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A NEW ECHIMYIDAE (RODENTIA, HYSTRICOMORPHA) FROM THE LATE MIOCENE OF SOUTHERN SOUTH AMERICA

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ABSTRACT—A new genus of echimyid rodent, †*Ullumys*, from the uppermost Miocene of northwestern Argentina is described. It includes two species, †*U. pattoni*, sp. nov., and †*Ullumys intermedius*, nov. comb. †*Ullumys pattoni* is known from a skull fragment and the corresponding right hemimandible coming from levels of Loma de Las Tapias Formation, underlying a tuff dated at 7.0 ± 0.9 Ma (Huayquerian age, San Juan Province). †*Ullumys intermedius* is represented by a left hemimandible from the ‘Araucanense’ of Valle de Santa María (Huayquerian age, Catamarca Province). A phylogenetic analysis in the context of octodontoids linked †*Ullumys* to the clade subtended by the extinct echimyids †*Pampamys* and †*Eumysops* and the living *Thrichomys*. †*Ullumys* has a peculiar craniomandibular morphology, shared only with †*Eumysops* among the Octodontoidea, involving specializations to open environments such as large and posteriorly extended orbits and related low mandibular condyles. Phylogenetic relationships of †*Ullumys* support the hypothesis that echimyids recorded since the latest Miocene in southern South America, and linked to those currently inhabiting Brazilian open biomes, represent a marginal sample of the great diversity evolving primarily in northern tropical areas.

<http://zoobank.org/urn:lsid:zoobank.org:pub:126592D1-0932-4374-AAD9-97FB59637DA7>

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Echimyidae is the most diverse family of hystricognath rodents in terms of both the number of living genera and species (Woods and Kilpatrick, 2005) and lifestyles (arboreal, terrestrial to fossorial, and semiaquatic; Eisenberg and Redford, 1999; Galewski et al., 2005; Emmons et al., 2015; Verzi et al., 2015). Living species are distributed mainly in northern South America (Leite and Patton, 2002; Woods and Kilpatrick, 2005; Upham and Patterson, 2012, 2015; Fabre et al., 2014; Verzi et al., 2014, 2015; Emmons et al., 2015). Echimyids inhabit Andean, Amazonian, and coastal tropical forests in the north of the continent (echimyines, dactylomyines, and eumysopines) and occasionally more open, xeric habitats in the Cerrado and Caatinga (*Thrichomys* and euryzygomatomyines; Eisenberg and Redford, 1999; Emmons and Feer, 1999; Emmons et al., 2015). *Myocastor* is the only extant echimyid distributed in southern South America (Woods et al., 1992; Patton, 2015).

The oldest fossils of the family come from the Paleogene of Santa Rosa, Peru, and are represented by, at least, the genus †*Eodelphomys* (late Eocene?–early Oligocene?; Frailey and Campbell, 2004). In southern South America, echimyids are

recorded since the late Oligocene (Patterson and Pascual, 1968; Verzi et al., 2015, 2016). Southern species recorded in the late Oligocene–middle Miocene (i.e., adelphomyines and †*Maruchito* from central-south Argentina and Chile; Patterson and Pascual, 1968; Vucetich et al., 1993; Flynn et al., 2008) are related to extant arboreal representatives (echimyines and dactylomyines; Emmons and Vucetich, 1998; Carvalho and Salles, 2004; Verzi et al., 2014, 2015, 2016; Olivares and Verzi, 2015), in accordance with the persistence of forests with tropical elements at high latitudes until the middle Miocene (Palazzesi and Barreda, 2007). Recently, the presence of dry and open forest and palm shrubland in Patagonia, with a brief regreening period during the middle Miocene, has been described (Dunn et al., 2015).

Echimyids recorded in southern South America since the latest Miocene are related to species that currently occupy Chacoan-type open environments in the Cerrado and Caatinga biomes (except for myocastorines; Reig, 1986; Verzi et al., 1994, 1995, 2002, 2014; Vucetich, 1995; Cartelle, 1999; Hadler et al., 2008; Olivares et al., 2012a; Olivares and Verzi, 2015). Systematic and phylogenetic studies of these southern late Miocene echimyids have suggested their relationship with the living fossorial euryzygomatomyines (sensu Emmons, 2005) and terrestrial ‘eumysopines’ (Reig, 1986; Verzi et al., 1995; Vucetich, 1995; Olivares et al., 2012b). This change in the taxonomic composition of echimyid fossil faunas is concurrent with palaeoenvironmental changes that

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took place in the middle to late Miocene, including the marine transgression of the Paranense Sea (Pascual et al., 1985; Webb, 1995) and the drying and cooling global trend that resulted in the expansion of open environments (Pascual and Ortiz Jaureguizar, 1990; Janis, 1993; Denton, 1999; Zachos et al., 2001; Arakaki et al., 2011; Palazzesi and Barreda, 2012; Dunn et al., 2015).

Here, we describe a new genus and species from the late Miocene of western Argentina, represented by a skull fragment and associated hemimandible, which improves knowledge about this stage in echimyid evolution. We describe its anatomy in order to assess its phylogenetic position and explore characters that could putatively indicate its occupation of one of the two major macro-environments, i.e., forested versus open. On this basis, we discuss the contribution of the southern fossil record of echimyids, and particularly of the new material, to the knowledge of the evolutionary history of the family.

Institutional Abbreviations—**GHUNLPam**, Cátedra de Geología Histórica, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa, Argentina; **MACN-Pv**, Museo Argentino de Ciencias Naturales, Bernardino Rivadavia, CONICET, Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MMP**, Museo de Ciencias Naturales de Mar del Plata, Lorenzo Scaglia, Mar del Plata, Argentina; **MN/UFRJ**, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **PVSJ**, Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **UnB**, Universidade de Brasília, Brasília, Brazil.

MATERIALS AND METHODS

Nomenclature of craniomandibular traits follows Hill (1935), Wahlert (1984), Novacek (1993), Verzi (1994, 2001), Wible et al. (2005), and Verzi et al. (2014, 2016). Dental nomenclature and homologies of crests follow Marivaux et al. (2004) and Verzi et al. (2016), respectively.

The morphological phylogenetic analysis of extinct and extant octodontoids is largely based on the matrices in Olivares and Verzi (2015) and Verzi et al. (2016). In addition, we add 10 new characters (characters 83–92; Supplementary Data 1, Appendix S1) resulting from the morphological revision of the new material PVSJ 24, the nominal species †*Eumysops intermedius* MACN-Pv 8378 (late Miocene, Argentina; Olivares et al., 2012b), †*Paramyocastor diligens* (Pliocene, Argentina; Verzi et al., 2002), and two living species of the cursorial genus *Thrichomys*, namely, *T. laurentius* and *T. apereoides*. This matrix includes a total of 73 taxa and 92 characters; *Dasyprocta* (Caviodea) was included for rooting purposes. The software TNT 1.1 (Goloboff et al., 2008a, 2008b) was used to find the most parsimonious trees and evaluate branch support. All characters were considered equally weighted, and multistate characters were coded as non-additive with the exception of characters 49 and 51. The analysis was based on 1000 random stepwise-addition replicates and tree bisection reconnection (TBR) branch swapping, saving 100 trees per replicate. In addition, we performed an extra round of TBR on the optimal trees to increase the possibility of finding all minimum-length topologies (Bertelli and Giannini, 2005). Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions (Coddington and Scharff, 1994). Branch support was calculated using absolute and relative Bremer support indices (Bremer, 1994).

