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A NEW RODENT (CAVIOIDEA, HYSTRICOGNATHI) FROM THE MIDDLE MIOCENE OF PATAGONIA, MANDIBULAR HOMOLOGIES, AND THE ORIGIN OF THE CROWN GROUP CAVIOIDEA SENSU STRICTO

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ABSTRACT—Cavioidea sensu stricto groups three traditionally recognized families that are characterized by hypsodont, double-heart-shaped cheek teeth and moderate hystricognathy: Eocardiidae, Caviidae, and Hydrochoeridae. Eocardiidae was erected to include a diverse assemblage of extinct and plesiomorphic taxa, whereas Caviidae and Hydrochoeridae (the crown group of Cavioidea) include the lineages with extant representatives (cuyes, maras, and capybaras). A new genus and species of Cavioidea sensu stricto, *Guiomys unica*, is described here from the middle Miocene of west central Patagonia (Argentina). The new taxon is known from mandibular and maxillary fragments with molars, and isolated cheek teeth. A phylogenetic analysis of Cavioidea sensu stricto shows *G. unica* as the sister taxon of the clade formed by the crown group of Cavioidea sensu stricto ('medialis series'). The new species displays characters states intermediate between eocardiids and the 'medialis series.' The most outstanding character of *Guiomys unica* is the autapomorphic position of the notch for the insertion of the masseter medialis pars infraorbitalis muscle, isolated from both the masseteric and horizontal crests. This notch is located at the anterior end of the masseteric crest in eocardiids and represents the plesiomorphic state for Cavioidea sensu stricto. In caviids and hydrochoerids, the notch is located at the anterior end of the horizontal crest, the derived state for this character. *G. unica* allows reinterpretation of the homologies of the mandibular crests in basal cavioids and clarifies the evolutionary origins of crown-group cavioids (Caviidae + Hydrochoeridae).

INTRODUCTION

The family Eocardiidae was established by Ameghino (1891) to group cavioid rodents that have high-crowned and double-heart-shaped teeth (similar to those of maras, cuyes, and capybaras), but that retain plesiomorphic character states such as fossettes/ids in their cheek teeth. These taxa are recorded from the Deseadan South American Land Mammal Age (SALMA) to the Colloncuran (late Oligocene–middle Miocene) in the austral region of South America (Ameghino, 1887, 1889, 1891, 1897, 1898, 1899, 1902, 1906; Scott, 1905; Wood and Patterson, 1959; Bondesio et al., 1980; Vucetich, 1984; Kramarz, 2006; Croft, 2007; Flynn et al., 2008). Eocardiids were traditionally considered as the ancestral group of the families Caviidae and Hydrochoeridae—cuyes/maras and capybaras—which are first recorded in the middle and late Miocene, respectively.

Patterson and Wood (1982:511) grouped the three families in Cavioidea sensu stricto (Cavioidea s. s.), which together with Dasyproctidae, Cuniculidae (= Agoutidae), and Dinomyidae form the more inclusive group Cavioidea sensu lato. Miller and Gidley (1918) and Ellerman (1940) informally grouped Caviidae and Hydrochoeridae in the 'medialis series' because they considered that the masseter medialis muscle was the main agent in modifying form of outer side of mandible. In addition to their peculiar euhypsodont and double-heart-shaped cheek teeth, members of the 'medialis series' (or crown-group of Cavioidea s. s.) are also characterized by apparently being non-hystricognathous (Landry, 1957; Patterson and Wood, 1982:510).

The aim of this work is to report a new cavioid from central Patagonia (Fig. 1), found in levels assigned to the middle–late Miocene (Goin and Carlini, 1993; Villafañe et al., 2008). This new species provides valuable information about the mandibular configuration in Cavioidea s. s., which leads to a reinterpretation of

the homologies of the mandibular crests for this superfamily, and provides insights on the evolutionary origins of the crown group of Cavioidea s. s. (Caviidae + Hydrochoeridae).

MATERIALS AND METHODS

Dental nomenclature used here follows Candela (1999) and Marivaux et al. (2004) (Fig. 2A–B), except for euhypsodont molars of Cavioidea s. s., for which a revised nomenclature is proposed (Fig. 2C–D). Mandibular nomenclature (Fig. 3A–B) is modified from Woods (1972) and Woods and Howland (1979). In order to test hypotheses of primary homology of mandibular crests in Cavioidea s. s., two cranio-mandibular dissections of different sized caviids—*Cavia aperia* and *Dolichotis patagonum*—were conducted. The cavioid taxa used for comparisons and phylogenetic analysis are listed in Table 1.

Taxonomic Nomenclature—Following Patterson and Wood (1982), Cavioidea sensu lato includes Dasyproctidae, Cuniculidae, "Eocardiidae," Caviidae, and Hydrochoeridae, whereas Cavioidea sensu stricto encompasses "Eocardiidae," Caviidae, and Hydrochoeridae. This study supports the paraphyly of "Eocardiidae," hence the use of quotation marks. The crown group of Cavioidea sensu stricto is formed by Caviidae + Hydrochoeridae, which is identical in taxonomic composition to the 'medialis series' sensu Miller and Gidley (1918).

Institutional Abbreviations—MPEF-PV, Museo Paleontológico Egidio Feruglio-Paleontología de Vertebrados, Trelew; MPEF-Zool, Museo Paleontológico Egidio Feruglio-Colección de Actuales, Trelew; MLP, Colección de Paleontología de Vertebrados y Colección de Mastozoología, Museo de La Plata, La Plata; MACN A, Colección Nacional Ameghino Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; MACN

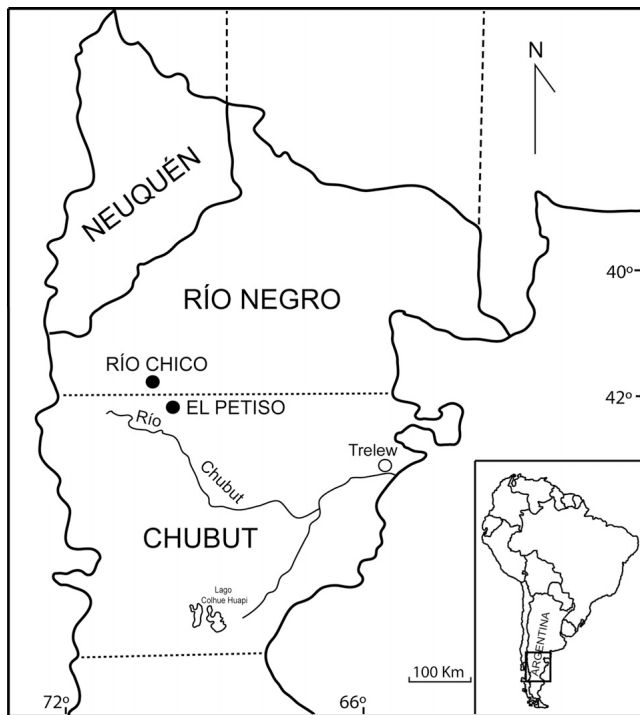


FIGURE 1. Location map of El Petiso (Chubut province) and Río Chico (Río Negro province) localities, Argentina.

Pv, Colección Nacional de Paleovertebrados Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”; **MMP**, Museo Municipal de Ciencias Naturales “L. Scaglia” de Mar del Plata.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
 Suborder HYSTRICOGNATHI Tullberg, 1899
 Superfamily CAVIOIDEA Kraglievich, 1930
GIUMYS UNICA, gen. et sp. nov.
 (Figs. 4–6)

Diagnosis—*G. unica* is diagnosed by the following autapomorphic characters: notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle located anteriorly and completely isolated from both the masseteric and the horizontal crests; presence of lingual flexids that are variable in length and that disappear with wear, but that do not form fossettids. Differing from members of the ‘medialis series’ in notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle connected to the horizontal crest and lacking flexi/ids (e.g., *Dolichotis*) or having them along the entire crown (e.g., *Hydrochoerus*) and remaining open throughout life without forming fossettes/ids. Differing from the rest of Caviioidea sensu stricto in notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle connected to the masseteric crest, and having flexi/ids that form fossettes/ids at least at some ontogenetic stage.

Etymology—The generic name is in honor of Dr. María Guiomar Vucetich, for her contributions to the systematics and anatomy of cavioid rodents. The specific epithet refers to the unique mandibular configuration of the new taxon.

Holotype—MPEF-PV 3504, fragment of right mandible with p4–m3.

Stratigraphic and Geographic Provenance—Most of the material was found in a new locality (El Petiso), located in northwest

Chubut Province, Argentina (see Fig. 1). The faunal assemblage found at this locality indicates a middle Miocene age, probably post-Colloncuran (Villafañe et al., 2008). Three additional specimens housed at the MLP collections were collected in the locality Río Chico, southwest Río Negro Province, Argentina (Goin and Carlini, 1993; see also Fig. 1). The latter locality has been considered as younger than the classic Colloncuran assemblages of Patagonia (Kay et al., 1997). Precise coordinates of the fossiliferous locality of the type material are housed at the MPEF collections and can be obtained from the author upon request.

