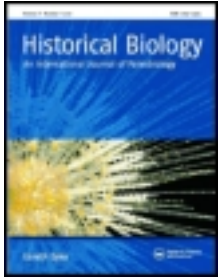


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## Mandibular remains of *Procardiomys martinoi* Pascual, 1961 (Hystricognathi, Caviioidea) from the Arroyo Chasicó Formation (early late Miocene) of Argentina: anatomy and the phylogenetic position of the genus within Caviidae

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Hydrochoerinae is a clade of caviomorph rodents broadly distributed in South America, which includes the maximum body size recorded among extant rodent taxa. The most basal forms of this group are an assemblage of small to medium body size extinct taxa with a plesiomorphic dentition, traditionally clustered in the group cardiomyines. One of the oldest known cardiomyine is *Procardiomys martinoi* (Chasicóan South American Land Mammal Age SALMA; early late Miocene), which was known only from the holotype, a fragmentary palate with the left and right molar series. New mandibular remains from the Arroyo Chasicó Formation (Chasicóan SALMA) are described and identified here as belonging to *P. martinoi* because they share a unique combination of characters (as well matching in size) with the upper dentition of the holotype. These materials help in critically reviewing the taxonomic identification of the mandibular remains previously assigned to *Procardiomys* and allow testing the phylogenetic affinities of this taxon within Caviidae. *P. martinoi* is depicted as one of the most basal forms of Hydrochoerinae, placed basally on the lineage leading to extant capybaras after the split between the common ancestor of *Kerodon* and *Hydrochoerus*.

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**Keywords:** *Procardiomys*; Caviidae; phylogeny; Chasicóan; Miocene; South America

### 1. Introduction

The family Caviidae is among the most diverse caviomorph rodents and includes three main extant lineages: Caviinae (cuyes or guinea pigs'), Dolichotinae (maras) and Hydrochoerinae (semi-aquatic capybaras and the rocky-dweller mocos) (Mares and Ojeda 1982; Woods 1984; Rowe and Honeycutt 2002; Woods and Kilpatrick 2005; Pérez and Vucetich 2011). Hydrochoerinae also includes the extinct cardiomyines, sometimes considered as more related to Caviinae (see Vucetich et al. 2011, 2012). Hydrochoerinae is currently broadly distributed in South America (from Colombia, Venezuela and Guyanas to Central Argentina), and their extant members inhabit a wide variety of lowland habitats in the proximity of water. These sub-aquatic rodents (i.e. *Hydrochoerus*) live in complex social groups (Herrera 2012) and have the maximum body size recorded among the extant rodents (Mones and Ojasti 1986). The origin and early evolution of hydrochoerines are poorly understood, hampering our understanding on the timing and pattern of acquisition of the highly differentiated morphology of modern members of this clade. Abundant fossil remains of already differ-

entiated members of Hydrochoerinae (*Cardiatherium*, *Xenocardia*, *Cardiomys*, *Procardiomys*) are known since the Chasicóan SALMA (early late Miocene) (e.g. Ameghino 1885, 1887; Pascual and Bondesio 1963, 1968; Vucetich et al. 2005, 2012). In particular, *Xenocardia*, *Cardiomys* and *Procardiomys* are of small to medium body size with a plesiomorphic dentition and have traditionally been clustered in the group Cardiomyinae, although the monophyly of this group has not been tested. Cardiomyines probably appeared during the Mayoan SALMA (middle Miocene) and lasted until the Chapadmalalan SALMA (late Pliocene) (Kraglievich 1930; Pascual 1961; Bondesio et al. 1980; Vucetich and Pérez 2011).

Four extinct genera, *Procardiomys*, *Cardiomys*, *Caviodon* and *Xenocardia*, have been regarded as cardiomyines and are characterised by the presence of a p4 composed of three lobes, the m1–m3 and P4–M2 formed by two lobes, an M3 formed by three to six main lobes and a smaller posterior projection, and a palate as broad as in *Hydrochoerus* (Kraglievich 1930; Pascual 1966). Although this group was originally allied to other caviid lineages (e.g. Dolichotinae, Caviinae; Pascual 1961), recent morphologi-

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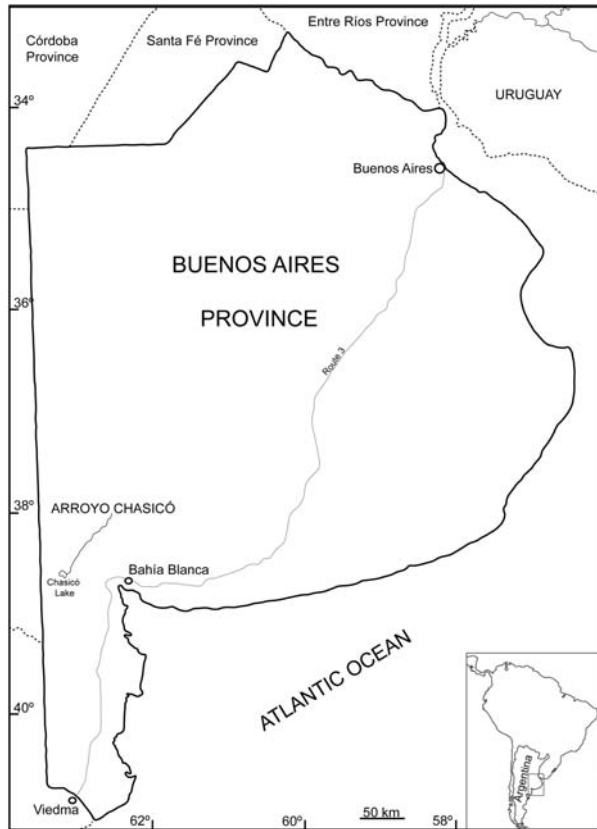


Figure 1. Location map of Arroyo Chasicó locality, Buenos Aires Province, Argentina.

cal phylogenetic analyses of Caviidae supported the proposal that cardiomyines are more closely related to hydrochoerines than to either Caviinae or Dolichotinae (Pérez 2010a; Pérez and Vucetich 2011). Those analyses only included a single cardiomyine taxon (*Cardiomyis*), which was placed basally within the lineage leading to the living capybara (*Hydrochoerus*).

