

# Capybaras, size, shape, and time: A model kit

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The capybaras (Hydrochoeridae) are outstanding rodents for their large size and euhyposodont and multilaminated cheek teeth. Although today they are represented by a single species, it was generally thought that their past diversity was much higher, especially during the late Miocene–early Pliocene. Such diversity is here analyzed taking into account the ontogenetic variation of the p4–m3 in different populations. Numerous isolated teeth of different size found in the upper levels of the Puerto Madryn Formation (late Miocene, Peninsula Valdés, Argentina) were interpreted as members of an ontogenetic series of a new species here described, *Cardiatherium patagonicum*. They provided clues to evaluate ontogenetic variation and a new framework to analyze the family diversity. In this context, it is proposed that multiple species described from the Ituzaingó Formation (late Miocene, Entre Ríos, Argentina) based on lower teeth, may actually represent specimens of different stages of the ontogenetic trajectory of a single species. Likewise, we found that several nominal taxa from other localities were based on juvenile specimens. According to these results, the diversity of the Hydrochoeridae during the late Miocene and early Pliocene was drastically reduced. The validity of the subfamily Cardiatheriinae is debated. Finally, it is suggested that the whole family should be revised taking into account the ontogenetic variation.

**Key words:** Rodentia, Hydrochoeridae, *Cardiatherium*, tooth development, allometry, Miocene, Puerto Madryn Formation, Argentina.

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## Introduction

The members of the family Hydrochoeridae, the capybaras, are semiaquatic rodents, outstanding for their large size and for their complex euhyposodont and multilaminated cheek teeth. The family is known since the late Miocene, and is represented today by a single species, *Hydrochoerus hydrochaeris*, which is the largest living rodent, inhabiting the area from Panama down to northeastern Argentina.

As in most extinct mammals, the systematics of hydrochoerids is based mainly on tooth morphology, especially the number and length of flexids. The great cheek teeth variability of these rodents, and their fragmentary fossil record led to the recognition of about 23 extinct genera and 56 species mostly based on slight morphological variations with typological criteria (Mones 1991). Many of these taxa were based on single specimens, and moreover, some of them exclusively on upper teeth, while others on lowers. Mones (1991), in his last review of the family, reduced the number of taxa to only 13 genera (grouped in four subfamilies) and 35 species, pointing out that some of these species still have a dubious status.

About half of these genera are assigned to the subfamily Cardiatheriinae, which includes taxa with primitive dental morphology for the family (basically fused prisms with relatively shallow flexids). Thus, it is presumed that this subfamily underwent a great diversification, especially during the Huayquerian Age (late Miocene; Mones 1991; Pascual et al. 1996). Mones (1991) recognized for this subfamily the genera *Anchimyris* (= *Eucardiodon*), *Cardiatherium* (= *Plexochoerus*), *Kiyutherium*, *Procardiatherium*, and *Phugatherium* (= *Neoanchimyris*) plus *Anchimyrisops*, which is based exclusively on upper teeth. *Phugatherium* was only found in Montehermosan (early Pliocene) sediments from the southern coast of the Buenos Aires Province. The other genera have wider geographic and stratigraphic distribution, but only in the “conglomerado osífero” of the Ituzaingó Formation (late Miocene; Entre Ríos Province; Cione et al. 2000) they are represented together (see Mones 1991). For each of these genera several species based mainly on size, and number and depth of the dental flexids, have been recognized (see Mones 1991). Although this subfamily is usually accepted by authors, Prado et al. (1998) stated that Cardiatheriinae appears as paraphyletic, and that taxa within this subfamily must be revised.

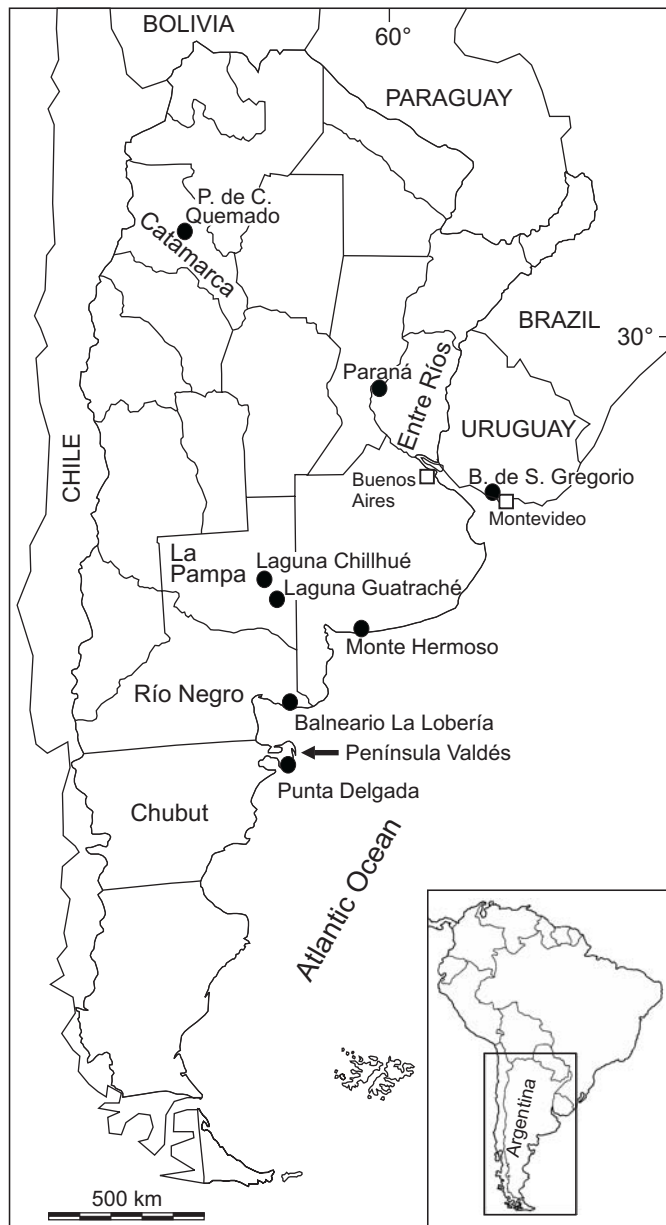


Fig. 1. Map showing the localities (black dots) and provinces yielding cardiatheriines. White squares—the capitals of Argentina and Uruguay.

It is known that the cheek teeth of the single living hydrochoerid are highly variable in occlusal morphology, especially p4, m3, and M3 (Kraglievich and Parodi 1921; Kraglievich 1941; Mones 1975, 1991; Pascual and Bondesio 1968; Reig et al. 1970). This diversity in tooth morphology represents both individual variability and ontogenetic changes (Mones 1991: figs. 7–10). Individual and ontogenetic morphological variation observed in the living species must be considered when studying the cheek teeth of fossil hydrochoerids. In fact, Reig et al. (1970) and Mones (1975) pointed out that many of these highly variable characters have been used to recognize and name extinct species based upon single specimens. Accordingly, Pascual and Bondesio (1961: 97) stated that differences between several cardiatheriine genera are not clear because

“[...] los caracteres convencionales usados para su distinción no resultan fácilmente aplicables [the characters traditionally used to distinguish them are not easily applicable]”.

At any rate, the fossil record had not yet yielded adequate collections to study variability in extinct species, since most of it consists of isolated fragmentary remains, some of them with dubious provenance. Actually, the single case in which such a study could be carried out is that of the specimens assigned to *Kiyutherium orientalis* from the Cerro Azul Formation (late Miocene, La Pampa Province; Montalvo and Casadío 1988; Rocha and Montalvo 1999).

In this paper we describe a new hydrochoerid species that represents the southernmost record of the family. It is part of a continental vertebrate association found in sediments of the upper part of the Puerto Madryn Formation (late Miocene), outcropping in Península Valdés, Chubut Province (Fig. 1; Dozo et al. 2002). This species offers a second chance to assess the dental variability within a population. In addition, this species allows an ontogenetic perspective, because it is based on relatively abundant material (more than 50 isolated teeth and a few bone fragments), ranging from a very small unborn specimen to cheek teeth 75% larger. The results lead us to a new approach to the analysis of the diversity of the family, through a better understanding of cheek tooth development.

*Institutional abbreviations* (all in Argentina).—CENPAT, Centro Nacional Patagónico, Puerto Madryn, Chubut; CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires; GHUNLPam, Cátedra de Geología Histórica, Universidad Nacional de La Pampa, Santa Rosa, La Pampa; MACN, Museo Argentino de Ciencias Naturales “B. Rivadavia”, Buenos Aires; MLP, Museo de La Plata, La Plata; MPEF, Museo Paleontológico “Egidio Feruglio”, Trelew, Chubut.

## Materials and methods

*Specimens examined*.—The new species *Cardiatherium patagonicum* was compared through quantitative analyses with Huayquerian cardiatheriines represented by lower dental series, because most of the specimens of the new species are lower teeth. Those taxa known exclusively through upper teeth were not taken into account, nor were those from the immediately older and younger South American Land Mammal Ages (Chasicosan and Montehermosan, respectively), clearly different in morphology. Materials are listed in Appendix 1.

*Nomenclature*.—Tooth nomenclature is given in Fig. 2. In order to conform to previous publications on the Hydrochoeridae, abbreviations are given in Spanish (see Frailey 1986). The tooth nomenclature follows Mones (1991), excepting that h.sn.i. is here considered as the flexid posterior to the h.2e. as originally defined (Francis and Mones 1965).

*Measurements*.—The measurements were taken with a stereomicroscope with micrometer eyepiece; see Fig. 3 for the method.

