

A New Extinct Genus of Caviioidea (Rodentia, Hystricognathi) from the Miocene of Patagonia (Argentina) and the Evolution of Cavioid Mandibular Morphology

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Abstract The family Caviidae is represented in modern faunas by caviés and maras, whereas the family Hydrochoeridae is represented by capybaras. The evolutionary origin of these families has been related to a diversity of plesiomorphic fossil forms (recorded from the late Oligocene up to the middle Miocene) traditionally grouped in the family “Eocardiidae”. These fossil forms were included, together with Caviidae and Hydrochoeridae, within the Caviioidea s.s. (*sensu stricto*), because they share high crowned cheek teeth, double-hearted occlusal surface, short lower incisors, and moderate hystricognathy. Within Caviioidea s.s., caviids and hydrochoerids were interpreted as forming its crown group, because they have unique craniomandibular and dental features. In this contribution, a new taxon of Caviioidea s.s. from the middle Miocene of central Patagonia, Argentina, is described, and its phylogenetic position is determined on the basis of a morphological cladistic analysis in which “eocardiids” were included. The study permits the understanding of the sequence of appearance of characters that originated the highly divergent morphology of crown-group cavioids. The analysis of the sequence of appearance of the characters that traditionally diagnosed the crown group indicates that these changes did not occur at the same time. On the contrary, many of these features seem to have appeared at different nodes of the evolutionary history of Caviioidea s.s. The remarkably derived morphology of modern

cavioids is the result of a stepwise appearance of a mosaic of evolutionary innovations that originated gradually along the history of Caviioidea during the late-middle Miocene.

Keywords Hystricognathi · Caviioidea · Phylogeny · Neogene · South America

Introduction

The family Caviidae is represented in modern faunas by caviés and maras, whereas the family Hydrochoeridae is represented by capybaras. Both families are the most morphologically divergent within South American Hystricognathi and probably form one of the most distinctive lineages among rodents as a whole (Mares and Ojeda 1982; Wood 1985; Vucetich and Verzi 1995). This can be seen, for example, in the structure of the mandible, which is highly modified for an enlarged *m. masseter medialis* or the fact that they are digitigrades (Landry 1999). They inhabit the entire neotropical region and occupy different habitats, ranging from open prairies, arid steppes, marginal forests, flooded areas, rocky mountains, and even highlands (4000 m). Additionally, cavioids are highly diverse and display a wide range of habits (e.g., epigeous, semiaquatic; Mares and Ojeda 1982; Woods 1984) and body sizes, with weights ranging from 0.4 kg (e.g., *Microcavia, Galea*) up to more than 60 kg reached by the largest living rodent, *Hydrochoerus hydrochaeris* (Mares and Ojeda 1982; Redford and Eisenberg 1992; Eisenberg and Redford 2000; Ojeda 2006; Álvarez and Martínez 2006).

The evolutionary origin of the families Caviidae and Hydrochoeridae has been related to a diversity of fossil forms that retain plesiomorphic characters (recorded from the late Oligocene up to the middle Miocene) traditionally grouped in the family Eocardiidae, a putative paraphyletic group (Pérez 2010a, b) that has been scarcely studied from a phylogenetic

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point of view. These fossil forms were included, together with Caviidae and Hydrochoeridae within the Cavoidea s.s. (Patterson and Wood 1982:511), because they share high crowned cheek teeth, double-hearted occlusal surface, short lower incisors, and moderate hystricognathy.

Within Cavoidea s.s., caviids and hydrochoerids were interpreted as forming its crown group, because they have unique craniomandibular and dental features (Pérez 2010a, b). Among them, the most outstanding are: 1) absence of fossettes/ids, 2) similar relative size of lower molariforms (except for Hydrochoeridae, in which m3 becomes more complex, formed by multiple laminae), 3) mandibular straight lateral crest, 4) mandibular robust horizontal crest, 5) mandibular masseteric crest slightly developed or not developed, and 6) notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis* (nMpi) in anterior position, connected to the horizontal crest and isolated from the masseteric crest. The strong modification of the muscles for mandibular adduction led Miller and Gidley (1918) to separate them from extinct cavioids as the ‘medialis series’, which is equivalent in terms of taxonomic composition to the crown-group of Cavoidea s.s.

In this paper, a new taxon of Cavoidea s.s. from the middle Miocene of central Patagonia, Argentina (Fig. 1) is described, and its phylogenetic position is determined on the basis of a morphological cladistic analysis in which a wide sample of basal forms of Cavoidea s.s. (i.e., “eocardiids”) was included. Thus, the study permits the understanding of the sequence of appearance of characters that originated the highly-divergent morphology of crown-group cavioids.

Materials and Methods

Nomenclature Dental nomenclature (Fig. 2) used here follows Candela (1999) and Marivaux et al. (2004), and modifications by Pérez (2010b). Mandibular nomenclature (Fig. 3) is modified from Woods (1972) and Woods and Howland (1979).

Dental Abbreviations Upper teeth: **aa**, anterior apex; **AL**, anterior lobe or prism; **Atl**, anteroloph; **c**, cement; **e**, enamel; **HF**, hypoflexus; **HY**, hypocone; **If**, interprismatic furrow; **LaW**, labial side or wall; **mes**, mesolophule; **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; **Prl**, protoloph; **PTF**, posterofossette. Lower teeth: **aa**, anterior apex; **AF**, anterofossetid; **AL**, anterior lobe or prism; **c**, cement; **e**, enamel; **Hd**, hypoconid; **Hf**, hypoflexid; **Hld**, hypolophid; **If**, interprismatic furrow; **LiW**, lingual side or wall; **Med I**, metalophulid I; **Med II**, metalophulid II; **MF**, mesoflexiid or mesofossettoid; **MFD**, metaflexid or metafossettoid; **pa**,

posterior apex; **PL**, posterior lobe or prism; **Prd**, protoconid; **Psd**, posterolophid.

Phylogenetic Analysis In order to test the phylogenetic position of the new species within the context of the Cavoidea s.s., a cladistic analysis was performed.

The matrix includes 89 morphological characters (See Appendix 1) and 35 taxa (See Table 1, Appendix 2, and Appendix 3). These characters were scored for the new taxon, 12 crown-group cavioids, 18 “eocardiids” (ingroup). In addition, some representatives of Dasyproctidae (*Dasyprocta azarae* Lichtenstein, 1823, and *Neoreomys australis* Ameghino, 1887b) and Cuniculidae (*Cuniculus paca* Linnaeus, 1766) were used as outgroup taxa (for testing monophyly of Cavoidea s.s.), because they were traditionally proposed in Cavoidea (e.g., Patterson and Wood, 1982). As group root we selected *Proechymis poliopus* Osgood, 1914. 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 and considering some multistate characters as additives (See Appendix 1). We use equally weights to minimize the number of postulated evolutionary transformations. Bremer indices were used as a metric of nodal support. In addition, an analysis was run without ordering states. The criteria used in the mapping of the phylogenetic changes (See Timing of Evolution of Cavioid Mandibular Morphology section) were Wagner optimization (Farris 1970); command Optimization: Character Mapping was done in TNT.

Institutional Abbreviations **AMNH**, America Museum of Natural History, Division of Paleontology. New York; **MACN A**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Ameghino. Buenos Aires; **MACN Ma.**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”. Mastozoología. Buenos Aires; **MACN PV**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Santa Cruz. Buenos Aires; **MLP PV**, Museo de La Plata, Paleontología de Vertebrados. La Plata; **MLP zool**, Museo de La Plata. Mastozoología. La Plata; **MMP**, Museo de Mar del Plata “Lorenzo Scaglia”. Mastozoología. Mar del Plata; **MPEF-PV**, Museo Paleontológico “Egidio Feruglio”, Paleontología de Vertebrados. Trelew; **MPEF-zool**, Museo Paleontológico Egidio Feruglio, Colección de Actuales. Trelew; **YPMPU**, Yale Peabody Museum Princeton University. New Haven.

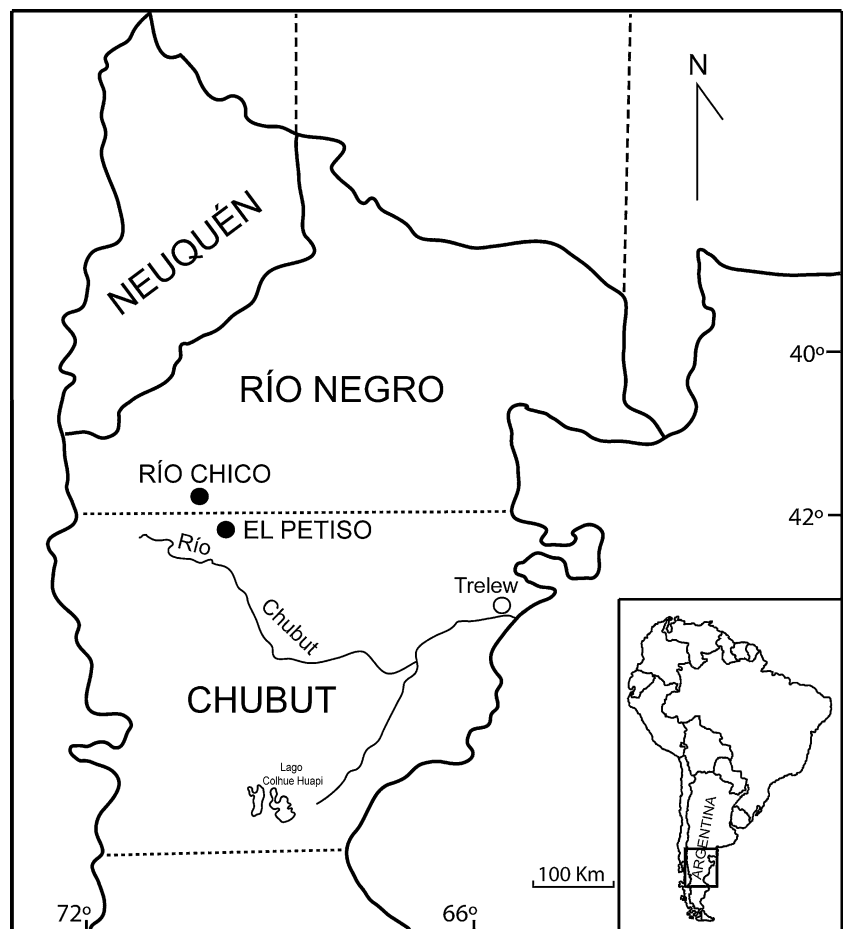
Systematic Paleontology

Order **Rodentia** Bowdich, 1821

Suborder **Hystricognathi** Tullberg, 1899

Superfamily **Cavoidea** Kraglievich, 1930

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



Microcardiodon, new genus

Type Species Microcardiodon williensis, new species.

Diagnosis As for type species.

Derivation of Name From Greek *micro* = very small, *cardia* = heart, *odon* = tooth; in reference to the small, heart-shaped premolar.

Ocurrence As for type species.

Microcardiodon williensis, new species
(Fig. 4; Table 2)

Diagnosis Cavioid diagnosed by the following unique combination of characters (autapomorphies marked with an asterisk): euhypsodont molariforms, without flexids or lingual fossettids at least in adult and senile ontogenetic stages; m1-m3 double-heart shaped; anterior lobe slightly anteroposteriorly shorter than the posterior one; hypoflexid extremely deep transversely and funnel-shaped; cement present in hypoflexid and enamel interrupted along the

lingual wall of both lobes; lingual furrow wide and relatively shallow, directed towards the posterior lobe; *p4 formed by two small lobes; the anterior labio-lingually short, subquadrangular in shape with rounded anterior margin, and the posterior lobe triangular; hypoflexid transversely shallow and without cement; mental foramen located dorsolaterally; nMpi connected to the masseteric crest and isolated from the horizontal crest; *horizontal crest developed as a wide and low ridge.

