

Phylogenetic affinities of the late Miocene echimyid †*Pampamys* and the age of *Thrichomys* (Rodentia, Hystricognathi)

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Phylogenetic affinities of the late Miocene echimyid †*Pampamys emmonsae* Verzi, Vucetich, and Montalvo, 1995 (Huayquerian South American Land Mammal Age, central Argentina), were analyzed. In the most-parsimonious tree obtained, subfamilies of Echimyidae were nonmonophyletic (except for Dactylomyiinae). Two major clades were recovered. One of them included the living fossorial Eumysopinae and the extinct †*Theridomysops*. The other clade grouped the terrestrial eumysopines *Thrichomys* (punaré) and *Proechimys-Trinomys* (spiny rats), and the arboreal eumysopines *Mesomys* (spiny tree-rats) + Echimyinae–Dactylomyiinae. †*Pampamys* was the sister genus of *Thrichomys*, suggesting the Huayquerian South American Land Mammal Age (>6.0 million years ago [mya] by biochronology) as a minimum age for the origin of the living genus. Both major echimyid clades recognized here are represented by simplified-molared species in the Huayquerian South American Land Mammal Age. This would be related to the expansion of open environments during the late Miocene, and the geographical bias of the fossiliferous Huayquerian deposits exposed mostly in southern South America.

Key words: caviomorph, Echimyidae, late Miocene, phylogeny, South America

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DOI: 10.1644/11-MAMM-A-176.1

Echimyidae is the most diverse family among the living New World hystricognath rodents (caviomorphs [Reig 1989: figure 1]). South American species belonging to Echimyidae are classified within 3 subfamilies: the arboreal Echimyinae and Dactylomyiinae, and the terrestrial and fossorial Eumysopinae (Emmons and Feer 1997; Galewski et al. 2005; Woods and Kilpatrick 2005). The semiaquatic *Myocastor coypus* (coypu) is included as a subfamily, Myocastorinae, in some classifications (McKenna and Bell 1997; Patterson and Pascual 1968). This taxonomic framework is unstable and has been debated in recent studies (Carvalho and Salles 2004; Emmons 2005; Galewski et al. 2005; Lara et al. 1996; Leite and Patton 2002).

Eumysopinae are 1st recorded in the late Miocene Huayquerian South American Land Mammal Age of Argentina and Brazil (Sant'Anna 1994; Verzi et al. 1994, 1995; Vucetich and Verzi 1996). The species recorded in this age show molars with reduced number of crests, and have been interpreted as members of a natural group of eumysopines

together with the living *Thrichomys* (punaré), *Clyomys* (broad-headed spiny rat), and *Euryzygomatomys* (guiara—Verzi et al. 1995). As part of this proposal, the species †*Pampamys emmonsae*, from the late Miocene of central Argentina, was interpreted as potentially ancestral to *Thrichomys* or alternatively to *Clyomys* and *Euryzygomatomys*. These living eumysopines currently inhabit open environments in north-eastern, central, and southeastern Brazil, eastern Paraguay, and, marginally, southeastern Bolivia (*Thrichomys*) and northeastern Argentina (*Euryzygomatomys*—Bezerra and Oliveira 2010; Eisenberg and Redford 1999; Oliveira and Bonvicino 2006).

The morphology of †*Pampamys* was known so far through mandibular fragments and lower dental series. The finding of skull remains, as well as new mandibular fragments, yields



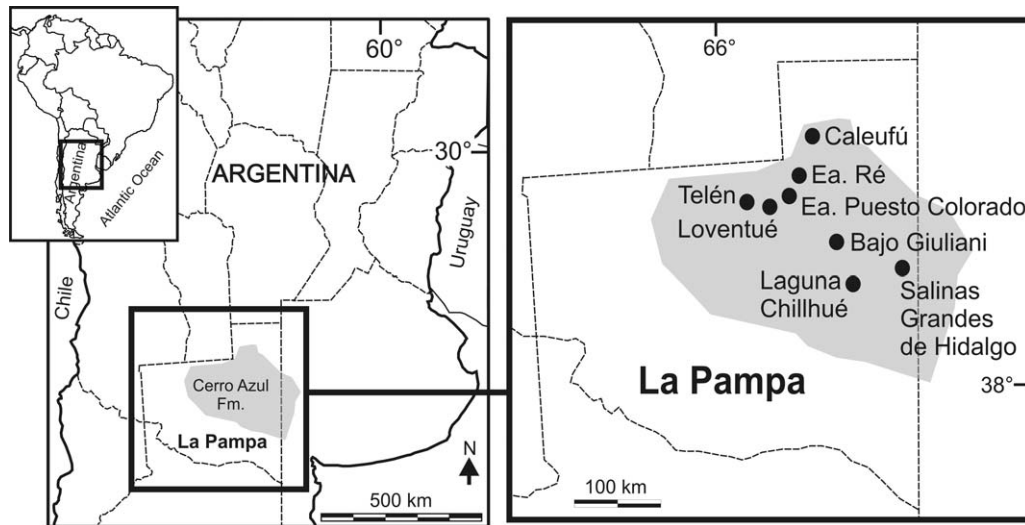


FIG. 1.—Location map of fossil-bearing deposits (gray) of the Cerro Azul Formation (Huayquerian South American Land Mammal Age, late Miocene, central Argentina). The †*Pampamys*-bearing localities are indicated with solid circles.

additional information to help understand the affinities of this echimyid. In this paper, the features of the new rostral and palatal remains are briefly described, and the contribution of this fossil echimyid to the interpretation of the evolution of living species is assessed through the analysis of its phylogenetic relationships.

MATERIALS AND METHODS

New materials of †*P. emmonsae* consist of 9 rostral and palatal remains and 22 hemimandible fragments from 8 localities of the Cerro Azul Formation (Huayquerian South American Land Mammal Age, late Miocene, La Pampa Province, central Argentina; Fig. 1). †*Pampamys* was included in the phylogenetic analysis together with the other 13 genera of Echimyidae, including 7 of the 9 genera of living Eumysopinae (Appendix I). Trees were rooted on the octodontid *Octodontomys* (mountain degu), according to the assumption that Octodontidae is the sister taxon of Echimyidae (Cook and Lessa 1998; Galewski et al. 2005; Reig 1986; Vilela et al. 2009; Winge 1941). In addition, *Octodontomys* has been interpreted as retaining several plesiomorphic characters among living octodontids (Verzi 2001). The matrix consisted of 15 taxa by 46 craniomandibular and dental characters (Appendices II and III). The software TNT 1.1 (Goloboff et al. 2008a, 2008b) was used to find the most-parsimonious trees and evaluate the level of support for branches. All characters were considered equally weighted and multistate characters were coded as nonadditive. Nomenclature of craniomandibular traits (Fig. 2) follows Grassé (1967), Lavocat (1971, 1976), Moore (1981), Novacek (1993), Verzi (1994, 2001), and Wahlert (1984). Dental nomenclature (Fig. 3) follows the proposal of Candela (2002) and Marivaux et al. (2004). Studied specimens of extinct and living octodontoids belong to the mammalogical and paleontological collections of the following institutions (Appendix I): Cátedra de Geología Histórica, Facultad de Ciencias Exactas y

