

DIVERSITY, PHYLOGENY AND BIOGEOGRAPHY OF THE SOUTH AMERICAN ‘CARDIOMYINE’ RODENTS (HYSTRICOGNATHI, CAVIOIDEA) WITH A DESCRIPTION OF TWO NEW SPECIES

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Abstract: ‘Cardiomyine’ rodents are extinct large terrestrial Caviidae closely related to capybaras, that inhabited large parts of South America during the middle Miocene and Pliocene. They are mostly preserved as isolated teeth, but also as skull and jaw fragments. Here we revise the taxonomy of this group and describe two new species, each pertaining to one of the two main late Miocene groups, represented by the genera *Caviodon* and *Cardiomyis*. This suggests that the diversity of ‘cardiomyines’ was higher than previously thought. Among the specimens studied there are two almost complete skulls; one from the Andalhuala Formation, Catamarca, and the other from the Arroyo Chasicó Formation, Buenos Aires. The first, housed in the Field Museum of Natural History, was originally catalogued as *Cardiomyis ameghinorum*, a common species for the late Miocene of north-western Argentina (NOA), but is here

transferred to the genus *Caviodon*. This is the first mention of the genus for NOA, enlarging its geographical distribution for the late Miocene. The second skull, assigned to *Cardiomyis* sp., is housed in the Museo de La Plata. Furthermore, from the revision of the holotypes of the species of *Caviodon* (*C. multiplicatus*, *C. bravardi*, *C. (Lelongia) paransensis*, *C. angustidens* and *C. scalai* from the Conglomerado osífero of the Ituzaingó Formation; late Miocene, Argentina) we propose their synonymy with the type species *C. multiplicatus*, decreasing the specific diversity in that locality. Finally, our phylogenetic analysis indicates that the species of ‘cardiomyines’ are paraphyletic, placing them in a basal position among the Hydrochoerinae.

Key words: Hydrochoerinae, ‘Cardiomyines’, Miocene, Pliocene, South America.

THE family Caviidae is among the most diverse groups of caviomorph rodents and includes three main extant lineages: Caviinae (cuyes or ‘guinea pigs’), Dolichotinae (maras), and Hydrochoerinae (capybaras and rock cavies) (Mares & Ojeda 1982; Woods 1984; Rowe & Honeycutt 2002; Woods & Kilpatrick 2005; Pérez 2010; Dunnum 2015).

‘Cardiomyines’ are extinct Caviidae that inhabited large parts of South America during the middle Miocene and Pliocene (Vucetich *et al.* 2010; Vucetich & Pérez 2011; Kerber *et al.* 2017) and were long considered to be related to the cavies and maras. They are now considered to be more closely related to Hydrochoerinae than to either

Caviinae or Dolichotinae on the basis of phylogenetic analysis (Pérez 2010; Pérez & Vucetich 2011; Pérez *et al.* 2014, 2017a; Vucetich *et al.* 2012, 2015). They were diverse and abundant, large terrestrial rodents apparently not strictly linked to living in association with permanent water bodies as capybaras do (‘cardiomyines’ are recorded in sediments of different origins; Esteban *et al.* 2014) and would have reached more than 15 kg (Vucetich *et al.* 2015). These rodents had a plesiomorphic dentition within hydrochoerines, characterized by the presence of a p4 composed of three prisms, the m1–m3 and P4–M2 formed by two prisms, the M3 formed by three to seven main prisms plus a small posterior projection that may

be present or not, and a palate as broad as that of the living capybara *Hydrochoerus hydrochaeris* (Kraglievich 1930; Pascual *in* Pascual *et al.* 1966; Pérez *et al.* 2014).

The oldest record of ‘cardiomyines’ is an isolated lower molar from the Río Frías Formation (Guenguel River; Mayoan SALMA assigned to the middle Miocene dated as 11.5 Ma; Dal Molin & Franchi 1996) that has been tentatively referred to *Cardiomyis? andinus* (Kraglievich 1930; Vucetich & Pérez 2011). However, ‘cardiomyines’ are well recorded from the early late Miocene to the Pliocene, as four genera with several species; *Xenocardia* Pascual & Bondesio, 1963, *Procardiomyis* Pascual, 1961, *Cardiomyis* Ameghino, 1885 and *Caviodon* Ameghino, 1885 (Figs 1, 2).

A revision of the material from various collections of Argentina and the USA suggested that the diversity of these rodents during the late Miocene was higher than so far known. One skull from the Andalhuala Formation of Catamarca (‘Araucanian’), notable for its preservation, was collected by the Second Marshall Field Paleontological Expedition to Argentina in 1926 together with some mandible remains, and is housed in the Field Museum of Natural History, Chicago, USA. This skull, FMNH P 14457, was catalogued as *Cardiomyis ameghinorum*, a common species for the late Miocene of north-western Argentina (Marshall & Patterson 1981): this determination is here revised. Another quite complete skull, housed in the Museo de La Plata (MLP 55-IV-28-11), was catalogued *in schedis* as *Cardiomyis* sp. but was unpublished. It was found in the Arroyo Chasicó Formation (late Miocene) cropping out on the banks of Arroyo Chasicó, south-west Buenos Aires Province. In this paper both skulls and other materials housed in the FMNH and MLP, referred to ‘cardiomyines’ are studied and scored for inclusion in a phylogenetic analysis, to improve our understanding of the relationships of the group. In addition, a synonymy of species of *Caviodon* from the Conglomerado osífero of the Ituzaingó Formation (late Miocene; also known as Mesopotamian) is proposed. Evolutionary and biogeographical issues resulting from the new taxonomic arrangement are also addressed.

MATERIAL AND METHOD

Taxonomic nomenclature. According with the taxonomic and phylogenetic analyses conducted here, ‘Cardiomyinae’ is not the valid status of this group; therefore quotation marks are used for this assemblage of basal hydrochoerines.

Dental and anatomical nomenclature. Nomenclature and abbreviations for dental structures (Fig. 3) refer to the Spanish names in order to conform to previous publications (Frailey 1986), and follow Vucetich *et al.* (2011).

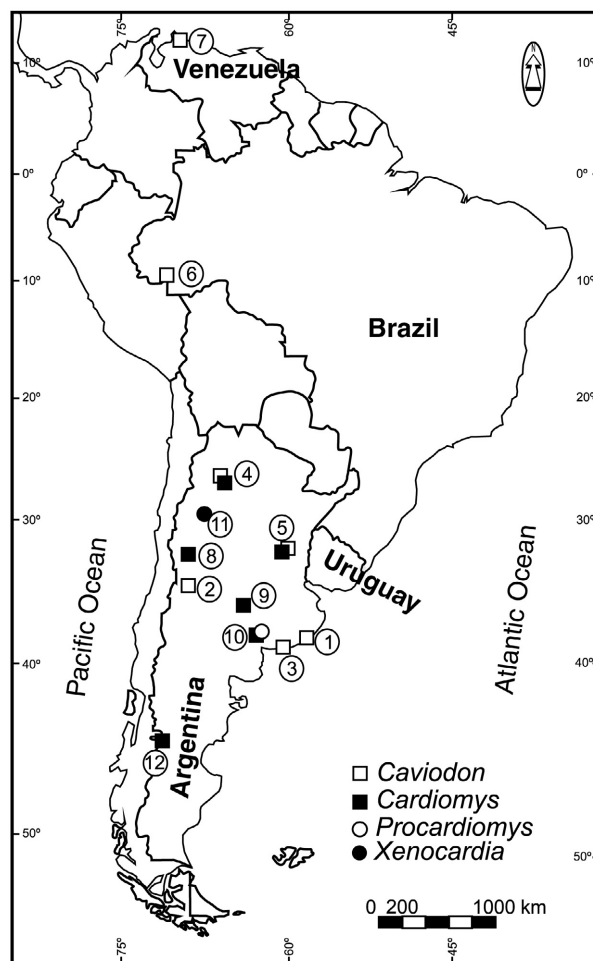


FIG. 1. Location map with the South American records of ‘cardiomyines’. 1, Chapadmalal Formation, Chapadmalal, Buenos Aires Province; 2, Aisol Formation, Arroyo Seco de la Frizada, Mendoza Province; 3, Monte Hermoso Formation, Farola Monte Hermoso, Buenos Aires Province; 4, Andalhuala Formation, Río de Yapes, Catamarca Province; 5, Conglomerado osífero of the Ituzaingó Formation, Paraná River Banks, Entre Ríos Province; 6, Madre de Dios Formation, Western Amazonia, Peru; 7, San Gregorio Formation, San Gregorio, Venezuela; 8, Huayquerías Formation, Huayquerías de San Carlos, Mendoza Province; 9, Cerro Azul Formation, several localities, La Pampa Province; 10, Arroyo Chasicó Formation, Arroyo Chasicó, Buenos Aires Province; 11, Huachipampa Formation, Loma del Camello, San Juan Province; 12, Río Frías Formation, Chubut Province. For temporal calibration of units see Deschamps *et al.* (2013), Vucetich *et al.* (2011), Milana *et al.* (2003).

The mandibular nomenclature follows that of Woods & Howland (1979) and Pérez (2010). The postcranial nomenclature follows that of Popesco *et al.* (2003) and Schaller (2007).

Upper and lower case letters refer to upper and lower teeth, respectively; i, p4, m1–3 and I, P4, M1–3 refer to lower and upper incisor, fourth premolar, and molars

FIG. 2. Stratigraphical and geographical distribution of 'cardiomyines'. 1, Chapadmalal Formation, Chapadmalal, Buenos Aires Province; 2, Aisol Formation, Arroyo Seco de la Frazada, Mendoza Province; 3, Monte Hermoso Formation, Farola Monte Hermoso, Buenos Aires Province; 4, Andahuala Formation, Río de Yapes, Catamarca Province; 5, Conglomerado osífero of the Ituzaingó Formation, Paraná River Banks, Entre Ríos Province; 6, Madre de Dios Formation, Western Amazonia, Peru; 7, San Gregorio Formation, San Gregorio, Venezuela; 8, Huayquerías Formation, Huayquerías de San Carlos, Mendoza Province; 9, Cerro Azul Formation, several localities, La Pampa Province; 10, Arroyo Chasicó Formation, Arroyo Chasicó, Buenos Aires Province; 11, Huachipampa Formation, Loma del Camello, San Juan Province; 12, Río Frías Formation, Chubut Province. For temporal calibration of units see Deschamps *et al.* (2013), Vucetich *et al.* (2011), Milana *et al.* (2003).