Derivation of Name From the native Mapuche language *willi* = south, in reference to the geographic provenance of the new taxon.

Holotype MPEF-PV 3500, fragment of left hemi-mandible with p4-m3.

Hypodigm MPEF-PV 3501, left hemi-mandible with p4-m2; MPEF-PV 3502, left hemi-mandible with p4-m1; MPEF-PV 3503, right hemi-mandible with p4-m3; MPEF-PV 3520, right hemi-mandible with p4-m2; MPEF-PV 3523, left hemi-mandible with m3; MPEF-PV 3532, left hemi-mandible with p4.

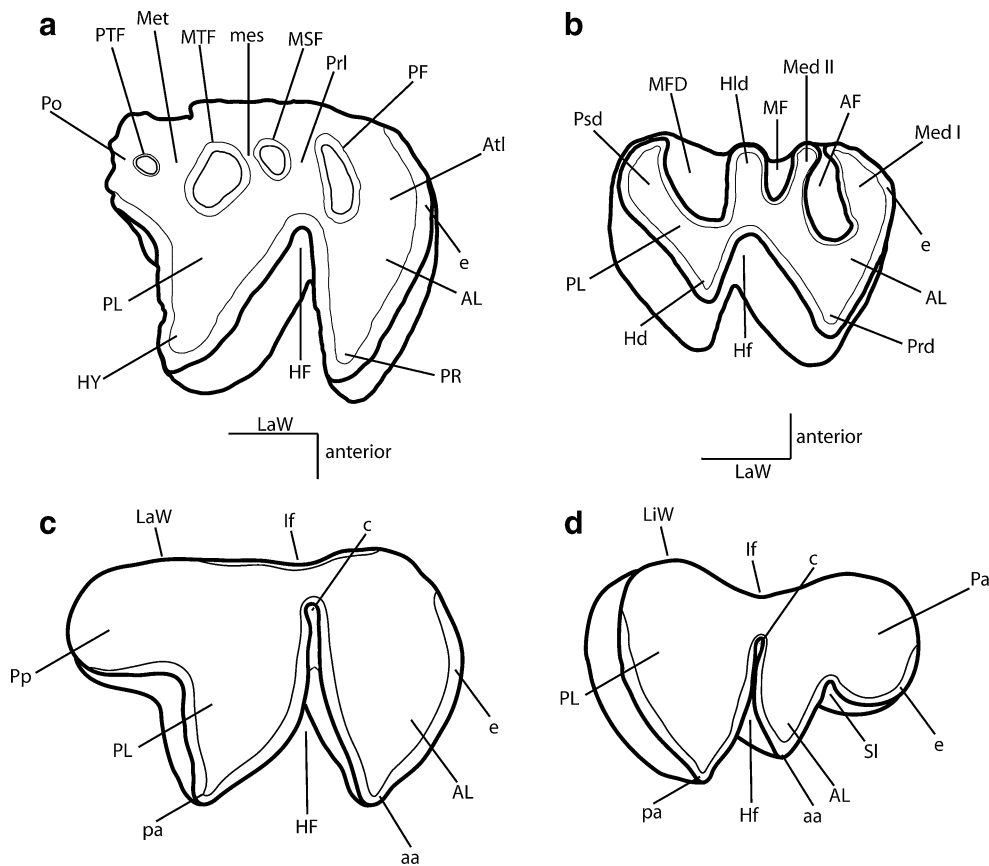


Fig. 2 Dental nomenclature. Occlusal dental morphology of upper and lower teeth and related nomenclature (Candela 1999; Marivaux et al. 2004). **a.** *Luantus minor*, MPEF PV 5028, right M3 in occlusal view. **b.** *Luantus minor*, MPEF PV 1154a, left m2 in occlusal view. **c.** *Guiomys unica*, MPEF PV 3535, right M3 in occlusal view. **d.** *Guiomys unica*, MPEF PV 3504, right p4 in occlusal view. **Abbreviations upper teeth:** aa, anterior apex; AL, anterior lobe or prism; Atl, anteroloph; c, cement; e, enamel; HF, hypoflexus; HY, hypocone; If, interprismatic furrow; LaW, labial side or wall; mes, mesolophule; 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; Prl, protoloph; PTF, posterofossette. **Abbreviations lower teeth:** aa, anterior apex; AF, anterofossetid; AL, anterior lobe or prism; c, cement; e, enamel; Hd, hypocone; Hf, hypoflexid; Hld, hypolophid; If, interprismatic furrow; LiW, lingual side or wall; Med I, metalophulid I; Med II, metalophulid II; MF, mesoflexiid or mesofossettid; MFD, metaflexid or metafossettid; pa, posterior apex; PL, posterior lobe or prism; Prd, protoconid; Psd, posterolophid

Geological Setting The material was found in a new locality (El Petiso), northwestern Chubut Province, central Patagonia, Argentina (Fig. 1). The faunal assemblage found at this locality indicates a middle Miocene age, probably post-Colloncuran (early-middle Miocene; Villafañe et al. 2008). Precise coordinates of the fossiliferous locality of the type material are housed at the MPEF-PV collections and can be obtained from the author upon request.

Description and Comparisons

Mandible The mandibular body is similar in size to that of *Eocardia robusta* Vucetich, 1984, although slightly smaller. At the base of the dentary it has a slightly developed alveolar protuberance of the m1 (Fig. 4a), unlike

Eocardia montana Ameghino, 1887a, which has the alveolar protuberances extremely developed. On the labial side (Fig. 4a), the mental foramen is dorsolaterally placed, but not as dorsally located as in basal Caviioidea s.s. or as laterally located as in the crown group. The lateral crest is straight or almost straight, as in the crown group of Caviioidea s.s. The nMpi is anteriorly located and connected to the masseteric crest, and remains isolated from the horizontal crest, as in basal Caviioidea s.s. The masseteric crest forms a well-developed ridge that does not project laterally on the dentary, as in *E. robusta* and *Luantus propheticus* Ameghino, 1898. The horizontal crest is developed as a low and wide ridge as in *Chubutomys leucoreios* Pérez et al., 2010, and extends anteriorly up to the level of the anterior lobe of the m3. On the lingual side, the root of the incisor reaches posteriorly the anterior lobe of m2, as in *Schistomys erro* Ameghino, 1887b, and

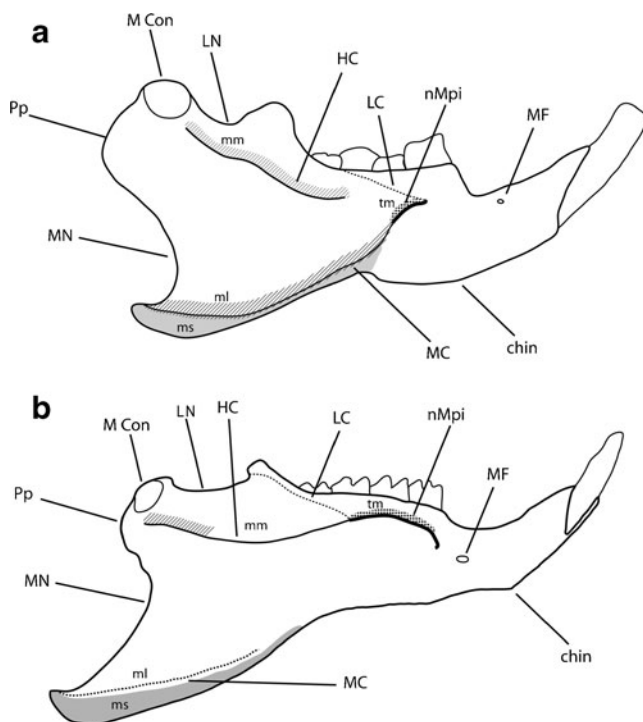


Fig. 3 Mandibular morphology and related nomenclature (Woods 1972; Woods and Howland 1979). **a.** *Dasyprocta azarae*, MLP 05. IX.97.02, right mandible in labial view. **b.** *Galea musteloides*, MLP 734, right mandible in labial view. **Abbreviations:** chin, posterior joint of the symphysis; HC, horizontal crest; LC, lateral crest; LN, lunar notch; MC, masseteric crest; MCon, mandibular condyle; MF, mental foramen; ml, masseter lateralis muscle; mm, masseter medialis muscle; MN, mandibular notch; ms, masseter superficialis muscle; nMpi, notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle; Pp, postcondyle process; tm, tendon of the masseter medialis pars infraorbitalis muscle

Dolichotis patagonum Zimmermann, 1780. The mandibular foramen is located below the crown of m3 as in all cavioids.

Lower Molars All molars are euhypsodont, as in the members of the crown group of Cavioides s.s. and derived forms among “eocardiids” (e.g., *Schistomys*, *Eocardia*).

The m1-m3 are bilobated (Fig. 4b–c), each molar double-heart shaped, all of them with the same morphology, but the m1 is smaller than the m2, and m2 smaller than m3 (Table 2), as in euhypsodont species of “eocardiids” (Pérez 2010a). Each lobe is heart-shaped, with convex walls and the labial apex is acute and labially oriented, lacking an anterior or posterior deflection (Fig. 4b–c). On the labial wall, they have a wide longitudinal furrow that is relatively deep and directed toward the posterior lobe, especially in the m3, a feature also present in *E. robusta*. The hypoflexid is funnel-shaped and deep in occlusal view, and the apex may be anteriorly directed. Molars have cement and the

enamel is continuous around the crown, except along the lingual wall of both lobes.

