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RESEARCH PAPER

A revision of the fossil genus *Phanomys* Ameghino, 1887 (Rodentia, Hystricognathi, Cavioidea) from the early Miocene of Patagonia (Argentina) and the acquisition of euhypsodonty in Cavioidea sensu stricto

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Abstract Cavioidea sensu stricto (Cavioidea s.s.) is one of the most divergent lineages within the South American Hystricognathi, and is currently represented by cavies, maras (Caviidae), and capybaras (Hydrochoeridae). Cavids and hydrochoerids have been interpreted as forming the crown group, whereas the stem group of Cavioidea s.s. is formed by "Eocardiidae", a paraphyletic group recorded in the late Oligocene to middle Miocene, mainly in Patagonia. One of the most interesting features of Cavioidea s.s. is the record of evolution of hypsodonty, which develops relatively slowly compared to other groups of caviomorphs, enabling this process to be followed in the fossil record. *Phanomys* is recorded in Patagonia during the late early Miocene, and since its description this genus has been considered close to euhypsodont genera. The objective of this paper is to: (1) report new material of *Phanomys*; (2) re-describe the two species of the genus; (3) determine the phylogenetic position of *Phanomys* among Cavioidea s.s. by morphological cladistic analysis; and (4) explore the sequence of appearance of characters related to the origin of euhypsodonty. The new materials assigned to *Phanomys mixtus* are the first mandibular fragments and palate known, yielding valuable morphological, ontogenetic, and phylogenetic information. *Phanomys vetulus* is recognized as a valid species, although better material is needed for a more robust definition. The phylogenetic analysis shows that *Phanomys* is the sister group of euhypsodont Cavioidea s.s. The evolutionary history of Cavioidea s.s. demonstrates that character states previously thought to correlate with the degree of hypsodonty (e.g. absence of fossettes/ids) do not all appear at the same time during the evolution of the group. Although the evolutionary trend in Cavioidea s.s. shows progressively increasing hypsodonty, the morphological changes inferred from this phylogenetic analysis indicate that hypsodonty and other character states were temporally decoupled during the evolution of the group during the Oligocene and early Miocene.

Keywords Cavioidea · Euhypsodonty · Phylogeny · Early Miocene · Patagonia

Kurzfassung Die Cavioidea *sensu stricto* repräsentieren eine der divergierenden Linien innerhalb der su?damerikanischen Hystricognathi und sind zurzeit durch Meerschweinchen, Maras (Caviidae), und Wasserschweine vertreten. Caviiden und Hydrochoeriden wurden als die Kronen-Gruppe der Cavioidea s.s. interpretiert, während die "Eocardiidae", eine paraphyletische Gruppe aus dem späten Oligozän bis mittleren Miozän aus Patagonien, als Stamm-Gruppe dargestellt wurden. Eine der interessantesten Merkmalsentwicklungen von Cavioidea s.s. ist die Evolution der Hypsodontie, die sich im Vergleich zu anderen Gruppen von Caviomorphen relativ langsam entwickelte; dies ermöglicht es, diesen Prozess bei Fossilien zu erkennen. *Phanomys* ist aus dem Ende des frühesten Miozän von Patagonien bekannt, und seit ihrer Erstbeschreibung wurde diese Gattung in die Nähe von euhypsodonten Taxa gestellt. Das Ziel dieses Beitrags ist es, neues

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Material von *Phanomys* vorzustellen, die beiden Arten dieser Gattung neu zu beschreiben, ihre phylogenetische Stellung innerhalb der Caviodea s.s. durch eine kladistische Analyse mit morphologischen Merkmalen zu untersuchen und die Sequenz des Merkmalserwerbes von mit Euhypsodontie verbundener Merkmale zu untersuchen. Bei dem neuen Material handelt es sich um den ersten Rest des Unterkiefers und des Gaumens von *Phanomys mixtus*, und diese Reste ergeben wichtige morphologische, ontogenetische und auch phylogenetische Informationen. Bei *Phanomys vetulus* handelt sich um eine gültige Art, obwohl besseres Material für eine befriedigende Definition nötig ist. Die phylogenetische Analyse zeigt, dass *Phanomys* die Schwestergruppe der euhypsodonten Cavioidea s.s. darstellt. Die Evolution der Cavioidea s.s. zeigt, dass die Merkmale, die bisher in direktem Zusammenhang mit dem Grad der Hypsodontie gestellt wurden (z.B. Abwesenheit von fossettes/ids) nicht zur gleichen Zeit während der Entwicklung der Gruppe erscheinen. Obwohl die evolutionäre Entwicklung bei den Caviodea s.s. einen Trend zu zunehmender Hypsodontie aufweist, zeigen die morphologischen Veränderungen, basierend auf dieser phylogenetischen Hypothese, dass diese Merkmale und der Erwerb der Hypsodenties in der Evolution der Gruppe im Oligozän und frühen Miozän zeitlich entkoppelt waren.

Schlüsselwörter Cavioidea · Mittleren Miozän · Phylogenie · Hypsodontie · Patagonien

Introduction

The superfamily Cavioidea *sensu stricto* (Cavioidea s.s.) (Patterson and Wood 1982) is one of the most divergent lineages within the South American Hystricognathi and one of the most distinctive lineages among rodents as a whole (Landry 1957; Mares and Ojeda 1982; Wood 1985; Vucetich and Verzi 1995). This group is currently represented by cavies, maras (i.e. Caviidae), and capybaras (i.e. Hydrochoeridae), and have the broadest body-size range among living rodents (Redford and Eisenberg 1992). Within Cavioidea s.s., caviids and hydrochoerids have been interpreted as forming the crown group, diagnosed by unique craniomandibular and dental features (Pérez 2010a, b; Pérez and Vucetich 2011). The stem group of Cavioidea s.s. is formed by "Eocardiidae", a paraphyletic group (Pérez 2010b) recorded in the Deseadan–Colloncuran South American Land Mammal Ages (SALMA; 28–15 Ma, late Oligocene—middle Miocene) of Patagonia.

One of the most interesting features of Cavioidea s.s. is the record of evolution of hypsodonty. In this group, the development of hypsodonty until the attainment of euhypsodonty took about eight million years enabling this process to be followed in the fossil record. The evolution of hypsodonty in Cavioidea s.s. would have evolved progressively in a scenario of a general tendency toward climatic deterioration and periods of intense volcanism that affected Patagonia and provided a great amount of glass to the sediments (Mazzoni 1985; Bellosi 2010; Barreda and Palazzesi 2010). These two elements, climatic deterioration and a large amount of abrasive materials, would have favored the development of hypsodonty (Kay et al. 1999).

The most basal "Eocardiidae", which have high-crowned teeth but develop roots (i.e. mesodont and protohypsodont; see definitions below), for example *Asteromys* Ameghino, 1897 and *Luantus* Ameghino, 1898, are recorded from the Deseadan to Santacrucian SALMAs (28–16.5 Ma; late Oligocene to late early Miocene). The first euhypsodont (i.e. high-crowned teeth that grow throughout life without developing roots) Cavioidea s.s., for example *Eocardia* Ameghino, 1887a, are registered in the Santacrucian SALMA, whereas mesodont and protohypsodont forms become extinct after this SALMA. The crown group of Cavioidea s.s. is recorded since the middle Miocene, and all known species are euhypsodont.

Phanomys Ameghino, 1887b, in particular, is recorded in Patagonia (Fig. 1) in the Santacrucian SALMA (Ameghino 1887b, 1891, 1900, 1902; Scott 1905; Kramarz and Bellosi 2005; Kramarz 2006). Since its description, *Phanomys* has been considered close to euhypsodont genera (e.g. *Eocardia*). Ameghino (1889) was first to propose such a hypothesis because *Phanomys* has semi rooted cheek teeth (i.e. atrophied and welded roots *sensu* Ameghino). Later, other authors pointed out that *Phanomys* shows the transition between Colhuehuapian (18.7–20.2 Ma, early Miocene; Flynn and Swisher 1995; Ré et al. 2010) eocardiids with rooted cheek teeth and those typical euhypsodont Santacrucian species (i.e. *Eocardia, Schistomys*; Scott 1905; Wood and Patterson 1959; Kramarz 2006). In a recent phylogenetic analysis, (Pérez 2010b; Pérez and Vucetich 2011) *Phanomys* is the sister group of euhypsodont eocardiids, corroborating the close relationship between this taxon and the common ancestor of euhypsodont cavioids.