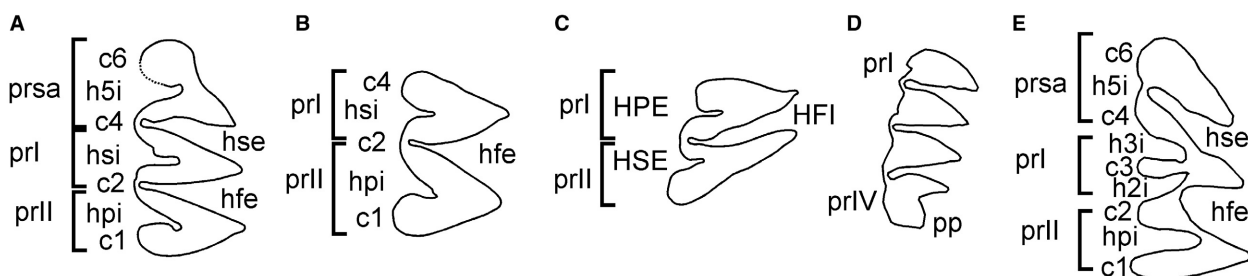
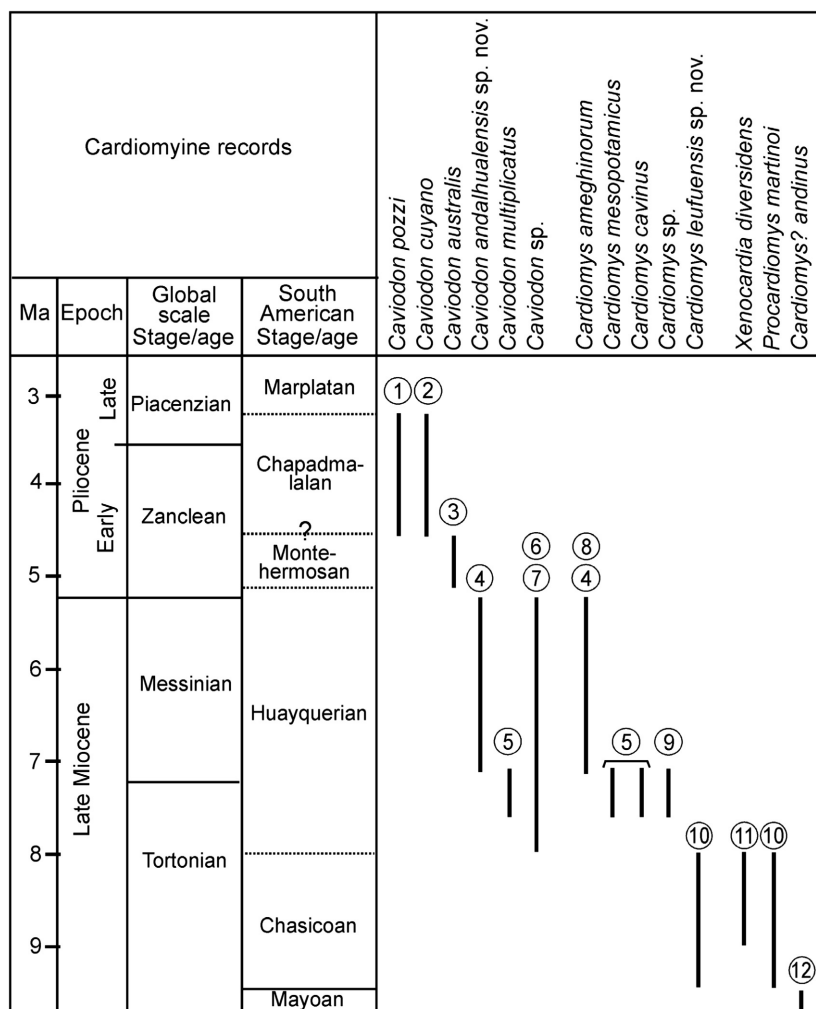


FIG. 3. Dental nomenclature of 'cardiomyines' and p4 of derived hydrochoerines. A, p4. B, m1 or m2. C, M1 or M2. D, M3. E, p4. *Abbreviations:* Upper and lower case letters refer to upper and lower teeth, respectively: i, p4, m1–3, and I, P4, M1–3 refer to lower and upper incisor, fourth premolar and molars 1–3; c1, c2, c3, c4, c6, columns 1, 2, 3, 4, 6; h2i/h3i/h5i, second/third/fifth internal fissure; hfe, fundamental external fissure (= hypoflexid); HFI, fundamental internal fissure (= hypoflexus); hpi/HPI, primary internal/external fissure; hse, secondary external fissure; hsi/HSE, secondary internal/external fissure; pp, posterior projection; prI–IV, prisms I–IV; prsa, supernumerary anterior prism.

1–3; c1, c2, c3, c4, c6 columns 1, 2, 3, 4, 6; hpi/HPI, primary internal/external fissure; hse, secondary external fissure; hsi/HSE, secondary internal/external fissure; h5i, fifth internal fissure; HFI, fundamental internal fissure

(= hypoflexus); hfe, fundamental external fissure (= hypoflexid); nMpi, notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle; prI–II, prisms I–II; prsa, supernumerary anterior prism.

The hsi in the simple lower premolars (i.e. three prisms with only hpi, hsi, and h5i) of Hydrochoerinae such as *Kerodon*, *Cardiomyis* and *Caviodon* is here interpreted as homologous to h3i (or h5i *sensu* Mones 1991) of complex lower premolars (i.e. three prisms with more lingual fissures than hpi, hsi and h5i) of most derived Hydrochoerinae such as *Cardiatherium*, *Phugatherium*, *Hydrochoeropsis*, *Nechoerus* and *Hydrochoerus* (Fig. 3E). This interpretation is based on that h3i (as hsi) is in prI in all species of Hydrochoerinae, whereas h2i is in prI or prII; moreover, h2i is usually shallower than h3i.

Dental measurements. AP, anteroposterior length; AW, anterior width measured at the first prism; HPEL, HPE length; HPIL, hpi length; HSEL, HSE/hse length; HSIL, hsi length; HFEL, hfe length; MW, middle width, prI width of p4; PW, posterior width measured at the last prism (Table 1).

Morphological analysis. The comparative morphological study of the material was made using the holotypes of ‘cardiomyine’ species; some of them are the single specimens of the taxon, even isolated teeth, and others from Argentine museums referred to ‘cardiomyines’ (Appendix).

Phylogenetic analysis. To test the phylogenetic position of the new species and the relationships of the ‘cardiomyines’ within Caviidae, a phylogenetic analysis was performed based on the data matrix of Pérez *et al.* (2017a). The combined matrix (Pérez *et al.* 2017b, suppl. data 1) for this analysis comprises 59 taxa (root: *Proechimys*; basal cavioids: *Cuniculus*, *Dasyprocta*, *Neoreomys*, ‘eocardiids’; and Caviidae: Caviinae, Dolichotinae and Hydrochoerinae), 133 morphological characters (mandibular, cranial, dental and postcranial) and 4014 characters from DNA sequences of nuclear and mitochondrial genes (Pérez *et al.* 2017b, suppl. data 2). The equally weighted parsimony analysis was conducted using TNT 1.1 (Goloboff *et al.* 2008a, b), performing a heuristic search of 1000 Wagner tree replicates followed by TBR branch swapping, collapsing zero-length branches under the strictest criterion. Unstable taxa in the set of the most parsimonious trees (MPTs) were identified using IterPCR (Pol & Escapa 2009) to derive an informative reduced consensus. Support values were calculated using Bremer indices and Bootstrap. Bremer support was calculated using the script BREMER.RUN provided with TNT, and resampling techniques were conducted with 1000 pseudoreplicates in TNT. Support analyses were conducted on the complete dataset, but the fossil taxon *Allocavia* (which was unstable in the MPTs) was pruned from the resulting trees to detect support values irrespective of the alternative positions of this fragmentary taxon in the suboptimal trees

(for Bremer support) and in the trees derived from the resampling techniques.

Institutional abbreviations. FMNH P, Paleontological Collection, Field Museum of Natural History, Chicago, USA; MACN A, Museo Argentino de Ciencias Naturales, Ameghino Collection, Buenos Aires, Argentina; MACN-Pv, Museo Argentino de Ciencias Naturales, Vertebrate Paleontology Collection, Buenos Aires, Argentina; MHNSR-PV, Museo de Historia Natural de San Rafael, Mendoza, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMH-CH, Museo Municipal de Monte Hermoso ‘Vicente Di Martino’, Colección Chasicó, Argentina; MMP, Museo Municipal de Mar del Plata, Mar del Plata, Argentina; UFAC, Universidade Federal do Acre (Campus Rio Branco).

SYSTEMATIC PALAEOLOGY

Order RODENTIA Bowdich, 1821

Suborder HYSTRICOGNATHI Tullberg, 1899

Superfamily CAVIOIDEA (Fischer de Waldheim, 1817)

Family CAVIIDAE Fischer De Waldheim 1817

Subfamily HYDROCHOERINAE Gray, 1825

Genus CAVIODON Ameghino, 1885

1888 *Diacartherium* Ameghino, pp. 10–11.

Type species. *Caviodon multiplicatus* Ameghino, 1885.

Diagnosis. Large caviomorphs with euhiposodont cheek teeth and bilobular P4–M2 and m1–m3 (modified from Pascual in Pascual *et al.* 1966). M3 formed by five to seven prisms, the last of which may have a posterior extension variably developed; p4 formed by three prisms; hpi and hsi of p4 present and similar in depth; m1–m3 and P4–M2 with his–hpi and HPE–HSE subequal in depth and proportionally deeper than in *Cardiomyis* and *Procardiomyis*, and located close to the middle of the prism; prisms transversely longer and with straighter margins than in *Cardiomyis* and *Procardiomyis*; prisms of M3 lanceolate except the first or two first prisms, which are heart-shaped; M1 anteroposteriorly shorter than P4 and M2; palate broad and almost flat, similar to the condition of *Cardiatherium*, and the most derived hydrochoerines (*Phugatherium*, *Hydrochoeropsis*, *Nechoerus* and *Hydrochoerus*; Fig. 3E); mesopterygoid fossa wide and rounded in ventral view; dorsal border of the skull at the level of the frontal-parietal bones, mainly flat; sagittal crest present; shallow temporal fossae.

Included species. The type species, *C. australis* (Ameghino, 1888), *C. pozzi* Kraglievich, 1927, *C. cuyano* Vucetich *et al.*, 2011 and *C. andalqualensis* sp. nov.

TABLE 1. Dental measurements (in mm).