Lower Premolar The p4 is much smaller than the molars (Table 2; Fig. 4b–g); it is obliquely oriented (anterolabial-posterolingual) and the lingual wall is straight. The p4 is characteristic and exclusive of this species, because its two lobes are not fully developed as in the other species of Cavioides s.s. (e.g., *E. montana*, *D. patagonum*). The anterior lobe is rounded (Fig. 4b–d) or subtriangular in

Table 1 Taxa used for comparisons and phylogenetic analysis

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., 2010
	† <i>Luantus propheticus</i> Ameghino, 1898
	† <i>Luantus toldensis</i> Kramarz, 2006
	† <i>Phanomys mixtus</i> Ameghino, 1887b
	† <i>Phanomys vetulus</i> Ameghino, 1894
	† <i>Eocardia montana</i> Ameghino, 1887a
	† <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, 1887b
	† <i>Schistomys rollinsii</i> Scott, 1905
	† <i>Matiamys elegans</i> Vucetich, 1984
	† <i>Microcardiodon williensis</i> , new genus and species
	† <i>Guimys unica</i> Pérez, 2010b
Caviidae	† <i>Prodolichotis pridiana</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, 1833
Hydrochoeridae	<i>Cavia aperea</i> Erxleben, 1777
	<i>Kerodon rupestris</i> Wied, 1820
	† <i>Cardiomyx cavinus</i> Ameghino, 1885
Cuniculidae	† <i>Phugatherium novum</i> Ameghino, 1908
	<i>Hydrochoerus hydrochaeris</i> Pallas, 1766
Dasyproctidae	<i>Cuniculus paca</i> Linnaeus, 1766
	† <i>Neoreomys australis</i> Ameghino, 1887b
Echimyidae	<i>Dasyprocta azarae</i> Lichtenstein, 1823
	<i>Proechimys poliopus</i> Osgood, 1914

†=extinct

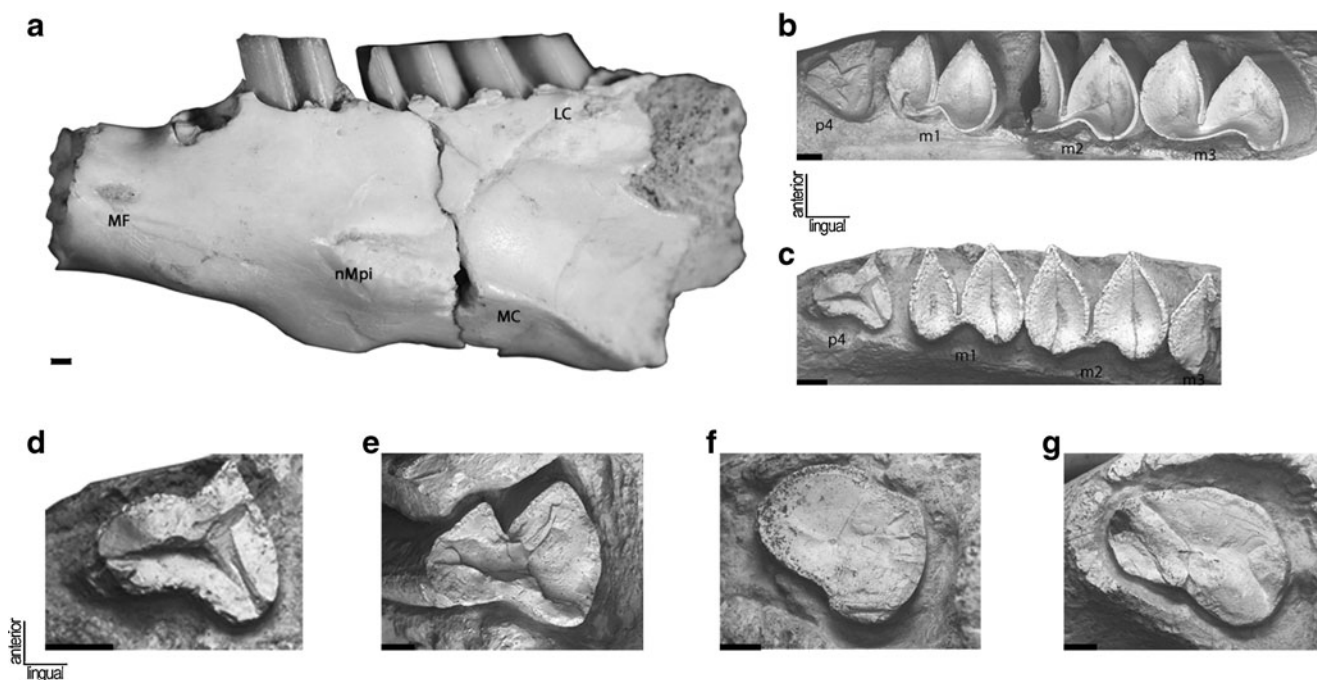


Fig. 4 *Microcardiodon williensis*, new genus and species, from the El Petiso locality. (Holotype) MPEF-PV 3500, **a**, lateral view, **b**, occlusal view. MPEF-PV 3503, **c**, occlusal view, **d**, p4. MPEF-PV 3520, **e**, p4. MPEF-PV 3502, **f**, p4. MLP 91-V-1-88, **g**, p4. **Abbreviations:** LC,

lateral crest; **m1-m3**, lower molars; **MC**, masseteric crest; **MF**, mental foramen; **nMpi**, notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*; **p4**, lower fourth premolar. Scale bar equals 1 mm

Table 2 Dental measurements of *Microcardiodon williensis*, new genus and species, in millimeters

		APL	AW	PW
MPEF-PV 3500 (Holotype)	p4	2.9	1.86	2.58
	m1	4.47	3.29	3.72
	m2		4.19	4.18
	m3	5.94	4.07	3.89
MPEF-PV 3501	p4	2.95	1.78	2.39
	m1		3.01	
	m2	4.92		3.89
MPEF-PV 3502	p4	2.88	1.89	2.33
	m1	4.36	2.86	
MPEF-PV 3503	p4	2.82	1.56	2.41
	m1	3.93	3.07	3.32
	m2	4.81	3.79	3.69
MPEF-PV 3520	m3		3.51	
	p4	2.59	1.7	
	m1	3.53	2.64	2.84
MPEF-PV 3523	m2		3.58	
	m3	4.73	3.27	3.43
MPEF-PV 3532	p4	2.95	1.76	2.57
MLP 91-V-1-88	p4	2.95	1.65	
	m1	3.84	3.18	3.46
	m2	4.79	3.60	3.72
	m3		3.79	

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

shape (Fig. 4e), and the labio-lingual diameter is shorter than that of the posterior prism. The posterior lobe is better defined and has a triangular shape. The hypoflexid is very shallow transversely and lacks cement.

None of the available specimens can be identified as a juvenile specimen (e.g., specimens with some teeth still in eruption) and none of the available cheek teeth has flexids or fossettids, a derived feature only found in the crown group and in adult and senile ontogenetic stages of the euhypsodont species of “eocardiids”.

One of the autapomorphic features of *M. williensis* is the above mentioned distinctive morphology of p4, which only resembles the condition found in *S. erro* and *E. robusta*. The p4 of adult specimens of *S. erro* is elliptical and shows a deep central fossettoid, probably a hypofossettoid; in senile specimens, the p4 is elliptical, small and lacks the fossettoid. On the other hand, the p4 of *E. robusta* has two well-defined and heart-shaped lobes. The anterior lobe is wide and rounded, and the apex is sharp, having its transverse diameter shorter than that of the posterior lobe. Additionally, on the anterolabial side is a small furrow delimited by an incipient longitudinal crest. The posterior lobe is narrower than the anterior one, and its posterior wall is convex. The hypoflexid reaches transversely more than half of the crown and has cement. The enamel is interrupted as in *M. williensis* along the lingual side of each lobe.

cf. *Microcardiodon williensis*

Referred Material MLP 91-V-1-88, right hemi-mandible with p4-m2 and part of m3.

Geological Setting MLP 91-V-1-88 was collected in the locality Río Chico, southwest Río Negro Province, Argentina (Goin and Carlini 1993; see also Fig. 1). This locality was considered intermediate in age between the classic Colloncuran assemblages of Patagonia and Laventan (Madden et al. 1997: 504, fig 29.1) or as Colloncuran (Forasiepi and Carlini 2010).

One additional specimen MLP 91-V-1-88 (Fig. 4g) is a fragment of right hemi-mandible that is tentatively assigned to *M. williensis* on the basis of the mandibular and molariform morphology. The p4 is broken at the level of the alveolus, and its shape is elliptical as in MPEF-PV 3520 (Fig. 4f), resembling the condition of adult specimens of *S. erro* (but see above).

Phylogenetic Position

Microcardiodon williensis is undoubtedly a Caviodea s.s. as indicated by the brief posterior extension of the lower incisors, which is a synapomorphy of the clade. In addition, *M. williensis* shows high-crowned teeth and double-hearted molars (Patterson and Wood 1982). As summarized in the diagnosis, *M. williensis* differs from other Caviodea s.s. by having a unique combination of plesiomorphic and apomorphic characters for Caviodea s.s. Some of the former include a horizontal crest developed as a low and wide margin, the absence of a dentine crest on the occlusal surface of the molars, the increasing size of the molars ($m1 < m2 < m3$), and nMpi connected to a well-developed masseteric crest and isolated from the horizontal crest. On the other hand, the presence of euhypsodonty, absence of flexids and fossettids, and a straight lateral crest are derived conditions among Caviodea s.s. Finally, the mental foramen is not as dorsally located as in euhypsodont “eocardiids”, but neither is it as lateral in the crown group species. This unique combination of plesiomorphies and apomorphies suggests that *M. williensis* can play a critical role in understanding the origins and early evolution of crown-group Caviodea.

The parsimony analysis resulted in ten most parsimonious trees of 276 steps (CI=0.442; RI=0.713). The strict consensus and the Bremer indices of the main nodes are shown in Fig. 5. The analysis with no additive multistate characters resulted in the same strict consensus as the first analysis, except the relations within the crown group, which fall out of the scope of the present study.

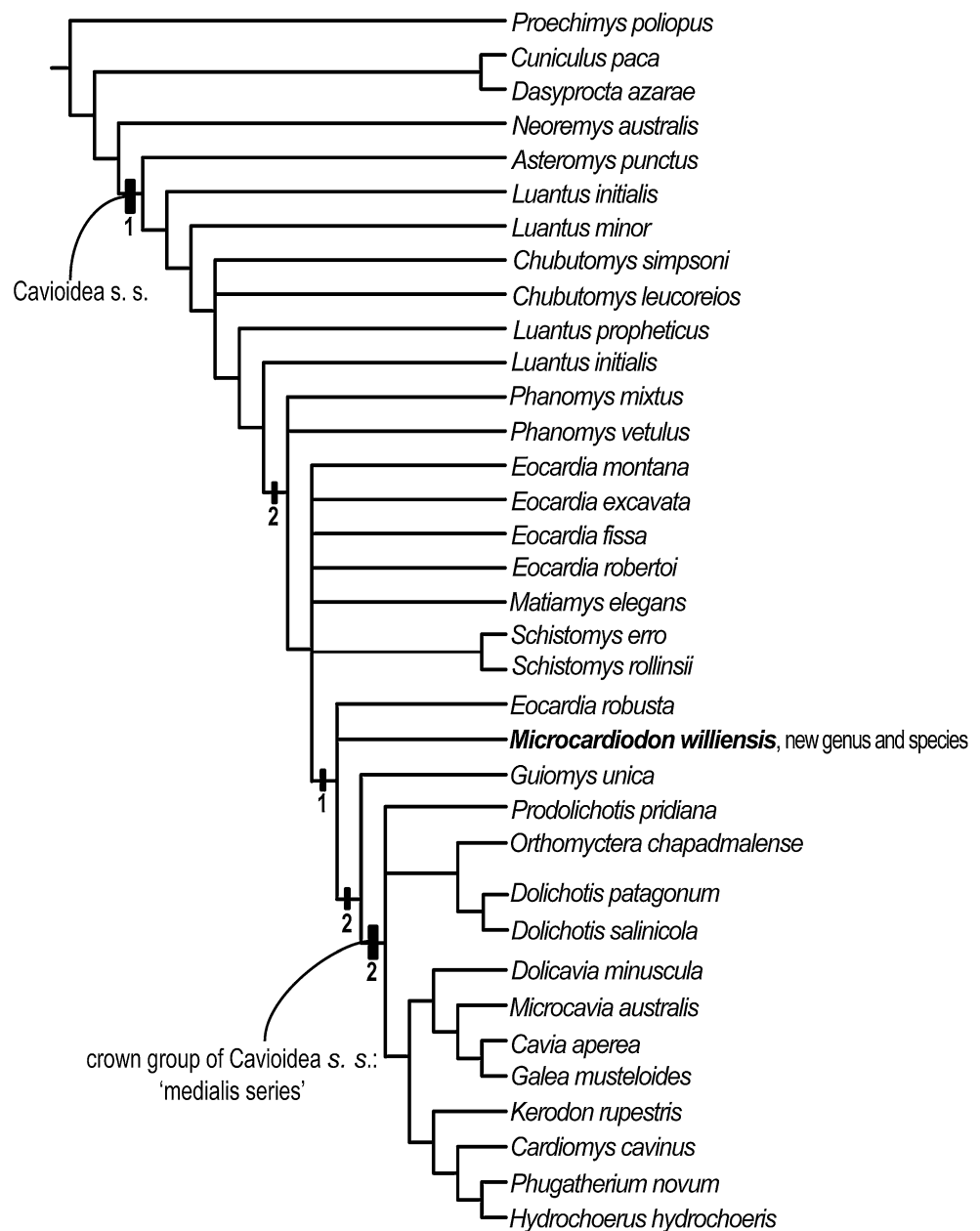
Microcardiodon williensis forms part of a polytomy together with *E. robusta* and the clade that includes *Guimys unica* Pérez, 2010b, and the crown group of Caviodea s.s. This polytomy is produced because no characters support either a more derived or a more basal position of *M. williensis* with respect to *E. robusta*. The node formed by *E. robusta*, *M. williensis*, and (*G. unica* + crown group) is supported by a single unambiguous synapomorphy in all the most parsimonious trees: the hypoflex/id funnel-shaped in occlusal view (character 34 [3]). Additionally, in some of the most parsimonious trees, this node is also supported by an unambiguous synapomorphy: the developed posterior projection of the posterior lobe of the M3 (character 55[1]). The position of *G. unica* as the sister taxon of the crown group is supported by six unambiguous synapomorphies: notch for the insertion of the tendon of the nMpi isolated, located between the masseteric crest and the horizontal crest (character 20[1]), masseteric crest absent or poorly developed as a thin and low ridge (character 21[2]), anterior origin of the masseteric crest with respect to the toothrow located below or posterior to m3 (character 23[2]), horizontal crest well developed, forming a laterally projected shelf and bearing a fossa on its dorsal surface (character 25[3]), length of p4-m1 approximately equal to the length of the m2-m3 length (character 38[1]), and lower molariforms subequal in size (character 39[1]). *Microcardiodon williensis* lacks the derived state of these six characters, and hence it is positioned more basally than *G. unica* + crown group.

