimonious trees, the strict consensus of which is shown in figure 4. Two basal polytomies in this topology contain nine plesiomorphic species that are currently classified in the genera *Marmosa*, *Micoureus*, and *Tlacuatzin*, but the remaining didelphines form a clade within which relationships are well resolved. *Cryptonanus*, *Gracilinanus*, and *Marmosops* were recovered as successive sister taxa to a large monophyletic group of nine other genera. Three of the latter form one clade in the sequence (*Chacodelphys*

TABLE 10
Molar Toothrow Measurements (mm) of *Cryptonanus* Species Samples

	N^a	Mean	SD	Observed range
C. agricolai	9	5.1	—	4.9–5.4
C. chacoensis	13	5.2	0.2	4.9–5.5
C. guahybae	2	5.2	—	5.2–5.3
C. ignitus	1	5.0	—	—
C. unduaviensis	14	5.6	0.2	5.3–5.9

[a] Sample size. Because sexual dimorphism is not apparent in molar measurements, sample statistics include data from both males and females.

(*Thylamys* + *Lestodelphys*)) and the remaining six form another (*Metachirus* (*Monodelphis* (*Chironectes* (*Lutreolina* (*Philander* + *Didelphis*))))). With the exception of *Marmosa*, *Micoureus*, and *Thylamys*, all genera represented by multiple species in this analysis were recovered as monophyletic groups. Bremer and bootstrap support for most clades are generally low with the conspicuous exception of the genus *Monodelphis*, a group consisting of the large $2n = 22$ opossums (*Chironectes*, *Lutreolina*, *Philander*, *Didelphis*), and *Thylamys* + *Lestodelphys*.

A heuristic parsimony analysis of IRBP sequences (which are not available for *Chacodelphys*) discovered 27 equally most-parsimonious trees, the strict consensus of which (fig. 5) differs from the nonmolecular results in several noteworthy details: (1) species of *Marmosa* and *Micoureus* form a monophyletic group; (2) *Monodelphis* is part of a basal polytomy rather than being nested within a larger clade of higher didelphines; (3) *Metachirus* is the sister taxon of the large $2n = 22$ opossums; (4) the remaining five genera were recovered in the sequence (*Marmosops* (*Cryptonanus* (*Gracilinanus* (*Lestodelphys* + *Thylamys*)))); and (5) *Thylamys* is monophyletic. *Marmosa* is the only genus represented by two or more species that does not appear as a monophyletic group in this analysis. Numerous IRBP clades are supported by large Bremer and bootstrap values, notably including the branch that associates *Cryptonanus* with *Gracilinanus*, *Lestodelphys*, and *Thylamys*.

We analyzed two supermatrices based on the combined nonmolecular and IRBP data. One supermatrix included *Chacodelphys* (for which all of the IRBP characters are missing), whereas the other did not. Because the analysis that included *Chacodelphys* resulted in a much less resolved tree than the analysis that omitted this taxon (table 12), and because the results of these analyses did not differ in any other respect (the clades recovered in the analysis that included *Chacodelphys* are a proper subset of those recovered in the analysis that omitted *Chacodelphys*), we illustrate only the results without *Chacodelphys*.[10] This topology (fig. 6) closely resembles the IRBP results described above, but it is less resolved due to conflict between morphological and molecular characters. The most noteworthy difference concerns relationships among three clades (*Cryptonanus*, *Gracilinanus*, and *Lestodelphys* + *Thylamys*) that are resolved in the IRBP consensus topology but not by the combined-data consensus tree. Most of the nodes that were strongly supported in the IRBP-only analysis, however, remain strongly supported in this combined-data analysis. In particular, support for the membership of *Cryptonanus* in the group that also includes *Gracilinanus*, *Lestodelphys*, and *Thylamys* is not eroded by data combination.

In order to understand the patterns of conflicting signal that resulted in the aforementioned polytomy in the combined-data analysis, we filtered the set of 510 MPTs whose strict consensus is illustrated in figure 6. Equal numbers of trees were found to support each of the three possible resolutions of this polytomy: 170 trees support ((*Cryptonanus* + *Gracilinanus*) (*Lestodelphys* + *Thylamys*)), whereas 170 trees support (*Cryptonanus* (*Gracilinanus* (*Lestodelphys* + *Thylamys*))), and 170 trees support (*Gracilinanus* (*Cryptonanus* (*Lestodelphys* + *Thylamys*))). Obviously there is no objective criterion in

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[10] A heuristic parsimony analysis of the supermatrix that included *Chacodelphys* resulted in a strict consensus topology with a large basal polytomy among the following nine clades: *Tlacuatzin*, *Chacodelphys*, *Monodelphis*, *Marmosa* + *Micoureus*, *Metachirus* + the large $2n = 22$ opossums, *Marmosops*, *Cryptonanus*, *Gracilinanus*, and *Thylamys* + *Lestodelphys*. Relationships within each of these clades were the same as those illustrated in figure 6 except for a complete loss of resolution within *Thylamys* + *Lestodelphys*.