The oldest record of cardiomyines is an isolated lower molar from the Río Frías Formation (Mayoan SALMA; middle Miocene; 11.5 Ma; Dal Molin and Franchi 1996) that has been tentatively referred to *Cardiomyis? andinus* (Kraglievich 1930; Vucetich and Pérez 2011). *Procardiomyis martinoi* is the first cardiomyine (Pascual 1961) represented by skull remains. It was found in the Arroyo Chasicó Formation (Chasicóan SALMA; early late Miocene; Figure 1). This species was known only from the holotype (MMP 471-M; Figure 2), a fragmentary palate with the left and right molar series. In the original description of the holotype, Pascual (1961) included a fragmentary right mandible with p4–m3 (Figure 3(A)). Vucetich and Pérez (2011) recently regarded this mandible (currently under the collection number MMP 5143-M) as belonging to a dolichotine, possibly related to *Orthomyctera*. As well, they suggested that another mandibular fragment (MLP 92-XI-19-4; Figure 3(B)) from the Arroyo Chasicó Formation could belong to *P.*

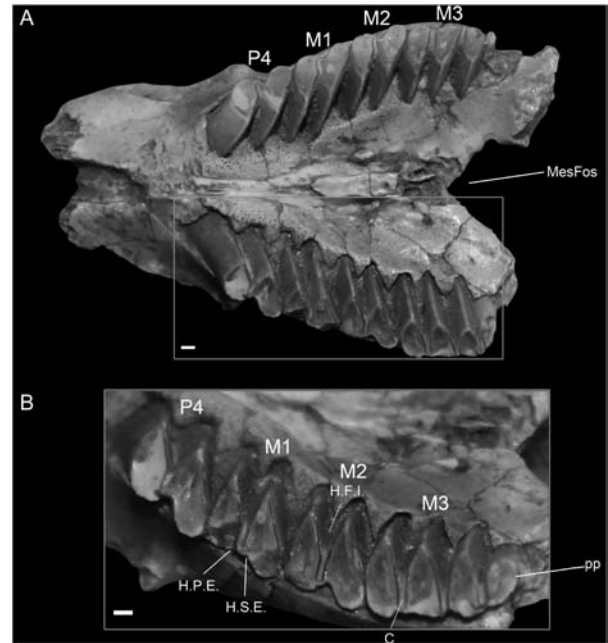


Figure 2. *Procardiomyis martinoi* holotype MMP 471, fragment of skull (A) in ventral view and (B) detail of right dental series. Abbreviations: c, cement; H.F.I., fundamental internal flexus; H.P.E., primary external flexus; H.S.E., secondary external flexus; MesFos, mesopterygoid fossa; P4–M3, upper teeth. Scale: 1 mm.

*martinoi*. However, a revision of undescribed remains from this unit revealed the presence of new mandibles (MMP 482-M; MMP 283-M; MLP 76-VI-12-143) that can be identified as *P. martinoi*, rejecting the previous identifications of the two mandibles made by Pascual (1961) and Vucetich and Pérez (2011) (see below).

In this contribution we describe these remains, discuss the taxonomic identification of the mandibular material

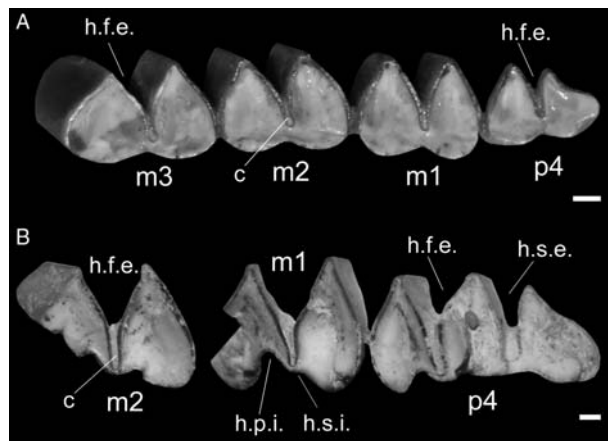


Figure 3. (A) Dolichotinae MMP 5143-M, right mandible with p4–m3. (B) MLP 92-XI-19-4 left mandible with p4–m1 and m2 isolated (occlusal view). Abbreviations: c, cement; h.f.e., fundamental external flexid; h.p.i., primary internal flexid; h.s.i., secondary internal flexid; p4–m3, lower teeth. Scale: 1 mm.

