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## Systematics, phylogeny and evolutionary pattern of the hystricognath rodent *Eumysops* (Echimyidae) from the Plio–Pleistocene of southern South America

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†*Eumysops* is a peculiar representative of the currently tropical family Echimyidae, which evolved in increasingly dry and cold Plio–Pleistocene environments of southern South America. The results of a systematic and stratigraphic review of the genus, and of phylogenetic analyses based on both morphology and a combined morphological–molecular dataset in the context of extant representatives, are presented here. Recognised diversity includes four previously described species plus a new one from the late Pliocene. These species form a well-supported monophyletic clade, sister to the late Miocene †*Pampamys* and the extant *Thrichomys*. The position of †*Eumysops*–†*Pampamys*–*Thrichomys* in a major clade including non-‘eumysopine’ echimyids constrains the traditional taxon Eumysopinae only to these three genera. Phylogeny and stratigraphic distribution of †*Eumysops* species suggest an essentially cladogenetic evolutionary pattern. Beyond this, a gradual directional change, involving increase in size and in molar hypsodonty, is shown by †*Eumysops chapadmalensis* as part of a late Pliocene faunal turnover interpreted as a local representation of the 2.5-Ma cooling global event. Distinctive skeletal and dental anatomy of †*Eumysops*, including large orbits, shortened braincase, marked hypsodonty and postcranial specialisations, would be a result of its southern history related to a particular palaeoclimatic context.

**Keywords:** Rodentia; caviomorph; Echimyidae; phylogeny; Plio–Pleistocene; 2.5-Ma palaeoclimatic event

### Introduction

In the living fauna, Echimyidae (spiny rats, tree rats and coypu) is the most diverse family of hystricomorph rodents (Reig 1989, fig. 1; Woods and Kilpatrick 2005; Upham and Patterson 2012). They have a deep evolutionary history; in accordance with molecular evidence, it extends as far back as the late Oligocene (Upham and Patterson 2012; Fabre et al. 2013; Voloch et al. 2013), while even older fossil echimyids have been recognised (late Eocene–early Oligocene; Frailey and Campbell 2004). The present distribution of echimyids is essentially in tropical forests (Amazonian, coastal and Andean forests), and occasionally more open, xeric habitats in the Cerrado and Caatinga, in northern South America (Hershkovitz 1958; Vucetich and Verzi 1999; Galewski et al. 2005; Upham and Patterson 2012; Figure 1). *Myocastor*, sometimes included in a family of its own (e.g. Woods and Kilpatrick 2005), is the only echimyid currently distributed in southern South America. However, part of the modern history (late Miocene to Pleistocene) of the family took place in open habitats of southern South America. Species related to the living terrestrial and fossorial, open biomes inhabitants, *Thrichomys*, *Clyomys* and *Euryzygomatomys* underwent a strong diversification in central and north-western Argentina since the late Miocene (Huayquerian; Rovereto 1914; Reig 1989; Verzi et al. 1994, 1995, in press; Vucetich and Verzi 1996; Olivares, Verzi, Vucetich and

Montalvo 2012). †*Eumysops* is part of this modern record and is the only echimyid with a long evolutionary history in southern South America (Vucetich and Verzi 1996). In addition, the genus is represented in the fossil record through abundant and well-preserved materials: †*Eumysops* gathers the most complete fossil record of the family, and even one of the most abundant and complete among caviomorphs, mostly recovered from the rich Plio–Pleistocene deposits of the coast of central Argentina (Reig 1958). Despite its uniqueness and rich record, systematic and evolutionary studies of this genus are very scarce (e.g. Kraglievich 1957, 1965) and have no reference to materials, whereby available samples are mostly unpublished.

In a previous paper, the earliest species of the genus were revised (Olivares, Verzi and Vucetich 2012). This revision is completed here through the analysis of the most abundant samples collected in the rich Pliocene coastal outcrops of the Chapadmalal area in central Argentina (Cione and Tonni 1995a). New data of anatomy, systematics, phylogeny and the stratigraphic distribution of the variation of †*Eumysops* are provided here. The diversity and phylogeny of the genus are analysed in the macrosystematic context of the Echimyidae; finally, the evolutionary pattern of this lineage, related to the uniqueness of its geographical and palaeoclimatic context, is analysed.

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## Material and methods

More than 250 skull, mandibular and postcranial remains of †*Eumysops* from the Plio–Pleistocene of central Argentina were studied (Figure 1; Supplementary Material 1). Morphological variation was assessed controlling for ontogeny by defining age categories based on tooth eruption and occlusal wear of upper and lower molars (Supplementary Material 2; Patton and Rogers 1983; Patton 1987; Malcolm 1992; Leite 2003; Bezerra and de Oliveira 2010; Olivares, Verzi and Vucetich 2012). The phylogenetic analysis was based on a matrix of 62 cranial, mandibular and dental characters from 25 extant and extinct genera of Echimyidae (Supplementary Material 3). The extant *Octodontomys* (Octodontidae) and *Dasyprocta* (Dasyproctidae) were used as outgroups. The data were analysed using the ‘traditional search’ option of TNT v. 1.1 (Goloboff et al. 2008a, 2008b). All characters were equally weighted and considered nonadditive. 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 topologies of minimum length (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 (BS) was calculated using absolute and relative Bremer support (RBS) indices (Bremer 1994; Goloboff and Farris 2001). In addition, we performed a

combined parsimony analysis of extinct and extant echimyids, based on our morphological dataset and five marker sequences obtained from GenBank (Supplementary Material 4): two mitochondrial genes (*Cytochrome b*, 1140 bp; *12S rRNA*, 932 bp) and three unlinked nuclear exons [growth hormone receptor exon 10, 801 bp; von Willebrand factor exon 28, 1149 bp; *RAG1*, part of the recombination activating gene, 1064 bp]. All of them were used in molecular phylogenies of octodontoids or echimyids (e.g. Leite and Patton 2002; Galewski et al. 2005; Patterson and Velazco 2008; Upham and Patterson 2012; Fabre et al. 2013). Sequences of each of the five genes were aligned using CLUSTAL X (Thompson et al. 1997) with the default values of gap opening and gap extension. The dataset of morphological traits was concatenated with the gene sequences, and extinct taxa were coded as missing for all molecular characters. This matrix contained a total of 39 taxa and 5150 characters; *Erethizon* (Erethizontoidea), *Cavia*, *Dasyprocta* (Cavioidea), *Chinchilla* (Chinchilloidea), *Abrocoma* (Octodontoidea, Abrocomidae), *Octomys*, *Octodontomys*, *Spalacopus*, *Octodon*, *Tympanoctomys*, *Pipanacoctomys* and *Aconaemys* (Octodontoidea, Octodontidae) were included as outgroups. The parsimony analysis was conducted treating gaps as missing data in TNT 1.1 (Goloboff et al. 2008a, 2008b). The heuristic search consisted in 10,000 replicates of a Wagner tree with random addition sequence of taxa and followed by TBR branch swapping. In addition, we performed an extra round of TBR

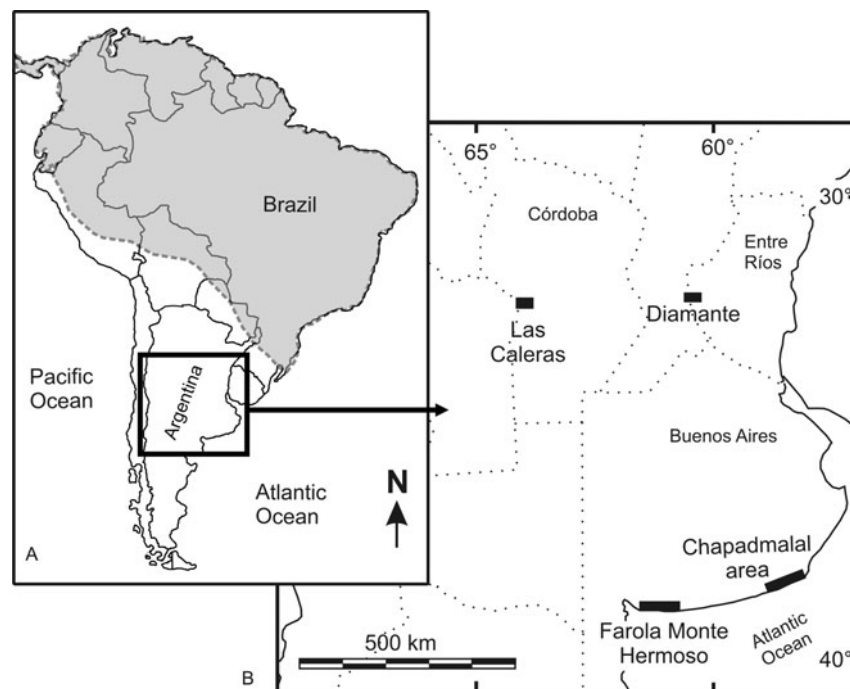


Figure 1. (A) Geographical distribution of the living echimyids (except for *Myocastor*) in South America. (B) Location of the †*Eumysops* bearing deposits in central Argentina (black rectangles).

on the optimal trees to increase the chance of finding all topologies of minimum length (Bertelli and Giannini 2005). Nomenclature of craniomandibular and postcranial traits follows Grassé (1967), Moore (1981), Wahlert (1984), Novacek (1993), Verzi (1994, 2001) and Rose and Chinnery (2004). Molar nomenclature corresponds to Marivaux et al. (2004) and Antoine et al. (2012); homologies follow Verzi et al. (in press) and results here. Hypsodonty indices (*H*) were determined as M1/m1 hypoflexus/id height divided by M1/m1 anteroposterior length.

### ***Institutional abbreviations***

The material studied in this paper is housed in the palaeontological and mastozoological collections of the MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; MD-FM, Museo Municipal de Ciencias Naturales ‘Charles Darwin’, Coronel Rosales, 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; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, CA, USA; UFBA, Museu de Zoologia, Universidade Federal da Bahia, Salvador, Brazil; UnB, Universidade de Brasília, Brasília, Brazil; USP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

### **Systematic palaeontology**

Order **RODENTIA** Bowdich, 1821

Infraorder **HYSTRICOGNATHI** Brandt, 1855

Superfamily **OCTODONTOIDEA** Waterhouse, 1839

Family **ECHIMYIDAE** Gray, 1825

**Genus *Eumysops*** Ameghino, 1888 non Wilson, 1935a

#### ***Eumysops chapalmalensis* (Rovereto, 1914)**

(Figures 2, 3(C)(D) and 4, Supplementary Material 5)

*Proaguti chapalmalensis* Ameghino, 1908: 424 (*nomen nudum*).

*Proaguti chapalmalensis* Rovereto, 1914: 188, Figure 73 (original description).

*Proaguti cavioides* Rovereto, 1914: 189.