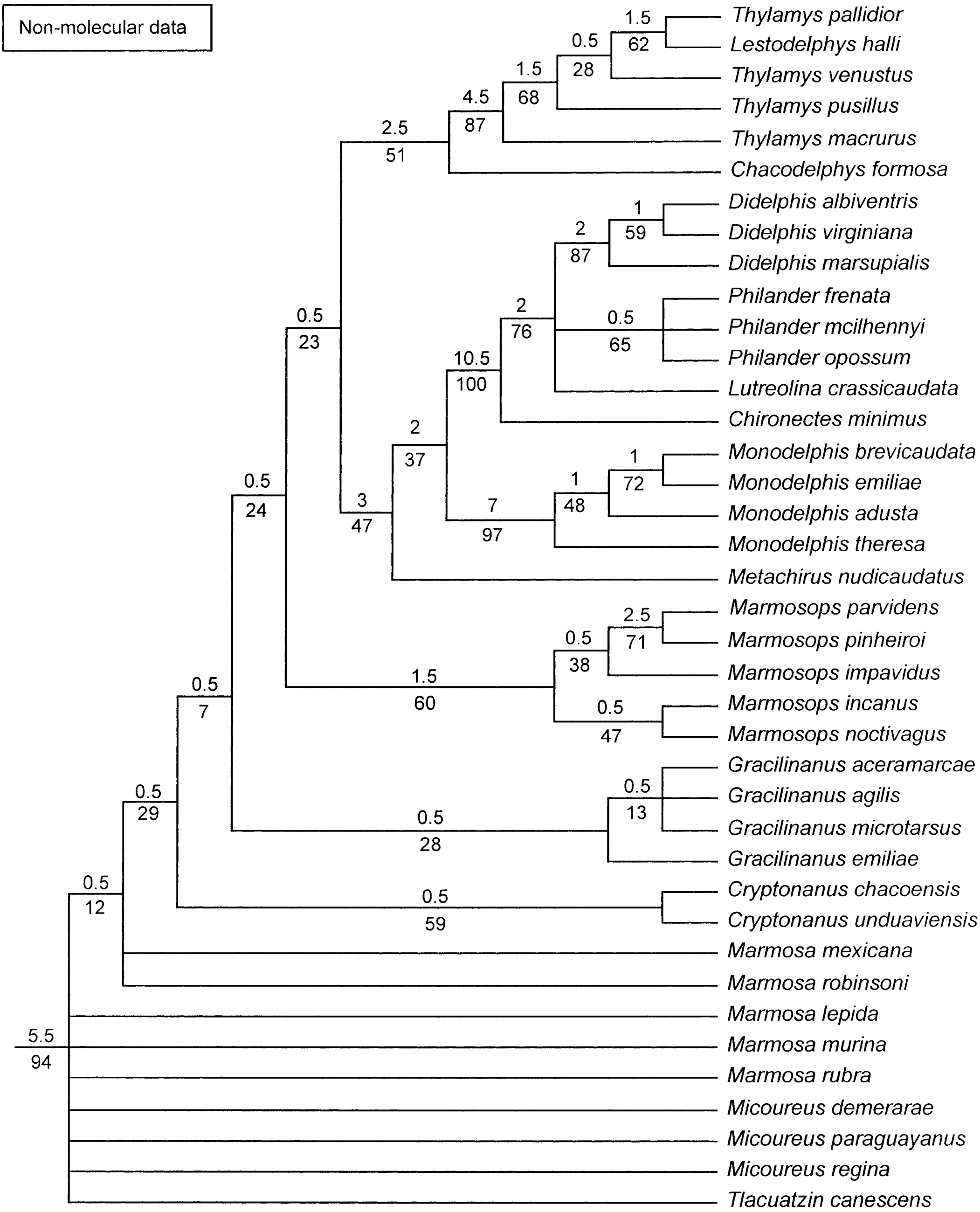

Fig. 4. Strict consensus of 1080 equally most-parsimonious trees discovered by a heuristic parsimony analysis of nonmolecular characters. Only ingroup (didelphine) relationships are illustrated; "caluromyine" outgroups (*Glironia venusta, Caluromysiops irrupta, Caluromys lanatus, C. philander*) are not shown. Bremer support and bootstrap values are provided above and below each branch, respectively. See table 12 for other tree statistics.

TABLE 11
Percent Completeness[a] of New Terminal Taxa

	Datasets		
	Nonmolecular	Molecular	Combined
Cryptonanus chacoensis	93%	70%	71%
Cryptonanus unduaviensis	90%	100%	99%
Gracilinanus aceramarcae	90%	100%	99%
Gracilinanus agilis	94%	100%	100%
Gracilinanus emiliae	93%	100%	100%
Thylamys macrurus	97%	100%	100%
Thylamys pusillus	99%	100%	100%

[a] Percent completeness was calculated as F/T × 100, where F is the number of filled matrix cells (excluding missing and inapplicable codes) and T is the total number of characters in each dataset (71 for the nonmolecular matrix, 1158 for the molecular matrix, and 1229 for the combined matrix). All tabulated values are rounded to the nearest whole percentage point.

such results for preferring any one of these hypotheses over the others.

BIOGEOGRAPHY AND NATURAL HISTORY

Known collecting localities of *Cryptonanus* are widely dispersed among a variety of tropical, subtropical, and temperate biomes between 7° and 35°S latitude (fig. 7). Although most of the ecological regions in which the genus has been taken—Caatinga, Cerrado, Chaco, Pantanal, and Pampas—are predominantly covered with savannas or other kinds of open vegetation, a few collection localities (e.g., 20, 23) are in mostly forested regions. However, the genus does not appear to have been collected in Amazonian rainforests, nor in the wet-tropical coastal zone of the Atlantic rainforest (Mata Atlantica).

Only a few of the specimens we examined are accompanied by habitat information, but several aspects of these scant data are noteworthy (table 13). First, all explicit descriptions record terrestrial captures of *Cryptonanus*, despite the fact that other sympatric marsupials were taken in trees. For example, P. Myers trapped one specimen of *C. chacoensis* (UMMZ 126105) on the ground in a marsh at Tobatí, Paraguay (locality 27), where a single specimen of *Gracilinanus agilis* (UMMZ 126104) had been caught the previous day about 2 m above the ground on a liana-covered tree in a nearby forest. Second, four of the eight available habitat descriptions mention marshes, the grassy borders of marshes, or seasonally flooded grasslands, which are unusual ecological circumstances for small didelphid marsupials. Third, two of the eight accounts mention anthropogenic habitats (woodpiles, houses), which are likewise seldom visited by most small didelphids.

Detailed habitat information is available from just one site from which vouchered captures of *Cryptonanus* have been reported. As described in field notes recorded by Barbara Phillips (personal commun.), two specimens of *C. unduaviensis* (IGP 154, 157) were trapped on a "forest island" consisting of a few bushes growing on a low hummock surrounded by seasonally flooded grasslands near the biological station of El Refugio in the Bolivian department of Santa Cruz (fig. 7: locality 13).[11] Situated in the floodplain of the Río Paraguá, this habitat (fig. 8) is characterized by standing water in the rainy season, but local soils dry out in the austral winter when plants suffer from a water deficit and fires are common. Woody plants are restricted to a peculiar topographic feature of this landscape (Killeen, 1998: 71–72):

> Inundated shrub savannas or termite pampas . . . are extensive grasslands covered by thousands of termite mounds that give this habitat a distinctive physiognomy. Termite mounds usually are located on top of a small platform 0.5–1.5 m higher than the surrounding flooded plains; this provides enough elevation above maximum water levels for trees and shrubs to grow. . . . Termite platforms are important for several species of animals who use them as nesting habitat and as a refuge during the rainy season.