Referred Material—MPEF-PV 3505, toothless right mandible; MPEF-PV 3506, left mandible with p4–m3; MPEF-PV 3508, 3513, 3514, left mandible with p4–m2; MPEF-PV 3512, 3519, right mandible with m1–m2; MPEF-PV 3524, 3526, 3529, right mandible with p4–m1; MPEF-PV 3527 and MLP 91-IX-4-3, left mandible with p4–m1; MPEF-PV 3533, maxilla with left P4–M2 and right P4–M1; MPEF-PV 3534, palate with right P4–M1 and M3; MPEF-PV 3535, 3537, right maxilla with M2–M3; MPEF-PV 3536, right maxilla with M2–M3; MPEF-PV 3538, left maxilla with M1–M2; MPEF-PV 3539, left maxilla with M3; MPEF-PV 3540, 3541, left maxilla with P4; MPEF-PV 3542, right maxilla with P4; MPEF-PV 3543, right maxilla with M1; MLP 91-IX-4-2, right mandible with p4–m2; MLP 91-IX-4-1, palate with both dental series.

Description and Comparison

Mandible—The material is fragmentary, but most specimens preserve part of the horizontal ramus, in which anatomical characters significant for phylogeny can be observed. The mandible is robust, larger than that of *C. aperea* and *Kerodon rupestris*, but smaller than in *Eocardia montana*, and has relatively conspicuous alveolar protuberances. The dorsal crest is subhorizontal (see ‘Homologies of Mandibular Crests,’ below) and robust, arising below m2, and the masseteric crest is not developed in the known specimens (although none have preserved the angular portion). The notch for the insertion of the masseter medialis pars infraorbitalis (Woods and Howland, 1979) is located anteriorly, below m1, and is completely isolated from the masseteric and horizontal crests (sensu Ellerman, 1940:237) (Fig. 4).

The mandibular foramen is located, as in all Caviioidea s. s., below m3; this could be related to the length of the incisor (Verzi, 1994), which extends only to the level of m2. The hystricognath fossa is relatively shallow, as in dolichotines, hydrochoerids, and euhypsodont ‘eocardiids.’

Lower Teeth—The morphology of the molariform teeth of *G. unica* is more uniform than that of euhypsodont ‘eocardiids’; the four molariforms are very similar in size and shape, and the hypoflexid has the same shape and disposition, whereas in euhypsodont ‘eocardiids’ there are differences in size and shape among molars, among lobes, and even among hypoflexids of different molariforms of a single specimen. Except for the highly derived condition of hydrochoerids, the uniform morphology of the molariform teeth of *G. unica* resembles the condition of caviines and dolichotines.

The p4 of *G. unica* has two well-developed lobes (Fig. 5A–B), of which the anterior is variable in shape and size. It has a strongly developed, blunt anterior projection, which does not form a true third lobe (Kraglievich, 1930; Contreras, 1964). This morphology is similar to that in *Dolicavia minuscula* and *Prodolichotis pridi-ana*, but in *G. unica* this tooth is proportionately smaller (Table 2). Two main characters of p4 are variable among the available material of *G. unica*: (1) the furrow between the first lobe and the anterior projection is variable in depth; (2) the apex of the anterior lobe follows the axis of the lobe (Fig. 5A) or is slightly anteriorly directed. These differences are considered as individual variations given that p4 is the most variable lower tooth both in size and shape in extant caviids (Kraglievich, 1930, Contreras,

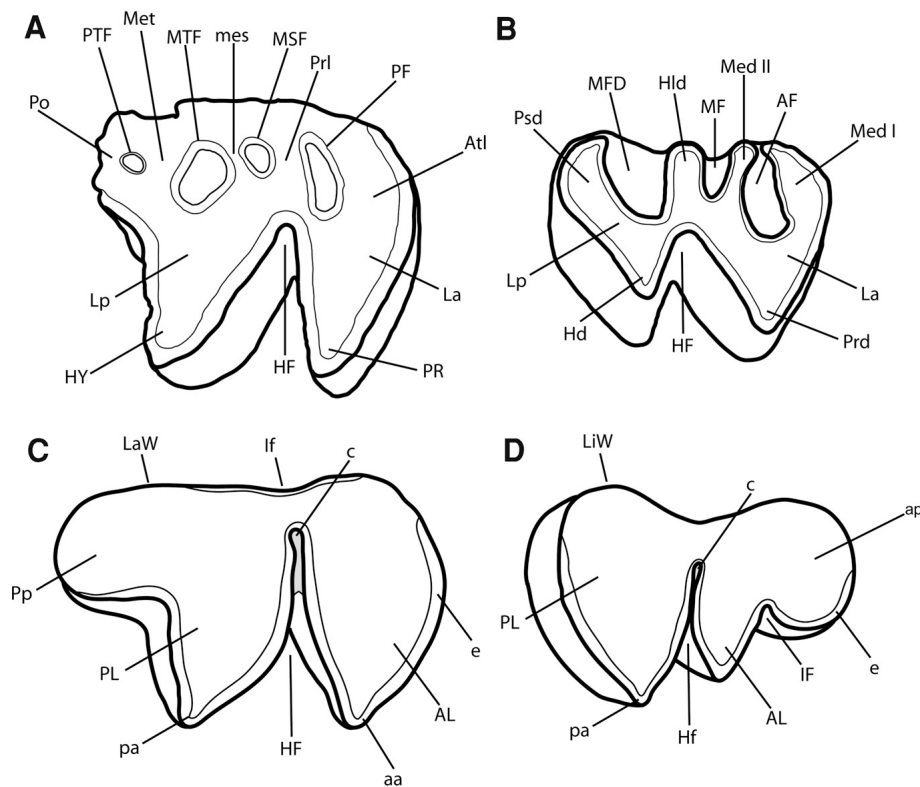


FIGURE 2. Occlusal dental morphology of upper and lower teeth and related nomenclature (Candela, 1999; Marivaux et al., 2004). **A**, *Luantus minor* Pérez et al. (2010), MPEF PV 5028, right M3 in occlusal view. **B**, *Luantus minor* Pérez et al. (2010), MPEF PV 1154a, left m2 in occlusal view. **C**, *Guiomys unica*, gen. et sp. nov., MPEF PV 3535, right M3 in occlusal view. **D**, *Guiomys unica*, gen. et sp. nov., MPEF PV 3504, right p4 in occlusal view. **Abbreviations:** aa, anterior apex; AF, anterofossetid; AL, anterior lobe or prism; AtI, anteroloph; c, cement; e, enamel; Hd, hypoconid; Hf, hypoflexid; HF, hypoflexus; Hld, hypolophid; HY, hypocone; If, interprismatic furrow; Med I, metalophulid I; Med II, metalophulid II; MF, mesoflexiid or mesofossettid; MFD, metaflexid or metafossettid; mes, mesolophule; LaW, labial side or wall; Met, metaloph; MSF, mesoflexus or mesofossette; MTF, metaflexus or metafossette; pa, posterior apex; PF, paraflexus or parafossette; PL, posterior lobe or prism; Po, posteroloph; Pp, posterior projection; PR, protocone; Prd, protoconid; Prl, protoloph; Psd, posterolophid; PTF, posterofossette.

1964). The p4 of *G. unica* differs significantly from the condition of both 'eocardiids' and crown-group cavioids. 'Eocardiids' either lack or have a small anterior projection of p4 (e.g., *E. montana*) that is never as well developed as in *G. unica*. An incipient anterior projection of the p4 also occurs in extant Caviinae and Dolichotinae (e.g., *Dolichotis patagonum*, *Cavia aperea*). In hydrochoerids (and *K. rupestris*), the anterior projection is even more developed than in *G. unica*, forming a true third lobe (Kraglievich, 1930).

The hypoflexid in p4 of *G. unica* has cement and is transversely deep (Fig. 5A). On the lingual side, the premolar has a wide interprismatic furrow. The enamel is distributed all around the crown, but is interrupted at the base of each lobe along the lingual side, and lingually at the anterior and posterior corners.

In the least worn specimen (MLP 91-IX-4-3; Fig. 5B-C), p4 is conical in lateral view, suggesting it has recently erupted; the projection of the anterior lobe is developed as in the adult specimens. A well-defined furrow is present on the lingual side of each lobe (Fig. 5C). This furrow is narrow and shallow, and is absent in the adult specimens due to wear. These furrows are probably homologous to the flexids of 'eocardiids' but much more ephemeral and failing to form fossettids. The enamel is continuous around the crown, and has cement at the lower half of the hypoflexid.