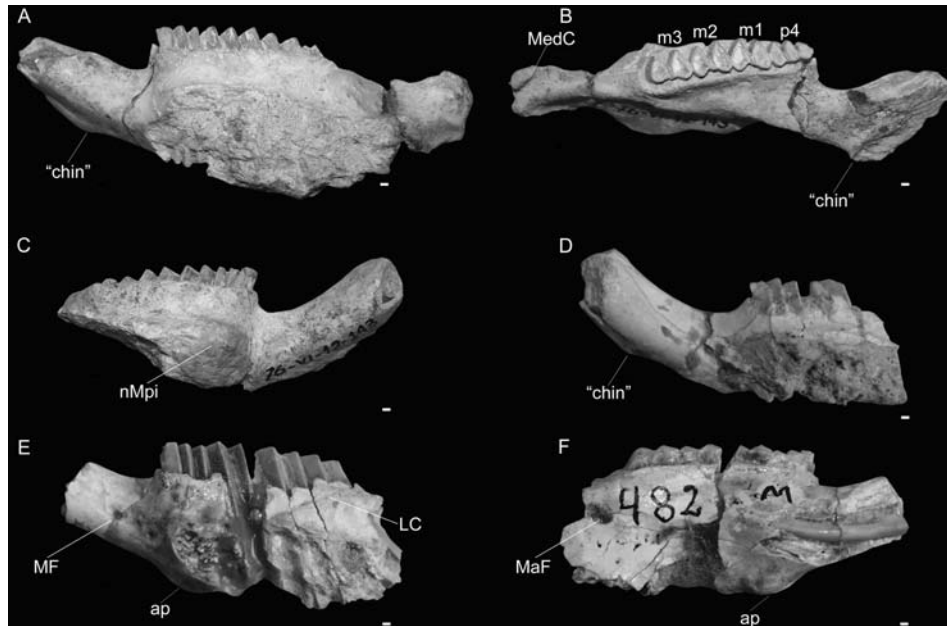


Figure 4. *Procardiomys martinoi*. MLP 76-VI-12-143 (A) left mandible, in labial view; (B) in occlusal view; (C) right mandible, in labial view. MMP 283-M (D) right mandible, in labial view. MMP 482 left mandible (E) in labial view and (F) in lingual view. Abbreviations: ap, alveolar protuberances; 'chin', posterior extension of the mandibular symphysis; LC, lateral crest; MaF, mandibular foramen; mf, mentonian foramen; MedC, medial condyle; nMpi, notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*. Scale: 1 mm.

previously assigned to *Procardiomys*, evaluate the new morphological information provided by the undescribed mandibular remains of the basal hydrochoerine *Procardiomys* and test the phylogenetic affinities of this taxon within Caviidae.

## 2. Materials and methods

### 2.1 Institutional abbreviations

MACN Pv, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' Vertebrate Paleontology Collection; MLP, Museo de La Plata; MMP, Museo Municipal de Ciencias Naturales de Mar del Plata 'Lorenzo Scaglia', Buenos Aires, Argentina.

### 2.2 Anatomical abbreviations

h.f.e., fundamental external flexid; h.s.e., secondary external flexid; H.S.E., secondary external flexus; H.P.E., primary external flexus; h.p.i., primary internal flexid; h.s.i., secondary internal flexid; nMpi, notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*.

### 2.3 Materials for comparison

The materials are compared with mandibles and teeth of extinct (†) and living Cavoioidea *sensu stricto* (Pérez

2010b, 2010c; Pérez and Vucetich 2011). Caviinae: †*Dolicavia*, *Cavia*, *Galea*; Dolichotinae: *Dolichotis salinicola*; Hydrochoerinae: †*Cardiomys*, †*Caviodon*, †*Cardiatherium*, †*Phugatherium*, *Hydrochoerus* and *Kerodon*; Cavoioidea *sensu stricto* indet.: †*Chubutomys navaensis* (see Supplementary data 1).

### 2.4 Phylogenetic analysis

In order to evaluate the phylogenetic position of *Procardiomys martinoi* within Caviidae, a cladistic analysis was performed using a modified version of the data-set of Pérez et al. (2012), which includes 39 cavioids *sensu stricto* scored for 94 morphological characters and DNA sequences of four genes (12s, Cyb, Tth and Ghr) for nine extant caviids (see Supplementary data 1–3). Fifteen multistate characters of the morphological partition were considered as additive based on increasing degrees of similarity between the character states or in cases of nested homologies. Some representatives of Cavoioidea *sensu lato* were used as outgroup taxa: *Dasyprocta azarae*, *Neoreomys australis* (Dasyproctidae) and *Cuniculus paca* (Cuniculidae). The phylogenetic trees were rooted with the octodontoid caviomorph *Proechimys poliopus*.

This data-set was analysed using equally weighted parsimony in Tree analysis using New Technology (TNT) 1.1 (Goloboff et al. 2008a, 2008b), treating gaps as missing data for the DNA sequences. Equally



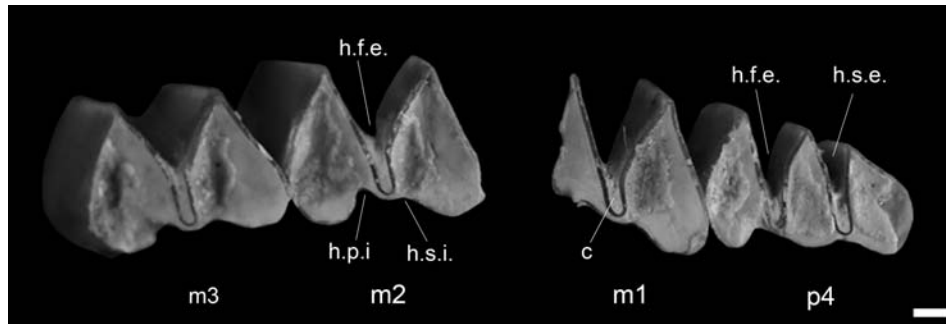


Figure 5. *Procardiomys martinoi*. MMP 482 in occlusal view. Abbreviations: h.f.e., fundamental external flexid; h.p.i., primary internal flexid; h.s.i., secondary internal flexid; p4–m3, lower teeth. Scale: 1 mm.

weighted parsimony was used to minimise the number of postulated evolutionary transformations. A heuristic trees search was conducted to find the most parsimonious trees (MPTs), which consisted of 1000 replicates of Wagner trees with random addition of taxa followed by TBR branch swapping, collapsing zero-length branches under the strictest criterion. After this procedure, a final round of TBR branch swapping was applied to find all the MPTs. Support values were calculated using Bremer indices, as well as bootstrap and jackknife resampling techniques. Unstable taxa in the set of MPTs were identified using IterPCR (Pol and Escapa 2009) to derive an informative reduced consensus.