Lacking any obvious semiaquatic adaptations, *Cryptonanus unduaviensis* is presumably among those species for which shrubby termite mounds are important seasonal rufugia. Essentially similar wetlands (locally known as pampas or patanos) are extensively

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[11] The two specimens of *Cryptonanus unduaviensis* collected at this locality were taken in Sherman traps placed inside larger funnel traps installed along a drift fence to capture snakes. Sherman traps were routinely placed in such situations at El Refugio to prevent captured rodents from chewing holes in the nylon mesh from which the snake traps were constructed (L.H. Emmons, personal commun.).

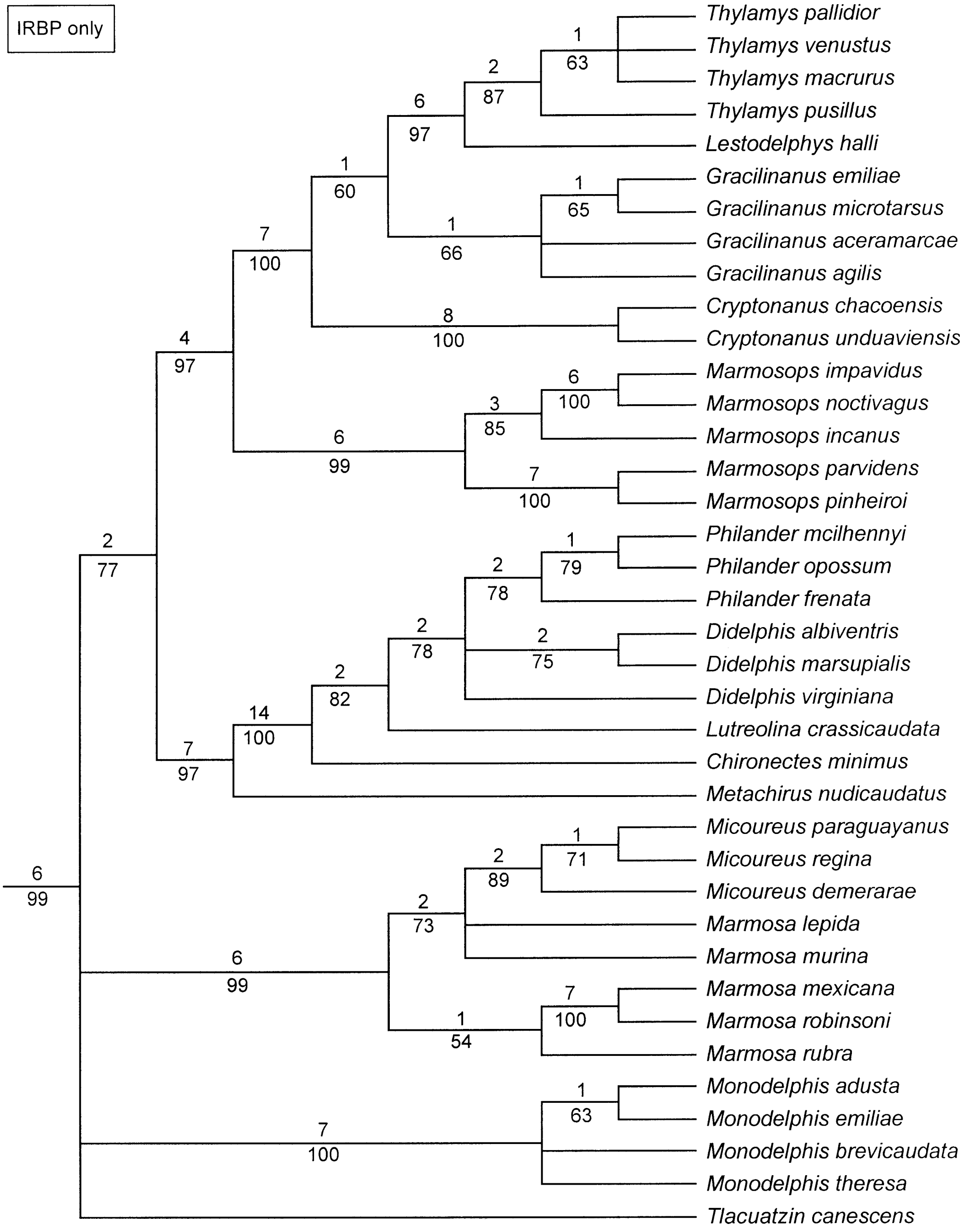

Fig. 5. Strict consensus of 27 equally most-parsimonious trees discovered by a heuristic parsimony analysis of IRBP exon 1 sequence data. Only ingroup (didelphine) relationships are illustrated; "caluromyine" outgroups (*Glironia venusta*, *Caluromysiops irrupta*, *Caluromys lanatus*, *C. philander*) are not shown. Bremer support and bootstrap values are provided above and below each branch, respectively. See table 12 for other tree statistics.

TABLE 12

Dataset Characteristics and Tree Statistics from Parsimony Analyses of Four Datasets

			Combined	
	Nonmolecular	IRBP	w/ *Chacodelphys*	w/o *Chacodelphys*
Number of terminal taxa[a]	43	42	43	42
Number of informative characters	66	159	225	225
Number of MPTs[b]	1080	27	437	510
Tree length[c]	173.5	436	625.5	619.5
Consistency index (CI)[d]	0.50	0.62	0.56	0.56
Retention index (RI)	0.84	0.84	0.83	0.83
Resolved ingroup nodes[e]	28	30	22	26
Total ingroup support[f]	55	118	110	144.5

[a] Including "caluromyine" outgroups (not illustrated in figs. 4–6).

[b] Equally most-parsimonious trees recovered by heuristic parsimony searchers.

[c] Including autapomorphies.

