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On the Relationships of “*Marmosa*” *formosa* Shamel, 1930 (Marsupialia: Didelphidae), a Phylogenetic Puzzle from the Chaco of Northern Argentina

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ABSTRACT

The holotype and only known specimen of *Marmosa formosa* Shamel, a nominal species currently synonymized with *Gracilinanus agilis* Burmeister, is strikingly unlike any other known didelphid marsupial. Phylogenetic analyses based on nonmolecular characters and IRBP sequences suggest that *formosa* is either the sister-taxon of *Thylamys* (including *Lestodelphys*) or *Monodelphis*. Because neither alternative is strongly supported by the data at hand, and because including *formosa* in *Thylamys* or in *Monodelphis* would compromise the diagnosability of those taxa, a new genus—*Chacodelphys*—is proposed to contain it. Currently known only from northern Argentina, *Chacodelphys formosa* may be widely distributed in the Chaco and other adjacent Neotropical biomes.

INTRODUCTION

Recent analyses of didelphid phylogeny based on nuclear gene sequences and morphology have provided an increasingly detailed perspective on relationships within this speciose group of American marsupials (Jansa and Voss, 2000; Voss and Jansa, 2003).

Among other conspicuous features in these results are a number of very long internal branches, corresponding to reconstructed phylogenetic lineages where many character-state transformations are hypothesized to have occurred in the absence of cladogenesis. On the assumption that long branches are ar-

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tifacts of extinction or sparse taxon sampling (Horovitz, 1999), they might be used to predict where significant taxonomic discoveries remain to be made. In ignorance of the facts reported below, Voss and Jansa (2003: 61) speculated that, “[a]lthough some of the ‘missing links’ that might occupy such long internodes are probably extinct, others may persist in the extant Neotropical fauna—either unnamed and undiscovered in some habitat neglected by collectors, or already named but yet unrecognized for what they really are.” Although the latter possibility may have seemed fanciful to some readers, subsequent revisionary research has revealed a striking example of a named but long-forgotten living taxon that appears to subdivide one or the other of two long branches in didelphid phylogeny.

In 1930, H.H. Shamel described a tiny mouse opossum collected in northern Argentina by the ornithologist Alexander Wetmore. Shamel (1930a) originally called it *Marmosa muscula*, but he promptly (Shamel, 1930b) proposed the replacement name *M. formosa* to avoid homonymy with *muscula* Cabanis (a synonym of *M. murina* Linnaeus). Unfortunately, Shamel’s original description emphasized small size, mouse-like coloration, and a very short tail, but provided few details of craniodental morphology. Tate (1933) recognized *formosa* as a valid species belonging to the “*Elegans* Group” of *Marmosa*, but cautioned that its relationships were obscure. Despite the fact that Shamel and Tate clearly stated that the type was a young adult, Cabrera (1958) considered it—sight unseen—to be a juvenile example of a local form of *M. velutina* (Wagner) in the subgenus *Thylamys*. Reig et al. (1985) raised *Thylamys* to generic rank and cited Kirsch and Calaby (1977) in recognizing *formosa* as a valid species, although Pine (1975) had earlier come to the same conclusion. Gardner and Creighton (1989), however, referred *formosa* to *Gracilinanus*, wherein it was listed as one of many putative synonyms of *G. agilis* (Burmeister). Hershkovitz’s (1992) revision of *Gracilinanus* also listed *formosa* as a synonym of *G. agilis*, and Shamel’s species has remained essentially forgotten in the subsequent literature.

We recently examined the type of “*Mar-*

mosa” *formosa* and found it to exhibit a unique combination of character states that does not fit the diagnoses of *Thylamys*, *Gracilinanus*, or any other currently recognized supraspecific taxon. In order to simplify the following analyses and discussion, we anticipate our taxonomic conclusions and provide a new generic name below.

Chacodelphys, new genus

Figures 1, 2

TYPE SPECIES: *Marmosa formosa* Shamel (1930b).

CONTENTS: Only the type species is referred to *Chacodelphys*.

DIAGNOSIS: As for the type species, below.

ETYMOLOGY: For the Chaco (a subtropical biome in northern Argentina, western Paraguay, and eastern Bolivia) + *delphys* (uterus), a traditional Greek suffix for New World marsupials.

Chacodelphys formosa (Shamel, 1930b)

Marmosa muscula Shamel, 1930a: 83. Original description.

Marmosa formosa Shamel, 1930b: 311. Replacement name.

Marmosa (Thylamys) velutina formosa: Cabrera, 1958: 33. New name combination.

Marmosa (Thylamys) formosa: Kirsch and Calaby, 1977: 14. New name combination.

Thylamys formosa: Reig, Kirsch, and Marshall, 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 generic assignment and synonymy, based on alleged conspecificity with *G. agilis* Burmeister.

HOLOTYPE: A young adult male specimen in the National Museum of Natural History (USNM 236330; original number 1081) collected by Alexander Wetmore on 9 August 1920 on an estancia called Linda Vista near the Riacho Pilagá, about 200 km northwest of Formosa, Provincia Formosa, Argentina. The type is preserved as a round skin with skull and hemimandibles, all of which are in good condition. Although Cabrera (1958) thought that Shamel’s type was a juvenile, the permanent dentition of USNM 236330 is fully erupted.

The type locality has been variously re-

TABLE 1
External and Craniodental Dimensions (mm)
of the Holotype of *Chacodelphys formosa*^a

Head-and-body length	68
Length of tail	55
Hind foot	11
Condylobasal length	20.6
Nasal breadth	8.3
Least interorbital breadth	3.4
Zygomatic breadth	11.6
Palatal length	11.1
Palatal breadth	7.1
Maxillary toothrow	8.2
Length of molars	4.7
Length M1-M3	4.2

^a Measurements defined by Voss et al. (2001: 18, fig. 7).

ported in the literature and merits comment. The original skin tag gives the collection locality of USNM 236330 as “Argentina/Formosa: Kilometro 182” on one side, and “Riacho Pilaga/10 mi. N.W.” on the other, but Shamel (1930a: 83) stated that the type was collected at “Kilometer 182” and did not mention Riacho Pilagá. Tate (1933: 232) correctly interpreted the type locality as “Riacho Pilaga, 10 mi. northwest of Kilom[eter]. 182.” Wetmore’s (1926) published itinerary (quoted at length below) states that his base of operations from 5 to 21 August 1920 was at Linda Vista, an estancia on the Riacho Pilagá, 15 km northwest of a station known as Kilometro 182 (now Comandante Fontana) on the railroad from Formosa. According to Paynter (1995), Linda Vista is about 100 m above sea level near 25°13’S, 59°47’W.

DIAGNOSIS: *Chacodelphys formosa* is a very small didelphid—possibly the smallest living form (see table 1 for measurements)—that can be distinguished from other confamilial taxa by numerous qualitative morphological characters, of which the following provide the most conspicuous points of comparison (see Voss and Jansa [2003] for character definitions and anatomical terminology).