The genus was based on syntype material consisting only of isolated teeth (Ameghino 1887b, 1889). Some authors considered it as one of the most outstanding eocardiids because it has a unique combination of characters among Cavioidea s.s. (Ameghino 1887b, 1889; Scott 1905; Wood and Patterson 1959). Recent work in early Miocene deposits (Kramarz 2006; Kay et al. 2008) yielded new materials that provide novel anatomical and phylogenetic information about *Phanomys*. The objective of this paper is to report the new material, to re-describe the two species of the genus, and to re-evaluate its phylogenetic position among Cavioidea s.s. by morphological cladistic analysis including the new materials, exploring the sequence of appearance of

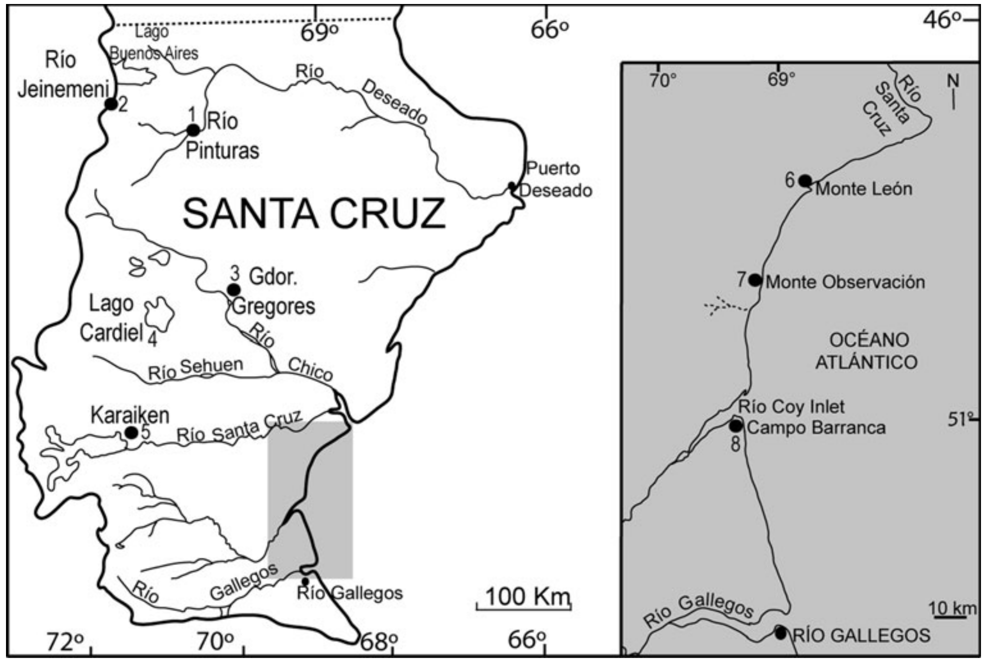


Fig. 1 Location map, modified from Kramarz (2006) and Kay et al. (2008), of the localities from which specimens of *Phanomys* derive. (*1*) Area of the upper valley of Pinturas River, (*2*) Río Jeinemení, (*3*) Gobernador Gregores, (*4*) Lago Cardiel, (*5*) Karaiken, (*6*) Monte León, (*7*) Monte Observación, (*8*) Campo Barranca

character states related to the origin of euhypsodonty, one of the most significant evolutionary transformations in the history of Cavioidea s.s.

Materials and methods

Anatomical nomenclature

Dental nomenclature follows Candela (1999), Marivaux et al. (2004) and Pérez (2010b). Mandibular nomenclature is modified from Woods (1972) and Woods and Howland (1979) (see Pérez 2010b).

Taxonomic nomenclature

We follow Patterson and Wood (1982) in their use of Cavioidea as a group that includes Dasyproctidae, Cuniculidae, "Eocardiidae", Caviidae, and Hydrochoeridae, but we exclude Dinomyidae because recent analyses consider this family a Chinchilloidea (Huchon and Douzery 2001; Opazo 2005; Blanga-Kanfi et al. 2009; Rowe et al. 2010). The use of Cavioidea s.s. follows the original proposal of Patterson and Wood (1982) that encompasses "Eocardiidae", Caviidae, and Hydrochoeridae (Pérez and Vucetich 2011). "Eocardiidae" is paraphyletic therefore quotation marks are used for this assemblage of basal cavioids (Pérez 2010b; Pérez and Vucetich 2011). The crown group of Cavioidea s.s. is formed by Caviidae + Hydrochoeridae, excluding the basal forms of Cavioidea s.s. (i.e., eocardiids) (Appendix 1).

Hypsodonty

Differences in the degree of hypsodonty of the taxa used in this analysis were defined qualitatively in moderately worn teeth because no unworn teeth are known for most species. Three states of hypsodonty were defined for Cavioidea (character 29 in Pérez and Vucetich 2011):

1. Mesodont: rooted teeth with antero-posterior length approximately equal to the crown height;
2. Protohypsodont: rooted teeth, crown height ≤50% than antero-posterior length; and
3. Euhypsodont: high-crowned teeth that grow continuously without developing roots (Mones 1982).

The species *Proechimys poliopus* (outgroup used to root typologies in the cladistic analysis) was considered "slightly hypsodont" because it is much lower crowned than the lowest crowned species considered in this analysis, but not brachydont.

Institutional abbreviations

MACN A, Colección Nacional Ameghino, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; MACN Pv, Colección Nacional de Paleovertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; MLP, Colección de Paleontología de Vertebrados and Colección de Mastozoología, Museo de La Plata, La Plata. MPM-PV, Museo Regional Padre Molina, Colección Paleontología de Vertebrados, Río Gallegos.

Results

Systematic revision

Order Rodentia Bowdich, 1821

Suborder Hystricognathi Tullberg, 1899
Superfamily Cavioidea Fischer de Waldheim, 1817
Genus *Phanomys* Ameghino, 1887b

Type species: *Phanomys mixtus* Ameghino, 1887b
Referred species: *Phanomys vetulus* Ameghino, 1891

Expanded diagnosis *Phanomys* is diagnosed by the following unique combination of characters (autapomorphies marked with an asterisk): protohypsodont molariforms, with the crown slightly higher than in *Luantus toldensis* Kramarz, 2006; in young-adult ontogenetic stages, enamel interrupted along the entire lingual, anterolingual, and posterolingual walls of lower teeth and labial, anterolabial, and posterolabial walls of the upper teeth; fossettes/ids less persistent during ontogeny than in any other protohypsodont species of Cavioidea s.s.; hypoflexus/id narrow, extending transversely more than half of the crown and bearing cement since early ontogenetic stages, as in *Eocardia* and *Schistomys*; *p4 with double-heart shaped occlusal surface with the anterior lobe transversely smaller than the posterior one, anterior surface obliquely oriented facing anterolingually and with a vertical furrow well developed, the labial apex of the anterior lobe is rounded and anteriorly directed; P4 unilobed. Differs from *Eocardia, Schistomys*, *Matiamys*, *Microcardiodon*, and *Guiomys* in having rooted cheek teeth. Also differs from *Schistomys*, and *Guiomys* in having P4 without a lingual flexus.

Geographic and stratigraphic provenance Pinturas Formation (late-early Miocene; Kramarz and Bellosi 2005), Santa Cruz province, Argentina; Santa Cruz Formation, Santacrucian SALMA (late-early Miocene, Fleagle et al. 1995), Santa Cruz province, Argentina. Río Jeinemení Formation, Santa Cruz province, Argentina.

Phanomys mixtus Ameghino, 1887b (Table 1; Figs. 2, 3)

Lectotype MACN A 11302, right maxillary fragment with P4–M2 (Ameghino 1889, Plate 10, Fig. 21–21a and Ameghino 1906, Fig. 313). See Taxonomic considerations below.

Neosyntype (Wood and Patterson 1959) MACN A 2022, nine isolated molariforms: (a) left juvenile p4 (Ameghino 1889, Plate 10, Fig. 24); (b) right lower molar (Ameghino 1889, Plate 10, Fig. 25); (c) juvenile right P4; (d) juvenile M1 or M2; (e) left m1 or m2; (f) left M1 or M2; (g) juvenile right M1 or M2; (h) right M1 or M2 with metafossette; (i) left DP4.

Referred material MLP 15–341, left maxillary fragment with P4-M2; MLP 15–217a, right mandibular fragment with m2–m3; MLP 91-II-25-3, right mandibular fragment with m2–m3 and left with p4–m2, assigned to a single individual because they match in size, morphology and stage of wear; MPM-PV 4375, palate fragment with right P4–M3 and left M1–M3; MACN Pv SC2583, left upper molar; MACN Pv SC2584, right upper molar; MACN Pv SC2832, cheek teeth; MACN Pv SC3450, left maxillary fragment with P4–M3; MACN Pv SC4040, several cheek teeth; MACN Pv SC4041, several cheek teeth; MACN Pv SC4058, 17 cheek teeth; MACN Pv SC4065, four cheek teeth; MACN Pv SC4074, six cheek teeth; MACN Pv SC4087, five cheek teeth; MACN Pv SC4095, left maxillary fragment with P4–M1; MACN Pv SC4096, 13 cheek teeth.

Taxonomical considerations Ameghino (1887b) described *Phanomys* and its type species *P. mixtus* on the basis of isolated molariforms deposited in the Museo de La Plata, but these specimens have been subsequently lost. In 1889 Ameghino illustrated five specimens and referred them to *P. mixtus* (Plate 10): a right maxillary fragment with P4–M2 (Ameghino 1889, Fig. 21) that is currently deposited as MACN A 11302, two specimens that have been lost after Ameghino′s publication (a left lower molar (Ameghino 1889, Fig. 22), an upper molar with two fossettes (Ameghino 1889, Fig. 23), a left lower premolar (MACN A 2022 a) considered M3 by Ameghino (Ameghino 1889, Fig. 24), and a very worn molar (MACN A 2022 b; Ameghino 1889, Fig. 25). Wood and Patterson (1959) named a group of nine molariforms deposited at the MACN A as neosyntypes. Two of these, MACN A a–b (Fig. 2a–e in this paper), are those originally illustrated by Ameghino (1889, Plate 10, Fig. 24–25). The other seven teeth were not illustrated by Ameghino (1889) but can be confidently referred to *P. mixtus* and were part of the Ameghino collection. The specimen MACN A 11302 (Ameghino 1889, Plate 10, Fig. 21–21a and Ameghino 1906, Fig. 313) was not included in the neosyntype (Wood and Patterson 1959) because it was lost at the time, but it was recently found in the collections and must be considered part of the type series. We designed MACN A 11302 as lectotype because this is the most complete specimen of the neosyntype.