Table 1. Dental measurements of *Procardiomys martinoi* and *Cardiomys* spp. in millimetres (in).

	APL	AW	PW	SAW
<i>Procardiomys martinoi</i>				
MMP 471-M holotype				
P4	4.69	4.05	4.74	
M1	4.48	4.24	4.24	
M2	4.90	4.33	4.45	
M3	7.55	4.22	3.98	
MMP 482-M				
p4	5.30	3.04	3.52	2.75
m1	–	3.94	–	
m2	5.04	3.89	4.01	
m3	5.16	3.46	3.66	
MLP 76-VI-12-143				
p4	5.41	2.97	3.27	2.51
m1	5.11	3.89	3.93	
m2	5.11	4.21	3.90	
m3	5.40	4.00	3.45	
MMP 283-M				
p4	5.50	2.77	3.50	2.68
<i>Cardiomys</i> sp.				
MLP 92-XI-19-4				
p4	9.82	5.21	5.5	5.05
m1	–	6.17	–	
m2	8.3	6.35	–	

Note: APL, anteroposterior length; AW, anterior lobe width; PW, posterior lobe width; SAW, anterior secondary lobe width.

### Systematic Palaeontology

#### Order RODENTIA Bowdich 1821

#### Infraorder HYSTRICOGNATHI Tullberg 1899

#### Superfamily CAVIOIDEA Fischer de Waldheim 1817

#### Family CAVIIDAE Waterhouse 1839

#### *Procardiomys martinoi* Pascual 1961

(Figures 2, 4 and 5, Table 1)

#### 2.5 Holotype

MMP 471-M, fragmentary palate with both P4 and M3.

#### 2.6 Referred material

MLP 76-VI-12-143, fragmentary right and left mandibles with p4–m3; MMP 283-M, fragmentary left mandible with p4–m1; MMP 482-M, fragmentary left mandible with p4–m3.

#### 2.7 Locality and horizon

Arroyo Chasicó Formation (early late Miocene, Chasicóan SALMA; ca. 7–9.43 Ma, see below), Arroyo Chasicó, southeastern Buenos Aires Province, Argentina (Figure 1). The Arroyo Chasicó Formation was originally defined by Fidalgo et al. (1979) from a lithological point of view. Later, Bondesio et al. (1980) incorporated the information of the fossil vertebrates from this unit and divided the Arroyo Chasicó Formation into the lower Vivero Member and the upper Las Barrancas Member. Recently, Zárata et al. (2007) proposed a different scheme for this unit based on the sedimentary succession sequence and recognised three distinct lithofacies.

Based on radioisotopic dates, Zárata et al. (2007) concluded that lithofacies 1 and 2 accumulated between 9.43 and 9.07 Ma and could extend up to 8.7 Ma. Later, Deschamps et al. (2009) considered that lithofacies 3 of the Arroyo Chasicó Formation could be biostratigraphically correlated with the Loma de Las Tapias Formation

(San Juan Province, Argentina), which had been radiometrically dated at  $7 \pm 0.9$  Ma. The holotype of *P. martinoi*, as well as the new mandibles referred to this taxon in this contribution, lacks the detailed information regarding the horizon in which they were found within the Arroyo Chasicó Formation. Hence, the age of these fossils is only constrained by the lower and upper bounds of the time of deposition of the Arroyo Chasicó Formation (i.e. ca. 7 and 9.43 Ma).

## 2.8 Emended diagnosis

Caviid diagnosed by the following unique combination of characters (autapomorphy marked with an asterisk): euhypsodont and heart-shaped teeth; m1–m3, and P4–M2 bilobed; p4 with three lobes; \*M3 with three lobes and a well-developed posterior projection; absent constriction on the apex of lobes; m1–m3 with shallow h.p.i. and h.s.i.; P4–M2 with shallow H.P.E. and H.S.E.; hypoflexus/id extremely deep transversely and with cement; enamel interrupted along the lingual wall of the lower teeth and labial wall of the upper teeth, except on h.p.i., h.s.i., H.P.E. and H.S.E.; mental foramen located at the dorsoventral midpoint.

## 3. Description

### 3.1 Dentary

The four mandibles referred to *Procardiomys martinoi* are incompletely preserved (Figure 4). MLP 76-VI-12-143 (Figure 4(A–C)) and MMP 482-M (Figure 4(E),(F)) lack the anteriormost and posteriormost portions of the dentary, but the p4–m3 series is complete. MMP 283-M (Figure 4(D)), instead, has preserved p4 and m1. These mandibles are similar in size to that of *Dolichotis salinicola* and have alveolar protuberances as in this taxon (Figure 4(D),(E)). In labial view, the mental foramen is located at the dorsoventral midpoint of the lateral surface of the dentary and opens laterally (Figure 4(D)), as in other caviids (e.g. *Cardiomys*, *Caviodon*, *Cardiatherium*, *Phugatherium*, *Hydrochoerus*, *Kerodon*, *Dolichotis*, *Dolicavia* and *Microcavia*). MMP 482-M has the posteroventral projection of the mandibular symphysis damaged, but MLP 76-XI-12-143 (Figure 4(A)) and MMP 283-M (Figure 4(D)) show that it is moderately developed (only a low bulge projects ventrally and it is marginally exposed in lateral view). The lateral crest is straight (Figure 4(E)), resembling the condition of other caviids, such as *Cardiomys*, *Caviodon*, *Kerodon*, *Hydrochoerus*, *Dolichotis*, *Dolicavia*, *Cavia* and *Galea*. The notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis* (nMpi) is located between p4 and m1 (MLP 76-XI-12-143; Figure 4(C)). The masseteric crest and the horizontal crest are broken in all specimens (Figure 4). The labial edge of the condyle lacks a distinct knob and is