Eye narrowly surrounded by mask of dark fur contrasting in color with fur of cheeks and crown; pale spot above eye absent; dark midrostral stripe absent; gular gland present (distinct but perhaps not fully developed on

holotype); dorsal fur brownish, somewhat darker middorsally than along flanks, but pelage not distinctly tricolored (sensu Tate, 1933); dorsal underfur gray-based; dorsal guard hairs very short and inconspicuous; ventral fur gray-based but superficially washed with buff-yellow from throat to anus (there is some self-colored buffy fur on the chin); third manual digit (dIII) longer than adjacent digits (dII and dIV); manual claws shorter than apical digital pads; central palmar surface of manus densely covered with small convex tubercles; fourth pedal digit (dIV) slightly longer than adjacent digits (dIII and dV); plantar epithelium of pes naked from heel to toes; body pelage not extending onto tail base; tail densely covered with short hairs (three per scale) and distinctly bicolored (dark above, pale below); tail scales arranged in annular series; caudal prehensile surface absent (tail tip completely hairy above and below); 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 very narrow, with subparallel lateral margins; maxillary turbinates large and elaborately branched; supraorbital margins smoothly rounded, without beads or processes; strongly marked interorbital and postorbital constrictions present; sagittal crest absent; parietal and alisphenoid bones in contact (no squamosal-frontal contact); petrosal exposed on lateral aspect of braincase through small fenestra between parietal and squamosal; maxillopalatine fenestrae very large; palatine fenestrae present but incompletely separated from maxillopalatine openings; maxillary fenestrae very small but bilaterally present near M1/M2 commissure; posterolateral foramina small, 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 bilaterally present; alisphenoid tympanic wing without anteromedial processes (secondary foramen ovale 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 exocci-



Fig. 1. Dorsal and ventral views of the skin of the holotype of *Chacodelphys formosa* (Shamel), both approximately life size.

tals; triangular stapes perforated by large obturator foramen; two mental foramina present on lateral aspect of mandible; angular processes apparently acute and strongly inflected (broken on both hemimandibles of holotype).

Upper incisor crowns symmetrically rhomboidal and increasing in breadth from front to back ($I2 < I5$); C1 without anterior or posterior accessory cusps; P1 present, smaller than posterior premolars but not vestigial; P2 distinctly taller 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 \ll width

M4); ectoflexus absent on M1, very shallow on M2, distinct only on M3; anterior cingulum incomplete on M3. Lower incisors with distinct lingual cusps; c1 without posterior accessory cusp; p2 taller than p3; hypoconid lingual to protoconid (not labially salient) on m3; entoconid distinct but small, subequal to hypoconulid on m1–m3.

COMPARISONS: *Chacodelphys formosa* differs by a large number of external and craniodental characters from members of other “marmosine” genera (comprising those species formerly classified as or allied with *Marmosa* sensu lato) and from *Monodelphis* as detailed in the following paragraphs.



Fig. 2. Dorsal, ventral, and lateral views of the skull of *Chacodelphys formosa* (Shamel), all approximately four times life size.

Chacodelphys differs from species of *Gracilinanus* sensu stricto⁴ by its long third manual digit (versus dIII and dIV subequal); densely tuberculate (versus smooth) central palmar surface of manus; very short tail (versus tail much longer than head-and-body); absence of a caudal prehensile surface (versus tail-tip modified for prehension); absence (versus presence) of a rostral process of the premaxillae; narrow nasals with subparallel lateral margins (versus nasals conspicuously widened posteriorly); absence (versus presence) of a secondary foramen ovale; incomplete (versus complete) anterior cingulum on M3; hypoconid not labially salient on m3 (versus m3 hypoconid labially salient); and an entoconid that is subequal in height to the hypoconulid on m1–m3 (versus entoconid much taller than the hypoconulid).

Chacodelphys differs from the monotypic genus *Lestodelphys* by not having distinctly tricolored pelage (versus pelage distinctly tricolored); gray-based ventral fur (versus ventral fur self-white); short manual claws (versus long manual claws that extend well beyond the apical digital pads); hindfoot with naked plantar epithelium from heel to toes (versus heel covered with coarse fur); long fourth pedal digit (versus dIII longer than dIV); tail not incrassate (versus incrassate); narrow nasals with subparallel lateral margins (versus nasals conspicuously widened posteriorly); presence (versus absence) of maxillary fenestrae; small posterolateral foramina (versus foramina large and usually

extending lingual to M4 protocones); absence (versus presence) of a secondary foramen ovale; triangular stapes with wide obturator foramen (versus stapes subtriangular and microperforate); fenestra cochleae laterally exposed (versus fenestra concealed in a sinus formed by the rostral and caudal tympanic processes of the petrosal); P2 distinctly taller than P3 (versus $P2 \ll P3$); and p2 taller than p3 (versus $p2 < p3$).

Chacodelphys differs from species of *Marmosa* and *Micoureus* by its long third manual digit (versus dIII and dIV subequal); densely tuberculate (versus smooth) central palmar surface of manus; very short tail (versus tail much longer than head-and-body); caudal scales in annular (versus spiral) series; absence of a caudal prehensile surface (versus tail-tip modified for prehension); absence (versus presence) of a rostral premaxillary process; narrow nasals with subparallel lateral margins (versus nasals conspicuously widened posteriorly); absence (versus presence) of postorbital processes; petrosal exposed laterally through a small fenestra between the parietal and squamosal (versus petrosal not so exposed); presence (versus absence) of maxillary fenestrae; P2 distinctly taller than P3 (versus P2 and P3 subequal); anterior cingulum on M3 incomplete (versus complete); hypoconid lingual to protoconid on m3 (versus m3 hypoconid labially salient); and entoconid subequal in height to hypoconulid on m1–m3 (versus entoconid much taller than hypoconulid).

Chacodelphys differs from species of *Marmosops* by its densely tuberculate (versus smooth) central palmar surface of manus; very short tail (versus tail longer than head-and-body); caudal scales in annular (versus spiral) series; caudal prehensile surface absent (versus tail-tip modified for prehension); presence (versus absence) of maxillary palatal vacuities; absence (versus presence) of a secondary foramen ovale; P2 distinctly taller than P3 (versus P2 and P3 subequal); hypoconid lingual to protoconid on m3 (versus m3 hypoconid labially salient); and entoconid subequal in height to hypoconulid on m1–m3 (versus entoconid much taller than the hypoconulid).