*Eumysops chapalmalensis* Kraglievich, 1965: 259–266, Figure 2.

### ***Holotype***

MLP 15-20a, part of the left maxillary with DP4–M3 and left hemimandible with m1–m3 (Figure 2(A)–(C)) from

the coastal cliffs of the Chapadmalal area (southeastern Buenos Aires Province, central Argentina; Figure 1).

### ***Referred material***

Holotype and specimens in Supplementary Material 1.

### ***Locality and horizon***

Coastal cliffs of the Chapadmalal area between the cities of Mar del Plata and Miramar (southeastern Buenos Aires Province, central Argentina); Chapadmalal, Barranca de los Lobos, Vorohué and San Andrés Formations; Chapadmalalan and Marplatan stages, Plio–Pleistocene; Las Caleras (Córdoba Province, central Argentina), Las Caleras Formation, Chapadmalalan, upper early Pliocene–late Pliocene; coastal cliff north of Mar del Plata city (Buenos Aires Province, Argentina), Ensenadan, middle Pleistocene, sediments below of unit 1 (*sensu* Verzi et al. 2002) (Figure 1; Supplementary Materials 1 and 6).

### ***Extended diagnosis***

The largest species of †*Eumysops*; interpremaxillary foramen long and broad; incisive foramina subrhomboidal to lyre-shaped; premaxillary portion of the premaxillary septum strongly developed, the vomer completes the septum; anterior portion of palatal bridge markedly more dorsal than alveolar margins of DP4, forming a deep fossa without a median ridge; paranasal sinus more inflated than in the remaining species; sphenopalatine foramen posterodorsally elongated, level with M1–M2; palatine foramen level with M1; foramen into the nasolacrimal duct dorsal to sphenopalatine foramen; orbital portion of lacrimal elongated and narrow; lacrimal foramen opening into the maxilla; jugal fossa broad, extended on the maxilla; masticatory and buccinator foramina distinct; postglenoid foramen in the anterior part of an anteroposterior canal below the posterior apophysis of the squamosal; lateral process of supraoccipital extending ventrally below the level of the mastoid process; paroccipital apophysis ventral to the auditory bulla; notch for tendon of the infraorbital part of the medial masseter muscle as an inconspicuous semicircular groove or rough area incorporated into the origin of the masseteric crest; mandibular condyle lower (with respect to the occlusal plane) than in the remaining species; bottom of hypoflexus anteriorly oriented in M1–M2 with labial fossettes; DP4 with labial fossettes in specimens with unworn M3; labial side of M1 with only mesofossette in specimens of age VI; lower molars with metaflexid slightly more persistent than the mesoflexid; neural apophyses of sacral vertebrae unfused; anterior iliac spine in more distal position than in remaining echimyids; gluteal ridge of femur strongly



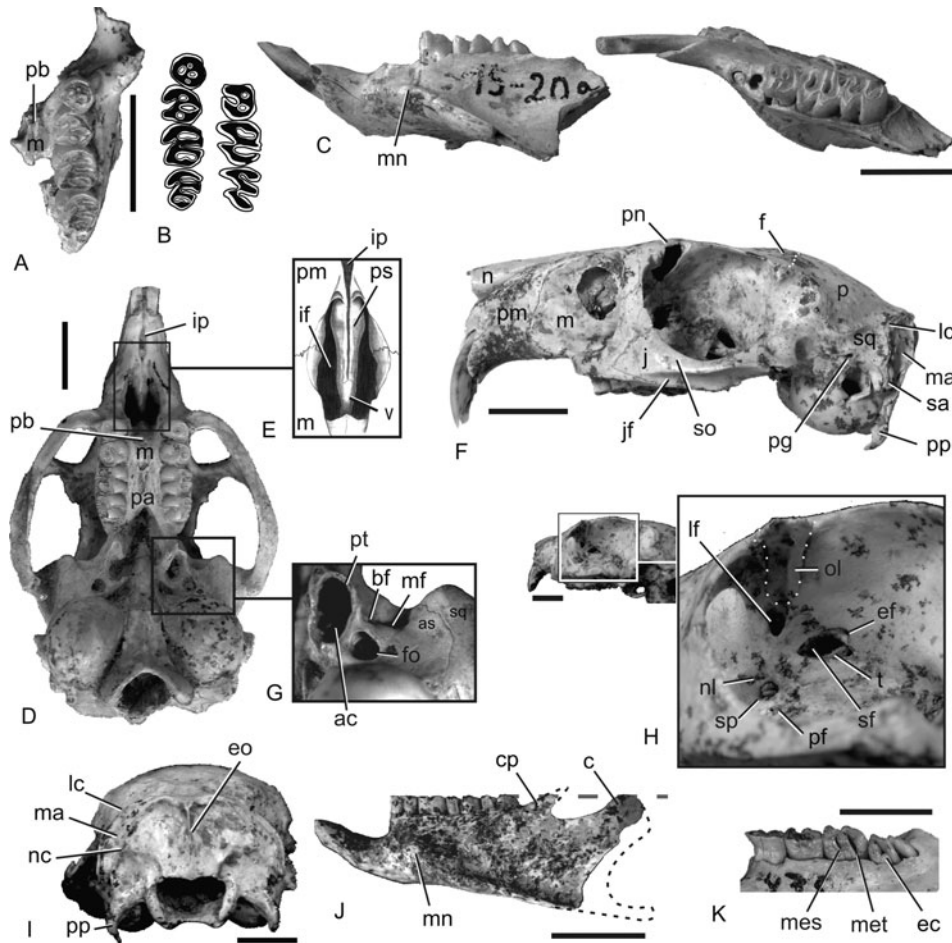


Figure 2. †*Eumysops chapalmalensis*. (A)–(C) MLP 15-20a holotype. (A) Ventral view of left maxillary portion. (B) Occlusal morphology of left DP4–M3 and left m1–m3. (C) Lateral and dorsal views of the left hemimandible. (D, E, G) MMP 834-M. (D) Ventral view of the skull. (E) Detail of the incisive foramina. (F) Lateral view of the skull MMP 4201-M. (G) Detail of left basitemporal region. (H) Detail of the orbital region of MMP 403-M. (I) Occipital view of MMP 4201-M. (J) Lateral view of left mandible MMP 2436-M. (K) Lingual view of right dp4–m3 of MMP 435-S. ac, alisphenoid canal; as, alisphenoid; bf, buccinator foramen; c, condyle; cp, coronoid process; ec, external column; ef, etmoid foramen; eo, external occipital crest; f, frontal; fo, foramen ovale; if, incisive foramina; ip, interpremaxillary foramen; j, jugal; jf, jugal fossa; lc, lambdoid crest; lf, lacrimal foramen; m, maxilla; ma, mastoid portion of bulla; mes, mesoflexus; met, metaflexus; mf, masticatory foramen; mn, masseteric notch; n, nasal; nc, nugal crest; nl, foramen into nasolacrimal duct; ol, orbital portion of lacrimal; p, parietal; pa, palatine; pb, palatal bridge; pf, palatine foramen; pg, postglenoid foramen; pm, premaxilla; pn, paranasal sinus; pp, paroccipital process; ps, premaxillary septum; pt, pterigoid fossa; sa, lateral apophysis of supraoccipital; sf, sphenopalatine fissure; so, suborbital fossa; sp, sphenopalatine foramen; sq, squamosal; t, turbinates; v, vomer. Scale: 10 mm.

developed, extending below femoral head; metatarsals I, II and V markedly reduced.

### Description

#### Skull

**Rostrum.** It is slender, especially in its anterior portion which accompanies the procumbency of upper incisors (Figure 2(D)). The interpremaxillary foramen is long and wide, similar to that of †*Eumysops formosus* (Olivares, Verzi and Vucetich 2012) and the new species, and markedly different from that of †*Eumysops gracilis*.

The incisive foramina are subrhomboidal (Figure 2(E)). The anterior margins of the incisive foramina are in contact with the interpremaxillary foramen. The premaxillary septum is long and wide. As in †*Eumysops formosus*, the vomer takes part of the premaxillary septum and is at the level of the premaxillary portion. The anterior portion of the palatal bridge is more dorsal than the alveolar margins of the DP4. It has no median ridge as in †*Eumysops formosus*; it is shorter and has a small anterior projection of the maxilla in its median point. Paranasal sinuses are more inflated than in the remaining species, forming externally visible prominences (Figure 2(F)), even in juveniles of age II (Supplementary Material 2).

**Orbital region.** It is wider and more posterior (with respect to the DP4) than in the other echimyid genera; the antorbital zygomatic bar is at the level of M1–M2 (Figure 2(F)). The zygomatic arch is very expanded laterally (Figure 2(D)). The anterior portion of the jugal fossa extends in front of the maxilla–jugal suture as in †*Eumysops laeviplicatus*. The suborbital fossa in the dorsal portion of the jugal is more anterior than in the remaining species (Figure 2(F)). The facial process of lacrimal is subtriangular and the orbital portion of lacrimal is long and narrow; as in the remaining echimyids, it does not contact with the lacrimal foramen, which opens in the maxillary (Figure 2(H)). The sphenopalatine foramen is posterodorsally elongated. Both this and the palatine foramen are in a long depression of the maxilla at the level of M1–M2, similar to that of †*Eumysops formosus* (Olivares, Verzi and Vucetich 2012) and the new species. In juveniles of age II, these foramina are at the level of DP4–M1. The ethmoid foramen is small and posterodorsal to the sphenopalatine fissure as in †*Eumysops laeviplicatus* (Figure 2(H)). In some specimens, turbinates are observed through the sphenopalatine fissure at the level of M2–M3.

**Cranial vault.** The post-dentary portion is shorter than in the living echimyids except for *Trinomys yonenagae*. The skull is posteriorly bowed and shortened (Figure 2(F)); this morphology is exclusive among echimyids, and more pronounced in juveniles and subadults. This posterior flexion and shortening of the skull is expressed through the vaulted parietals, markedly shortened and descending, the posteroventral orientation of basisphenoid and basioccipital, and in the more ventral position of the occipital condyle with respect to the tympanic bulla (Figure 2(D),(F)). The auditory bulla is rounded in lateral view and slightly elongated in ventral view as in the rest of the species of the genus (it is unknown in †*Eumysops formosus*). The postglenoid foramen is observed inside the anteroposterior canal formed between the squamosal and the external auditory meatus; this morphology is similar to that of †*Eumysops laeviplicatus* and markedly different from that of †*Eumysops gracilis* in which there is no canal. The mastoid bulla is narrower than in †*Eumysops gracilis* (Figure 2(F),(I)). The pterygoid fossa is semicircular and wide, and the alisphenoid canal (*sensu* Woods and Howland 1979) is short. The palatine shapes much of the lateral margin of the pterygoid fossa. The foramen ovale (Hill 1935) communicates with the pterygoid fossa and with the buccinator and masticatory foramina (Figure 2(G)), as in *Trichomys*, *Proechimys* and *Trinomys*. The buccinator foramen (Hill 1935) is rounded and small, and is located between the lateral–external wall of the pterygoid fossa and the masticatory foramen (Hill 1935), behind an anteroposterior groove (Figure 2(G)). The pterygoid apophysis preserved in MMP 403-M is long and its end contacts the anteromedial margin of the bulla.