Additionally, a combined parsimony analysis was performed based on the data set of morphological characters and four gene fragments obtained from GenBank (Supplementary Data 1, Appendix S2, Table S1; Verzi et al., 2016): one mitochondrial gene (12S rRNA, 979 bp) and three unlinked nuclear exons (GHR, 814 bp; RAG1, 1072 bp; vWF, 1173 bp). Gene selection followed Upham and Patterson (2012). Gene sequences were aligned using BioEdit 7.2.0 (Hall, 1999) with the default values

of gap opening and gap extension. The data set of morphological traits was concatenated with the gene sequences, and extinct taxa were coded missing for all molecular characters. This matrix contained a total of 4232 characters and 79 taxa, including *Cavia*, *Hydrochoerus*, *Cuniculus*, *Dasyprocta* (Caviodea), *Chinchilla*, (Chinchilloidea), and *Erethizon* (Erethizontoidea) as outgroups. The parsimony analysis of the combined morphological and DNA matrix was carried out treating gaps as missing data in TNT 1.1 (Goloboff et al., 2008a, 2008b). The heuristic search consisted of 10,000 replicates of a Wagner tree with random addition sequence of taxa followed by TBR branch swapping. In addition, we performed an extra round of TBR on the optimal trees to increase the chance of finding all minimum-length topologies (Bertelli and Giannini, 2005).

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOMORPHA Brandt, 1855
Superfamily OCTODONTOIDEA Waterhouse, 1839
Family ECHIMYIDAE Gray, 1825
Subfamily EUMYSOPINAE Rusconi, 1935
ULLUMYS, gen. nov.

Included Species—The type species, *Ullumys pattoni*, sp. nov., and *Ullumys intermedius*, nov. comb.

Derivation of Name—Ullum, for the fossil-bearing locality Ullum, -mys, Greek-derived suffix for rodents.

Distribution—Late Miocene of northwestern Argentina (Fig. 1A).

Diagnosis—Medium-sized echimyid; nasals broad with parallel lateral margins; frontals narrow; sphenopalatine fissure broad at level of M1–2; orbital portion of lacrimal short; lacrimal and maxilla forming the first part of the lacrimal canal; lacrimal foramen opening into the maxilla; antorbital zygomatic bar at level of M1–2; parietals vaulted, markedly shortened, and descending; diastema in front of dp4 at level of alveolar margin, without ledge; mandibular condyle low, nearly level with occlusal plane of molars; DP4–M1 trilophodont, with a composite posterior loph as evidenced in the tetralophodont M2–3; mesolophule without contact with hypocone area in the M2; protoloph thin; dp4 tetralophodont, with a second crest discontinuous in its mesial portion (metalophulid II); closure of lingual flexids almost synchronous in m1; thin lophids of m1–3, separated by broad flexids; metaflexid more persistent than mesoflexid in m2–3; mesoflexid deep on the occlusal surface; m1–3 trilophodont with mesial end of their flexid rounded.

ULLUMYS PATTONI, sp. nov.
(Figs. 2–4)

Holotype—PVSJ 24, skull without basicranial region, with both DP4–M3 series, and right hemimandible with dp4–m3.

Derivation of Name—*pattoni* to honor the evolutionary biologist James L. Patton for his comprehensive contribution to the knowledge of the echimyids.

Distribution—Loma de Las Tapias Formation, Arenisca Albardón Member (Huayquerian, upper late Miocene), Ullum, San Juan Province, northwestern Argentina. The holotype comes from the areas northeast from Ullum dam (Fig. 1B, C). The geological and stratigraphic context of the Loma de Las Tapias Formation is described in Serafini et al. (1986), Rodriguez (2004), Suvires and Contreras (2011), and Contreras and Baraldo (2011, and literature cited therein). The Loma de Las Tapias Formation is divided into two members (Rodriguez, 2004): a lower one named Limolita La Colmena and an upper one, Arenisca Albardón. The Arenisca Albardón Member consists of layers of conglomeratic and tuffaceous sandstones