Timing of the Evolution of Cavioid Mandibular Morphology

The phylogenetic position of *Microcardiodon williensis*, and *Guimys unica* from the middle Miocene of Central Patagonia, as the closest sister groups of the crown group provides critical information for understanding the evolutionary origins of Caviodea s.s. (i.e., Caviidae and Hydrochoeridae) and the sequence of appearance of characters that resulted in the great morphological differentiation of modern cavioids with respect to other caviomorph groups.

The remarkable modification of mandibular and dental characters that clearly differentiated the families Caviidae and Hydrochoeridae from other families of living rodents as well as from the members of the stem group (e.g., modification of mandibular crests—masseteric, lateral and horizontal—and position of the nMpi, the presence of a central crest of dentine on each molar lobe, the similar relative size of lower molars, and the absence of fossettids) is here analyzed on the basis of the phylogenetic study. In this way, we aim to identify the time of appearance of each

Fig. 5 Strict consensus of the ten most parsimonious trees (tree length=276) resulting from cladistic analysis of 35 Caviioidea sensu lato taxa using 89 morphological characters. *Microcardiodon williensis*, new genus and species, is the sister group of *Guimys unica* + crown group of Caviioidea s.s. The numbers indicate Bremer indices at the main nodes



character in the evolutionary history of the group, considering both the phylogenetic and the chronostratigraphic information. In this way, we also aim to evaluate whether these features arose simultaneously or if the innovations of masseteric musculature preceded the changes in the dental morphology (or vice versa) in the evolution of Caviioidea s.s.

The most outstanding modifications of these structures are listed below, according to their phylogenetic appearance in the history of Caviioidea s.s.

- 1- Among the characters that previously defined the crown group of Caviioidea s.s., the one that was first acquired along the evolutionary history of the group is

the straight or almost straight lateral crest (sensu Woods 1972). This character is ambiguously optimized and one of the possible reconstructions indicates that it was acquired at the node formed by *M. williensis* and more derived forms (Fig. 6: Node A), a transformation that must have occurred at least by the early-middle Miocene (Colloncuran age), approximately six million years before the appearance of definitive members of caviids and hydrochoerids. Alternatively, this character can be reconstructed as convergently acquired by *M. williensis* and the crown group (given that *G. unica* has the plesiomorphic curved lateral crest; Fig. 6). The discovery of more taxa closely related to the crown group will help resolve this ambiguity.

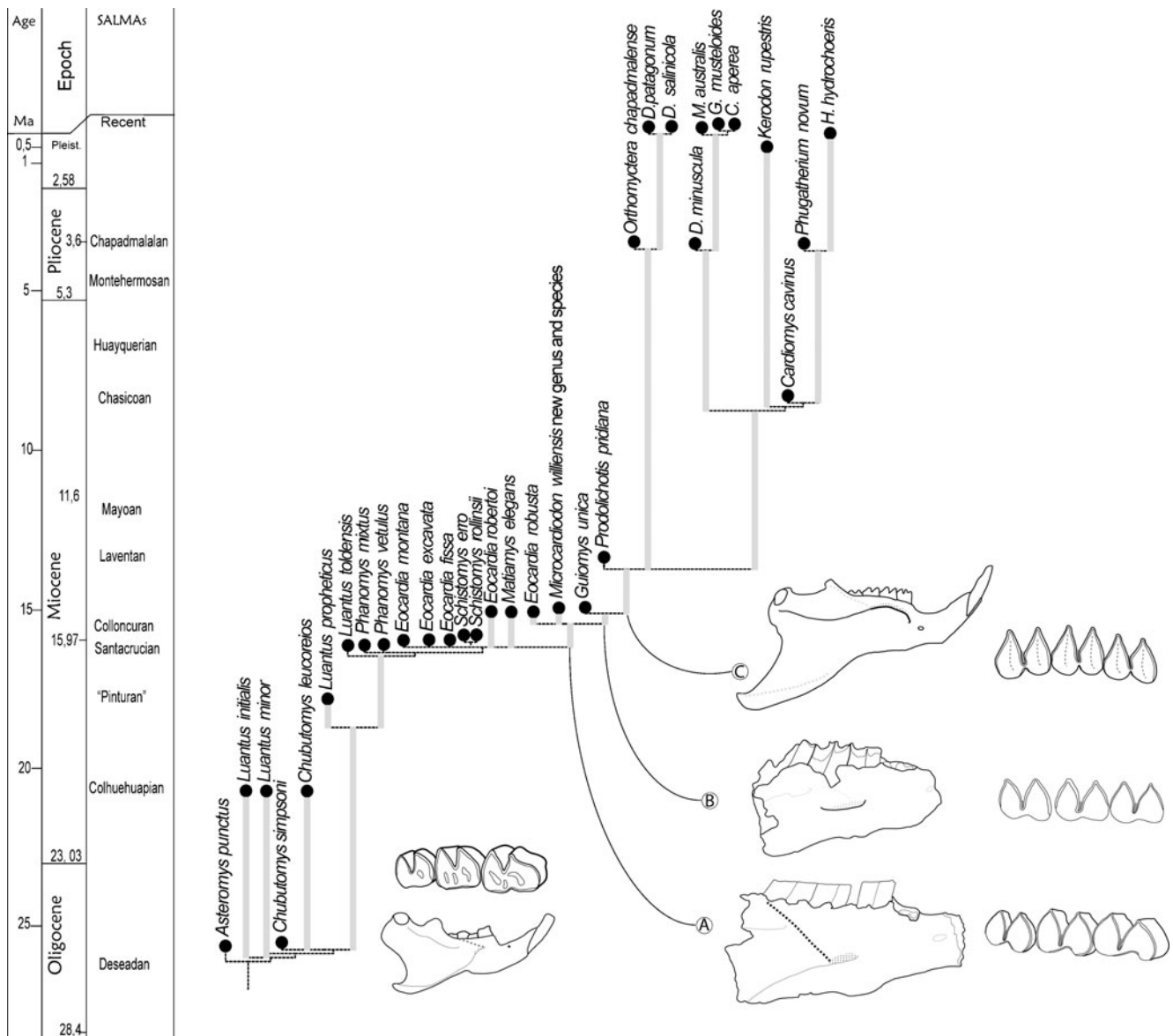


Fig. 6 Major stages in the evolution of crown group of Cavioidae s.s. representing mandibular and dental innovations: (Node A) acquisition of a straight lateral crest; (Node B) nMpi completely isolated from masseteric crest and horizontal crest; (Node B) acquisition of similar

relative size of the lower molars; (Node B) absence of fossetids in all ontogenetic stages; (Node C) nMpi completely isolated from masseteric crest but joined to horizontal crest; (Node C) acquisition of the dentine crest on the occlusal surface of each lobe of molariform

2- The absence of fossettes/ids in all the ontogenetic stages is a condition that appears in *G. unica*+ crown group of Cavioidae s.s., as more basal forms have fossettes/ids at least in early ontogenetic stages. The absence of juvenile specimens of *M. williamsi* precludes determining their absence during the earliest ontogenetic stages (Fig. 6). Therefore, this derived feature of modern cavioids must have appeared at least at Node B (Fig. 6), and possibly at Node A if *M. williamsi* lacked fossettes/ids in the earliest ontogenetic stages. More specimens of this taxon will provide the information to resolve this

ambiguity. In any case, this transformation must have also occurred at least by the lower-middle Miocene (Colloncuran age), also predating by six m.y. the appearance of caviids and hydrochoerids in the fossil record.

3- The similar relative size of the lower molars (i.e., $m1 = m2 = m3$) is a condition acquired by the clade of *G. unica*+crown group (Fig. 6: Node B). The plesiomorphic condition of *M. williamsi* indicates that no ambiguity exists in the optimization of this character. As in the above characters, the appearance of this character must also be inferred to occur at least by the

lower-middle Miocene (Colloncuran age). Note that this condition reverts in Hydrochoeridae due to the complexity of molars by development of multiple laminae, especially in m3.

- 4- The mental foramen in lateral position is acquired by the crown group of Caviioidea s.s., whereas *G. unica* and basal forms have it in dorsolateral position. In this case, *M. williensis*, has an intermediate condition between both states (Fig. 6). The evolutionary history of this character indicates a gradual modification occurred along Nodes A and B, a series of transformations that also must have occurred at least by the lower-middle Miocene (Colloncuran age).
- 5- One of the most outstanding characters of the crown group is the peculiar disposition and morphology of the mandibular crests (Fig. 6). The most basal forms of Caviioidea s.s., including *M. williensis*, have the plesiomorphic mandibular configuration present in other caviomorphs, in which the nMpi is placed anteriorly and connected to the masseteric crest, being isolated from the horizontal crest. In these forms the masseteric crest is always well developed, whereas the horizontal crest may be developed to a greater or lesser extent. *Guiomys unica*, which is the sister group of the cavioid crown group, has a unique mandibular shape, in which the mMpi is placed completely isolated from both the masseteric crest and the robust horizontal crest, showing an intermediate condition. Finally, the crown group of Caviioidea s.s. has the nMpi connected to the horizontal crest and completely isolated from the masseteric crest. The horizontal crest of the crown taxa is robust and the masseteric crest is slightly developed (e.g., *Cavia*) or absent (e.g., *Dolichotis*). The evolutionary history of the modification of the mandibular crests, therefore, also shows a series of gradual transformations that are inferred to occur between Nodes A and C (Fig. 6). The first modification is the isolation of the nMpi from both crests (masseteric and horizontal) and the reduction of the masseteric crest (Node A). This transformation must have occurred at least by the middle Miocene (Colloncuran age). A later transformation involves the connection of the nMpi to the horizontal crest that appears in the crown group (Fig. 6: Node C). The time of appearance of this characteristic morphology is inferred to occur at least by the upper-middle Miocene (Laventan South American land Mammal Age, SALMA), as it is present in *Prodolichotis pridiani*, approximately 3 m.y. before the appearance of definitive members of caviids and hydrochoerids.
- 6- Finally, the dentine crest on the occlusal surface of each molar lobe appears in the crown group of Caviioidea

s.s. (Fig. 6: Node C). This condition also is currently restricted to the crown group and its minimum age of appearance is also inferred to be in the upper-middle Miocene (Laventan SALMA), as it is also present in the basal crown taxon *P. pridiani*. The appearance of this derived character also predates the appearance of fossil forms of caviids and hydrochoerids by three m.y.