Chacodelphys differs from species of *Monodelphis* by having a dark mask sur-

⁴ As construed herein, *Gracilinanus* sensu stricto comprises the following valid species, all of which conform to Gardner and Creighton's (1989) original generic diagnosis: *aceramarcae* Tate, *agilis* Burmeister (including *beatrice* Thomas, *buenavistae* Tate, and *peruanus* Thomas), *dryas* Thomas, *emiliae* Thomas (including *longicaudus* Hershkovitz), *marica* Thomas (including *perijae* Hershkovitz), and *microtarsus* Wagner. Explicitly excluded from our concept of *Gracilinanus* sensu stricto are five nominal taxa (currently treated as synonyms of *agilis*, *emiliae*, or *microtarsus*; see Gardner, 1993) that belong to an unnamed clade to be described in a manuscript currently in preparation. These include *agricolai* Moojen; *chacoensis* Tate; *guahybae* Tate; *ignitus* Díaz, Flores, and Barquez; and *unduviensis* Tate. We have not examined material of three nominal taxa (*blaseri*, *rondoni*, and *herhardi*) originally described by Miranda-Ribeiro (1936) and currently assigned to *Gracilinanus* (sensu Gardner, 1993); their membership in one or the other of the groups mentioned above seems probable but remains to be determined.

rounding the eyes (versus circumocular mask absent); short manual claws (versus long manual claws that extend beyond the apical digital pads); densely tuberculate (versus smooth or sparsely tuberculate) central palmar surface of manus; long fourth pedal digit (versus dIII longer than dIV); narrow nasals with subparallel lateral margins (versus nasals conspicuously widened posteriorly); maxilloturbinals large and elaborately branched (versus maxilloturbinals small and unbranched); petrosal exposed laterally through a small fenestra between the parietal and squamosal (versus petrosal not so exposed); presence (versus absence) of palatine fenestrae; presence (versus absence) of maxillary fenestrae; maxillary and alisphenoid separate (versus contacting on orbital floor); and P2 distinctly taller than P3 (versus P2 < P3).

Chacodelphys differs from species of *Thylamys* in not having distinctly tricolored pelage (versus pelage distinctly tricolored); hindfoot with naked plantar epithelium from heel to toes (versus heel covered with coarse fur); absence of a caudal prehensile surface (versus tail-tip modified for prehension; tail not incrassate (versus incrassate); posterolateral palatal foramina small (versus foramina large and usually extending lingual to M4 protocones); absence (versus presence) of a secondary foramen ovale; fenestra cochleae exposed laterally (versus concealed in a sinus formed by the rostral and caudal tympanic processes of the petrosal); P2 distinctly taller than P3 (versus P2 < P3); p2 taller than p3 (versus p2 subequal to p3 or p2 < p3); hypoconid lingual to protoconid on m3 (versus m3 hypoconid labially salient); and entoconid subequal in height to hypoconulid on m1–m3 (versus entoconid much taller than hypoconulid).

Chacodelphys differs from the monotypic genus *Tlacuatzin* by its possession of a gular gland (versus gular gland absent in *Tlacuatzin*); long third manual digit (versus dIII and dIV subequal); densely tuberculate (versus smooth) central palmar surface of manus; very short tail (versus tail longer than head-and-body); absence of a caudal prehensile surface (versus tail-tip modified for prehension); narrow nasals with subparallel lateral margins (versus nasals conspicuously wid-

ened posteriorly); absence (versus presence) of postorbital processes; petrosal exposed laterally through a small fenestra between the parietal and squamosal (versus petrosal not so exposed); presence (versus absence) of palatine fenestrae; second through fifth upper incisor crowns increasing in breadth from front to back (versus I2–I5 crowns subequal in breadth); P2 distinctly taller than P3 (versus P2 and P3 subequal in height); anterior cingulum of M3 incomplete (versus complete); hypoconid lingual to protoconid on m3 (versus m3 hypoconid labially salient); and entoconid subequal in height to hypoconulid on m1–m3 (versus entoconid much taller than hypoconulid).

SPECIMENS EXAMINED: The holotype is the only known specimen.

PHYLOGENETIC RELATIONSHIPS

The morphological and molecular datasets recently compiled by Voss and Jansa (2003) provide an appropriate basis for analyzing the relationships of *Chacodelphys*, but our very limited material is a significant problem. With only one specimen of *C. formosa* at hand, we are unable to evaluate character variability in this taxon, which might be polymorphic for some attributes exhibited by the holotype. A more serious deficiency in our data, however, are missing values for many characters that might be important for accurate phylogenetic inference.

For example, we are unable to score *Chacodelphys* for 12 of the 71 nonmolecular (morphological and karyotypic) characters defined by Voss and Jansa (2003). Missing nonmolecular data for this taxon include state assignments for characters 1 (number of ventrolateral rhinarial grooves), 12 (presence/absence of lateral carpal tubercles), 13 (presence/absence of medial carpal tubercles), 17 (presence/absence of pouch), 18 (morphology of pouch), 19 (mammary complement), 20 (cloacal morphology), 61 (dental eruption sequence), and 68–71 (Robertsonian chromosomal transformations). Scoring these characters is often problematic from dried skins of very small species (1), or requires reproductively mature adults of the appropriate sex (12, 13, 17, 18, 19), intact

TABLE 2
Dataset Characteristics of Tree Statistics from Parsimony Analyses Without and With *Chacodelphys*

	Nonmolecular analysis		Combined analysis	
	Without ^a	With	Without ^a	With
Terminal taxa	35	36	35	36
MPTs ^b	2161	4	34	18
Tree length ^c	158	163.5	567	573
Consistency index ^d	0.55	0.53	0.59	0.59
Retention index	0.85	0.84	0.83	0.83
Resolved ingroup nodes ^e	20	26	23	27
Total ingroup support ^f	42	54	138	116

^a Results from Voss and Jansa (2003: table 4).

^b Maximally parsimonious trees recovered by heuristic searches.

^c Including autapomorphies.

^d Excluding autapomorphies.

^e In strict-consensus topologies illustrated by Voss and Jansa (2003: figs. 17, 21) and in this report (figs. 3, 4).

^f Sum of Bremer support values over resolved ingroup nodes in strict-consensus topologies illustrated by Voss and Jansa (2003: figs. 17, 21) and in this report (figs. 3, 4).

fluid-preserved material (20), age series (61), or live material for karyotyping (68–71).

The absence of molecular data is also unfortunate. The 83-year-old holotype is not available for destructive tissue sampling, which would, in any case, be unlikely to yield high-quality nuclear DNA. Therefore, all of the IRBP sequence characters (N = 1158) analyzed by Voss and Jansa (2003) are missing for *Chacodelphys*.

We carried out two phylogenetic analyses, one based only on the nonmolecular data (appendix 1), for which *Chacodelphys* is 83% complete, and the other based on the combined data (nonmolecular + IRBP; Voss and Jansa, 2003), for which *Chacodelphys* is only 5% complete. Both analyses were executed using the same heuristic search parameters, nodal support algorithms, and rooting conventions employed by Voss and Jansa (2003). The results are summarized statistically in table 2 and illustrated in figures 3 and 4.