The fossa for the temporal muscle (main part) is little developed compared with that of the living ‘echimyines’ and dactylomyines. Laterally, the posterior apophysis of the squamosal is elongate and its dorsal margin is markedly sigmoid as in †*Eumysops laeviplicatus* and †*Eumysops gracilis* (unknown in †*Eumysops formosus*), and similar to *Proechimys*. In the lateral apophysis of the supraoccipital, there is a lambdoid crest more pronounced than in other echimyids (Figure 2(F)). The paroccipital process exceeds the auditory bulla, ending in a sharp tip anteriorly directed. The occipital external crest is long (Figure 2(I)) as in living ‘eumysopines’ and strongly different from ‘echimyines’ and dactylomyines in which it is very short. The orientation of the distal portion of the paroccipital process is rotated so that its external margin becomes posterolateral as in other echimyids (Figure 2(I)).

#### Mandible

The mandible is slender (Figure 2(J)) as in the remaining species of †*Eumysops*. The diastema is moderately excavated in front of dp4, less than in †*Eumysops laeviplicatus*. The anterior portion of the diastema is somewhat more dorsal than the dorsal alveolar edge of dp4 in adults. The notch for the tendon of the infraorbital part of the medial masseter muscle is an inconspicuous, semicircular step incorporated into the origin of the masseteric crest, as in the remaining species of the genus, the late Miocene †*Pampamys*, and the living *Trichomys*. The external margin of the masseteric crest curves dorsally. The anterior margin of the coronoid process is at the level of the posterior portion of m3. The mandibular condyle and coronoid process are lower than in the remaining echimyids, near the occlusal level of molars. This is common to all species of †*Eumysops*, but in †*Eumysops chapalmalensis* the condyle is lower than in the remaining species of the genus (Figure 2(J)).

#### Molars

†*Eumysops chapalmalensis* has unilateral hypsodonty as in the remaining species of the genus. The molars of †*Eumysops chapalmalensis* have crowns lower than those of †*Eumysops gracilis* and of the new species. In occlusal view, the bottom of the hypoflexus is anteriorly oriented in M1–M2 with labial fossettes (ages IV–VI; Figure 3(A), (C)), as in †*Eumysops laeviplicatus* (Olivares, Verzi and Vucetich 2012). In specimens of age III, the DP4 has already labial fossettes, unlike †*Eumysops laeviplicatus* in which para- and mesoflexus are more persistent (Olivares, Verzi and Vucetich 2012). Specimens of †*Eumysops chapalmalensis* of age IV have labial fossettes in M1 and the hypoflexus shallow in lateral view, almost becoming a hypofossette. In specimens of the same age of †*Eumysops*

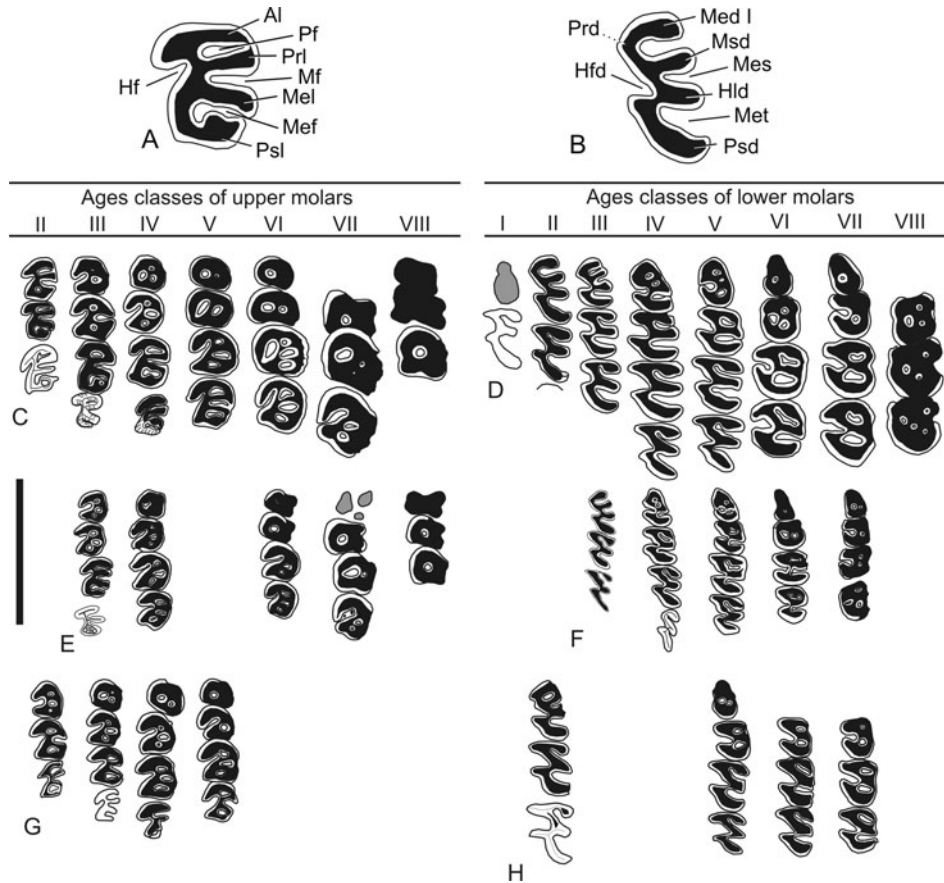


Figure 3. Ocusular morphology of the molars of †*Eumysops*. (A, B) Nomenclature of lophs/ids and flexi/ids in (A) left M1 of MMP 4172-M and (B) left DP4 of MMP 632-S. (C, E, G) Left upper molars. (D, F, H) Left lower molars. (C, D) †*Eumysops chapalmalensis*. (E, F) †*Eumysops gracilis*. (G, H) †*Eumysops marplatensis*. All molars are sorted by age classes (description of age classes is in Supplementary Material 2). (C) DP4-M1, MMP 4172-M (II); DP4-M3, MLP 88-VII-5-5 (III); DP4-M3, MACN-PV 100 (IV); DP4-M3, MMP 832-M (V); DP4-M3, MMP 4201-M (VI); M1-M3 (reversed right), MMP 1362-M (VII); DP4-M1, MLP 51-VI-11-50 (VIII). (D) m1 (reversed right), MMP 668-S (I); dp4-m1, MMP 632-S (II); dp4-m2 (reversed right) MLP 91-IV-5-228 (III); dp4-m3, MMP 623-M (IV); dp4-m3 (reversed right) MACN-Pv 10963 (V); dp4-m3 (reversed right), MMP 4201 (VI); dp4-m3 (reversed right), MMP 546-M (VII); m1-m3 (reversed right), MMP 454-S (VIII). (E) DP4-M3, MMP 798-M (III); DP4-M3 (reversed right), MLP 62-VII-27-75 (IV); DP4-M3, MMP 410-M (VI); m1-m3, MMP 799-M (VII); dp4-m2, MACN-Pv 19335 (VIII). (F) dp4-m2 (reversed right), MLP 91-IV-5-224 (III); dp4-m3 (reversed right), MMP 798-M (IV); dp4-m3 (reversed right), MMP 559 (V); dp4-m3, MMP 782-S (VI); dp4-m3, MMP 451-S (VII). (G) DP4-M2, MMP 1052 (II); DP4-M3, MMP 1056-M (III); DP4-M3, MMP 1055-M (IV); DP4-M3, MMP 482-M (holotype) (V). (H) dp4-m2 (reversed right) MACN-PV 19705 (II); dp4-m3, MMP 482-M (holotype) (V); m1-m3, MACN-Pv 19702 (VI); m1-m3, MACN-Pv 19699 (VII). al, anteroloph; hf, hypoflexus; hfd, hypoflexid; hld, hypolophid; med I, metalophulid I; mef, metaflexus; mel, mesolophule; mes, mesoflexid; met, metaflexid; mf, mesoflexus; msd, mesolophid; pf, paraflexus; prd, protoconid; prl, protoloph; psd, posterolophid; psl, posteroloph + metaloph. Scale: 10 mm.

*gracilis* and the new species, the hypoflexus is deeper and shows no sign of closing. In specimens of age VI of †*Eumysops chapalmalensis*, the labial side of M1 has only mesofossette, whereas age-equivalent specimens of †*Eumysops laeviplicatus* have meso- and metafossette (Olivares, Verzi and Vucetich 2012), and there are no labial fossettes in †*Eumysops gracilis* (Figure 3(E)). In lower molars of †*Eumysops chapalmalensis*, the metaflexid closes shortly after the mesoflexid (Figure 3(B),(D)), as in †*Eumysops laeviplicatus*. In some specimens, there is a small external column (of the mesoflexid?) joined to the posterior margin of the metalophulid I (Figure 2(K)).

Those materials of †*Eumysops chapalmalensis* from the Vorohué and San Andrés Formations (Figure 9) have differences in the skull and molars compared with the specimens from the Chapadmalal Formation (see Stratigraphic distribution of the variation of †*Eumysops*).

#### Postcranial skeleton

The record of †*Eumysops chapalmalensis* includes most of the postcranial elements (Horovitz 1991; Olivares 2009). A detailed study is currently in progress (Olivares, Morgan



and Verzi, unpublished data). Only distinctive features are briefly mentioned here.

The neural apophyses of sacral vertebrae are unfused (Figure 4(A),(B)). In the pelvic girdle, the anterior iliac spine forms a very prominent tuberosity, located more anteriorly with respect to the acetabular fossa than in the remaining echimyids or even other caviomorphs (Figure 4(C),(D)). The gluteal crest, on the greater trochanter, is very developed and extends below the femur head (Figure 4(E),(F)). The morphology of the metatarsus is unique among caviomorphs; metatarsals (mt) III and IV are strongly larger than mt I, II and V (mt IV > mt III >> mt II > mt V > mt I) (Figure 4(G),(H)).

#### Remarks

Rovereto (1914) stated that *Proaguti cavioides* Ameghino (1908: 424) has similarities with *Proaguti chapalmalensis*.

However, there are no illustrations of this taxon, and no materials can be assigned to it; hence, its inclusion in the synonymy of *Eumysops chapalmalensis* is tentative. Kraglievich (1965) proposed the name *Eumysops paracavioides* for a species allegedly descendant from *Eumysops chapalmalensis*. According to the related chronological information, this name could correspond to what is here interpreted as more modern (post-Chapadmalalan materials) representatives of *Eumysops chapalmalensis*. However, Kraglievich (1965) did not describe nor illustrate or design materials, for which *Eumysops paracavioides* is a *nomen nudum* (Vucetich and Verzi 1995; Verzi and Quintana 2005).

