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## Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujvp20>

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Available online: 08 Nov 2011

To cite this article: María G. Vucetich & María E. Pérez (2011): The putative cardiomyines (Rodentia, Caviioidea) of the middle Miocene of Patagonia (Argentina) and the differentiation of the Family Hydrochoeridae, *Journal of Vertebrate Paleontology*, 31:6, 1382-1386

To link to this article: <http://dx.doi.org/10.1080/02724634.2011.618194>

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## THE PUTATIVE CARDIOMYINES (RODENTIA, CAVIOIDEA) OF THE MIDDLE MIOCENE OF PATAGONIA (ARGENTINA) AND THE DIFFERENTIATION OF THE FAMILY HYDROCHOERIDAE

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### INTRODUCTION

The crown group of Caviioidea sensu stricto (Patterson and Wood, 1982; Pérez, 2010a, 2010b) comprises Caviidae (Caviinae [Cuyes] and Dolichotinae [Maras]) and Hydrochoeridae. The latter encompasses the gigantic semiaquatic Hydrochoerinae (Capybaras), the small and rock dweller *Kerodon* (Mocos), and the extinct Cardiomyinae, a group of large rodents that share with the hydrochoerines ever-growing double-heart-shaped cheek teeth with accessory fissures on lingual (lowers) and labial (uppers) walls, enlarged M3 and p4, and a broad palate. In spite of these similarities, cardiomyines were classically classified as Caviidae (e.g., MacKenna and Bell, 1997). However, Pérez (2010a, 2010b) and Vucetich and Deschamps (in press) considered cardiomyines as more closely related to hydrochoerines. Caviioidea also includes ‘eocardiids,’ the stem group of Caviioidea sensu stricto (s.s.) (Pérez, 2010a, 2010b), which became extinct during the middle Miocene, plus the extant Dasyproctidae and Cuniculidae (Huchon and Douzery, 2001; Pérez, 2010a, 2010b).

The crown group of Caviioidea s.s. is first recorded in the middle Miocene of Colombia (Laventan South American Land-mammal Age [SALMA]; Madden et al., 1997; Figs. 1, 2) with *Prodolichotis pridianae* (see Field, 1957; Walton, 1997; Pérez, 2010a). Additionally, Kraglievich (1930a), based on two isolated lower molars, described two species from the late middle Miocene of Patagonia that tentatively assigned to the cardiomyine *Cardiomys* (*Cardiomys?* *huemulensis* and *C.?* *andinus*). But it is in the early late Miocene (Chasicuan SALMA; Fig. 2) when the fossil record shows the Caviioidea s.s. fully differentiated.

The most important turnover in the history of caviomorph rodents occurred precisely during the middle Miocene, especially after the Colloncuran age (early middle Miocene; Fig. 2). It involved the extinction of most of the ancient genera as well as the appearance of several new clades usually classified as ‘families’ and ‘subfamilies’ (Vucetich et al., 1999, in press). For Caviioidea in particular, this turnover involved the extinction of ‘eocardiids’ as well as other primitive cavioids (e.g., *Neoreomys* and allied taxa) on the one hand, and the differentiation of the members of the crown group (Hydrochoerinae, Cardiomyinae, Dolichotinae, and Caviinae) on the other. Because the middle Miocene has been underrepresented, the events and processes occurred in this period are inferred mostly through the record of the late Miocene (Chasicuan and Huayquerian SALMAs; Fig. 2) of central Argentina. Fortunately, the early and middle Miocene cavioids of Patagonia have been recently restudied (Pérez, 2010a, 2010b; Pérez and Vucetich, 2011), greatly increasing the knowledge about their diversity, phylogenetic relationships, processes related to the differentiation of its dental and mandibular characters, and the sequences in which these characters appeared.

In addition, the time of differentiation of the crown group of Caviioidea s.s. has been estimated through molecular analyses, and different schemes of relationships among the taxa of this crown group were proposed (Rowe and Honeycutt, 2002; Opazo, 2005; Rowe et al., 2010). None of these papers considered the Cardiomyines.