Naturales, Universidad Nacional de La Pampa, Santa Rosa, Argentina (GHUNLPam); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina (MACN); Museo de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia,” Mar del Plata, Argentina (MMP); Museo de La Plata, La Plata, Argentina (MLP); Museu de Zoologia, Universidade Federal de Bahia, Bahia, Brazil (UFBA); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MN-UFRJ); Museum of Vertebrate Zoology, University of California, Berkeley, California (MVZ); Universidade de Brasília, Brasília, Brazil (UnB). In addition, unpublished photographs of *Carterodon sulcidens* (owl’s spiny rat) from the P. W. Lund mammal collection (Zoological Museum, Natural History Museum of Denmark, University of Copenhagen) were reviewed.

RESULTS

Order Rodentia Bowdich, 1821
 Suborder Hystricomorpha Brandt, 1855
 Infraorder Hystricognathi Brandt, 1855
 Superfamily Octodontoidea Waterhouse, 1839
 Family Echimyidae Gray, 1825
 Subfamily Eumysopinae Rusconi, 1935
 †*Pampamys emmonsae* Verzi, Vucetich and Montalvo, 1995
 Figs. 2–4; Table 1

Material

Holotype and hypodigm (Verzi et al. 1995:192), and GHUNLPam 2229, left hemimandible with m2; GHUNLPam 5021, palatal fragment with right M1–3; GHUNLPam 5078, rostrum and palatal fragment with both incisors and left DP4–M3; GHUNLPam 5083, palatal fragment with right M1–3 and anterior portion of left M2; GHUNLPam 5235, left hemimandible with Dp4; GHUNLPam 5244, palatal portion with

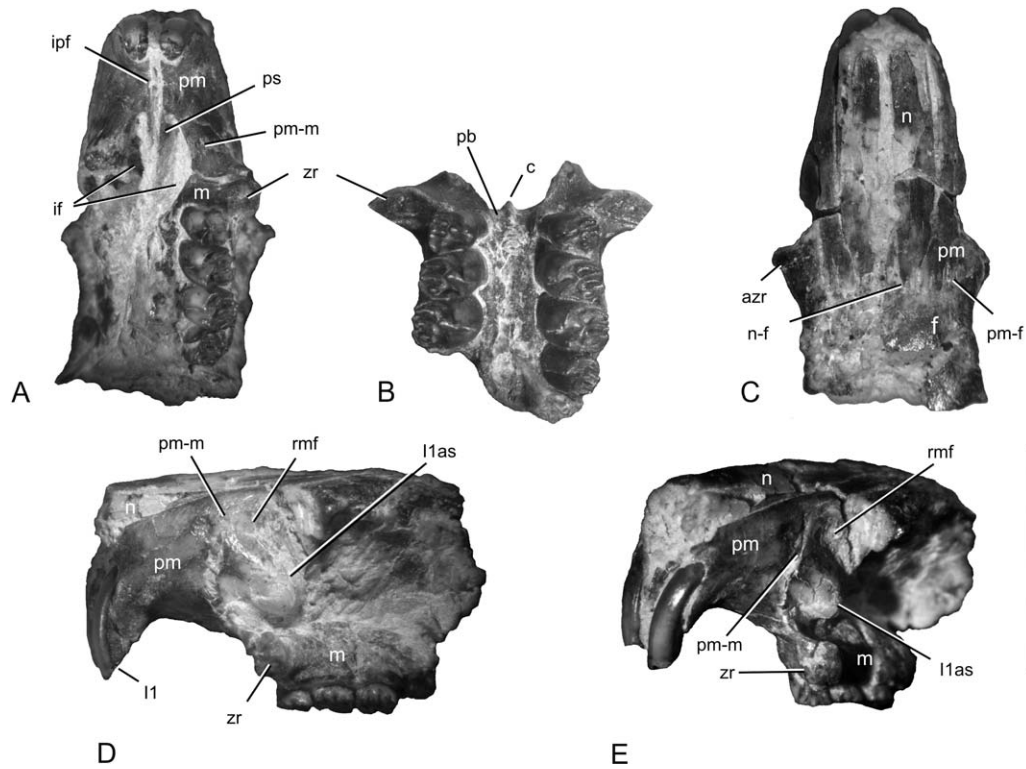


FIG. 2.—Skull morphology of †*Pampamys emmonsae*. A, C, D, and E) Ventral, dorsal, lateral, and anterolateral view, respectively, of GHUNLPam 5078; B) ventral view of GHUNLPam 5244. Abbreviations: azr, root of the antorbital zygomatic ramus; c, crest of palatal bridge; if, incisive foramina; ipf, interpremaxillary foramen; I1, upper incisive; I1as, alveolar sheath of upper incisive; f, frontal; m, maxillary; n, nasal; n-f, nasal–frontal suture; pb, anterior portion of palatal bridge; pm, premaxillary; pm-f, premaxillary–frontal suture; pm-m, premaxillary–maxillary suture; ps, premaxillary septum; rmf, rostral masseteric fossa; zr, anterior zygomatic root. Scale = 5 mm.

right DP4–M2 and left DP4–M3 and anterior portion of zygomatic root of both sides; GHUNLPam 5316, left hemimandible with m1–3; GHUNLPam 5318, Dp4 and anterior portion of m1; GHUNLPam 5455, right hemimandible with m1–2 and i1; GHUNLPam 5456, palatal fragment with right DP4–M2; GHUNLPam 5967, right hemimandible

with m1–3; GHUNLPam 6637, left hemimandible with m1–2; GHUNLPam 8557, left hemimandible with Dp4–m2; GHUNLPam 8558, right hemimandible with a portion of Dp4, and m1–3; GHUNLPam 8571, palatal fragment with anterior portion of zygomatic root and DP4–M1; GHUNLPam 8977, right hemimandible with Dp4–m1; GHUNLPam 9187, right hemimandible with Dp4–m3; GHUNLPam 9188, left hemimandible with Dp4–m3; GHUNLPam 9620, right hemimandible with Dp4–m1; GHUNLPam 9621, right hemimandible with Dp4–m1; GHUNLPam 9927, right hemimandible with Dp4–m2; GHUNLPam 12883, left hemimandible with Dp4–m1; GHUNLPam 14126, left hemimandible with Dp4–m2; GHUNLPam 14128, palatal fragment with left M1–3; GHUNLPam 14421, left hemimandible with Dp4–m1; GHUNLPam 14423, right hemimandible with m1; GHUNLPam 14992, left hemimandible with Dp4–m2; GHUNLPam 14331, right hemimandible with Dp4–m3; GHUNLPam 19606, right hemimandible with m1; GHUNLPam 22585, left hemimandible with m1–2; GHUNLPam 22586, right maxilla with DP4–M3; MLP 65-VII-29-88, palatal fragment with left and right DP4–M2.