Species	Tooth	AP	prIW	prIIW	prsaW	npr
<i>Caviodon andalqualensis</i> sp. nov.						
FMNH P 15287	p4	9.12	4.41	4.26	4.36	
FMNH P 14434	p4	9.81	4.78	4.85		
	m1	7.59		4.36		
	m2		5.01			
FMNH P 14457	P4					
Holotype	M1	6.44	5.69	5.13		
	M2	7.11	5.51	6.34		
	M3	16.6	5.85			6
<i>Caviodon multiplicatus</i>						
MACN-Pv 5891	M3	10.8	4.9			5
<i>Caviodon cuyano</i>						
MHNSR-PV 1101	p4	14.24	6.56	7.04	6.08	
Holotype	m1	9.76	7.04	7.2		
	m2	9.6	7.68	8.08		
	m3	12	7.84	8.04		
	P4	8.96	5.76	7.2		
	M1	7.36	6.72	7.36		
	M2	8	6.72	8.16		
	M3	19.56	7.74			7
<i>Caviodon australis</i>						
MACN-Pv 14481	m1	7.5	4.95	5.4		
	m2	7.5	5.55	5.55		
MACN A-1099	P4	9.41	5.88	7.01		
Holotype	M1	7.55	6.25	6.81		
	M2	8.21	6.31	7.01		
	M3	19.3	6.26			6
<i>Caviodon pozzi</i>						
MACN-Pv 6915	p4	10.35	5.1	5.25	4.8	
	m1	7.25	5.25	5.1		
	m2	7.8	6	6		
MMP 525-M	P4	7.36	5.12	6.24		
	M1	5.92	5.44	6.08		
	M2	6.4	5.44	5.76		
	M3	14.45	5.42			6
<i>Cardiomyis leufuensis</i> sp. nov.						
MLP 76-VI-12-92	p4	11.2	5	5.51	4.9	
	m1	7.8	6	5.7		
	m2	8.6	5.6	6.8		
MLP 55-IV-28-11	P4	7.25		5.54		
Holotype	M1	5.19	4.8	4.93		
	M2	6.8	5.2	5.7		
	M3	11.9	4.95			4
<i>Cardiomyis cavinus</i>						
MACN-Pv 4593	m1	6.59	4.78	4.95		
Metatype (1)	m2	6.47	5.16	5.02		
<i>sensu</i>	m3	8.63	5.61	5.44		
Kraglievich 1932						
<i>Cardiomyis ameghinorum</i>						
MACN-Pv 8247	p4	10.6	5.23	5.84		
Holotype	m1	7.81	5.92	5.92		
	m2	7.44	5.89	5.91		
	m3	8.68	6.16	6.55		

(continued)

TABLE 1. (Continued)

Species	Tooth	AP	prIW	prIIW	prsaW	npr
MACN-Pv 8246	P4	7.4		5.54		
	M1	5.19	4.8	4.93		
	M2	5.8	4.72	5.21		
	M3	12.9	4.54			4

AP, anteroposterior length; npr, number of prisms; prI/IIW, width of prism I/II; prsaW, width of supernumerary anterior prism.

Geographical and stratigraphical distribution. Late Miocene (Huayquerian; Conglomerado osífero of the Ituzaingó Formation, Paraná, Entre Ríos); early Pliocene (Montehermosan; Monte Hermoso Formation, Farola Monte Hermoso, Buenos Aires); late Pliocene (Chapadmalalan; Chapadmalal Formation, Buenos Aires; Aisol Formation, Arroyo Seco de la Frazada, Mendoza; late Miocene (Huayquerian) of Solimoes Formation, Patos, Brazil; and Pliocene of the San Gregorio Formation, San Gregorio, Venezuela (Fig. 1).

Caviodon multiplicatus Ameghino, 1885

1927 *Caviodon bravardi* Kraglievich, p. 593.

1930 *Caviodon (Lelongia) paranensis* Kraglievich, pp. 181–184, fig. 1.

1932 *Caviodon (Paracaviodon) angustidens* Kraglievich, p. 179.

1932 *Caviodon scalai* Kraglievich, p. 176.

Holotype. MACN-Pv 5891: right M3.

Remarks. These species of *Caviodon* were based on isolated M3 from the same geographical and stratigraphical provenance (see Appendix). They differ only in increasing size and depth of labial fissures, as well as in the addition of posterior prisms with size/age (Table 1). In this regard, Vucetich *et al.* (2011) had already suggested that *Caviodon bravardi* and *C. (Lelongia) paranensis* are synonymous; they interpreted their differences as ontogenetic variation (Vucetich *et al.* 2005). The holotypes of *C. (Paracaviodon) angustidens* and *C. scalai* are lost; however, the description and measurements given by Kraglievich (1932) are within the range of ontogenetic variation of *C. multiplicatus*. In this context, we propose that these species are synonyms of *C. multiplicatus*.

Caviodon andalqualensis sp. nov.

Figures 4–7

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Derivation of name. In reference to the bearing unit, the Andalhuala Formation.

Holotype. FMNH P 14457: skull, atlas, axis and three cervical vertebrae.

Type locality. Locality 4, Río de Yapes, level XX (Marshall & Patterson 1981).

Diagnosis. *Caviodon andalhualensis* sp. nov. differs from other species of *Caviodon* by a unique set of characters: skull more robust than *C. pozzi* but less robust than *C. cuyano*; cheek teeth with relatively thin prisms with HPE and HSE shallower than in *C. pozzi* and *C. cuyano*, deeper than in *C. multiplicatus*, and more transversal than in *C. australis*; M3 with six prisms plus a thin and long posterior projection (Fig. 5A) transversally oriented as in *C. pozzi* (Fig. 5E), but different from the condition of *C. cuyano* which has seven prisms (Fig. 5D), *C. australis* which has five prisms plus a rounded posterior projection, and *C. multiplicatus* which has five prisms plus a thin posterior projection (Fig. 5F–H); mesopterygoid fossa relatively narrower than in *C. cuyano* and *C. pozzi*.

Horizon and locality. Valle de Santa María, Locality 4, Río de Yapes, level XX; Puerta de Corral Quemado, above level 19 (Marshall & Patterson 1981). Levels XX and 19 belong to the Andalhuala Formation and are below level 23, which is dated as 5.30 ± 0.2 Ma and 5.64 ± 0.16 (Butler *et al.* 1984 and Latorre *et al.* 1997, respectively), and above level 15, dated as 6.70 ± 0.05 Ma and 7.14 ± 0.02 Ma (Butler *et al.* 1984 and Latorre *et al.* 1997, respectively) (see Esteban *et al.* 2014). Therefore, a late Miocene Messinian age is proposed for the fossil-bearing sediments.

Referred material. FMNH P 14434, right jaw fragment with p4–m2, from level 15–32 (*in schedis* ‘above level 19’) and FMNH P 15287, left jaw fragment with p4 (no horizon), were assigned to *Cardiomys ameghinorum latidens in schedis* and by Marshall & Patterson (1981). However, because of their deep hsi and hpi in the middle of the prisms, including in the middle prism (prI) of p4, similar to those of upper teeth of *C. andalhualensis* sp. nov., they are here transferred to this taxon.

Description

Skull. The premaxilla occupies the anterior portion of the rostrum and has a conspicuous anterior ridge, dorsal to the incisor alveolus and anteroventral to the nasal cavity; it is more vertical

than that of *C. pozzi*, which is oblique. It cannot be compared with other species of *Caviodon* because the specimens are broken. The skull of *C. andalhualensis* is narrower than that of *C. cuyano* (Fig. 6A–C).

In dorsal view (Fig. 4A), the nasals are flat (these bones are missing in *C. pozzi*, and are broken in *C. cuyano*). The anterior end of the nasals is posterior to the anteriormost part of the premaxilla. The frontals are also flat, like those of *C. pozzi*. The parietals are slightly convex posteriorly and have a medial sagittal crest. Laterally there is a shallow temporal fossa.

In lateral view (Fig. 4B), the ascendant ramus of the premaxilla is wider at the posterior margin, and more backwardly extended (surpassing the naso-frontal suture) than in *C. pozzi* (in which it extends up to this suture). The masseteric fossa is anteriorly formed by the premaxilla and posteriorly by the maxilla; the fossa is deeper and its dorsal, anterior and ventral margins are more developed than in *C. pozzi* (this feature cannot be seen in *C. cuyano*). In both species (*C. andalhualensis* and *C. pozzi*) the diastema is shorter than the cheek teeth series (Table 1), but in *C. pozzii* the diastema has a different height and inclination, as the incisor alveolus is above the line of the cheek teeth series. The orbit appears to be displaced backwards relative to the tooth row as in *C. pozzi*. Above the dorsal root of the antorbital bar there is a horizontal canal (Fig. 4B), which is very conspicuous as a double wave in *Cardiatherium* and *Phugatherium*, but is shorter in other caviomorphs.

In ventral view (Fig. 4C), the palate of *C. andalhualensis* is narrower than in *C. australis* and *C. cuyano*. The maxilla–palatine suture does not contact the palatine foramina, unlike *C. pozzi* in which it does. The maxillary area of the palate occupies 50% of the palate, as in *C. pozzi* and *C. australis*, unlike *C. cuyano* in which this area is short and narrow, although in the three species the suture is at the level of the posterior lobe of M2. The posterior margin of the anterior root of the zygomatic arch is, as in *C. cuyano*, slightly posterior than in *C. pozzi*. The mesopterygoid fossa is narrower than in *C. pozzi* and *C. cuyano*. The pterygoids (right and left) of the new species are closer to each other than those of *C. pozzi*. The posterolateral extensions of the palatine are wider than in *C. pozzi* and *C. cuyano*. The mesopterygoid fossa occupies 50.84% the width of the palatine at the level of the last prism of M3 (60% in *C. cuyano* and 61% in *C. pozzi*).

The basicranium is rather complete with the sphenoid complex (orbitosphenoid, presphenoid, basisphenoid, alisphenoid), the basioccipital and the ectotympanic (Fig. 4C). The presphenoid is long and narrow; it is anteriorly fused to the orbitosphenoid, laterally to the alisphenoid and posteriorly to the basisphenoid. This latter is anteriorly thin, posteriorly wide and fused to the basioccipital. The alisphenoid is a thin lamina slightly sloping and laterally joined to the glenoid cavity of the squamosal. The basioccipital is robust, wide and laterally in contact with the ectotympanic, which is globose but relatively small in comparison with the skull (similar to other hydrochoerines). The occipital condyle is dorsoventrally elongated (Fig. 4C). The occipital is slightly posteriorly concave and has a dorsal ridge through its entire border.