In this paper, the materials from the Pliocene of Las Caleras Formation (central Argentina; Tauber 2000; Figure 1) are assigned to †*Eumysops chapalmalensis*, as well as unpublished isolated molars from the Pleistocene of northern Mar del Plata city in central Argentina (Verzi

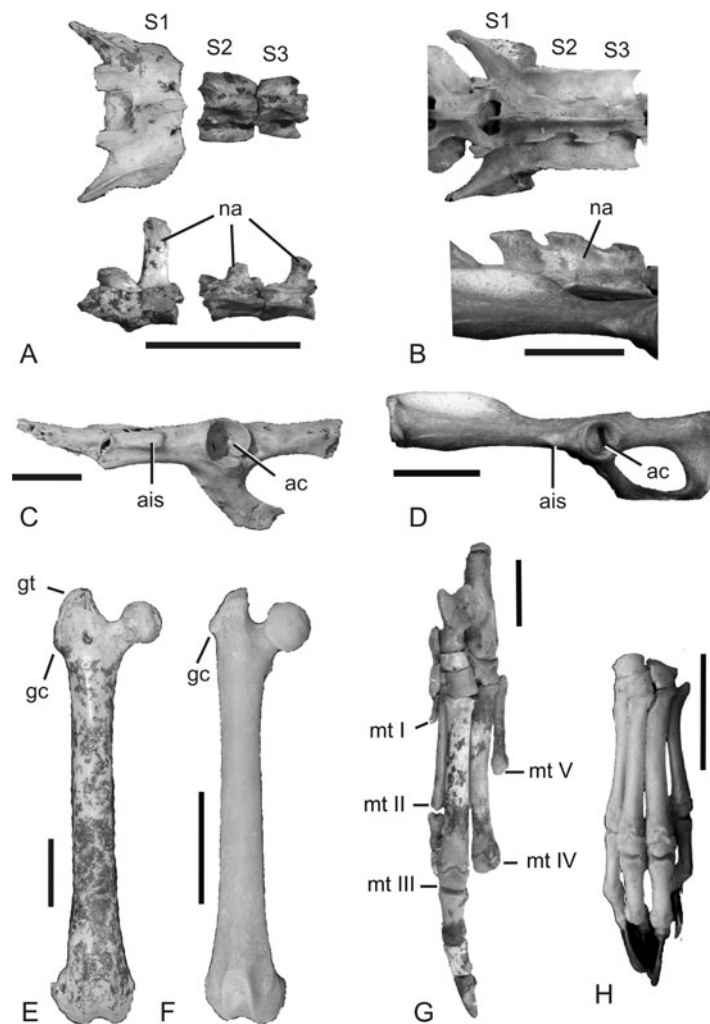


Figure 4. Postcranial skeleton of †*Eumysops chapalmalensis* (A, C, E, G) and the living *Thrichomys* (B, D, F, H). (A, B) Dorsal and lateral views of sacral vertebrae S1 to S3. (C, D) Lateral view of pelvic girdle. (E, F) Anterior view of right femur. (G, H) Dorsal view of left foot. ac, acetabular fossa; ais, anterior iliac spine; gc, gluteal crest; gt, greater trochanter; mt, metatarsus; na, neural apophyses; S, sacral vertebrae. Scale: 10 mm.



et al. 2002); these later extend the biochron of the genus to the middle Pleistocene (ca. 1.0 Ma).

***Eumysops gracilis* (Rovereto, 1914)**

(Figures 3(E)(F) and 5, Supplementary Material 5)

*Proaguti gracilis* Ameghino, 1908: 424 (*nomen nudum*).

*Proaguti complicatus* Ameghino, 1908: 424 (*nomen nudum*).

*Proaguti gracilis* Rovereto, 1914: 190.

*Eumysops formosus* Kraglievich, 1957: 38 (*partim*).

**Holotype**

MACN-A 53-2, damaged left hemimandible with m1–m3 (Figure 5(A),(B)) from the coastal cliffs of the Chapadmalal area (southeastern Buenos Aires Province, central Argentina; Figure 1).

**Referred material**

Holotype and specimens in Supplementary Material 1.

**Locality and horizon**

Coastal cliffs of the Chapadmalal area between the cities of Mar del Plata and Miramar (southeastern Buenos Aires Province, central Argentina); Chapadmalal, Vorohué and San Andrés Formations; Chapadmalalan stage, upper Marplatan stage (Vorohuean and Sanandresian substages), upper early Pliocene–early Pleistocene (Figure 1; Supplementary Materials 1 and 6).

**Extended diagnosis**

The smallest species of †*Eumysops*; interpremaxillary foramen small; incisive foramina oval; premaxillary septum principally formed by premaxillae and an anterior maxillary apophysis; anterior portion of palatal bridge at the same level or slightly more dorsal than alveolar margins of DP4, without median ridge; orbital portion of lacrimal at the level of the margin of lacrimal foramen; lacrimal foramen opening into the maxilla; paraorbital process formed by jugal; jugal fossa short and posterior to maxilla–jugal suture; inferior jugal process posteriorly oriented, slightly anterior to the level of paraorbital process; postglenoid foramen small; lateral process of the supraoccipital extending ventrally below the level of the mastoid process; mastoid portion of the bulla broad; molar crowns higher than those of †*Eumysops chapalmalensis*, and lower than those of the new species; all molars with labial fossettes in specimens of age IV; M1 with only hypofossette in specimens of age VI; lower molars with metaflexid notably more persistent than the mesoflexid.

**Description**

**Skull**

**Rostrum.** The interpremaxillary foramen is small and is closer to the incisive foramina (Figure 5(C),(D)) than in †*Eumysops laeviplicatus*. Unlike the other species, the premaxillary septum is completed by an anterior apophysis of the maxillary. The vomer is dorsal to the septum and is not involved in its formation. The anterior portion of the palatal bridge has no medial crest.

**Orbital region.** It is more posterior (with respect to the DP4) than in the other echimyid genera, the antorbital zygomatic bar being at the level of M1–M2 as in the remaining species of the genus (Figure 5(E)). The lower apophysis of the jugal is posteriorly oriented. The anterior portion of the jugal is dorsally extended on the antorbital zygomatic bar. The suborbital fossa is deep. The jugal fossa is more posterior than in the rest of the species. The sphenopalatine foramen is elongated in specimens of ages III and IV by influence of the alveolar sheath of the M1, which protrudes dorsally into the orbital floor. In specimens of ages VI–VIII, it is rounded because molars are more worn and do not invade the orbit. There is no sphenopalatine fissure. The orbital portion of the lacrimal reaches the margin of the lacrimal foramen (Figure 5(G)).

**Cranial vault.** The postglenoid foramen is small, semicircular in shape (Figure 5(E)); this foramen is not included in a canal as in †*Eumysops laeviplicatus* (Olivares, Verzi and Vucetich 2012) and †*Eumysops chapalmalensis* (Figure 2(F)). The alisphenoid has a particular morphology; it has no buccinator and masticatory foramina; one foramen on the lateral wall of the pterygoid fossa, ventral-medially to the oval foramen (Figure 5(F)), may correspond to the posterior opening of the alisphenoid canal described by Iack-Ximenes et al. (2005) for some living ‘echimyines’, or be the equivalent to the external alisphenoid canal of Hill (1935). The mastoid bulla is broader than in †*Eumysops chapalmalensis* (Figure 5(H)).

**Mandible**

The mandible is more slender than in the remaining species of the genus (Figure 5(I)). The mandibular condyle is lower than in †*Eumysops laeviplicatus* and higher than in †*Eumysops chapalmalensis*.

**Molars**

The molars of †*Eumysops gracilis* are lower than those of the new species and higher than those of the remaining species. The hypoflexus penetrates deeply in the occlusal surface in molars with labial fossettes (ages IV–VII; Figure 3(E)). The morphology of lower molars is similar to that of †*Eumysops formosus* in that its metaflexid is notably more persistent than the mesoflexid, which causes that

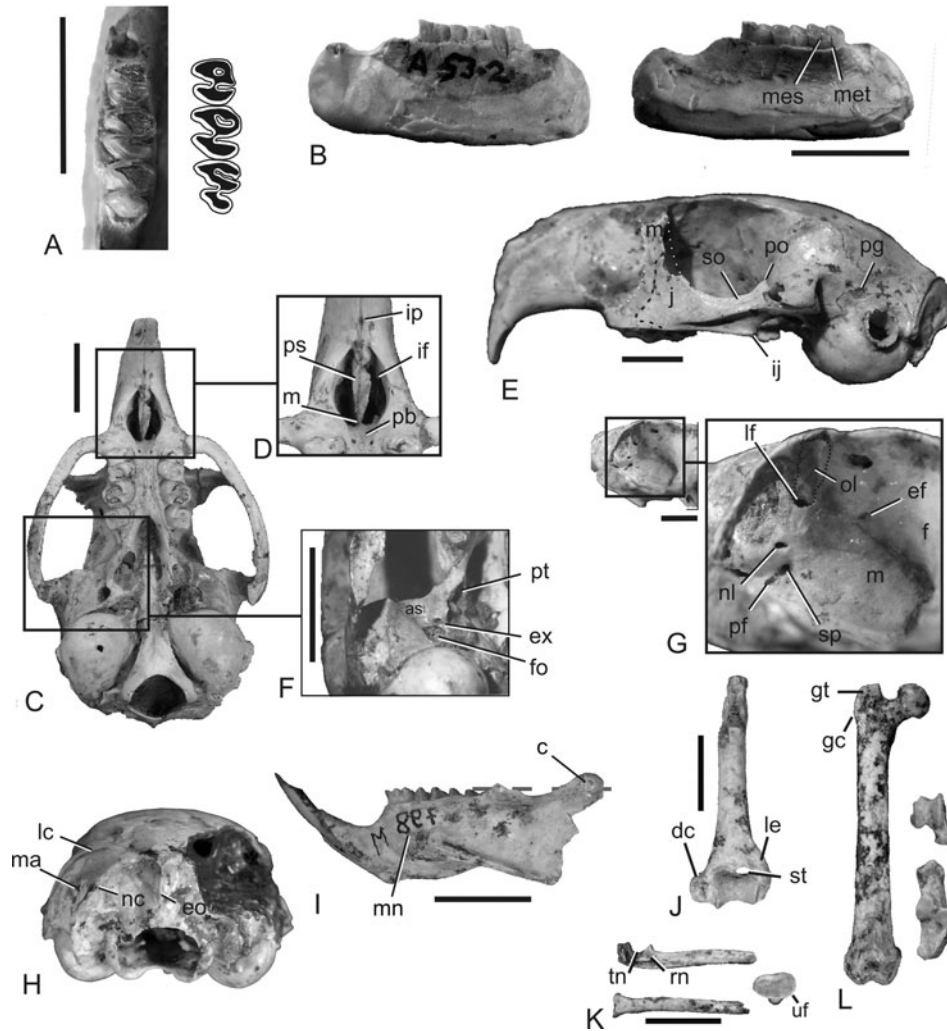


Figure 5. †*Eumysops gracilis*. (A, B) MACN-A 53-2 holotype. (A) Dorsal view of left hemimandible and occlusal morphology of m1–m3. (B) Labial and lingual (reversed) view of left hemimandible. (C)–(H) skull MMP 410-M. (C) Ventral view. (D) Detail of the incisive foramina. (E) Lateral view. (F) Detail of the right basitemporal region. (G) Detail of the orbital region. (H) Occipital view. (I)–(L) MMP 798-M. (I) Lateral view of right hemimandible (reversed). (J) Anterior view of the distal portion of right humerus. (K) Lateral view of the proximal portion of the right ulna, dorsal view of right radius and radius head. (L) Anterior view of right femur and dorsal view of astragalus and calcaneus. dc, deltoide crest; ex, external canal; ij, inferior jugal process; le, lateral epicondylar ridge; po, paraorbital process; rn, radial notch; st, supratrochlear foramen; tn, trochlear notch; uf, ulnar facet. The remaining abbreviations as in Figures 2 and 4. Scale: 10 mm.