continuous with the lateral wall of the dentary in posterior view (MLP 76-VI-12-143; Figure 4(A)). The medial edge of the condyle is poorly developed and forms a small knob (MLP 76-VI-12-143; Figure 4(B)). In lingual view, the mandibular foramen is positioned below the m3 (Figure 4(F)), resembling the condition of other Caviioidea *sensu stricto* except for *Chubutomys navaensis* (Pérez et al. 2012).

### 3.2 Dentition

The incisors of all mandibles are broken, but it can be determined that they extended up to the level of the posterior lobe of the m1 (Figure 4(B),(F)). The cheek teeth of *P. martinoi* are euhypsodont and with heart-shaped lobes. The enamel is interrupted along the entire lingual wall of lower teeth except for h.p.i. and h.s.i. The teeth have cement in the hypoflexid (or h.f.e.; Figure 5).

The p4 is anteroposteriorly longer than the molars (Figures 4(B) and 5; Table 1) and has three lobes, differing from the molars with only two lobes. This condition resembles that of *Cardiomys*, *Caviodon*, *Kerodon*, *Cardiatherium* and *Hydrochoerus*. The lobes lack a constriction in the apex, and the lingual wall is convex along the base of each lobe. In MMP 283-M and MMP 482-M, the anterior wall of the most anterior lobe (anterior secondary prism *sensu* Mones, 1991) is broken, but in both MLP 76-VI-12-143 this lobe is wider than the other two lobes. In the four referred mandibles, this lobe has straight anterior and posterior walls (Figures 4(B) and 5). The middle lobe (prism I *sensu* Mones, 1991) is narrow and lanceolate (Figures 4(B) and 5). The posterior lobe (prism II *sensu* Mones, 1991) is heart shaped, with the anterior wall straight and the posterior wall convex (Figures 4(B) and 5). The secondary external flexid (h.s.e.) and the fundamental external flexid (h.f.e.) are very similar in shape and depth. Both flexids are relatively narrow with a rounded end and extend beyond the transverse midpoint of the crown (Figures 4(B) and 5). On the lingual wall, the premolar has an anterior flexid opposite to the h.s.e. and a slightly deeper posterior flexid that is located at the anterior portion of the lingual wall of the posterior lobe.

In occlusal view, the m1–m3 are bilobed, with heart-shaped lobes. The anterior wall of each lobe is relatively straight, but the posterior wall is convex (Figures 4(B) and 5). The hypoflexid (h.f.e.) is funnel shaped, extremely long, and extends beyond the transverse midpoint of the crown (Figures 4(B) and 5). The m1 and m2 are similar sized, but anteroposteriorly shorter than m3 (Figures 4(B) and 5). On the lingual wall, these molars bear two shallow flexids located one on each lobe, with the anterior (h.s.i.) shallower than the posterior one (h.p.i.) (Figures 4(B) and 5). The m1 and m2 lack the constriction in the apex of the