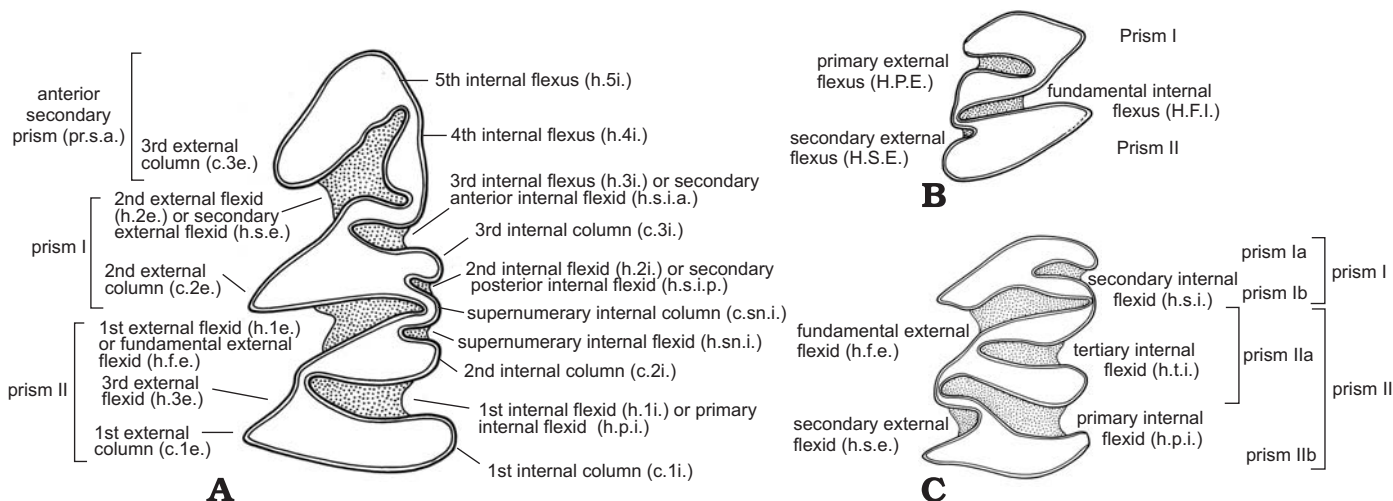


Fig. 2. *Cardiatherium patagonicum* sp. nov. Nomenclature of dental features (occlusal surfaces) in: p4 (A); P4 (B); m1–m2 (C).

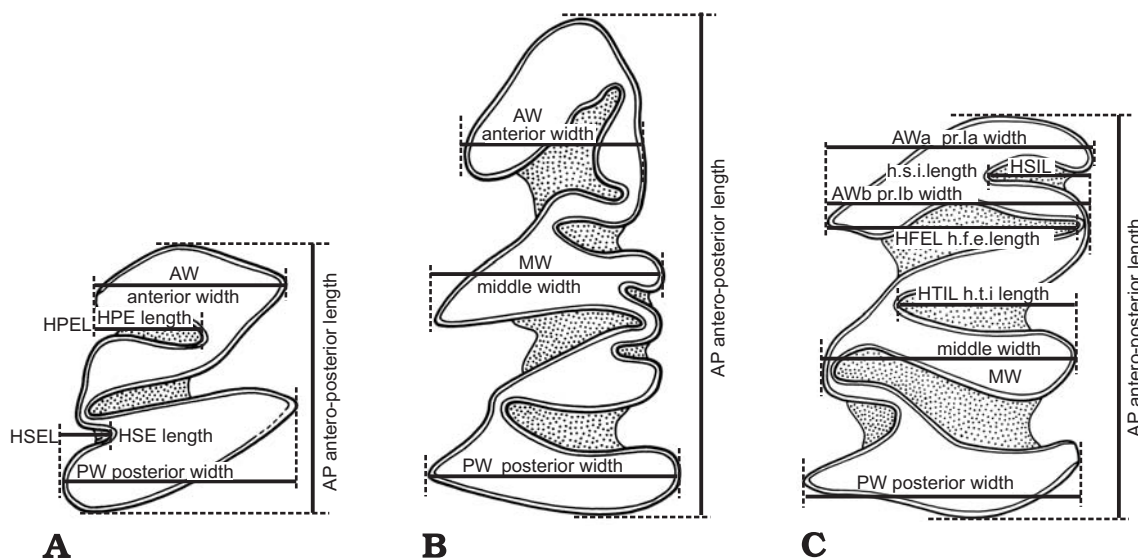


Fig. 3. *Cardiatherium patagonicum* sp. nov. Dental measurements of occlusal surfaces in: P4 (A); p4 (B); m1–m2 (C).

**Data analysis.**—Quantitative analysis was carried out for M1, M2 and m1, m2, because they are the best represented cheek teeth in the sample of the new species, and in addition, because they have lesser morphological variability than p4. Since isolated M1 and m1 cannot be differentiated from M2 and m2 respectively, they were considered as a whole M1–M2 and m1–m2, although slight differences in size and development cannot be discarded. Consequently, the materials used for comparisons were studied in the same way. For this analysis, measurements (AP, AW1, AW2, HFEL, HPEL, HSEL, HSIL, HTIL, MW, and PW, see Fig. 3) were log<sub>10</sub> transformed and examined through Principal Components Analysis (PCA) based on a correlation matrix (Bookstein et al. 1985; Legendre and Legendre 1998).

**Allometric analysis.**—Given the nature of the record (isolated teeth) no classical size estimates, like basicranial skull

length (basioccipital-basisphenoid; Radinsky 1985), are available. Consequently, in order to evaluate molars as size estimates, AP and MW (Fig. 3, see above) of m1–m2 were plotted against basicranial length in *Hydrochoerus hydrochaeris* (Appendix 1) in a simple regression analysis, Model II (Sokal and Rohlf 1994; Legendre and Legendre 1998). Results were significant ( $P < 0.005$ ) since both variables showed isometric growth respect to basicranial length [AP:  $y = -0.45x^{0.97}$ ;  $a = (-0.61, -0.31)$ ;  $b = (0.88, 1.06)$ . MW:  $y = -0.82x^{1.06}$ ;  $a = (-1.15, -0.54)$ ;  $b = (0.89, 1.26)$ ]. Since AP had higher correlation coefficient ( $r^2 = 0.92$ ) than MW ( $r^2 = 0.78$ ), it was selected as size estimate.

On the fossil samples, growth allometries of flexid depth (HSIL, HTIL and HPE, HSE) versus AP of m1–m2 and M1–M2, were studied through a simple regression analysis, Model II (Sokal and Rohlf 1984; Legendre and Legendre 1998).



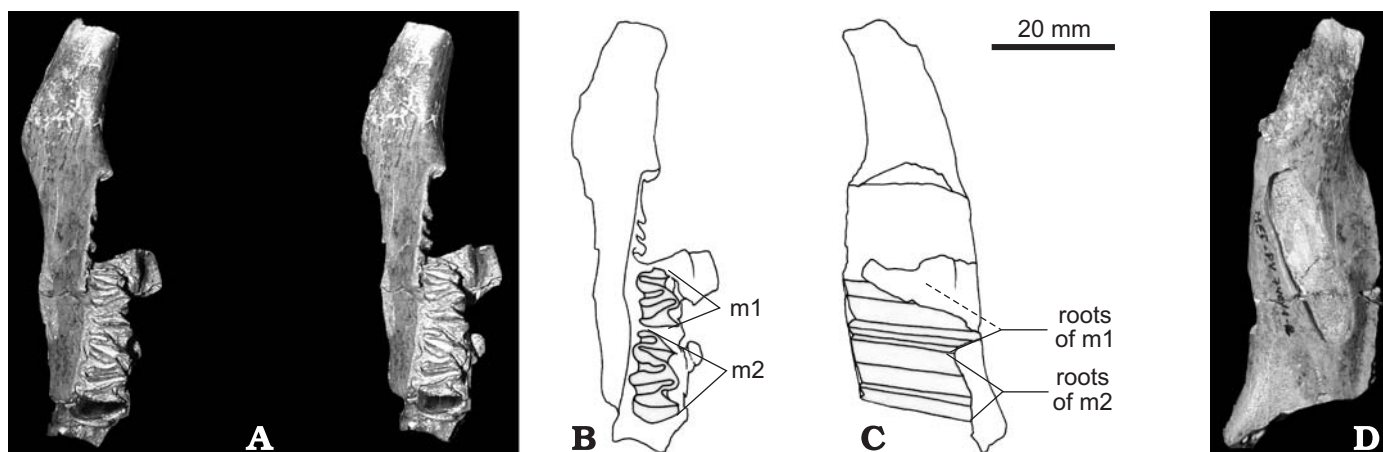


Fig. 4. *Carditherium patagonicum* sp. nov. Puerto Madryn Formation, Punta Delgada, Chubut. Holotype, right mandible with m1–m2, MPEF-PV 740/1. Stereopair in occlusal view (A); schematic drawing in occlusal view (B) showing m1–m2; schematic drawing in labial view (C) showing the roots of m1–m2; photograph in lingual view (D).

## Systematic paleontology

Order Rodentia Bowdich, 1821

Suborder Hystricognathi Tullberg, 1899

Family Hydrochoeridae Gill, 1872

Genus *Carditherium* Ameghino, 1883

*Synonyms*: *Procarditherium* Ameghino, 1885: 55–59; *Anchimys* Ameghino, 1886: 71–72; *Kiyutherium* Francis and Mones, 1965: 47.

*Carditherium patagonicum* sp. nov.

Figs. 4–6 and Table 1.

*Synonym*: *Kiyutherium* cf. *orientalis* Pascual and Bondesio, 1985; cf. *Kiyutherium*, Dozo et al. 2002.

*Holotype*: MPEF-PV 740/1, right mandibular fragment with m1–m2. Figs. 4 and 5A.

*Hypodigm*: The holotype and MPEF-PV 740/9 and 26, left p4s; MPEF-PV 740/10 and 41, anterior fragments of right p4; MPEF-PV 740/27, right p4; MPEF-PV 740/11, 12, and 34, anterior fragments of left p4; MPEF-PV 740/2, 3, 4, 5, 24, 25, 30, and 36, isolated right m1 or m2; MPEF-PV 740/29, 31, and 39, isolated left m1 or m2; MPEF-PV 740/6, small right mandibular fragment with m2; MPEF-PV 740/7, fragment of left m3; MPEF-PV 740/20 and 40, fragment of right m3; MPEF-PV 740/22, fragment of palate with left P4; MPEF-PV 740/28, isolated left P4; MPEF-PV 740/14, isolated right P4; MPEF-PV 740/8, damaged right M1 or M2; MPEF-PV 740/13, isolated right M1 or M2; MPEF-PV 740/15 and 16, left M1 or M2; MPEF-PV 740/17, small fragment of left palate with M1; MPEF-PV 740/19, fragment of lower incisor; MPEF-PV 740/23, isolated left M1 or M2; MPEF-PV 740/18, isolated right M3; MPEF-PV 740/33, fragment of right M3; MPEF-PV 740/32 and 38, fragments of left M3; MPEF-PV 740/35, isolated left M3; MPEF-PV 740/37, fragment of a juvenile palate with right M3; MPEF-PV 740/21, right mandibular fragment with p4–m1 probably of an unborn specimen, and MJG 22-IV-1976, anterior fragment of p4.