The m1 and m2 of *G. unica* have the anterior lobe equal to or slightly smaller than the posterior one (Fig. 5A). The hypoflexid has cement, is transversely deep, and its apex is transversely directed, or slightly bent anteriorly. The hypoflexid is anteroposteriorly wide labially and very markedly narrow lingually. This last character is similar to the condition of colloncuran 'eocardiids' (e.g., *Eocardia robertoi*) but differs from both the more plesiomorphic 'eocardiids' in which the hypoflexid is wide and transversely less penetrating (e.g., *Luantus propheticus*), and the Santacrucian 'eocardiids' (e.g., *E. montana*) in which the

hypoflexid is very narrow all along its length, and transversely deeper. A single wide lingual furrow is present opposite to the hypoflexid as in *Prodolichotis* and dolichotines. Enamel surrounds the crown, but is interrupted at the base of each lobe on the lingual side, and on the antero- and posterolingual corners of all molars, as in *D. patagonum*. The m3 differs from other molars because it is slightly larger, its lobes are more heart-shaped, and it shows the posterior inclination typical of euhyposodont dentitions.

On the m1 of the juvenile specimen (MLP 91-IX-4-3; Fig. 5B-C) the hypoflexid has cement, the enamel is distributed around the crown, and on the lingual side of the anterior lobe there is a shallow flexid variable in length, which does not form a true fossettid. This is an interesting character as it may be an intermediate condition between 'eocardiids,' which are characterized by having fossettes/ids at least during some ontogenetic stages, and the complete absence of fossettes/ids in cavioids. In addition, a break in the mandible exposes the base of the molar crown, which has the morphology of adult specimens, without lingual flexids.

Although associated skull and mandible remains have been found neither in El Petiso nor in Río Chico, in this paper upper dentitions collected in these localities are tentatively assigned to *G. unica* because of similar occlusal morphology, enamel and cement distribution, and size.

Maxilla—Dental series are anteriorly convergent (Fig. 6A), as in *Eocardia* spp. and *K. rupestris*. This convergence is not as evident as in *Dolichotis patagonum*, *Cavia aperea*, *Microcavia australis*, or *Galea musteloides*. MLP 91-IX-4-1 preserves the anterior part of the zygomatic arches with part of the maxilla and the jugal. The ventral zygomatic root arises at the level of P4.

Upper Teeth—Molars show strong unilateral hypsodonty; P4, M1, and M2 are bilobate and the anterior lobe smaller than the posterior one (Fig. 6B). The P4 is slightly smaller than molars, as in *Schistomys rollinsii*, whereas M1 and M2 are approximately

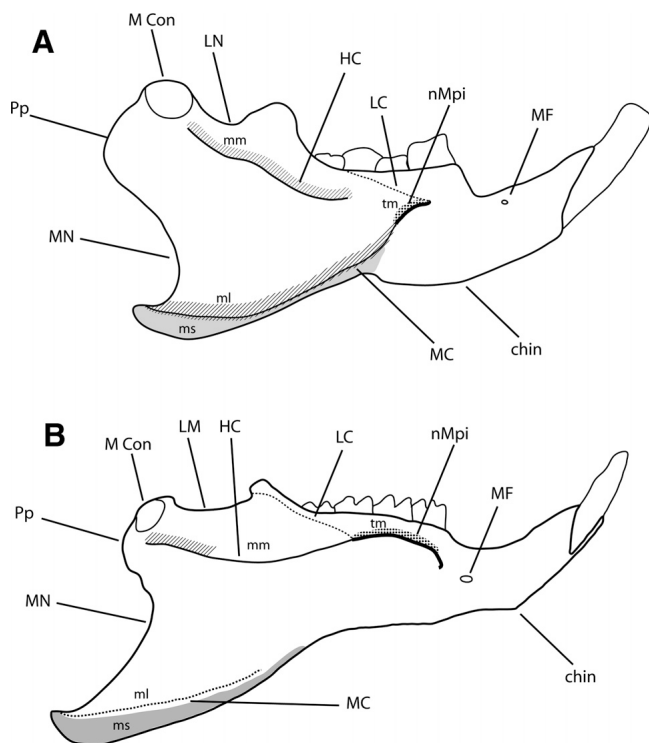


FIGURE 3. Mandibular morphology and related nomenclature (Woods, 1972; Woods and Howland). **A**, Mandibular morphology: *Dasyprocta azarae*, MLP 05.IX.97.02 right mandible in labial view. **B**, *Galea musteloides*, MLP 734, right mandible in labial view. **Abbreviations:** **HC**, horizontal crest; **chin**, posterior joint of the symphysis; **LC**, lateral crest; **MC**, masseteric crest; **MCon**, mandibular condyle; **MF**, mental foramen; **ml**, masseter lateralis muscle; **LM**, lunar notch; **mm**, masseter medialis muscle; **MN**, mandibular notch; **nMpi**, notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle; **ms**, masseter superficialis muscle; **Pp**, postcondylear process; **tm**, tendon of the masseter medialis pars infraorbitalis muscle.

equal in size. The enamel is continuous around the crown but interrupted at the base of each prism along the labial surface. The hypoflexus has cement, extending beyond the transverse midpoint of the crown and directed posteriorly, especially in M2 and M3. On the labial side, opposite the hypoflexus, there is a wide but relatively shallow longitudinal interprismatic furrow.

The M3 is similar to the other molars, but the posterior lobe has a large projection directed posteriorly, perpendicular to the prisms (Fig. 6C). This projection is more developed than in 'eocardiids' (except for *Eocardia robusta* and *Matiamys elegans*). Among living caviids, in *G. musteloides* and *K. rupestris* this projection is as in *G. unica*. However, in *C. aperea* the projection is smaller, whereas in *D. patagonum* and *M. australis* it forms a third lobe, because the flexus between this and the preceding lobe is extremely deep, narrow, and blunt (Kraglievich, 1930).

HOMOLOGIES OF THE MANDIBULAR CRESTS

Hystricognath rodents are characterized by a major mandibular specialization due to modifications related to the insertion of the masseter lateralis muscle. The hystricognath condition consists of the lateral deflection of the angular process exteriorly to the incisor alveolus (Ellerman, 1940; Hoffstetter, 1975).

Woods (1972) and Woods and Howland (1979) identified the mandibular masseteric crest as the area of insertion of two impor-

TABLE 1. Taxa used for comparisons and phylogenetic analysis († = extinct).

Family	Species
"Eocardiidae"	† <i>Asteromys punctus</i> Ameghino, 1897
	† <i>Chubutomys simpsoni</i> Wood and Patterson, 1959
	† <i>Chubutomys leucoreios</i> Pérez et al., 2010
	† <i>Luantus initialis</i> Ameghino, 1902
	† <i>Luantus minor</i> Pérez et al, in press
	† <i>Luantus propheticus</i> Ameghino, 1898
	† <i>Luantus toldensis</i> Kramarz, 2006
	† <i>Phanomys mixtus</i> Ameghino, 1887
	† <i>Phanomys vetulus</i> Ameghino, 1894
	† <i>Eocardia montana</i> Ameghino, 1887
	† <i>Eocardia excavata</i> Ameghino, 1894
	† <i>Eocardia fissa</i> Ameghino, 1891
	† <i>Eocardia robusta</i> Vucetich, 1984
	† <i>Eocardia robertoi</i> Vucetich, 1984
† <i>Schistomys erro</i> Ameghino, 1887	
† <i>Schistomys rollinsii</i> Scott, 1905	
† <i>Matiamys elegans</i> Vucetich, 1984	
† <i>Guimys unica</i> , gen. et sp. nov.	
Caviidae	† <i>Prodolichotis pridiiana</i> Fields, 1957
	† <i>Orthomyctera chapadmalense</i> Ameghino, 1889
	† <i>Dolicavia minuscula</i> Ameghino, 1908
	<i>Dolichotis patagonum</i> Zimmermann, 1780
	<i>Dolichotis salinicola</i> Burmeister, 1876
	<i>Microcavia australis</i> Geoffroy and d'Orbigny, 1833
	<i>Galea musteloides</i> Meyen, 1832
<i>Cavia aperea</i> Erxleben, 1777	
<i>Kerodon rupestris</i> Wied, 1820	
Hydrochoeridae	† <i>Cardiomys cavinus</i> Ameghino, 1885
	† <i>Phugatherium novum</i> Ameghino, 1908
	<i>Hydrochoerus hydrochaeris</i> Pallas, 1766
Cuniculidae	<i>Cuniculus paca</i> Linnaeus, 1766
Dasyproctidae	† <i>Neoreomys australis</i> Ameghino, 1887
	<i>Dasyprocta azarae</i> Lichtenstein, 1823
Echimyidae	<i>Proechimys poliopus</i> Osgood, 1914

tant muscles in caviomorph rodents: the masseter lateralis pars anterior and the masseter superficialis pars principalis (Fig. 3A). The first one inserts dorsal and lateral to the masseteric crest, and the second inserts ventral to this crest. In caviomorph rodents (except Caviidae and Hydrochoeridae), the masseteric crest is always clearly developed (e.g., *Proechimys poliopus*, *Dasyprocta azarae*, *Cuniculus paca*) and is anteriorly connected to the notch for the insertion of the tendon of the masseter medialis pars infraorbitalis (Woods and Howland, 1979; Fig. 3A).