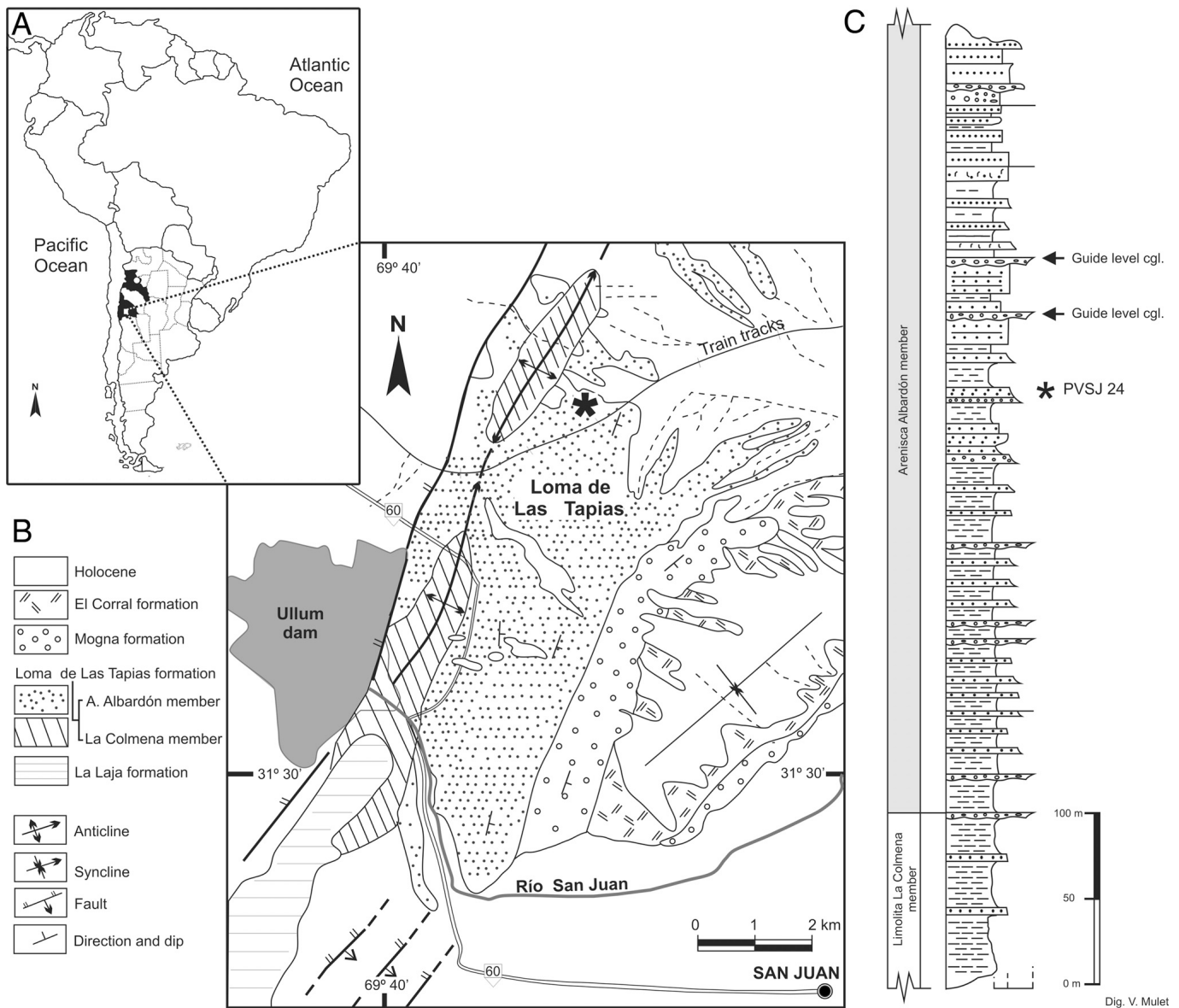


FIGURE 1. **A**, location map of Valle de Santa María, Catamarca Province (white circle), and Ullúm, San Juan Province (white square). **B**, geologic map of Loma de Las Tapias Formation. **C**, stratigraphic section, located in the north area of rail tracks, of Loma de Las Tapias Formation. Asterisk indicates the location of PVSJ 24. Modified from Contreras and Baraldo (2011).

interbedded with fine- to coarse-grained sandstones, gray and buff gray in color. This member is 1350 m thick (Suvires and Contreras, 2011). Radiometric analysis of a tuff from the middle levels of the Arenisca Albardón Member yielded a date of 7.0 ± 0.9 Ma (Bercowski et al., 1986). Based on numerical ages and local history of magnetic polarity (Bercowski et al., 1986), these members are accepted as late Miocene in age, between 9.0 and 5.4 Ma (Contreras and Baraldo, 2011). The most conspicuous fossiliferous levels occur in the upper portion of the La Colmena Member and the lower half of the Arenisca Albardón Member, below the dated tuff (Contreras and Baraldo, 2011), where two faunal assemblages are recognized. The specimen PVSJ 24 was recovered from the middle levels of the Arenisca Albardón Member and is included in the most modern faunal Association B considered to be of Huayquerian age (upper late Miocene; Contreras and Baraldo, 2011).

Diagnosis—Skull traits as in the diagnosis of the genus; mandible slender; base of coronoid process level with posterior portion

of m3; lateral crest starting at level of m1–2; labial end of protoconid of m1–2 slightly more extended than that of hypoconid; anterior lophid of m2 with a small spur; crowns lower than those of †*Ullumys intermedius*; hypoflexid shallower than that of †*U. intermedius*.

DESCRIPTION

Skull

The skull is similar in size to that of *Thrichomys laurentius*. The nasals are damaged, their lateral and posterior margins of the right side being best preserved. They are broad up to their posterior margin, as in the Plio-Pleistocene †*Eumysops*, with straight lateral margins. Their posterior ends are at the level of the dorsal root of the antorbital zygomatic bar. In dorsal view the premaxillae are narrower than in †*Eumysops*, †*Pampamys*, and living echimyids (Olivares et al., 2012a, 2012b; Olivares and Verzi, 2015). They contact the frontals at the same level as the