In this paper we restudy the middle Miocene teeth referred to *Cardiomys?* by Kraglievich and reanalyze their affinities with other cavioids, their bearing in the comprehension of the evolutionary events occurred during the middle Miocene in Patagonia, as well as the origin and diversification of modern cavioids. We also restudy the holotype of the Chasicuan *Procardiomys martinoi* Pascual, 1961, in order to elucidate some doubts on its anatomy and correct definition expressed by Pascual himself, and to understand its bearing in the cardiomyine evolution.

**Institutional Abbreviations**—MACN Pv, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Vertebrate Paleontology collection, Buenos Aires, Argentina; MHNSR-PV, Museo de Historia Natural de San Rafael, Vertebrate Paleontology collection, San Rafael, Mendoza, Argentina; MMP, Museo de Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia,” Buenos Aires, Argentina.

**Anatomical Abbreviations**—Tooth nomenclature is simplified from that used for hydrochoerines and follows Vucetich et al. (2005) and Vucetich et al. (2011) (Fig. 3A–B). Following the common use in cardiomyines, hypoflexus/hypoflexid is used instead of fundamental external fissure (H.F.E./h.f.e.) of hydrochoerines. Abbreviations for dental structures refer to the Spanish names in order to conform to previous publications (e.g., Frailey, 1986): **h.p.i.**, primary internal fissure; **h.s.i.**, secondary internal fissure; **hyd/Hyp**, hypoflexid/us; **Pr.I**, prism I; **Pr.II**, prism II; **H.P.E.**, primary external fissure; **H.S.E.**, secondary external fissure.

**Materials**—The comparative morphological study was made using the holotypes of most nominal species of Cardiomyinae: *Caviodon bravardi* Kraglievich, 1927, MACN Pv 4495, left M3; *Cardiomys cavinus* Ameghino, 1885, MACN Pv 4593, right mandible with m1–m3; *Caviodon pozzii* Kraglievich, 1927, MACN Pv 6915, right mandible fragment with p4–m2; *Cardiomys ameghinorum* Rovereto, 1914, MACN Pv 8538, mandible with p4–m3; *Caviodon (Lelongia) paranensis* Kraglievich, 1930b, MACN Pv 13471, right M3; *Xenocardia diversidens* Pascual and Bondesio, 1963, MLP 57-XII-23-5, skull fragment with damaged right and left P4–M3; *Procardiomys martinoi* Pascual, 1961, MMP 471 (M), skull fragment with right and left P4–M3; *Caviodon* sp. nov. MHNSR-PV 1101, large part of a deformed skull with left and right P4–M3, fragments of both hemimandibles with left p4, left m2–m3, and right p4–m3, and associated postcranium.

**Systematics**—Recent studies have provided different schemes of relationships among taxa of the Caviioidea crown group (e.g., Pérez, 2010a, vs. Rowe et al., 2010). We use a traditional systematic scheme with two families, Caviidae and Hydrochoeridae, until a cladistic analysis, including cardiomyines (Pérez and