The mandible of caviomorph rodents has, in addition, another crest that is horizontally directed and has the masseteric fossa dorsal to it (Verzi, 1994). This is the area of insertion of the masseter medialis muscle (Woods and Howland, 1979). This crest is variable in thickness, extent, and depth (e.g., *P. poliopus*, *D. azarae*, *C. paca*) but is always isolated from the notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle (Fig. 3A).

Caviidae and Hydrochoeridae have a derived condition (Fig. 3B), different from other caviomorphs. The masseteric crest is absent (e.g., *D. patagonum*, *D. salinicola*, *Hydrochoerus hydrochaeris*) or poorly developed as a thin and low ridge (e.g., *M. australis*, *G. musteloides*, *K. rupestris*, *C. aperea*). Previous authors (Woods, 1972; Woods and Howland, 1979) confirmed that the poorly developed crest located in the ventral and posteroventral area of the angular process in *Cavia* is the area of insertion of the masseter lateralis muscle. Therefore, the poorly developed crest can be postulated as homologous to the masseteric crest of other caviomorphs. Even in forms that completely lack this crest, such as *D. patagonum*, the masseter lateralis muscle inserts on

TABLE 2. Dental measurements of *Guiomys unica*, gen. et sp. nov., in millimeters.

		APL	AW	PW
MPEF-PV 3504 (Holotype)	p4	3.4	2.2	2.5
	m1	3.5	2.9	3.1
	m2	4.0		
	m3		2.8	
MPEF-PV 3506	p4	3.0	1.9	2.2
	m1	3.4	2.6	2.7
	m2	3.6	2.7	2.8
	m3	4.4	2.9	2.7
MPEF-PV 3508	p4	3.4	2.5	2.8
	m1	3.9		3.2
MPEF-PV 3512	m1	4.1	3.2	3.1
MPEF-PV 3513	p4			2.6
	m1	3.9	3.0	3.0
	m2	4.2	3.0	3.0
	p4	3.5	2.5	3.0
MLP 91-IX-4-2	m1	3.7	3.0	3.1
	m2	3.8	3.2	2.9
MLP 91-IX-4-3	p4	3.8	1.9	2.0
	m1	3.3	2.5	2.1
MPEF-PV 3524	p4	3.19	2.15	2.49
	m1	3.81	2.95	3.05
MPEF-PV 3526	p4	3.08	2.03	2.29
	m1	3.45	2.68	2.94
MPEF-PV 3529	p4	3.25	2	2.54
	m1		3.01	
MPEF-PV 3527	p4	2.92		
	m1	3.56		
MPEF-PV 3533	P4	3.29	2.57	3.02
	M1	4.05	2.96	3.52
	M2		3.43	
MPEF-PV 3534	M1	3.43	3.64	3.16
	M3	4.92	3.03	2.7
	M2	3.73	3.32	2.87
MPEF-PV 3535	M3	3.34	3.26	3.29
	M2		3.58	3.42
	M3		3.22	
MPEF-PV 3536	M2	3.54	3.2	3.07
MPEF-PV 3538	M3	5.2	3.01	2.97
MPEF-PV 3539	P4	2.97		
MPEF-PV 3540	P4			3.01
MPEF-PV 3541	P4	3.28	2.81	2.79
MPEF-PV 3542	M1 or M2	3.1	2.73	2.57
MPEF-PV 3543	P4	3.13	2.67	2.67
MLP 91-IX-4-1	M1	3.22	3.02	2.99
	M2	3.26	2.96	3.12

Abbreviations: APL, anteroposterior length; AW, anterior width; PW, posterior width.

the lateral and posteroventral region of the angular process (observed in dissections MPEF-Zool 204). Unlike the condition of other caviomorphs, in Caviidae and Hydrochoeridae, the masseteric crest is isolated from the notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle (Fig. 3B).

The horizontal crest of caviids and hydrochoerids is well developed, forms a laterally projected shelf bearing a fossa on its dorsal surface and, as in other caviomorphs, it is the area of insertion of the masseter medialis muscle (Miller and Gidley, 1918; Woods, 1972; Woods and Howland, 1979). In caviids and hydrochoerids, the horizontal crest is joined anteriorly to the notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle (Fig 3B).

Although the homologies of these crests have been correctly established in neontological papers focused in musculature of caviomorph rodents (Woods, 1972; Woods and Howland, 1979), they were erroneously identified by several authors in fossil forms of the families Caviidae and Hydrochoeridae (Ameghino, 1887, 1902; Scott, 1905; Kraglievich, 1930; Wood and Patterson, 1959; Patterson and Wood, 1982). These authors considered the

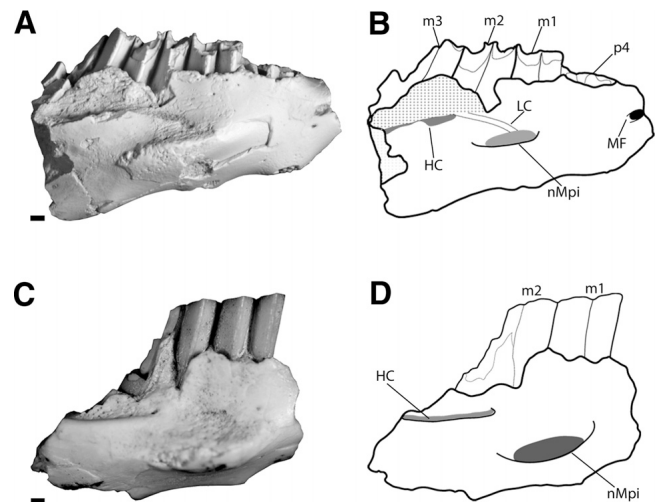


FIGURE 4. *Guiomys unica*, gen. et sp. nov., from the El Petiso locality. **A-B**, MPEF-PV 3504, fragment of right mandible with p4-m3, in labial view; **C-D**, MPEF-PV 3512, fragment of right mandible with m1-m2 in labial view. **Abbreviations:** HC, horizontal crest; LC, lateral crest; MF, mental foramen; nMpi, notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle; p4, lower premolar; m1-m3, lower molars. Scale bars equal 1 mm.

conspicuous horizontal crest of Caviidae and Hydrochoeridae as homologous to the masseteric crest of the other caviomorphs.

In 'eocardiids' the masseteric crest is well developed, conspicuous along its length, and connected to the notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle. This suite of characters resembles the plesiomorphic condition of the Caviomorpha (e.g., *D. azarae*, *C. paca*).

The horizontal crest of 'eocardiids' is always present; although it is more developed in the most derived and modern forms (e.g., *Eocardia*). The horizontal crest lacks a fossa above it and is always separated from the notch for the insertion of the masseter medialis pars infraorbitalis muscle. Thus, 'eocardiids' show the same disposition of the notch with respect to the

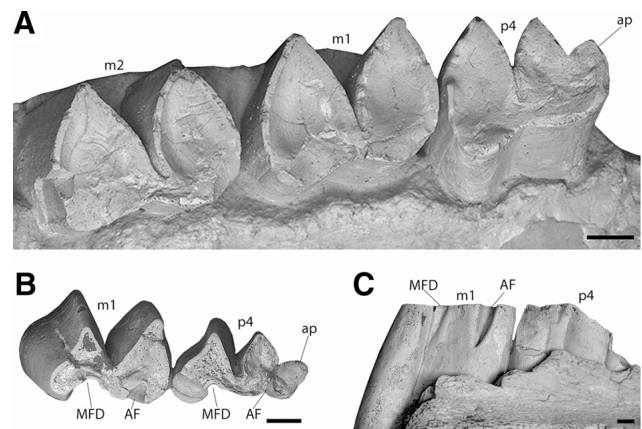


FIGURE 5. *Guiomys unica*, gen. et sp. nov., from Río Chico locality. **A**, MLP 91-IX-4-2, fragment of right mandible with p4-m2, in occlusal view; **B-C**, MLP 91-IX-4-3, fragment of left mandible with p4-m1, in occlusal and lingual views. **Abbreviations:** ap, anterior projection; MFD, metaflexid; p4, lower premolar; m1-m2, lower molars. Scale bars equal 1 mm.