Stratigraphic and geographic provenance The neosyntype of *P. mixtus* (MACN A 2022), MACN A 11302, MLP 15–341 and MLP 15–317a are from "Formación Santacruceña" (= Santa Cruz Formation) at the cliff of the Santa Cruz River (Ameghino 1887b, 1889, 1891, 1900,

Table 1 Dental measurements of *Phanomys mixtus*, in millimeters

	APL	AW	PW
Phanomys mixtus			
MACN A 2022 (Neosyntype)			
(a) p4	4.14	2.02	2.87
(b) m1 or m2	3.16	2.6	3.00
(c) P4	3.08	3.30	
(d) M1 or M2	3.55	3.20	3.12
(e) M1 or M2	3.9	3.83	3.45
(f) M1 or M2		3.55	3.14
(g) M1 or M2	3.26		
(h) M1 or M2	3.92	3.67	3.41
(i) DP4	3.07	2.84	2.54
MACN A 11302 (Lectotype)			
P4	4.3	3.3	
M1	3.6	4.2	4.1
M2		4.4	
MLP 15–341			
P4	3.64	3.55	
M1	3.33	3.94	3.77
M2	4.08	4.06	4.99
MACN Pv SC3450			
P4		2.63	
M1	3.1	3.08	3.13
M2	3.52	3.38	3.55
M3	4.51	3.26	29.3
MPM-PV 4375			
P4	3.6	4.15	
M1	3.83	4.17	3.83
M2	4.25	4.49	
M3			3.59
M3		4.08	
MLP 91-II-25-3			
p4	4.37	2.47	3.26
m1	3.55	3.47	3.55
m2	4.32	3.95	3.99
m2	4.31	3.93	3.96
m3	5.09	3.8	
MLP 15–217a			
m2	4.3	3.8	4.0
m3		4.0	
MACN Pv SC2832			
p4	3.8	2.07	3.09
MACN Pv SC2832			
m1 or m2	4.14	3.51	3.89
MACN Pv SC2832			
m1 or m2	4.55	4.05	4.03
MACN Pv SC2832			
m3	5.12		
MACN Pv SC2832			
m3	5.24	4.12	3.35
MACN Pv SC2832			
P4	3.97	4.14	
MACN Pv SC2832			
M1 or M2	4.52	4.19	4.19
MACN Pv SC2832			
M1 or M2	4.3	4.72	4.43
MACN Pv SC2832			
M1 or M2		4.41	4.39
MACN Pv SC2832			
M3	5.49	4.16	4.09

APL anteroposterior length, *AW* anterior width, *PW* posterior width

1902); MLP 91-II-25-3 is from Río Jeinemení Formation, Jeinemení River; MPM-PV 4375 is from Santa Cruz Formation, Campo Barranca, (Kay et al. 2008); MACN Pv SC2583, 2584, 2832, and 3450 are from Pinturas Formation, Los Toldos Sur; MACN Pv SC4040, 4041, 4058, and 4068 are from Pinturas Formation, Gobernador Gregores; MACN Pv SC4074, 4087, 4095, and 4096 are from Lago Cardiel (see Bown and Larriestra 1990; Bown and Fleagle 1993); Santa Cruz Province, Argentina (Fig. 1).

Diagnosis All characters mentioned in the diagnosis of *Phanomys* are present in *P. mixtus*. This species differs from *P. vetulus* in its larger size.

Description Among the specimens of the neosyntype MACN A 2022, two were illustrated by Ameghino (1889, Plate 10). One of these (MACN A 2022 a) is an isolated juvenile left lower premolar (Fig. 2a–c) with antero, meso, and metafossettids; the mesofossettid is circular whereas the other two are narrow and elongate. The lingual wall is straight. The anterior lobe is transversely smaller than the posterior lobe, the antero-labial wall bears a relatively marked vertical furrow, the apex of the tooth is strongly directed anteriorly and its posterior wall (i.e., the anterior wall of the hypoflexid) is markedly convex. The posterior lobe is narrower and transversely much longer, and its anterior and posterior walls are slightly convex. In this stage of wear, the hypoflexid reaches more than halfway across the occlusal surface, it has cement (Fig. 2a–b) and the enamel is interrupted from the base of the lingual wall upward, and slightly more on the posterior lobe (Fig. 2c). The other tooth illustrated by Ameghino is an isolated lower right molar (MACN A 2022b) extremely worn (Fig. 2d–e); it has double-heart shaped occlusal surface,

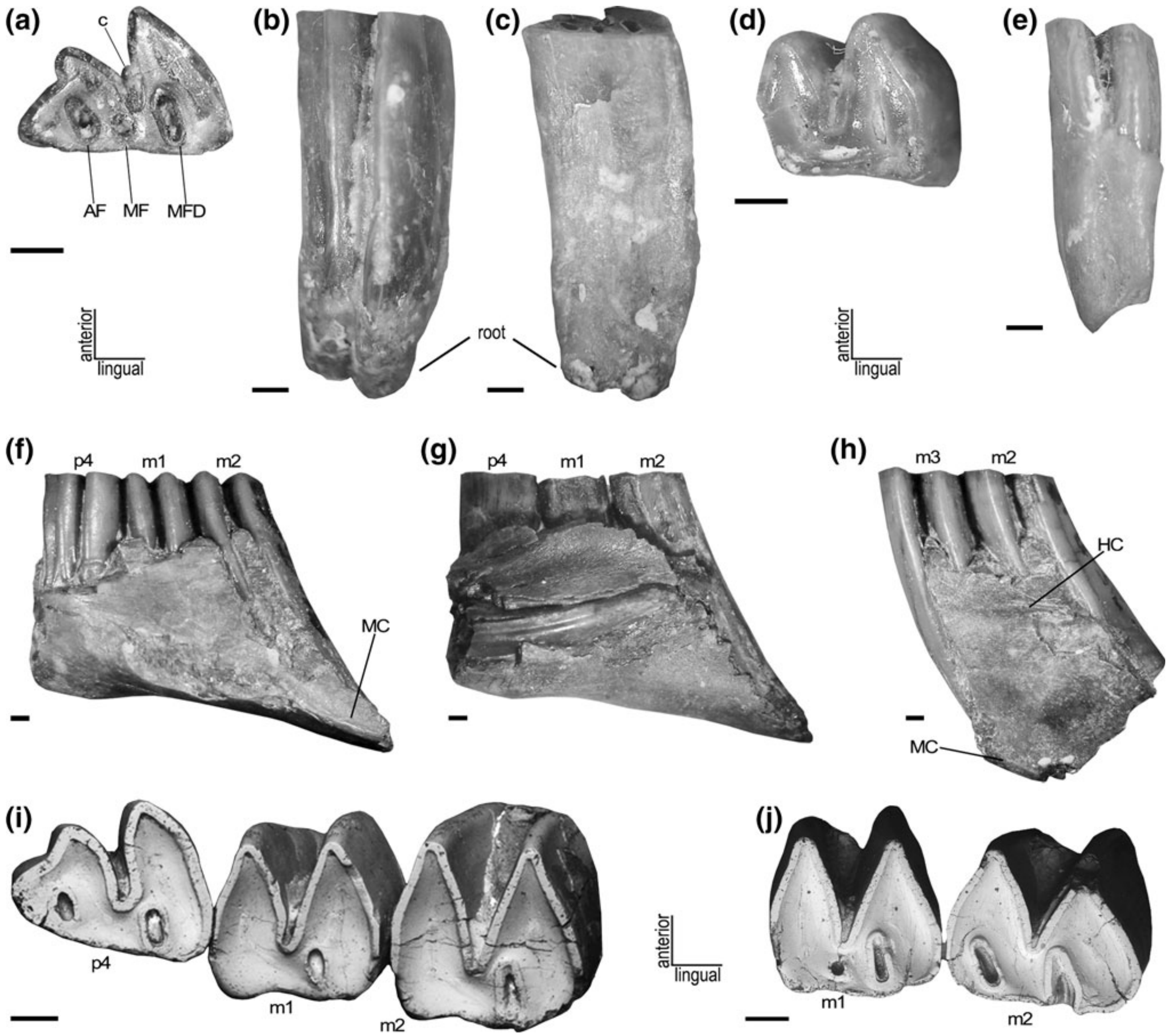
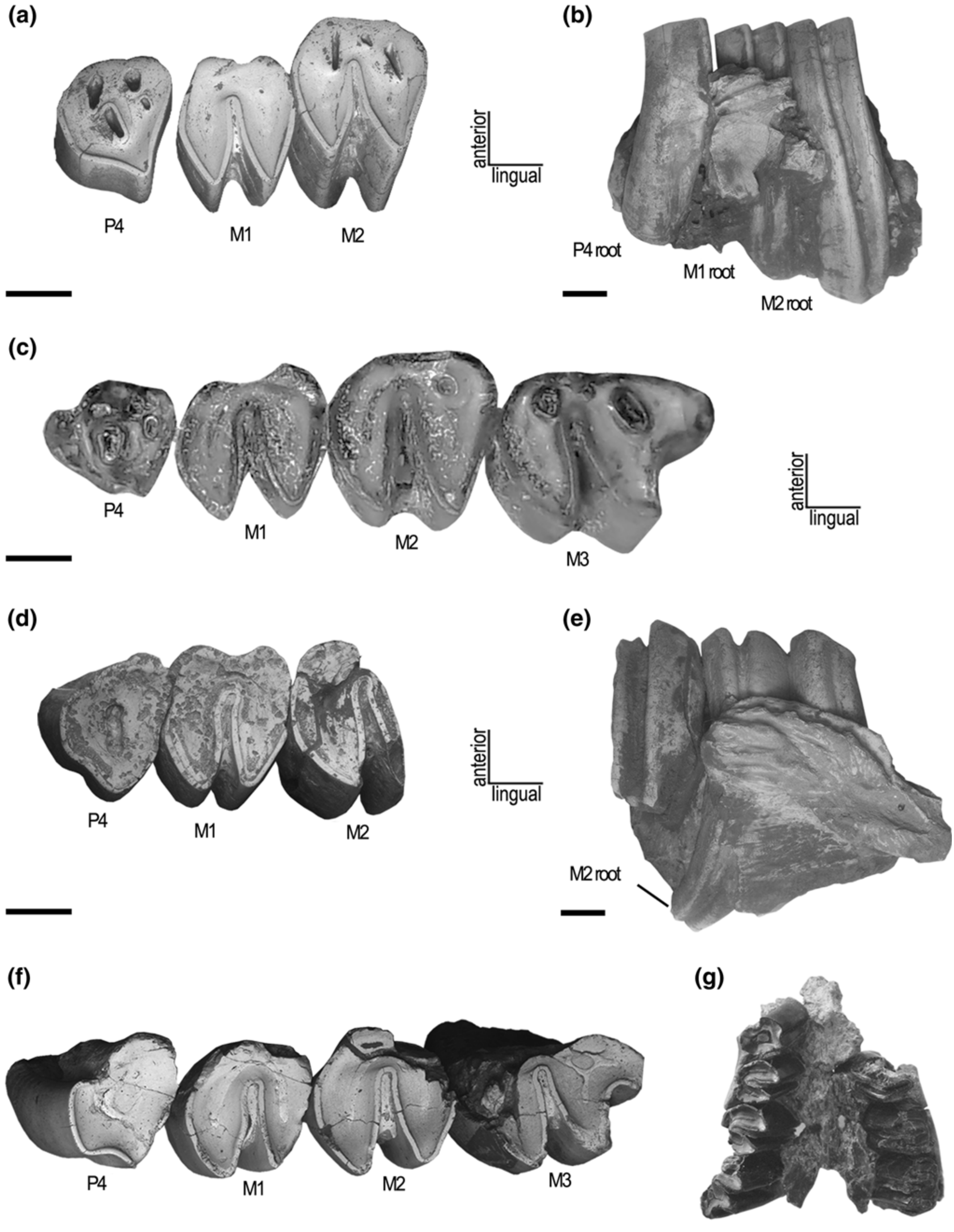