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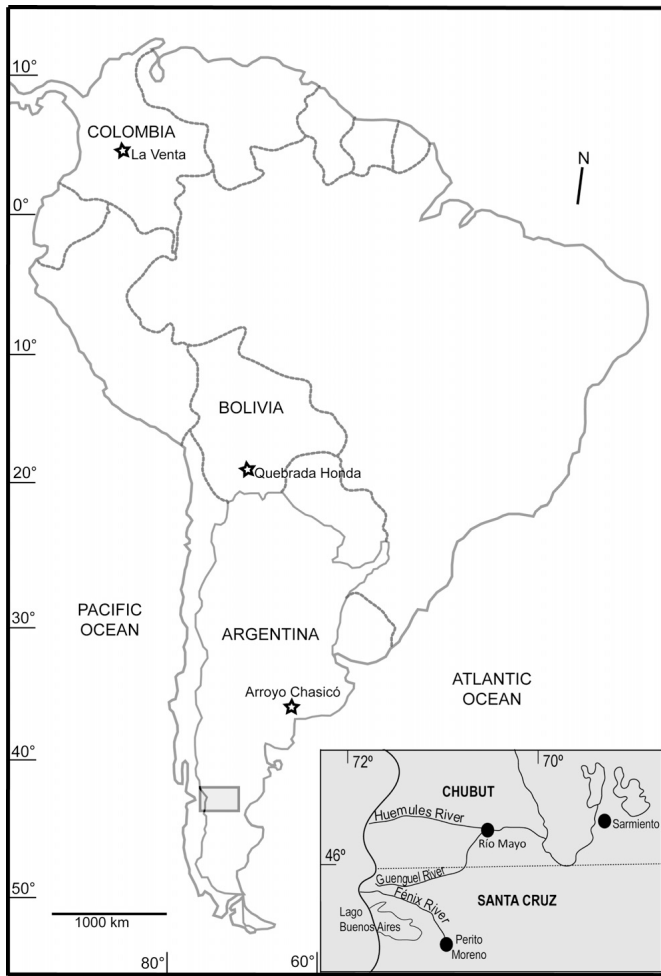


FIGURE 1. Map showing the localities mentioned in the text.

Vucetich, in prep.) sheds light on the relationships among these taxa.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821  
 Infraorder HYSTRICOGNATHI Tullberg, 1899  
 Superfamily CAVIOIDEA Fischer de Waldheim, 1817  
 Family indet.

*MICROCARDIODON* Pérez and Vucetich, 2011  
*MICROCARDIODON HUEMULENSIS* (Kraglievich, 1930),  
 nov. com.  
 (Fig. 4A–C; Table 1)

**Holotype**—MLP 79-II-1-1, isolated left m1 or m2.  
**Geographic and Stratigraphic Provenance**—Huemules River, Chubut (Fig. 1), Río Frías Formation.  
**Extended Diagnosis**—Double-heart-shaped euhypsodont cheek teeth without flexids or fossettids, prisms subequal and with well-developed apical constriction on each one. Posterior prism with well-developed h.p.i.

**Description and Comparison**—The material is an isolated left lower molar, probably m2 because of the curve of the crown, whose base directs slightly backward with respect to the occlusal surface (Fig. 4A). This molar is euhypsodont, bilobated with each prism heart-shaped and convex walls, without flexids or fosset-

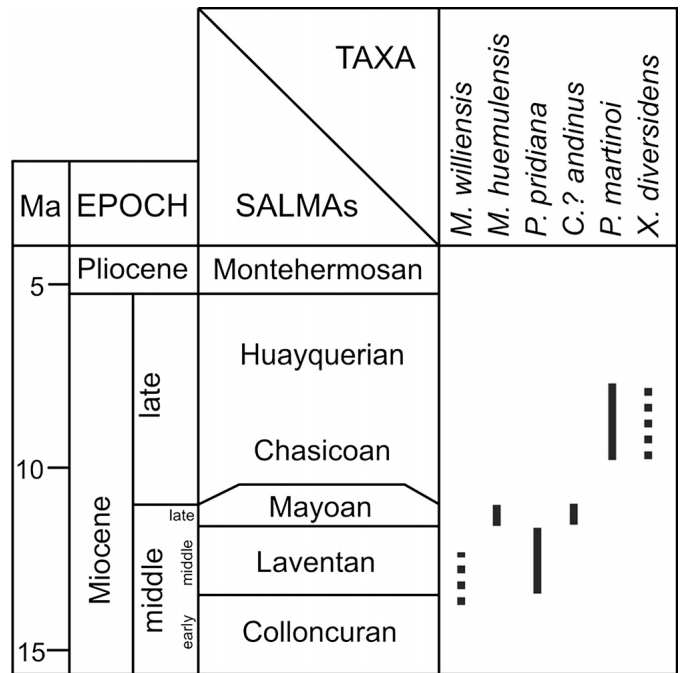


FIGURE 2. Stratigraphic chart of the middle–late Miocene with the SALMAs mentioned in the text. Following Flynn and Swisher, 1995, Zárate et al., 2007, and references therein. Dotted line dubious temporal assignment.