[d] Excluding autapomorphies.

[e] In strict consensus topologies (figs. 4–6).

[f] Sum of Bremer support values over ingroup nodes illustrated in figures 4–6.

distributed elsewhere in eastern Bolivia, notably along the floodplain of the Río Iténez where a much larger series of *C. unduaviensis* was collected at the Pampa de Meio (fig. 7: locality 7) by S. Anderson and A. Ximenez in 1964.

Massoia and Fornes (1972) characterized a small marsupial that they called *Marmosa agilis chacoensis* as an inhabitant of gallery forests, but they also noted captures in osier (*Salix* sp.) plantations and in thickets of pampas grass (*Cortaderia* sp.) and bulrushes (*Scirpus giganteus*). Nests that appeared to have been occupied by this species, manufactured from various materials, were found in tree holes and branches from near ground level to 1.6 m above the ground. Numerous skulls, mandibles, and other skeletal elements were recovered from the regurgitated pellets of the owl *Tyto alba*.

On the assumption that Massoia and Fornes's (1972) material—which we have not seen—was correctly identified, *Cryptonanus* might plausibly be considered an inhabitant of ecotonal habitats in mosaics of wet grasslands and forest. Such mosaics are widespread in most of the biomes where specimens have been collected, and anthropogenic habitats (e.g., agricultural fields and weedy secondary growth around houses) might resemble natural ecotones in certain essential structural features. Where *Cryptonanus* occurs sympatrically with *Gracilinanus* in tropical and subtropical landscapes (e.g., at localities represented in table 13), it is possible that it is more consistently associated with nonforest vegetation than where it occurs allopatrically at temperate latitudes (the main source of Massoia and Fornes' observations), but such conjectures are perhaps premature in the absence of appropriately designed transect-trapping studies.

DISCUSSION

Phylogenetic analyses of the morphological and molecular data at hand suggest that *Cryptonanus* and *Gracilinanus* are reciprocally monophyletic taxa, but other aspects of their historical relationships are not consistently indicated by our results. However, large Bremer and bootstrap values in the IRBP analysis (fig. 5) and in the combined-data analysis without *Chacodelphys* (fig. 6) provide impressive support for the hypothesis that *Cryptonanus* and *Gracilinanus* belong to a clade that also includes *Lestodelphys* and *Thylamys*. The position of *Marmosops* as the closest sister group to this clade is moderately to strongly supported by the same analyses. By contrast, the nonmolecular data analyzed separately do not strongly support the recovered consensus pattern of relationships among these and other higher didelphines (fig. 4), whereas combined-data analyses that include *Chacodel-*

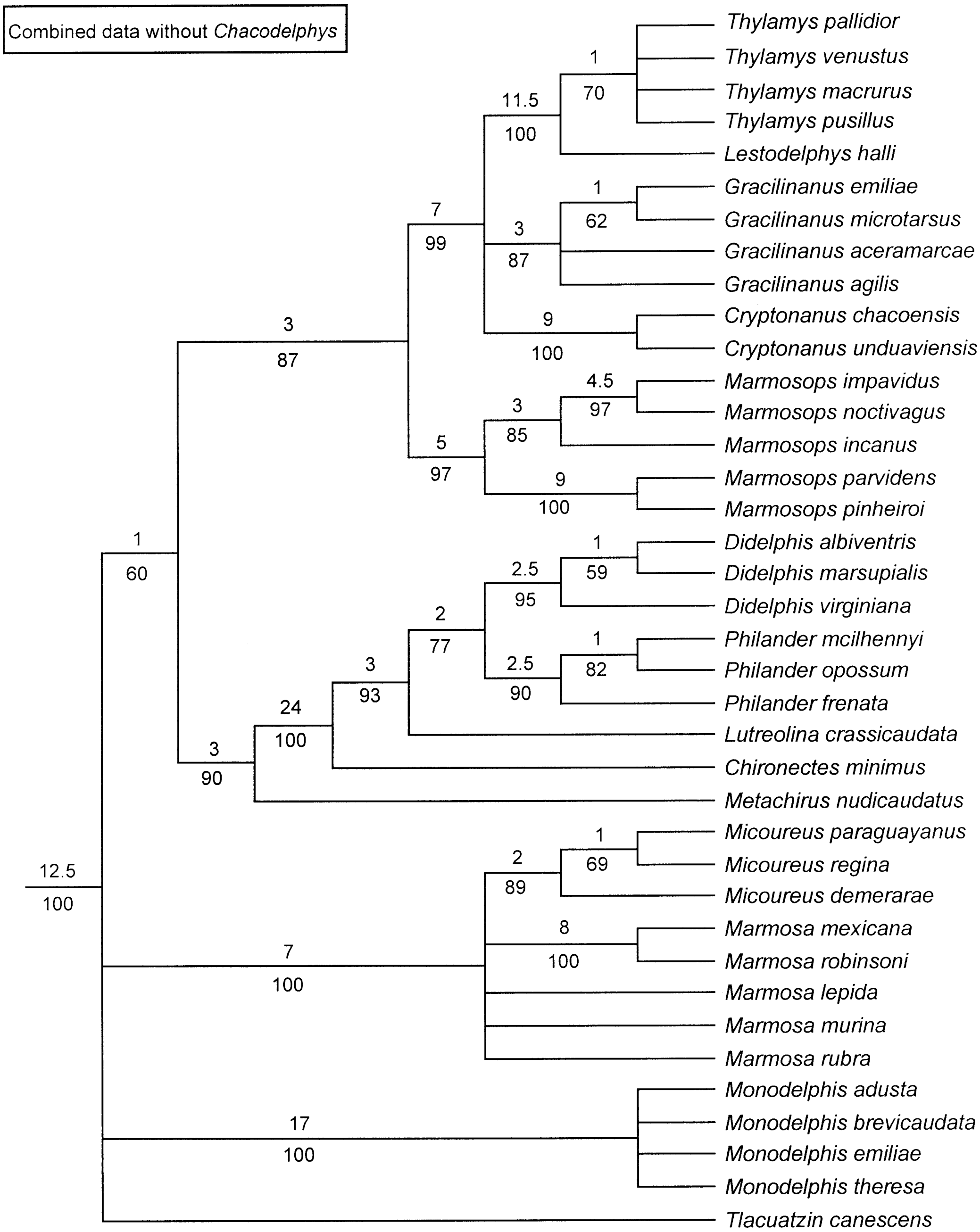

Fig. 6. Strict consensus of 510 equally most-parsimonious trees discovered by a heuristic parsimony analysis of the combined (nonmolecular + IRBP) data with *Chacodelphys* omitted (see text). Only ingroup (didelphine) relationships are illustrated; "caluromyine" outgroups (*Glironia venusta*, *Caluromysiops irrupta*, *Caluromys lanatus*, *C. philander*) are not shown. Bremer support and bootstrap values are provided above and below each branch, respectively. See table 12 for other tree statistics.