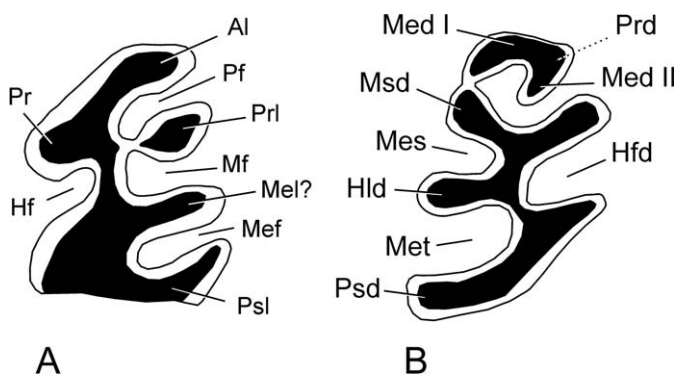


FIG. 3.—Nomenclature for upper and lower teeth of †*Pampamys emmonsae* (following Candela [2002] and Marivaux et al. [2004]). A) DP4 of GHUNLPam 5078; B) Dp4 of GHUNLPam 2344. Abbreviations: Al, anteroloph; Hf, hypoflexus; Hfd, hypoflexid; Hld, hypolophid; Med I, metalophulid I; Med II, metalophulid II; Mef, metaflexus; Mel, metaloph; Mes, mesoflexid; Met, metaflexid; Mf, mesoflexus; Msd, mesolophid; Pf, paraflexus; Pr, protocone area; Prd, protoconid; Prl, protoloph; Psd, posterolophid; Psl, posteroloph.

Stratigraphic and Geographic Provenance

Cerro Azul Formation, Huayquerian South American Land Mammal Age (late Miocene), La Pampa Province (central Argentina). Laguna Chillhué (Zone of *Chasichimys scagliai*;

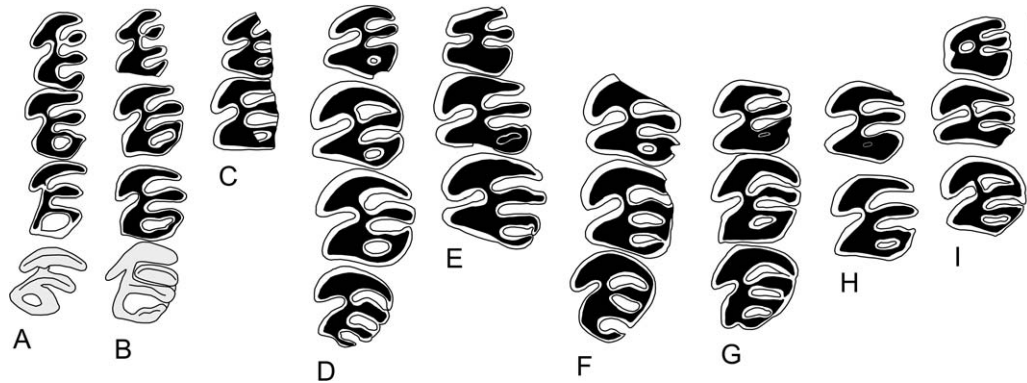


FIG. 4.—Occlusal morphology of left DP4–M3 of †*Pampamys emmonsae*. A) GHUNLPam 22586, inverted; B) GHUNLPam 5078; C) GHUNLPam 8571; D) GHUNLPam 5244; E) GHUNLPam 5456, inverted; F) GHUNLPam 14128; G) GHUNLPam 5021, inverted; H) GHUNLPam 5083, inverted; I) MLP 65-VII-29-88, inverted. Scale = 1 mm.

GHUNLPam 2229, 5078, 5083, 5235, 5244, 5316, 5318, 5455, 2 5456, 8557, 8558, 8571, 8977, 14423, 14992); Bajo Giuliani (Zone of *Chasichimys* morphotype a; GHUNLPam 5021, 5967), Caleufú (Zone of *Xenodontomys elongatus*; GHUNLPam 19606); Estancia Puesto Colorado (GHUNLPam 6637, 14126, 14128); Estancia Ré (GHUNLPam 22585, 22586); Loventué (GHUNLPam 9187, 9188); Salinas Grandes de Hidalgo (GHUNLPam 14331, MLP 65-VII-29-88); Telén (GHUNLPam 9620, 9621, 9927, 12883)—Fig. 1; Verzi et al. 2008).

Extended Diagnosis

Smaller than *Thrichomys*. Rostrum short and wide; width of incisive foramina nearly 50% of rostrum width. Anterior portion of palatal bridge forming a vertical wall at level of alveolar margins of DP4. Anterior zygomatic root with its anterior margin markedly convex and slightly ahead of the DP4; this root is anteroposteriorly broader than that of *Thrichomys* and narrower than those of *Clyomys* and *Euryzygomatomys*. Nasals and premaxillaries extending posteriorly up to level of root of antorbital zygomatic ramus. Rostral masseteric fossa short, posterior to premaxillary–

maxillary suture. Lateral flange for infraorbital nerve absent. Cheek teeth enamel proportionally thinner than in *Thrichomys*. Upper cheek teeth tetralophodont and unilaterally hypsodont. Protoloph with lingual end markedly narrowed in juveniles. Mandibular masseteric crest very bowed. Anterior end of lower diastema level with or slightly below occlusal plane of cheek teeth. Anterior wall of Dp4 alveolus without a marked step. Dp4 tetralophodont and with metalophulid II forming a spur larger than that of *Clyomys* and *Euryzygomatomys*. The most anterior flexid open both labially and lingually in juveniles, with the labial opening more persistent. Lower molars tetralophodont, with metaflexid more persistent than mesoflexid.