tids. It belonged probably to an adult because the occlusal surface and the base are equal in size (Table 1). The h.p.i. is wide and its end slightly surpasses the end of the hypoflexid, and has the same size and shape at both the occlusal surface and the base (Fig. 4B–C). The isthmus that joins both lobes is long and relatively wide. There is cement in the hypoflexid and a dentine track at the lingual wall of each prism.

*Microcardiodon huemulensis* differs from *M. williensis* Pérez and Vucetich, 2011, by a wider hypoflexid, narrower h.p.i., subequal and more elongated prisms, and more developed apical constriction on each prism. *M. huemulensis* differs from *Eocardia robusta* Vucetich, 1984 (Colloncuran), because in m1–m3 of the latter the anterior prism is smaller. It differs from caviids because it lacks the dentine crest in the midline of the occlusal surface (Pérez, 2010b). We consider it is not a cardiomyine because the walls of the crown are parallel, showing no evidence of allometric growth (see below). Moreover, there is only h.p.i., instead

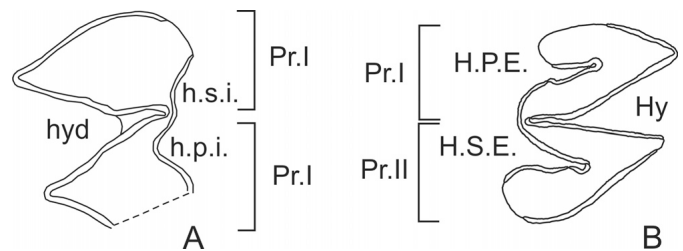


FIGURE 3. Tooth nomenclature and abbreviations. **A**, MLP 92-XI-19-4, left m1 of *Procardiomys?* sp.; **B**, MHNSR-PV 1101 right P4 of *Caviodon*, sp. nov. **Abbreviations:** H.P.E., primary external fissure; h.p.i., primary internal fissure; H.S.E., secondary external fissure; h.s.i., secondary internal fissure; hyd/Hyp, hypoflexid/us; Pr.I, prism I; Pr.II, prism II.

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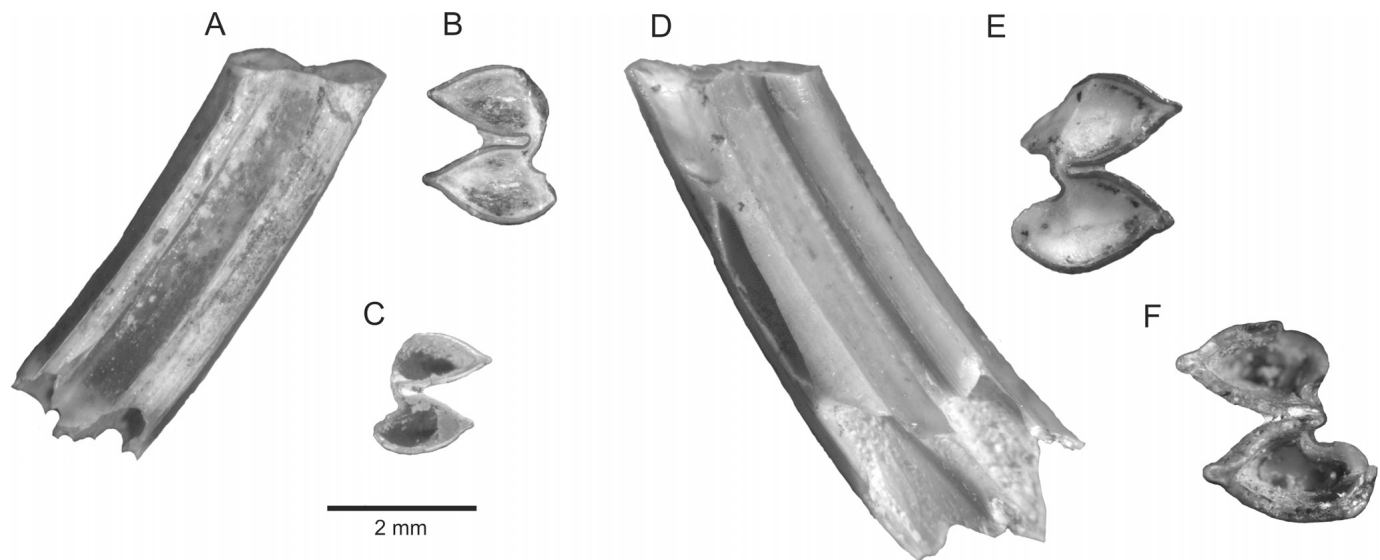