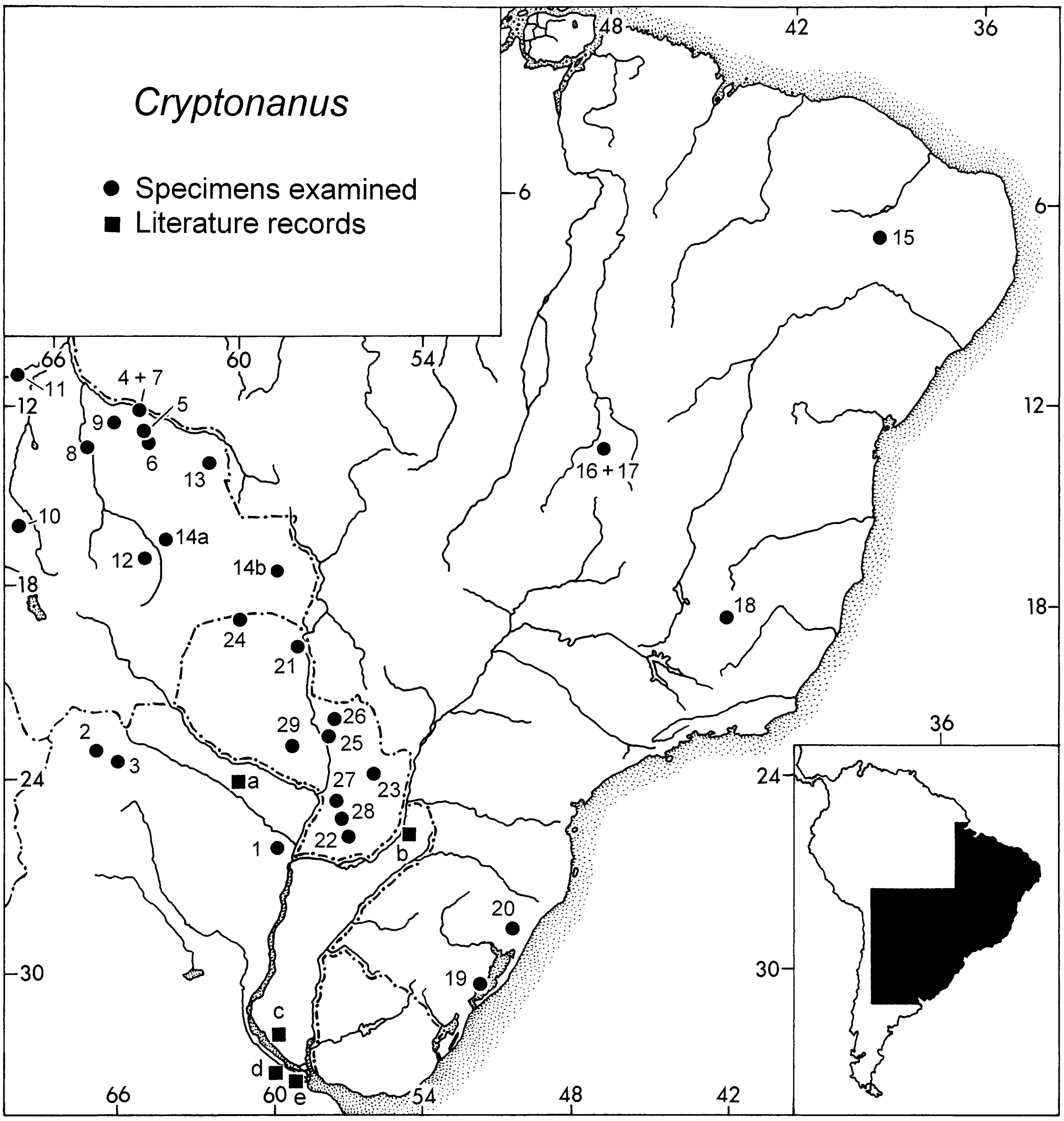

Fig. 7. Known collection localities of *Cryptonanus* based on specimens examined (●) and literature records (■). Localities based on specimens examined are keyed to numbered entries in the gazetteer (appendix 3). The following collection localities in Argentina are from Massoia and Fornes (1972): **a,** Formosa, Pozo del Tigre (24°54′S, 60°19′W; Paynter, 1995); **b,** Misiones, Río Urugua-í (25°54′S, 54°36′W; Paynter, 1995); **c,** Entre Ríos, Brazo Largo (33°47′S, 58°36′W; Paynter, 1995); **d,** Buenos Aires, Zárate (34°06′S, 59°02′W; Paynter, 1995); **e,** Buenos Aires, Campana (34°10′S, 58°57′W; Paynter, 1995).

phys lack any useful resolution (see footnote 10, above).