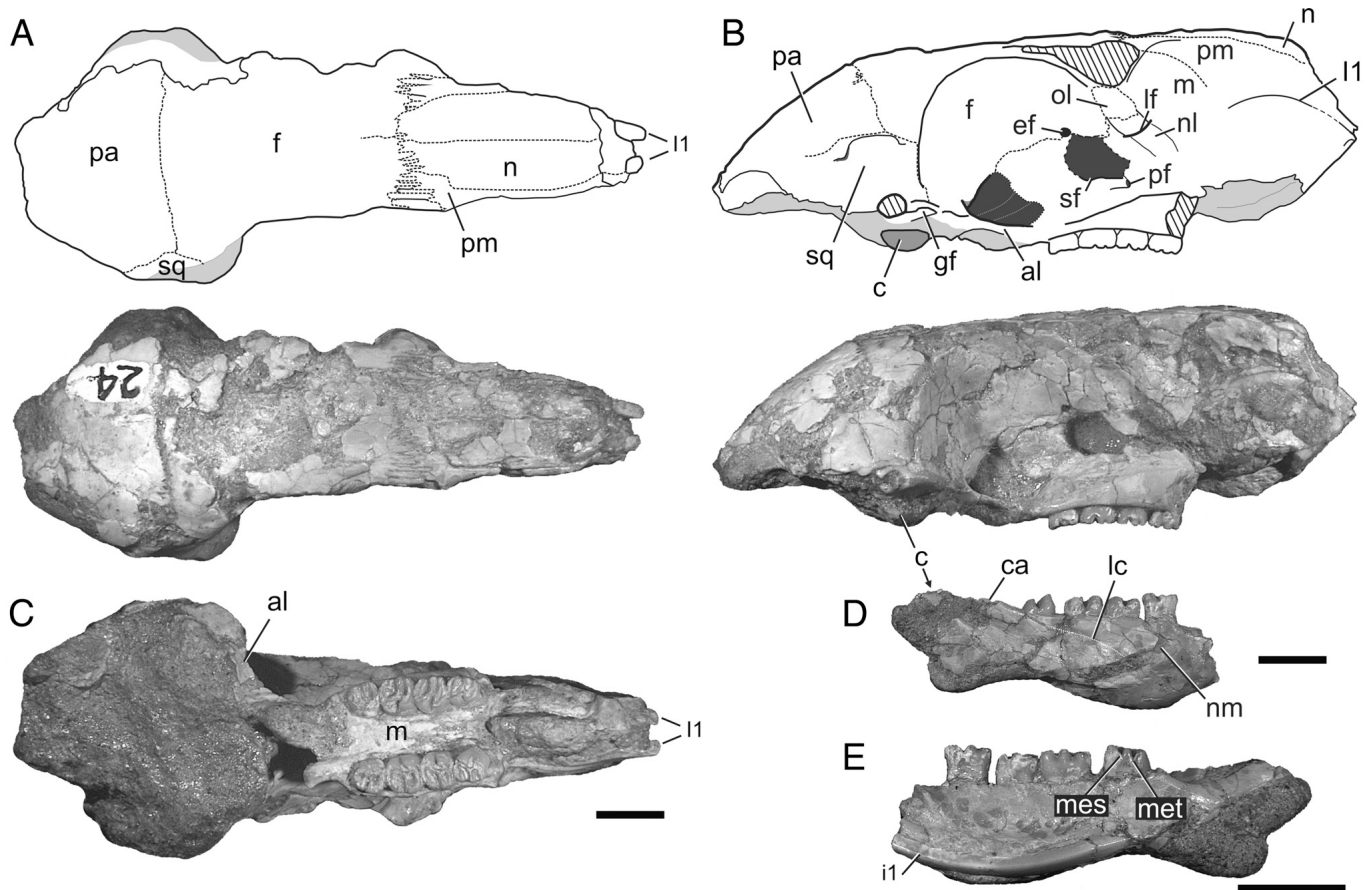


FIGURE 2. Skull and mandible of †*Ullumys pattoni* PVSJ 24. **A**, dorsal view of skull (line drawing and photograph); **B**, right lateral view of skull (line drawing and photograph); **C**, ventral view of skull; **D**, lateral view of right hemimandible; **E**, lingual view of the right hemimandible. **Abbreviations:** **al**, alisphenoid; **c**, condyle; **ca**, coronoid apophysis; **ef**, ethmoidal foramen; **f**, frontal; **gf**, glenoid fossa; **I1/i1**, upper and lower incisors; **j**, jugal; **lc**, lateral crest; **lf**, lacrimal foramen; **m**, maxilla; **mes**, mesoflexid; **met**, metaflexid; **n**, nasal; **nl**, foramen into nasolacrimal canal; **nm**, notch for the tendon of medial masseter muscle; **ol**, orbital portion of lacrimal; **pa**, parietal; **pf**, palatilar foramen; **pm**, premaxilla; **sf**, sphenopalatine fissure; **sq**, squamosal. All scale bars equal 5 mm.

frontonasal suture (Fig. 2A). As in †*Eumysops*, the orbital region is larger and more posterior than in the remaining echimyids, 80% of it being placed behind the level of the molar tooth row (Figs. 2B, 3). The orbital process of the lacrimal is preserved on the right side; it is short as in *Thrichomys* and †*Eumysops formosus* (Olivares et al., 2012A) and does not contact the lacrimal foramen that opens onto the maxilla. The preserved cast of the nasolacrimal canal is anteroventrally oriented (Fig. 2B). The frontomaxillary suture contacts the ventral part of a small ethmoidal foramen, as in the rest of echimyids. A large hollow anteroventral to the ethmoidal foramen and dorsal to the maxillary lateral wall corresponds to the area in which the sphenopalatine fissure would have developed. Its preserved maxillary ventral margin extends at the level of M1–2 (Fig. 2B) as the sphenopalatine fissure of *Thrichomys*. Below this fissure, the anteromedial floor of the orbital region bears a palatine foramen similar to that of †*Eumysops*. On the left side, a concavity posterodorsal to the M3 could correspond to the anterior portion of a broad sphenopalatine vacuity; on the right side, this area is covered by fragmented bone. The cranial vault is very short and wide. It is markedly shorter than in living echimyids and similar to that of †*Eumysops* (Fig. 3), the parietals being shorter in the midline than both the frontals (40%) and the nasals (32%) (Fig. 2A, B). The origin of the temporal orbital muscle delimits a fossa on the squamosal bone (preserved on the right side; Figs. 2, 3), located more ventrally than in †*Eumysops* (Fig. 3C, D). The right

alisphenoid is partially preserved (Fig. 2C). The distance between the M3 and the anterior margin of the alisphenoid is greater than in †*Eumysops* and the remaining echimyids, a condition related to the greater posterior extension of the orbit (Figs. 2C, 3). The mandibular condyle came away from the mandible during preparation of the specimen, and is preserved attached to the glenoid fossa (Fig. 2B, D).

Mandible

The mandible is represented by a partially preserved right hemimandible lacking the anterior part of the diastema, coronoid process, masseteric crest, and angular process. The body of the hemimandible is slender (Fig. 2D, E). The posterior portion of the diastema is slightly excavated, without a ledge in the anterior alveolar border of the dp4. The notch for the tendon of the infraorbital part of the medial masseter muscle is damaged. The masseteric crest has been partially lost, its origin on the mandibular corpus being occupied by a narrow fracture; in the ventral border of this fracture, the ventral margin of the masseteric crest is partially preserved and is continuous with the notch. The masseteric fossa is shallow. The base of the coronoid process is posterior to the m3, and its anterior border is posterodorsally oriented, rising at an angle of about 30° to the mandibular body. The mandibular condyle is low, located nearly level with the occlusal plane of the molars, as in †*Eumysops*.