FIGURE 4. *Microcardiomys huemulensis* (A–C) and *Cardiomys? andinus* (D–F). A, D, lingual view; B, E, occlusal view; C, F, base of the teeth.

of the h.p.i. and h.s.i. of cardiomyines, and the walls of each prism are very convex (Fig. 4B–C).

Family HYDROCHOERIDAE Gill, 1872  
Subfamily CARDIOMYINAE Kraglievich, 1930  
*CARDIOMYS? ANDINUS* Kraglievich, 1930  
(Fig. 4D–F; Table 1)

**Holotype**—MLP 15-11: isolated right m1 or m2 of a juvenile.

**Geographic and Stratigraphic Provenance**—Guenguel River, Chubut (Fig. 1), Río Frías Formation.

**Extended Diagnosis**—Euhypsodont cavioid with double-heart-shaped cheek teeth with convex walls. It has an accessory fissure on each prism, being the h.p.i. deeper than the h.s.i. Posterior prism with conspicuous lingual projection; with a dentin track on the lingual wall of each prism, and a well-marked constriction on each prism.

**Description**—The material is an isolated lower molar that lacks the anterior inner angle and the base is much damaged. It is a juvenile because the anteroposterior length of the apex is remarkably smaller than that of the base (Table 1). It has cement in the hypoflexid; the enamel is interrupted in the most lingual portion of each prism. The hypoflexid is comparatively short with respect to the posterior transverse diameter. The h.p.i. reaches the level of the bottom of the hypoflexid, whereas the h.s.i. is very shallow. The isthmus that joins both lobes is relatively short and wide.

TABLE 1. Measurements (in mm) of lower teeth of the studied cardiomyine taxa.

	<i>M. huemulensis</i> m1 or m2	<i>C? andinus</i> m1 or m2	<i>P. martinoi?</i> m1 (MLP 92-XI-19-4)
AP	4.59	5.2	8.16
AP base	4.59	6.12	
AW			6.12
PW	3.67	4.38	
Hy	2.8	3.06	4.59
Hy base	2.8	3.57	

**Abbreviations:** AP, anteroposterior length; AW, anterior width; PW, posterior width; Hy, hypoflexid.

However, the relationship among these structures changes at the base of the tooth: the h.p.i. slightly surpasses the level of the hypoflexid bottom, the h.s.i. reaches the level of the hypoflexid bottom, and the isthmus connecting both prisms becomes very narrow (Fig. 4E–F). The apices of each prism are well marked. All the walls of the prisms are very convex.