Despite their superficial similarity, at least with respect to external morphological characters, *Cryptonanus* and *Gracilinanus* do not appear as sister taxa in any of the analyses reported here. Therefore, ranking them as distinct genera is the only phylogenetically defensible option consistent with stable binomial nomenclature. Other alternatives (e.g., treating all of the species herein referred to *Cryptonanus*, *Gracilinanus*, *Lesto-*

TABLE 13

Ecological Information Associated with Specimens of *Cryptonanus*

Specimen	Species	Notes
BMNH 4.1.5.48	*chacoensis*	"Caught in hollow log" (skin label: W. Foster, 10 August 1903; Sapucay, Paraguay)
BMNH 5.8.1.8	*chacoensis*	"Caught in wood pile" (skin label: W. Foster, 11 September 1903; Sapucay, Paraguay)
UMMZ 126105	*chacoensis*	On wet ground in rank marsh vegetation (paraphrased from field notes: P. Myers, 1 September 1978; near Tobatí, Paraguay)
UMMZ 134552	*chacoensis*	"On ground in high grass at edge of small marsh" (field catalog: G.K. Creighton, 8 September 1979; Paso Horqueta, Paraguay)
UMMZ 137143	*chacoensis*	"At base of fruiting bromeliad stalks on ground" (field catalog: P. Myers, 17 July 1979; near Curuguaty, Paraguay)
IGP 157	*unduaviensis*	"Pampa" (skin label: I.G. Phillips, 15 August 2001; El Refugio, Bolivia). According to Barbara Phillips and L.H. Emmons (personal commun.), this specimen and another that we did not examine (IGP 154, collected 8 August 2001) were trapped on a "tree island" surrounded by seasonally flooded grassland (see text for more detailed description of the local habitat at this site).
MSB 57000	*unduaviensis*	On ground in grass at the edge of a marshy stream (paraphrased from field notes: L.A. Ruedas, 26–27 July 1986; Independencia, Bolivia)
USNM 364718	*unduaviensis*	"Casado [sic] en la casa" (skin label: M.L. Kuns, 14 June 1966; San Joaquin, Bolivia)

delphys, and *Thylamys* as congeneric) would needlessly disrupt traditional taxonomic usage for ecologically and morphologically divergent groups of species that are usefully known by different generic names.

It is an interesting fact that adding *Chacodelphys* to the earlier versions of our nonmolecular and combined-data analyses resulted in a net *increase* in phylogenetic resolution (Voss et al., 2004a), whereas *Chacodelphys* is now acting to *decrease* resolution in more taxonomically comprehensive analyses of the same character data. To more fully explore the latter phenomenon, we calculated the average number of nodes that differ between MPTs recovered in the latest combined-data analyses with and without *Chacodelphys*. On average, the 437 MPTs recovered by the analysis with *Chacodelphys* differed by 13.4 nodes, whereas the 510 MPTs recovered in the analysis without *Chacodelphys* differed (on average) by only 9.0 nodes. This result suggests that *Chacodelphys* is now acting as a ''wildcard'' taxon (sensu Nixon and Wheeler, 1992) that can occupy numerous relatively deep positions in parsimony-equivalent trees. Obtaining sequence data from this problematic terminal, currently known only from the type skin and skull, is a clear priority for future work.

Much remains to be learned about the taxonomy, distribution, and natural history of *Cryptonanus*, all of which are worthy topics for future research. In particular, the distinctness of the five species provisionally recognized above remains to be demonstrated convincingly. Sequence data from rapidly evolving mitochondrial genes such as cytochrome *b* and collections from geographically intermediate localities would both be useful for evaluating whether these names represent evolutionarily distinct lineages or weakly differentiated populations of a single geographically variable species.

Although *Cryptonanus* ranges from tropical to temperate latitudes, the genus may be even more widely distributed than currently available records suggest. We expect that pitfall trapping in savanna landscapes, a relatively recent practice, will soon provide abundant new material that may fill in many of the distributional gaps apparent in our geographic data and might result in substan-

Fig. 8. Two views of seasonally flooded termite savannas near El Refugio in the Bolivian department of Santa Cruz (appendix 3, locality 13). **Top:** General aspect with grass-dominated microhabitat (flooded to a depth of ca. 20 cm during the rainy season; Killeen, 1998) in foreground. **Bottom:** Closeup with ‘‘tree islands’’ (woody vegetation growing on emergent termite platforms) where two specimens of *Cryptonanus unduaviensis* were trapped in August 2001. Both photos courtesy of L.H. Emmons.

tial range extensions. For example, many vertebrate taxa that are widespread in the Chaco and Cerrado also occur on Ilha de Marajó and in isolated Amazonian savannas, where it would not be surprising to find *Cryptonanus* as well.

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APPENDIX 1

NEW MORPHOLOGICAL MATERIAL SCORED FOR PHYLOGENETIC ANALYSIS

Skins, skulls, and fluid-preserved material that we examined to score morphological characters for didelphid taxa whose relationships are newly analyzed in this report (i.e., those not previously analyzed by Voss and Jansa [2003] or Voss et al. [2004a]) are listed below.

Cryptonanus chacoensis—Skins: 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 adult 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: MSB 70752.

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

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).

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 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).

APPENDIX 2

NEW SPECIMENS SEQUENCED FOR IRBP

The specimens newly sequenced for this report are listed below by Latin binomial, geographic origin (country, province/department/state, locality name), and museum catalog number (in parentheses; see Materials and Methods for institutional acronyms). Other identifying numbers associated with samples preserved in institutional tissue collections are provided in square brackets.

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]).

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]).

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

Thylamys pusillus: Bolivia, Tarija, Estancia Bolívar (MSB 67016 [NK 25139]).

APPENDIX 3

Gazetteer

Below are listed all localities from which we examined specimens of *Cryptonanus* in the course of this study. Italicized place names are those of the largest political divisions (state/department/province) within countries; boldface identifies collection localities as they appear in the text of this report. Unless recorded by the collector, geographic coordinates and elevation above sea level (in meters, m) are provided in square brackets with a cited secondary source for these data. The species name, name(s) of collector(s), and date(s) of collection are separated from the locality entry by a colon. Numbered localities are plotted on the accompanying map (fig. 7).

ARGENTINA

1. *Chaco*, **Las Palmas** [27°04′S, 58°42′W, ca. 50 m; Paynter, 1995]: *Cryptonanus chacoensis* (coll. A. Wetmore, 13 July 1920).
2. *Jujuy*, **Santa Barbara** [23°36′S, 65°04′W, ca. 1800 m; Paynter, 1995]: *Cryptonanus chacoensis* (coll. F. Contino, 20 June 1960).
3. *Jujuy*, **Yuto** [23°38′S, 64°28′W, ca. 349 m; Paynter, 1995]: *Cryptonanus chacoensis* (coll. F. Contino, 10 November 1961) and *C. ignitus* (coll. F. Contino, 28 March 1962).