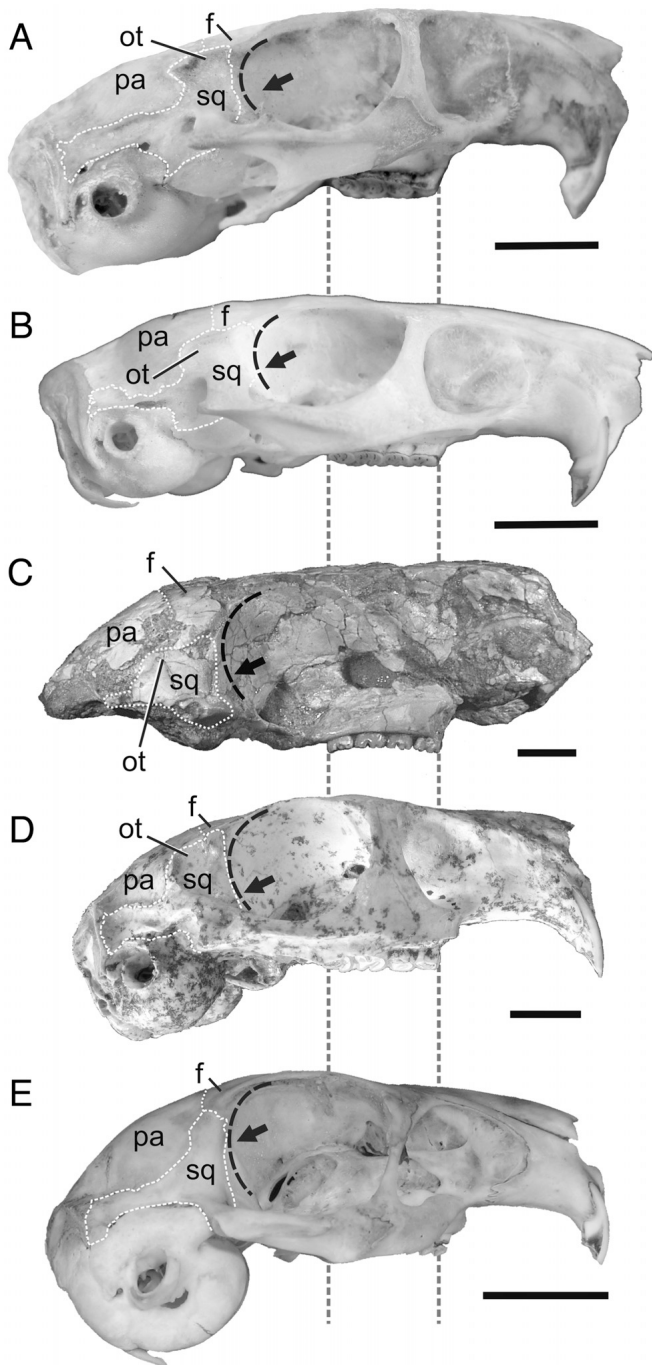


FIGURE 3. Comparisons of the posterior portion of the skull (in right lateral view) and the position of the posterior margin of the orbital region (black arrow and black dotted line) with respect to the molar series (gray dotted line) of **A**, *Thrichomys* UnB 189; **B**, *Proechimys* MLP 22.II.00.7; **C**, †*Ullumys pattoni* PVSJ 24; **D**, †*Eumysops* MMP 403-M; **E**, *Microcavia* MLP 26.VIII.01.22. **Abbreviations:** f, frontal; ot, origin of the orbital portion of the temporal muscle; pa, parietal; sq, squamosal. All scale bars equal 10 mm except for †*U. pattoni* (scale bar 5 mm).

Teeth

Upper and lower incisors are transversely narrow and antero-posteriorly deep.

Both upper molar rows are preserved (Figs. 2C, 4; Table 1). Molars are lower crowned than those of *Thrichomys*. According

to the degree of wear of M3 and m3, the specimen is subadult (see Neves and Pessôa, 2011). The DP4 and M1 are trilophodont, but the posterior loph is broad, indicating that it is a composite structure. This loph is anterolabially oriented. The composite nature of this posterior loph is evident in the M2, in which a remnant of the mesolophule is still present and joined to the postero-loph + metaloph; this remnant is separated from the hypocone area. The M3 is tetralophodont. A similar molar pattern can be observed in juveniles and subadults of *Thrichomys laurentius* (Fig. 4D), *Thrichomys pachyurus* (Neves and Pessôa, 2011), and *Thrichomys apereoides*, but not in *Thrichomys inermis*. The DP4–M3 of *T. inermis* show the mesolophule as a distinct crest contacting the mure (Neves and Pessôa, 2011), similar to †*Pampamys* (Fig. 4C). In the unworn M2 of †*Eumysops chapalmalensis* MLP 48-IV-14-1, the complete mesolophule is posterolaterally oriented and contacts the postero-loph plus a relic of the metaloph (Fig. 4B). The proto-loph of †*U. pattoni* is thin. In occlusal view, the mesial portion of the hypoflexus is close to the mesial portion of the paraflexus in DP4–M3.

The dp4 is tetralophodont (Fig. 4E). Although the anterolateral side is damaged, a shallow indentation is retained that can be interpreted to be the same one occurring behind the trigonid in juveniles of *Thrichomys* (Fig. 4F), †*Pampamys* (Fig. 4H), *Clyomys*, some specimens of *Proechimys*, and echimyines. The root of the mesolophid, when present, is posterior to this sulcus, as observed in the above-mentioned genera. If this is the case, at least the root of the second lophid in †*Ullumys* would be the metalophulid II (Fig. 4E). This pattern is different from the tetralophodont dp4 of both *Thrichomys* (Fig. 4F, I) and †*Eumysops* (Olivares and Verzi, 2015) and the pentalophodont dp4 of †*Pampamys* (Fig. 4H). The m1–3 are trilophodont, with the protoconid area labially projected, thin lophids, and equally broad flexids. Flexids are narrower in †*Pampamys*, †*Eumysops*, and *Thrichomys*. The mesial portion of the hypoflexid is close to the mesial portion of the metaflexid. The anterior lophid of the m2 has a small spur.

ULLUMYS INTERMEDIUS, nov. comb. (Fig. 5)

Eumysops intermedius Rovereto, 1914:67, fig. 34.
Thrichomys intermedius (Bond, 1977):312 (partim).

Holotype—MACN-Pv 8378, fragment of left hemimandible with m1–2.

Distribution—‘Araucanense’ sensu Rovereto (1914), late Miocene–Pliocene?, Valle de Santa María, Catamarca Province, northwestern Argentina (Fig. 1A); its precise stratigraphic provenance is unknown (Rovereto, 1914). The ‘Araucanense’ of Valle de Santa María represents the late Miocene–Pliocene interval (Marshall and Patterson, 1981; Bossi and Muruaga, 2009; Reguero and Candela, 2011; Esteban et al., 2014).

Emended Diagnosis—Base of coronoid process level with posterior portion of m2; lateral crest starting at level of m1; crowns of m1–2 higher than those of †*Ullumys pattoni*; labial end of protoconid slightly more extended than that of hypoconid in m2; lingual portion of hypolophid in m1–2 slightly oriented anteriorly; anterior lophid of m2 without the small spur present in †*U. pattoni*; lingual flexids more ephemeral (with regard to persistence of the hypoflexid) than in †*U. pattoni*.

DESCRIPTION

Mandible

The single specimen of †*U. intermedius*, MACN-Pv 8378, is a fragmentary left hemimandible of a juvenile (compare Fig. 4G and I). The posterior portion of the diastema is slightly excavated, without a ledge in the anterior alveolar border of the