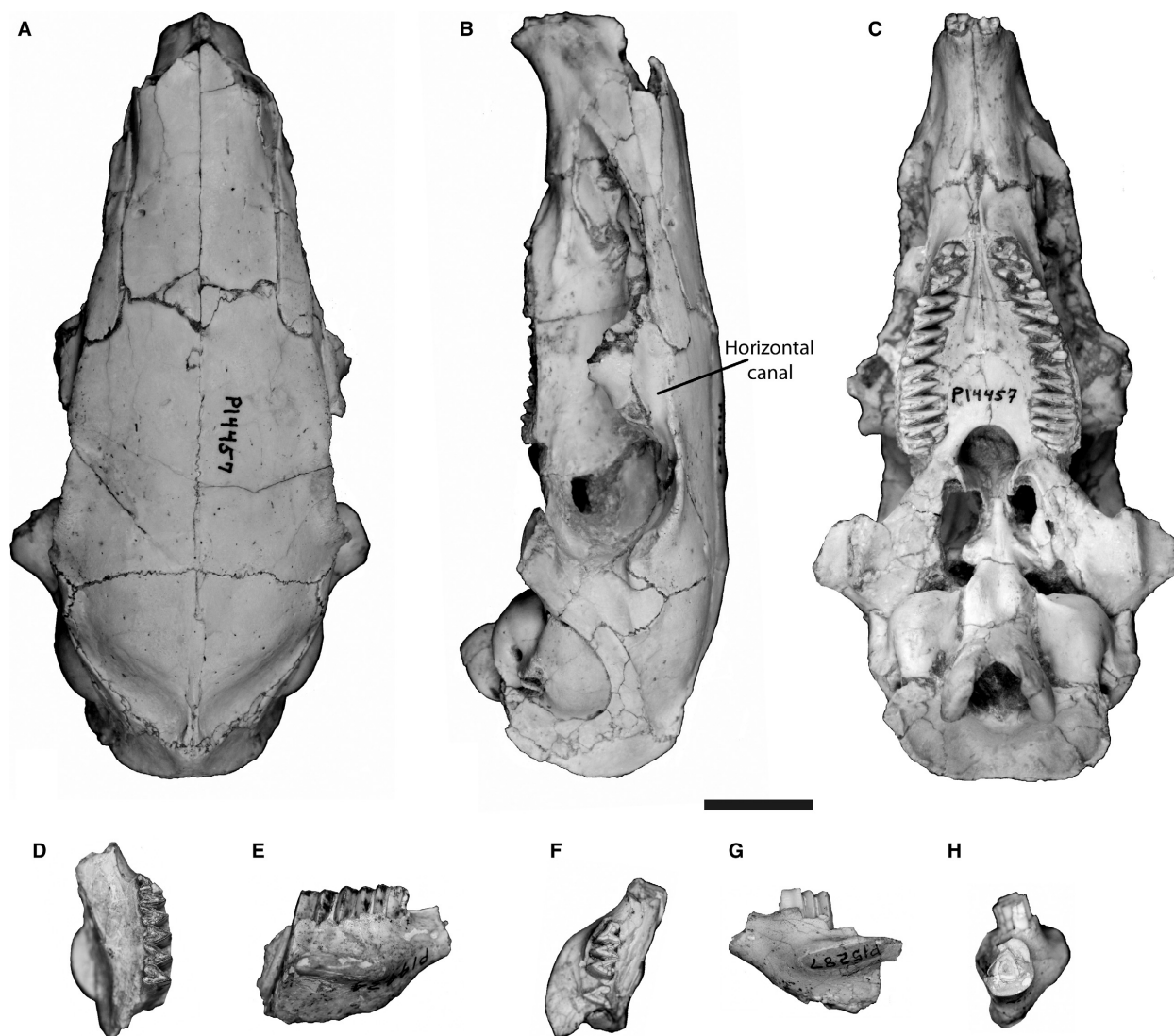


FIG. 4. *Caviodon andalhuensis* sp. nov. A–C, FMNH P 14457, skull: A, dorsal; B, lateral; C, ventral view. D–E, FMNH P 14372, right mandible fragment: D, occlusal; E, labial view. F–H, FMNH P 15287, left mandible fragment: F, occlusal; G, labial; H, frontal view with fragment of incisor. Scale bar represents 20 mm.

Mandible. The preserved fragments of the dentary in FMNH P 14434 and FMNH P 15287 (Fig. 4D–H) are robust. The nMpi is placed between p4 and m1 below the alveolar line; it is large and forms a continuous and thick border that extends from the anterior margin of the p4 ascending posteriorly (Fig. 4E, G). The mental foramen is located anteriorly to p4 and at little above the level of nMpi.

Dentition. The incisor is preserved only in the intraalveolar portion; it is triangular in cross-section, being the proximal angle very acute (Fig. 4H). P4–M2 and m1–m3 are double-hearted; M3 has six prisms and a small posterior projection; p4 has three prisms. Some features participate in the shape of molariforms, mainly the anteroposterior length of each prism, the location of the fissure, its depth and its shape, as well as the shape of the hypoflex. All of the molariforms of the new species are narrower

than those of *C. cuyano* and *Cardiomyis*, and thicker than *C. pozzi* and *C. australis*.

Upper teeth. HPE and HSE of P4–M2 of *C. andalhuensis* (Fig. 5A) penetrate less than 30% of the occlusal surface of the prism as in *C. australis* (Fig. 5B, C), in contrast with the condition of *C. cuyano* and *C. pozzi* (Fig. 5D, E) in which these fissures penetrate up to almost 50% of the width of the occlusal surface. The M3 of *C. andalhuensis* has six prisms and a small posterior projection, as in *C. pozzi* (Fig. 5A, E). *C. australis* has six prisms (the last one thicker, Fig. 6D) and *C. cuyano* has seven prisms on the right dental series, while on the left it has seven prisms plus a small posterior projection (Fig. 6B). The fissures of the new species are deeper, especially those of prisms 1–4, than those of *C. multiplicatus* and *C. australis*, but shallower than in *C. pozzi* and *C. cuyano*.

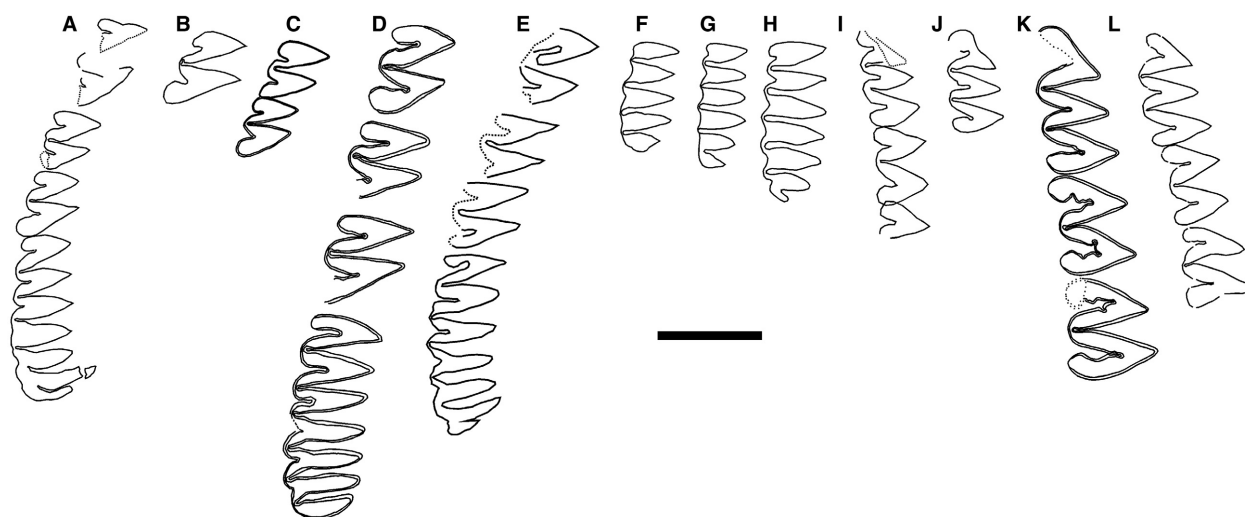


FIG. 5. Occlusal schemes of the dental series of the species of *Caviodon*. A–H, upper teeth; I–L, lower teeth. A, I–J, *Caviodon andalhalensis* sp. nov. B–C, *Caviodon australis*. D, K, *Caviodon cuyano*. E, L, *Caviodon pozzi*. F–H, *Caviodon multiplicatus*. A, FMNH P 14457 (holotype), right P4–M3. B, MACN A-1099 (holotype of *Diacartherium australe*) left P4 (reversed). C, MACN-Pv 7326, left M1–M2 (reversed). D, MHNSR-PV 1101 (holotype) right P4–M3. E, MMP 525-M, right P4–M3. F, MACN-Pv 5891 (holotype) right M3. G, MACN-Pv 4495 (holotype of *Caviodon bravardi*, left M3. H, MACN-Pv 13471 (holotype of *Caviodon (Lelongia) paranense*), right M3. I, FMNH P 14434, right p4–m1 and prI of m2. J, FMNH P 15287 right p4. K, MHNSR-PV 1101 right p4–m2. L, MACN-Pv 6915 (holotype) right p4–m2. Scale bar represents 10 mm.

Lower teeth. The lower molariforms of *C. andalhalensis* are wider than in *C. pozzi* and *C. australis* and narrower than in *C. cuyano* (Fig. 5).

The prsa of p4 is linguallong due to an anterolingual widening (Fig. 5I, J). The prI is the narrowest and has a single deep fissure, unlike *Cardiomys* in which this prism lacks hsi or has two very shallow ones. The hse and hfe are very deep and have cement. The h5i, hsi and hpi are deep, with different curvature and orientation. The enamel is interrupted in c1 and c4 (Fig. 4).

The m1–m2 are bilobed and double heart-shaped with funnel-shaped hfe, and the hsi and hpi relatively deep (Fig. 5I, J).

Postcranium. Among the cardiomyines, only a few postcranial elements of *Caviodon cuyano* have been described (Vucetich *et al.* 2011). However, the preserved bones (sacrum, femora, knee joint, some phalanges and sesamoids) are different from those preserved in *C. andalhalensis*, and thus cannot be compared. Only the atlas, axis and the following three cervical vertebrae (3–5) are known for *C. andalhalensis*. The atlas (Fig. 7A) is mostly complete, showing the spinous process dorsally, the transverse process, the cranial articular fovea, transverse foramen, and foramen of wing. The cranial articular fovea is covered with sediment. The axis (Fig. 7B, C) presents in anterior (or cranial) view the conspicuous spinous process and the vertebral arch, whereas the transverse process is broken. The caudal articular process and caudal extremity of corpus (vertebral fossa), both relatively large, are seen in posterior (or caudal) view; the little ventral tubercle is seen in ventral view. The other three cervical vertebrae 3–5 (Fig. 7D) are smaller, still articulated, and with part of the spinous process; the cranial extremity of body and the ventral plate are seen in anterior view. The vertebral

arch, caudal articular process, caudal extremity of corpus and the ventral plate are preserved.

Genus *CARDIOMYS* Ameghino, 1885

non 1780 *Procavia* Storr

1885 *Procavia* Ameghino

1889 *Neoprocavia* Ameghino

1932 *Parodimys* Kraglievich, p. 111, fig. 5q.

Type species. *Cardiomys cavinus* Ameghino, 1885.