Discussion

The most important turnover in the history of caviomorph rodents occurred during the middle Miocene, especially after the Colloncuran age. It involved the extinction of most of the ancient taxa as well as the appearance of several new families and subfamilies (Vucetich et al. 1999, 2011). For the Caviioidea s.s. in particular, this modernization phase implied the extinction of the “eocardiids” and the “sudden” record of already well differentiated caviids and hydrochoerids in the Chasicuan SALMA—although a basal member of the crown group is present in the Laventan SALMA (Figs. 5 and 6). Because the middle Miocene is underrepresented, the events and processes that occurred in this period are inferred mostly through the record of the late Miocene (Chasicuan and Huayquerian SALMAs) of central Argentina. The new findings, the phylogenetic analysis of these forms, and the analysis of the anatomical characters allow a better understanding of the origin of the crown group of Caviioidea s.s. and add to the comprehension of the processes involved in this turnover.

Many of the mandibular and dental innovations characterizing caviids and hydrochoerids appear in forms that are closely related to the crown group (i.e., *M. williensis* and *G. unica*) from the early-middle Miocene of Patagonia (post Colloncuran), predating the appearance of the most ancient records of caviids and hydrochoerids. The analysis of the sequence of appearance of these characters (Fig. 6) indicates that these changes did not occur at the same time. On the contrary, many of these features seem to have appeared at different nodes of the evolutionary history of Caviioidea s.s. In fact, in some characters a series of gradual transformations can be inferred from the character optimization on the phylogenetic trees.

Both the fossil record and the phylogenetic analysis show that the loss of the fossettids, and the acquisition of a straight lateral crest, and a similar relative size of lower molars, occurred first (Fig. 6: Node A). In an intermediate phylogenetic and stratigraphic position (Fig. 6: Node B) the nMpi became isolated from the masseteric crest. Finally, the

connection of the nMpi to the horizontal crest and the appearance of the dentine crest on the occlusal surface of each molar lobe occurred somewhat later in the Laventan SALMA (Fig. 6: Node C). This shows that the remarkably derived morphology of modern cavioids is the result of a stepwise appearance of a mosaic of evolutionary innovations that originated gradually during the middle-late Miocene. All these changes predate the appearance of the most ancient records of caviids and hydrochoerids (Chasicuan SALMA), and occurred after the Colloncuran and before the Chasicuan SALMA, corroborating that the middle Miocene was a critical time for the evolution of modern cavioids.

Based on molecular data, Opazo (2005) estimated the radiation of the Caviodea s.s. (as used in this paper), at 18.5 \pm 2.5 m.y. (see also Dunnum and Salzar-Bravo 2010a, b). However, none of the morphological characters that diagnose the crown group are present in the taxa recorded for that moment (Kramarz et al. 2010), nor during the rest of the early Miocene (Kramarz and Bellosi 2005; Pérez 2010a). Hypsodonty in particular is significant to understand the evolution of this group. Among “eocardiids” hypsodonty evolved progressively through the late Oligocene to early Miocene in a scenario of a general tendency toward climatic deterioration that occurred after the Eocene-Oligocene transition cooling (Barreda and Palazzesi 2010). Moreover, during the Paleogene, periods of intense volcanism affected Patagonia, providing a great amount of glass to the sediments (Mazzoni 1985; Bellosi 2010). These two elements, climatic deterioration and a large amount of abrasive materials, favored the development of hypsodonty (Kay et al. 1999). For the early Pinturan (18.7 m.y., see Kramarz et al. 2010), which includes Opazo’s (2005) estimation for the Caviodea s.s. radiation, “eocardiids” were protohypsodont with long lasting fossette/ids. “Eocardiids” achieved euhypsodonty in the Santacrucian SALMA (late-early Miocene), but still showed an apical portion of the crown with fossettes/ids in juveniles. This ancestral apical portion bearing the fossettes/ids is retained until the Colloncuran, although fossettes/ids were then reduced in size and ontogenetic duration.

During the middle Miocene, many environmental, climatic, and paleogeographic changes modified the scenario of Patagonia (see Vucetich et al. 2011). For example, sedimentology and the paleontological record indicate a climate cooling and a marked seasonality (Vucetich 1986; Pascual et al. 1996; Ortiz Jaureguizar and Cladera 2006). However, the influence of the environmental change in the development of the mentioned characters is not clear. New discoveries of material from the middle and early-late Miocene will surely shed more light on the origin and early evolution of crown group cavioids.

Although it was not the aim of this paper to analyze the internal relationships of the crown group, which is currently under study by one of us (MEP), the use of Hydrochoeridae instead of Hydrochoerinae deserves a short discussion, and was queried by both anonymous reviewers. The relationships among the members of the crown group are still controversial, thus its internal systematics remains unstable. The conflicts lay mainly on two issues. One is the position of *Kerodon*, which was alternatively related to the Caviidae (both to Dolichotinae and Caviinae; Quintana 1998 and literature therein) and Hydrochoeridae (Woods and Kilpatrick 2005 and literature therein). The other issue concerns the relationships of Dolichotinae. While usually considered as caviids in the classical meaning, Rowe and Honeycutt (2002) considered them to be the sister group of *Hydrochoerus* + *Kerodon*. Our results suggest that Dolichotinae is the sister group of Caviinae + Hydrochoeridae. The enamel microstructure of cheek teeth also supports this hypothesis (Vieytes 2003). In turn, Vucetich and Deschamps (2010), in opposition to the classical proposal, postulated that the extinct Cardiomyinae are more closely related to hydrochoerids than to caviids (see also Pérez 2010a, b). Therefore, while the internal relationships of the group are not resolved we prefer to maintain a classical position on this issue.

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Appendix 1. Description of Characters Used in Phylogenetic Analyses.

The following characters are treated as ordered: 12, 14, 16, 18–21, 23–25, 29, and 33

- (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: absent (0); present (1).
- (6) Development of posteroventral projection of the posterior end of the mandibular symphysis in lateral view: well developed, forming an elongate peg exposed in lateral view (0); moderately developed, only a low bulge projects ventrally and is marginally exposed in lateral view (1).
- (7) Labial edge of the condyle, that is the 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).
- (8) Medial edge of the condyle that is the insertion point of *m. pterygoideus externus*, in posterior view: projecting medially forming a shelf that overhangs the medial surface of the dentary (0); poorly developed projecting medially forming a small knob with respect to medial wall of the dentary (1).
- (9) Shape of the post-condylar process, in lateral view: squared-off, forming approximately a 90° angle (0); rounded (1).
- (10) Length of the post-condylar process: equal or longer than the anteroposterior length of the condyle (0); shorter than anteroposterior length of the condyle (1).
- (11) Height of the coronoid process compared to the position of the condyle: located at the same dorsoventral level as the condyle (0); located more ventrally than the condyle (1).
- (12) Anterior margin of the coronoid process: convex (0); straight (1); concave (2). This character treated as ordered.
- (13) Dorsal end of the coronoid process: pointed and posterodorsally projected (0); pointed and dorsally projected (1); blunt (2).
- (14) Dorsoventral position of the mandibular notch: located above the occlusal surface of the dental series (0); located at the same height as the occlusal surface of the dental series (1); located ventral to the occlusal surface of the dental series (2). This character treated as ordered.
- (15) Shape of the mandibular notch: concave (0); almost straight (1).
- (16) Dorsoventral position of the anteriormost point of the lunar notch: low, located ventral to the dorsoventral midpoint of the dentary (between the ventral edge of the dentary and the condyle) (0); located at the approximate dorsoventral midpoint of the dentary (1); high, located above the dorsoventral midpoint of the dentary (2). This character treated as ordered.
- (17) Posterior extension of the angular process: level with the post-condylar process (0); ending anterior to the post-condylar process (1); ending posterior to the post-condylar process (2).
- (18) Posterior extension of the root of the lower incisors: extending up to the level of m3 (0); extending up to the level of the posterior lobe of m2 (1); extending up to the level of the anterior lobe of m2 (2); extending up to the level of m1 (3). This character treated as ordered.
- (19) Location of the notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis* with respect to the toothrow: located between p4 and m1 (0); located below m1 (1); located between m1 and m2 (2). This character treated as ordered.
- (20) Notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*: connected to the masseteric crest (0); isolated, located between the masseteric crest and the horizontal crest (1); connected to the horizontal crest (2). This character treated as ordered.
- (21) Development of the masseteric crest: well developed, forming a shelf that projects laterally with respect to the lateral surface of the dentary (0); forming a well-developed ridge that fails to project with respect to the lateral surface of the dentary (1); absent or poorly developed as a thin and low ridge (2). This character treated as ordered.
- (22) Shape of the lateral crest (sensu Woods 1972): straight, projecting anteroventrally from the base of the coronoid process (0); curved, deflecting anteroventrally from the base of the coronoid process (1).
- (23) Anterior origin of the masseteric crest with respect to the toothrow: located below m1 (0); located below m2 (1); located below m3 or posterior to m3 (2). This character treated as ordered.
- (24) Posterior extension of the horizontal crest, in lateral view: extending up to the anterior margin of the mandibular condyle (0); approximately ending at the anteroposterior midpoint of the mandibular condyle (1); extending up to the posterior margin of the