*Locality and age*: All the specimens labeled as MPEF-PV 740/ were found at the marine cliffs between Punta Delgada and Punta Lobo (about three kilometers west from Punta Delgada; 42°47' S, 63°40' W; Fig. 1), Estancia Rincón Chico, southeastern Peninsula Valdés, Chubut Province, Argentina; upper levels of the Puerto Madryn Formation (late

Miocene; Dozo et al. 2002); MJG 22-VI-1976 was found at Bahía Creek, Río Negro Province, Río Negro Formation “capa d” (Angulo and Casamiquela 1982), late Miocene (Marshall et al. 1983).

*Etymology*: *patagonicum* in reference to its Patagonian distribution.

*Diagnosis*.—The new species differs from “*Procarditherium*” *chasicense*, *Carditherium isseli*, and *C. talicei* in having a p4 with h.sn.i. It differs from *C. paranense* (and its synonyms, see below), “*Kiyutherium*” *orientalis*, and “*K.*” *rosendoi* in that the h.sn.i. overlaps the lingual end of h.1e. It differs from all the mentioned species in having (1) a very deep h.1e. reaching the lingual wall, forming a c.sn.i., which is lingually leveled with c.2i and c.3i.; (2) h.2e. bifurcate at the lingual end in adults, and with isthmus joining pr.I, and pr.s.a. globose; (3) m1–m2 with deeper h.s.i. and h.t.i. (up to 40% and 72% of the MW respectively) for equivalent sizes, and h.s.i. labiolingually oriented. It shares with *C. paranense* and “*K.*” *orientalis* the arched pr.I of m3, but differs in having a very deep h.t.i. also in young individuals. It differs from “*Kiyutherium*” *octolaminatum*, *Anchimysops villalobosi*, and ?*A. dubius* in having higher number of laminae in M3 (10 or 11 versus 6 or 8).

*Description*.—The sample consists almost exclusively of isolated cheek teeth of different sizes, interpreted as representatives of individuals of different ages within a single population. Cheek teeth are gracile, somewhat longer than wide, with elongate joined prisms, and with deep flexids. The mandible MPEF-PV 740/21 is considered an unborn specimen because its preserved teeth are only slightly worn (Kraglievich 1941), and the bone shows incomplete ossification. In addition it is the smallest specimen of the sample.

The p4: as in all hydrochoerids p4 has 3 prisms; Pr.II lingually bears a long h.1i. and a shorter h.sn.i. In some specimens (MPEF-PV 740/27, 9, and 34; Fig. 5B, E, and H), the h.1i. is very deep and forms a protrusion of the posterior margin of the h.1e. The h.sn.i. is longer than in other carditheriines, and its labial end exceeds the lingual end of h.1e. Pr.I has two lingual flexids, h.2i. and h.3i. As the h.sn.i., the h.2i.

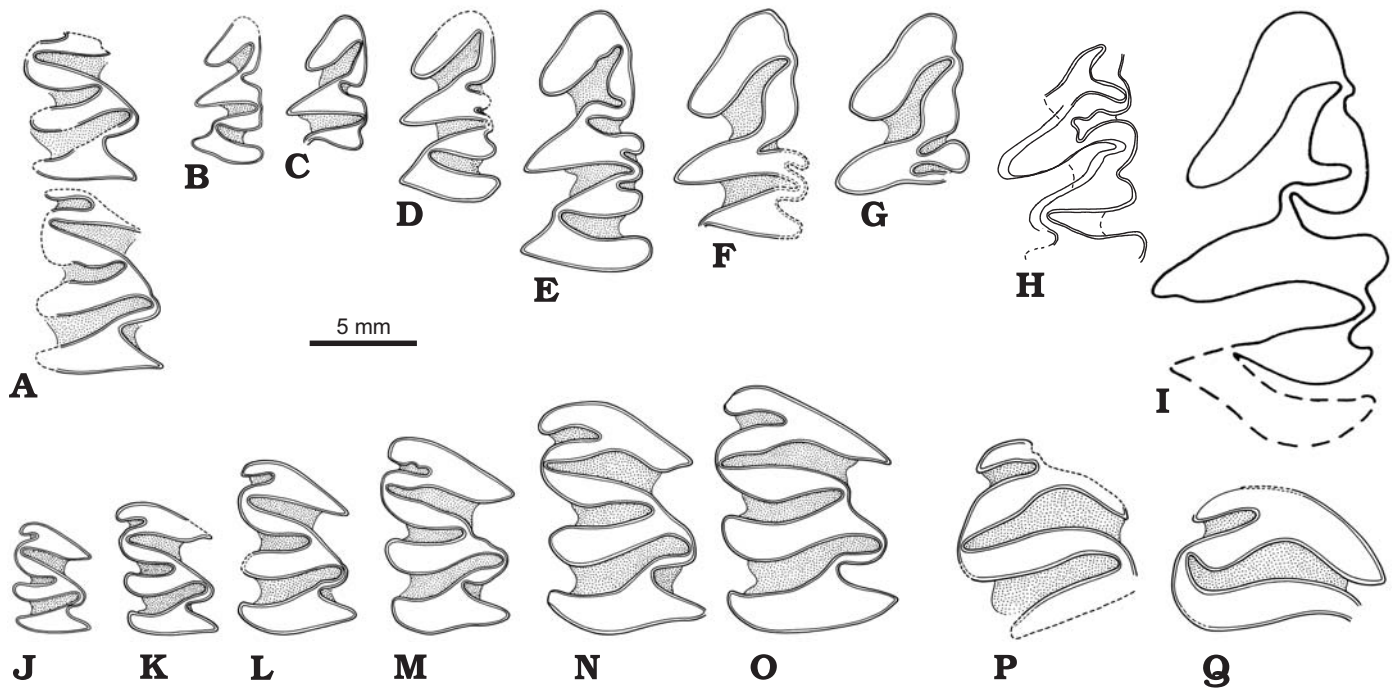


Fig. 5. *Cardiatherium patagonicum* sp. nov. occlusal surfaces of the lower cheek teeth: right m1–m2 (A, J–O), right p4 (B, C), left p4 (D–I), right m3 (P), left m3 (Q). A. MPEF 740/1 (holotype, m1–m2). B. MPEF 740/27 (inverted). C. MPEF 740/10 (inverted). D. MPEF 740/26. E. MPEF 740/9. F. MPEF 740/11. G. MPEF 740/12. H. MPEF 740/34. I. MJG 22-IV-1976. J. MPEF 740/25. K. MPEF 740/4. L. MPEF 740/3. M. MPEF 740/5. N. MPEF 740/24. O. MPEF 740/2. P. MPEF 740/20. Q. MPEF 740/7 (inverted). I, modified from Pascual and Bondesio (1985).

overlaps the lingual end of the h.1e. However, this middle lingual portion of p4 is very variable, and part of this variation depends on size. For example, in MPEF-PV 740/27 (Fig. 5B) both h.2i. and h.sn.i. are scarcely outlined in the occlusal surface, but on the basal surface they exceed slightly the bottom of h.1e. In MPEF-PV 740/10 (Fig. 5C) the h.sn.i. is scarcely developed and h.2i. is not yet outlined on the occlusal surface, but it can be seen on the basal surface. Instead, in MPEF-PV 740/26 (Fig. 5D), which is somewhat larger than the former two teeth, both flexids already exceed the bottom of the h.1e. in the occlusal surface. In most specimens the h.3i. is deeper than h.2i. and h.sn.i., but in MPEF-PV 740/12 (Fig. 5G) it is slightly shorter than the h.2i., which is very long in this specimen. Instead, in MPEF-PV 740/41 h.3i. is only slightly longer than h.2i. One of the largest specimens (MPEF-PV 740/34; Fig. 5H) has a single flexid in pr.II (h.3i.?), which is very deep and bifurcate at the end. The c.3 (limited by h.2i. and h.3i.) is variable in shape and size, depending on the development and orientation of h.2i. In large specimens (MPEF-PV 740/9, 11, 12, and 34; Fig. 5E–H) there are outlines of h.4i. and h.5i. The h.1e. penetrates up to the lingual border of the tooth, placing the c.sn.i. at the lingual margin of the tooth. The pr.s.a is separated from pr.1 by a deep h.2e. This is bifurcate at the labial end, with a deep anterior ramus anteriorly oriented, and a less developed posterior ramus, slightly backwardly oriented. Both rami are separated by a widened portion of the isthmus that joins internally pr.s.a and pr.I. In the three smallest specimens (MPEF-PV 740/10, 26, and 27; Fig. 5B–D) the h.2e. is not bifurcate and the isthmus is not widened. In the unborn

specimen the p4 lacks h.sn.i., h.2i. and h.3i., the h.1e. traverse the entire width of the tooth and the h.2e. is nearly labially closed.

The m1–m2: as in the other hydrochoerids, m1 is probably smaller than m2, as suggested by the holotype (Figs. 4, 5A, Table 1). The h.s.i. is narrow and encompasses from 24% up to 46% of the molar width with increasing AP. The h.t.i. extends more than half the occlusal surface, from 57% to 78% of the molar width with increasing AP. The h.f.e. and h.p.i. are deep and reach the opposite side of the tooth. The h.s.e. is wide, deep and reaches up to 30% the width of pr.lib. In the unborn specimen, m1 has the h.t.i. already formed although very short, h.s.i. is only hinted, while the h.s.e. is only barely developed.