Diagnosis. Medium size caviomorphs with euhypsodont cheek teeth and bilobular P4–M2 and m1–m3 (modified from Pascual in Pascual *et al.* 1966). M3 composed of four main prisms and a posterior extension, more or less developed; all prisms relatively compressed antero-posteriorly, with an external fissure in each one, or with two very shallow fissures in the third and fourth prisms; p4 composed by three prisms, prsa with very shallow h5i or not present, prI with hsi absent forming a convex lingual margin, or with two very shallow fissures next to columns c2 and c4, the margin being straight, depressed with respect to the lingual margin, prII with deeper hpi next to c2; the remaining molars with hsi and hpi/HPE and HSE shallower, different in depth, and closer to c2 than in *Caviodon*; temporal fossae relatively deep. It differs from *Procardiomys* which has only three prisms in



FIG. 6. Comparison of 'cardiomyine' skulls in ventral view. A, FMNH P 14457, *Caviodon andalhualensis* sp. nov. B, MHNSR-PV 1101, *Caviodon cuyano*. C, MMP 525-M, *Caviodon pozzi*. D, MACN-Pv 7326, *Caviodon australis*. E, MACN-Pv 8246, *Cardiomyis ameghinorum*. F, MLP 55-IV-28-11, *Cardiomyis leufuensis* sp. nov. Scale bar represents 20 mm.

the M3 and the external fissures are shallower; from *Kerodon* because it has two prisms in M3, and from *Xenocardia*, *Caviodon*, *Cardiatherium*, *Phugatherium*,

Hydrochoeropsis, *Nechoerus* and *Hydrochoerus* because these all have five or more prisms in M3 with deeper labial flexi.

Included species. *Cardiomyx ameghinorum* Rovereto, 1914 (including *C. ameghinorum* var. *latidens* Rusconi, 1914); *Cardiomyx mesopotamicus* (Ameghino, 1885); *Cardiomyx? andinus* Kraglievich, 1930; *Cardiomyx* (*Pseudocardiomyx*) *intermedius* Kraglievich, 1932; *Cardiomyx* (*Pseudocardiomyx*) *minutus* Kraglievich, 1932; *Cardiomyx* (*Pseudocardiomyx*) *paranensis* Kraglievich, 1932; *Cardiomyx* (*Pseudocardiomyx*) *puelchensis* Rusconi, 1944.

Remarks. *Cardiomyx vignatii* Kraglievich, 1932 based on the specimen MACN-Pv 3944 probably belongs to *Caviodon* (see Discussion, below).

Geographical and stratigraphical distribution. Middle Miocene (Mayoan; Río Frías Formation, Chubut Province; 11.5 Ma; Dal Molin & Franchi 1996); early late Miocene (Chasicóan; Arroyo Chasicó Formation, Buenos Aires); late Miocene (Huayquerian; Conglomerado osífero of the Ituzaingó Formation, Paraná, Entre Ríos; Cerro Azul Formation, La Pampa; Huayquerías Formation, Mendoza; Chiquimil, Andalhuala and Corral Quemado formations, Puerta de Corral Quemado, Valle de Santa María, Catamarca). The reports of *Cardiomyx* from the Montehermosan and Chapadmalalan (Pascual *et al.* 1966; Tonni *et al.* 1992a, b) have not been corroborated. Probably the mention for the Montehermosan refers to lists including materials from the 'Mesopotamian' assemblage of the Conglomerado osífero, that was considered to range from the Chasicóan to the Montehermosan before the paper by Cione *et al.* (2000), and subsequent revisions of rodents (Vucetich & Verzi, 1995; Vucetich *et al.* 2011, 2015, 2016). Even, in their revision of the mammals from Farola Monte Hermoso, Tomassini *et al.* (2013) reported *Cardiomyx* sp. with doubts, from data taken from the literature. Its presence in Chapadmalal mentioned by Pascual *et al.* (1966) is probably a mistake because no material of this genus from this locality could be found.

Cardiomyx leufuensis sp. nov.

Figures 6F, 8, 9A, C–F

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Derivation of name. From *leufú*, the Pampa word for Arroyo (Creek) in reference to the provenance, Arroyo Chasicó.

Holotype. MLP 55-IV-28-11: partial skull with right P4, M2–M3 and left P4–M3 (Fig. 8A–C).

Type locality. Campo Quinteros, margin of the Arroyo Chasicó, Buenos Aires Province; Arroyo Chasicó Formation, Late Miocene.

Diagnosis. The hpi and hsi of m1–m2 shallower than in *C. cavinus* (Fig. 9K); m1–m2 with narrower prisms than the molar of *Cardiomyx? andinus* which is more heart-shaped or convex; skull more slender and palate narrower than in *C. ameghinorum*; prI of p4 has no hsi and the lingual wall is slightly convex, differing from *C. ameghinorum* in which the prI presents two small and very shallow fissures next to columns c2 and c4. It differs from *C. mesopotamicus* (Fig. 9I) in that the prI of *C. leufuensis* more lingually extended, the prII is wider, the apex of hfe is directed forward, and hsi shallower. *Cardiomyx* (*Pseudocardiomyx*) *paranensis* has two small fissures in prI of the M2 in contrast with *C. leufuensis* that has only the HPE. *Cardiomyx intermedius*, *C. minutus* and *C. puelchensis* are lost, but according to the descriptions, they would be different from *C. leufuensis* sp. nov. because: *C. intermedius*, coincides with the description of *C. mesopotamicus* especially in the morphology of p4; p4 of *C. minutus* presents the two small fissures in prI, differing from *C. leufuensis* which has only HPE; and p4 of *C. puelchensis* is smaller, and has two external fissures in prII (Rusconi 1944).

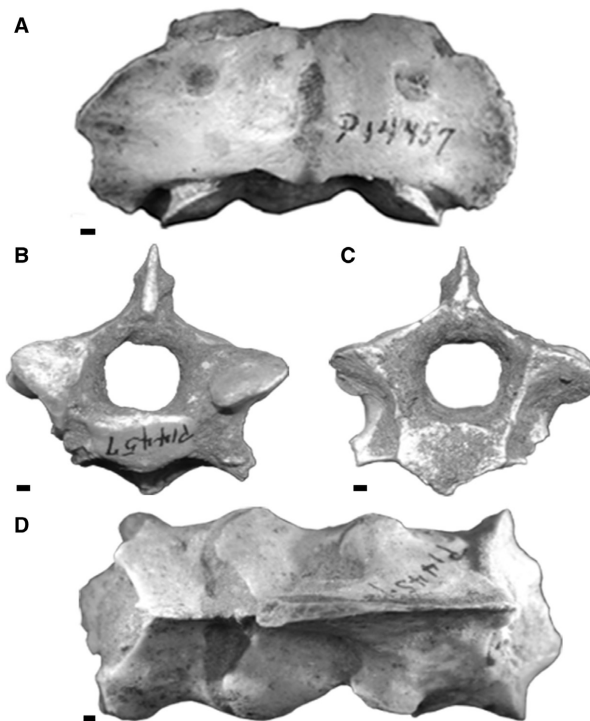


FIG. 7. *Caviodon andalhualensis* sp. nov. A, atlas. B–C, axis. D, cervicals (3–5). All scale bars represent 1 mm.

Horizon and locality. Arroyo Chasicó, Arroyo Chasicó Formation, Vivero and Las Barrancas members, Quebrada del Hacha, Bajada de los Toros.

Referred material. MLP 76-VI-12-18a, fragment of palate with right P4-M1 and left P4 (Fig. 8F); MLP 76-VI-12-18b, right mandible fragment with p4-m3 and left mandible fragment with p4-m1 (Fig. 8G); MLP 76-VI-12-92, left mandible fragment with p4-m2 (Fig. 8D); MLP 92-XI-19-4, left mandible fragment with p4-m1; MLP 92-XI-19-19, palate fragment with right P4-M3 and left P4-M2, and both anterior rami of the zygomatic arch (Fig. 8E). The specimens MLP 76-VI-12-18a, b with palate and mandible fragments allow assignment of the mandibles MLP 92-XI-19-4 and MLP 76-VI-12-92 to this species. MLP 92-XI-19-4 has previously been referred to *Procardiomyis martinoi* (Vucetich & Pérez 2011), but later Pérez *et al.* (2014) considered it tentatively as *Cardiomyis*.

Description

Skull. Specimen MLP 55-IV-28-11 consists of a partially preserved skull, without the anterior portion of the rostrum; its left side is the best preserved (Fig. 8A–C). It can only be compared with *Cardiomyis ameghinorum*, which is a fragmentary skull that lacks the anterior portion (Fig. 6E).

In dorsal view (Fig. 8A), the nasals are wide and slightly dorsally convex, and the anterior margin is pointed. The lateral margins of the frontals are damaged but the beginning of the anterior margin of the orbit can be seen on the left side. The middle suture of the temporals has a conspicuous crest in the posterior region. The posterior margin of the skull is very sharp with a marked crest formed by the occipitals.

In lateral view (Fig. 8B), the premaxilla is deformed and broken and the ascendant ramus is wide but does not surpass the naso-frontal suture. The masseteric fossa is deformed and broken; it is anteriorly formed by the premaxilla and posteriorly by the maxilla. It has a longitudinal furrow more or less parallel to the margin of the masseteric arch; this arch is anteroposteriorly elongated. The anterior ramus of the zygomatic arch begins anterior to the P4. Only the dorsal root of the maxillary zygomatic process is preserved and is relatively wide. In the orbital region, the maxilla is posteriorly broken and deformed, but similar in length to the maxillary orbital portion of *Cardiomyis ameghinorum*. The squamosal is broad and extends posteriorly forming a downward curve, covering the ectotympanic. The ectotympanic is relatively small, with the auditory meatus opened posteriorly. Occipitals are oblique, projecting anteriorly downward.

In ventral view (Fig. 8C, E), the palate is relatively flat; the palatine foramina are elongated from the posterior margin of the M2, merging at the level of P4; the tooth rows are slightly convergent. Diastema length is approximately equal to the combined length of P4–M3 (30 mm). The rostrum width in front of the anterior root of the zygomatic arch is 16 mm, half the width

between both M3 (30 mm). The base of the anterior ramus of the zygomatic arch is posterolaterally oriented. The suture between maxilla and palatine runs from the posterior margin of the posterior palatine foramen toward the alveolar margin of M3, where it cannot be clearly seen because of a fracture. The mesopterygoid fossa is triangular in shape, with the middle anterior point at the level of prII of M3.

Mandible. The dentary (Fig. 8D, F, G) is robust and the nMpi is placed between p4 and m1 below the alveolar line; it is large and forms a continuous and thick border that extends from the anterior margin of the p4 ascending posteriorly, similar to other 'cardiomyines'. The mental foramen is located anterior to p4 and at the dorsoventral midpoint of the lateral surface of the dentary; it opens laterally (Fig. 8F).

Dentition. In *Cardiomyis* the prisms of all molariforms are heart-shaped, with the anteroposterior diameter proportionally long, the accessory fissures are relatively shallow and displaced toward c2, and M3 has four prisms plus a blunt posterior extension.