Adding *Chacodelphys* to the nonmolecular dataset of Voss and Jansa (2003) dramatically reduces the number of maximally parsimonious trees (MPTs)—from 2161 in their heuristic analysis of 35 terminals to 4 in our analysis of 36 terminals. Correspondingly, the number of resolved ingroup nodes in the strict-consensus topology increases from 20

(in Voss and Jansa's results) to 26 in the present study. In effect, adding *Chacodelphys* resolves the large polytomy of *Marmosa* and *Micoureus* species that Voss and Jansa observed at the base of the didelphine radiation. Species of *Marmosa* and *Micoureus* are now (fig. 3) recovered as a clade (within which *Marmosa* remains stubbornly paraphyletic) that is sister to a novel cluster containing *Tlacuatzin*, *Gracilinanus*, *Chacodelphys*, *Thylamys*, and *Lestodelphys*. Within the latter group, *Chacodelphys* is sister to a clade containing species of *Thylamys* and *Lestodelphys* in the sequence (*Thylamys venustus* (*T. pallidior* (*Lestodelphys halli*))). Among the remaining didelphines, the genera *Monodelphis*, *Metachirus*, and *Marmosops* appear as successively distant outgroups to the large $2n = 22$ opossums. Unfortunately, most measures of nodal support are small, including all of those that support relationships in which figure 3 differs from the corresponding nonmolecular results of Voss and Jansa (2003: fig. 17).

Including *Chacodelphys* also reduces the number of MPTs and increases the number of resolved ingroup nodes when the combined (nonmolecular + IRBP) dataset of Voss and Jansa (2003) was reanalyzed. The resulting strict-consensus topology, however, is quite different from that obtained in the

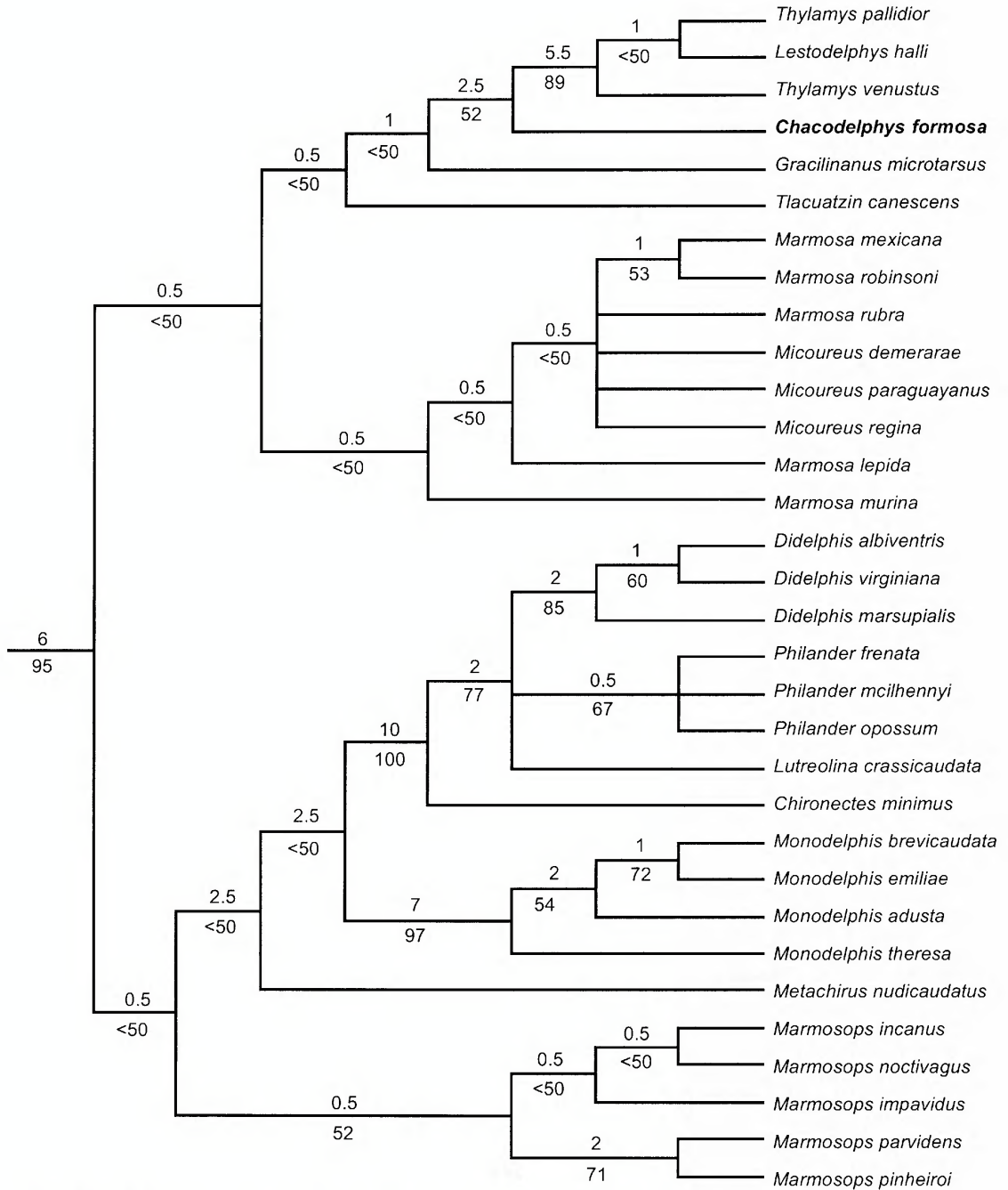


Fig. 3. Strict consensus of four equally most-parsimonious trees obtained by a heuristic analysis of nonmolecular characters. Only ingroup (didelphine) terminal taxa are illustrated; “caluromyine” outgroups (*Glironia venusta*, *Caluromysiops irrupta*, *Caluromys lanatus*, and *C. philander*) are not shown. Bremer support and bootstrap values are shown above and below each branch, respectively. See table 2 for other tree statistics.