- mandibular condyle (2). This character treated as ordered.
- (25) Development of the horizontal crest: absent or extremely reduced (0); present as a low and broad ridge (1); present as a conspicuous crest, forming a 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). This character treated as ordered.
- (26) Depth of the fossa located dorsal to the horizontal crest with respect to the dorsoventral depth of the notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*: notch deeper than fossa (0); fossa deeper than notch (1); notch and fossa equal in depth (2).
- (27) Alveolar protuberances (ventral outgrowth of the base of some molariform alveoli that projects ventrally from the ventral surface of the dentary): absent (0); present (1).
- (28) Development of alveolar protuberances: present as a small but distinct convexity on the ventral margin of the dentary (0); present as well-developed bulge on the ventral margin of the dentary (1).
- (29) Degree of hypsodonty: slightly hypsodont, having the root and the anteroposterior length of the occlusal surface longer than the height of the crown (0); mesodont, having the root and the anteroposterior length of the occlusal surface approximately equal to the height of the crown (1); protohypsodont, having the root and the anteroposterior length of the occlusal surface less than half the height of the crown (2); euhypsodont, lacking roots (3). This character treated as ordered.
- (30) Shape of the molars, in occlusal view: not forming lobes (0); formed by triangular lobes (1); formed by heart-shaped lobes (2); formed by two laminar lobes, the posterior one being formed by a single lamina (3); formed by two laminar lobes, the posterior one being formed by at least four laminae (4).
- (31) Constriction of the apex in each lobe of the molars: absent (0); present (1).
- (32) Development of constriction of the apex in each lobe of the molars: poorly developed, with the apex of the lobes bearing a minor constriction (0); well developed, the constriction is present in both lobes of each tooth (1).
- (33) Transverse extension of the hypoflexus/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). This character treated as ordered.
- (34) Shape of the hypoflexus/id in occlusal view: very narrow and short (0); V-shaped (1); narrow and very long (2); funnel shaped (3).
- (35) Longitudinal furrow on the labial wall of the upper molars and lingual wall of the lower molars: absent (0); present (1).
- (36) Position of the longitudinal furrow on the labial wall of the upper molars and the lingual wall of the lower molars: one furrow opposite the hypoflexus/id (0); one furrow on the posterior lobe (1); one furrow on each lobe (2).
- (37) Transverse dentine crest on the occlusal surface, located at the middle of each molar lobe: absent (0); present (1).
- (38) Length of p4-m1 with respect to the length of the m2-m3 (Wood and Patterson 1959): p4-m1 shorter than m2-m3 (0); p4-m1 approximately equal to m2-m3 (1).
- (39) Relative size of lower molars: $m1 < m2 < m3$ (0); $m1 = m2 = m3$ (1).
- (40) Relative size of the upper molars: $P4 < M1 < M2$ (0); $P4 = M1 = M2$ (1).
- (41) Replacement of deciduous premolar: unreplaced (0); with replacement (1).
- (42) Type of replacement: postnatal replacement (0); prenatal replacement (1).
- (43) Orientation of left and right molar series: parallel to each other (0); anteriorly convergent (1).
- (44) Cement in late ontogenetic stages: absent (0); present (1).
- (45) Cement in young-adult ontogenetic stages: absent (0); present (1).
- (46) Cement in juvenile ontogenetic stages: absent (0); present (1).
- (47) 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).
- (48) 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 flexus/ids opposite to the hypoflexus/id (4); interrupted along the entire lingual wall and anterolingual and posterolingual walls (5).

- (49) Fossettes/ids in late ontogenetic stages: present (0); absent (1).
- (50) Fossettes/ids in young-adult ontogenetic stages: present (0); absent (1).
- (51) Fossettes/ids in juvenile ontogenetic stages: present (0); absent (1).
- (52) Shape of the fossettes/ids: elongated (0); subcircular (1).
- (53) Number of lobes in P4: two (0); one (1).
- (54) Posterior projection of M3: absent (0); present (1).
- (55) Development of posterior projection of M3: incipient (0); developed (1); M3 with multiple laminae (2).
- (56) Mesofossettoid in young-adult stages: present (0); absent (1).
- (57) Fusion of the mesolophid with the anterolophid (metalophulid II and metalophulid I respectively sensu Marivaux et al. 2004): no (0); yes (1). (Kramarz 2005: character 15).
- (58) Reduction of the mesolophid (metalophulid II sensu Marivaux et al. 2004): complete (0), reduced (1). (Kramarz 2005: character 16).
- (59) Mesoflexid remains opened: no (0); yes (1). (Kramarz 2005: character 17).
- (60) Size of oval foramen: small (1); large (0). (Quintana 1998: character 1)
- (61) Apex of mesopterygoid fossa with respect to M2: level with M2 (0); apex in front of M2 (1). (Quintana 1998: character 2)
- (62) Articulation of nasals with respect to premaxillae: nasals articulate with premaxillae throughout their length (0); anterior half of nasals do not articulate with premaxillae (1). (Quintana 1998: character 6)
- (63) Interorbital width: longer or equal to braincase (0); shorter than braincase (1). (Quintana 1998: character 14)
- (64) Shape of frontals: markedly convex posteriorly (1); not convex (0). (Quintana 1998: character 15; Ubilla et al. 1999: character 14)
- (65) Extension of pterygoids: short (0); long and oriented posteriorly (1). (Quintana 1998: character 17).
- (66) Pterygoids: free (0); fused to the auditory bullae (1). (Quintana 1998: character 18).
- (67) 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).
- (68) Position of the posterior margin of the upper diastema: not vertical (0); vertical (1). (Quintana 1998: character 23; Ubilla et al. 1999: character 23).
- (69) Shape of palate: concave (0); plane (1). (Quintana 1998: character 24; Ubilla et al. 1999: character 12)
- (70) Upper zygomatic process of the maxilla: not extended as plate-shaped in the rostrum (0); plate-shaped (1). (Quintana 1998: character 25; Ubilla et al. 1999: character 24)
- (71) Shape of upper margin of the infraorbital foramen: not straight (0); with straight upper margin (1). (Quintana 1998: character 26; Ubilla et al. 1999: character 5).
- (72) Incisive foramina: not reduced (0); reduced (1). (Quintana 1998: character 27).
- (73) Jugular and carotid foramina: fused (0); not fused (1). (Quintana 1998: character 28; Ubilla et al. 1999: character 36).
- (74) 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).
- (75) Postfrontal spinous process of the jugal: absent (0); present (1). (Quintana 1998: character 33; Ubilla et al. 1999: character 31).
- (76) Orbital foramen: fused to the foramen rotundum (0); separated from the foramen rotundum (1). (Quintana 1998: character 34).
- (77) Position of upper incisors: orthodont (0); inclined (1). (Quintana 1998: character 35).
- (78) Enamel of upper and lower incisors: uncolored (0); with color (1). (Quintana 1998: character 36; Ubilla et al. 1999: character 13).
- (79) Shape of nasals: not anteriorly vaulted (0); greatly vaulted anteriorly (1). (Quintana 1998: character 38; Ubilla et al. 1999: character 3).
- (80) Shape of palatines: without posterior flat expansion (0); with posterior flat expansion (1). (Quintana 1998: character 39; Ubilla et al. 1999: character 11).
- (81) Position of parietals: in the same plane with respect to the nasals (0); in different plane with respect to the nasals (1). (Quintana 1998: character 40; Ubilla et al. 1999: character 25).
- (82) 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).
- (83) Supraorbital foramen or notch: conspicuous (0); absent (1). (Quintana 1998: character 42).
- (84) Position of P4 alveolar prominence: near to the nasolacrimal foramen margin (0); far anterior to this margin (1). (Ubilla et al. 1999: character 4).
- (85) Masseteric fossa of the zygomatic arch: shallow and not well delimited (0); deep and well delimited (1). (Ubilla et al. 1999: character 9).
- (86) Position of the boundary between the mastoid and paraoccipital processes: at the same level or above

Appendix 2

Table 3 Character-taxon matrix used for phylogenetic analysis. Characters between brackets represent polymorphic or uncertain scorings. Data matrix modified of Pérez 2010b

Taxon	10	20	30	40	50	60	70	80	89
<i>Proechimys poliotus</i>	00?0110000	00000000000	0000000?00	0?000?0000	0?00000000	00?0?01100	0010110010	00?0?0?1?0	011?0?001
<i>Dolicavia minuscula</i>	01110?1111	??22111302	2?10311?32	1?23111111	??111?3411	??1111?0	1012110010	0000011010	011001011
<i>Prodolichotis pridiiana</i>	0111?0?0?0	??0?0?0?0?0	2?0?0?0?0?0	1?22101111	??111?3[45]1?	??1111?0	101?1010?0	?0?0?0?0?0?0	?0?0?0?0?0
<i>Orthomyctera chapadmalense</i>	01110?1011	012001?222	2021322?32	2?23101111	??111?2411	??1111?0	0011?01010	00?0?0?0?0?0	?0?0?0?0?0
<i>Plugatherium novum</i>	011?0?0?0	??0?0?0?0?0	202?320?34	1?23120000	??111?4411	??1121?0	2?00?0?11?	?0?0?0?0?0?0	?00?00111
<i>Hydrochoerus hydrochoeris</i>	111101111	0122022312	2021320?34	2?23120000	1111104411	1?1121?0	2000001010	0000000?00	000?00111
<i>Cardiomyx cavinus</i>	11110?0?0	??0?0?0?0?0	202?322?32	2?2312?011	??111?4411	1?111?0?0	1?00?0?01?	?0?0?0?0?0?0	?0?0?0?0?0
<i>Kerodon rupestris</i>	01110?0000	1?12012312	2020320?32	2?22120111	1111114511	1?1101?0	0010101001	1110100100	001100011
<i>Cavia aperea</i>	0101100001	1?02022112	2020312?33	1?22111111	1111112411	1?1101?0	1011001011	1100010000	011011101
<i>Galea musteloides</i>	0111010011	0?00122102	2022301?32	1?2?111111	1111112411	1?1111?0	1011000011	10?0?0?1?0	?11?11101
<i>Microcavia australis</i>	0111110011	1?02012322	2020310?32	1?2?1?1000	1011112410	0?1111?0	1011000111	1011010010	010111001
<i>Dolichotis patagonum</i>	01110?1111	0220022222	20?1322?32	2?231?1111	1111112411	1?1111?0	0000001000	0010010100	100?01100
<i>Dolichotis salinicola</i>	01110?1111	0220022222	20?322?32	2?231?1111	1111112411	1?1111?0	0100001000	0010010100	110?01100
<i>Dasyprocta azarae</i>	01000?1110	1222101000	000000?10	0?000?0111	1000000000	00?0?01?01	00111?1010	01?1?001?0	?01?00011
<i>Cuniculus paca</i>	00?00?1011	0021010?00	1001110?10	0?000?0011	1000000000	10?0?00?11	001100?011	0?0?0?01?0	?01?11011
<i>Neoreomys australis</i>	1100111111	?1?0?02000	100000?21	0?110?0000	1011101000	0000?0?0?11	00?0?0?01?	?0?0?0?0?0	?0?0?0?0?0
<i>Asteromys punctus</i>	?10111?0?0	?0?0?0?0?0	110?120?11	0?010?011?	10?0000000	00?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0
<i>Chubutomys simpsoni</i>	?0?0?0?0?0	?0?0?0?0?0	?1?0?0?0?0	10210?0?0?	?0?00?2?0	00?0?1?0?	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0
<i>Chubutomys leucoreios</i>	?10111?0?0	?0?0?0?0?0	111?110?21	10?110000?	10?001?0	00?0?10?	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0
<i>Luantus initialis</i>	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0	10110?000?	10?1001000	000?0?110?	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0
<i>Luantus minor</i>	?0?0?0?0?0	?0?0?0?0?0	1?1?0?0?21	10110?0?0?	?0?100?000	000?0?110?	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0
<i>Luantus propheticus</i>	?10111?0?0	?0?0?0?0?0	111?210?21	101100000	101101200	000100110?	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0
<i>Luantus toldensis</i>	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0	1021100?0?	10?1111310	000100110?	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0
<i>Phanomys mixtus</i>	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0	1022100?0?	10?1111510	000101110?	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0
<i>Phanomys vetulus</i>	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0	1022100?0?	10?1111510	01010?1110?	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0
<i>Eocardia fissa</i>	01011?0?0	?0?0?0?0?0	111?221032	10112210000	1011111[45]11	010101110?	1011?0?01?	?0?0?0?0?0	?11?0?0?0
<i>Eocardia montana</i>	0101101?0	11210?120	0110221132	101122110000	1011113411	010101110?	?0?11?0?01?	?0?0?0?0?0	?11?1?0?0
<i>Eocardia excavata</i>	?10110?0?0	?0?0?0?0?0	011?220?32	101122110000	1011111411	010101110?	?0?1?0?0?0	?0?0?0?0?0	?0?0?0?0?0
<i>Eocardia robusta</i>	010111?0?0	?0?0?0?0?0	111?221032	1123110000	101111141?	?10111010?	?0?1?0?0?0	?0?0?0?0?0	?111?0?0?0
<i>Eocardia robertoi</i>	0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0	1122100?0?	10?111?411	010111?0?0	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0
<i>Schistomys erro</i>	?101110?11	01100?0?220	0111220?32	101122100000	1011111[45]10	011111?10?	?0?11?0?01?	?0?0?0?0?0	?111?0?0?0
<i>Schistomys rollinsii</i>	0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0	?0?22100?0?	1011?0?0[45]1?	?11111?0?0	?0?1?0?0?0	?0?0?0?0?0	?111?0?0?0
<i>Matiamys elegans</i>	1?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0	1122100?0?	10111?0?410	010111?0?0	?0?1?0?0?0	?0?0?0?0?0	?111?0?0?0
<i>Guimys unica</i>	?101?0?0?0	?0?0?0?0?0	212321032	1023100111	??11113411	1?1111?0?	1?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0
<i>Microcardiodon williamsi</i>	?10111?0?0?0	?0?0?0?0?0	101?121032	102310000?	?0?1?0?041?	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0	?0?0?0?0?0