Fig. 2 *Phanomys mixtus*, *lower* teeth: Neosyntype MACN A 2022a, *left* p4 **a** occlusal view (reversed), **b** labial view, **c** lingual view, and MACN A 2022b, *right* m1 or m2 (reversed) **d** occlusal view, **e** labial view. MLP 91-II-25-3, *left* mandibular fragment with p4–m2 **f** labial view, **g** lingual view (reversed), and *right* mandibular fragment with m2–m3 **h** labial view (reversed). MLP 91-II-25-3, *left* mandibular fragment with p4–m2 **i** occlusal view (reversed), and *right* mandibular fragment with m2–m3 **j** occlusal view. *AF* anterofossettid, *c* cement, *HC* horizontal crest, *m1–m3 lower* molars, *MC* masseteric crest, *MF* mesoflexid or mesofossettid, *MFD* metaflexid or metafossettid, *p4 lower* fourth premolar. *Scale bar* equals 1 mm

with the anterior lobe slightly smaller than the posterior lobe (Fig. 2d), without lingual flexids or fossettids, and with cement in the hypoflexid; this tooth closes basally without forming roots.

In the most juvenile specimens of *P. mixtus*, the enamel is continuous around the entire crown. With wear, the enamel disappears at the base and along the lingual wall of the posterior lobe of the lower molars and the labial wall of the upper molars. In more advanced ontogenetic stages the enamel interrupts along the entire lingual, anterolingual, and posterolingual walls of the lower teeth and labial, anterolabial, and posterolabial walls of the upper teeth. Kramarz (2006: 774) stated that not all the specimens of the neosyntype have a dentine track on the labial wall of the upper molars and the lingual wall of the lowers. This is

Fig. 3 *Phanomys mixtus*, *upper* teeth: MLP 15–341, *left* maxillary fragment with P4–M2 **a** occlusal view, **b** lingual view. MACN Pv SC3450, *left* maxillary fragment with P4–M3 **c** occlusal view. Lectotype MACN A 11302 *right* maxillary fragment with P4–M2 (reversed), **d** occlusal view, **e** lingual view. MPM-PV 4375, palate fragment with *right* P4–M3 and *left* P4–M2 **f** *right* P4–M3 in occlusal view (reversed), **g** palate fragment. *M1–M3 upper* molars, *P4 upper* fourth premolar. *Scale bar* equals 1 mm ▶


(a)
P4
M1
M2
anterior
lingual
(b)
P4 root
M1 root
M2 root
(c)
P4
M1
M2
M3
anterior
lingual
(d)
P4
M1
M2
anterior
lingual
(e)
M2 root
(f)
P4
M1
M2
M3
(g)

because of the different stages of wear of the molariforms of the neosyntype. Cement is abundant since juvenile stages in all molariforms and covers entirely the walls of the hypoflexid.

The specimen MLP 91-II-25-3 (Fig. 2f–j) can be assigned undoubtedly to *P. mixtus* because of the p4 morphology.

Mandible The preserved portion of the left mandible (MLP 91-II-25-3) has on its labial side (Fig. 2f) the notch for the insertion of the tendon of the m. *masseter medialis pars infraorbitalis* (nMpi) and the masseteric crest broken but connected to each other as in all eocardiids; on the lingual side (Fig. 2g) it can be seen that the incisors extend up to the level of the anterior lobe of m2. The fragment of right mandible shows the anterior portion of the horizontal crest, which is low and forms a broad ridge (Fig. 2h). The alveolar protuberances are not developed in these specimens. The specimen MLP 15–217a coincides with this description.

Lower teeth The p4 of MLP 91-II-25-3 (Fig. 2i) matches, in general, that of the neosyntype (MACN A 2022; Fig. 2a) but is slightly more worn and with some differences related to ontogeny. The vertical furrow of the anterior wall becomes shallower toward the base but does not reach it. The antero and metafossettid are narrow and elongate, the mesofossettid has already disappeared. On the lingual wall the enamel is interrupted from the base up to three quarters upwards of the preserved height of the crown (Fig. 2g). The m1–m2 are very similar to each other (Fig. 2i), but m2 is slightly larger; the lobes are narrow, although the posterior is somewhat wider than the anterior; the hypoflexid with cement, is narrow, elongate, with almost straight walls, and reaches transversely more than halfway across the crown. The m1 (Fig. 2i) bears on the lingual wall a wide and shallow vertical furrow, opposite to the hypoflexid. The enamel is interrupted along the entire lingual wall. The occlusal surface bears a small and elongate metafossettid. The m2 (Fig. 2i) also bears a vertical furrow on the lingual wall, but somewhat narrower than that of the m1. On the m2 of the right mandible (Fig. 2j) the anterofossettid has already disappeared, but the small subcircular mesofossettid and the narrow and elongate metafossettid are still present. In the left mandibular fragment (Fig. 2i) only the narrow and elongate metafossettid still persists. The m3 (Fig. 2j) has slightly narrower lobes than m1–m2, the posterior lobe being transversely narrower and mesiodistally longer than the anterior one. The hypoflexid has cement, is triangular and reaches transversely half of the crown. The lingual furrow is not present, and the lingual wall is straight. The enamel is interrupted on the entire antero-lingual corner, and on the lingual base of the anterior lobe and part of the posterior lobe. The anterofossettid is narrow and elongated mediolaterally and the metaflexid is still open and is also elongated. The m3 lacks a mesofossettid.

Among the new specimens assigned to *P. mixtus*, there are four maxillary fragments with upper teeth preserved (Fig. 3), on the basis of which, a dental ontogenetic series can be established.

Maxillary The maxillary fragments are much damaged, but they show the base of the lower zygomatic root placed above the P4.

Upper teeth In all upper teeth the enamel is interrupted at the labial wall and labial portion of the posterior one.

The undescribed specimen MLP 15–341 is a juvenile (Fig. 3a–b). The cheek teeth are markedly high-crowned, and their bases are in the process of closing, becoming circular in outline, but the rudimentary roots that are present in later ontogenetic stages (e.g. MACN A 11302) are not already formed. The P4 is unilobed. (Fig. 3a), it has the posterior wall slightly concave and becomes convex toward the labial side. The anterior surface bears a subrectangular projection in occlusal view. This projection is limited lingually (Fig. 3b) by a shallow vertical furrow located on the antero-lingual wall, and an even shallower furrow on the antero-labial side. In occlusal view (Fig. 3a) it has four fossettes; the anterior ones seem to be the parafossette divided into lingual and labial ones. Alternatively, the more lingual fossette may be interpreted as a hypofossette. Posteriorly there is a very small fossette, almost completely worn away, and another one, large and rounded, located more labially. The M1 is approximately equal in size to the P4 (Fig. 3a), double-heart shaped occlusal surface, with a narrow hypoflexus, reaching transversely 2/3 the distance across the crown, and has cement; it lacks fossettes, except for a remnant of the metafossette on the posterior lobe. On the labial wall (Fig. 3a) there is a vertical furrow that is shallow and located in front of the hypoflexus. The anterior wall is convex, becoming straight toward the labial wall; whereas the posterior wall is slightly convex along its entire length. The M2 is much larger than M1 (Fig. 3a), with convex anterior, posterior and labial walls. It has three fossettes; the parafossette and metafossette are narrow and elongated, whereas the mesofossette is smaller and subcircular.

The undescribed specimen MACN PV SC3450 (Fig. 3c), referred to *P. mixtus* by Kramarz (2006) is a left maxillary fragment with P4–M3 somewhat more worn than those of the juvenile MLP 15–341. It has the same morphological features as MLP 15–341, but M1 completely lacks fossettes and M2 has only a small metafossette. The M3 is slightly larger than M2 and has a posterior projection of the posterior lobe; the parafossette and metafossette are large, whereas the mesofossette is smaller.