BOLIVIA

4. *Beni*, **Boca del Río Baures** [12°30′S, 64°18′W; Anderson, 1997]: *Cryptonanus unduaviensis* (S. Anderson, 28 September–5 October 1964).
5. *Beni*, **Campo Alegre** (13°11′S, 64°13′W), 230 m: *Cryptonanus unduaviensis* (coll. B.H.F. Bol, 11 September 1994).
6. *Beni*, **Magdalena** [13°20′S, 64°08′W, 233 m; Paynter, 1992]: *Cryptonanus unduaviensis* (coll. M.L. Kuns, 13 June 1969).
7. *Beni*, **Pampa de Meio** [ca. 12°30′S, 64°15′W; Anderson, 1997] on Río Itenez: *Cryptonanus unduaviensis* (coll. S. Anderson and A. Ximenez, 15–19 September 1964).
8. *Beni*, **Puerto Caballo** [13°43′S, 65°21′W; Anderson, 1997] on Río Mamoré: *Cryptonanus unduaviensis* (coll. D.E. Añez, 23 September 1965).
9. *Beni*, **San Joaquín** [13°04′S, 64°49′W; Anderson, 1997]: *Cryptonanus unduaviensis* (coll. M. L. Kuns, 7 May–5 June 1964, 14 June 1966).
10. *La Paz*, **Pitiguaya** [ca. 16°21′S, 67°47′W; Anderson, 1997], 5600–5800 ft [1707–1768 m]: *Cryptonanus unduaviensis* (coll. G.H.H. Tate, 10–12 May 1926).
11. *Pando*, **Independencia** [11°26′S, 67°34′W; Anderson, 1997]: *Cryptonanus unduaviensis* (coll. C.K. Malcolm and L.A. Ruedas, 27 July–7 August 1986).
12. *Santa Cruz*, **2 km S Caranda** [17°33′S, 63°32′W; Anderson, 1997]: *Cryptonanus unduaviensis* (coll. R.L. Humphrey, 10 August 1987).
13. *Santa Cruz*, **El Refugio** (14°45′S, 61°01′W): *Cryptonanus unduaviensis* (coll. I.G. Phillips, 15 August 2001).

14a. *Santa Cruz*, **Estancia Cachuela Esperanza** [16°47′S, 63°14′W; Anderson, 1997], 300 m: *Cryptonanus unduaviensis* (coll. J.A. Cook, 25 August 1984).

14b. *Santa Cruz*, 4 km N and 1 km W **Santiago de Chiquitos** (18°18′S, 59°36′W), 700 m: *Cryptonanus unduaviensis* (coll. D.W. Moore, 1 October 1984).

BRAZIL

15. *Ceará*, **Crato** [7°14′S, 39°23′W, 422 m; Paynter and Traylor, 1991]: *Cryptonanus agricolai* (coll. A.L. de Carvalho, 26 September 1936).
16. *Goiás*, **20 km NW Colinas do Sul** [ca.14°12′S, 48°03′W; Paynter and Traylor, 1991]: *Cryptonanus agricolai* (collector and date unknown).
17. *Goiás*, **Serra Negra region** on left bank Rio Bagagem [ca. 17 km NW of locality 16; L. Flamarion, in litt.]: *Cryptonanus agricolai* (collector and date unknown).
18. *Minas Gerais*, **Lagoa Santa** [19°38′S, 43°53′W, 760 m; Paynter and Traylor, 1991]: *Cryptonanus agricolai* (coll. J. Reinhardt, 14 March 1855–29 September 1856).
19. *Rio Grande do Sul*, **São Lourenço** [31°22′S, 51°58′W, sea level; Paynter and Traylor, 1991]: *Cryptonanus guahybae* (collector and date unknown).
20. *Rio Grande do Sul*, **Taquara** (29°39′S, 50°47′W, 29 m; Paynter and Traylor, 1991): *Cryptonanus guahybae* (coll. H. von Ihering, date unknown).

PARAGUAY

21. *Alto Paraguay*, **Estancia Doña Julia** (20°11′S, 58°10′W, 60 m): *Cryptonanus chacoensis* (coll. TTU field party, 14–16 February 1996).
22. *Caazapá*, **Estancia Dos Marias** (26°46′S, 56°32′W), Río Tebicuary: *Cryptonanus chacoensis* (coll. G. D'Elia, 7 May 2001).
23. *Canendiyú*, **13.3 km N Curuguaty** [ca. 24°31′S, 55°42′W, 255 m; Paynter, 1989]: *Cryptonanus chacoensis* (coll. P. Myers, 17 July 1979).

24. *Chaco*, **Palmar de las Islas** (19°38′ S, 60°37′ W): *Cryptonanus chacoensis* (coll. H. Amarilla, 5 May 1997).
25. *Concepción*, **Concepción** [23°25′S, 57°17′W, ca. 175 m; Paynter, 1989]: *Cryptonanus chacoensis* (coll. E. Weiske; date unknown, but not later than 1911).
26. *Concepción*, **Paso Horqueta** [23°07′S, 57°20′W; DMA, 1992] on Río Aquidaban: *Cryptonanus chacoensis* (coll. G.K. Creighton, 8 September 1979).
27. *Cordillera*, **1.6 km S Tobatí** [25°15′S, 57°04′W, ca. 100 m; Paynter, 1989]): *Cryptonanus chacoensis* (coll. P. Myers, 1 September 1978).
28. *Paraguarí*, **Sapucay** [= Sapacuaí at 25°40′S, 56°55′W, ca. 220 m; Paynter, 1989]: *Cryptonanus chacoensis* (coll. W. Foster, 10 August–11 September 1903).
29. *Presidente Hayes*, **Estancia La Victoria** (23°40′S, 58°35′W, 120 m): *Cryptonanus chacoensis* (coll. TTU party, 4 August 1995).

APPENDIX 4

NONMOLECULAR DATA MATRIX

The matrix of nonmolecular characters analyzed in this report is reproduced below. An electronic version of the same data in Nexus format can be downloaded from ftp://ftp.amnh.org/pub/mammalogy.