- the external auditory meatus (0); beneath the external auditory meatus (1). (Ubilla et al. 1999: character 15).
- (87) Shape of the squamosal process: straight (0); curved (1). (Ubilla et al. 1999: character 18).
- (88) Shape of the external auditory meatus: long and tube-shaped (0); short (1). (Ubilla et al. 1999: character 19).
- (89) Posterior apophysis of the squamosal: partially covering the epitympanic sinus (0); completely covering the epitympanic sinus (1). (Vucetich 1975, 1984).

Appendix 3. Analyzed Specimens of Taxa Used in Phylogenetic Analysis and Comparison

List of specimens of ingroup.

Asteromys punctus—MACN A 52-110 (holotype), R mandibular fragment with i, p4-m3; MLP 59-II-26-97, L mandibular fragment with i, dp4, p4-m3. *Chubutomys simpsoni*—AMNH 29557 (holotype), L mandibular fragment with m2-m3. *Chubutomys leucoreios*—MPEF-PV 1153 (holotype), L mandibular fragment with p4-m3. *Luantus initialis*—MACN A 52-164 (lectotype), L mandibular fragment with i, p4-m2; MPEF-PV 6056, R maxillary fragment with P4-M2; MPEF-PV 7979, R upper molar; MLP 85-VII-3-7, R lower molar; MLP 93-XI-18-28, L lower molar. *Luantus minor*—MPEF-PV 5007 (holotype), R mandibular fragment with m1-m2; MPEF-PV 1154a, L lower molar; MPEF-PV 5028, R M3; MPEF-PV 1154b, R upper molar. *Luantus propheticus*—MACN A 2018 (holotype), R mandibular fragment with p4-m3. And see Appendix in Kramarz (2006). *Luantus toldensis*—MACN Pv SC2574 (holotype), R lower molar. And see Appendix in Kramarz (2006). *Phanomys mixtus*—MACN A 2022 (neosintype): MACN A 11-302, R maxillary fragment with P4-M2; MLP 15-341, L maxillary fragment with P4-M2; MLP 15-217a, R mandibular fragment with m2-m3; MLP 91-II-25-3, R mandibular fragment with m2-m3 and L mandibular fragment with p4-m2. And see Appendix in Kramarz (2006). *Phanomys vetulus*—P4 superior isolated and M superior isolated (iconotype; Fig. 25, Ameghino 1891). *Eocardia montana*—(neointype). MACN A 336, L mandibular fragment with i, p4-m2; MACN A 337, R mandibular fragment with p4-m2; MACN A 338, L maxillary fragment with M1-M2; MACN A 339 L mandibular fragment with p4; MACN A 340, L mandibular fragment with p4-m3 (holotype of *Eocardia perforata*); MACN A 446, R mandibular fragment with i, p4-m2 (holotype of *Dicardia maxima*); MACN A 4475 (holotype of *Tricardia divisa*); YPMPU 15323, L mandibular fragment with i, p4-m2 (holotype of *Eocardia petersoni*); MLP 15-98, L mandibular fragment with m2-

m3; MLP 15-112, L mandibular fragment with p4-m3; MLP 63-XII-19-44, L mandibular fragment with i, p4-m1; MLP 63-XII-19-46, R mandibular fragment with i, p4-m2; MLP 63-XII-19-47, R mandibular fragment with p4-m2; MLP 63-XII-19-49, R mandibular fragment with p4-m3; MLP 63-XII-19-51 R mandibular fragment with i, p4-m1; MLP 63-XII-19-54, R maxillary fragment with M1-M2; MLP 63-XII-19-56, L maxillary fragment with P4-M2; MLP 63-XII-19-71, R mandibular fragment with m1-m2; MLP 67-V-23-3, R mandibular fragment with m1-m3; MLP 68-I-16-5, L mandibular fragment with i, p4-m3; MACN A 341, L mandibular fragment with m1-m2; MACN A 2009, four M3 isolated; MACN A 2015 L mandibular fragment with i, p4-m3 and R mandibular fragment with i, p4-m2; MACN A 4455, L mandibular fragment with m1-m3; MACN A 4456, L mandibular fragment with p4-m3; MACN A 4457, R mandibular fragment with m2-m3; MACN A 4503, R mandibular fragment with p4-m1; MLP 15-325, R mandibular fragment with p4-m3; MLP 15-326, R mandibular fragment with m1-m2; MLP 15-327, L mandibular fragment with p4-m1; MLP 15-328, R mandibular fragment with m1; MPEF-PV 1349, L mandibular fragment with i, m2-m3; MACN A 10204, R mandibular fragment with dp4-m2; MACN A 10205, R mandibular fragment with dp4-m2; MACN A 10206a, R mandibular fragment with p4-m1; MACN A 10206b, R mandibular fragment with dp4-m1; MACN A 10207/8, Rdp4, Ldp4 and LM3; MACN A 10215, R mandibular fragment with p4 and m1; MACN A 10216, L mandibular fragment with p4-m1; MACN A 10227, L mandibular fragment with p4-m1; MACN A 10931, molar; MACN A 4483, L maxillary fragment with P4-M3; MLP 90.III.5.15, R mandibular fragment with m1-m2; MLP 90.III.5.37, L mandibular fragment with p4-m1; MLP 90.III.5.12, L mandibular fragment with dp4-m1; MLP, 91.I.10.8, three molars; MLP 91.I.10.1, R mandibular fragment with m1-m2; AMNH 97683, R mandibular fragment with m1-m3; AMNH 97733, L mandibular fragment with dp4-m1; AMNH 97748, L mandibular fragment with i, p4-m3; AMNH 99307, L mandibular fragment with m1; AMNH 99313, R mandibular fragment with p4-m1; R maxillary fragment with M2-M3; AMNH 9590, R mandibular fragment with p4-m3 and L mandibular fragment with i, p4-m3; AMNH 97656, m2 and m3; AMNH 97667, R mandibular fragment with P4-M2 and L P4-M1; AMNH 94594, R maxillary fragment with P4-M3 and L P4-M3; YPMPU 15058, R mandibular fragment with i, p4-m1; YPMPU 15574, R and L mandibular fragment with incisors and L p4-m3; YPMPU 15583, R mandibular fragment with m2-m3; YPM PU 15372, R mandibular fragment with i, p4-m3; YPMPU 15635, L mandibular fragment with p4-m2; YPMPU 15874, maxillary fragment with L and R P4-M1 and L M2. *Eocardia fissa*—R mandibular fragment

with i, p4-m3 (iconotype; Ameghino 1891: fig. 24). MACN A 4468, R mandibular fragment with p4-m1; MACN A 10407, R mandibular fragment with p4-m3; MACN A 4461, L mandibular fragment with p4-m1; MACN A 4463 R mandibular fragment with i, p4-m3; MACN A 4458, L mandibular fragment with p4-m2; MACN A R mandibular fragment with p4-m3; MACN A 2009, 15 M3; MACN A 2009, two molars; MACN A 10211, skull fragment with two molariforms series and L incisor; MACN A 10957a, palate fragment with two molar series; MACN A 10957b, maxillary fragment with two molar series; MACN A 10957c, maxillary fragment with two molar series; MACN A 10957d, maxillary fragment with two molar series; MACN A 10931, R mandibular fragment with m1-m2; MACN A 10931, R mandibular fragment with m1; MACN A 10931, upper molar, MACN A 10931, five molars; MACN A 10931, 40 molars; MACN A 10210, R mandibular fragment with p4-m3; MACN A 10210, maxillary fragment with L P4-M3 and R M1; MACN A 4485, maxillary fragment with L P4-M3 and R M2-M3; MACN A 10729, maxillary fragment with R P4-M2; MACN A 10203, skull fragment with R I, M1-M3; MACN A 4469, R mandibular fragment with p4-m1; MACN A 4470, R mandibular fragment with p4; MACN A 4471, L mandibular fragment with p4-m1; MACN A 4489, maxillary fragment with R P4-M3 and L M1-M3; MACN A 10212, maxillary fragment with two molar series; MACN A 4486, maxillary fragment with two molar series; MACN A 10957, L mandibular fragment with i, p4-m2; MACN A 10957, R mandibular fragment with p4-m1; MACN A 10957, L mandibular fragment with p4-m2; MACN A 10957, L mandibular fragment with m1-m2; MACN A 10957, R mandibular fragment with p4-m2; MACN A 10957, L mandibular fragment with p4-m2; MACN A 10957, R mandibular fragment with p4-m2; MACN A 10957, L mandibular fragment with p4-m1; MACN A 10957, maxillary fragment with L P4-M2; MACN A 4490, upper molar; MACN A 4493, maxillary fragment with L P4; MACN A 4497, maxillary fragment with L P4-M2; MACN A 4498, maxillary fragment with R P4-M2; MACN A 4499, maxillary fragment with L P4-M1 and R P4-M2; MPEF-PV 1507, R mandibular fragment with i, p4-m3; MPEF-PV 1659, maxillary fragment with two molar series; MPEF-PV 1621, fragment of skull with two dental series; MLP 15-97, L mandibular fragment with m1-m2; MLP 15-313, R mandibular fragment with i, p4-m2; MLP 15-316, maxillary fragment with L P4-M2; MLP 15-291, maxillary fragment with two molar series; MLP 15-394, L mandibular fragment with p4-m2; MLP 63-XII-19-70 L mandibular fragment with p4-m2; MACN A 2016, R mandibular fragment with p4-m2; MACN A 10214, L mandibular fragment with p4-m3; YPMPU 15010, fragment of skull with two dental series;