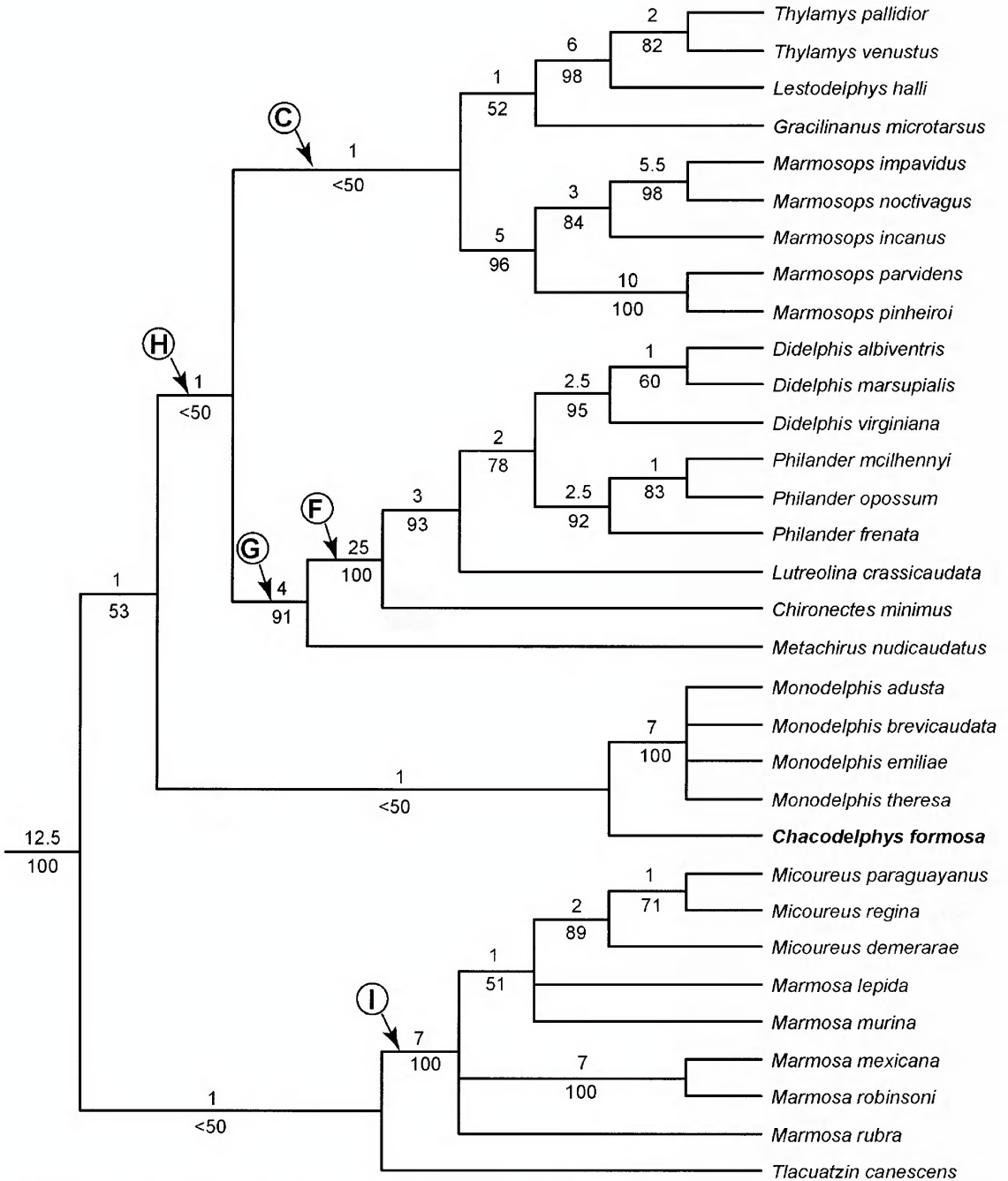


Fig. 4. Strict consensus of 18 equally most-parsimonious trees obtained by a heuristic analysis of the combined (nonmolecular + IRBP) dataset. Only ingroup (didelphine) terminal taxa are illustrated; "caluromyine" outgroups (*Glironia venusta*, *Caluromysiops irrupta*, *Caluromys lanatus*, and *C. philander*) are not shown. Bremer support and bootstrap values are shown above and below each branch, respectively. See table 2 for other tree statistics. Labelled clades (C, F, G, H, I) are defined and discussed in the text.

TABLE 3
Apomorphy Lists for Selected Clades Recovered in the Nonmolecular Analysis^a

Clade	Character ^b	CI ^c	Locally derived condition
<i>Chacodelphys</i> + <i>Thylamys</i> ^d	10 (relative length manual digits)	0.667	dIII longest
	11 (central palmar surface manus)	1.000	densely tubercular
	33 (nasal shape)	0.333	uniformly narrow
	60 (M3 anterior cingulum)	0.333	incomplete
<i>Chacodelphys</i>	25 (tail tip)	0.200	nonprehensile
	55 (relative height P2, P3)	0.500	P2 > P3
	65 (m3 hypoconid position)	0.333	lingual to protoconid
	66 (entoconid size m1—m3)	0.500	reduced
<i>Thylamys</i> ^d	7 (pelage color pattern)	1.000	distinctly tricolored
	16 (pedal plantar pelage)	1.000	tarsus furred
	28 (tail incassation)	1.000	present
	41 (posterolateral palatal foramina)	1.000	lingual to M4 protocones
	47 (fenestra cochleae)	0.250	concealed in a sinus
	55 (relative height P2, P3)	0.500	P2 < P3
	63 (relative height p2, p3)	0.500	p2 ≈ p3

^a Only unambiguous character-state transitions (from both ACCTRAN and DELTRAN optimizations) are tabulated for clades illustrated in figure 3.

^b As numbered and defined by Voss and Jansa (2003).

^c Consistency index.

^d Including *Lestodelphys*.

nonmolecular analysis discussed above. Here (fig. 4) *Chacodelphys* appears as the sister taxon of *Monodelphis*, whereas clades C (*Marmosops* + *Gracilinanus* + *Thylamys* + *Lestodelphys*), G (*Metachirus* + the large 2n = 22 opossums), and H (clades C + G) of Jansa and Voss (2000) are recovered intact, and *Tlacuatzin* appears as the basal lineage of another group (clade I) containing *Marmosa* and *Micoureus* species. Although this topology contrasts in several respects from that obtained in the combined analysis of Voss and Jansa (2003: fig. 21), none of the new results just described are supported by large Bremer or bootstrap values. In fact, *Chacodelphys* was recovered as a member of clade C in 48% of our bootstrap pseudoreplicates, slightly more often than it appeared as the sister-group to *Monodelphis* (44%).

We optimized our morphological character data on most-parsimonious trees to assess patterns of anagenetic evolution implied by these alternative phylogenetic hypotheses (tables 3, 4). Only a few character-state transitions unambiguously support each of the alternative sister-group relationships for *Chacodelphys*. By contrast, the monophyly of

Thylamys (including *Lestodelphys*) is unambiguously supported by seven synapomorphies in the nonmolecular analysis, and the monophyly of *Monodelphis* is unambiguously supported by six synapomorphies in the combined analysis.