The m3: the anterior wall is very curved and the h.t.i. very deep, reaching almost the external margin of the tooth (Fig. 5P–Q), as in the m3 of *Cardiatherium paranense* and *C. isseli*. The anterior wall of h.f.e. is S-shaped, with a middle sector wider than the rest, like that of *C. isseli*. The h.s.i. is deeper than in the m1–m2. and the h.t.i. reaches the labial border of the tooth. In MPEF-PV 740/40, the h.t.i. also reaches the labial portion of the tooth, although it is a small tooth in which the occlusal surface is still smaller than the base.

The i1: slightly wider than high, with its anterior face gently curved, the enamel extends slightly on each side.

The P4: two of the isolated upper cheek teeth (MPEF-PV 740/14 and 22; Fig. 6A and B) are considered P4 because the anterior side is more curved than in the other specimens, and





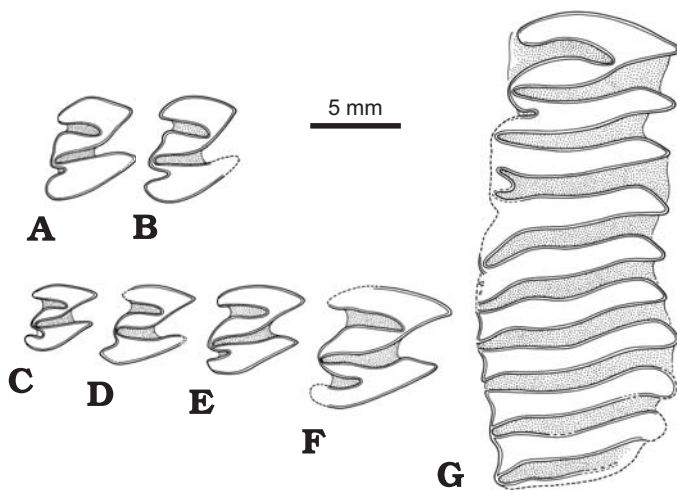


Fig. 6. *Carditherium patagonicum* sp. nov. occlusal surfaces of the upper cheek teeth: right P4 (A), left P4 (B), left M1–M2 (C, D, F), right M1–M2 (E), right M3 (G). A. MPEF 740/14. B. MPEF 740/22 (inverted). C. MPEF 740/16 (inverted). D. MPEF 740/15 (inverted). E. MPEF 740/13. F. MPEF 740/23 (inverted). G. MPEF 740/18.

the external side of the posterior lobe of Pr. I (between H.P.E. and H.S.E.) is long and anteroposteriorly oriented. Consequently, the longest anteroposterior diameter of this lobe lies on the labial side and not in the middle as in molars. Except for these characters, the structure is very similar to that of M1–M2, but with wider lobes, especially the anterior of Pr.I.

The M1–M2: assignment to tooth locus is difficult, but one specimen (MPEF-PV 740/17) included in a small left palate fragment, is considered M1 because it lies just behind the beginning of the zygomatic arch as in other cardiatheriines. The rest are considered M1–M2 (Fig. 6C–F). The H.P.E. penetrates into the Pr.I more than 50% of the width, while the H.S.E. is shorter, but deeper than in *Kiyutherium orientalis*, *K. scillatoyanei*, *K. rosendoi*, and *Carditherium paranense*. In one of the specimens (MPEF-PV 740/15; Fig. 6D) the H.S.E. is superficial. In the largest specimens, the enamel disappears in the postero external apices of the posterior lobe.

The M3: there are two complete M3; the largest (MPEF-PV 740/35) has 10 long laminae plus a shorter posterior one; the other (MPEF-PV 740/37) is a juvenile specimen with nine long laminae plus a shorter one with a posterior projec-

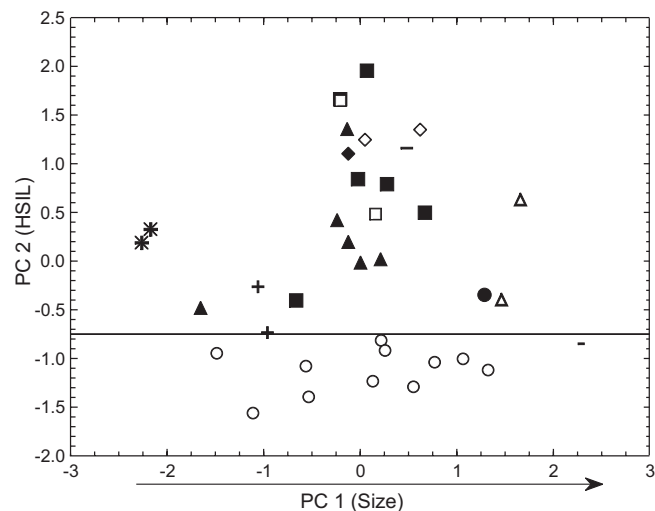
tion on the labial side. Another large but incomplete specimen (MPEF-PV 740/18; Fig. 6G) has 9 long laminae and the remains of another broken lamina also long. According to the structures of the M3 of all Hydrochoeridae, it may be assumed that this specimen had at least 10 complete laminae plus another shorter one. The Pr.I is split by a deep H.P.E., which encompasses approximately 70% the prism width. Pr.II, Pr.III, and Pr.IV have a conspicuous external flexid, while more posterior ones only have a smooth depression. In MPEF-PV 740/18 the internal flexid that separates Pr.III from IV (H.3I.) is bifurcated at the bottom, limiting a short lobe as wide as the laminae, and rising from the external wall. The lingual end of each prism is pointed and curved backward up to Pr.VIII, while from Pr.IX on, the ends are rounded and have no torsion. The lobes are joined by the external wall as in all cardiatheriines, but the enamel seems too thin in the external column of each prism.

Mandible: the only fragment of an adult, the holotype, is quite damaged. The diastema is elongate, slightly concave on the upper side, and rises anteriorly (diastema length >22.75 mm; height in front of p4 = 19.95 mm). The mental foramen is placed in front of p4 and at half height of the ramus. The angular region rises below the m2 and from this point it is oriented downward. The bottom of the i1 alveolus is placed internally to the anterior half of the m2. In the unborn specimen the upper margin of the diastema is gently concave in front of the p4 and slopes upward anteriorly (diastema length 8.90 mm, height in front of p4 = 7.3 mm); the symphysis is very smooth and the chin is almost undeveloped; the fossae for the masseters are very shallow.

## Quantitative analysis

**Multivariate analysis.**—The multivariate analysis of selected variables (see Data analysis) of m1–m2 and M1–M2 among Huayquerian cardiatheriines discriminated *Carditherium patagonicum* sp. nov. from the other Huayquerian species. In a PCA with m1–m2 (Fig. 7), PC1 explained 86% of the total variability, and reflected mainly size because variables had high positive loadings (Fig. 7; Lessa and Stein 1992); h.t.i. length, although with lesser loading, is also reflected. PC1 does not discriminate taxa clearly, but some groups can be recognized: from small species with very small h.t.i. to large species with long h.t.i. The middle-sized species, represented by the holotypes of *Carditherium petrosus*, *Kiyutherium orientalis* (and referred material from the Cerro Azul Formation), *K. scillatoyanei*, *K. rosendoi*, and other middle-sized specimens of the “conglomerado osífero” were not discriminated from each other. The series of *C. patagonicum* encompasses almost the whole size range of the other taxa. This suggests an alternative interpretation of the Huayquerian cardiatheriines, in which the mandibles assigned to different taxa could be individuals of different ontogenetic stages. Although using size to estimate age is considered problematic (Godfrey and Sutherland 1995 and

← Table 1. Dental measurements of *Carditherium patagonicum* and cardiatheriines from other localities (Cerro Azul Formation, La Pampa; Ituzaingó Formation, Entre Ríos; Puerta de Corral Quemado, Catamarca; Río Negro Formation, Río Negro; Kiyú Formation, Barrancas de San Gregorio, Uruguay). \* = type specimens (see Appendix 1). AP, antero-posterior length; AW, anterior width of upper molariforms; AWa, prism Ia width; AWb, prism Ib width; HFEL, h.f.e. (fundamental external flexid) length; HPEL, HPE (primary external flexus) length; HSEL, HSE (secondary external flexus) length; HSIL, h.s.i (secondary internal flexid) length; HTIL, h.t.i (tertiary internal flexid) length; MW, middle width; PW, posterior width.



	PC1	PC2	
AP	*0.980	0.119	* <i>Anchimys marshii</i> Type
AWA	*0.980	0.052	○ <i>Cardiatherium patagonicum</i>
HSIL	0.690	*-0.714	— <i>Cardiatherium petrosum</i> Type
AWB	*0.980	0.129	● <i>Cardiatherium doeringi</i> Type
HFEL	*0.975	0.087	▲ <i>Cardiatherium paranense</i> Type
MW	*0.988	0.038	▲ <i>Cardiatherium paranense</i>
HTIL	*0.804	-0.064	- cf. <i>Cardiatherium isseli</i>
PW	*0.962	0.133	□ <i>Kiyutherium orientalis</i> Type
eigenvalue	6.855	0.574	■ <i>Kiyutherium orientalis</i>
total variance	86%	7%	◆ <i>Kiyutherium rosendoi</i> Type
			◇ <i>Kiyutherium scillatoyanei</i> Type
			+ <i>Procardiatherium simplicidens</i> Type

Fig. 7. Scatter plot of scores and Factor loadings of PC1 and PC2 of m1–m2 dental measurements. AP, antero-posterior length; AWA, anterior lamina of lower molar prisms width; AWB, posterior lamina of lower molar prisms width; HFEL, fundamental external flexid length; HSIL, secondary internal flexid length; HTIL, tertiary internal flexid length; MW, middle width; PW, posterior width. Asterisk: loadings >0.7.

references therein), in this case it may be accepted as legitimate, because teeth of euhypsodont rodents grow throughout or at least through most of life. PC2 explains 7% of the total variation, and discriminated the new species from the rest of the late Miocene cardiatheriines in the greater relative depth of h.s.i. of m1–m2. *C. isseli* is placed in a position similar to *C. patagonicum*, but it differs from the latter in many morphological characters of the p4 (h.2e. short and opposed to h.2i., h.2i. and h.3i. long and similar in length, h.sn.i. absent) and of pr.I of m1–m3 (anteroposteriorly long with h.s.i. curved and anteriorly oriented).