Description

Skull.—The rostrum is partially preserved in GHUNLPam 5078 (Fig. 2); it is wider and shorter than in the living echimyids *Thrichomys*, *Clyomys laticeps*, and *Euryzygomatomys spinosus*. The interpremaxillary foramen is small (Fig. 2A). The incisive foramina are wide, approximately half the rostrum width, as in *Thrichomys*. The premaxillary–maxillary suture is close to the anterior end of the incisive foramina. The premaxillary septum is moderately wide and narrows gradually backward as in *Thrichomys laurentius* (see Neves and Pessôa [2011]: Fig. 4A); in *E. spinosus* and *C. laticeps*, the anterior portion is markedly wider. The septum is not visible in lateral view because it is hidden inside the incisive foramina as in *Thrichomys*. The anterior portion of the palatal bridge forms a vertical plate with a medial crest, located at the level of the anterior edge of DP4 (Fig. 2B). This plate is more vertical than in *Thrichomys*.

Nasals and premaxillaries extend more posteriorly than in *Thrichomys*, *C. laticeps*, and *E. spinosus*, behind the level of the root of the antorbital zygomatic ramus (Fig. 2C). The lateral margins of the nasals are straight as in *Thrichomys*. The rostral masseteric fossa (for the origin of the infraorbital part of the medial masseter muscle [Woods and Howland 1979]) is short as in *Thrichomys*; it is posterior to the premaxillary–maxillary suture and dorsal to the incisive alveolus (Fig. 2D).

TABLE 1.—Measurements (in mm) of upper molars of †*Pampamys emmonsae*; anterior–posterior length (AP), transversal width (TW); right series except where indicated by an asterisk (*). Museum acronyms are as defined in the “Materials and Methods.”

	GHUNLPam								MLP
	5021	5078*	5083	5244*	5456	8571*	14128*	22586	65-VII-29-88
DP4 AP	—	1.66	—	1.83	1.66	1.41	—	1.71	1.48
DP4 TW	—	1.24	—	1.58	1.58	1.16	—	1.25	1.54
M1 AP	1.74	1.74	1.83	1.99	1.74	1.66	1.83	1.54	1.60
M1 TW	1.74	1.41	1.83	2.07	2.07	1.49	—	1.25	1.94
M2 AP	2.16	1.83	2.07	2.24	2.24	—	1.99	1.71	1.88
M2 TW	2.07	1.66	1.91	2.24	2.32	—	2.16	1.25	1.94
M3 AP	2.07	1.74	—	1.91	—	—	2.16	1.48	—
M3 TW	1.99	1.41	—	1.91	—	—	2.07	1.43	—
DP4–M3	—	6.89	—	7.64	—	—	—	6.78	—

The anterior zygomatic root is anteroposteriorly broader than that of *Thrichomys* and narrower than those of *Clyomys* and *Euryzygomatomys*. Its anterior margin is markedly convex. It is more posterior than in *Thrichomys*, *C. laticeps*, and *E. spinosus*, level with DP4. There is no lateral flange for the infraorbital nerve (Fig. 2E); this flange shows different degrees of development in *Thrichomys*, *C. laticeps*, *E. spinosus*, and *Proechimys* (spiny rats).

Upper teeth.—The upper incisor is narrow, with short bevel; in lateral view, its base markedly protrudes in the rostrum dorsally to the DP4 (Fig. 2D); in *Thrichomys* this protrusion is more anterior and less marked.

The upper cheek teeth are tetralophodont, with unilateral hypsodonty. DP4 is the smallest molariform, whereas M2 is the largest. The M3 is narrower posteriorly than anteriorly. In M1–3 the protocone area is wider than in *Thrichomys*, *C. laticeps*, and *E. spinosus*. Lophes are long in adults. In juveniles the protoloph has a marked constriction on the lingual end (Figs. 3, 4A, and 4B). In *Thrichomys* this constriction is less marked; in the late Miocene †*Theridomysops parvulus*, and especially in *C. laticeps* and *E. spinosus*, the protoloph is reduced to a labial tubercle that joins the anteroloph in adults (Montalvo et al. 1998; Vucetich 1995). As a result, in adults of *C. laticeps* and *E. spinosus*, the 2nd loph is the mesoloph, not the protoloph as in *Thrichomys* and †*Pampamys* (Fig. 3). The bottom of the hypoflexus is oriented toward the bottom of the paraflexus. The mesoflexus is the most persistent flexus, whereas the metaflexus is the most ephemeral. The latter, or its corresponding fossette, is comparatively more persistent than in *Thrichomys* (Fig. 4; Neves and Pessôa 2011). The DP4 of GHUNLPam 5456 (Fig. 4E) and MLP 65-VII-29-88 (Fig. 4I), and the M1 of this latter and GHUNLPam 5083 (Fig. 4H) lack the metafossette, resulting in a trilophodont morphology with the 3rd loph wider anteroposteriorly than in *Thrichomys*.

Remarks

Vucetich and Verzi (1996) reported aff. *Thrichomys* from the Huayquerian South American Land Mammal Age of the Cerro Azul Formation on the basis of a palatal fragment (MLP 65-VII-29-88, Fig. 4I, collection number not mentioned by the authors) here assigned to †*Pampamys*. We support the assignment of the skull remains described here to †*P. emmonsae* based on a comparison with an ontogenetic series of the closely related *Thrichomys* (Verzi et al. 1995, 1999). The skull and mandibular remains assigned to †*P. emmonsae* show close correspondence in size and dental morphology to each other, analogous to that seen in the living genus (cf. Table 1 and Figs. 3 and 4 with Neves and Pessôa [2011], Petter [1973:figure 2], and Verzi et al. [1995:table 1; plate 2]). Although no associated remains have been found, the skull materials come from localities in which mandibular remains of this species have been found. In addition, no other rodent skull or upper teeth exhumed from these localities match these mandibles.

Phylogenetic Analysis

One most-parsimonious tree of 71 steps (consistency index = 0.746, retention index = 0.877) was found using the implicit enumeration search option. Bremer support (Bremer 1994) and relative Bremer support values for the nodes are given in Fig. 5.