Upper teeth. P4–M2 bilobed with very shallow HPE and HSE penetrating less than 10% of the width of the prism, but the HSE seems to be deeper because of the labial extension of c1; both HPE and HSE are located toward the middle of the tooth, i.e. close to c2.

M3 has four prisms, the posterior one with a conspicuous posterior projection; prI similar to that of the other cheek teeth; prII with the labial side straight, depressed (Figs 8C, E; 9A, B).

Lower teeth. The p4 has three prisms, prI being very characteristic of the genus and different from that of *Caviodon* in which there is a single, relatively deep, hsi. In *C. leufuensis* this prI has the lingual margin convex, without hsi (Fig. 9C–F). In *C. ameghinorum* (Fig. 9G, H), especially those specimens from the Santa María Valley (Catamarca), this margin is straight, depressed with respect to the lingual margin, and limited by two narrow and shallow fissures (Fig. 9G), which give a concave labial margin. The m1–3 are bilobed with hsi and hpi close to c2; hpi is deeper and wider than hsi (Figs 8D, 9C–F).

Phylogenetic analysis

The combined analysis resulted in a total of 37 224 MPTs of 3290 steps, and a strict consensus of all trees was calculated (Pérez *et al.* 2017b). Hydrochoerinae is a monophyletic group; however, it shows a basal polytomy due to the unstable fragmentary fossil taxon *Allocavia chasicense* that takes different positions within this clade in the most parsimonious trees (MPTs). When the alternative positions of this species are ignored, the reduced consensus corroborates the paraphyly of 'cardiomyines' that are shown as basal forms of Hydrochoerinae (Fig. 10), and retrieves *Kerodon rupestris*, *Cardiomyis? andinus* and

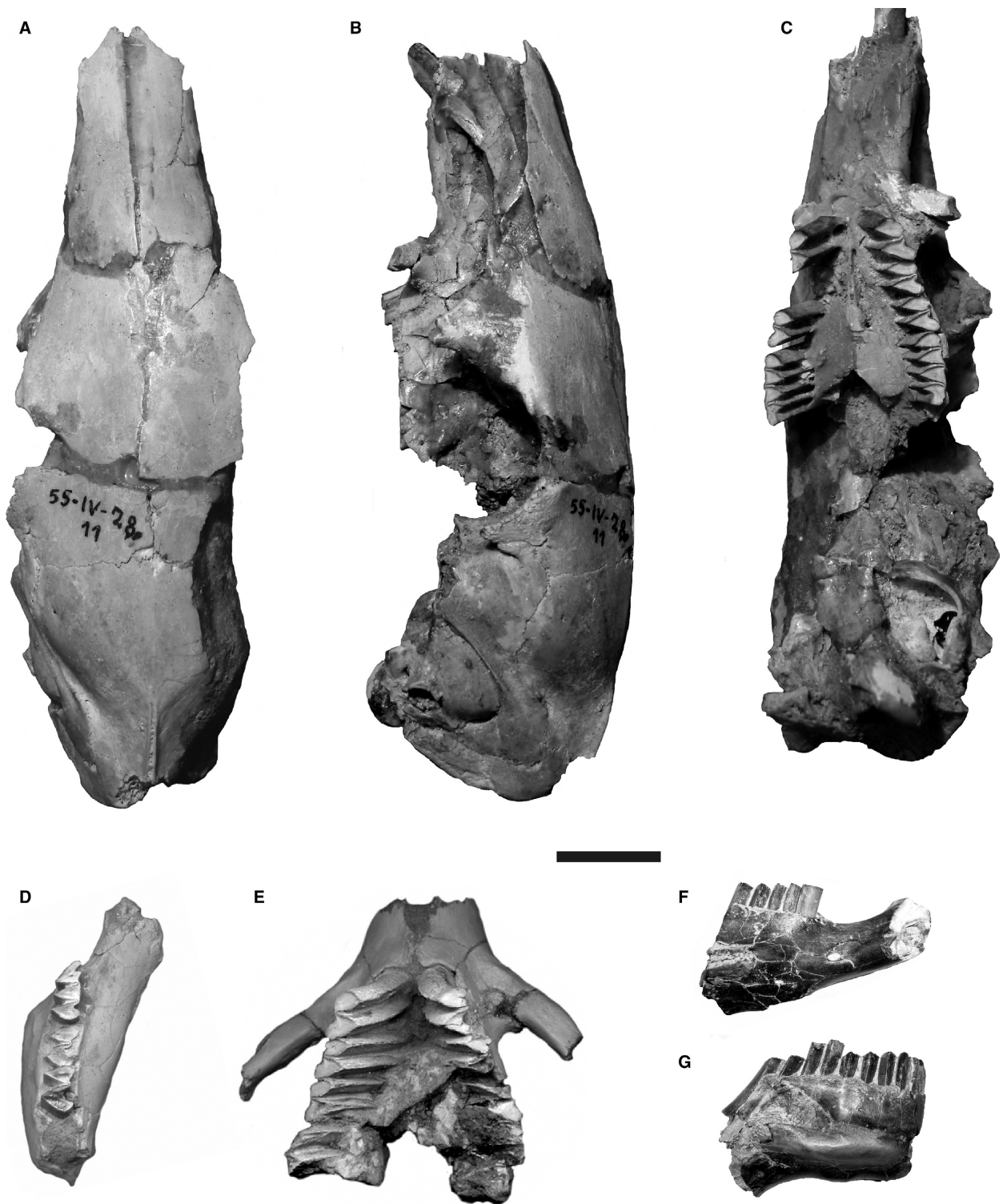


FIG. 8. *Cardiomys leufuensis* sp. nov. A–C, MLP 55-IV-28-11, skull: A, dorsal; B, lateral; C, ventral view. D, MLP 76-VI-12-92, left mandible fragment in occlusal view, with p4–m2. E, MLP 92-XI-19-19, skull fragment in ventral view, with right P4–M2 and fragment of M3 and left P4–M2. F, MLP 76-VI-12-18a, left mandible fragment in labial view with diastema and p4–m1 (reversed). G, MLP 76-VI-12-18b, right mandible fragment in labial view with p4–m3. Scale bar represents 20 mm.

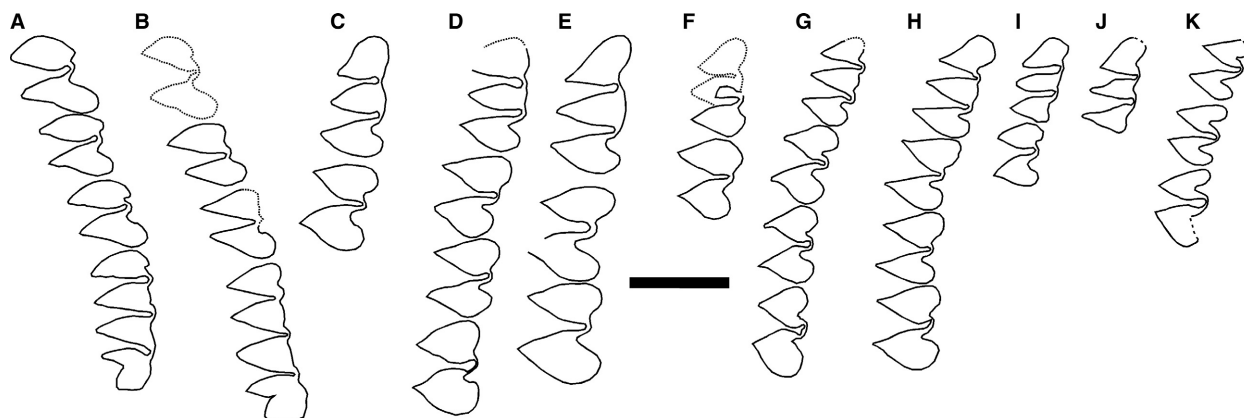


FIG. 9. Occlusal schemes of left dental series of the species of *Cardiomyys*. A–B, upper teeth. C–K, lower teeth. A, C–F, *Cardiomyys leufuensis* sp. nov. B, G–H, *Cardiomyys ameghinorum*. I, *Cardiomyys mesopotamicus*. J–K, *Cardiomyys cavinus*. A, MLP 55-IV-28-11 (holotype), left P4–M3. B, MACN-Pv 8246 (holotype), left P4–M3. C, MLP 76-VI-12-18a, left p4–m1. D, MLP 76-VI-12-18b, right p4–m3 (reversed). E, MLP 76-VI-12-92, left p4–m2. F, MLP 92-XI-19-4, left p4–m1 (reversed; broken p4). G, MACN-Pv 8247, left p4–m3. H, MACN-Pv 8538 (holotype of *C. ameghinorum* var. *latidens*) right p4–m3 (reversed). I, MACN-Pv 3832, left p4–m1. J, MLP M 28, cast of the holotype of *Cardiomyys cavinus* (the original is lost); MACN-Pv 4593, right mandible with m1–3 (reversed). Scale bar represents 10 mm.

Procardiomyys martinoi as the most basal forms of Hydrochoerinae. Support analyses (Fig. 10) yielded low values (both Bremer support and bootstrap) because of the low resolution of the basal forms within Hydrochoerinae.

Hydrochoerinae (Fig. 10, node A) is supported by eight morphological unambiguous synapomorphies: character 8 [state 1]: medial edge of the condyle, that is the insertion point of *m. pterygoideus externus* in posterior view, poorly developed projecting medially forming a small knob with respect to the medial wall of the dentary; ch. 20 [3]: the root of the lower incisors extending up to the level of the posterior lobe of m1; ch. 45 [1]: anteroposterior length of incisive foramina, short; ch. 53 [0]: position of the boundary between the mastoid and paraoccipital processes at the same level or above the external auditory meatus; ch. 77 [3]: p4 with prsa; ch. 94 [1]: presence of hse in p4; ch. 100 [1]: presence of hsi in m1–m2; ch. 122 [1]: presence of HPE in M1–M2. Additionally, 36 molecular data are shared between *Kerodon rupestris* and *Hydrochoerus hydrochaeris*.

The basal position of *Kerodon rupestris*, *Cardiomyys andinus* and *Procardiomyys martinoi*, arises because they lack derived characters such as more than three prisms in M3, or deeper fissures in p4. The p4 of *K. rupestris* has three prisms (a derived character within Caviidae); however, this tooth has very shallow fissures. Moreover, *Kerodon* has only two prisms in M3, which is a plesiomorphic character for this group. *Cardiomyys andinus* has only one lower molar with very shallow hpi and hsi and with heart-shaped prisms. *Procardiomyys martinoi* presents only three prisms in M3, in contrast with the condition of more derived Hydrochoerinae, in which the M3 has more than three prisms.