PCA of M1–M2 included only *C. patagonicum* and *K. orientalis*, because this latter is the only Huayquerian species with lower and upper molars undoubtedly associated. The result was similar to that for m1–m2. PC1 explained 79% of the total variability and species were distributed according to their size (AP, AW, PW, HPEL had positive loading >0.9), without clear discrimination between them. PC2 explained 13% of the total variability, and variable HSIL with significant loading (>0.6) produced discrimination of *C. patagonicum* from *K. orientalis*.

**Regression analysis.**—Since the PCA showed that h.s.i. and h.t.i. are important characters to discriminate species, and the qualitative study of *Cardiatherium patagonicum* suggests that the depth of both flexids depends on specimen size, variation of these characters was quantitatively analyzed and compared with *Kiyutherium orientalis* from the Cerro Azul Formation. Regression analysis AP versus HSIL and HTIL (Fig. 8), showed that in *C. patagonicum* h.t.i. and h.s.i. increase length by positive allometry with respect to AP. In contrast, *K. orientalis* h.t.i. increases its length isometrically, but with a low correlation coefficient ( $r^2 = 0.73$ ); no significant relationship between the development of h.s.i. and tooth size could be found. This indicates no defined growing pattern, or alternatively, that the limited size range of the sample would impede the evaluation of the ontogenetic pattern. To assess whether the different growth patterns depend on different size range, the analysis was repeated in *C. patagonicum* including only the specimens within the available size range for *K. orientalis*. Results were as for the whole size range [AP versus HSIL:  $y = -1.25x^{1.61}$ ;  $a = (-1.81, -0.87)$ ;  $b = (1.23, 2.17)$ ;  $P < 0.005$ . AP versus HTIL:  $y = -0.69x^{1.34}$ ;

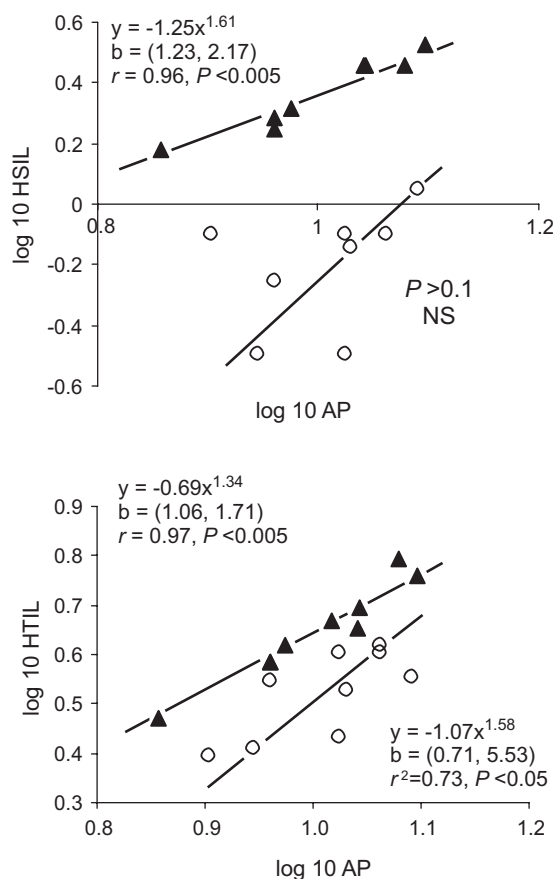


Fig. 8. Graphics of allometric equations ( $y = ax^b$ , Model II regression) between log 10 of antero-posterior length (AP) vs. log 10 of secondary internal flexid length (HSIL) and log 10 of tertiary internal flexid length (HTIL). *Cardiatherium patagonicum*, black triangle and *Kiyutherium orientalis*, open circle. Confidence intervals of b (slope) between brackets; r, correlation coefficient.



$a = (-1.07, -0.42)$ ;  $b = (1.06, 1.71)$ ;  $P < 0.005$ ], showing that each ontogenetic trajectory actually follows somewhat different patterns.

In the upper molars of *C. patagonicum*, HPEL and HSEL grow isometrically with respect to AP [HPEL:  $y = -0.11x^{0.76}$ ;  $a = (-1.14, 0.35)$ ;  $b = (0.18, 2.07)$ ;  $P < 0.005$ . HSEL:  $y = -0.89x^{1.38}$ ;  $a = (-2.02, -0.41)$ ;  $b = (0.77, 2.82)$ ;  $P < 0.05$ ]. In *K. orientalis* HPEL grows isometrically [ $y = -0.43x^{1.08}$ ;  $a = (-0.88, -0.14)$ ;  $b = (0.73, 1.63)$ ;  $P < 0.005$ ], but HSEL seems to be independent from AP [ $y = -4.45x^{5.38}$ ;  $P > 0.1$ ].

## Cheek tooth growth in hydrochoerids

Capybaras are born with all cheek teeth already erupted, even with occlusal wear, and teeth keep growing in all dimensions as long as skull and mandible grow, as in other euhypsodont mammals (Francis 1960; Kramarz 2002). How long dental growth in transverse and anteroposterior diameter lasts, or if it only slows down in adults, is still unknown. The descriptive and quantitative dental analyses of *Cardiatherium patagonicum* and *K. orientalis* reveal other general characteristics of cheek tooth development in hydrochoerids. A highly relevant feature provided by the numerous teeth of the new species is that the occlusal morphology keeps changing as long as teeth grow, implying that the base of the teeth enlarges and keeps folding through life (or at least most of it). The morphology of the occlusal surface becomes more complex with age, contrary to protohypsodont teeth which change toward a more simple pattern with wear. Another interesting feature revealed by our study is that some flexids appear after the tooth has already erupted; consequently, the number of flexids depends, at least in part, on the age of the specimen. In addition, we found that flexids grow in length at different rates: some with positive allometry, others isometrically, while the length of others is apparently independent of tooth size. When flexids grow with positive allometry they increase their relative depth with increasing tooth size. The design of the occlusal surface varies accordingly. When they are isometric, they maintain their relative depth, and the design of the occlusal surface does not change with size. When the development of a flexid is not related to tooth size, its expression is quite varied within a population.

Consequently, the definition of a taxon based upon number and depth of flexids of a single specimen is quite risky in hydrochoerids. However, this has been a common practice, partly because of the way in which tooth growth has been understood. When euhypsodont cheek teeth erupt, their apices are conspicuously smaller than bases, and so juveniles are easily identifiable. Somewhat later in ontogeny, this difference is not evident, and specimens at this state previously were assumed to have reached their final size and shape. This led to the use of several morphologies as typical of different

genera. Hence, the characteristics of growth pattern here reported provide a new framework to reevaluate hydrochoerid systematics.

## The case of the cardiatheriines from the “conglomerado osífero”

The most remarkable case of hydrochoerid diversity is that of the “conglomerado osífero”, because this unit is the richest in capybara taxa. Mones (1991) recognized eight genera for this unit, five genera and 12 species belong to the Cardiatheriinae, and two monospecific genera to the peculiar Anatochoerinae. These latter and four genera of the cardiatheriines are exclusively known through upper teeth. There is also a single upper tooth referred to the Protohydrochoerinae. According to Mones (1991), this great diversity could be due to the wide temporal span encompassed by the “conglomerado osífero”. Several authors (e.g., Kraglievich 1930; Scillato Yané 1981) proposed that the “conglomerado osífero” included faunas of Chasicosan, Huayquerian, and Montehermosan ages (late Miocene–early Pliocene). However, a recent revision of the vertebrates of this unit suggested that its age would be restricted to the Huayquerian (Cione et al. 2000).

Contrary to the classical view, the PCA (Fig. 7) suggested that the high hydrochoerid diversity of this unit could be based on specimens of different ontogenetic stages. The smallest species, *Anchimys leidyi* and *A. marshi* (Fig. 9A) are those with most simple occlusal figures: p4 lacks h.2i. and h.3i., and in m1–m2 the h.s.i. is scarcely developed and h.t.i. is absent or shorter than h.s.i. Bearing in mind that some flexids appear after the tooth has already erupted, we propose that the holotypes of these species belong to juvenile specimens (newborn?). Accordingly, the types of both species (the only material known from this unit) display characters observed in juvenile specimens of *Hydrochoerus hydrochaeris*: diastema very thin ahead of p4 and sloping anteriorly upwards, posterior margin of the symphysis placed anteriorly with respect to the p4, and fossae for insertion of masseter muscles relatively shallow (Fig. 9A<sub>1</sub>).

One isolated left m1 or m2 (MLP 61-VI-8-6; Fig. 9B), somewhat larger than those of *A. leidyi* and *A. marshi*, has the h.t.i. already developed, but remarkably smaller than the h.s.i. *Procardiatherium simplicidens* (Fig. 9C), whose m1–m2 are slightly larger still, already has the h.2i. and h.3i. on p4, while the h.s.i. and h.t.i. of m1–m2 are similar in length.