Two major clades were recovered. One of them, including the living fossorial *Carterodon*, *Clyomys*, and *Euryzygomatomys* and the extinct †*Theridomysops*, was supported by 5 nonambiguous synapomorphies. The late Miocene †*Theridomysops* and *Euryzygomatomys*–*Clyomys* shared the morphology of the protoloph of M1–2, which is reduced forming a labial tubercle isolated or fused to the anteroloph (character-state 45 [1]). The other clade included the remaining species analyzed. The basal node of this clade was supported by 2 nonambiguous synapomorphies: lack of a crest in the maxillary septum (character-state 3 [1]), and the lateral palatine plate low and posteriorly extended (character-state 30 [1]). *Proechimys*–*Trinomys* (spiny rats) and *Mesomys* (spiny tree-rat) were clustered with species traditionally included in the subfamilies Echimyinae and Dactylomyinae (Woods and Kilpatrick 2005). This clade was supported by having a laterally oriented inferior margin of the posterior process of the squamosal (character-state 36 [1]), and a vertical postcondyloid process (character-state 40 [1]). The grouping †*Pampamys*–*Thrichomys* was strongly supported (Fig. 5). These 2 genera shared wide incisive foramina (character-state 8 [1]), the posterior margin of incisive foramina level with the anterior margin of the DP4 (character-state 9 [1]), and the notch for the tendon of the medial masseter muscle incorporated into the origin of the masseteric crest and scarcely evident (character-state 42 [1]).

DISCUSSION

Echimyids are morphologically conservative caviomorphs (Reig 1986). This has hindered the understanding of their systematic relationships; thus, the traditional subfamilial groupings have not, or have only partially, been recovered in phylogenetic analyses (Carvalho and Salles 2004; Emmons 2005; Galewski et al. 2005; Leite and Patton 2002). Our results, based on morphological characters, produced similar results. In line with previous morphological (Emmons 2005) and molecular (Galewski et al. 2005) phylogenies, 2 major clades were recovered. One of them included the living fossorial eumysopines (tribe Euryzygomatomyini of Emmons [2005]) and †*Theridomysops* (Montalvo et al. 1998; Vucetich 1995), and the other clustered the terrestrial eumysopines *Thrichomys*–†*Pampamys* and *Proechimys*–*Trinomys* with arboreal echimyines–dactylomyines. Thus, neither the traditional subfamily Eumysopinae (Woods and Kilpatrick 2005) nor the more restricted grouping of eumysopines with simplified molars proposed by Verzi et al. (1995; see also Carvalho and Salles 2004) were monophyletic in this analysis, as also shown in previous analyses (Emmons 2005; Galewski et al. 2005; Leite and Patton 2002). The reduction in the number of crests in these latter simplified-molared species would have followed at least 2 independent evolutionary pathways of change.

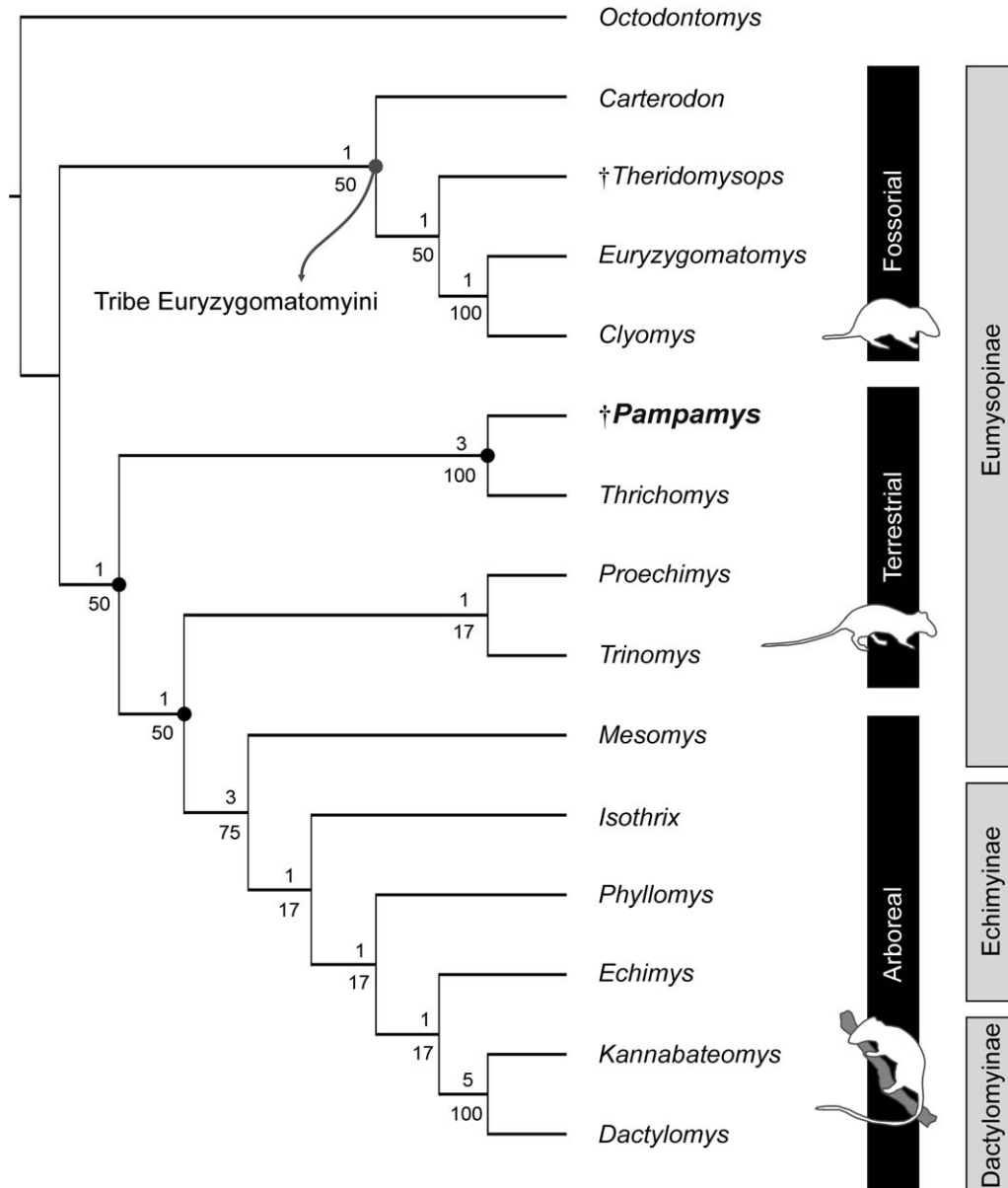


FIG. 5.—Most-parsimonious tree (length = 71 steps, consistency index = 0.746, retention index = 0.877) for the 14 genera of Echimyidae analyzed. Bremer support and relative Bremer support values are shown above and below the nodes, respectively.