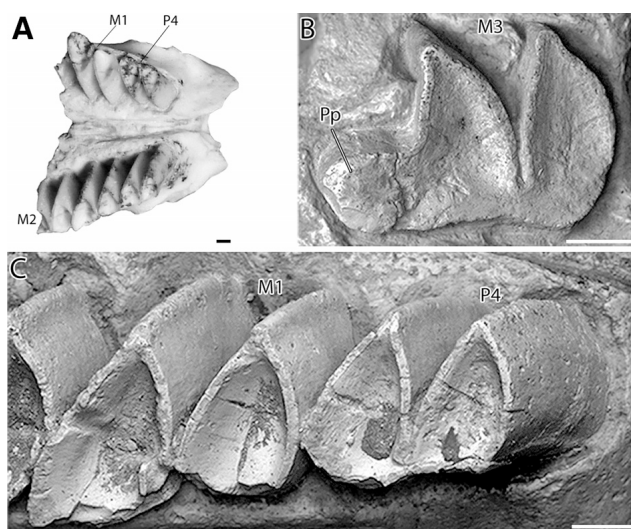


FIGURE 6. *Guiomys unica*, gen. et sp. nov., from the El Petiso locality. **A**, MPEF-PV 3533, fragment of maxilla with left P4–M2 and right P4–M1; **B**, MPEF-PV 3533, left P4–M1, in occlusal view; **C**, MPEF-PV 3534, right M3, in occlusal view. **Abbreviations:** Pp, posterior projection; P4, upper premolar; M1–M3, upper molars. Scale bars equal 1 mm.

masseteric and horizontal crests as in Caviomorpha, except for Caviidae and Hydrochoeridae.

In *G. unica*, although the angular process is not preserved in any specimen, there are no signs of a masseteric crest in the area of insertion of the masseter lateralis muscle (Fig. 4A). The condition of *G. unica* could be similar to that of some caviids (e.g., *G. musteloides* or *K. rupestris*) in which the masseteric crest is not developed anterior to the angular process, but is present posteriorly as a slightly developed ridge. Irrespective of the possible development of the masseteric crest in *G. unica*, its condition is different from that of ‘eocardiids.’

In *G. unica*, the horizontal crest extends anteriorly up to the level of m2 and bears a deep fossa above it, but it is shallower than in caviids and hydrochoerids. Consequently, *G. unica* displays an intermediate morphology between the characteristic condition of ‘eocardiids’ and the derived morphology of caviids and hydrochoerids.

The notch for the insertion of the masseter medialis pars infraorbitalis muscle is conspicuous, wide, and located anterodorsal to the horizontal crest. This notch is isolated both from the masseteric and the horizontal crests (Fig. 4). This is an autapomorphic character of *G. unica* and contrasts with the generalized condition of ‘eocardiids’ (and caviomorphs other than the ‘medialis series’) in which the notch is isolated from the horizontal crest. It also contrasts with the condition of Caviidae and Hydrochoeridae, in which the notch is isolated from the masseteric crest but joined to the horizontal crest.

PHYLOGENETIC ANALYSIS

In order to test the phylogenetic position of *G. unica* within the context of the Cavoioidea s. s., a cladistic analysis was performed. The phylogenetic trees were rooted with an octodontoid caviomorph, *Proechimys poliopus*, of the family Echimyidae, because it has been interpreted as a relatively plesiomorphic form among the living octodontoids (i.e., it is a generalized rodent, with mesodont to protohypsodont teeth, and lacks the conspicuous specializations for digging or tree-dwelling habits seen in other octodontoids; Corti et al. 2001; Leite and Patton,

2002; Galewsky et al., 2005; Olivares, 2009). In order to test the monophyly of the Cavoioidea s. s., three Cavoioidea sensu lato taxa were also included: *Dasyprocta azarae*, *Neoreomys australis* (Dasyproctidae), and *Cuniculus paca* (Cuniculidae).

Fossil and living representatives of Cavoioidea s. s. were selected as the ingroup. Because of the similarities between *G. unica* and ‘eocardiids’ and derived forms of Caviidae and Hydrochoeridae, the data set included the 17 valid species of ‘eocardiids,’ three fossil and six extant species of Caviidae, and two fossil and the single living species of Hydrochoeridae (see Table 1). The extant taxa were selected because they represent morphological variability within Caviidae. Fossil taxa were selected because they have been traditionally considered as primitive forms of each family (e.g., *Cardiomys cavinus*) and because they have enough cranio-mandibular information (e.g., *Dolicavia minuscula*, *Phugatherium novum*). For each species, 83 morphological cranio-mandibular and dental characters were scored, 33 of which were taken from the literature (Vucetich, 1984; Quintana, 1998; Ubilla et al., 1999; Kramarz, 2001, 2005), 11 were modified, and 39 are new (see Appendix 1). The matrix consisted of 34 taxa by 83 characters (Appendix 2). An equally weighted parsimony analysis was conducted using TNT 1.1 (Goloboff et al., 2008a, 2008b), performing a heuristic search of 100 Wagner tree replicates followed by TBR that resulted in 18 most parsimonious trees, 272 steps long. The strict consensus is shown in Figure 7. The 18 phylogenetic hypotheses show *G. unica* as the sister group of caviids and hydrochoerids (i.e., the crown group of Cavoioidea s. s. or ‘medialis series’). Additionally, the strict consensus shows all ‘eocardiids’ as a paraphyletic assemblage of basal forms of Cavoioidea s. s.

The position of *G. unica* as the sister group of caviids and hydrochoerids is supported (in all most parsimonious trees) by eight unambiguous synapomorphies: notch for the insertion of the tendon of the m. masseter medialis pars infraorbitalis isolated, located between the masseteric crest and the horizontal crest (character 19[1]); masseteric crest absent or poorly developed as a thin and low ridge (character 20[2]); anterior origin of the masseteric crest with respect to the toothrow located below or posteriorly to m3 (character 22[2]); horizontal crest well developed, forming a laterally projected shelf and bearing a fossa on its dorsal surface (character 24[3]); length of p4–m1 approximately equal to the length of the m2–m3 length (character 34[1]); lower molariforms subequal in size (character 35[1]); upper molariforms subequal in size (character 36[1]); and two lobes in P4 (character 48 [1]).

In all most parsimonious trees *E. robusta* is the most derived ‘eocardiid,’ and is the sister taxon of the clade formed by *G. unica* and the crown group. This clade is supported in all trees by a single unambiguous synapomorphy: funnel-shaped hypoflex/id (character 31[3]). In some of the most parsimonious trees, this clade is also supported by two additional unambiguous synapomorphies: p4 with two lobes and an anterior projection separated from the anterior lobe by a well-developed interprismatic furrow (character 42[3]) and well-developed posterior projection of M3 (character 49[2]).

In this analysis, the crown group of Cavoioidea s. s. is supported in all trees by three unambiguous synapomorphies: mental foramen located at the dorsoventral midpoint of the lateral surface of the dentary and opening laterally (character 3[1]); notch for the insertion of the tendon of the m. masseter medialis pars infraorbitalis joined to the horizontal crest (character 19[2]); and shape of the lateral crest straight, projecting anterodorsally from the base of the coronoid process (character 21[0]).

The monophyly of the Cavoioidea s. s. is supported in all trees by four unambiguous synapomorphies: 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 17[1]); lateral crest rounded and deflecting