molars to acquire a transitory eight-shaped occlusal morphology (Figure 3(F)). Unlike †*Eumysops formosus*, in juveniles of ages III–V, meso- and metaflexid are more penetrating, and hence, their bottoms exceed that of the hypoflexid (Figure 3(F); Olivares, Verzi and Vucetich 2012).

The single known mandible of †*Eumysops gracilis* from the Vorohuean has higher crowned molars than the specimens from the Chapadmalalan.

#### Postcranial elements

The postcranial elements of this species are known only by the juvenile specimen MMP 798-M (age III; Figure 5(J)–(L)). Only the distal portion of the humerus is preserved

(Figure 5(J)). This has the lateral epicondylar ridge more marked and the entepicondyle more medially protruding than in †*Eumysops laeviplicatus* (Olivares, Verzi, Vucetich and Montalvo 2012b). The olecranon fossa is perforate as in the other species of the genus in which it has been preserved, †*Eumysops laeviplicatus* and †*Eumysops chapadmalensis*. The olecranon process of the ulna is partially preserved; the trochlear and radial notch are broad as in †*Eumysops laeviplicatus* (Figure 5(K)). In the radius, only the proximal portion of the shaft is preserved. The head of the radius is slightly suboval, and the ulnar facet is rounded, unlike in †*Eumysops laeviplicatus* and †*Eumysops chapadmalensis* in which it is subrectangular. Femur, astragalus and calcaneus are preserved

(Figure 5(L)). These elements are very similar to those of †*Eumysops chapalmensis* but smaller.

Remarks

Here, *Eumysops complicatus* is considered a synonym of *Eumysops gracilis*, as stated by Rovereto (1914, as *Proaguti*). Kraglievich (1957) considered *Eumysops gracilis* as a junior synonym of *Eumysops formosus*, which is not accepted here. This author also related *Eumysops gracilis* with ‘*Proaguti*’ *intermixtus* Ameghino, 1908; however, the limited available description of this latter species, supplied by Rovereto (1914, p. 190), and the lack of referred materials do not allow to elucidate its taxonomic status.

*Eumysops marplatensis* sp. nov.

(Figures 3(G)(H) and 6, Supplementary Material 5)  
*Eumysops* sp. Verzi and Quintana, 2005: 310–316 (partim).

Etymology

*Eumysops marplatensis*, in reference to stratigraphic and geographic distribution of the species in Marplatan outcrops of the coastal cliffs south of Mar del Plata city.

Holotype

MMP 482-S, maxillary with both DP4–M3 series and zygomatic arches partially preserved; right hemimandible

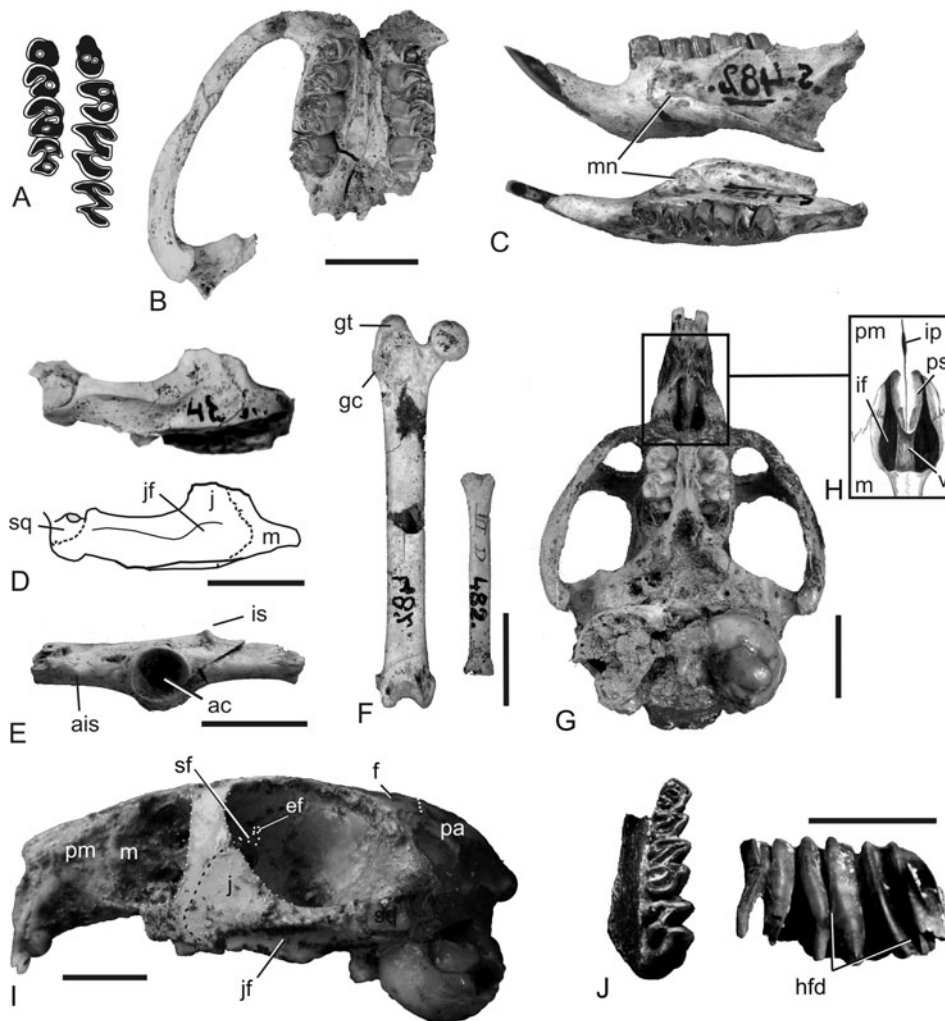


Figure 6. †*Eumysops marplatensis* sp. nov. (A)–(F) MMP 482-S holotype. (A) Occlusal morphology of left DP4–M3/dp4–m3. (B) Ventral view of maxillary portion with right zygomatic arch. (C) Lateral and dorsal views of right hemimandible (reversed). (D) Lateral view of the right zygomatic arch. (E) Lateral view of left pelvic girdle. (F) Anterior view of left femur (reversed) and dorsal view of metatarsus III. (G)–(I) MMP 1052-M. (G) Ventral view of skull. (H) Detail of the incisive foramina. (I) Lateral view of skull. (J) Occlusal and labial (reversed) views of right dp4–m2 MACN-PV 19705. hfd, hypoflexid; is, ischial spine. The remaining abbreviations as in Figures 2 and 4. Scale: 10 mm.

with dp4–m3; acetabular portion of the left pelvic girdle, left femur without distal epiphysis and right metatarsus III (Figure 6(A)–(F)).

### Hypodigm

MACN-Pv 19698, 19699, 19700, 19701, 19702, 19704, 19705; MMP 484-S, 1052-M, 1055-M, 1056-M (Supplementary Material 1).

### Locality and horizon

Coastal cliffs of the Chapadmalal area between the cities of Mar del Plata and Miramar (southeastern Buenos Aires Province, central Argentina), Vorohué and San Andrés Formations; upper Marplatan stage (Vorohuean and Sanandresian substages), late Pliocene–early Pleistocene. The holotype comes from Baliza San Andrés, General Pueyrredón, Buenos Aires Province, Argentina; San Andrés Formation; Sanandresian substage, late Pliocene–early Pleistocene (Figure 1; Supplementary Materials 1 and 6).

### Diagnosis

Medium-sized species of †*Eumysops*; interpremaxillary foramen very narrow; incisive foramina lyre shaped; vomer forming part of the premaxillary septum; anterior portion of palatal bridge at the same level of the alveolar margins of DP4, with a median ridge; antorbital zygomatic bar very wide, especially at its base; jugal notably extended in the antorbital zygomatic bar; jugal fossa high at the anterior portion; suborbital fossa absent; mandible robust, with a strong notch for the tendon of the infraorbital part of the medial masseter muscle; masseteric fossa deeper and masseteric crest more protruding than in the remaining species; molars with the highest crown among the echimyids; flexids more ephemeral than in the remaining species of the genus; upper and lower molars narrow, with enamel of the leading edge very thin; hypoflexus very deep in lateral view with respect to the labial flexids; hypolophid anteroposteriorly broader than in the remaining species; metaflexid slightly deeper than mesoflexid.

### Description

#### Skull

The skull is medium sized, with crests and fossae for muscular attachment stronger than in the remaining species.

**Rostrum.** The interpremaxillary foramen is narrower than that of †*Eumysops chapadmalensis*. The vomer forms the posterior part of the premaxillary septum, being more dorsal than the premaxillae (Figure 6(G)(H)).

**Orbital region.** As in the other species of the genus, the orbital portion is more posterior than in the remaining echimyids; the antorbital zygomatic bar is at the level of M1–M2 (Figure 6(I)). The zygomatic arch is robust. The antorbital zygomatic bar is very wide, especially ventrally, similar to that of the most modern specimens of †*Eumysops chapadmalensis*. The anterior portion of the jugal is very high and extends on the antorbital bar forming more than half of the posterior margin of this bar. The jugal fossa is notably deeper than in the remaining species, and its anterior portion is rounded and high (Figure 6(D),(I)), similar to that in *Clyomys* and *Euryzygomatomys*. The area for attachment of the lateral masseter muscle on the ventral surface of the zygomatic arch reaches the jugal, unlike the remaining species in which it is restricted to the maxillary. The alveoli of molars protrude into the orbit in the juvenile MMP 1052-M. The sphenopalatine and palatine foramina are arranged in a posterodorsally oblique groove as in †*Eumysops chapadmalensis* and †*Eumysops formosus*. The sphenopalatine fissure is small.