It differs from the Caviidae in the absence of a dentine crest in the midline of the prisms. Both the evident enlargement toward the base of the crown and the morphological change between the occlusal and basal surfaces, due to allometric growth, suggests affinities with the hydrochoerids (Vucetich et al., 2005). Allometric growth among cardiomyines has been previously detected in the holotypes of *Cavidon bravardi* and *C. (L.) paransensis* (Vucetich et al., 2011).

*PROCARDIOMYS MARTINOI* Pascual, 1961  
(Fig. 5; Tables 1 and 2)

**Holotype**—MMP 471-M, fragmentary palate with both P4–M3.

**Tentatively Referred Material**—MLP 92-XI-19-4, fragmentary left mandible with damaged p4–m1.

**Provenance**—Arroyo Chasicó Formation. Arroyo Chasicó, southeast of Buenos Aires Province (Fig. 1).

**Emended Diagnosis**—P4–M2 with anterior prism smaller than the posterior one, anterior wall of the posterior prism straight, labial wall of the posterior prism very projected outward and only H.E.P. M3 with three main prisms and a fourth one wide but shorter.

**Comments**—When Pascual (1961) described *P. martinoi*, he expressed his doubts about whether the mandible that finally became part of the holotype pertains to the same individual as the skull fragment, because of “the apparent disparity in the structure between upper and lower cheek teeth” (translated from Pascual, 1961:67). Detailed restudy of the cheek teeth of the mandible showed that they bear a dentine crest on the midline (Fig. 5A), which is a caviine and dolichotine character (Pérez, 2010b). Besides, it has a bilobed p4 and only one accessory lingual fissure opposed to the hypoflexid on m1–m3, characters that led Pascual to recognize its close morphological similarities with the dolichotines. We consider that this mandible pertains indeed to

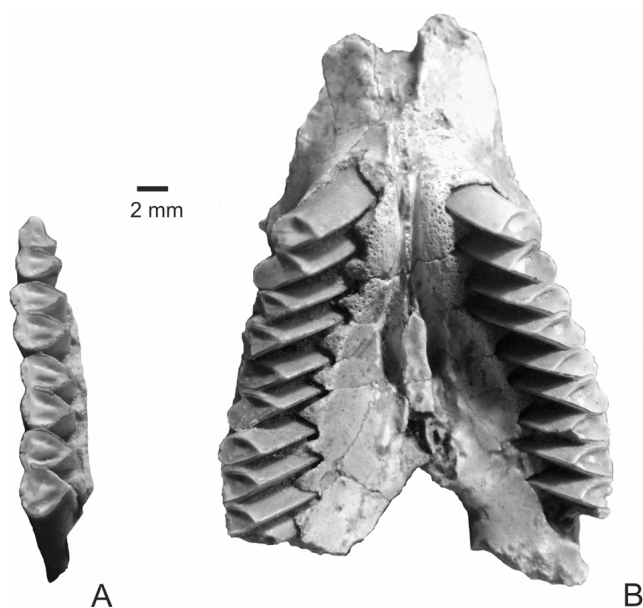


FIGURE 5. *Procardiomys martinoi*. A, MMP 5143-M right mandible with p4-m3 in dorsal view (formerly part of the holotype of *P. martinoi*); B, MMP 471 holotype fragment of skull in ventral view.

a dolichotine, maybe close to *Orthomyctera*. It is now under the collection number MMP 5143-M.

On the contrary, the skull fragment can be assigned to the cardiomyine, because the palate is posteriorly broad with enlarged palatine and very shallow mesopterygoid fossae, enlarged M3, cheek teeth lacking the midline dentine crest, and the walls forming the hypoflexus somewhat straight (Fig. 5B). Taking into account the difference in anteroposterior (AP) length between the occlusal surface and the base of M3 (Table 2), we consider that this specimen corresponds to a juvenile individual.