MACN A 11302 (Lectotype, Fig. 3d–e), illustrated by Ameghino (1889, Plate 10, Figs. 22–25 and 1906, Fig. 313) consists of a right maxillary fragment with P4–M2 that is more worn than MACN SC-3540. The P4 (Fig. 3d) has only an elongate central fossette, of uncertain homologies. In this stage of wear M1 and M2 lack fossettes. The hypoflexus is narrow, with cement. On the labial wall there is a vertical furrow relatively shallow and opposed to the xus. In this stage of wear teeth are rooted (Fig. 3e).

New material found in Campo Barranca (Santa Cruz Province; Kay et al. 2008), MPM-PV 4375 (Fig. 3f–g), is the first palate of *P. mixtus* with almost complete molariform series. The P4, M1, and M2 are similar in morphology to MACN A 11302, but the teeth are more worn and the P4 lacks fossettes. The M3 is similar in width to M2, and it has a conspicuous posterior projection, more developed than in *L. propheticus* (Kramarz 2006). The M3 show an acute angle between this projection and the posterior lobe like MACN SC 2832, and in contrast with the condition in MACN SC-3540. The palate is triangular and the dental series are more convergent anteriorly than in *L. propheticus*.

Comments *P. mixtus* differs from *Luantus propheticus, L. minor* and *L. toldensis* in a greater degree of hypsodonty, the presence of cement in earlier stages of wear, more ephemeral fossettes/ids, enamel discontinuities along the entire labial wall of upper cheek teeth and the lingual wall of lower cheek teeth (Kramarz 2006; Pérez et al. 2010). On the other hand, *Luantus* lacks the anterior extension of the anterior lobe of p4 or it is smaller than in *Phanomys* (*L. toldensis*; Kramarz, 2006), whereas p4 of *P. mixtus* has an extension similar in occlusal shape to *Eocardia excavata*.

Phanomys vetulus Ameghino, 1891 (Table 2; Fig. 4)

Syntype MACN A 2024, nine isolated molariforms: (a) left p4; (b) right m1 or m2; (c) left m1 or m2; (d) right m1 or m2; (e) very damaged lower molar; (f) juvenile left P4 and maxillary fragment; (g) left M1 or M2; (h) left M1 or M2 with mesofossette and metafossette; (i) left M1 or M2 with metafossette.

Table 2 Dental measurements of *Phanomys vetulus*, in millimeters

	APL	AW	PW
Phanomys vetulus			
MACN A 2024 (Syntype)			
(a) p4	3.00	1.67	2.18
(b) m1 or m2	3.53	3.11	3.55
(c) m1 or m2	2.84	–	–
(d) m1 or m2	–	–	2.66
(e) Damaged teeth	–	–	–
(f) P4	2.73	2.74	
(g) M1 or M2	2.86	–	2.58
(h) M1 or M2	2.81	2.37	2.40
(i) M1 or M2	2.86	2.78	2.70

APL anteroposterior length, *AW* anterior width, *PW* posterior width

Taxonomical considerations This species is known from nine isolated molariforms, currently catalogued as the syntype (MACN A 2024; Wood and Patterson 1959). The specimens that form currently the syntype are not those originally illustrated (right P4 isolated and left M2) by Ameghino (1891, Fig. 25), but they coincide with the original description. On the other hand, one of the molars of the syntype (MACN A b) was later illustrated by Ameghino (1894). The specimens illustrated by Ameghino (1891) are currently lost.

Geographic and stratigraphic provenance The syntype of *P. vetulus* (MACN A 2024) is from "Formación Santacruceña" at the Santa Cruz River cliff, Santa Cruz Province (Ameghino 1891, 1894).

Diagnosis All characters mentioned in the diagnosis of *Phanomys* are present in *P. vetulus*. However, the p4 is markedly worn and consequently, this morphology has to be corroborated in younger specimens. The adult specimens of *P. vetulus* are smaller than the adult specimens of *P. mixtus*.

Description The specimens of the syntype have the same morphological features as *P. mixtus,* but smaller (Table 2), being similar in size to that reported by Ameghino in the original description of *P. vetulus*. One of the syntype specimens (MACN A 2024 a) is an isolated left p4 (Fig. 4a–b) very worn, and broken on the lingual side, but with the characteristic outline of the genus with the anterior lobe labio-lingually shorter than the posterior one; a more complete knowledge of morphological details depends on future findings of young specimens. The specimen MACN A2024 b consists in a right lower molar in an advanced stage of wear without fossettids (Fig. 4c–d). The lower molars MACN A 2024 c (left m1 or m2), and MACN A 2024 d (right m1 or m2) lack fossettids, but they are less worn that MACN A 2024 b; whereas MACN A 2024 e is a much damaged lower molar. MACN A f consists in a left P4 juvenile with four fossettids like *P. mixtus* but smaller (Fig. 5; Tables 1, 2). The upper molars MACN A 2024 g (left M1 or M2), MACN A 2024 h (left M1 or M2) and MACN A 2024 i (left M1 or M2) are similar in size, they have metafossette, and MACN A 2024 h has also a mesofossette.

All teeth of the syntype are smaller than in *P. mixtus* except MACN A 2024 b which is larger than and very similar to MACN A 2022 b of *P. mixtus* (Fig. 5). This difference could be explained because MACN A 2022 b is more worn than MACN A 2024 b of *P. vetulus*. The crown diameter of the protohypsodont cheek-teeth of basal Cavioidea becomes smaller toward the base.

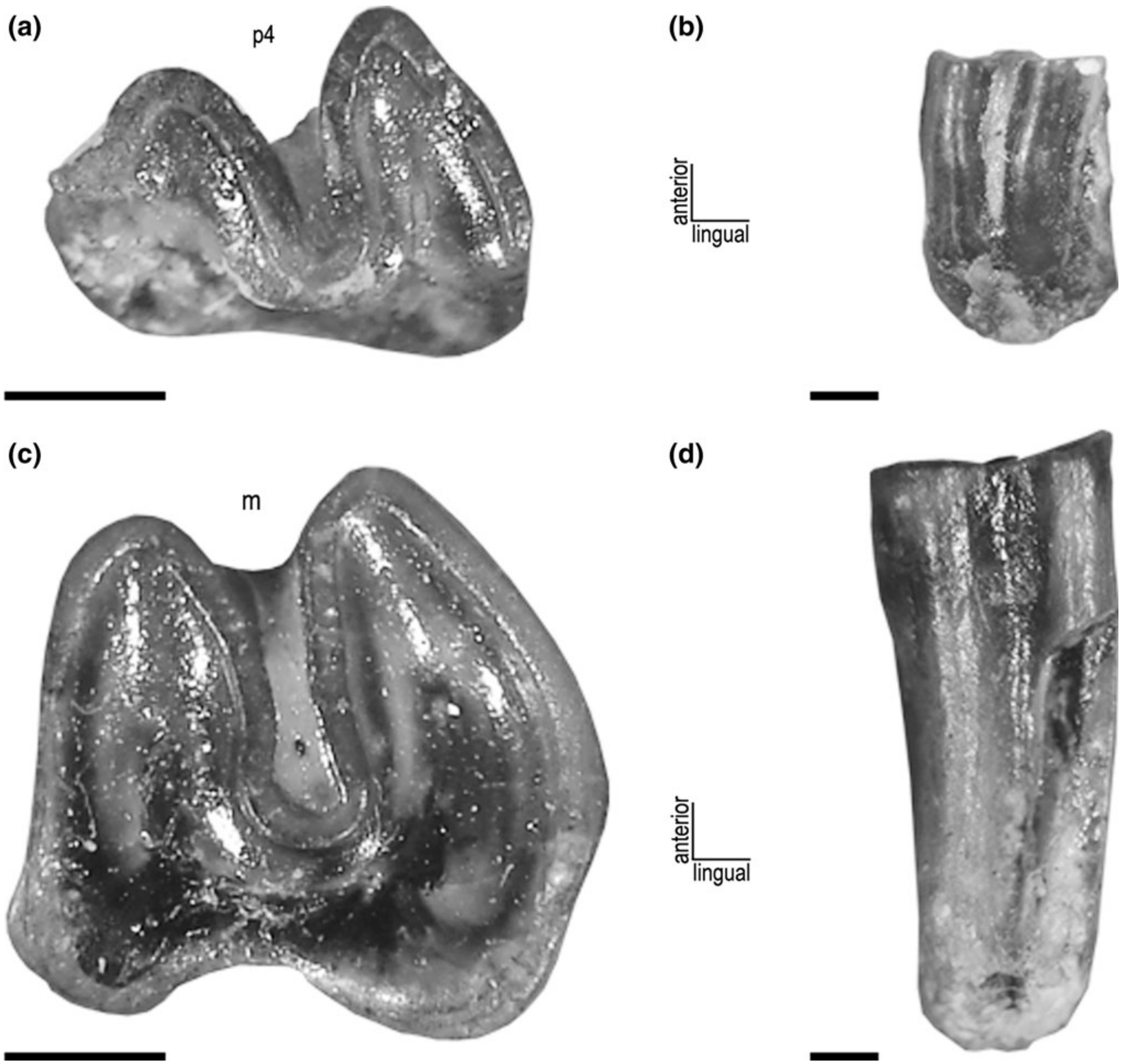


Fig. 4 *Phanomys vetulus*, Syntype MACN A 2024a *left* p4 **a** occlusal view (reversed), **b** labial view, and MACN A 2024b *left* m1or m2, **c** occlusal view (reversed), **d** lingual view. *m lower* molar, *p4 lower* fourth premolar. *Scale bar* equals 1 mm

Phylogenetic position of *Phanomys*

To test the phylogenetic position of *Phanomys* within Cavioidea s.s. a morphological cladistic analysis was performed using the matrix of Pérez and Vucetich (2011) re-scoring some characters of *Phanomys* and including the information given by the new specimens (Appendix 2). An equally weighted parsimony analysis was conducted using TNT 1.1 (Goloboff et al. 2008a, b), performing a heuristic search of 100 Wagner tree replicates followed by TBR that resulted in 10 most parsimonious trees of 277 steps (CI = 0.444; RI = 0.713). The strict consensus of each node is shown in Fig. 5.