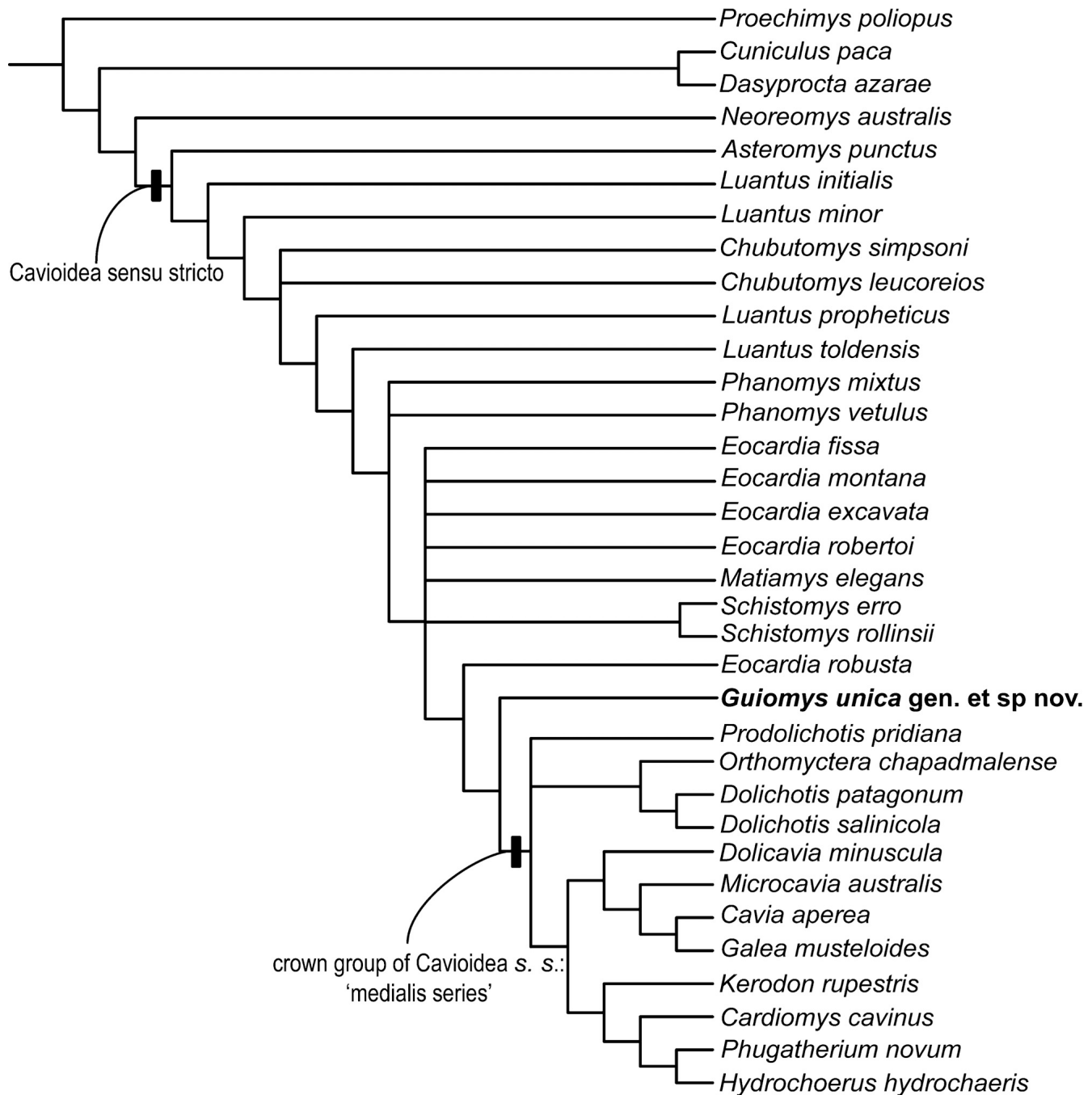


FIGURE 7. Strict consensus of the 18 most parsimonious trees (tree length = 275) resulting from cladistic analysis of 34 Cavioidea sensu lato taxa using 83 morphological characters. *Guiomys unica*, gen. et sp. nov., is the sister group of 'medialis series.'

anteroventrally from the base of the coronoid process (character 21[1]); and horizontal crest well developed as low and broad ridge (character 24[1]).

DISCUSSION AND CONCLUSIONS

Although the taxonomic content of Cavioidea sensu lato has varied significantly according to different authors (Kraglievich, 1930; Landry, 1957; Simpson, 1945; Reig, 1980; Patterson and Wood, 1982), the affinities of the families "Eocardiidae," Caviidae, and Hydrochoeridae have traditionally been recognized

(i.e., Cavioidea s. s.) given their slight hystricognathy and their short lower incisors. Furthermore, recent phylogenetic studies based on DNA sequences corroborate the close relationships of Caviidae and Hydrochoeridae (da Silva Neto, 2000; Rowe and Honeycutt, 2002; Opazo, 2005; Blanda-Kanfi et al., 2009). In this analysis, the monophyly of Cavioidea s. s. is corroborated and the characters used by Patterson and Wood (1982) to establish the superfamily Cavioidea s. s. are optimized as synapomorphies of the clade.

In addition, "Eocardiidae" was traditionally considered as ancestral to Caviidae and Hydrochoeridae (Ameghino, 1887, 1891;

Scott, 1905; Vucetich, 1984; Walton, 1990, 1997; Quintana, 1998, Ubilla et al., 1999, Vieytes, 2003; Kramarz, 2006). The paraphyly of “Eocardiidae” is consistent with this hypothesis, although it clearly means that it should not be recognized as valid as taxonomic family. Thus, ‘eocardiids’ should be regarded as an assemblage of basal and plesiomorphic cavioids that form the stem of Cavoioidea s. s.

Vucetich (1975, 1984) considered the Colloncuran *E. robusta* and *M. elegans* as the ‘eocardiid’ species most closely related to the origin of caviids because they have dental characters intermediate between “Eocardiidae” and Caviidae (e.g., posterior projection of M3). Here, *E. robusta* is the sister group of *G. unica*, whereas *M. elegans* forms a polytomy with the other species of *Eocardia* and *Schistomys*. The phylogenetic analysis performed in this paper shows *G. unica* as the sister group of the clade formed by the ‘medialis series.’ This new species shows characters with intermediate states between ‘eocardiids’ and the ‘medialis series.’ The most outstanding character of *G. unica* represents an apomorphy that is the notch for the insertion of the masseter medialis pars infraorbitalis muscle isolated both from the masseteric and horizontal crests. As explained above, this notch is connected to the masseteric crest in ‘eocardiids’ and represents a plesiomorphic state within Cavoioidea s. s., shared by all the caviomorphs except those of the ‘medialis series.’ In caviids and hydrochoerids, the notch is connected only to the horizontal crest. Another autapomorphic character of *G. unica* is the presence of lingual flexiids variable in length that disappear with wear but that do not form fossettid. This is also an intermediate state between ‘eocardiids’ and the ‘medialis series,’ the former having flexiids that form fossettes/ids at least at some ontogenetic stage and the latter lacking flexiids (e.g., *Dolichotis*) or having them along the entire crown (e.g., *Hydrochoerus*) and remaining open during wear without forming fossettes/ids.

The importance of *G. unica* lies not only on its unique combination of derived and plesiomorphic characters but also on its impact on the completeness of the fossil record of Cavoioidea s. s. The most recent record of ‘eocardiids’ occurs in Colloncuran beds of Patagonia (Bondesio et al., 1980; Vucetich et al., 1993; Vucetich, 1984), whereas the first undisputed record of the ‘medialis series’ comes from La Venta in Colombia (*Prodolichotis pridiiana* Fields, 1957). The faunal assemblage associated with *G. unica* suggests a post-Colloncuran age but possibly pre-Laventan SALMA. Therefore, *G. unica* may partially fill a gap in the record of Cavoioidea s. s. at a critical moment for understanding the origin and early diversification of the crown group of this clade.

Furthermore, the diversity of cavioids with intermediate morphology between ‘eocardiids’ and ‘medialis series’ might have been much broader than previously recognized. Walton (1997) recognized two cavioid taxa from La Venta beds that were referred preliminary to Dolichotinae, which are characterized by having the anterior prism of the p4 slightly developed. One of these, Dolichotinae, gen. 2 small sp. (IGM 183212), has the notch for the insertion of the masseter medialis pars infraorbitalis muscle completely isolated both from the masseteric and the horizontal crests, as in *G. unica*.

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APPENDIX 1. Description of characters used in phylogenetic analyses. The following characters are treated as ordered: 11, 13, 15, 17, 18, 19, 20, 22, 23, 24, 26, 27, 30, 31, 33, 37, 47, 49.

1. Length of the upper diastema: equal or longer than the molariform series (0); shorter than molariform series (1).
2. Mental foramen: absent (0); present (1).
3. Location of the mental foramen on the anterior region of the dentary: close to the dorsal margin of the dentary and opening dorsolaterally (0); at the dorsoventral midpoint of the lateral surface of the dentary and opening laterally (1).
4. Position of the mandibular foramen: behind the retromolar fossa (0); below the m3 (1).