#### DISCUSSION

Recent studies on Caviioidea systematics, morphological evolution, and phylogeny (Vucetich et al., 2005; 2011; Pérez, 2010a, 2010b; Pérez and Vucetich, 2011) allow us reanalyze the putative middle Miocene cardiomyines from Patagonia with a renewed perspective. The very convex walls of the prisms, and the relative short accessory fissures, especially the h.s.i., of *Cardiomys?* *andinus* suggest a primitive morphology for the subfamily, more similar to that of *Cardiomys* or *Procardiomys* (shallow accessory fissures and h.s.i./H.S.E much shorter than h.p.i./H.P.E.) than that of *Caviodon* or *Xenocardia*. These latter have deeper and subequal in length accessory fissures. This may signify either that *C.?* *andinus* is more closely related to *Cardiomys* and/or

TABLE 2. Measurements (in mm) of the teeth of the holotype of *Procardiomys martinoi* MMP 471-M.

	AP occlusal	AP base	AW	PW
DP4	4.69		4.05	4.74
M1	4.48		4.24	4.24
M2	4.895		4.33	4.45
M3	7.05	7.83	4.22	ca. 3.98

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

*Procardiomys*, or that it is the sister group of all the other cardiomyines, being its h.s.i. in the beginning of its phylogenetical development.

The oldest undoubted hydrochoerids, the hydrochoerine *Cardiatherium chasicoense* (Pascual and Bondesio, 1968; see Deschamps et al., 2007), and the cardiomyine *Procardiomys martinoi* come from the Chasicoan age (early late Miocene); *Xenocardia diversidens* Pascual and Bondesio, 1963, may be similar in age. Vucetich et al. (in press) proposed that the differentiation of the family was older and that it may have occurred in the lapse between the Colloncuran and the Chasicoan (Fig. 2), probably outside Patagonia. However, neither hydrochoerines nor cardiomyines have been recorded yet from middle middle Miocene deposits of Quebrada Honda (Bolivia; Chick, 2009) or La Venta (Colombia; Walton, 1997). Therefore, *C.?* *andinus* from the late middle Miocene is the oldest hydrochoerid yet recorded. Opazo (2005) estimated the origin of the crown group of Caviioidea s.s. (sensu Pérez 2010a, 2010b; second radiation of Opazo) in  $18.5 \pm 2.5$  Ma, but for that moment only protohypsodont cavioids with a generalized mandible structure (Pérez, 2010b) have been recorded. Vucetich and Deschamps (in press) stated that the differentiation of hydrochoerids would have been relatively rapid, explaining the absence of potential close ancestors in the middle Miocene. In agreement, the oldest record of the family, the primitive *C.?* *andinus*, is late middle Miocene in age. This also suggests that the evolution of the group was rapid. If *Xenocardia* is coeval with *P. martinoi*, it would mean that two lineages (with H.S.E./h.s.i. as long as H.P.E./h.p.i., respectively, or shorter) have already been differentiated for the Chasicoan. Moreover, a preliminary study of unpublished Chasicoan remains suggests that the actual diversity of the early late Miocene cardiomyines is larger than supposed.

The reassignment of "*Cardiomys?*" *huemulensis* to *Microcaviodon* results in a longer biochron and a larger diversity of the genus, and the persistence of derived forms of the stem group of cavioids s.s. up to the late middle Miocene. Likewise, it shows that members of the stem and crown groups of cavioids were living simultaneously at least during the late middle Miocene. This also corroborates Vucetich et al.'s (in press) statement that the middle Miocene turnover was not as abrupt as interpreted from the evidence provided by the fossil record (Vucetich et al., 1999).

#### ACKNOWLEDGMENTS

We thank A. Dondas, A. Elissamburu, and F. Scaglia for access to material and kind help at the MMP, I. Olivares helped with *P. martinoi* measurements, and D. Verzi and C. Deschamps for taking the photos of the type material and for fruitful discussions. PICT 38112 and Subsidio Automático UNLP no. 568 partially supported this research.

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Submitted June 10, 2011; revisions received August 3, 2011; accepted August 23, 2011.

Handling editor: Thomas Martin.