In the strict consensus (Fig. 6) *P. mixtus* and *P. vetulus* forms a polytomy with the node formed by euhypsodont Cavioidea s.s. as previously reported by Pérez and Vucetich (2011). The resolutions of this polytomy in the most parsimonious trees show that *P. mixtus* and *P. vetulus* may form a monophyletic group basal to the clade of euhypsodont Cavioidea s.s., or that *P. mixtus* and *P. vetulus* are successive sister taxa to such a clade (*P. vetulus* being more basal in some trees and *P. mixtus* more basal in

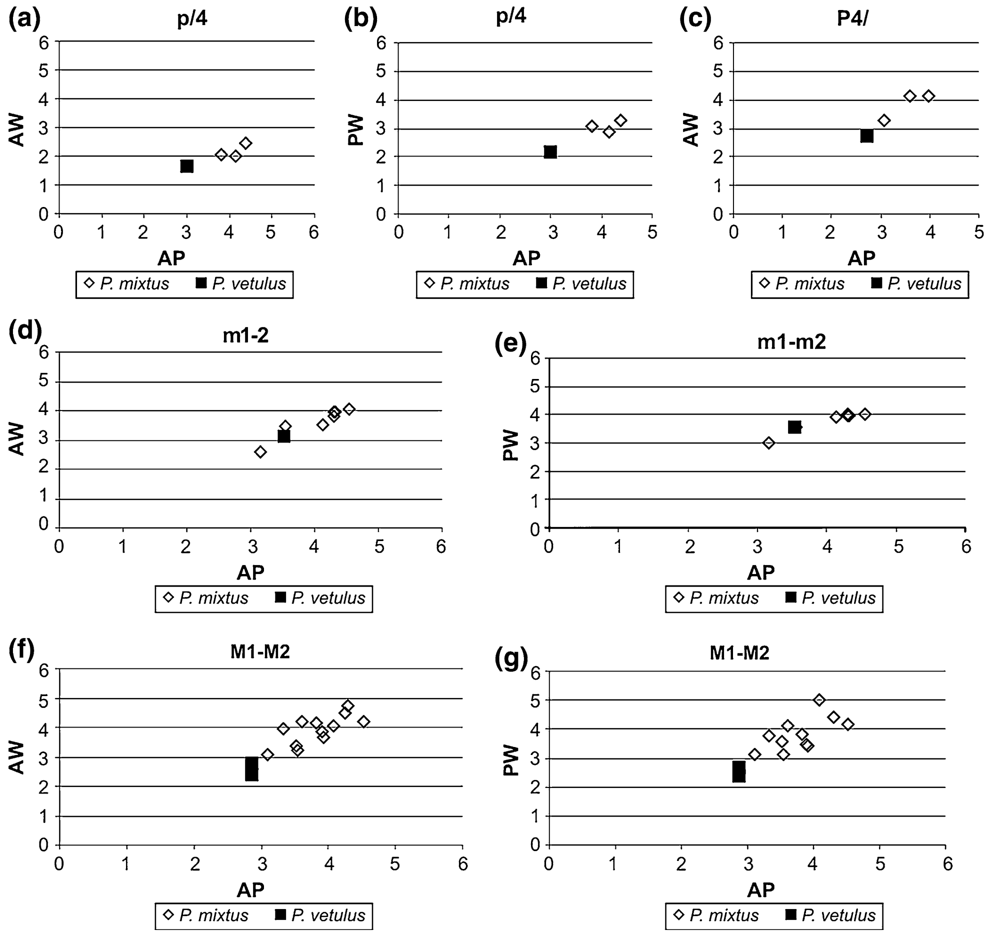


Fig. 5 Graphic of teeth measurements of *P. mixtus* and *P. vetulus*. p4 **a** AW versus AP, **b** PW versus AP; P4 **c** AW versus AP; m1–m2 **d** AW versus AP, **e** PW versus AP; M1–M2 **f** AW versus AP, **g** PW versus AP. *AP* anteroposterior length, *AW* anterior width, *PW* posterior width, *p/4 lower* fourth premolar, *m1–m2 lower* molars, *P4/upper* fourth premolar, *M1–M2 upper* molars

others). A detailed analysis shows that these possible resolutions have no character support to place *P. mixtus* and *P. vetulus* conforming a monophyletic clade or as successive sister group of euhypsodont Cavioidea s.s. Hence, the collapse of these branches is because of the presence of zero-length branches (Coddington and Scharff 1994) indicating the lack of characters enabling better assessment of the affinities of *P. mixtus* and *P. vetulus*.

The node of euhypsodont Cavioidea s.s. (Fig. 6) is supported in all the most parsimonious trees by two unambiguous synapomorphies: euhypsodont teeth, (character 29[3]), distribution of the enamel in molars interrupted along the entire labial wall of the upper molars (lingual of the lower molars) except for the furrow opposite to the hyopflexus/id (character 48[4]). Additionally, in some of the most parsimonious topologies this clade is supported by two unambiguous synapomorphies: constriction of the apex in each lobe of upper molars well developed in both lobes of each tooth (character 32[1]), and absent fossettes/ids in young-adult ontogenetic stage (character 50[1]). The abundance of missing entries in *P. vetulus* and its alternative phylogenetic positions create ambiguous optimizations for some characters that are possibly diagnostic of node A. If this taxon is pruned (Pol and Escapa 2009) from the most parsimonious trees, this node is also diagnosed by two additional synapomorphies: fossettids subcircular shaped (character 52[1]) and posterior projection of M3 well developed (character 55[1]) (Fig. 7).

The node formed by *P. mixtus* + *P. vetulus* + euhypsodont Cavioidea s.s. (Fig. 6) is supported in all most parsimonious trees by two unambiguous synapomorphies: shape of the molariform teeth, in occlusal view with heart-shaped lobes (character 30[2]), and shape of the hypoflexus/id in occlusal view, narrow and very long (character 34[2]). In some of the most parsimonious trees, this clade is also supported by one additional unambiguous synapomorphy: mesofossettid present in young-adult stage (character 56[1]).

The node formed by *L. toldensis* and more derived species of Cavioidea s.s. (Figs. 6, 7) is supported in all most parsimonious trees by two unambiguous synapomorphies: cement in juvenile ontogenetic stage present (character 46[1]) and fossettes/ids in late ontogenetic stage absent (character 49[1]).

The node formed by *L. propheticus* and more derived species of Cavioidea s.s. (Figs. 6, 7) is supported in all the most parsimonious trees by two unambiguous synapomorphies: development of the horizontal crest

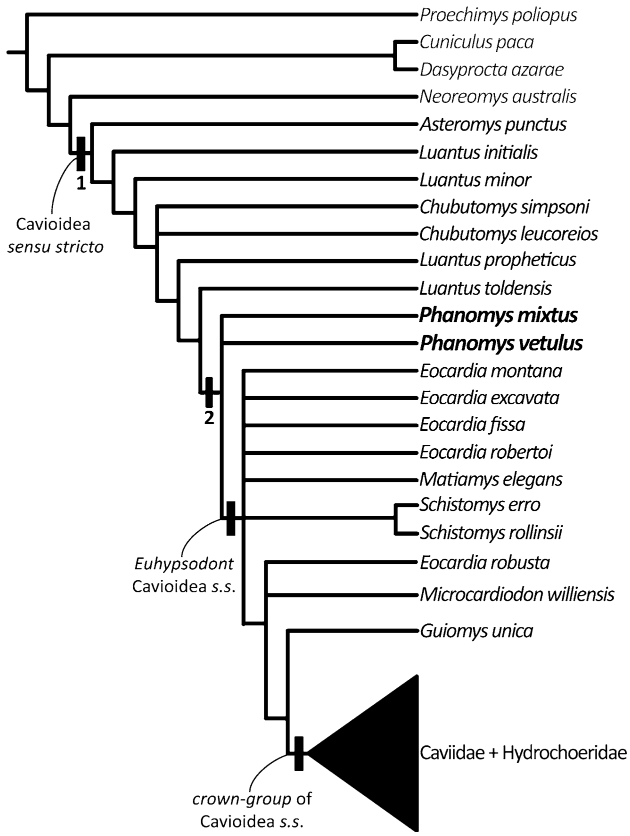


Fig. 6 Strict consensus of the ten most parsimonious trees (tree length = 277) resulting from cladistic analysis of a modified matrix of Pérez and Vucetich (2011; and see Appendix 2 of this paper). *P. mixtus* and *P. vetulus*, form a polytomy with the node formed by euhypsodont Cavioidea s.s. The numbers indicate Bremer indices at the main nodes

present as a conspicuous crest, forming laterally projected shelf but lacking a dorsal fossa (character 25[2]) and cement in young-adult ontogenetic stage present (character 45[1]).

The node formed by *Chubutomys simpsoni* + *C. leucoreios* + more derived Cavioidea s.s. (Figs. 6, 7) is supported in all most parsimonious trees by a single unambiguous synapomorphy: distribution of enamel in molars interrupted at the base and the corner of the lingual wall (character 48[2]).

The node formed by *L. minor* and species of more derived Cavioidea s.s. (Figs. 6, 7) is supported in all most parsimonious trees by one unambiguous synapomorphy: protohypsodont, having roots and the anteroposterior length of the occlusal surface less than half the height of the crown (character 29[2]).

The node formed by *L. initialis* and species of more derived Cavioidea s.s. (Figs. 6, 7) is supported in all most parsimonious trees by one unambiguous synapomorphy: constriction of the apex in each lobe of the molars present (character 31[1]).