In the original description based on mandibular remains, Verzi et al. (1995) pointed out that †*Pampamys* could be related to the differentiation of the living *Thrichomys*, or alternatively to *Clyomys* and *Euryzygomatomys*. According to the phylogenetic results reported here, †*Pampamys* is the sister taxon of *Thrichomys*; moreover, the analyzed characters do not contradict a relationship of direct ancestry with the living genus (Verzi et al. 1999). Beyond the latter, we consider †*Pampamys* as the sister genus of *Thrichomys*, and consequently its oldest record in Laguna Chillhué (Zone of *Chasichimys scagliai*, late Huayquerian, >6.0 million years ago [mya] by biochronology [Deschamps et al. 2009; Verzi et al. 2008]) would provide a minimum age (Benton and Donoghue 2007) for the origin of the *Thrichomys* lineage. Pascual (1967; Reig 1989) extended the biochron of *Thrichomys* up to the lower late

Miocene (approximately 9.0 mya by radiometric dates) based on a Chasicoan species of “*Cercomys*” (a nonvalid senior synonym of *Thrichomys* [see Petter 1973]) that was later reassigned to the family Octodontidae (Verzi 2002; Verzi and Arnal 2007; Vucetich et al., in press).

In the Huayquerian South American Land Mammal Age, echimyids are represented by species with simplified molars related to terrestrial and fossorial living taxa (Marshall and Sempere 1991; Verzi et al. 1994, 1995; Vucetich and Verzi 1996). Although dental similarities among these echimyids have been previously interpreted as synapomorphics (Verzi et al. 1995), the results of this analysis suggest that these most likely represent independently acquired adaptations. Simplification of molar occlusal morphology occurs among unrelated rodents that inhabit open areas (Moojen 1948; Rocha 1995;

Schmidt-Kittler 1984; Verzi et al. 2004). The Huayquerian record of simplified-molared species belonging to the 2 major clades of Echimyidae would be related with the expansion of open environments during the late Miocene (Ortiz Jaureguizar and Cladera 2006 and literature therein), as well as with the geographical bias of the fossiliferous deposits, mostly exposed in southern South America (Verzi and Montalvo 2008). Moreover, the absence or scarcity in this record of species related to echimyid clades that are currently diversified in forested habitats of northern South America (Emmons 2005; Emmons and Feer 1997; Lara and Patton 2000) also could be due to these same causes (Verzi et al. 1995).

RESUMEN

Se describen nuevos restos craneanos y se analizan las afinidades filogenéticas del equímido †*Pampamys emmonsae* Verzi, Vucetich, and Montalvo, 1995 (Mioceno tardío, Argentina central). En la filogenia obtenida, las subfamilias de Echimyidae resultaron no monofiléticas (a excepción de Dactylomyinae). Se recuperaron dos clados principales; uno de ellos resultó integrado por los Eumysopinae fosoriales *Carterodon*–*Clyomys*–*Euryzygomatomys* y el extinto †*Theridomysops*; el restante por los Eumysopinae terrestres *Thrichomys* y *Proechimys*–*Trinomys* junto a los arborícolas *Mesomys* + Echimyinae–Dactylomyinae. †*Pampamys* se ubicó como género hermano de *Thrichomys*, lo que sugiere el Huayqueriense tardío (>6.0 millones de años por biocronología) como edad mínima para el origen del género viviente. En el Huayqueriense, los 2 clados de equímidos aquí reconocidos están representados por especies con molares simplificados. Este registro, y la ausencia de taxones actualmente diversificados en hábitats forestados del norte de América del Sur, serían consecuencia de la expansión de ambientes abiertos en el Mioceno tardío y la distribución esencialmente austral de los yacimientos portadores.

ACKNOWLEDGMENTS

We thank E. Lacey, J. Patton, C. Conroy, J. Oliveira, W. Kliem, A. Dondas, E. Tonni, M. Reguero, A. Kramarz, D. Romero, D. Flores, and T. Hatting for granting access to materials under their care. We are especially grateful to E. Lacey, J. L. Patton, J. Oliveira, P. Rocha, and A. Bezerra for generously and actively facilitating access to materials. Photographs of the Lund specimen of *Carterodon* were kindly taken by G. Brovad. We thank 2 anonymous reviewers for their valuable suggestions that helped us improve the manuscript. Access to the software TNT was available thanks to the sponsorship of the Willi Hennig Society. C. M. Deschamps and C. C. Morgan assisted with translation. This paper is a contribution to ANPCyT PICT 2007-01744, CONICET PIP 0270, and FCEyN Universidad Nacional de La Pampa 209 projects.

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- acquire, late Miocene, Telén, La Pampa Province, Argentina (GHUNLPam 9473); Huayqueriense, late Miocene, Loventhue, La Pampa Province, Argentina (GHUNLPam 14772). *Clyomys laticeps*: Parque Estadual Serra de Caldas Novas, Brazil (UnB 2077 and 2079); Brazil (MN-UFRJ 63851, 63853, and 68967). *Dactylomys dactylinus*: Echarte, Convención, Cusco, Peru (MLP 8.V.95.6) and Colocação Vira-Volta, left bank Juruá River on Igarapé Arabidi, Brazil (MVZ 190620); Juruá River on Igarapé Arabidi, Brazil (MVZ 190620). *Echimys* sp.: Ecuador (MACN 31.160, 31.161, and 3.28). *Euryzygomatomys spinosus*: Cuñá Pirú, Aristóbulo del Valle, General San Martín, Misiones, Argentina (MLP 16.VII.02.11) and Misiones, Argentina (MACN 18103). *Isothrix bistrata*: Opposite Altamira, left bank Juruá River, Amazonas, Brazil (MVZ 190629); Brazil (MLP 1447). *Kannabateomys* sp.: Misiones, Argentina (MACN 15457 and 49359). *Mesomys hispidus*: Nova vida, right bank Juruá River, Acre, Brazil (MVZ 190653). *Phyllomys pattoni*: Fazenda Sao Jose da Serra, Bonsucesso, Sumidouro, Rio de Janeiro, Brazil (MVZ 183139). *Proechimys brevicauda*: Huampami, Cenepa River, Amazonas, Peru (MVZ 153623). *Proechimys poliopus*: Zulia, Sierra de Parijá, El Tokuko, Venezuela (MLP 22.II.00.8 and 22.II.00.7). *Proechimys roberti*: Parque Nacional de Brasília, Brazil (UnB 316 and 326); Reserva Ecológica Cristalino, 40 km N Alta Floresta, Mato Grosso, Brazil (MVZ 197578). *Thrichomys* (Neves and Pessôa 2011): Palmeiras, Brazil (MMP 1242–1245); Pernambuco, Brazil (MMP 1246); Brazil (MMP 1247 and 1292); Pacoti, Fortaleza, Brazil (MMP 1293 and 1297); Baturite, Fortaleza, Brazil (MMP 1294); Santana do Ipanema, Brazil (MMP 1295 and 1296); unknown locality (MMP 150-USB 542); 7 km south east Cristalina, Brazil (UnB 188–190); Bela Vista, Mato Grosso do Sul, Brazil (MN-UFRJ 46896); Jaborandi, Bahia, Brazil (MN-UFRJ 616599); Brazil (MN-UFRJ 34406). *Trinomys dimidiatus*: Parque Nacional da Serra dos Órgãos (UnB 723 and 739); Parnaioaca, Iiha Grande, Angra dos Reis, Rio de Janeiro, Brazil (MN-UFRJ 62273, 62275, and 62278). *Trinomys yonenagae*: Ibiraba, Barra, Bahia, Brazil (UFBA 00467–00473). *Octodontomys gliroides*: Route between Uquía and Calpalá, Jujuy, Argentina (MLP 25.XI.98.1 and 25.XI.98.2); Pucará de Tilcara, Jujuy, Argentina (MLP 12.VII.88.10, MACN 17832–17837, MMP 755, 2200, 2532, 3057, and 3557); Maimará, Jujuy, Argentina (MACN 27.92–27.94, 27.96, and 31.39); Sierra de Zenta, Jujuy, Argentina (32.15, 32.16, and 32.59); Pucapampa, Jujuy, Argentina (MACN 49.101); Cochinota, Jujuy, Argentina (MLP 11.XII.35.19); San Antonio de Los Cobres, Salta, Argentina (MACN 30.51, 30.52, 30.54 and 30.55); Chorrillos, Salta, Argentina (MACN 30.112).