Caluromys lanatus: 01100 00002 00020 01100 00211 00011 00010 00000 00000 11000 11010 00100 00000 00000 0

Caluromys philander: 01100 00002 00020 01000 10201 00011 00010 00000 00000 11000 11010 00100 00000 00000 0

Caluromysiops irrupta: 000–0 02002 00020 01?00 00211 00001 00011 00000 00002 11000 11010 00000 00000 01??? ?

Chacodelphys formosa: ?0100 10000 1??20 0???? 20000 00000 00100 02211 01010 00000 00000 11211 ?00?1 10??? ?

Chironectes minimus: 10120 01000 20021 01201 11200 00000 01021 00200 01012 10101 00002 11111 21000 00111 1

Cryptonanus chacoensis: 00100 10001 01020 00–00 20001 00000 00000 02210 01010 00000 00102 11211 00000 00??? ?

Cryptonanus unduaviensis: 00100 10001 01020 0???0 20001 00000 00000 02210 01010 00000 00202 11210 00020 00??? ?

Didelphis albiventris: 10100 00110 00010 01100 11201 00000 01021 00210 01012 10110 01002 11111 21000 00111 1

Didelphis marsupialis: 10100 00110 00020 01100 11201 00000 01021 00210 01012 10110 01002 11111 21000 00111 1

Didelphis virginiana: 10100 00110 00010 01100 11201 00000 01021 00210 01012 10110 01002 11111 21000 00111 1

Glironia venusta: 00100 ?0001 0??20 00–00 00–11 ??000 00010 00100 00010 00000 01001 01110 000?0 00??? ?

Gracilinanus aceramarcae: 00100 10001 01020 00–00 20001 00010 00000 02211 01011 00000 00001 11210 ?00?0 00??? ?

Gracilinanus agilis: 00100 10001 01020 0???0 20001 00010 00000 02211 01011 00000 00001 11210 ?0020 00000 0

Gracilinanus emiliae: 00100 10001 01020 00–00 20101 00010 00000 02211 01011 00000 00101 11210 00020 00??? ?

Gracilinanus microtarsus: 00100 10001 01020 0???0 20001 00010 00010 02211 01011 00000 00001 11210 000?0 00000 0

Lestodelphys halli: 10100 16000 10000 10–10 20000 ?0100 00000 01210 11011 01000 00002 11211 00221 00000 0

Lutreolina crassicaudata: 100–0 00000 00000 01200 11200 10000 01021 00210 01212 10110 01002 11111 21000 00111 1

Marmosa lepida: 00100 00001 01020 00–00 20201 00010 00010 00200 01010 00000 00101 11210 00020 00??? ?

Marmosa mexicana: 00100 10001 01120 00–00 20101 00010 00010 00210 01010 00000 00001 11210 00020 00000 0

Marmosa murina: 00100 00001 00020 00–00 20201 00010 00010 00200 01010 00000 00001 11210 00020 00000 0

Marmosa robinsoni: 00100 10001 01120 00–00 20101 00010 00010 00200 01010 00000 00001 11210 00020 00000 0

Marmosa rubra: ?0100 00001 01120 00–0? 20201 00010 00000 00200 01010 01000 00001 11210 00020 00??? ?

Marmosops impavidus: 00100 00000 01020 00–00 20201 01010 00000 02210 01011 00000 00001 11211 00000 00000 0

Marmosops incanus: 00100 10000 01020 00–10 20201 010?0 00100 01210 01011 00000 00001 11211 000?0 00000 0

Marmosops noctivagus: 00100 10000 01020 00–00 20201 01010 00000 01210 01011 00000 00001 11211 00000 00000 0

Marmosops parvidens: 00100 00000 01020 00–00 20201 01010 00000 02200 01011 00000 00201 11210 00000 00??? ?

Marmosops pinheiroi: 00100 00000 01020 00–00 20201 01010 00000 02200 01011 00000 00201 11211 00000 00??? ?

Metachirus nudicaudatus: 10121 10000 00020 00–00 20100 00000 00000 10200 01011 00110 00001 11211 10000 00000 0

Micoureus demerarae: 00100 00001 01120 00–00 20201 00010 00010 00200 01010 00000 00001 11210 00020 00000 0

Micoureus paraguayanus: 00100 00001 01120 00-?0 10201 00010 00010 00200 01010 00000 00001 11210 ?00?0 00000 0

Micoureus regina: 00100 00001 01120 00–00 20201 00010 00010 00200 01010 00000 00001 11210 00020 00000 0

Monodelphis adusta: 100–0 10000 00000 00–00 20000 00000 10000 00200 01210 00000 00002 11211 001?1 10??? ?

Monodelphis brevicaudata: 100–0 14000 00000 00–00 00000 00000 10000 00200 01210 00000 00002 11211 10101 10010 1

Monodelphis emiliae: 100–0 15000 00000 00–00 00000 00000 10000 00200 01210 01000 00002 11211 ?0201 10010 1

Monodelphis theresa: 100–0 03000 00000 0???0 20000 00000 10000 00200 01212 00000 00002 11211 ?01?1 10??? ?

Philander frenata: 10111 00000 00020 01100 11201 10000 01021 00210 01012 10110 01002 11111? 10?0 00111 1

Philander mcilhennyi: 10121 00000 00020 01100 11201 10000 01021 00210 01012 10110 01002 11111 21000 00111 1

Philander opossum: 10121 00000 00020 01100 11201 10000 01021 00210 01012 10110 01002 11111 21000 00111 1

Thylamys macrurus: 00100 16000 10020 10–10 20001 00000 00100 02211 01011 01000 00002 11211 001?0 00000 0

Thylamys pallidior: 10100 16000 10020 1???0 20001 00100 00100 02210 11011 01000 00002 11211 00120 00000 0

Thylamys pusillus: 00100 16000 10020 10–10 20001 00100 00100 02211 11011 01000 00002 11211 00110 00000 0

Thylamys venustus: 00100 16000 10020 1???0 20001 00100 00100 02211 11011 01000 00002 11211 00120 00000 0

Tlacuatzin canescens: 00100 00001 01020 00–00 20001 00000 00010 00201 01010 00000 00001 11210 00020 00111 1