Cardiomyys ameghinorum, *C. leufuensis*, and the lineage that leads to the other hydrochoerines are placed in a more derived position (Fig. 10, node B). The basal position of these taxa with respect to *Xenocardia*, *Caviodon*, *Cardiatherium* and more derived hydrochoerines, is supported by ten morphological unambiguous synapomorphies: ch. 70 [0]: absence of constriction of the apex in each prism of molars; ch. 21 [0]: nMpi with respect to the toothrow, located between p4 and m1; ch. 26 [0]: dorsoventral length of the scar, high; ch. 31 [1]: posterior extension of the horizontal crest, in lateral view, approximately ending at the anteroposterior midpoint of the mandibular condyle; ch. 37 [1]: anteroposterior length of the upper diastema, shorter than molariform series; ch. 41 [1]: apex of mesopterygoid fossa, curved; ch. 46 [0]: palate plane; ch. 89 [1]: presence of h5i in prsa of p4; ch. 108 [1]: depth of hpi in m2 up to 25% of the occlusal surface; ch. 126 [3]: four prisms in M3.

A polytomy in a more derived position (Fig. 10, node C) includes *Xenocardia diversidens*, *Cardiomyys cavinus*, *Caviodon multiplicatus*, *C. australis*, *C. pozzi*, *C. cuyano*, *C. andalhuensis*, and the clade of *Cardiatherium* and more derived Hydrochoerinae. The 12 unambiguous synapomorphies that support this group are: ch. 42 [1]: margins of the mesopterygoid fossa, parallel; ch. 80 [23]: depth of hpi in p4 25–50%; ch. 84 [1]: presence of h3i (hsia) or hsi in p4; ch. 90 [1]: depth of h5i in prsa in p4, up to 50%; ch. 91 [1]: depth of hpi with respect to h5i, equally deep; ch. 101 [12]: depth of hsi in m1–m2, less than 50%, approximately half of the prism (50%); ch. 107 [0]: depth of hsi respect to hpi in m1, equally deep; ch. 108 [2]: depth of hpi in m2, up to 50%; ch. 124 [0]: depth of HPE respect to HSE, equally deep; ch. 125 [3]:

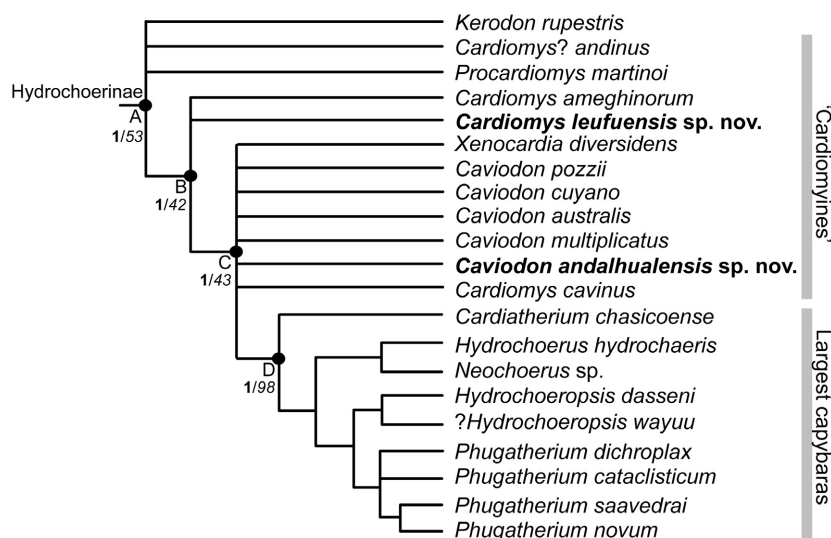


FIG. 10. Reduced strict consensus of Hydrochoerinae (Node A), ignoring the unstable fossil taxon *Allo-cavia chasicoense*. ‘Cardiomyines’ is a paraphyletic group and includes the most basal forms among Hydrochoerinae. Upper case letters indicate the nodes within Hydrochoerinae. The numbers in bold indicate Bremer support values, those in italics represent bootstrap values.

P4>M1>M2; ch. 126 [4]: 5–6 lobes in M3; ch. 127 [1]: lobes in M3 lanceolate shaped (with three or more prisms, in which the first ones is/are heart-shaped). A discussion about the position of *Xenocardia* and *Cardiomyis cavinus* is provided below.

The clade of *Cardiatherium* and more derived hydrochoerines (i.e. *Phugatherium*, *Hydrochoeropsis*, *Neochoerus* and *Hydrochoerus*) is supported by 21 morphological synapomorphies (see Pérez *et al.* 2017b).

DISCUSSION

Systematic considerations

Taxonomic and phylogenetic analyses of the species traditionally considered to be ‘cardiomyines’ corroborate the paraphyly of these forms, which are the most basal among Hydrochoerinae, and the following considerations arise.

The species of *Caviodon* described from the Conglomerado osífero of the Ituzaingó Formation (*C. paranensis*, *C. angustidens* and *C. scalai*) are here synonymized with *Caviodon multiplicatus* because all the remains of this genus are considered to pertain to different ontogenetic stages of a single species. The material of *Caviodon* shows a progressive increase in deepening of the fissures and addition of prisms to the M3 from the oldest (*C. andalhualensis* and *C. multiplicatus*) toward the youngest species (*C. pozzii* and *C. cuyano*).

Cardiomyis cavinus and *C. vignatii* from the Conglomerado osífero deserve further study. The metatype (Kraglievich 1932) of the type species (*Cardiomyis cavinus*) consists in a hemimandible fragment with m1–m3 (Fig. 9K), which has relatively deep hpi and hsi, equal in depth near the middle of the prism (which are diagnostic characters of *Caviodon*). The phylogenetic analysis indicates a more

derived position for *Cardiomyis cavinus* with respect to the other *Cardiomyis* species, probably more closely related to *Caviodon*; however, the resolution in the cladistical analysis is poor (Fig. 10, Node C). *Cardiomyis vignatii* has narrower prisms than other species of *Cardiomyis*, and the M3 has five prisms, not four as is typical of *Cardiomyis*. Here, we maintain *Cardiomyis cavinus* and *C. vignatii* within *Cardiomyis*, pending the discovery of new and more complete material from the Conglomerado osífero that would allow a more thorough taxonomic analysis.

The holotype of *Cardiomyis intermedius* is lost; hence, although the original description coincides with the morphology of *C. mesopotamicus*, their synonymy cannot be confirmed.

Allo-cavia chasicoense is a species represented by a single specimen, a right maxillary fragment with P4–M1; in the phylogeny it takes different alternative positions within Hydrochoerinae. The AP of its molariforms is 4 mm, and the HPE and HSE are very shallow, especially the HPE. Following the proposal of ontogenetic change for capybaras proposed by Vucetich *et al.* (2005), it cannot be rejected that this specimen (and taxon) represents a juvenile of *C. leufuensis* or alternatively *Procardiomyis martinoti*, the two ‘cardiomyines’ found in the Arroyo Chasicó Formation.

Xenocardia diversidens consists of a fragmentary maxilla and palate with both molariform series. This taxon is similar to *Caviodon* because its M3 has five prisms plus a posterior projection, narrow prisms with HPE and HSE relatively deep (typical of *Caviodon*). In our phylogenetic analysis, *X. diversidens* collapses with the species of *Caviodon*. Although the resolution is low, *X. diversidens* seems to be closely related to *Caviodon*.

The most important features that allow differentiation of the new material assigned to *Caviodon andalhualensis* from *Cardiomyis ameghinorum*, to which it was previously referred, are the p4 with a deep and single hsi in pr1, the

M3 with six prisms plus a small posterior projection, relatively deep fissures (and equally deep) in the middle of the prisms and in all molariforms, wider palatine rami, and rounded shape of the mesopterygoid fossa (Figs 4C, 6, 8C). Instead, in *C. ameghinorum* the p4 has two very shallow fissures in p1 next to columns c2 and c4, the M3 has four prisms and a thick posterior projection, all of them without fissures, shallow fissures in all molariforms and toward c2, the palatine rami are thinner, and the mesopterygoid fossa is ogival (Figs 6, 7).

This review brings up again the issue of the boundary between *Cardiomyis* and *Caviodon* because the m1–m3 of some isolated jaws from the Andalhuala Formation have internal fissures with intermediate depth, position in the prism, and relative development to each other. Riggs & Patterson (1939) did not recognize *Caviodon* as a distinct genus, but commented about materials that were similar to the 'Lelongia type' (= *Caviodon* (*Lelongia*)) of Kraglievich (1932). It is very likely that they were considering the materials FMNH P 14457, P 14434 and P 15287, here assigned to *Caviodon andalhualensis*. Later, Marshall & Patterson (1981) recognized only the species *Cardiomyis ameghinorum* among the 'cardiomyines' of Catamarca. However, our revision of this material housed in the Field Museum showed that the only specimens that can be assigned to *Cardiomyis ameghinorum* are FMNH P 15251, P 15298 and P 14513, while the other three specimens (FMNH P 14457, P 14434 and P 15287) represent *C. andalhualensis* and the first reports of *Caviodon* for the Andalhuala Formation.

'Cardiomyinae Genus and Species Indeterminate A' from Western Amazonia (Frailey 1986) is a Dolichotinae because M1 or M2 have double heart-shaped lobes, dentine crest, a furrow opposite the HFI (hypoflexus), with HPE and HSE absent; and 'Cardiomyinae Genus and Species Indeterminate B' is a Neopiblemyidae because of the straight and parallel lobes with a wide cement layer in the hypoflexus.

Diversity

The modern diversity of hydrochoerines is very low, represented by two species of the gigantic semiaquatic capybaras (*Hydrochoerus hydrochaeris* and *H. isthmius*, the most derived living Hydrochoerinae) and two small rocky cavies (*Kerodon rupestris* and *K. acrobata*, the most basal in the clade). However, in the past hydrochoerines were more diverse, in part because of the presence of 'cardiomyines'. Their acme is recorded in the late Miocene (7 species of the capybara *Cardiatherium*, and 11 'cardiomyines': 6 species of *Cardiomyis*, 1 of *Xenocardia*, 1 of *Procardiomyis*, and at least 3 of *Caviodon*). They declined in the Pliocene when *Cardiomyis* became extinct, *Caviodon* was restricted to three species (Fig. 2), and the largest capybaras were represented

by four species of *Phugatherium* and two species of *Hydrochoeropsis*. In the Pleistocene, 'cardiomyines' became extinct and hydrochoerines were restricted to the extinct *Neochoerus*, and the living *Hydrochoerus* and *Kerodon* (Vucetich et al. 2012, 2015; Pérez et al. 2017a).