APPENDIX II

Description of characters used in the phylogenetic analysis.

Character 1.—Anterior ends of the incisive foramina: (0) separated by a wide root of the premaxillary septum; (1) very close or joined, root of premaxillary septum narrow.

Character 2.—Premaxillary septum (Emmons 2005; Patton 1987): (0) not joined to the anterior portion of the palatal bridge, or slightly joined by a plate of the premaxillary or vomer; (1) broadly fused, developing a wide suture.

Character 3.—Crest in the root of the premaxillary septum: (0) present; (1) absent.

Character 4.—Premaxillary septum: (0) subhorizontal, level with margins of incisive foramina; (1) posterodorsally oriented, dorsal to the margins of incisive foramina.

Character 5.—Palatal bridge (Olivares 2009): (0) dorsal to the alveolar margin of molars, the lateral margins of the alveoli are acute;

Submitted 6 May 2011. Accepted 15 August 2011.

Associated Editor was Elizabeth R. Dumont.

APPENDIX I

List of taxa and specimens examined (other than †*Pampamys emmonsae*). Institutional acronyms are as in the “Materials and Methods.”

†*Theridomysops parvulus*: Araucanense, late Miocene, Andahualá, Catamarca Province, Argentina (MACN 8380); Huayquer-

(1) slightly ventral to the alveolar margin of molars, lateral margins are wide to moderately convex, sometimes swollen.

Character 6.—Medial margins of the maxillary fossae (Olivares 2009): (0) separated; (1) very close to each other or fused on the midline and generally forming a crest.

Character 7.—Medial margins of the maxillary fossae (Olivares 2009): (0) curved; (1) straighter, subparallel.

Character 8.—Width of the incisive foramina at the level of premaxillary–maxillary suture (Olivares 2009; Verzi 2008): (0) nearly one-third of width of the rostrum (at the same level); (1) nearly half or of a little more than the width of the rostrum; (2) nearly one-fourth or less than the width of the rostrum.

Character 9.—Posterior margins of the incisive foramina: (0) markedly anterior to the DP4; (1) at the level of the anterior side of the DP4 or a little in front.

Character 10.—Anterior portion of premaxillary in front of the incisive alveolus (Carvalho and Salles 2004; Olivares 2009): (0) low to very low; (1) high, forming the lateroventral side of a tube that is dorsally completed by the nasal.

Character 11.—Lateral margins of the nasals (Iack-Ximenes et al. 2005; Olivares 2009): (0) subparallel or slightly convex; (1) widened anteriorly.

Character 12.—Jugal (Emmons 2005; Olivares 2009): (0) narrower anteriorly than posteriorly; (1) higher anteriorly or equal in height to the posterior portion.

Character 13.—Jugal (Olivares 2009): (0) moderately high, with the dorsal margin concave and ascending at the paraorbital process; (1) markedly high, with the dorsal margin very slightly concave or straight and not ascending, or only slightly, at the level of the paraorbital process.

Character 14.—Dorsal margin of the jugal fossa (Emmons 2005; Olivares 2009): (0) subhorizontal or slightly descending anteriorly; (1) strongly descending, oriented toward the posterior part of the maxillary–jugal suture.

Character 15.—Anterior end of the jugal fossa (Emmons 2005; Olivares 2009): (0) acute; (1) wide, rounded to subquadrangular.

Character 16.—Suborbital fossa in the jugal (Olivares 2009; Verzi 2008): (0) absent; (1) present.

Character 17.—Inferior jugal process (Emmons 2005; Olivares 2009): (0) level with or slightly anterior to paraorbital process; (1) behind paraorbital process.

Character 18.—Lateral wall of the nasolacrimal canal (Olivares 2009): (0) formed by the orbital portion of the lacrimal; (1) formed by the maxillary.

Character 19.—Orbital portion of the lacrimal: (0) forming the margin of the lacrimal foramen; (1) not forming the margin; (2) forming only a part of the margin; it extends as a thin plate posterolaterally to the margin of the lacrimal foramen.

Character 20.—Dorsal part (“first part” sensu Hill 1935:123) of the nasolacrimal canal (Olivares 2009): (0) with posterior margin; (1) without posterior margin.

Character 21.—Lateral wall of the nasolacrimal canal: (0) moderately convex, distinguishable on the maxillary wall in lateral view; (1) smooth, not distinguishable in lateral view; (2) strongly swollen.

Character 22.—Foramen into nasolacrimal canal: (0) very reduced; (1) conspicuous.

Character 23.—Sphenopalatine foramen or anterior portion of the sphenopalatine fissure (Olivares 2009): (0) ventral or anteroventral to the lacrimal foramen; (1) posteroventral to the lacrimal foramen.

Character 24.—Portion of the maxillary dorsal to the sphenopalatine fissure and posterior to the nasolacrimal canal: (0) narrow, little extended behind the canal; (1) wide, markedly extended behind the canal.