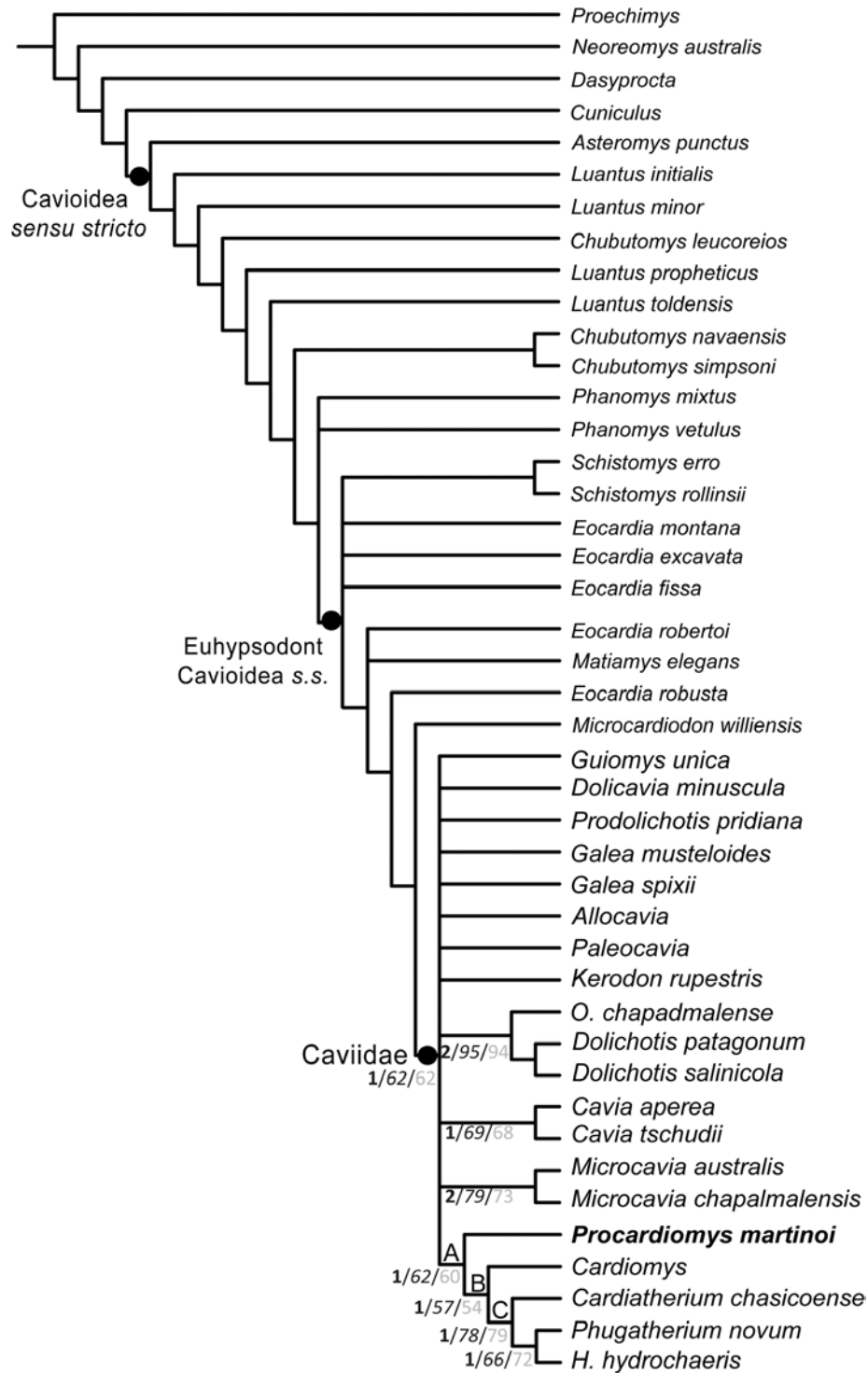


Figure 6. Strict consensus of the 408 MPTs (length = 3191; CI = 0.636; RI = 0.477) resulting from the parsimony combined phylogenetic analysis of morphological and molecular data-set using TNT (see Supplementary data 1 and 3 of this paper). The numbers in bold indicate Bremer indices, numbers in italics represent absolute jackknife values and numbers in grey represent absolute bootstrap values.

lobes. The anteroposterior length (APL) of both lobes in m1 and m2 is approximately equal (Figures 4(B) and 5).

#### 4. Taxonomic identity

As noted above, two different mandibular fragments from the Arroyo Chasicó Formation were previously referred to *Procardiomys martinoi* by Pascual (1961) and Vucetich and Pérez (2011). In the original description, Pascual (1961: 67) raised questions about the correspondence of the holotype (palatal remains; Figure 2) and the supposedly associated mandible (MMP 5143-M; Figure 3(A)), given the differences in their tooth morphology. This mandible likely belongs to a Dolichotinae, given the presence of a dentine crest on the midline of each lobe, a bilobed p4 with an incipient anterior projection and one furrow opposite the hypoflexus/id (Figure 3(A)) (Vucetich and Pérez 2011). None of these characters are present in the upper teeth of the holotype of *P. martinoi* (Figure 2) but are found in lower and upper teeth of dolichotines (e.g. *Orthomyctera*).

Vucetich and Pérez (2011) recently referred a second mandible (MLP 92-XI-19-4; Figure 3(B)) to *P. martinoi*, which is a fragmentary left mandible with a damaged p4–m1 and isolated m2. A more detailed analysis of MLP 92-XI-19-4 allows recognising some characters that differ from the upper teeth of the holotype of *P. martinoi*. In general terms, the teeth of MLP 92-XI-19-4 are anteroposteriorly longer, their lobes are labiolingually broader, and their walls are more convex than the teeth of the holotype of *P. martinoi* (Figure 2). In particular, the p4 of MLP 92-XI-19-4 is almost twice the length of the P4 of the holotype of *P. martinoi* (MMP 471-M), the p4 of hydrochoerines and cardiomyines is always longer than P4 (>20%; Vucetich et al. 2011 and personal observation). Several characters of the m1 of MLP 92-XI-19-4 differ from the M1 of the holotype: (1) the lobes are somewhat different: they are transversely oriented and with convex walls, whereas in the holotype of *P. martinoi*, the posterior lobe of P4–M2 is oblique with the posterior wall straight and anteroposteriorly oriented; (2) the hypoflexid (h.f.e.) of m1 is narrower in the apex than the hypoflexus (H.F.I.) of the M1 of the holotype; (3) the h.p.i. of m1 is deeper than in the M1 of the holotype. The m1 and m2 of MLP 92-XI-19-4 have a constriction in the apex of the lobes, whereas the M1 and M2 of the holotype of *P. martinoi* lack this constriction (Figure 2). Finally, the h.p.i. and h.s.i. of m2 of MLP 92-XI-19-4 are deeper than in the M2 of the holotype of *P. martinoi*.

These differences are not as marked as those of the holotype of *P. martinoi* and the mandible originally referred by Pascual (1961), but nonetheless they suggest that MLP 92-XI-19-4 belongs to a different caviid taxon, as these features are usually consistent between the upper

and the lower teeth among caviids and we consider it tentatively *Cardiomys* sp.