In order to assess the potentially confounding effects of missing molecular data for *Chacodelphys* in the combined-data analysis, we carried out a missing-entry replacement exercise in the spirit of Norell and Wheeler (2003), although the details of our procedure differ somewhat from theirs.⁵ When the missing IRBP sequence for *Chacodelphys* is replaced by random nucleotides,

⁵ One hundred simulated datasets were obtained by replacing missing molecular data for *Chacodelphys formosa* with nucleotide character-states randomly drawn from a probability distribution based on the observed frequencies of each state in the other taxa (0.21 for A, 0.36 for C, 0.28 for G, 0.15 for T) using the "Fill Random" option in MacClade 4.02 (Maddison and Maddison, 2001). Missing molecular entries for other didelphids (constituting <0.1% of the IRBP2 matrix analyzed by Voss and Jansa, 2003) and missing morphological entries were not replaced. Heuristic parsimony analyses were carried out with some multistate morphological characters ordered as by Voss and Jansa (2003).

TABLE 4
Apomorphy Lists for Selected Clades Recovered in the Combined-Data Analysis^a

Clade	Character ^b	CI ^c	Locally derived condition
<i>Chacodelphys</i> + <i>Monodelphis</i>	23 (tail scale arrangement)	0.250	annular
	65 (m3 hypoconid position)	0.500	lingual to protoconid
	66 (entoconid size m1–m3)	1.000	reduced
<i>Chacodelphys</i>	11 (central palmar surface manus)	0.500	densely tubercular
	33 (nasal shape)	0.333	uniformly narrow
	37 (lateral petrosal exposure)	0.286	exposed laterally
	39 (palatine fenestrae)	0.200	present
	40 (maxillary fenestrae)	0.250	present
	55 (relative height P2, P3)	0.400	P2 > P3
<i>Monodelphis</i>	3 (circumocular mask)	0.333	absent
	14 (relative length pedal digits)	0.250	dIII longest
	31 (maxilloturbinal morphology)	1.000	small and unbranched
	43 (maxillary-alisphenoid contact)	0.500	present
	55 (relative height P2, P3)	0.400	P2 < P3
	63 (relative height p2, p3)	0.500	p2 ≈ p3

^a Only unambiguous character-state transitions (from both ACCTRAN and DELTRAN optimizations) are tabulated for clades illustrated in figure 4.

^b As numbered and defined by Voss and Jansa (2003).

^c Consistency index.

few consistent patterns of relationships were found (fig. 5). For example, *Chacodelphys* was recovered as the sister-group of *Monodelphis* in only 15 of 100 simulated datasets, as the sister-group of *Tlacuatzin* in 31, and as the sister-group of one or more members of clade C in 36. However, *Chacodelphys* never appeared within clades F (the large $2n = 22$ opossums) or I (*Marmosa* + *Micoureus*), nor did it ever appear as the sister group of either *Lestodelphys* or *Thylamys* alone.

ECOGEOGRAPHIC PROVENANCE

The only available information about the habitat of *Chacodelphys formosa* was recorded by the collector of the holotype, Alexander Wetmore, an ornithologist dispatched to Argentina in 1920 by the U.S. Biological Survey to study the winter habitats of migratory North American shore birds. Traveling by rail from the provincial capital of Formosa, Wetmore (1926: 4–5) described the local landscape in these words:

As the railroad leaves Formosa it enters the Chaco, a broad nearly level area of alternate forest and marshy savanna, cut by several large streams. . . . For miles our train traversed a roadbed built through an inter-

minable estero, with broad swamps and prairies on either hand, dotted with slender trunked palms interspersed with stands of saw-edged grass and rushes, and bordered by bands of low-growing hardwoods, prominent among which was the quebracho, valuable for its dye product. Hundreds of acres were covered with ant-hills built up 3 or 4 feet above the surrounding level to raise them above inundations caused by the summer rains. At intervals we crept out to higher ground and stopped at some little station, with a cluster of low houses or grass-thatched huts about it. Elsewhere no signs of man were visible; bands of rheas, flocks of maguari storks, courlans, and other strange birds were numerous. In mid-afternoon I reached my destination, Kilometer 182 (known locally as Fontana), and there left the railroad at the hospitable invitation of Don Pedro Upitz to continue by oxcart northwest for 15 kilometers to the estancia Linda Vista on the Riacho Pilaga. . . . For several miles on either side of the railroad the forest had been cut away, but at the Riacho Pilaga tree growth was in its original condition. Open savannas, often of a marshy nature, mingled with scattered groves, while near the small sluggish streams, known as riachos, were extensive forests with a jungle undergrowth that, as it was not grazed [by livestock], required a machete to penetrate. . . . The savannas were grown with bunch grass that seldom attained great height as it was burned yearly by the Indians to drive out concealed game. . . . The country as a whole was higher than that immediately west of Formosa and was now comparatively dry. It is inundated extensively during the summer rains. Frost was frequent; the first intimation of spring came toward the close of my stay with the