The node of Cavioidea s.s. (Figs. 6, 7) is supported in all most parsimonious trees by four unambiguous synapomorphies: position of the mandibular foramen below the m3 (character 4[1]), posterior extension of the root of the lower incisors extending up to the level of the posterior lobe of m2 (character 18[1]), shape of the lateral crest curved, deflecting anteroventrally from the base of the coronoid process (character 22[1]), development of the horizontal crest present as a low and broad ridge (character 25[1]).

Phylogenetic robustness and the affinities of *Phanomys*

The phylogenetic position of *Phanomys* as the sister group of euhypsodont forms of Cavioidea s.s. has important implications for understanding the origin of this type of dentition. Therefore a thorough evaluation of the robustness of its phylogenetic position among the stem group of Cavioidea s.s. is needed to evaluate the robustness of the inferences made on the most parsimonious trees. Support values are low for most nodes of basal cavioids s.s. in the reduced consensus (Fig. 7), with Bremer support values of 1 and only a few nodes with frequency values above 50% in the bootstrap and jackknife analyses. Nevertheless, ignoring the alternative positions of *P. vetulus* the node of *P. mixtus* + euhypsodont Cavioidea s.s. has Bremer support values of 2 and bootstrap and jackknife frequencies above 80%. In this case, the node of euhypsodont Cavioidea s.s. has Bremer support values of 3 and values above 70% in the bootstrap and jackknife analyses. Furthermore, forcing *Phanomys* either into a more basal position among protohypsodont cavioids or a more derived position (within the euhypsodont node A) requires a minimum of three extra steps. Thus, despite the general low support values, the phylogenetic placement of *P. mixtus* is robustly supported as the most derived protohypsodont cavioid and the closest relative of the clade of euhypsodont forms of Cavioidea s.s. (Fig. 7; node A).

Biostratigraphic remarks

The stratigraphic distribution of *P. mixtus* allows some correlation to be done. This species was originally described as coming from the "Barrancas del río Santa Cruz, Piso Santacruceño" (Ameghino 1887b, 1889). Later, Ameghino (1900, 1902) listed *P. mixtus* among the taxa that possibly come from the Notohippidian Horizon from Karaiken (type locality of the Notohippidian), which bears a fauna somewhat older than that of typical Santacrucian localities. Kramarz and Bellosi (2005) and Kramarz (2006) correlated the upper sequence of the Pinturas Formation with the Notohippidian Horizon at Karaiken (Ameghino 1900,

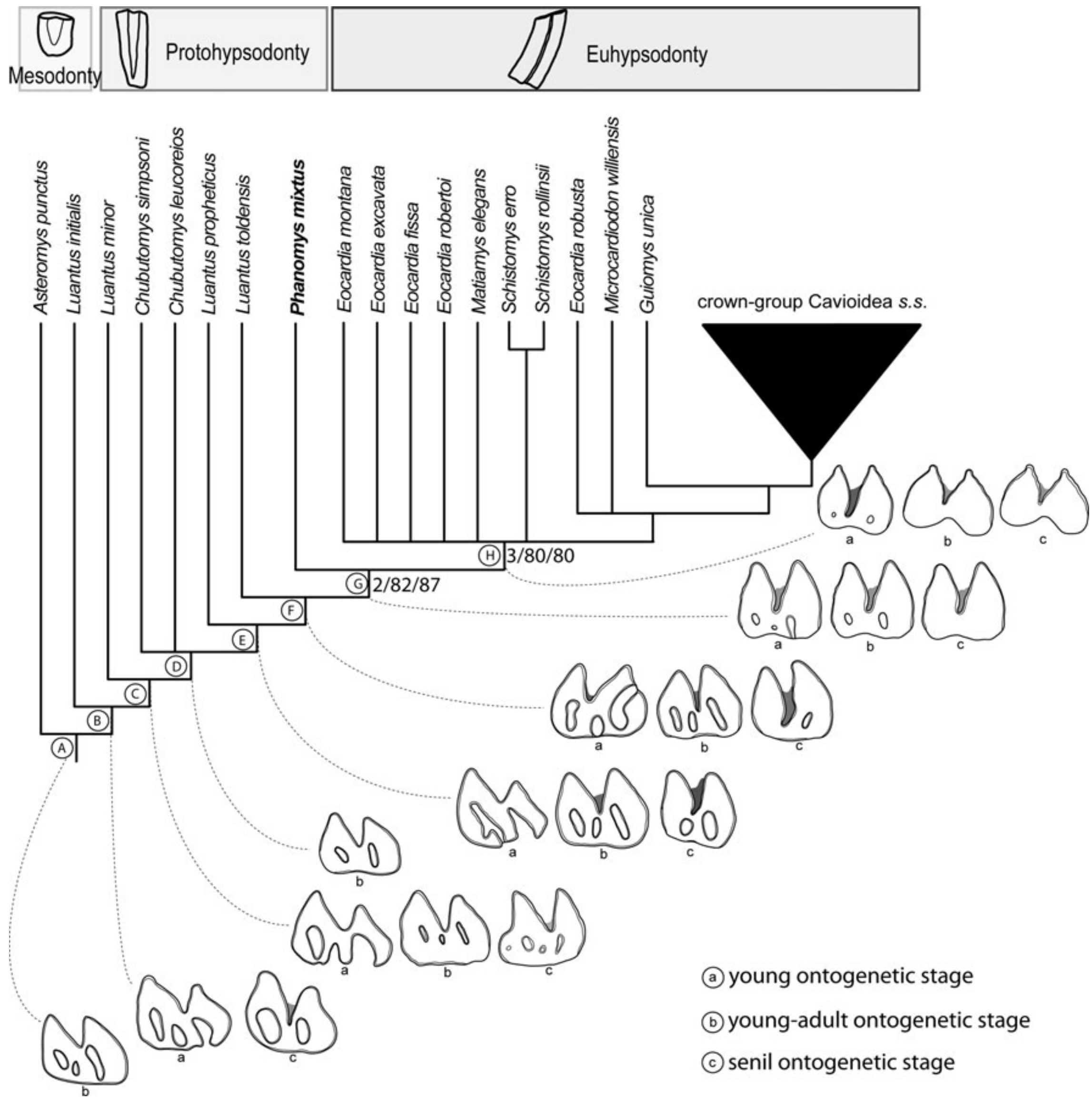


Fig. 7 Reduced consensus showing the major stages in the acquisition of euhypsodonty in Cavioidea s.s. Node **a** plesiomorphic condition for the entire clade of Cavioidea s.s. Node **b** presence of cement in senile ontogenetic stages. Node **c** acquisition of the protohypsodont. Node **d** appearance of discontinuities in the enamel. Node **e** cement appears in young-adult specimens. Node **f** cement appears in juvenile specimens. Node **g** disappearance of fossettids in senile ontogenetic stages. Node **h** appearance of euhypsodont dentition in Cavioidea s.s. The numbers indicate Bremer index, Bootstrap, and Jackknife values, respectively, at the main nodes

1902, 1906; Marshall and Pascual 1977) because they shared the rodent species *P. mixtus* and *Spaniomys modestus*. They also correlated that sequence with the lower levels of the Santa Cruz Formation at Monte León and Monte Observación because they share *Spaniomys modestus.* Recently, Kay et al. (2008) considered the Santa Cruz Formation at Campo Barranca as old as or even older than the levels cropping out at the costal localities of Monte León and Monte Observación. Thus, Campo Barranca would be partially contemporaneous with the upper levels of the Pinturas Formation at western Santa Cruz Province. The presence of *P. mixtus* at Campo Barranca corroborates this hypothesis.

The Río Jeinemení Formation represents the lower part of the Río Zeballos Group, while the Cerro Boleadoras Formation represents the middle part of Group Río Zeballos, and was assigned to the early Miocene (Ugarte 1956; Escousteguy et al. 2002), and Vucetich (1994) more specifically considered the fauna of Cerro Boleadoras as Santacrucian in age. The presence of *P. mixtus* in the Río Jeinemení Formation enables its correlation with the lower levels of the Santa Cruz Formation at the costal localities, the upper sequence of the Pinturas Formation, and probably also with the Notohippidian Horizon at Karaiken.

Discussion

Taxonomic status of *P. vetulus*

As shown above, the phylogenetic results indicate that both *P. mixtus* and *P. vetulus* are close relatives of the node of euhypsodont cavioids (Fig. 6) and corroborate the close affinities of both species. However, the fragmentary remains known for *P. vetulus* only enables limited knowledge of this species. The syntype material of *P. vetulus* consists of nine isolated molariforms with different degrees of wear, some of which are damaged. Ameghino (1891) characterized *P. vetulus* as being 50% smaller than *P. mixtus*. The evaluation of size performed here does not support such a great difference. Nevertheless, the material assigned to *P. vetulus* is consistently smaller than that of *P. mixtus* (Fig. 5), hence we accepted it as a valid species, although only more complete specimens will provide the necessary information for solving its actual status.

Evolution of the euhypsodonty in Cavioidea s.s.

It has long been recognized that one of the major evolutionary trends in the history of Cavioidea s.s. is the progressive acquisition of hypsodonty (Ameghino 1887b; Kraglievich 1932; Wood and Patterson 1959; Kramarz 2006). These authors have in fact mentioned that the evolutionary trend in the group involves the modifications of several features, possibly related with the acquisition of euhypsodonty, for example absence of fossettes/ids, presence of cement, discontinuities of enamel, continuous growth of crown evidenced by the absence of roots. Furthermore, some of the characters classically related to hypsodonty, for example the appearance of cement or the presence of fossettes/ids in molariforms vary through the ontogeny in some cavioid taxa. All these features were analyzed as independent characters in this phylogenetic study in order to test their sequence of appearance. The presence of ontogenetically variable characters was therefore defined in separate characters for three different ontogenetic stages (juvenile, young-adult and senile) that were recognized by the degree of wear of the preserved teeth (Pérez and Vucetich 2011).