5. Posteroventral projection of the posterior end of the mandibular symphysis in lateral view: well developed, forming a elongate peg (0); moderately developed, only a low bulge projects ventrally and is marginally exposed (1); absent (2).
6. Labial edge of the condyle (i.e., insertion point of *m. masseter posterior*) in posterior view: projecting laterally with respect to wall of the dentary, forming small knob (0); lacking a distinct knob, continuous with lateral wall of the dentary (1).
7. Medial projection of medial edge of the condyle (i.e., insertion point of *m. pterygoideus externus*) in posterior view: forming a shelf that overhangs the medial surface of the dentary (0); poorly developed, forming a small knob with respect to medial wall of the dentary (1).
8. Shape of the post-condylar process in lateral view: squared-off, forming an angle approximately 90° (0); rounded (1).
9. Length of the post-condylar process: equal to or longer than the anteroposterior length of the condyle (0); shorter than anteroposterior length of the condyle (1).
10. Height of the coronoid process compared to the position of the condyle: located at the same dorsoventral level of the condyle (0); located ventrally than condyle (1).
11. Anterior margin of the coronoid process: convex (0); straight (1); concave (2).
12. Dorsal end of the coronoid process: pointed and posterodorsally projected (0); pointed and dorsally projected (1); blunt (2).
13. Dorsoventral position of the mandibular notch: located above the occlusal surface of the dental series (0); located at the same height than the occlusal surface of the dental series (1); located ventrally from the occlusal surface of the dental series (2).
14. Shape of the mandibular notch: concave (0); almost straight (1).
15. Dorsoventral position of the anterior most point of the lunar notch: low, ventral to midpoint of dentary (between the ventral edge of dentary and condyle) (0); approximately at midpoint of dentary (1); high, above midpoint of the dentary (2).
16. Posterior extension of the angular process: level with the post-condylar process (0); anterior to the post-condylar process (1); posterior to the post-condylar process (2).
17. Posterior extension of the root of the lower incisors: to level of m3 (0); to level of posterior lobe of m2 (1); to level of anterior lobe of m2 (2); to level of m1 (3).
18. Location of the notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis* with respect to the toothrow: between p4 and m1 (0); below m1 (1); between m1 and m2 (2).
19. Notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*: connected to masseteric crest (0); isolated, located between masseteric crest and horizontal crest (1); connected to horizontal crest (2).
20. Masseteric crest: well developed, forming a shelf that projects lateral to lateral surface of dentary (0); forming a well-developed ridge that fails to project lateral to dentary (1); absent or poorly developed as thin, low ridge (2).
21. Shape of the lateral crest (sensu Woods, 1972): straight, projecting anteroventrally from the base of the coronoid process (0); rounded, deflecting anteroventrally from the base of the coronoid process (1).
22. Anterior origin of the masseteric crest with respect to the toothrow: below m1 (0); below m2 (1); below or posterior to m3 (2).
23. Posterior extension of the horizontal crest, in lateral view: to anterior margin of mandibular condyle (0); approximately to anteroposterior midpoint of mandibular condyle (1); to posterior margin of the mandibular condyle (2).
24. Development of horizontal crest: absent or extremely reduced (0); present as low, broad ridge (1); present as a conspicuous crest, forming laterally projected shelf but lacking a dorsal fossa (2); well developed, forming a laterally projected shelf and bearing a fossa on its dorsal surface (3).
25. Depth of the fossa dorsal to horizontal crest with respect to the dorsoventral depth of the notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*: shallower than notch (0); deeper than notch (1); equal in depth to notch (2).
26. Alveolar protuberances (ventral outgrowths molariform alveolar bases that project ventrally from dentary): absent (0); present as small but distinct convexities (1); present as well-developed bulges (2).
27. Degree of hypsodonty: slightly hypsodont, rooted with anteroposterior length of occlusal surface greater than crown height (0); mesodont, rooted, with the anteroposterior length of occlusal surface approximately equal to crown height (1); protohypsodont, rooted with anteroposterior length of occlusal surface less than half crown height (2); euhypsodont, lacking roots (3).
28. Shape of the molariform teeth, in occlusal view: unlobed (0); with triangular lobes (1); with heart-shaped lobes (2); with two laminar lobes, the posterior one formed by a single lamina (3); with two laminar lobes, the posterior one formed by at least four laminae (4).
29. Constriction of the apex in each lobe of upper molars: absent (0); poorly developed, bearing a minor constriction (1); well developed, the constriction present in both lobes of each tooth (2).
30. Transverse extension of the hypoflex/id: transversely shorter than half of the width of the crown (0); extending from the margin up to the transverse midpoint of the crown (1); extending beyond the transverse midpoint of the crown (2).
31. Shape of the hypoflex/id in occlusal view: very narrow and short (0); V-shaped (1); narrow and very long (2); funnel-shaped (3).
32. Longitudinal furrow on the labial wall of upper molars and lingual wall of lower molars: absent (0); one furrow opposite hypoflex/id (1); one furrow on posterior lobe (2); one furrow on each lobe (3).
33. Transverse dentine crest on the occlusal surface, located at the middle of each lobe: absent (0); present (1).
34. Length of p4–m1 with respect to length of m2–m3 (Wood and Patterson, 1959): p4–m1 shorter than m2–m3 (0); p4–m1 approximately equal to m2–m3 (1).
35. Relative size of lower molariforms: m1 < m2 < m3 (0); m1 = m2 = m3 (1).
36. Relative size of the upper molariforms: P4 < M1 < M2 (0); P4 = M1 = M2 (1).
37. Replacement of deciduous premolar: unreplaced (0); postnatal (1); prenatal (2).
38. Orientation of left and right molar series: parallel (0); anteriorly convergent (1).
39. Cement in late ontogenetic stage: absent (0); present (1).
40. Cement in young-adult ontogenetic stage: absent (0); present (1).
41. Cement in juvenile ontogenetic stage: absent (0); present (1).
42. Lobes in p4: two incipient lobes (0); two well-developed lobes, but lacking an anterior projection (1); two lobes and one incipient anterior projection that is not separated from the anterior lobe by an interprismatic furrow (2); two lobes and one developed anterior projection separated from the anterior lobe by a well-developed interprismatic furrow (3); three lobes (4).

43. Distribution of enamel in molars: covering the entire crown (0); interrupted at the base of the lingual wall (1); interrupted at the base and the corner of the lingual wall (2); interrupted at the base and in two strips (3); interrupted along the entire labial wall of the upper molars (lingual of the lower molars) except for the flex/ids opposite to the hyopflex/id (4); interrupted along the entire lingual wall and anterolingual and posterolingual walls (5).
44. Fossettes/ids in late ontogenetic stage: present (0); absent (1).
45. Fossettes/ids in young-adult ontogenetic stage: present (0); absent (1).
46. Fossettes/ids in juvenile ontogenetic stage: present (0); absent (1).
47. Shape of the fossettes/ids: elongated (0); subcircular (1).
48. Number of lobes in P4: two (0); one (1).
49. Posterior projection of M3: absent (0); incipient (1); developed (2); M3 with multiple laminae (3).
50. Mesofossettoid in young-adult stage: present (0); absent (1).
51. Fusion of the mesolophid with the anterolophid (metalophulid II and metalophulid I, respectively, sensu Marivaux et al., 2004): absent (0); present (1). (Kramarz, 2005:character 15).
52. Reduction of the mesolophid (metalophulid II sensu Marivaux et al., 2004): complete (0), reduced (1). (Kramarz, 2005: character 16).
53. Mesoflexid remains opened: absent (0); present (1). (Kramarz, 2005: character 17).
54. Size of oval foramen: small (1); large (0). (Quintana, 1998: character 1).
55. Apex of mesopterygoid fossa: level with M2 (0); in front of M2 (1). (Quintana, 1998: character 2).
56. Articulation of nasals with respect to premaxillae: along entire length (0); anterior half unarticulated (1). (Quintana, 1998: character 6).
57. Interorbital width: longer or equal to braincase (0); shorter than braincase (1). (Quintana, 1998: character 14).
58. Shape of frontals: markedly convex posteriorly (1); not convex (0). (Quintana, 1998:character 15; Ubilla et al., 1999:character 14).
59. Extension of pterygoids: short (0); long and posteriorly oriented (1). (Quintana, 1998:character 17).
60. Pterygoids: free (0); fused to the auditory bullae (1). (Quintana, 1998:character 18).
61. Shape of the margins of the incisive foramina: with rounded margins (0); with straight and parallel margins (1). (Quintana, 1998:character 21; Ubilla et al., 1999:character 6).
62. Position of the posterior margin of the upper diastema: not vertical (0); vertical (1). (Quintana, 1998:character 23; Ubilla et al., 1999:character 23).
63. Shape of palate: concave (0); flat (1). (Quintana, 1998:character 24; Ubilla et al., 1999:character 12).
64. Upper zygomatic process of the maxilla: not extended as a plate-shape in the rostrum (0); plate-shape (1). (Quintana, 1998:character 25; Ubilla et al., 1999:character 24).
65. Shape of upper margin of the infraorbital foramen: not straight (0); straight (1). (Quintana, 1998:character 26; Ubilla et al., 1999:character 5).
66. Incisive foramina: unreduced (0); reduced (1). (Quintana, 1998:character 27).
67. Jugular and carotid foramina: fused (0); unfused (1). (Quintana, 1998:character 28; Ubilla et al., 1999:character 36).
68. Position of lacrimal: totally interposed between maxilla and premaxilla (0), partially interposed between maxilla and premaxilla (1). (Quintana, 1998:character 32; Ubilla et al., 1999:character 8).
69. Postfrontal spinous process of the jugal: absent (0); present (1). (Quintana, 1998:character 33; Ubilla et al., 1999:character 31).
70. Orbital foramen: fused to the round foramen (0); separated from the round foramen (1). (Quintana, 1998:character 34).
71. Position of upper incisors: orthodont (0); inclined (1). (Quintana, 1998:character 35).
72. Enamel of upper and lower incisors: unpigmented (0); pigmented (1). (Quintana, 1998:character 36; Ubilla et al., 1999:character 13).
73. Shape of nasals: not anteriorly vaulted (0); greatly vaulted anteriorly (1). (Quintana, 1998:character 38; Ubilla et al., 1999:character 3).
74. Shape of palatines: without posterior flat expansion (0), with posterior flat expansion (1). (Quintana, 1998:character 39; Ubilla et al., 1999:character 11).
75. Position of parietals in the same plane as nasals (0); in different plane as nasals (1). (Quintana, 1998:character 40; Ubilla et al., 1999:character 25).
76. Position of the occipital condyles: below the lower limit of the auditory bullae (0); above the lower limit of the auditory bullae (1). (Quintana, 1998:character 41; Ubilla et al., 1999:character 27).
77. Supraorbital foramen or notch: conspicuous (0); absent (1). (Quintana, 1998:character 42).
78. Position of P4 alveolar prominence: near margin of nasolacrimal foramen (0); far anterior to this margin (1). (Ubilla et al., 1999:character 4).
79. Masseteric fossa of zygomatic arch: shallow and not well delimited (0); deep and well delimited (1). (Ubilla et al., 1999:character 9).
80. Position of the boundary between mastoid and paraoccipital process relative to auditory meatus: at the same level or above (0); below (1). (Ubilla et al., 1999:character 15).
81. Shape of the process of squamosal: straight (0); curved (1). (Ubilla et al., 1999:character 18).
82. Shape of the external auditory meatus: long and tube-shaped (0); short (1). (Ubilla et al., 1999:character 19).
83. Posterior apophysis of squamosal: partially covering the epitympanic sinus (0); completely covering the epitympanic sinus (1). (Vucetich, 1975, 1984).