**Cranial vault.** The basicranial region and the cranial vault are badly damaged in the single specimen that preserves this area, MMP 1052-M. As far as can be seen, this entire portion is largely shortened and the parietals strongly curve downward. The auditory bullae are rounded and are moderately inflated as in the other species of †*Eumysops* (Figure 6(I)).

#### Mandible

The mandible is more robust than in the other species (Figure 6(C)). It is deeper, and the crests and fossae for muscular attachment are stronger. The notch for the tendon of the infraorbital part of the masseter muscle is very conspicuous; it is wide and markedly protruding, as protruding as the origin of the masseteric crest. The masseteric fossa is deeper than in the other species. The projecting crest is more protruding than in the other species, and in lateral view its anterior portion is very thick (Figure 6(C)).

#### Molars

Molars are higher crowned than in the other species of the genus and are the highest (Figure 6(J)) among echimyids (more than 20% higher than in the late Miocene hypsodont †*Reigechimys*). They are narrower than in the other species of the genus. The enamel thins at the labial side of the upper molars and at the lingual side of the lower molars (Figure 3(G),(H)). The bottom of the hypoflexus is oriented towards the paraflexus as in †*Eumysops formosus* and †*Eumysops gracilis*, unlike †*Eumysops laeviplicatus* and †*Eumysops chapadmalensis* in which it is more anteriorly oriented. The labial flexus are less deep



(ontogenetically more ephemeral) than in the other species (Figure 3(G)). The hypoflexus is deeper because it increases its depth with increasing hypsodonty. Consequently, it is more persistent than in the other species and remains open in the M1 of specimens of age V. The anterior margin of the hypoflexus remains transverse longer (up to age IV in M2). In three specimens of the sample, the M3 has a marked reduction of the mesolophule and metaloph + posteroloph (Figure 3(G), age IV). In the lower molars, the labial side is straighter than in the other species (Figure 3(H)). The hypolophid is anteroposteriorly wide. The mesoflexid is anterolabially oblique. Despite molars are very high crowned, the difference in height (and in consequent ontogenetic persistence) between meso- and metaflexid is slight, unlike what is observed in †*Eumysops formosus* and †*Eumysops gracilis*, and even in other echimyids with high molars such as †*Reigechimys* and †*Dicolpomys*, in which the metaflexid is notably more persistent. The lower incisor is more sharply recurved; thus, its base and the accompanying mandibular foramen are more anterior than in the other species.

#### Postcranial elements

The postcranial remains belong to the holotype and MACN-Pv 19700. In the first one, the pelvic girdle, femur and metatarsus III have been preserved, and in the second, only the tibia.

The ischial spine of the pelvic girdle is rounded and less prominent than in †*Eumysops chapalmalensis*. The anterior iliac spine is distalised as in the latter (Figure 6(E)). The femur of the adult MMP 482-M is more columnar (i.e. with more constant transverse diameter) than in that of †*Eumysops chapalmalensis* MMP 4201-M of comparable age (compare Figures 4(E) and 6(F)). The diaphysis is suboval in section, anteroposteriorly flatter than in †*Eumysops chapalmalensis* and †*Eumysops gracilis*. The gluteal crest is more prominent and is more distalised than in the remaining species. The greater trochanter is lower than in †*Eumysops chapalmalensis* and surpasses slightly the head of the femur (compare Figures 4(E) and 6(F)). The distal portion preserved of the tibia is similar to that of †*Eumysops chapalmalensis*. The metatarsus III is long, approximately half the length of the femur (Figure 6(F)). It is similar in length to that of the juvenile (age II) of †*Eumysops chapalmalensis* MMP 4172-M.

#### Phylogeny

##### Morphological data analysis

Three most parsimonious trees 112 steps long (CI = 0.643; RI = 0.833) were recovered in the phyloge-

netic analysis based on morphological data (Figure 7(A), Supplementary Material 3).

†*Eumysops* was recovered as a monophyletic clade, sister to the extinct †*Pampamys* and the living *Thrichomys*. The monophyly of †*Eumysops* is supported by six unambiguous synapomorphies: the anterior portion of the upper diastema markedly narrow (character-state 10-1); the antorbital zygomatic bar broad, with its anterior margin at the level of M1–M2 (character-state 26-1); the orbital region extended behind the level of the M2 (character-state 27-1); the parietals markedly descendant and short (character-state 36-1); the mandibular condyle markedly low (character-state 43-1); and the occlusal surface of upper incisors long, extended along the whole exposed portion of crown (character-state 49-1). This node had the highest support (Figure 7(A)).

Within †*Eumysops*, the morphologically divergent †*Eumysops gracilis* is the sister taxon of a clade including the remaining species of the genus. In this latter clade, †*Eumysops laeviplicatus* clusters with †*Eumysops marplatensis* + †*Eumysops chapalmalensis*–†*Eumysops formosus* by the narrow mastoid bulla (character-state 39-1). The new species, †*Eumysops marplatensis*, is grouped with †*Eumysops chapalmalensis* and †*Eumysops formosus* by the morphology of the incisive foramina with the anterior margins located lateral to the interpremaxillary foramen (character-state 6-1). Sister species †*Eumysops chapalmalensis* and †*Eumysops formosus* share the lack of medial ridge in the anterior portion of the palatal bridge (character-state 8-1). This pattern of relationships among species of †*Eumysops* shows moderate support.

The clade comprising the living *Thrichomys*, and the extinct †*Pampamys* and †*Eumysops*, is supported by three unambiguous synapomorphies: wide incisive foramina (character-state 5-1), the posterior margin of incisive foramina level with the anterior margins of the DP4 (character-state 7-1) and the notch for the tendon of the infraorbital part of the medial masseter muscle incorporated into the origin of the masseteric crest (character-state 46-1). The fragmentary remains of †*Pampamys* hinder the resolution of relationships in this clade.

The assemblage *Thrichomys*–†*Pampamys*–†*Eumysops* belongs to one of the major clades recovered together with the terrestrial spiny rats *Hoplomys*, *Proechimys* and *Trinomys*, the semiaquatic coypu *Myocastor*, the spiny tree-rat *Mesomys*, the arboreal ‘echimyines’–dactylomyines and fossil echimyids from the early to middle Miocene. These taxa share a more elongated pterygoid fossa (character-state 32-1), and the origin of the lateral apophysis of supraoccipital anteriorly deflected (character-state 34-1) (unknown in fossils). The other major clade includes the fossorial spiny rats *Carterodon*, *Clyomys* and *Euryzygomatomys* (*Euryzygomatomyini sensu* Emmons 2005), as well as the extinct †*Theridomysops*, and is

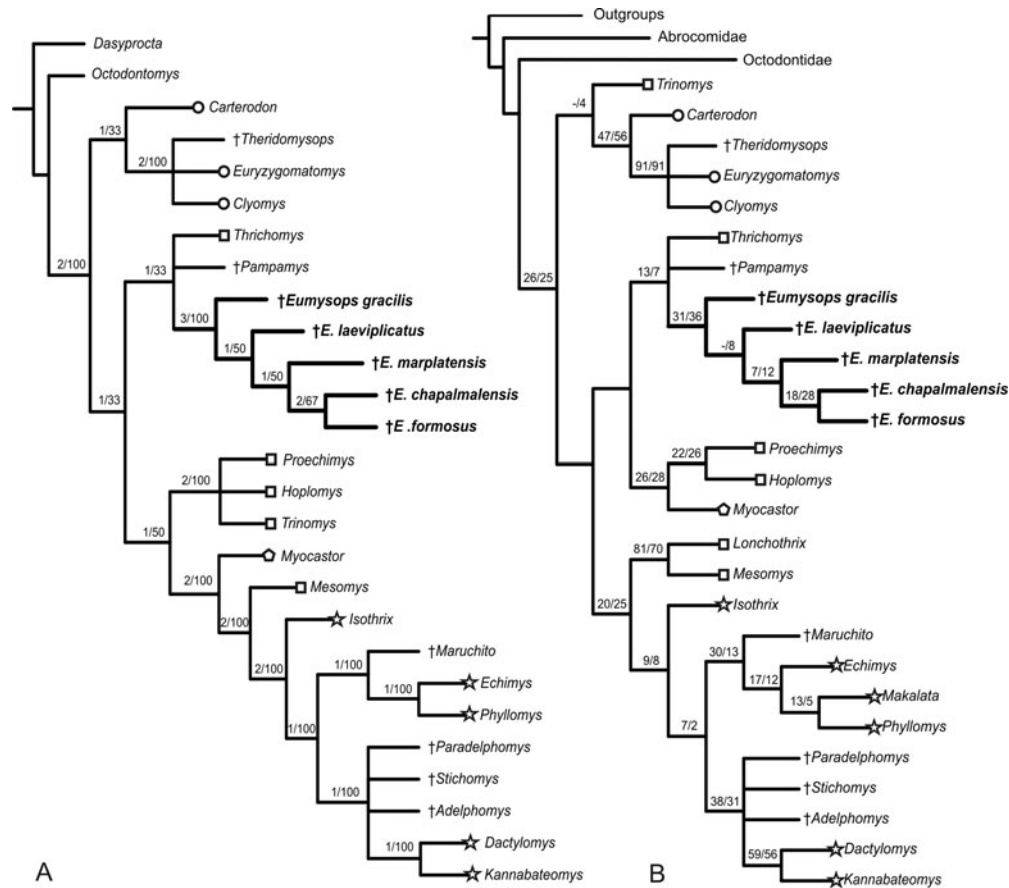


Figure 7. Strict consensus of three most parsimonious trees resulting from parsimony analysis of (A) morphological data (112 steps length) and (B) combined morphological and molecular data (6156 steps length). Bremer support/RBS values (A) and bootstrap CG frequency/jackknife CG frequency values (B) are shown above of each node. Open square, terrestrial; open circle, fossorial; open polygon, semiaquatic; open star, arboreal.

supported by the morphology of the zygomatic arch, not preserved in *†Theridomysops* (character-states 20-1, 24-1 and 25-1).

Support for nodes is low. However, except for the most internal nodes within Echimyidae, and those within the clade of *†Eumysops*, the remaining show low character conflict (high RBS values) (Figure 7(A)).