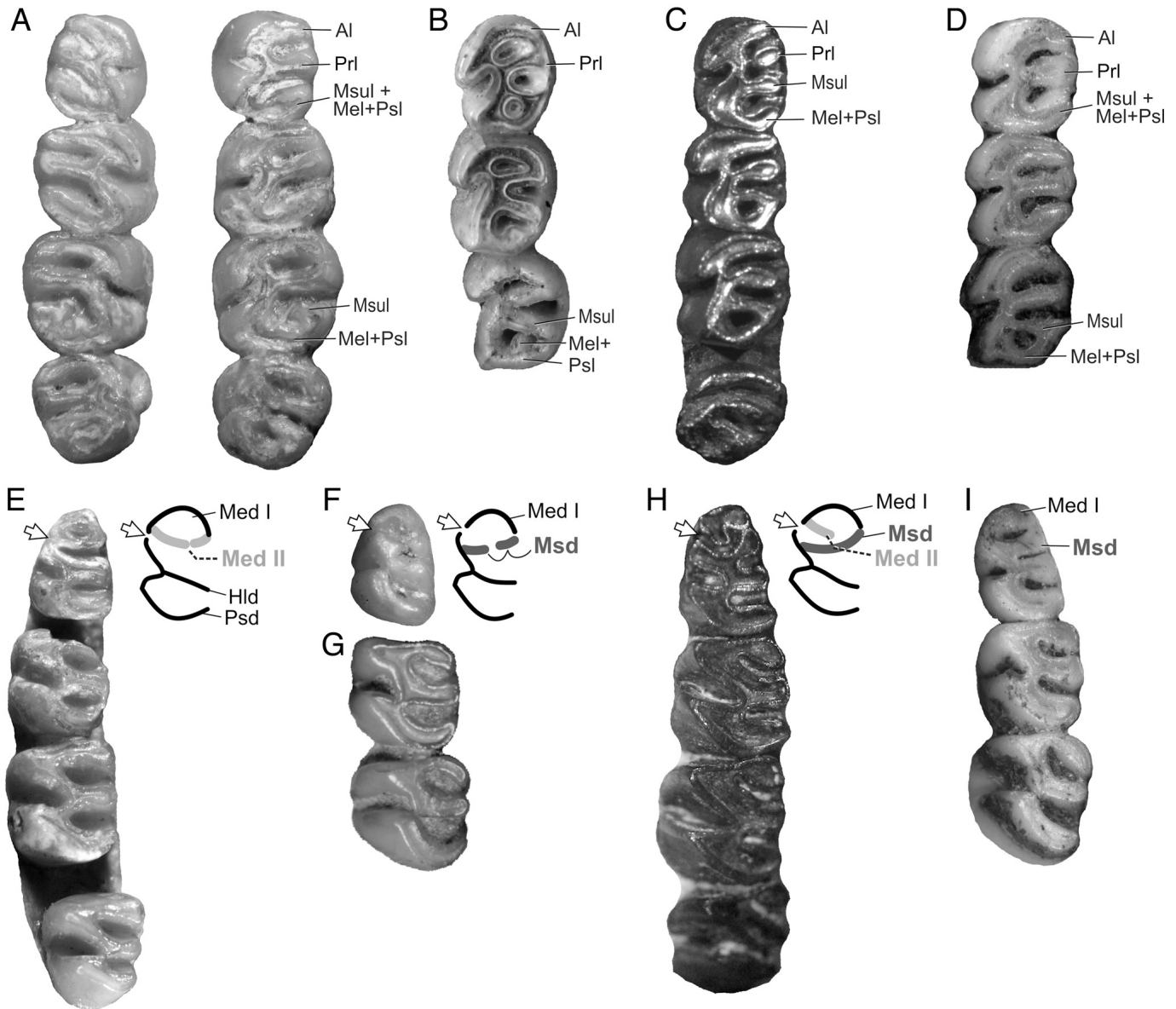


FIGURE 4. Upper and lower molars. **A**, right and left DP4–M3 of †*Ullumys pattoni* PVSJ 24; **B**, right DP4–M2 (inverted) of †*Eumysops chapalmalensis* MLP 48-IV-14-1; **C**, left DP4–M3 of †*Pampamys emmonsae* GHUNLPam 22586; **D**, left DP4–M2 of *Thrichomys laurentius* MN/UFRJ 42411; **E**, right dp4–m3 (inverted) of †*Ullumys pattoni* PVSJ 24; **F**, right juvenile dp4 (inverted) of *Thrichomys* MN/UFRJ 14511; **G**, left m1–2 of †*Ullumys intermedius* MACN-Pv 8378; **H**, right dp4–m3 (inverted) of †*Pampamys emmonsae* GHUNLPam 2214 (holotype); **I**, right dp4–m2 (inverted) of *Thrichomys laurentius* MN/UFRJ 42457 (juvenile with unerupted m3). **E**, **F**, **H**, with schematic illustrations of crest homologies. White arrows indicate the sulcus behind the trigonid. Not to scale. **Abbreviations:** **AI**, anteroloph; **Hld**, hypolophid; **Med I**, metalophulid I; **Med II**, metalophulid II; **Mel**, metaloph; **Msd**, mesolophid; **Msul**, mesolophule; **Prl**, protoloph; **Psd**, posterolophid; **Psl**, posteroloph.

dp4 as in †*U. pattoni*. Its lateral crest is more anterior than in †*U. pattoni*; this could be an ontogenetic difference, considering that in the ontogenetic sequence of *Thrichomys laurentius*, the lateral crest is more anterior in juveniles than in adults. The base of the coronoid process is more anterior in †*U. intermedius* (lateral to m3) than in †*U. pattoni* (lateral to the posterior portion of m3). This could be an ontogenetic difference as well. The masseteric fossa is deeper than in †*U. pattoni*.

Teeth

The lower incisor is transversely narrow and anteroposteriorly deep as in †*U. pattoni*.

†*Ullumys intermedius* has higher crowned molars than †*U. pattoni* (Figs. 2, 5). Their morphology and wear stage are comparable to those in juveniles of *Thrichomys* (i.e., with unerupted m3; compare Fig. 4G and I, and see Neves and Pessôa, 2011). Given that †*U. pattoni* and †*U. intermedius* are not fully adult specimens either, this morphology of †*U. intermedius* could be additionally influenced by its greater hypsodonty. The anterior lophid is more curved than in †*U. pattoni*, especially in the m2 (Fig. 4E, G). The anterior lophid of the m2 lacks the small spur present in †*U. pattoni*. The lingual portion of the hypolophid of the m1–2 is anteriorly oriented, whereas in †*U. pattoni* it is posteriorly oriented in the m1 and straight in the m2. The enamel at the mesial portion of the hypoflexid is oriented anteroposteriorly, especially in m1, and becomes abruptly labial at the protoconid area. In †*U.*

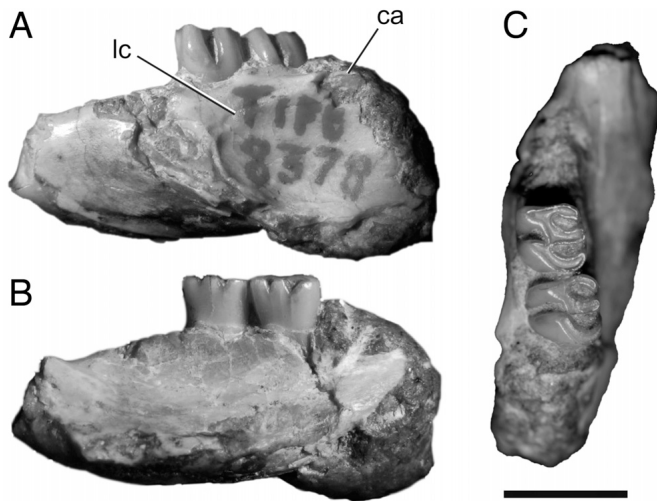


FIGURE 5. **A**, lateral, **B**, medial, and **C**, occlusal views of left hemimandible of †*Ullumys intermedius* MACN-Pv 8378. **Abbreviations:** **ca**, coronoid apophysis; **lc**, lateral crest. Scale bar equals 5 mm.

pattoni, this enamel edge is oriented anterolabially. The hypolophid still remains separated from the anterior arm of the hypocoind in m2 of †*U. intermedius* (Fig. 4G).