The most basal species of Cavioidea s.s. (*A. punctus*) is a mesodont taxon that lacks cement, has fossetids, and the enamel is continuous around the entire surface of the crown in all known ontogenetic stages, representing the plesiomorphic condition for the entire clade of Cavioidea s.s. (Fig. 7, node A). The first of the changes related to the evolution of hypsodonty is the presence of cement in senile ontogenetic stages. This condition is present in *L. initialis* and all more derived forms (Fig. 7, node B).

The second modification recorded in the phylogenetic analysis is the acquisition of the protohypsodont stage (present in *L. minor* and more derived species; Fig. 7, node C), characterized by a high crown and presence of roots (see "Materials and methods" and Mones 1982). Subsequently, in node D (Fig. 7), the phylogenetic analysis indicates the appearance of discontinuities in the enamel (present in *Chubutomys* and more derived forms).

The two subsequent characters related to the origin of hypsodonty are changes in the ontogenetic timing of appearance of cement. First the cement appears in young-adult specimens (a change optimized in node E, given its presence in *L. propheticus*) and then in juvenile specimens (Fig. 7, node F, as indicated by the juvenile specimens of *L. toldensis* and *P. mixtus*).

Phanomys represents the most advanced protohypsodont cavioid characterized by an increase in the discontinuities of enamel which are already present in juvenile specimens, and disappearance of fossettes/ids in senile specimens (Fig. 7, node G). Furthermore, *Phanomys* and more derived forms lack mesofossettid in young-adult ontogenetic stages. This derived character is also present in the more basal *Chubutomys*, and therefore is ambiguously optimized in the most parsimonious trees. One of the possible reconstructions is that disappearance of mesofossettid in young-adult ontogenetic stages occurred convergently in *Chubutomys* and *Phanomys* + euhypsodont cavioids s.s. The other equally parsimonious reconstruction is that mesofossettids were lost earlier in the evolutionary history of Cavioidea s.s. (at node D: *Chubutomys* + more derived Cavioidea s.s.) but reappeared in *L. propheticus* and *L. toldensis*. These are the last changes recorded before the appearance of euhypsodont dentition in node H.

The appearance of euhypsodont dentition is characterized by the complete absence of roots. This change is accompanied by the ephemeral presence fossettes/ids (disappearing in young-adult ontogenetic stages in most euhypsodont taxa). Further modifications of the characters related to hypsodonty are also inferred to occur later in the phylogeny of the group. For instance, *Microcardiodon williensis* and more derived forms (*Guiomys* and the crown group) lack fossettes/fossettids in all (postembryonic) ontogenetic stages.

As shown above, the result of the phylogenetic analysis indicates that the modifications related to an increase in the degree of hypsodonty (e.g., mesodont, protohypsodont, euhypsodont; Fig. 7) as the presence of cement and the disappearance of fossettes/ids do not appear at the same time in the evolution of Cavioidea s.s. In fact, most of the characters traditionally associated to hypsodonty have appeared gradually during the evolution of the group, having independent evolutionary histories and therefore being phylogenetically independent characters.

The increasing degree of hypsodonty has been interpreted as progressive adaptations to the environmental change recorded during the early evolution of the group in the Oligocene–early Miocene. During this time, South America (and especially Patagonia) experienced a marked cooling and aridization, and an increase in the volcanism that provided a great amount of glass to the sediments (Mazzoni 1985; Bellosi 2010; Barreda and Palazzesi 2010).

An important consequence of this phylogenetic analysis is that although the morphological changes associated with hypsodonty (e.g. formation and later reduction of fossettes/ids, acquisition of cement) may be functionally related or their presence explained by a common evolutionary trend (or selective environmental pressure), the sequence of appearance of morphological changes inferred from the fossil record indicates that they were temporally decoupled along the evolution of the group during the late Oligocene–early Miocene. An increase in the degree of hypsodonty might affect the subsequent evolution (loss or acquisition) of certain characters, but the dependence among these characters would be biological but not phylogenetic (Kluge 1989).

Although the evolutionary trend in Cavioidea s.s. shows a progressive increase in the hypsodonty and the acquisition of robust and simple occlusal surfaces (through the loss of fossettids, appearance of cement, and discontinuities of enamel), the evolution of these features is more complex than previously supposed. The phylogenetic analysis shows that some structures have a homoplastic evolutionary history. For example, although *Chubutomys* is a relatively basal cavioid (given the protohypsodont stage, absence of cement, poorly developed discontinuities in the enamel) it has lost the mesofossettid in young-adult specimens (Fig. 7), an evolutionary novelty convergently acquired in *Phanomys* and euhypsodont cavioids.

Conclusions

Phanomys mixtus was known by a few isolated teeth and fragments of maxilla (Ameghino 1887b, 1889, 1891, 1894; Scott 1905; Wood and Patterson 1959; Kramarz 2006). The new materials assigned to *P. mixtus* in this paper are the first mandibular fragments (MLP 91-II-25-3, and MLP 15–217a) and the first palate known (MPM-PV 4375) of this species, yielding valuable morphological, ontogenetic, and phylogenetic information. The new findings of *P. mixtus* at different Miocene localities of Santa Cruz Province (i.e. Campo Barranca and Río Jeinemení) widens its known geographic distribution, which together with its short stratigraphic range, suggest that this species could be a useful biostratigraphic indicator.

On the other hand, although *P. vetulus* is recognized as a validate species, more material is needed to corroborate its status.

The phylogenetic analysis shows that *Phanomys* is the latest-diverging protohypsodont eocardiid and positions *Phanomys* as the sister group of euhypsodont Cavioidea s.s. In this way, this analysis confirms the close relationship of *Phanomys* to euhypsodont eocardiids (e.g. *Eocardia*) and corroborates previously proposed hypotheses (Ameghino 1887b; Scott 1905; Wood and Patterson 1959; Kramarz 2006). The new evidence (taxonomic and phylogenetic) is crucial to understanding the origin of euhypsodonty in Cavioidea s.s.

The evolutionary history of Cavioidea s.s. reflects that the characters previously related to the degree of hypsodonty (e.g. absence of fossettes/ids, presence of cement, discontinuities of enamel) do not appear at the same time during the evolution of the group and thus are phylogenetically independent characters. Although the evolutionary trend in Cavioidea s.s. shows a progressive increase in the hypsodonty, the morphological changes inferred from the fossil record indicate that they were temporally decoupled along the evolution of the group during the late Oligocene- early Miocene. These morphological changes may be related to a general tendency toward climatic deterioration, in addition to periods of intense volcanism that affected Patagonia from Eocene to Miocene. The climatic deterioration (cooling and aridization) and a large amount of abrasive materials would have been a selective pressure that favored the development of hypsodonty in the evolution of Cavioidea s.s.

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Appendix 1

See Table 3

Table 3

Family	Species
"Eocardiidae"	†*Asteromys punctus* Ameghino, 1897
	†*Chubutomys simpsoni* Wood and Patterson, 1959
	†*Chubutomys leucoreios* Pérez et al., 2010
	†*Luantus initialis* Ameghino, 1902
	†*Luantus minor* Pérez et al., 2010
	†*Luantus propheticus* Ameghino, 1898
	†*Luantus toldensis* Kramarz, 2006
	†*Phanomys mixtus* Ameghino, 1887
	†*Phanomys vetulus* Ameghino, 1894
	†*Eocardia montana* Ameghino, 1887
	†*Eocardia excavata* Ameghino, 1894
	†*Eocardia fissa* Ameghino, 1891
	†*Eocardia robusta* Vucetich, 1984
	†*Eocardia robertoi* Vucetich, 1984
	†*Schistomys erro* Ameghino, 1887
	†*Schistomys rollinsii* Scott, 1905
	†*Matiamys elegans* Vucetich, 1984
	†*Microcardiodon williensis*, Pérez and Vucetich, 2011
	†*Guiomys unica* Pérez, 2010b
Caviidae	†*Prodolichotis pridiana* Fields, 1957
	†*Orthomyctera chapadmalense* Ameghino, 1889
	†*Dolicavia minuscula* Ameghino, 1908
	Dolichotis patagonum Zimmermann, 1780
	Dolichotis salinicola Burmeister, 1876
	Microcavia australis Geoffroy and d′Orbigny, 1833
	Galea musteloides Meyen, 1833
	Cavia aperea Erxleben, 1777
	Kerodon rupestris Wied, 1820
Hydrochoeridae	†*Cardiomys cavinus* Ameghino, 1885
	†*Phugatherium novum* Ameghino, 1908
	Hydrochoerus hydrochaeris Pallas, 1766
Cuniculidae	*Cuniculus paca* Linnaeus, 1766
Dasyproctidae	†*Neoreomys australis* Ameghino, 1887
	Dasyprocta azarae Lichtenstein, 1823
Echimyidae	*Proechimys poliopus* Osgood, 1914

Taxa used for comparisons and phylogenetic analysis († = extinct)

Appendix 2

See Table 4.

Table 4 Character-taxon matrix (Pérez and Vucetich 2011) used for phylogenetic analysis was re-scored by *Phanomys mixtus* and *Phanomys vetulus*

Taxon	10	20	30	40	50	60	70	80	89
Phanomys mixtus	??????????	???????2?0	??????0?22	1022100??0	10?1111510	000101110?	??????????	??????????	?????????
Phanomys vetulus	??????????	??????????	????????22	1022100???	10?1111510	0[01]0??1110?	??????????	??????????	?????????

Characters between brackets represent polymorphic or uncertain scorings

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