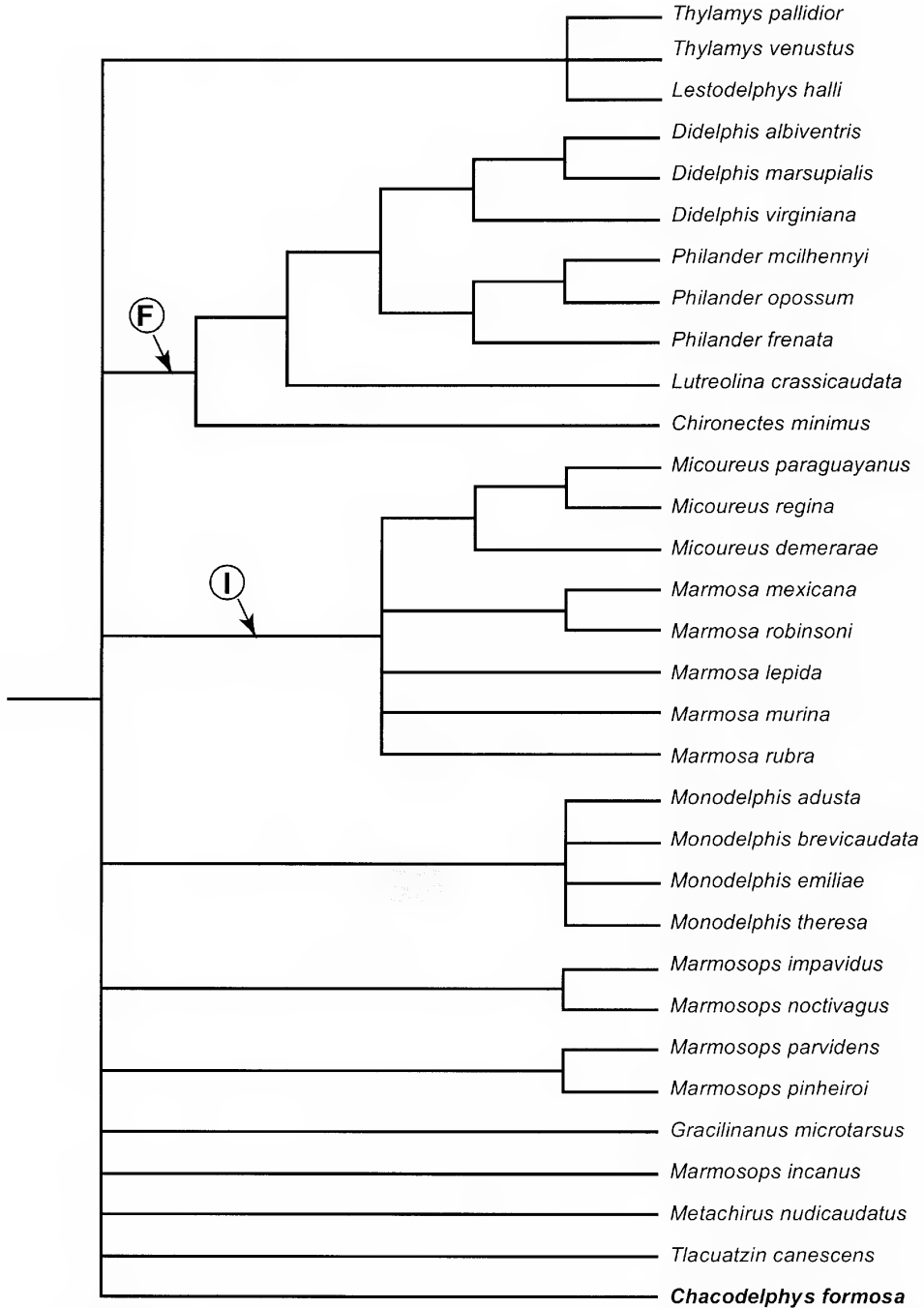


Fig. 5. Strict consensus of all MPTs recovered from heuristic analyses of 100 simulated datasets in which the missing molecular data for *Chacodelphys formosa* were replaced by random nucleotide sequences (see text). “Caluromyine” outgroups (*Glironia venusta*, *Caluromysiops irrupta*, *Caluromys lanatus*, and *C. philander*) are not shown. Labelled clades (F, I) are defined and discussed in the text.



Fig. 6. The savanna-woodland border at Linda Vista near the Riacho Pilagá, Provincia Formosa, Argentina, type locality of *Chacodelphys formosa*. Photographed by Alexander Wetmore in August 1920 (courtesy of the Smithsonian Institution Archives).

blossoming of the tree known as lapacho (*Tecoma obtusata*).

Photographs taken by Wetmore at Linda Vista (e.g., fig. 6) illustrate habitats like those found throughout the eastern Chaco (Chaco Oriental; Bucher, 1980). Although Wetmore's field journal (archived in the USNM Division of Birds) mentions that a number of small mammals were collected by trapping at Linda Vista, no additional information is provided about the habitat in which the holotype of *Chacodelphys formosa* was taken, which might have been either the savannas or the gallery forests mentioned above. Wetmore's field catalog of mammals (preserved as Smithsonian Archive Record Unit 107021 in the USNM Division of Mammals), has only the pencilled word "opossum" on the line corresponding to his field number 1081.

DISCUSSION

Creating a monotypic genus is seldom useful, but no alternative classification of Sha-

mel's species seems phylogenetically acceptable. Based on our analyses of the data at hand, *formosa* clearly does not belong in either *Marmosa* or *Gracilinanus*. Although our nonmolecular analysis (fig. 3) suggests that *formosa* could be referred to *Thylamys*, only a few character transformations can be unambiguously optimized as apomorphies of *Thylamys* in this expanded sense, which would necessarily include *Lestodelphys* as a junior synonym. A second option (based on the combined analysis; fig. 4) would be to refer *formosa* to *Monodelphis*, but with a similar cost in terms of morphological diagnosability. Given that the two analyses provide conflicting estimates of where *formosa* belongs, no assignment of it to any previously recognized genus is defensible.

Reanalyzing the data of Voss and Jansa (2003) with *Chacodelphys* included is an interesting exercise in taxon sampling. Adding taxa with many missing entries to a phylogenetic analysis often decreases resolution in

strict-consensus topologies (Kearney and Clark, 2003; Wilkinson, 2003), but including *Chacodelphys* actually improves resolution for both the nonmolecular and combined-data analyses described herein. Unfortunately, including *Chacodelphys* only slightly increases congruence between our nonmolecular and combined-data analyses (figs. 3 and 4 have ten resolved ingroup nodes in common) by comparison with those previously reported by Voss and Jansa (whose nonmolecular and combined-data consensus topologies have nine resolved ingroup nodes in common).

Both of the internal branches to which *Chacodelphys* attaches in our results are among the longest in didelphine phylogeny: in the combined-data analysis of Voss and Jansa (2003: fig. 21), the branch leading to *Thylamys* + *Lestodelphys* had a Bremer support value of 11.5, whereas the branch leading to *Monodelphis* had a Bremer support value of 18. Although long-branch attraction is alleged to be a common problem in parsimony analyses, we note that *Chacodelphys* is not a particularly long branch in either topology that we recovered, nor does it exhibit noteworthy patterns of derived similarity with didelphine clades other than *Monodelphis* and *Thylamys* + *Lestodelphys*. It is therefore reasonable to assume that its nearest relationships are with one or the other of these groups.

Whereas the combined-data supermatrix might be thought to provide a more persuasive basis for phylogenetic inference than the nonmolecular data, the results of our missing-entry replacement exercise suggest that the relationships of *Chacodelphys* resolved by the former analysis (fig. 4) may be an artifact of the uniquely compliant behavior of missing data. As originally noted by Platnick et al. (1991), analyses of data matrices that include missing entries ("?") can sometimes yield spurious results that are not supported by any observable data. In the present application of missing-entry replacement, the sister-group of *Chacodelphys* appears to be genuinely equivocal, although *Monodelphis* or some member of clade C still seem like plausible alternatives.

Despite being known only from the type locality, we suspect that *Chacodelphys* is

geographically widespread. Not only is the Chaco itself spatially extensive (occupying much of northern Argentina, western Paraguay, and eastern Bolivia), but many Chacoan vertebrates are also widely distributed in neighboring biomes (Short, 1975; Gallardo, 1979; Myers, 1982; Myers and Wetzel, 1983). Of course, *Chacodelphys* might be narrowly endemic to some particular set of ecogeographic conditions found only in northern Argentina, but alternative explanations for its apparent rarity should be considered.

Most mammalogical collectors use traps designed and baited to capture small to medium-size (ca. 20–200 g) rodents, but such equipment is not effective for taking either very small species (too light to depress trap triggers) or those unattracted to commonly used vegetable baits. *Chacodelphys* probably weighs no more than about 10 g, and its carnassialized molars suggest an almost-exclusive diet of insects and other arthropods. Plausibly, it is simply hard to capture using standard methods. Pitfall trapping, a useful technique for collecting otherwise elusive species of small marsupials and insectivorans (Raxworthy and Nussbaum, 1994; Stanley et al., 1996; Voss et al., 2001), remains underutilized in Neotropical mammal inventory work. Future applications of pitfall trapping in the Chaco, Pantanal, and Cerrado may result in more material of *Chacodelphys* and a considerable expansion of its known ecogeographic distribution.