The four mandibular remains from the Arroyo Chasicó Formation described in this contribution (i.e. MLP 76-VI-12-143 left and right, MMP 482-M and MMP-283), in contrast, show a congruent dental morphology in the above-noted features with the upper dentition of the holotype of *P. martinoi* and therefore are referred to this taxon: (1) the APL of the lower teeth of the newly referred material (MLP 76-VI-12-143, MMP 482-M and MMP-283) is congruent with the length of the teeth of the holotype (see Table 1); (2) the teeth lack the constriction in the apex of the lobes, and the lobes are labiolingually narrow with their walls only slightly convex, as in the holotype of *P. martinoi*; (3) the h.p.i. and h.s.i. of the teeth of the mandibular remains are shallow like the labial furrow of the holotype; (4) the shape and orientation of the lobes are alike: the anterior walls of m1–m3 are straight and posterolabially anterolingually directed, resembling the condition of P4–M2 of the holotype of *P. martinoi* in which the posterior wall of the posterior lobe is straight and anterolingually posterolabially directed.

This list of features (as well as the ones mentioned above) not only underscore the unique combination of characters shared between the four mandibles described here and the holotype of *P. martinoi* but also distinguish them from the two mandibles previously identified as *P. martinoi* (MLP 92-XI-19-4; MMP 5143-M) and allow rejecting the taxonomic referral made by Pascual (1961) and Vucetich and Pérez (2011).

#### 5. Phylogenetic analysis

The parsimony analysis resulted in a total of 408 MPTs of 3191 steps (CI = 0.636; RI = 0.477). Caviidae shows a basal polytomy in the strict consensus (Figure 6) because †*Allocavia*, †*Prodolichotis*, †*Paleocavia* and †*Dolicavia* take different positions within this clade in the MPTs.

*Procardiomys martinoi* is depicted in all MPTs as the most basal form of the lineage leading to modern capybaras (Figure 6), and six unambiguous synapomorphies support its inclusion in the lineage leading to modern capybaras: (1) alveolar protuberances present, as well as a developed bulge on the ventral margin of the dentary (character 27[1]), (2) p4 with three lobes (character 44[4]), (3) H.S.E deeper than H.P.E. (character 55[1]), (4) H.S.E. less than half of the lobe (in occlusal view) (character 56[1]), (5) M3 with three lobes and one posterior projection (character 57[3]) and (6) apex of the mesopterygoid fossa at the level of the middle point of M3 (character 63[3]). This node has only moderate support values in the phylogenetic analysis (Bremer = 1; jackknife absolute/GC frequency = 62/60; bootstrap absolute/GC frequency = 60/57; see Figure 6, node A).



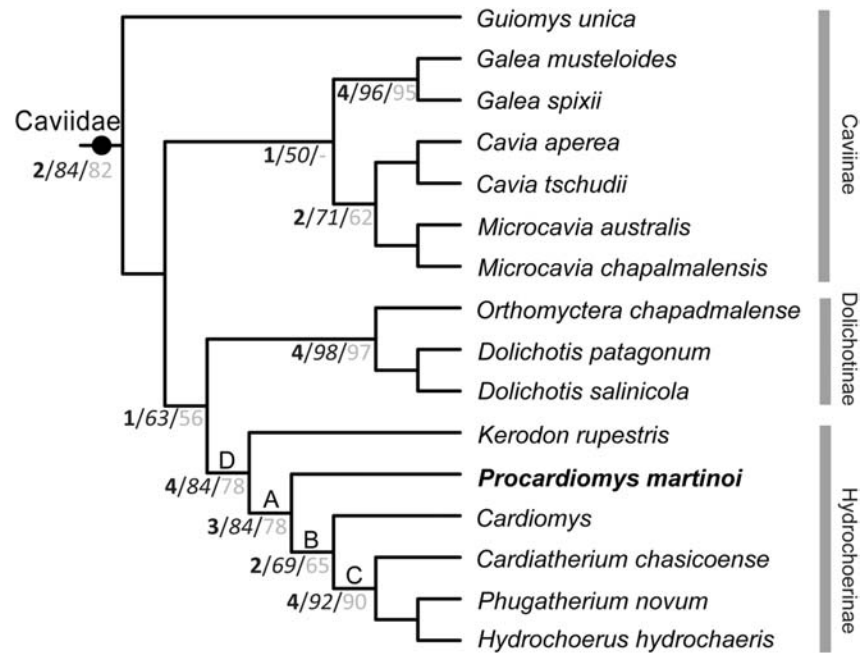


Figure 7. Node Caviidae in the reduced consensus ignoring the fossil taxa, *Allocavia*, *Dolicavia*, *Paleocavia* and *Prodolichotis*. The numbers in bold indicate Bremer indices, numbers in italics represent absolute jackknife values and numbers in grey represent absolute bootstrap values.

*Procardiomyx* is placed as the sister group of the clade formed by *Cardiomyx* and more derived hydrochoerines (Figure 6, node B). *Procardiomyx* is excluded from this clade because it lacks three unambiguous synapomorphies that diagnose this clade: (1) length of p4–m1 shorter than the length of m2–m3 (character 35[0]), (2) relative size of lower molars: m1 < m2 < m3 (character 36[2]) and (3) M3 with four lobes and one posterior projection (character 57[4]). More derived hydrochoerines, such as *Cardiatherium chasicoense*, *Phugatherium novum* and *Hydrochoerus hydrochaeris* (Figure 6, node C) are clustered in a monophyletic group that is supported by seven unambiguous synapomorphies: (1) lack of alveolar protuberances (character 26[0]), (2) laminated posterior lobe of m1–m2 (character 29[3]), (3) hypoflexus/id canal-shaped (character 32[4]), (4) H.P.E. deeper than H.S.E. (character 55[3]), (5) M3 with five to six lobes (character 57[5]), (6) laminated anterior lobe of m1–m2 (character 58[1]) and (7) apex of the mesopterygoid fossa at the level of the posterior half of M3 (character 63[4]).