Those specimens larger than *P. simplicidens* [*Kiyutherium scillatoyanei* (Fig. 9D), neotype of *Cardiatherium paranense* (Fig. 9E), the holotypes of its synonyms and undescribed materials; see Appendix 1] have the h.t.i. longer than h.s.i., and the latter proportionally longer in the largest specimens. In fact, the h.s.i. varies greatly among middle to large-sized specimens, from very short, as in *K. scillatoyanei*

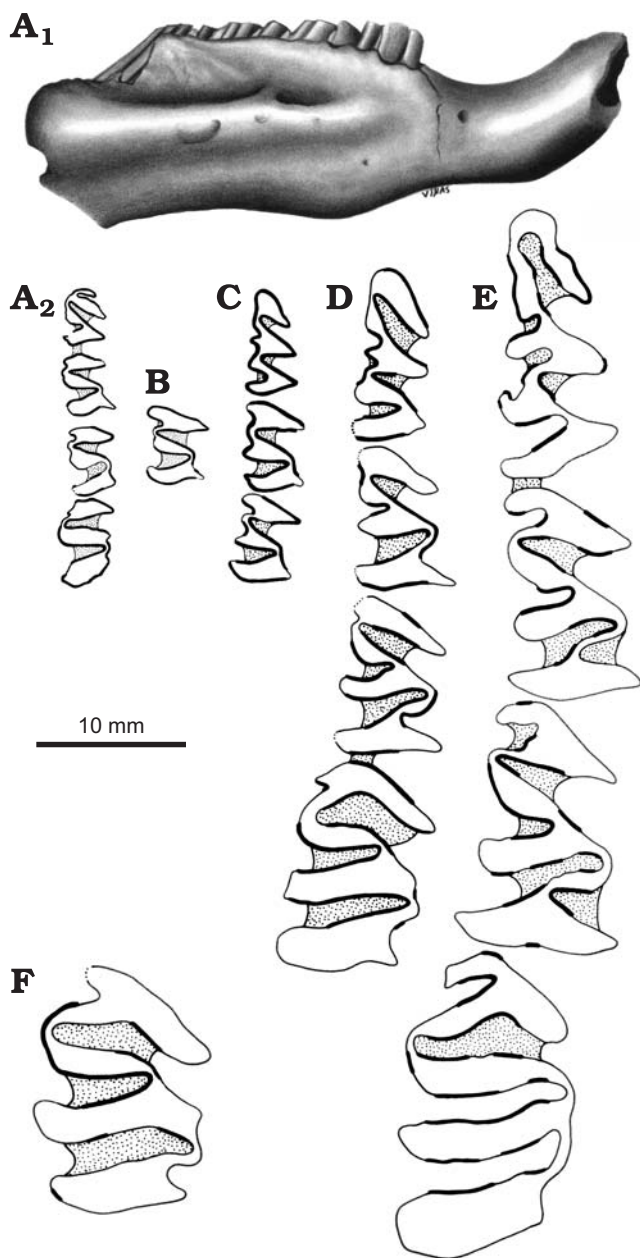


Fig. 9. Cardiatheriines from the Ituzaingó Formation. A. *Anchimys marshi*, MLP 73-I-10-7, holotype. A<sub>1</sub>. Right mandible in lateral view. A<sub>2</sub>. Right p4-m3 in occlusal view. B-F. Occlusal view of right lower cheek teeth. B. MLP 61-VI-8-6, m1 (inverted). C. *Procardiatherium simplicidens*, MLP 73-I-10-8, p4-m2 (inverted). D. *Kiyutherium scillatoyanei*, MLP 78-II-27-1, p4-m3. E. *Cardiatherium paranense*, MLP 40-XI-15-1, neotype, p4-m3. F. *Cardiatherium* sp. A, MLP 61-VI-8-2, m3.

and “*K. denticulatum*”, to very long as in the holotypes of *C. paranense* and “*C. doeringi*”.

A similar analysis may be done for m3, which is considered the tooth that changes the most in the phylogeny of the family (Pascual and Bondesio 1968: 244). In *Anchimys marshi* the h.s.i. is very short, while the h.t.i. is scarcely developed. In the remaining specimens (much larger than *A. marshi*) the ratio h.t.i./MW increases gradually with increas-

ing AP (MLP 61-VI-8-1: 52%, *Kiyutherium scillatoyanei*: 69%, *Cardiatherium* sp. A (Fig. 9F): 76%, neotype of *C. paranense*: 97%, and MLP 61-VI-8-5: 98%). Moreover, the h.t.i. of the two largest specimens is so long that it forms an extra column in the external side of the tooth.

**Regression analysis.**—The small specimens (*Anchimys leidyi*, *A. marshi*, *Procardiatherium simplicidens*, and MLP 61-VI-8-6) were excluded because if they actually represent very young individuals of the same species as the large ones, they could have a different allometric pattern from the adults (Godfrey and Sutherland 1995). The allometric study performed in m1-m2 (AP versus HSIL and HTIL; Fig. 10) of middle to large sized specimens, shows that the h.s.i. scales as in *Cardiatherium patagonicum*, with positive allometry with respect to the AP, although with a low correlation coefficient  $r^2 = 0.59$ . The h.t.i. instead, was isometric, as in *Kiyutherium orientalis*, with a high correlation coefficient  $r^2 = 0.89$ . To check the behavior of this species in the range size of *K. orientalis*, the analysis was repeated without the largest specimens. The results showed that for this range size, the h.s.i. does not rely significantly on AP, and that h.t.i. remains isometric. These results agreed with those of *K. orientalis*, suggesting that both species had similar growth patterns. Contrary to what happens in *C. patagonicum*, these results yielded a low correlation coefficient ( $r^2 = 0.70$  and  $P < 0.01$ ). The dispersion observed in the length of h.s.i. reflects in part differences between m1 and m2, and suggests that the growth of the flexid in this range size is not clearly related to AP.

**Discussion.**—We think that these specimens, which display a great morphological change associated with increasing size, may be interpreted as a relatively complete ontogenetic series of a single species, instead of as representing a high taxonomic diversity as classically considered. If this interpretation is correct, the name for this taxon should be *Cardiatherium paranense*, and the ontogenetic sequence would be formed as follows: (1) *A. leidyi* and *A. marshi* (newborns?), (2) MLP 61-VI-8-6, (3) *Procardiatherium simplicidens*, (4) MLP 61-VI-8-1, (5) *Kiyutherium scillatoyanei*, “*K. denticulatum*”, and *Cardiatherium* sp. A, and (6) *C. paranense* (and its synonyms), and *P. crassum*.

In this species the h.t.i. would appear later than h.s.i., it would grow constantly with size, more quickly and with positive allometry during the first stages. The growth of the h.s.i., in contrast, is less easily understood. On the one hand it has more pronounced differences between m1 and m2 than is the case with h.t.i. On the other hand its ontogenetic trajectory may be interpreted either as not related to tooth growth in intermediate size range, or as “choppy-filled with starts and stops” (Godfrey and Sutherland 1995). Hence, h.s.i. and h.t.i. in this species would have very different ontogenetic trajectories.

Consequently, some characters previously considered useful to separate taxa at the species level, have a different interpretation within this framework. For example, a short

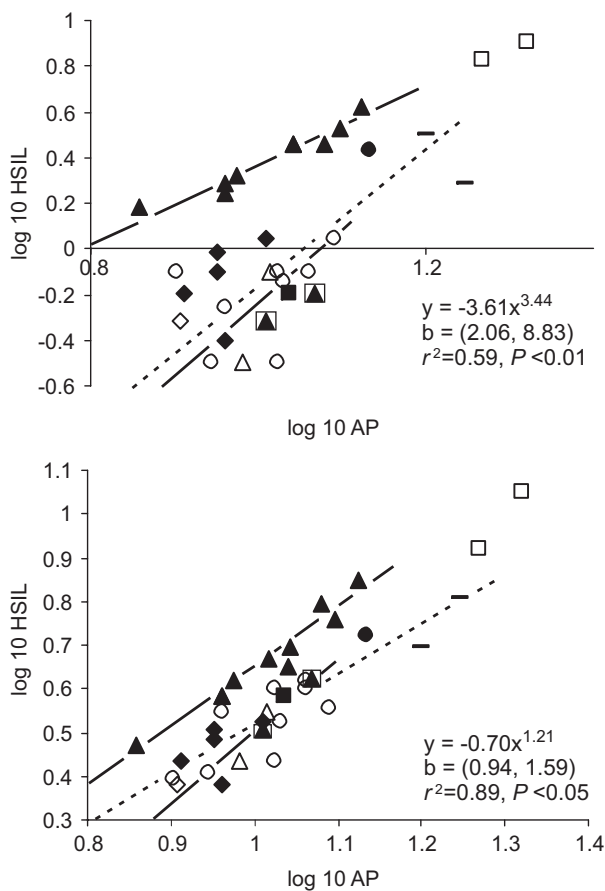


Fig. 10. Graphics of allometric equations ( $y = ax^b$ , Model II regression) between log 10 of antero-posterior length (AP) versus log 10 of secondary internal flexid length (HSIL) and log 10 of tertiary internal flexid length (HTIL). *Cardiatherium patagonicum*, black triangle, *Kiyutherium orientalis*, open circle, and cardiatheriines from the “conglomerado osífero” (dotted line and parameters): *C. paranense*, black diamond; *C. paranense* Type, dash; *C. petrosum* Type, black square; *C. doeringi* Type, black circle; *K. scillatoyanei* Type, black triangle in open square. The types of *K. rosendoi* (open diamond) and *K. orientalis* (open triangle) and cf. *C. isseli* (open square) were drawn to show their position, but they were not considered in the regression analysis. Confidence intervals of  $b$  (slope) between brackets;  $r$ , correlation coefficient.

h.s.i. in *K. scillatoyanei* (Bondesio 1985a) would have no systematic value because the relationship h.s.i./AP is complex in this species, and the relatively short h.t.i. of the m3 of *Cardiatherium* sp. A would mean that it is a younger (= smaller) specimen than the neotype of *C. paranense*.

## The cases of other late Miocene and early Pliocene cardiatheriines

The holotypes of species from other localities than Punta Delgada and “conglomerado osífero” can also be analyzed taking into account this proposal of ontogenetic growing pattern of molars. The holotype of *Kiyutherium orientalis*, type

species of the genus found in Uruguay (see Fig. 1 and Appendix 1), is a middle-sized specimen (similar to *Kiyutherium scillatoyanei*) with relatively short flexids, and thus it could be a young individual. There are no significant morphological differences between this specimen and the series of the “conglomerado osífero” as to think it represents a different species.

The holotype of *Kiyutherium rosendoi* (Bondesio 1985b; Puerta de Corral Quemado, Fig. 1) is also within this range size, and morphologically very similar to *Cardiatherium paranense*, but its m2 has special characters (two flexids in pr.I, this paper) that make its assignment to any of the other species difficult.

Nevertheless, in both cases it would be hasty to establish identity with *C. paranense* on the basis of single specimens. More specimens from the same localities have to be found in order to evaluate individual variation and analyze ontogenetic trajectories.