Character 25.—Sphenopalatine foramen and fissure (Olivares 2009): (0) joined; (1) separated into an anterior oblique foramen, and a posterior fissure; (2) fissure reduced or absent.

Character 26.—Sphenopalatine fissure or foramen: (0) limited posteriorly by the frontal; (1) limited posteriorly by the maxillary.

Character 27.—Anterior end of the orbitosphenoid (Olivares 2009): (0) level with the M2 or M2–3; (1) level with or behind M3.

Character 28.—Interorbital constriction of frontals, behind the lacrimals (Olivares 2009): (0) present; (1) absent or barely marked.

Character 29.—Sphenopalatine vacuities (Carvalho and Salles 2004; Emmons 2005; Olivares 2009): (0) large; (1) very reduced or absent.

Character 30.—Lateral palatine plate in basitemporal region, in lateral view (Verzi 2001:267): (0) high, moderately convex and forming the anterior margin of the pterygoid fossa; (1) low and extended posteriorly, forming the anterior and lateral margins of the fossa; (2) low and anteroposteriorly short, forming the anterior and lateral margins of the pterygoid fossa; without a prominent lateral margin.

Character 31.—Alisphenoid (Verzi 2008): (0) without contact with the maxillary; (1) widely extended anteriorly, with its anterior margin joined to the maxillary.

Character 32.—Base of the mastoid area (Olivares 2009): (0) wide; (1) anteroposteriorly compressed between the nuchal crest and the lateral process of the supraoccipital.

Character 33.—Lateral process of supraoccipital (Woods 1984:434): (0) short, dorsal to the mastoid process; (1) ventrally extended below level of the mastoid process.

Character 34.—Nuchal crest: (0) continuous with the paroccipital process; (1) not continuous with the paroccipital process.

Character 35.—Lower margin of the posterior process of the squamosal: (0) thin; (1) thick.

Character 36.—Lower margin of the posterior process of the squamosal: (0) ventrally oriented; (1) ventrolaterally or laterally oriented.

Character 37.—Anterior margin of the base of the coronoid process (Olivares 2009): (0) level with m3 or behind it; (1) level with m2.

Character 38.—Tip of the coronoid process (Emmons 2005; Olivares 2009): (0) level with or below the mandibular condyle; (1) above the mandibular condyle.

Character 39.—Tip of the coronoid process (Leite 2003; Olivares 2009): (0) posteriorly or posterolaterally oriented, anterior margin of the sigmoid notch strongly excavated; (1) dorsally oriented, anterior margin of the sigmoid notch not excavated.

Character 40.—Dorsal portion of the postcondyloid process in posterior view (Olivares 2009): (0) oblique ventrolaterally; (1) vertical.

Character 41.—Origin of the masseteric crest (Verzi 2001, 2008): (0) not forming a shelf; if a shelf is present, it is behind the notch for the tendon of the medial masseter muscle and separated from it; (1) forming a shelf from the level of the notch or its posterior part.

Character 42.—Notch for the tendon of the medial masseter muscle: (0) as a semicircular step anterior to the origin of the masseteric crest; (1) incorporated into the origin of the masseteric crest, as an inconspicuous groove or rough area.

Character 43.—Protuberance of the bottom of the upper incisor alveolar sheath lateral to DP4 (Hadler et al. 2008): (0) absent; (1) present.

Character 44.—Lower incisor (Hadler et al. 2008): (0) long, the bottom of the alveolar sheath forming a bulbous protuberance on the external wall of mandible at posterior level of m3; (1) shorter, with the bottom not reaching the posterior part of m3.

Character 45.—Protoloph of M1–2 (Carvalho and Salles 2004): (0) present; (1) reduced to its labial portion forming a tubercle isolated or fused to the anteroloph.

Character 46.—Anterior portion of the Dp4 (Carvalho and Salles 2004): (0) with metalophulid II and mesolophid present; occasionally, the metalophulid II is joined to the metalophulid I by loss of the fossetid; (1) metalophulid II reduced or absent and the 2nd crest

formed by the mesolophid; (2) metalophulid II and mesolophid reduced to a spur or absent, 2nd crest formed by the hypolophid; (3) 2nd crest complex formed by the union of the metalophulid II and the mesolophid (crest C of Carvalho and Salles [2004]).

APPENDIX III

Data matrix analyzed. Polymorphic character: A (0 and 1); multistate characters were treated as unordered.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46		
<i>Octodontomys</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?		
† <i>Pampamys</i>	0	0	1	0	0	0	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	?	?	?	?	1	1	0	0	0	1
<i>Thrichomys</i>	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	
<i>Clyomys</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	0	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	1	0	1	2
<i>Euryzomatomys</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	0	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	1	0	1	2	
<i>Carterodon</i>	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	1	1	1	0	?	1	0	0	0	0	?	?	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	2	
† <i>Theridomysops</i>	?	0	?	?	0	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Proechimys</i>	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	2	1	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	1	A	0	0	0	0
<i>Trinomys</i>	0	A	1	0	0	0	0	0	1	0	0	0	A	0	0	0	1	1	1	0	1	1	2	1	0	0	A	1	0	0	1	0	0	1	0	0	1	0	0	0	1	1	A	0	0	0	3	
<i>Isothrix</i>	1	0	1	1	1	0	1	2	0	0	1	0	0	0	0	0	0	1	2	0	1	1	1	1	1	0	0	1	1	2	0	0	1	0	1	1	1	0	0	1	1	0	0	1	0	0		
<i>Phyllomys</i>	1	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	1	1	2	0	1	0	1	1	2	1	0	1	1	2	0	0	1	0	1	1	1	1	0	0	1	1	0	0	1	0	0	
<i>Echimys</i>	1	1	1	1	1	0	1	2	0	0	1	0	0	1	0	0	1	1	2	0	1	1	1	1	0	1	0	1	1	2	0	0	1	0	1	1	1	1	0	0	1	1	0	0	1	0	0	
<i>Mesomys</i>	1	0	1	1	0	0	1	2	0	0	1	0	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	1	0	2	0	0	1	0	1	1	1	0	0	1	1	0	0	1	0	0		
<i>Kannabateomys</i>	1	1	1	1	1	1	1	2	0	0	1	0	0	1	0	0	1	1	2	0	1	0	1	1	1	1	0	1	1	2	1	1	1	0	1	1	1	0	1	1	1	0	0	1	0	1		
<i>Dactylomys</i>	1	1	1	1	1	1	1	2	0	0	1	0	0	1	0	0	1	1	2	0	1	0	1	1	1	1	0	1	1	2	1	1	1	0	1	1	1	0	1	1	1	0	0	1	0	1		