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REFERENCES

- Bucher, E.H. 1980. Ecología de la fauna chaqueña: una revisión. *Ecosur* 7: 111–159.
- Cabrera, A. 1958 [“1957”]. Catálogo de los mamíferos de América del Sur [part 1]. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”* (Ciencias Zoológicas) 4: 1–307.
- Gallardo, J.M. 1979. Composición, distribución, y origen de la herpetofauna chaqueña. Monograph of the University of Kansas Museum of Natural History 7: 299–307.
- Gardner, A.L. 1993. Order Didelphimorphia. In D.E. Wilson and D.M. Reeder (editors), *Mammal species of the world*, 2nd ed: 15–23. Washington, DC: Smithsonian Institution Press.
- Gardner, A.L., and G.K. Creighton. 1989. A new generic name for Tate’s *microtarsus* group of South American mouse opossums (Marsupialia: Didelphidae). *Proceedings of the Biological Society of Washington* 102: 3–7.
- Hershkovitz, P. 1992. The South American gracile mouse opossums, genus *Gracilinanus* Gardner and Creighton, 1989 (Marmosidae, Marsupialia): a taxonomic review with notes on general morphology and relationships. *Fieldiana Zoology* (New Series) 39: 1–56.
- Horovitz, I. 1999. A phylogenetic study of living and fossil platyrrhines. *American Museum Novitates* 3269: 1–40.
- Jansa, S.A., and R.S. Voss. 2000. Phylogenetic studies on didelphid marsupials. I. Introduction and preliminary results from nuclear IRBP gene sequences. *Journal of Mammalian Evolution* 7: 43–77.
- Kearney, M., and J.M. Clark. 2003. Problems due to missing data in phylogenetic analyses including fossils: a critical review. *Journal of Vertebrate Paleontology* 23: 263–274.
- Kirsch, J.A.W., and J.H. Calaby. 1977. The species of living marsupials: an annotated list. In B. Stonehouse and G. Gilmore (editors), *The biology of marsupials*: 9–26. Baltimore MD: University Park Press.
- Maddison, D.R., and W.P. Maddison. 2001. *MacClade 4: Analysis of phylogeny and character evolution* [version 4.02]. Sunderland, MA: Sinauer Associates.
- Miranda-Ribeiro, A. de. 1936. Didelphia ou Mammalia-Ovovivipara. *Revista do Museu Paulista* 20: 245–424.
- Myers, P. 1982. Origins and affinities of the mammal fauna of Paraguay. In M.A. Mares and H.H. Genoways (editors), *Mammalian biology in South America*: 85–93. Pittsburgh PA: Pyramtuning Laboratory of Ecology (Special Publication Series, vol. 6).
- Myers, P., and R.M. Wetzel. 1983. Systematics and zoogeography of the bats of the Chaco Boreal. University of Michigan Museum of Zoology Miscellaneous Publication 165: I–iv, 1–59.
- Norell, M.A., and W.C. Wheeler. 2003. Missing entry replacement data analysis: a replacement approach to dealing with missing data in paleontological and total evidence data sets. *Journal of Vertebrate Paleontology* 23: 275–283.
- Paynter, R.A., Jr. 1995. *Ornithological gazetteer of Argentina*, 2nd ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).
- Pine, R.H. 1975. A new species of *Monodelphis* (Mammalia: Marsupialia: Didelphidae) from Bolivia. *Mammalia* 39: 320–322.
- Platnick, N.I., C.E. Griswold, and J.A. Coddington. 1991. On missing entries in cladistic analysis. *Cladistics* 7: 337–343.
- Raxworthy, C.J., and R.A. Nussbaum. 1994. A rainforest survey of amphibians, reptiles, and small mammals at Montagne d’Ambre, Madagascar. *Biological Conservation* 69: 65–73.
- Reig, O.A., J.A.W. Kirsch, and L.G. Marshall. 1985. New conclusions on the relationships of the opossum-like marsupials, with an annotated classification of the Didelphimorphia. *Ameghiniana* 21: 335–343.
- Shamel, H.H. 1930a. A new murine opossum from Argentina. *Journal of the Washington Academy of Sciences* 20: 83–84.
- Shamel, H.H. 1930b. A new name for *Marmosa muscula* Shamel. *Journal of Mammalogy* 11: 311.
- Short, L.L. 1975. A zoogeographic analysis of the South American Chaco avifauna. *Bulletin of the American Museum of Natural History* 154: 163–352.
- Stanley, W.T., S.M. Goodman, and R. Hutterer. 1996. Notes on the insectivores and elephant shrews of the Chome Forest, South Pare Mountains, Tanzania (Mammalia: Insectivora et Macroscelidea). *Zoologische Abhandlungen Staatliches Museum für Tierkunde Dresden* 49: 131–148.
- Tate, G.H.H. 1933. A systematic revision of the marsupial genus *Marmosa* with a discussion of the adaptive radiation of the murine opossums (*Marmosa*). *Bulletin of the American Museum of Natural History* 66: 1–250 + 26 pls., folded tables in pocket.
- Voss, R.S., and S.A. Jansa. 2003. Phylogenetic studies on didelphid marsupials. II. Nonmolecular data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. *Bulletin of*

- the American Museum of Natural History 276: 1–82.
- Voss, R.S., D.P. Lunde, and N.B. Simmons. 2001. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna. Part 2. Nonvolant species. Bulletin of the American Museum of Natural History 263: 1–236.
- Wetmore, A. 1926. Observations on the birds of Argentina, Paraguay, Uruguay, and Chile. Bulletin of the United States National Museum 133: I–iv, 1–448.
- Wilkinson, M. 2003. Missing entries and multiple trees: instability, relationships, and support in parsimony analysis. Journal of Vertebrate Paleontology 23: 311–323.

APPENDIX 1

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

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 microtarsus: 00100 10001 0??20
00–10 20001 00010 00000 02211 01011 00000
00001 11210 000?0 00000 0

Lestodelphys halli: 10100 16000 10000 10–10
20000? 0100 00000 01210 11011 01000 00002
11211 00211 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 00010 00????

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

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

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

Marmosa rubra? 0100 00001 01120 00–0?
20201 00010 00000 00200 01010 01000 00001
11210 00010 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 00010 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 00010 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 pallidior: 10100 16000 10020 1??0
20001 00100 00100 02210 11011 01000 00002
11211 00110 00000 0

Thylamys venustus: 00100 16000 10020 1??0
20001 00100 00100 02211 11011 01000 00002
11211 00110 00000 0

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