The holotypes of the Montehermosan (early Pliocene from Monte Hermoso; Fig. 1) species *Phugatherium cataclisticum* and *Anchimylops villalobosi* represent juvenile specimens. This assertion is based on molar characters, and mandibular morphology of the former (holotype of “*Neoanchimys pisanoi*”, see Mones 1991), which resembles that of *Anchimys marshi* and *A. leidy* (i.e., diastema in front of p4 slender, and posterior margin of the symphysis ahead p4). The only other hydrochoerid known from these levels is the Protohydrochoerinae *Chapalmaterium perturbidum* (see Prado et al. 1998); therefore, the two former species may be juveniles of the latter. If this were so, the correct name for the single Montehermosan species would be *Phugatherium cataclisticum*.

## Conclusions

The new species here described, *Cardiatherium patagonicum* sp. nov., represents the southernmost hydrochoerid, and is more derived than the remaining Huayquerian hydrochoerids classically referred to the subfamily Cardiatheriinae because it has longer flexids at similar molar sizes, and the onset of the development of h.t.i and h.s.i is predisplaced in relation to *C. paranensis* (the h.t.i. is already developed in the unborn in *C. patagonicum*, but not in the newborns of *C. paranense*).

The material of *C. patagonicum* allowed the first description of the ontogenetic trajectory of some dental traits in an extinct hydrochoerid. These new data about molar development result in new criteria for the study of the hydrochoerid diversity.

Based on these ontogenetic criteria, all the species of the “conglomerado osífero” represented by lower dental series could be considered as different ontogenetic stages of *Cardiatherium paranense*. Hence, all the cardiatheriines of this level might represent a single species, but the status of the peculiar Anatochoerinae (*Anatochoerus* and *Contra-*



*cavia*) must be reanalyzed. If these genera proved to be good taxa, some of the mandibles here analyzed could belong to them. This would yield an alternative explanation for the peculiar growth pattern of the h.s.i.

In any case, we consider that the hydrochoerid diversity for the “conglomerado osífero” was much lower than so far supposed. From a chronological standpoint, less diversity among capybaras is in agreement with a restricted age for the “conglomerado osífero” (Cione et al. 2000).

The genus *Kiyutherium* Francis and Mones, 1965 is considered a junior synonym of *Cardiatherium* Ameghino, 1883, and the status of *K. orientalis* and *K. rosendoi* has to be revised within the parameters of ontogenetic development described in this paper. *Phugatherium cataclisticum* and *Anchimylops villalobosi* are based on juvenile individuals, probably of *Chapalmatherium perturbidum* (senior synonym of *P. cataclisticum*).

In this context the subfamily Cardiatheriinae has no phylogenetic meaning, and should be abandoned. In doing so the subfamilial arrangement of hydrochoerids weakens, and should be cautiously considered until the systematics of the whole family is reanalyzed. Therefore, in this paper we do not propose a subfamily rank placement for the genus *Cardiatherium*.

It is acknowledged that the differentiation of hydrochoerids was associated with increasing size accompanied by enlargement and morphological complexity of cheek teeth. For example, in m1–m3 this complication is obtained through the enormous enlargement of h.p.i., which labially defines an h.s.e., and the development of h.t.i., which is a novelty within the superfamily. This phenomenon was probably subordinate to several heterochronic processes, for example, a predisplacement at the onset of some flexid development, and an increase in growth rates of some flexids.

We postulate that the beginning of familial differentiation was a relatively rapid process, which would explain the absence of potential close ancestors in middle Miocene strata of Patagonia (Vucetich 1984; Vucetich et al. 1993) and Colombia (Walton 1997). On the contrary, from the upper Miocene on, together with the first undoubted hydrochoerids, there were recorded other middle sized cavioids, with several laminae in the M3, p4 with three lobes, a lengthening of flexids, and a wide palate, that are usually referred to the subfamily Cardiomyinae of the family Caviidae (e.g., *Caviodon*, Kraglievich 1941). However, some of these cavioids have been alternatively referred to the Cardiatheriinae (i.e., *Xenocardia*, Pascual and Bondesio 1963 versus Mones 1991). Cardiomyines may actually be the sister group of the hydrochoerids. Recently, some authors debated classical cavioid classification. Among them, Walton et al. (1997) stated that the hydrochoerids should be classified with the Caviidae, Rowe and Honeycutt (2002) suggested the close relationships among *Hydrochoerus* and *Kerodon*, while Vieytes (2003) proposed that the Caviinae are more closely related to the hydrochoerids than to the Dolichotinae (Caviidae). Our proposal that hydrochoerids

and cardiomyines are more closely related to each other than to other cavioids would join this debate.

These hypotheses require testing through the detailed study of the superfamily as a whole (but especially cardiomyines and hydrochoerids), taking into account the ontogenetic trajectory of cheek tooth traits.

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## References

- Ameghino, F. 1883. Sobre una nueva colección de mamíferos fósiles recogidos por el Profesor Pedro Scalabrini en las barrancas del Paraná. *Boletín de la Academia Nacional de Ciencias en Córdoba* 5: 257–306.
- Ameghino, F. 1885. Nuevos restos de mamíferos fósiles oligocenos recogidos por el Profesor Pedro Scalabrini y pertenecientes al Museo Provincial de la ciudad de Paraná. *Boletín de la Academia Nacional de Ciencias en Córdoba* 8: 5–207.
- Ameghino, F. 1886. Contribución al conocimiento de los mamíferos fósiles de los terrenos terciarios antiguos del Paraná. *Boletín de la Academia Nacional de Ciencias en Córdoba* 9: 5–228.
- Angulo, R.J. and Casamiquela, R.M. 1982. Estudio estratigráfico de las unidades aflorantes en los acantilados de la costa norte del Golfo San Matías (Río Negro y extremo austral de Buenos Aires) entre los meridianos 62°30' y 64°30' W. *Mundo Ameghino* 2: 20–73.
- Bookstein, F.L., Chernoff, B., Elder, R.L., Humphries, J.M., Smith, G.R., and Strauss, R.E. 1985. Morphometric in evolutionary biology. *Special Publication Academy of Natural Sciences Philadelphia* 15: 1–277.
- Bondesio, P. 1985a. *Kiyutherium scillatoyanei* n. sp. (Rodentia, Hydrochoeridae, Cardiatheriinae) de la Formación Ituzaingó de la Provincia de Entre Ríos (República Argentina). *Ameghiniana* 21 (2–4): 275–279.
- Bondesio, P. 1985b. Un nuevo roedor Cardiatheriinae (Hydrochoeridae) del departamento de Belén, Provincia de Catamarca. Inferencias paleoambientales. Probable edad de los sedimentos portadores. *Ameghiniana* 21 (2–4): 280–284.
- Bowdich, T.E. 1821. *An Analysis of the Natural Classification of Mammalia, for the Use of Students and Travellers*. 115 pp. J. Smith, Paris.
- Cione, A.L., Azpelicueta, M.M., Bond, M., Carlini, A.A., Casciotta, J., Cozzuol, M., de la Fuente, M., Gasparini, Z., Goin, F., Noriega, J., Scillato-Yané, G., Soibelzon, L., Tonni, E.P., Verzi, D.H., and Vucetich, M.G. 2000. Miocene vertebrates from Entre Ríos, eastern Argentina. In: F. Azeñolaza and R. Herbst (eds.), *El Mio-Plioceno Argentino. INSUGEO Serie de Correlación Geológica* 14 (1–2): 191–237.
- Dozo, M.T., Monti, A., Bouza, P., Vucetich, M.G., Cione A.L., Tonni, E.P., and Scillato-Yané, G.J. 2002. Geología y Vertebrados Continentales en cercanías de Punta Delgada (Neógeno de Península Valdés, Chubut, Argentina). In: N. Cabaleri, C.A. Cingolani, E. Linares, M.G. López de