#### Combined analysis of molecular and morphological data

The analysis resulted in three most parsimonious trees 6156 steps long (CI = 0.552, RI = 0.436), in which the sister relationship between monophyletic Octodontidae and Echimyidae, and relationships (topologies) within Echimyidae were consistent with previously published molecular phylogenies (Figure 7(B)). Unlike the trees obtained with only morphological data, *Trinomys* resulted the sister group of Euryzygomatomyini, and *Myocastor* + *Proechimys*–*Hoplomys* were sister to *Thrichomys*–*†Eumysops*–*†Pampamys*.

As in the morphological trees, support for most nodes is low, except for *Euryzygomatomys*–*Clyomys*–*†Theridomysops*, *Lonchothrix*–*Mesomys* and *Dactylomys*–*Kannabateomys* (Figure 7(B)). Both in the morphological trees, and in those obtained through combined data, alternative topologies result from the unstable position of the Miocene genera *†Stichomys*, *†Adelphomys* and *†Paradelphomys*.

#### Stratigraphic distribution of the variation of *†Eumysops*

Except for a few fragmentary records of eastern (late Pliocene–Pleistocene of Entre Ríos Province; Vucetich et al. 2005; Candela et al. 2007) and central Argentina (Pliocene of Córdoba Province, Tauber, 2000; early Pliocene of the ‘Irene Formation’, Buenos Aires Province, Olivares, Verzi and Vucetich 2012), the record of *†Eumysops* is concentrated in the coastal cliffs of Farola Monte Hermoso and Chapalmalal area (Figure 1, Supplementary Material 6). These exposures have been largely

studied from a geological and palaeontological standpoint (e.g. Ameghino 1888, 1906, 1908; Kraglievich 1934; Kraglievich 1952; Reig 1958, 1978; Simpson 1972; Fidalgo and Tonni 1982; Marshall et al. 1983, 1984; Zárate and Fasano 1989; Tonni et al. 1992; Zavala 1993; Alberdi et al. 1995; Cione and Tonni 1995a, 1995b, 1996; Deschamps et al. 2012; Tomassini et al. 2013). A geologic and stratigraphic synthesis of the Monte Hermoso Formation in Farola Monte Hermoso can be found in Zavala (1993), Fidalgo and Tonni (1982), Cione and Tonni (1995b), Tomassini et al. (2013) and literature therein. There are neither numerical ages nor magnetostratigraphic data for the Monte Hermoso Formation; on the basis of geology and biochronology, it is accepted that these deposits represent the early Pliocene interval between <5.28 and >4.5 Ma (Zárate 2005; Verzi et al. 2008; Deschamps et al. 2013; Tomassini et al. 2013). The outcrops of the Chapadmalal area, 30 km of almost continuous coastal cliffs, 25 m in thickness (Kraglievich

1952; Zárate and Fasano 1989; Cione and Tonni 1995c; Supplementary Material 6), are among the richest Plio–Pleistocene deposits in South America (Reig 1958). In particular, the sequential Chapadmalal, Barranca de los Lobos, Vorohué and San Andrés Formations encompass the upper early Pliocene–early Pleistocene interval. According to radiometric, magnetostratigraphic and biochronological data, this interval extends between <4.5 and ca. 2.0 Ma (e.g. Cione and Tonni 1995a, 1995b, 1996, 1999, 2001; Schultz et al. 1998; Verzi and Quintana 2005; Bidegain and Rico 2012).

Supplementary Material 6 details the geographic and stratigraphic provenance of the specimens of †*Eumysops* from the exposures of Farola Monte Hermoso and Chapadmalal area. The information corresponds to the materials with accurate provenance. The pattern of stratigraphic distribution of †*Eumysops* is characterised by the presence of two species in the early Pliocene levels of the Monte Hermoso Formation, †*Eumysops formosus*

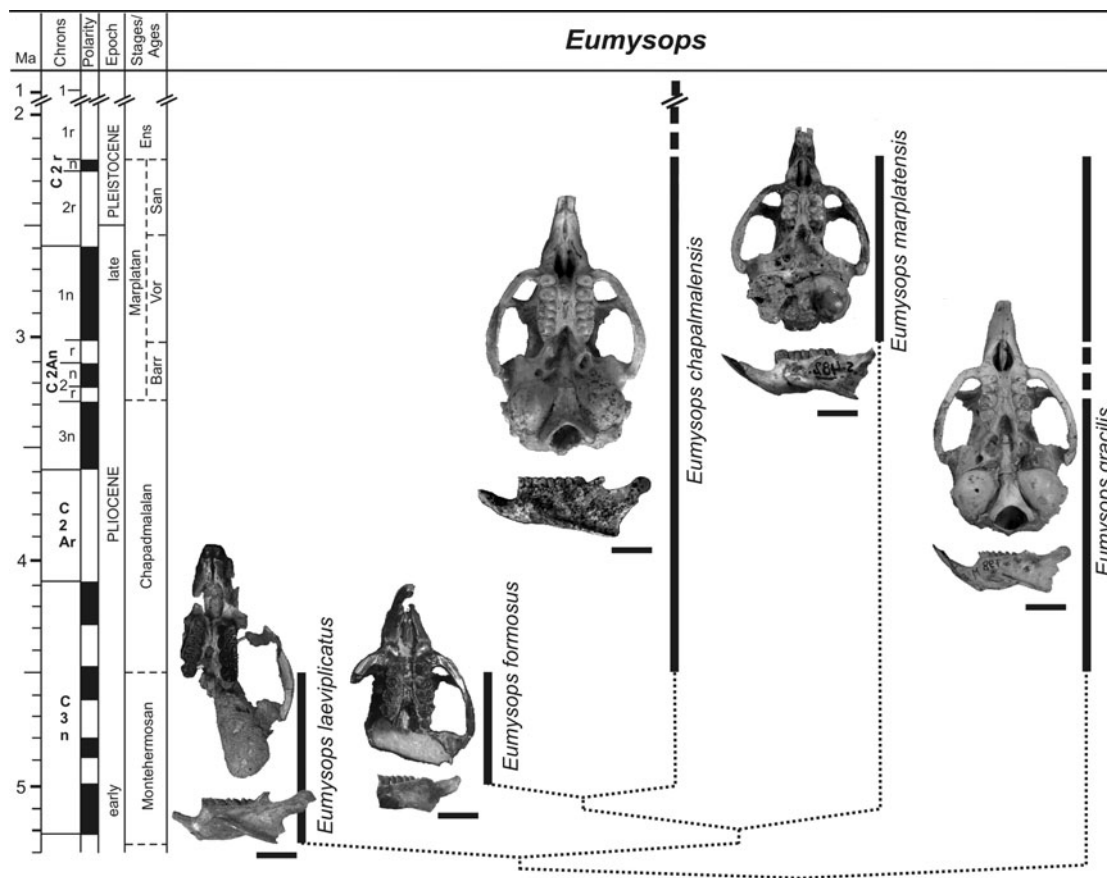


Figure 8. Chronological distribution of the species of †*Eumysops*. Time scale after Gradstein et al. (2008); stratigraphy modified from Cione and Tonni (1999), Verzi and Quintana (2005) and Verzi et al. (2008); magnetostratigraphic scale follows Berggren et al. (1995). Ventral view of skull and lateral view of mandible of †*Eumysops laeviplicatus* (MACN-A 1623 holotype and MMP 457-M, respectively), †*Eumysops formosus* (MACN-A 7327 holotype and MACN-Pv 7315, respectively), †*Eumysops chapalmalensis* (MMP 834-M and MMP 2432-M, respectively), †*Eumysops marplatensis* (MMP 482-S) and †*Eumysops gracilis* (MMP 410-M and 798-M, respectively). Bar, Barrancalobian; Ens, Ensenadan; San, Sanandresian; Vor, Vorohuean. Scale: 10 mm.

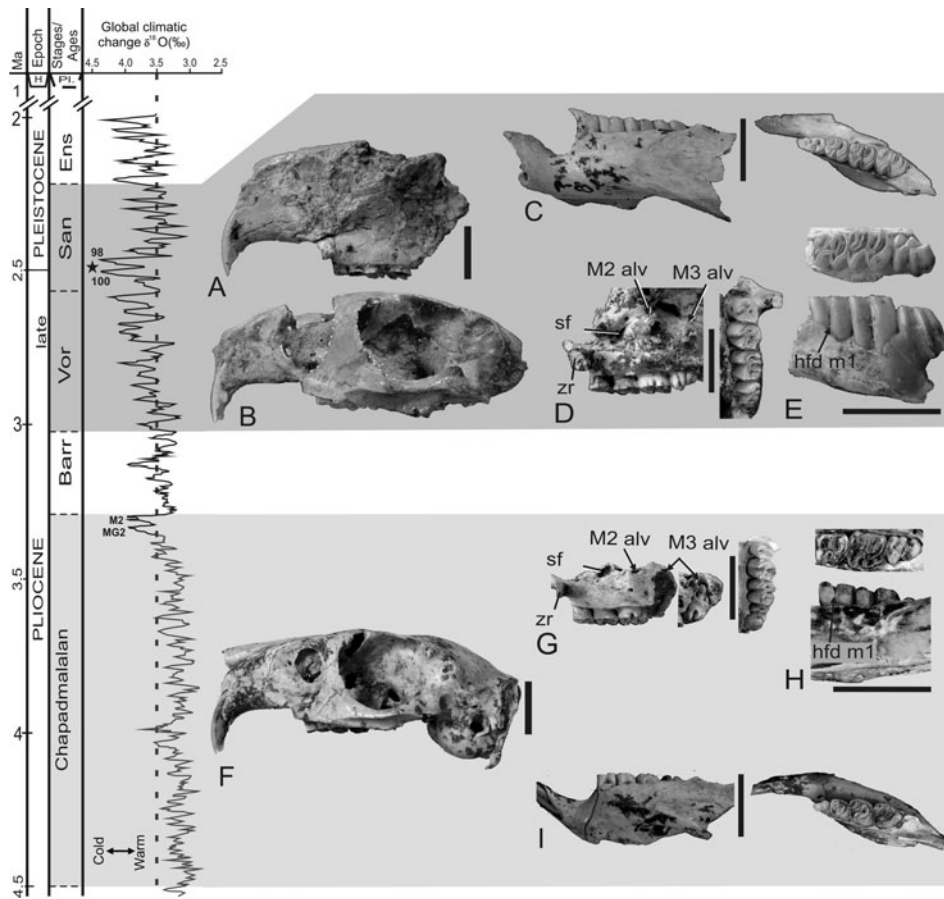


Figure 9. Chapadmalalan and Vorohuean-Sanandresian specimens of †*Eumysops chapalmalensis* showing morphological and size changes detected. Lateral view of skull (A) MMP 03\_1, (B) MMP 1053-S, (F) MMP 4201-M. Lateral and dorsal views of left hemimandibles (C) MMP 03\_5, (I) MMP 4102-M. (D) Detail of the alveolar sheaths of upper molars protruding into the orbit and occlusal morphology of MLP 96-II-2-1. (E) Lateral and occlusal views of right m1–m3 (reversed) of 56-X-17-2. (G) Detail of the alveolar sheaths of upper molars and occlusal morphology of MLP 88-VII-5-5. (H) Lateral and occlusal views of left m1–m3 of MLP 48-IV-22-3. Isotopic curve after Shackleton (1995). Black star indicates the 2.5-Ma cooling and drying event. Bar, Barrancalobian; Ens, Ensenadan; hfd m1, hypoflexid of the m1; M2 alv, alveolar sheath of the M2; M3 alv, alveolar sheath of the M3; San, Sanandresian; sf, sphenopalatine foramen; Vor, Vorohuean; zr, zygomatic root. Scale: 10 mm.

and †*Eumysops laeviplicatus* (Olivares, Verzi and Vucetich 2012), whereas the three remaining, more modern species, are recorded in the upper early Pliocene–late Pliocene of the Chapadmalal area (Figure 8; Supplementary Materials 1 and 6; Olivares, Verzi and Vucetich 2012; Deschamps et al., 2012). †*Eumysops laeviplicatus* defines the biostratigraphic unit (*Eumysops laeviplicatus* Range Zone) supporting the early Pliocene Monterhermosan Stage/Age (Tomassini et al. 2013). Isolated molars of †*Eumysops chapalmalensis* recorded in the upper Ensenadan from the north of Mar del Plata (ca. 1.0 Ma; Verzi et al. 2002) extend the biochron of this species up to the middle Pleistocene.