Comments

In addition to †*Eumysops intermedius*, Rovereto (1914) included within the variation of †*Eumysops* two fragmentary mandibles with m1–2, which were originally named †*Eumysops ponderosus* (holotype MACN-Pv 8377) from Valle de Santa Maria, Catamarca Province, and †*E. serridens* (holotype MACN-Pv 8564) from Huayquerías de San Carlos, Mendoza Province, all from the late Miocene–early Pliocene of western Argentina. These species are currently not considered as belonging to †*Eumysops* (Bond, 1977; Olivares et al., 2012a). They were assigned to the living *Proechimys* and *Thrichomys*, respectively, by Bond (1977; although see Reig, 1989). The differences between these fossils and the species here described do not allow their inclusion within the variation of †*Ullumys*.

PHYLOGENETIC ANALYSIS

A parsimony analysis of octodontoids based on morphological characters resulted in six most parsimonious trees, 198 steps long (consistency index [CI] = 0.571, retention index [RI] = 0.854; Fig. 6; Supplementary Data 1, Fig. S1). In the trees obtained, the monophyly of †*Ullumys* is supported by two synapomorphies: thin lophids separated by broad flexids (character 87[1]), and

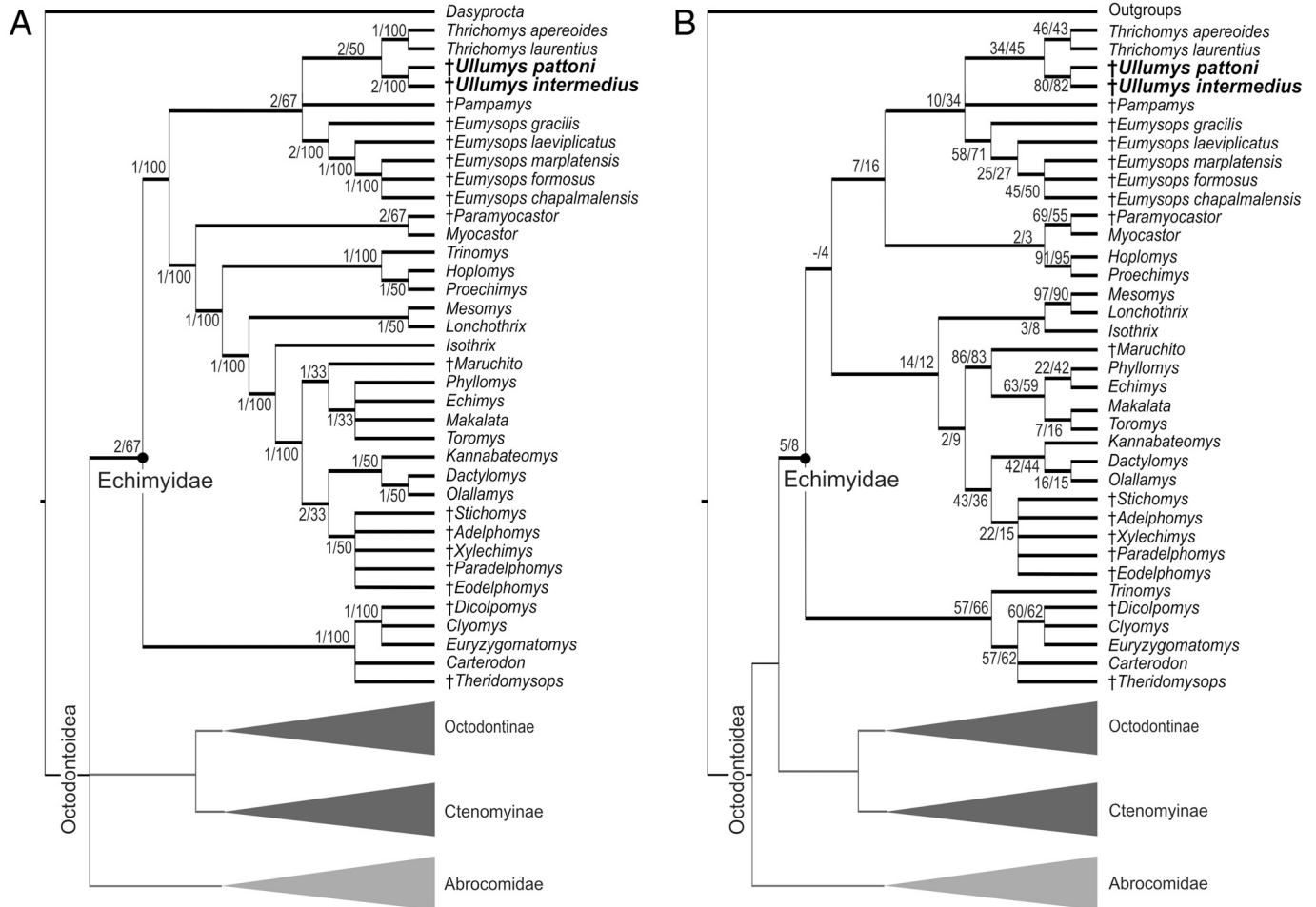


FIGURE 6. Phylogenetic analysis. **A**, strict consensus of six most parsimonious trees of 198 steps resulting from parsimony analysis of morphological data, with Bremer support/relative Bremer support values shown for each node. **B**, a single most parsimonious tree of combined morphological and molecular data (3611 steps in length), with bootstrap CG frequency/jackknife CG frequency values shown for each node.

TABLE 1. Measurements (mm) of molars.

| Tooth | AP/TW | |
|-------|------------------------|----------------------------|
| | <i>Ullumys pattoni</i> | <i>Ullumys intermedius</i> |
| DP4 | 1.78 / 1.48 | — |
| M1 | 1.69 / 1.71 | — |
| M2 | 1.96 / 1.65 | — |
| M3 | 1.87 / 1.77 | — |
| dp4 | 2.14 / 1.42 | — |
| m1 | 2.05 / 1.69 | 2.14 / 1.76 |
| m2 | 2.23 / 1.78 | 2.23 / 1.5 |
| m3 | 1.69 / 1.60 | — |

Abbreviations: AP, anteroposterior length; TW, transverse width.

diastema in front of dp4 without ledge (character 91[1]); this grouping showed moderate support but no character conflict. †*Ullumys* formed a monophyletic group with *Thrichomys*, with which it shares a reduced or absent mesolophule on DP4 (character 51[2]), posterior loph of adult M1 fused forming a single composite loph (character 56[1]), and different pattern of reduction of the posterior crests in M1 with respect to that in M2 (character 88[1]). *Thrichomys* species share conspicuous supra-orbital ridges, extending almost in parallel along the anterior half of the frontals and diverging toward the squamosal-parietal suture (character 89[1]; Neves and Pessôa, 2011; Pessôa et al., 2015). †*Ullumys* and *Thrichomys* form a clade with †*Pampamys* and the species of †*Eumysops*, supported by two synapomorphies: notch for tendon of medial masseter muscle incorporated into origin of masseteric crest (character 46[1]), and trilophodont m1–2 with the mesial portion of hypoflexid facing the mesial portion of metaflexid (character 86[1]). The relationships within the clade ((*Thrichomys* + †*Ullumys*) †*Pampamys* + †*Eumysops*) remain unresolved (as in Olivares and Verzi, 2015); this clade has moderate support but no character conflict (Fig. 6).