- Luchi, H.A. Oстера, and H.O. Panarello (eds.), *XV Congreso Geológico Argentino* CD-ROM, N° 118 and *Actas* 1: 536–541.
- Frailey, C.D. 1986. Late Miocene and Holocene mammals, exclusive of the Notoungulata, of the río Acre region, Western Amazonia. *Contribution in Sciences, Natural History Museum of Los Angeles County* 374: 1–46.
- Francis, J.C. 1960. Análisis de algunos factores de confusión en la sistemática genérica de los Mesotheriinae (Notoungulata, Typotheria). *Ameghiniana* 2 (2): 29–36.
- Francis, J.C. and Mones, A. 1965. Sobre el hallazgo de *Kiyutherium orientalis* n. g., n. sp. (Rodentia Hydrochoeridae) en la Formación Kiyú, de Barrancas de San Gregorio, Departamento de San José, República Oriental del Uruguay. *Kragleviana* 1 (2): 45–54.
- Gill, T. 1872. Arrangement of the families of mammals with analytical tables. *Smithsonian Miscellaneous Collections* 11 (1): vi + 1–98.
- Godfrey, L.R. and Sutherland, M.R. 1995. Flawed inferences: Why size-based tests of heterochronic processes do not work. *Journal of Theoretical Biology* 172: 43–61.
- International Commission on Zoological Nomenclature 1999. *International Code of Zoological Nomenclature* (4th edition). 306 pp. International Trust for Zoological Nomenclature, London.
- Kraglievich, L. 1930. La Formación Friaseana del río Frias, río Fenix, laguna Blanca, etc., y su fauna de mamíferos. *Physis* 10 (35): 127–161.
- Kraglievich, L. 1941. Morfología normal y morfogénesis de los molares de los carpinchos y caracteres filogenéticos de este grupo de roedores. (La primera parte en colaboración con el Sr. Lorenzo J. Parodi). In: A.J. Torcelli and C.A. Morelli (eds.), *Obras de Geología y Paleontología 3* (Obras póstumas e inéditas), 438–484. Ministerio de Obras Públicas de la Provincia de Buenos Aires.
- Kraglievich, L. and Parodi, L.J. 1921. Morfología normal y variaciones de los molares del carpincho (*Hydrochoerus hydrochoeris*). *Physis* 9 (34): 454–455.
- Kramarz, A.G. 2002. Roedores chinchilloideos (Hystricognathi) de la Formación Pinturas, Mioceno temprano-medio de la provincia de Santa Cruz, Argentina. *Revista del Museo Argentino de Ciencias Naturales*, n.s. 4: 167–180.
- Legendre, P. and Legendre, L. 1998. *Numerical Ecology*, 2<sup>nd</sup> edition. 853 pp. Elsevier, Amsterdam.
- Lessa E.P. and Stein, B.R. 1992. Morphological constraints in the digging apparatus of pocket gophers (Mammals: Geomyidae). *Biological Journal of the Linnean Society*, London 47: 439–453.
- Marshall, L.G., Hoffstetter, R., and Pascual, R. 1983. Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. *Palaeovertebrata*, Mémoire extraordinaire: 1–93.
- Mones, A. 1975. Estudios sobre la Familia Hydrochoeridae (Rodentia), V. Revalidación de sus caracteres morfológicos dentarios con algunas consideraciones sobre la filogenia del grupo. *I Congreso Argentino de Paleontología y Bioestratigrafía* 2: 463–476.
- Mones, A. 1991. Monografía de la Familia Hydrochoeridae (Mammalia, Rodentia). Sistemática–Paleontología–Bibliografía. *Courier Forschungsinstitut Senckenberg* 134: 1–235.
- Montalvo, C. and Casadío, S. 1988. Algunas consideraciones sobre los géneros *Procardiatherium* y *Kiyutherium* (Rodentia, Hydrochoeridae, Cardiatheriinae). *V Jornadas Argentinas de Paleontología de Vertebrados*, Resúmenes: 50.
- Pascual, R. and Bondesio, P. 1961. Un nuevo Cardiatheriinae (Rodentia, Hydrochoeridae) de la Formación Monte Hermoso (Plioceno superior) de la Provincia de Buenos Aires. Algunas consideraciones sobre la evolución morfológica de los molariformes de los Cardiatheriinae. *Ameghiniana* 2 (6): 93–111.
- Pascual, R. and Bondesio, P. 1963. Un nuevo tipo de morfología dentaria en un Cardiatheriinae (Rodentia, Hydrochoeridae) del Plioceno inferior de Hauchipampa (San Juan). *Ameghiniana* 3 (2): 43–49.
- Pascual, R. and Bondesio, P. 1968. Los Cardiatheriinae (Rodentia, Caviomorpha) de la Formación Arroyo Chasicó (Plioceno inferior) de la provincia de Buenos Aires. *Ameghiniana* 5 (7): 237–251.
- Pascual, R. and Bondesio, P. 1985. Mamíferos terrestres del Mioceno medio-tardío de las cuencas de los ríos Colorado y Negro (Argentina): Evolución ambiental. *Ameghiniana* 22 (1–2): 133–145.
- Pascual, R., Ortiz Jaureguizar, E., and Prado, J.L. 1996. Land mammals: Paradigm for Cenozoic South American geobiotic evolution. In: G. Arratia (ed.), *Contributions of Southern South America to Vertebrate Paleontology. Münchner Geowissenschaftliche Abhandlungen* 30: 265–319.
- Prado, J.L., Cerdeño, E., and Roig-Juñent, S. 1998. The giant rodent *Chapalmatherium* from the Pliocene of Argentina: new remains and taxonomic remarks on the Family Hydrochoeridae. *Journal of Vertebrate Paleontology* 18: 788–798.
- Radinsky, L.B. 1985. Approaches in evolutionary morphology: a search for patterns. *Annual Review of Ecology and Systematics* 16: 1–14.
- Reig, O.A., Soriano, P., and Ojasti, J. 1970. Variabilidad del último molar superior en una población de chigüires (*Hydrochaeris hydrochaeris*) de los llanos de Apure. *Acta Científica Venezolana* 21 (1): 33.
- Rocha, A.M. and Montalvo, C.I. 1999. Variabilidad morfológica de los molariformes inferiores de *Kiyutherium* (Rodentia, Hydrochoeridae, Cardiatheriinae). *VII Jornadas Pampeanas de Ciencias Naturales*, 279–287.
- Rowe, D.L. and Honeycutt, R.L. 2002. Phylogenetic relationships, ecological correlates, and molecular evolution within the Caviodea (Mammalia, Rodentia). *Molecular Biology and Evolution* 19 (3): 263–277.
- Scillato Yané, G.J. 1981. Nuevo Mylodontinae (Edentata, Tardigrada) del “Mesopotamiense” (Mioceno tardío) de la Provincia de Entre Ríos. *Ameghiniana* 18 (1–2): 29–34.
- Sokal, R.R. and Rohlf, F.J. 1994. *Biometry*, 3<sup>rd</sup> edition. 880 pp. Freeman, New York.
- Tullberg, T. 1899. Ueber das System der Nagethiere, eine phylogenetische Studie. *Nova Acta Regiae Societatis Scientiarum Upsalensis* (3) 18 (2, Sectio Medica et Historiae Naturalis): 1–514.
- Vieytes, E.C. 2003. *Microestructura del esmalte de roedores Hystricognathi sudamericanos fósiles y vivientes. Significado morfofuncional y filogenético*. 295 pp. Unpublished Doctoral thesis, Universidad Nacional de La Plata.
- Vucetich, M.G. 1984. Los roedores de la Edad Friasense (Mioceno medio) de Patagonia. *Revista del Museo de La Plata (Nueva Serie)* 8 *Paleontología* 50: 47–126.
- Vucetich, M.G., Mazzoni, M.M., and Pardiñas, U.F.J. 1993. Los roedores de la Formación Collón Cura (Mioceno medio) y la Ignimbrita Pilcaniyeu. *Ameghiniana* 30 (4): 361–381.
- Walton, A.H. 1997. Rodents. In: R.F. Kay, R.H. Madden, R.L. Cifelli, and J.J. Flynn (eds.), *Vertebrate Paleontology in the Neotropics. The Miocene Fauna of La Venta, Colombia*, 392–409. Smithsonian Institution Press, Washington.
- Walton, A.H., Nedbal, M.A., and Honeycutt, R.L. 1997. Molecular evidence for the monophyly of the New World Hystricognath rodents (Caviomorpha) and interrelationships of caviomorph families. *Seventh International Therological Congress, Abstracts of Oral and Poster Papers*, 381.

## Appendix 1

Taxa and specimens examined. Fossil material is listed with geographic and stratigraphic provenance.

*Hydrochoerus hydrochaeris*: MLP 211, MLP 17.V.02.10, MLP 17.V.02.12, MLP 1.XII.00.8, MLP 10-VI.98.2, MLP 18.VIII.92.16, MLP 4.X.94.5, MLP 14.IX.55.1, MLP 17.V.02.11, MACN-Ma 47.220, MACN-Ma 49.302, MACN-Ma 50.310, MACN-Ma 50.309, MACN-Ma 33.119, MACN-Ma 14040, MACN-Ma 52.66, MACN-Ma 16329, MACN-Ma 38.248, MACN-Ma 16324, MACN-Ma 28.13, MACN-Ma 243, MACN-Ma 39.954, MACN-Ma 20956.

### Fossil material

1. Ituzaingó Formation (“Conglomerado osífero”), “Mesopotamiense”, Entre Ríos Province, Argentina: *Cardiatherium paranense*, MLP 40-XI-15-1 (neotype), right mandibular fragment with p4–m3; MLP 61-VI-8-1, right mandibular fragment with p4–m3; MLP 61-VI-8-3, left m3; MLP 61-VI-8-5, fragmented right m3; MLP 61-VI-8-6, left m1; MLP 69-XII-2-16 (holotype of *Cardiatherium petrosus*), left mandibular fragment with i1, p4–m1; MLP 73-I-10-11 (holotype of *Cardiatherium doeringi*), left mandibular fragment with p4–m2; MLP 87-XI-1-15, right mandibular fragment with p4–m1; MLP 87-XI-1-150, right mandibular fragment with p4–m2; *Cardiatherium* sp. A, MLP 61-VI-8-2, right m3; *Anchimyus leidyi*, MLP 73-I-10-6 (syntype, referred to in the MLP collection as cotype, the term not recommended by the International Code of Zoological Nomenclature 1999, Recommendation 73E), right mandibular fragment with i1, p4–m2; *Anchimyus marshi*, MLP 73-I-10-7 (holotype), right mandibular fragment with p4–m3; *Procardiatherium simplicidens*, MLP 73-I-10-8

(holotype and only specimen), left mandibular fragment with p4–m2; *Kiyutherium scillatoyanei*, MLP 78-II-27-1 (holotype and only specimen), right mandibular fragment with p4–m3; *Kiyutherium denticulatum*, isolated right m1 or m2 (since the type and single specimen is lost, only the cast of the type, numbered MLP-M-27 is available, consequently it was not included in numerical analyses).

2. Kiyú Formation, Barrancas de San Gregorio, Uruguay: *Kiyutherium orientalis*, cast of the holotype SPV-FHC 27-XI-64-20, right p4–m3.

3. Puerta de Corral Quemado, Catamarca Province, Argentina, “Araucanian” (late Miocene). *Kiyutherium rosendoi*, MLP 29-X-8-26 (holotype and single specimen), left mandibular fragment with p4, m1 and part of m2.

4. Río Negro Formation, Río Negro Province: *Cardiatherium isseli*, MLP 97-VIII-1-1 (cast of MJG 12-II-1977), right mandibular fragment with i1, p4–m3.

5. Cerro Azul Formation, Huayquerian Age (late Miocene), La Pampa Province, Argentina: *Kiyutherium orientalis*. Laguna Chillhué: GHUNLPam 138, right mandibular fragment with p4–m1 and damaged m2; GHUNLPam14661 right mandibular fragment with p4–m3; GHUNLPam 19030, fragment of left p4. Laguna Guatraché: GHUNLPam 2013, right mandibular fragment with m1–m2 and left mandibular fragment with p4–m1; GHUNLPam 9157, both mandibles with i1–m3; GHUNLPam 9158, right mandibular fragment with p4–m3; GHUNLPam 19141, left mandibular fragment with p4–m2; GHUNLPam 19142, isolated left m3.