APPENDIX 2. Character-taxon matrix used for phylogenetic analysis. The letters represent polymorphic or uncertain scorings (i.e., A = states 0 and 1; B = states 1 and 2; C = states 2 and 3; D = states 4 and 5).

Taxon	10	20	30	40
<i>Proechimys polioopus</i>	00?0100000	0000000000	0000000000	0000000000
<i>Dolicavia minuscula</i>	011121111?	??21113022	?103113212	321111?111
<i>Prodolichotis pridiani</i>	0111??????	????????222	???32?3212	211111?111
<i>Orthomyctera chapadmalense</i>	0111210110	12001?2222	0213223222	311111?111
<i>Phugatherium novum</i>	011?2?????	???????3122	02?3203412	330000?111
<i>Hydrochoerus hydrochaeris</i>	1111011110	1220223122	0213203422	3300002111
<i>Cardiomys cavinus</i>	11112?????	???????022	02?3223222	33? ?11?111
<i>Kerodon rupestris</i>	0111200001	?120123122	0203203222	2301112111
<i>Cavia aperea</i>	0111000011	?020221122	0203123312	2211112111
<i>Galea musteloides</i>	0111100110	?001221022	0223013212	?211112111
<i>Microcavia australis</i>	0111100111	?020123222	0203103212	?110001111
<i>Dolichotis patagonum</i>	0111211110	2200222222	0?13223222	3111112111
<i>Dolichotis salinicola</i>	0111211110	2200222222	0??3223222	3111112111
<i>Dasyprocta azarae</i>	0100211101	2221010000	0000001000	0001111000
<i>Cuniculus paca</i>	00?0210110	021010?001	0011101000	0000111000
<i>Neoreomys australis</i>	110011111?	1?0?020001	0000002101	0000001111
<i>Asteromys punctus</i>	?1011?????	???????1001	10?1201100	10011?1?00
<i>Chubutomys simpsoni</i>	???????????	???????????	1?????2112	100???????
<i>Chubutomys leucoreios</i>	?1011?????	???????1101	11?1102112	11001?1?00
<i>Luantus initialis</i>	???????????	???????????	???????1111	1000001?10
<i>Luantus minor</i>	???????????	???????1101	?1????02111	100?????10
<i>Luantus propheticus</i>	?1011?????	???????1101	11?2102111	1100001111
<i>Luantus toldensis</i>	???????????	???????????	???????2112	110?????1?11
<i>Phanomys mixtus</i>	???????????	???????????	???????2212	210?????1?11
<i>Phanomys vetulus</i>	???????????	???????????	???????2212	210?????1?11
<i>Eocardia fissa</i>	0101???????	?1?????2201	11?22132B2	2100001111
<i>Eocardia montana</i>	010101?????	1210??1200	11022232B2	2200001111
<i>Eocardia excavata</i>	?1010???????	???????2200	11?22032B2	2100001111
<i>Eocardia robusta</i>	01011???????	???????3201	11?2213222	3200001111
<i>Eocardia robertoi</i>	0???????????	???????????	???????3222	???????1?111
<i>Schistomys erro</i>	?10110?110	1100??2200	11122032B2	2100001111
<i>Schistomys rollinsii</i>	0???????????	???????????	???????32?2	210?????111?
<i>Matiamys elegans</i>	1???????????	???????????	???????3222	210?????1111
<i>G. unica, gen. et sp. nov.</i>	?101???????	???????1212	12?3213212	310111?1111

Taxon	50	60	70	80	83
<i>Proechimys polioopus</i>	0000000?00	1100001011	001000?0??	?1?0011?0?	001
<i>Dolicavia minuscula</i>	?3411??121	???0101211	0010000001	1010011001	011
<i>Prodolichotis pridiani</i>	?3D1????121	???1101?10	10????0?0??	???????????	?01
<i>O. chapadmalense</i>	?2411??121	?????0011??	101000?0??	???????0?0?	101
<i>Phugatherium novum</i>	?4411??1?1	?????2?00??	111??0?0???	?????00?00	111
<i>H. hydrochaeris</i>	044111?1?1	???0200000	1010000000	0?00000?00	111
<i>Cardiomys cavinus</i>	?44111?111	?????1?00??	?01???????	???????0?0??	111
<i>Kerodon rupestris</i>	145111?111	???0001010	1001111010	0100001100	011
<i>Cavia aperea</i>	124111?111	???0101100	1011110001	0000011011	101
<i>Galea musteloides</i>	124111?121	???0101100	001110?0??	?1????1?11	101
<i>Microcavia australis</i>	124100?121	???0101100	0111101101	0010010111	001
<i>Dolichotis patagónica</i>	124111?121	???1000000	1000001001	0100100?01	100
<i>Dolichotis salinicola</i>	124111?121	???1010000	1000001001	0100110?01	100
<i>Dasyprocta azarae</i>	0000000?00	1?0100111?	101001?1??	01????01?00	011
<i>Cuniculus paca</i>	0000010?00	0?11001100	?0110?????	01????01?11	011
<i>Neoreomys australis</i>	0100000000	??1100????	?01???????	?????????00	???
<i>Asteromys punctus</i>	0000000?00	?0????????	???????????	???????????	???
<i>Chubutomys simpsoni</i>	0?2?000??1	?10???????	???????????	???????????	???
<i>Chubutomys leucoreios</i>	012?000?11	?10???????	???????????	???????????	???
<i>Luantus initialis</i>	01000000?0	110???????	???????????	???????????	???
<i>Luantus minor</i>	0?00000?00	010???????	???????????	???????????	???
<i>Luantus propheticus</i>	0120000010	110???????	???????????	???????????	???
<i>Luantus toldensis</i>	1131000010	110???????	???????????	???????????	???
<i>Phanomys mixtus</i>	1151000011	110???????	???????????	???????????	???
<i>Phanomys vetulus</i>	115100A0?1	110???????	???????????	???????????	???
<i>Eocardia fissa</i>	11D1101011	110?1011??	?01???????	0?????1???	???
<i>Eocardia montana</i>	1341101011	110????11??	?01???????	0?????11???	???
<i>Eocardia excavata</i>	1141101011	110????1???	???????????	???????????	???
<i>Eocardia robusta</i>	1C41??1021	010?????1??	?0????????	0?????11???	??0
<i>Eocardia robertoi</i>	1?41101021	???????????	???????????	???????????	???
<i>Schistomys erro</i>	11D1001121	?10?1?11??	??1???????	???????11???	??1
<i>Schistomys rollinsii</i>	??D1??1121	???1?111??	??1???????	??1???????	???
<i>Matiamys elegans</i>	1?41001021	?????????1??	???????????	0?????11???	??1
<i>G. unica, gen. et sp. nov.</i>	134111?121	??0?1?1????	??1???????	???????????	???

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