Although the alternative positions taken by the four unstable taxa do not affect the resolution within the above-mentioned hydrochoerines, the strict consensus does not reflect the affinities between *Kerodon* and hydrochoerines that are supported in all the MPTs. When the four unstable taxa (*Allocavia*, *Prodolichotis*, *Paleocavia* and *Dolicavia*) were pruned from the MPTs, the resulting reduced strict consensus retrieves as monophyletic group, the three major living lineages of Caviidae: Caviinae, Hydrochoer-

inae and Dolichotinae (Figure 7). In this topology, *Kerodon rupestris* is positioned as the most basal form of Hydrochoerinae, being the sister group of the clade formed by *Procardiomyx* and more derived hydrochoerines (Figure 7, node D). The affinities of *Kerodon* with hydrochoerines is supported by five unambiguous synapomorphies of the morphological partition: (1) mandibular notch located ventral to the occlusal surface of the dental series (character 12[2]), (2) posterior extension of the root of the lower incisors extending up to the level of the m1 (character 17[3]), (3) p4 with three lobes (character 44[4]), (4) frontals not convex (character 65[0]) and (5) position of the boundary between the mastoid and paraoccipital processes at the same level or above the external auditory meatus (character 86[0]). In addition, this node is supported by 34 unambiguous synapomorphies of the molecular partition. By ignoring the alternative positions of the four unstable taxa during support calculations, the values retrieved for hydrochoerines are markedly increased (Bremer = 3; jackknife absolute/GC frequency = 84/80; bootstrap absolute/GC frequency = 78/72; see Figure 7, node A).

## 6. Discussion and conclusions

*Procardiomyx martinoi* was known only from the type specimen, a fragmentary palate with both P4 and M3 (MMP 471-M; Figure 2). Two different mandibles referred to this taxon by Pascual (1961) and Vucetich and Pérez

(2011) are here interpreted as belonging to different taxa (Figure 3). Four new mandibular remains are described in this work (MLP 76-VI-12-143 left and right, MMP 283-M and MMP 482-M; Figures 4 and 5) and identified as *P. martinoi* because they share a unique combination of characters (matching in size as well) with the upper dentition of the holotype. Thus, these new materials clarify the taxonomic identity of caviid mandibular remains from the Arroyo Chasicó Formation, increase our anatomical knowledge on *P. martinoi* and allow testing the phylogenetic position of this taxon with broader empirical bases.

In the phylogenetic analysis, *P. martinoi* is positioned as one of the most basal forms of Hydrochoerinae, placed basally on the lineage leading to extant capybaras after the split between the common ancestor of *Kerodon* and *Hydrochoerus* (Figure 7). Such a basal position for *P. martinoi* is justified since it lacks some derived aspects of the dentition present in *Cardiomyis* and more derived hydrochoerines (e.g. more number of lobes in M3).

Although the taxon sampling of cardiomyines of this analysis is not complete, the position of *Procardiomyis* and *Cardiomyis* as successive sister taxa of more derived hydrochoerines suggests that this group may be a paraphyletic assemblage of basal hydrochoerines. Further studies, expanding character and taxon sampling of these forms (e.g. *Caviodon cuyano*, *Caviodon pozii*, *Cardiomyis cavinus* and *Cardiomyis ameghinorum*) are needed to thoroughly test the monophyly of cardiomyines.

The morphological differences noted above between the basal forms (cardiomyines) and the derived members of hydrochoerines could also reflect differences in the paleobiology of this group and the evolutionary pattern of acquisition of their peculiar body plan, social structure and habitat preferences. Derived forms of Hydrochoeridae are always found in water-related sediments, including their oldest records in the Chasicóan SALMA (e.g. *Cardiatherium*). Furthermore, it is common to find adults and juveniles of different ages in different localities, suggesting the existence of a complex social structure (Vucetich et al. 2012). Meanwhile, although the remains are scarcer, there is no evidence that cardiomyines had social habits or physiological dependence on water. Moreover, even the most derived cardiomyines (e.g. *Caviodon cuyano* Vucetich et al. 2011) never acquired the complex dental morphology characteristic of hydrochoerines. This suggests that semi-aquatic, social habits and the characteristic body size and complex dental morphology of modern hydrochoerines might have appeared simultaneously in the evolutionary history of hydrochoerines (Deschamps et al. 2009; Vucetich et al. 2012).

Despite the morphological gap (and the possible ecological differences) between the basal (cardiomyines) and derived forms of Hydrochoeridae, multiple lineages of hydrochoerines are found in the Chasicóan SALMA

(i.e. *Procardiomyis*, *Cardiomyis*, and *Cardiatherium*). The occurrence of these forms at this age places a robust minimum divergence time for Hydrochoeridae (see Pérez and Pol 2012). Moreover, this paleontological dating of the diversification of Hydrochoeridae agrees with molecular clock estimates of this evolutionary event (Pérez and Pol 2012). These lines of evidence indicate that the Chasicóan SALMA was a key moment in the evolution of Hydrochoeridae, during which the clade not only diversified but also recorded the appearance of the highly differentiated anatomy and ecology of modern capybaras.

The Chasicóan hydrochoerines are critical to understand the early evolution of the group as they record the appearance of some dental features that progressively approach the highly apomorphic dentition of capybaras (e.g. teeth with deeper and additional fissures, M3 with an increasingly high number of lobes). Therefore, the study of hydrochoerines from this age (Chasicóan SALMA), and even older records of this lineage (currently known by a single tooth from the Mayoan SALMA; middle Miocene), and their inclusion in a phylogenetic context will provide the basis for fully understanding the unique evolutionary history of the lineage that led to the largest extant rodents.

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