YPMPU 15022, maxillary fragment with L P4-M3; YPMPU 15463, R mandibular fragment with p4-m2 and maxillary fragment with two molar series; YPMPU 15380, R mandibular fragment with p4-m2; YPMPU 15327, maxillary fragment with L and R M1-M3; YPMPU 15276, maxillary with two molar series. *Eocardia excavata*—MACN A 4472 (holotype) p4-m2; MACN A 107, L mandibular fragment with i, p4-m2; MACN A 4476 (holotype *Tricardia gracilis*), L mandibular fragment with p4-m2; MACN A 4467 (holotype *Dicardia proxima*), R mandibular fragment with i, p4-m3; MACN-A 10226, R mandibular fragment with p4-m3; MACN A 10219, L mandibular fragment with p4-m2; MACN A 10222, R mandibular fragment with m1-m2; MACN-A 10223, R mandibular fragment with p4-m2; MACN A 10225, L mandibular fragment with p4-m2; MACN A 4470, R mandibular fragment with p4; MACN A 4471, L mandibular fragment with p4-m1; MACN A 4460, R mandibular fragment with p4-m1; MLP 15-302, R mandibular fragment with p4-m3; MLP 15-114, R mandibular fragment with p4-m2; MLP 15-329, L mandibular fragment with m1-m2; MLP 15-383, L mandibular fragment with p4-m2; MLP 63-XII-19-48, R mandibular fragment with m1; MLP 15-303, maxillary fragment with R M2-M3; MACN A 4459, L mandibular fragment with p4-m1; MACN-A 10209, maxillary fragment with two molar series; MACN A 4454, skull; MACN A 10931, three molars; MACN A 10931, five upper molars and three lower molars; MACN A 2008, L mandibular fragment with; MACN A 2009, L mandibular fragment with p4-m1; MACN A 2009, 11 M3; MACN A 2011, R mandibular fragment with i, m1; MACN A 2012, L mandibular fragment with p4; MACN A 425-434, 10 molars; MACN A 2020, R mandibular fragment with M2-M3; MACN A 2020, two upper molars; MACN A 342, L mandibular fragment with p4-m1; MACN A 343, L mandibular fragment with m1-m2; MACN A 4500, maxillary fragment with R P4-M3; MACN A 4501, maxillary fragment with R P4-M2; MACN A 10957, L mandibular fragment with p4-m3; MACN A 10957, R mandibular fragment with p4-m1; MACN A 10957, R mandibular fragment with p4-m2; MACN A 10957, R mandibular fragment with p4-m1; MACN A 10957, L mandibular fragment with m2-m3; MACN A 10220, L mandibular fragment with m1-m2; MACN A 4496, L mandibular fragment with m2-m3; MACN A 10213, p4-m1; MACN A 10221, R mandibular fragment with p4-m3; AMNH 97665, R mandibular fragment with p4-m3; AMNH 97682, R mandibular fragment with p4-m1; AMNH 99308, R mandibular fragment with m2-m3; AMNH 99309, L mandibular fragment with m1-m2; AMNH 99310, R mandibular fragment with p4-m1; AMNH 99311, R mandibular fragment with p4-m1; AMNH 99312, L mandibular fragment with p4-m2;

YPMPU 15126, L mandibular fragment with m1-m3; YPMPU 15205, maxillary fragment with R and L M1-M2 and R mandibular fragment with i, p4-m1; YPMPU 15326, R mandibular fragment with m1-m3; YPMPU 15383, fragment of skull with R DP4-M3 and L DP4-M2; YPMPU 15550, R mandibular fragment with i, p4-m2; YPMPU 15810, maxillary fragment with R M1-M2; YPMPU 15977, R mandibular fragment with m2-m3; YPMPU 15054, maxillary fragment with R P4-M3; YPMPU 15621, maxillary fragment with R and L P4-M3; AMNH 99330, maxillary fragment with R M1-M3. *Eocardia robusta*—MLP 15-414 (holotype), skull with two molar series; MLP 74-II-1-7, maxillary fragment with L DP4-M3; MLP 15-417, L mandibular fragment with i, p4-m3; MLP 91-IX-2-93, skull with R P4-M3 and L P4-M2; MLP 92-V-10-3, L mandibular fragment with m1-m2; MLP 91-IX-2-81, R mandibular fragment with i, p4-m3; MLP 91-V-1-89, R mandibular fragment with m1-m3; MLP 92-V-10-67, L mandibular fragment with p4-m2; MLP 92-V-10-68, R mandibular fragment with m2-m3; MLP 92-V-10-70, R mandibular fragment with p4-m2; MLP 92-V-10-71, L mandibular fragment with m1 and m2 isolated; MLP 92-V-10-73, R mandibular fragment with m3; MLP 92-V-10-74, R mandibular fragment with incisor; MLP 92-V-10-75, maxillary fragment of; MLP 91-V-1-73, R maxillary fragment with DP4-M2; MLP 91-V-1-74, R mandibular fragment with p4-m1; MLP 91-V-1-75, L mandibular fragment with m2-m3; MLP 92-V-10-69, R mandibular fragment with p4-m1; MLP 91-IX-2-1, L mandibular fragment with p4-m1; MLP 74-II-1-34, maxillary fragment with M1-M3; MJHG 76-III-1-1, rostral region with L dental series and two incisors. *Eocardia robertoi*—MLP 80-VII-1-1 (Holotype), maxillary fragment L P4-M3 and R M1-M3. *Matiamys elegans*—MACN Pv 14565 (holotype), skull with two dental series; MLP 90-XII-25-I, maxillary fragment with L DP4-M3 and R P4-M3. *Schistomys erro*—MLP 68-I-16-7, maxillary fragment with L I, P4-M3, R I, P4-M1; MACN A 4479 (holotype of *Schistomys crassus*), skull with two dental series; MACN A 2019 (holotype of *Procardia elliptica*), R mandibular fragment with i, p4-m3; MACN A 4480b, maxillary fragment with L and R P4; MLP 63-XII-19-50, R maxillary fragment with P4-M3; MLP 63-XII-19-55, L maxillary fragment with P4-M2; MLP 63-XII-19-58, L maxillary fragment with M1-M3; YPMPU 15648, skull and mandible; MLP 15-330, R maxillary fragment with M1-M3; YPMPU 15420, fragment of skull with R dental series; YPMPU 15620, fragment of skull with L P4-M3 and R M1-M3; YPMPU 15587, fragment of skull with R P4-M2; AMNH 9539, fragment of skull with R M1-M3 and L M3. *Schistomys rollinsii*—YPM 15969 [SIC] = YPMPU 15959 (holotype), skull with two molariforms series. *Guimys unica*—MPEF-PV 3504 (Holotype), R mandibular fragment of with p4-m3; MPEF-PV 3505, R mandibular fragment; MPEF-PV 3506, L mandibular fragment with p4-m3; MPEF-PV 3508, L mandibular fragment with p4-m2; MPEF-PV 3513, L mandibular fragment with p4-m2; MPEF-PV 3514, L mandibular fragment with p4-m2; MPEF-PV 3512, R mandibular fragment with m1-m2; MPEF-PV 3519, R mandibular fragment with m1-m2; MPEF-PV 3524, R mandibular fragment with p4-m1; MPEF-PV 3526, R mandibular fragment with p4-m1; MPEF-PV 3529, R mandibular fragment with p4-m1; MPEF-PV 3527, L mandibular fragment with p4-m1; MLP 91-IX-4-3, L mandibular fragment with p4-m1; MPEF-PV 3533, maxillary fragment with L P4-M2 and R P4-M1; MPEF-PV 3534, maxillary fragment with R P4-M1 and M3; MPEF-PV 3535, R maxillary fragment with M2-M3; MPEF-PV 3537, R maxillary fragment with M2-M3; MPEF-PV 3536, R maxillary fragment with M2-M3; MPEF-PV 3538, L maxillary fragment with M1-M2; MPEF-PV 3539, L maxillary fragment with M3; MPEF-PV 3540, L maxillary fragment with P4; MPEF-PV 3541, L maxillary fragment with P4; MPEF-PV 3542, R maxillary fragment with P4; MPEF-PV 3543, R maxillary fragment with M1; MLP 91-IX-4-2, R mandibular fragment with p4-m2; MLP 91-IX-4-1, maxillary fragment with both dental series. *Prodolichotis pridiani*—skull and mandible have been scored from the literature (Fields 1957: holotype UCMP 38761). *Orthomyctera chapadmalense*—MLP 15-229 (holotype), skull and mandible. *Dolicavia minuscula*—MLP 34.V.10.10, skull; MLP 91.IV.5.333, skull and mandible; MLP 95.IX.4.1 L mandibular fragment with p4-m2; MPEF-PV 1398a, fragment of skull with I, R P4-M3 and L P4-M1; MPEF-PV 1398b, R mandibular fragment with p4-m3, L p4 and incisors.; MPEF-PV 1398c, maxillary fragment with L M2-M3 and R M1-M2; MPEF-PV 1398d, maxillary fragment with L P4-M2; MPEF-PV 1398e, L M2-M3; AMNH 98823, L mandibular fragment with I, p4-m2. *Cardiomyx cavinus*—MLP 55.IV.28.11, skull; MLP 76.VI.12.18, L mandibular fragment with p4-m1. *Phugatherium novum*—Fcs 92-5-15/1, skull; Fcs 92-5-15/2, skull; Fcs 92-5-15/3, R mandibular fragment with I, p4-m2. *Dolichotis salincola*—MLP 672, skull and mandible; MLP 673, skull and mandible. *Dolichotis patagonum*—MLP 640, skull and mandible; MPEF-PV 41, skull and mandible; MPEF-PV 42, skull and mandible. *Cavia aperea*—MLP 1.XI.95.7, skull and mandible; MLP 12.II.92.4, skull and mandible; MMPMa 2239, skull and mandible; MMPMa 2318, skull and mandible; MMPMa 2319, skull and mandible; MMPMa 2320, skull and mandible; MMPMa 2322, skull and mandible; MMPMa 2324, skull and mandible; MMPMa 2367, skull and mandible; MMPMa 3233, skull and mandible; MMPMa 144, skull and mandible; MMPMa 4099, skull and mandible. *Galea musteloides*—MLP 738, skull and mandible; MLP 14.IX.98.4, skull and mandible;

MMPMa 2698, skull and mandible. *Microcavia australis*—MLP 518, skull and mandible; MLP 684(1), skull and mandible; MLP 684(2), skull and mandible; MLP 684(3), skull and mandible; MLP 684(5), skull and mandible; MLP 684(11), skull and mandible; MLP 684(12), skull and mandible; MLP 684(13), skull and mandible; MLP 684(14), skull and mandible; MLP 684(18), skull and mandible; MLP 13.IX.95.7, skull and mandible. *Kerodon rupestris*—MMPMa 1257, skull and mandible; MMPMa 1470, skull and mandible. *Hydrochoerus hydrochoeris*—MLP 1.XII.008, skull and mandible; MLP 5.V.99.1, skull and mandible; MLP 4.X.94.5, skull and mandible; MLP 8.X.97.3, skull.

List of specimens of outgroup.

Neoreomys australis—MPEF-PV 1651, skull; MPEF-PV 1636, L mandibular fragment with i, p4-m3; MPEF-PV 1348, R mandibular fragment with p4-m3; MPEF-PV 1346, R mandibular fragment with p4-m2; MPEF-PV 1727, L mandibular fragment with m1-m2; MPEF-PV 1726, R mandibular fragment with m1-m3; MPEF-PV 1725, R mandibular fragment with I and p4. *Dasyprocta azarae*—MLP 1420, skull and mandible; MLP 1421, skull and mandible; MLP 05.IX.97.02, skull and mandible. *Cuniculus paca*—MLP 24.IX.01.24, skull and mandible; MLP 1105, skull and mandible. *Proechimys poliopus*—MLP 22.II.00.7, skull and mandible; MLP 22.II.00.8, skull and mandible.

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