Data of the stratigraphic distribution by locality suggest the coexistence of species during the Pliocene: †*Eumysops laeviplicatus* and †*Eumysops formosus* in the late Montehermosan; †*Eumysops chapalmalensis* and

†*Eumysops gracilis* in the Chapadmalalan; †*Eumysops chapalmalensis*, †*Eumysops gracilis* and †*Eumysops marplatensis* in the Vorohuean and Sanandresian (Figure 8).

Materials of †*Eumysops chapalmalensis* from the Vorohué and San Andrés Formations show some differences in the skull and molars compared with those from the underlying Chapadmalal Formation. In general, an increase in the size and robustness of the skull and jaw, and in the crown height of molars is observed (Figure 9). Vorohuean–Sanandresian specimens show a deeper and wider rostrum, an antorbital bar antero-posteriorly wider, especially at the base and a jugal fossa anteriorly deeper (Figure 9(A),(B),(F)). In the specimen of age IV MLP 56-X-17-2 from the Vorohuean, the m1 is clearly higher ( $H = 0.83$ ) than that of the age-equivalent specimen MLP 91-II-20-3 from the Chapadmalalan ( $H = 0.51$ ). In



addition, the higher hypsodonty may be observed through the markedly greater height of the alveolar sheaths protruding in the orbital region. These alveolar sheaths influence the morphology and disposition of the sphenopalatine foramen and fissure in the specimens from the Vorohuean and Sanandresian (Figure 9(D),(G)). Interestingly, the change of hypsodonty in †*Eumysops chapalmalensis* does not modify the relative persistence of flexi/ids at occlusal level (Figure 9(E),(H); see Verzi et al. 2011).

## Discussion

†*Eumysops* shows a peculiar skeletal morphology that permits its recovery as a monophyletic taxon with a high support within the context of living and fossil echimyids. Its species show some consistency in tooth morphology, frequent among echimyids (Patton and Reig 1989), but the richness and quality of preservation of the materials allow the use of craniomandibular characters and ontogenetic variation for species delimitation.

Phylogenies obtained here support the monophyly of Echimyidae including *Myocastor* (Patterson and Pascual 1968; Leite and Patton 2002; Galewski et al. 2005; Candela and Rasia 2012; Upham and Patterson 2012; Fabre et al. 2013; Verzi et al., *in press*). In our morphological dataset, it is supported by the morphology of the lacrimal canal, the long lateral process of the supraoccipital and the orientation of the paroccipital process. Relationships among echimyids are in agreement with those of previous phylogenies based on both morphology (Emmons 2005; Olivares, Verzi, Vucetich and Montalvo 2012) and molecules (Galewski et al. 2005; Fabre et al. 2013; Upham and Patterson 2012), especially in recovering one major subclade comprising fossorial echimyids and one comprising terrestrial, arboreal and semiaquatic representatives, respectively. Furthermore, results from all these studies do not support the traditional taxonomic arrangement of the South American echimyids in three subfamilies, Echimyinae, Eumysopinae and Dactylomyiinae (four if *Myocastorinae* is accepted as a subfamily of Echimyidae; Patterson and Pascual 1968). In particular, the monophyly of the first two is not recovered, and the two major clades most frequently recognised in phylogenetic analyses are not consistent with previous classificatory schemes (see discussion of this issue in Emmons et al. 2015).

In the trees obtained here from both morphological data and combined molecular and morphological evidence, the †*Eumysops*–†*Pampamys*–†*Thrichomys* grouping was included in a major clade of terrestrial, arboreal and semiaquatic non-‘eumysopine’ echimyids. This same result was obtained in a morphological analysis including a wider sample of octodontoids (Verzi et al., *in press*; Figure 7). Thus, the resultant clade Eumysopinae, limited

to these three genera, is notably more restricted than the traditional taxon (Woods and Kilpatrick 2005), and even more restricted than the grouping of ‘eumysopines with simplified molars’ proposed by Verzi et al. (1995; see Olivares, Verzi, Vucetich and Montalvo 2012). This latter grouping was recovered by Candela and Rasia (2012; see also Carvalho and Salles 2004) in one analysis based on dental morphology.

Kraglievich (1965) interpreted †*Eumysops* as an austral radiation represented by two lineages with gradual directional evolution (ver Rasskin-Gutman and Esteve-Altava 2008). Unfortunately, it is very difficult to test this pattern because Kraglievich assigned no materials, and furthermore, two of the included names (*Eumysops cavioides* and *Eumysops paracavioides*) are not applicable (Vucetich and Verzi 1995; Verzi and Quintana 2005; Olivares, Verzi and Vucetich 2012; results here). The phylogeny and stratigraphic distribution of †*Eumysops* species suggest an essentially cladogenetic evolutionary pattern. The possible coexistence of species detected for †*Eumysops* is a unique pattern among Pliocene octodontoids of the Pampasia, the genera of which are represented by a single species, or a single chronomorph (of an individual lineage), in each Stage/Age (e.g. Reig in Marshall et al. 1984, Figure 6; Vucetich and Verzi 1995; Deschamps 2005; Deschamps et al. 2012). In addition, although the stratigraphic distribution of the sister species †*Eumysops formosus* and †*Eumysops chapalmalensis* does not prevent the assumption of a relationship ancestor–descendant between both [as stated by Kraglievich (1965) for these nominal species], the presence of an autapomorphy in the lacrimal and the relatively greater persistence of the metaflexid in the older †*Eumysops formosus* reject this possibility.

Beyond this, a gradual directional change (*sensu* Rasskin-Gutman and Esteve-Altava 2008) was detected within the variation of †*Eumysops chapalmalensis* between the Chapdamalalan and Vorohuean–Sanandresian (Figure 9). The polarity of these changes results in larger skulls and mandibles, with stronger crests and fossae for muscular attachment, and higher molars. The same skull and mandibular features are concurrent in †*Eumysops marplatensis* from the Vorohuean–Sanandresian. The preservation of †*Eumysops gracilis* prevents the assessment of whether this species underwent changes during this interval. According to radiometric dates for the top of the underlying Chapdamal Formation (Schultz et al. 1998), and magnetostratigraphic and biochronological data, the interval Vorohuean–Sanandresian extends between ~3.0 and 2.0 Ma (Orgeira 1987, 1990, 1991; Cione and Tonni 1995a, 2001; Zárate 2005; Bidegain and Rico 2012). During this interval, one of the most important environmental and climatic changes of the late Neogene is recorded at the global level (Denton 1999; McKay et al. 2012). This corresponds to a cooling and drying trend (involving expansion of the Antarctic ice sheets onto the

continental shelf; McKay et al. 2012), initiated at  $\sim 3.3$  Ma and that culminates in three large glacial events around 2.5 Ma ( $\delta^{18}\text{O}$  stages 100, 98 and 96, Shackleton 1995; Denton 1999; Figure 9) which had significant biological consequences (expansion of open environments and first appearances of arid adapted species; e.g. Janis 1993; Marshall and Sempere 1993; Vrba 1985, 1989, 1992; Vrba et al. 1995; Denton 1999; de Menocal 2004). The important faunal turnover recorded in the lower levels of the San Andrés Formation (in which also the Sanandresian materials of †*Eumysops* have been recovered; Verzi and Quintana 2005) has been interpreted as the local representation of the 2.5-Ma event (Tonni and Cione 1994, 1995; Verzi 2001; see Bidegain and Rico 2012). This turnover has been characterised by the sudden first appearance of the caviomorph extinct fauna most clearly indicative of arid environments so far recorded (Verzi and Quintana 2005). In this context, †*Eumysops* is one of the caviomorphs recorded in levels underlying this turnover, and that during the faunistic change shows a trend towards the increase in size and development of robust and markedly hypsodont morphotypes. This pattern is concurrent with that observed in the octodontid lineage †*Eucelophorus chapalmalensis*, which also shows increasing size and robustness in the Vorohuean–Sanandresian (Reig and Quintana 1992; Verzi et al. 2015). Increase in size in independent lineages of African bovids concordant with the cooling event of  $\sim 3.0$ –2.5 Ma has been reported by Vrba (2005).

The fossil record of echimyids from southern South America is an impoverished, marginal sample of the astonishing diversity achieved by this group in the tropical and subtropical areas of northern South America. Fossils linked to the extant arboreal species are present in Patagonia only until the Middle Miocene, coinciding with the persistence of tropical forests at this latitude (Palazzesi and Barreda 2007). By contrast, echimyids from late Miocene to Pleistocene of central Argentina are linked to the few representatives that currently inhabit more open areas, i.e. *Clyomys*–*Euryzygomatomys* and *Thrichomys* (Verzi et al., in press). This latter, modern record has been interpreted as a southern expansion of more northern, Chacoan, radiations occurring after the withdrawal of the Paranense Sea (Verzi 2002; see Pascual et al. 1985; Webb 1995). Among these modern echimyids, †*Eumysops* is the only genus whose evolution occurred in southern South America (together with *Myocastor* if this is accepted within Echimyidae). Its distinctive skeletal and dental anatomy within the family, including large orbits, shortened braincase, marked hypsodonty and postcranial specialisations (Horovitz 1991; Olivares 2009), could be related to its austral history. This is consistent with the hypothesis that derived environments out of the tropics would have promoted the development of peculiar morphologies.

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