The combined parsimony analysis resulted in one most parsimonious tree, 3611 steps long (CI = 0.557; RI = 0.595; Fig. 6). The topology is similar to that in Verzi et al. (2016), except for the inclusion of †*Ullumys*, the †*Eumysops* species, and †*Paramyocastor*. Unlike the trees obtained here with morphological data only, in the combined tree, *Trinomys* was sister group of euryzygomatomyines (sensu Emmons 2005) and ((*Myocastor* + †*Paramyocastor*) (*Proechimys* + *Hoplomys*)) were sisters to ((*Thrichomys* + †*Ullumys*) †*Pampamys* + †*Eumysops*). In addition, in the combined tree, *Isothrix* was sister to *Mesomys* + *Lonchothrix*, and echimyines showed greater resolution.

DISCUSSION AND CONCLUSIONS

The new genus †*Ullumys* increases the southern diversity of the clade that includes extinct echimyids and the living rodent *Thrichomys*. This clade also includes the late Miocene †*Pampamys emmonsae* and the Plio-Pleistocene species of †*Eumysops*. †*Ullumys pattoni* is the first echimyid described from the late Miocene Lomas de Las Tapias Formation, in western Argentina. The holotype and only known specimen comes from levels below a tuff dated at 7.0 ± 0.9 Ma (Bercowski et al., 1986), and it is part of an association of mammals considered to be Huayquerian in age (late Miocene; Contreras and Baraldo, 2011). The precise provenance of †*Ullumys intermedius* is unknown (Rovereto, 1914), whereas the genus is recorded with certainty only for the Huayquerian older than 6.0 Ma. The variation between †*Ullumys* species primarily reflects ontogeny and a variable degree of hypsodonty, with †*U. intermedius* being clearly more hypsodont than the type species. There is a possibility that these two species represent two morphologies of a temporal pattern of change along a continuous lineage, which cannot at present be ruled out.

The topology of the major clades of fossil and living Octodontidae, and in particular of Echimyidae, is similar to those presented in the proposals of Olivares and Verzi (2015) and Verzi et al. (2015, 2016), except for the inclusion of †*Ullumys* and †*Paramyocastor*. The latter genus grouped with *Myocastor*, as in the phylogenetic analysis of Candela and Rasia (2012). The phylogenetic position of †*Ullumys* is consistent with the previously detected temporal pattern of the southern fossil record of echimyids, which follows distinct phases of palaeoenvironmental change: fossils as part of the clades of arboreal ‘echimyines’ and dactylomyines are recorded until the middle Miocene, whereas the clades of terrestrial ‘eumysopines’ and euryzygomatomyines, which currently inhabit more open, Chacoan areas (Cerrado, Caatinga, Pantanal) are represented since the late Miocene (Olivares and Verzi, 2015; Verzi et al., 2015, 2016).

Morphometric analyses of a broad sample of hystricognath rodents suggest that the posterior position of the orbits occurs in species that inhabit open environments (Hautier et al., 2012; Alvarez et al., 2013, 2015). †*Ullumys*, like †*Eumysops*, has large orbits that extend posteriorly (Fig. 3C, D) and a low mandibular condyle whose position would be constrained by the location of the orbit (see Hautier et al., 2009, 2012); the cranial vault is shortened, with markedly short and downward-oriented parietals (Fig. 3C, D; Olivares and Verzi, 2015). This cranial morphology is not found in other echimyids (Fig. 3A, B), but resembles that of the caviid *Microcavia* (Fig. 3E; Olivares, 2009), an inhabitant of arid environments of the Monte and Patagonia biomes in southern South America (Dunnum, 2015). In †*Eumysops*, known from more complete remains, this cranial morphology is combined with postcranial specializations that enable half-bound locomotion (Horovitz, 1991; Olivares, 2009). Fossil southern echimyids of the modern stage (since the late Miocene) shown specializations for the occupation of open environments that are not present in living echimyids (Verzi et al., 1994; Olivares and Verzi, 2015).



The late Miocene †*Ullumys* and †*Pampamys* represent a minimum age in the fossil record for the separation of *Thrichomys* from its sister clade *Myocastor* + *Proechimys-Hoplomys* (Olivares and Verzi, 2015). A similar minimum age for this divergence is provided by the presence of *Myocastor* in the late Miocene of eastern Argentina (Candela and Noriega, 2004). However, molecular dating indicates that this split must have taken place earlier, during the middle or even the early Miocene (Galewski et al., 2005; Fabre et al., 2014; Upham and Patterson, 2015; Verzi et al., 2016:online resource 3). The divergence time of euryzygomatomyines, the other clade present in southern South America since the late Miocene (Vucetich, 1995; Olivares et al., 2012; Verzi et al., 2016), is more uncertain. In recent molecular phylogenies (Upham and Patterson, 2015), this clade is recovered as sister to the remaining Echimyidae in a five-gene completely sampled tree, whereas it clusters with the Caribbean Capromyidae in an alternative analysis based on a taxonomically more exhaustive supermatrix. In any case, euryzygomatomyines would have diverged from the remaining echimyids during the early Miocene (Galewski et al., 2005; Upham and Patterson, 2012, 2015; Fabre et al., 2014) or even the late Oligocene (Verzi et al., 2016:online resource 3). Thus, our phylogenetic hypothesis that suggests that the absence of fossils related to *Thrichomys*, *Myocastor*, and euryzygomatomyines in the rich late Oligocene–middle Miocene Patagonian deposits implies a bias in the fossil record. In addition, the presence of fossils belonging to the above-mentioned clades in the uppermost Miocene (Huayquerian age) of central and western Argentina (Verzi et al., 1995; Vucetich, 1995; Olivares and Verzi, 2015; Sostillo et al., 2015) is preceded by an absence of echimyids in lower strata of the upper Miocene (Chasicóan) fossil beds (Verzi, 2002:312) that are rich in small octodontoids (e.g., Pascual, 1967; Bondesio et al., 1980; Verzi, 1999; Montalvo et al., 2015). This supports the idea that

late Miocene echimyids from central and western Argentina would represent a southern extension of Brazilian radiations (Verzi, 2002) that occurred after the withdrawal of the middle-late Miocene Paranense Sea (Pascual et al., 1985; Webb, 1995; Hernández et al., 2005). Recent phylogenies including both living and extinct taxa, although still incomplete, suggest that echimyid species were less numerous in the fossil record of Argentina than previously thought, in contrast to octodontids and abrocomids (Verzi et al., 2014, 2015, 2016, in press). This supports the idea that the presence of this family in southern South America has always represented an impoverished, marginal sample of its extraordinary diversity in the northern tropical areas.

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