Biogeography

This revision raises some points concerning the geographical distribution of the 'cardiomyines'. Although the geographical distribution of most genera overlaps at mid latitudes, they show some differences. Only basal 'cardiomyines' (*Cardiomyis*, *Cardiomyis?* and *Procardiomyis*) have been recorded at high latitudes during the middle to early late Miocene (Mayoan–Chasicóan SALMAs), Chubut (Fig. 1, 12) and southern Buenos Aires province (Fig. 1, 10), and *Cardiomyis* in particular is also recorded in mid latitudes during the Huayquerian, Mendoza (Fig. 1, 2), Catamarca (Fig. 1, 4), Entre Ríos (Fig. 1, 5), La Pampa (Fig. 1, 9) and San Juan (Fig. 1, 11) provinces. Instead, the more derived *Caviodon* and *Xenocardia*, are first recorded at low/mid latitudes, western Amazonia (Fig. 1, 6), San Juan (Fig. 1, 11), Catamarca (Fig. 1, 4) and Entre Ríos (Fig. 1, 5) provinces, and only in the Pliocene at higher latitudes, southern Mendoza (Fig. 1, 2) and Buenos Aires (Fig. 1, 1, 1, 3) provinces. This distribution suggests that *Caviodon* could originated in mid or low latitudes, and later migrated southward.

CONCLUSIONS

The diversity of Hydrochoerinae in the past was much higher than at present; however, the oldest forms remain poorly known. Here the taxonomic diversity of 'cardiomyines' is enlarged and a phylogenetic analysis corroborates the paraphyly of these forms. Two new 'cardiomyine' species are recognized for the late Miocene: *Caviodon andalhualensis* (from the Huayquerian of Catamarca Province) and *Cardiomyis leufuensis* (from the Chasicóan of Buenos Aires Province). *C. andalhualensis* represents the first *Caviodon* recognized for the Andalhuala Formation, while *Cardiomyis leufuensis* is the first *Cardiomyis* formally reported from the Arroyo Chasicó Formation. Revision of *Caviodon* suggests that only one species of this genus, the type species *Caviodon multiplicatus*, is valid for the material found in the Conglomerado osífero. Our taxonomic and phylogenetic analyses indicate that *Xenocardia diversidens* is more closely related to *Caviodon* than to *Cardiomyis*.

The geographical and temporal distribution shows that two 'cardiomyine' genera and species (*Cardiomyis leufuensis* and *Procardiomyis martinoi*) occur in the Arroyo Chasicó

Formation, while *Allocavia chasicoense* may be a juvenile of one of these two. The record of the genus *Cardiomy*s is restricted to the late Miocene, whereas that of *Caviodon* spans from the late Miocene to the Pliocene. *Cardiomy*s was restricted to southern South America whereas *Caviodon* was found also in western Amazonia and Venezuela.

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DATA ARCHIVING STATEMENT

This published work, and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/References/CFDB051D-FA79-4EA1-8A07-4621CABEEBE9>

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pj562>

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APPENDIX

Material used in this study with their geographical and stratigraphical provenance.

Xenocardia diversidens Pascual & Bondesio, 1963

Huachipampa, San Juan; Huachipampa Formation, early late Miocene: MLP 57-XII-23-5, skull fragment with damaged right and left P4–M3, holotype and single specimen.

Procardiomyis martinoi Pascual, 1961

Arroyo Chasicó, Buenos Aires; Arroyo Chasicó Formation (= Cerro Azul Formation *sensu* Folguera & Zárate 2009), early late Miocene: MMP 471-M, fragmentary palate with right and left P4–M3 (holotype); MMH-CH-88-6-77, incomplete skull with right and left M1–M3; 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.

Caviodon multiplicatus Ameghino, 1885

Paraná, Entre Ríos; Conglomerado osífero, Ituzaingó Formation: MACN-Pv 5891 isolated right M3 (holotype and single specimen); MACN-Pv 4495, left M3 (holotype and single specimen of *Caviodon bravardi* Kraglievich, 1927); MACN-Pv 13471, right M3 (holotype and single specimen of *Caviodon (Lelongia) paransis* Kraglievich, 1930).

Caviodon australis (Ameghino, 1888) (including *Caviodon obtusus* Ameghino, 1888)

Farola Monte Hermoso, Buenos Aires; Monte Hermoso Formation, early Pliocene: MACN A-1657, fragment of left mandible and isolated molar fragment (see Rovereto 1914); MACN A-1099, maxillary fragment with left P4 and isolated M3 (holotype of *Diacartherium australe*); MACN-Pv 7326, skull fragment with palate and both dental series; MACN-Pv 7526, skull fragment; MACN-Pv 14841, fragment of right mandible with m1–m2.

Caviodon pozzii Kraglievich, 1927

Chapadmalal, Buenos Aires; Chapadmalal Formation, early late Pliocene: MACN-Pv 6915, right jaw fragment with p4–m2 (holotype); MMP 525-M, skull with right P4–M3 and left M1–M3; MLP 61-VII-10-8, left M3.

Caviodon cuyano Vucetich *et al.*, 2011

Arroyo seco de la Frazada, Mendoza; middle section of the La Huertita Formation (Garrido *et al.* 2014; = SM of the Aisol Formation *sensu* Forasiepi *et al.* 2011), Pliocene?: MHNSR-PV 1101, large part of a deformed skull with left and right P4–M3, fragments of both jaws with left p4, m2–m3 and right p4–m3, and postcranium (holotype and single specimen).

Caviodon andalhualensis sp. nov.

Valle de Santa María, Andalhuala Formation, Locality 4, Arroyo (= Río) de Yapes: FMNH P 14457 (assigned to *Cardiomyis ameghinorum* by Marshall & Patterson 1981), skull, atlas–axis and other vertebrae (holotype), level XX; FMNH P 14434, right jaw fragment with p4–m2, level 15–32 (above 19 *in schedis*); FMNH P 15287, left jaw fragment with p4 (no horizon).

Caviodon sp.

Paraná, Entre Ríos; Conglomerado osífero, Ituzaingó Formation: MLP 87-XI-1-12b, right p4; MLP 87-XI-1-11, right M3; MACN-Pv 2483, right m3; MACN-Pv 3410, left m1 or m2; MACN-Pv 13459, right mandible fragment with p4–m3 (the three latter are assigned *in schedis* to *Cardiomyis*).

San Gregorio Formation, San Gregorio, Venezuela: UNEFM-VF-53 (left M1 or M2) (Vucetich *et al.* 2010).

Solimões Formation, Patos locality, Acre River, Brazil: UFAC 5465 (M1 or M2) (Kerber *et al.* 2017).

Cardiomyinae

Paraná, Entre Ríos; Conglomerado osífero, Ituzaingó Formation: MACN-Pv 9033, right mandible fragment with p4–m3; MACN-Pv 17693, right mandible fragment with m1–m3; MLP 87-XI-1-4,

isolated M1 or M2; MLP 87-XI-1-8, left jaw fragment with i, p4–m2; MLP 87-XI-1-20, right palatal fragment with M3.

Cardiomyx cavinus Ameghino, 1885

Paraná, Entre Ríos, Conglomerado osífero, Ituzaingó Formation: MLP M 28: cast of the holotype, right p4; MACN Pv 4593, right jaw with m1–m3 (metatype).

Cardiomyx mesopotamicus (Ameghino, 1885)

Paraná, Entre Ríos, Conglomerado osífero, Ituzaingó Formation: MACN-Pv 3832, fragment of left mandible with p4–m1 (holotype); MLP 52-X-1-84, right jaw fragment with p4(damaged)–m3.

Cardiomyx leufuensis sp. nov.

Arroyo Chasicó, Buenos Aires; Arroyo Chasicó Formation (= Cerro Azul Formation *sensu* Folguera & Zárate 2009), early late Miocene: MLP 55-IV-28-11, partial skull with right P4, M2–M3 and left P4–M3 (holotype); MLP 92-XI 19-4, left mandible fragment with p4–m1, Vivero Member; MLP 92-XI-19-19, palate fragment with right P4–M3 and left P4–M2, and both anterior rami of the zygomatic arch, Las Barrancas Member; MLP 76-VI-12-18, fragment of palate with right P4–M1 and left P4, right mandible fragment with p4–m3 and left mandible fragment with p4–m1, Las Barrancas Member, Bajada de los Toros; MLP 76-VI-12-92, left mandible fragment with p4–m2, Las Barrancas Member, Quebrada del Hacha.

Cardiomyx ameghinorum Rovereto, 1914

Andalhuala, Catamarca; Andalhuala Formation, late Miocene: MACN-Pv 8247, left jaw with p4–m3 (holotype); MACN-Pv 8246, skull without rostrum, with right and left P4–M3 partially damaged; MACN-Pv 8248, incomplete skull; MACN-Pv 4831, symphysis with both i–p4; MACN-Pv 8252, right palate fragment with M1–M2.

Puerta de Corral Quemado, Andalhuala Formation: FMNH P 15251 (no horizon), left mandibular fragment with p4–m2;

FMNH P 15298 (no horizon), left mandibular fragment with symphysis (*in schedis* assigned to *Cardiomyx ameghinorum latidens*, but the material is not sufficient to make a definite assignment); FMNH P 14513 (level 20), partial skull with right M3 (*in schedis* assigned to *Cardiomyx ameghinorum* var. *latidens*).

Cardiomyx ameghinorum var. *latidens* Rovereto, 1914

Huayquerías de San Carlos, Mendoza; Huayquerías Formation, late Miocene; these levels were dated as 5.8 ± 0.1 Ma (Marshall *et al.* 1986): MACN-Pv 8538, right jaw with p4–m3 (holotype); MACN-Pv 8539, skull fragment with right P4–M3 and left P4, and both hemimandibles with incisors, right p4–m2 and left p4.

C. aff. ameghinorum

Paraná, Entre Ríos, Conglomerado osífero, Ituzaingó Formation: MACN-Pv 3823, right mandibular fragment with p4–m3.

Cardiomyx sp.

Puerta de Corral Quemado, level 23: FMNH P 14491, right jaw with p4–m3; left jaw with m1–m3; femur, atlas, axis, ribs (*in schedis* *Cardiomyx ameghinorum* var. *latidens*).

Valle de Santa María; Andalhuala Formation; Locality 1, Entre Ríos (= Chiquimil), level XVIIIb: FMNH P 14372 (assigned *in schedis* to *Cardiomyx*; it was not mentioned by Marshall & Patterson 1981), lower right dentition with p4–m3 and incisor fragment.

Puerta de Corral Quemado, El Jarillal Member of the Chiquimil Formation (Esteban *et al.* 2014), Catamarca, without other data: MACN-Pv 15313, right mandible fragment with p4–m3.

Conglomerado osífero, Ituzaingó Formation: MLP 41-XII-13-178, left jaw with p4–m2.

Adolfo Alsina: MLP 49-XI-18-15, two isolated right m3.

Salinas de Hidalgo, Buenos Aires; Cerro Azul Formation (*sensu* Folguera & Zárate 2009), late Miocene: MLP 65-VII-29-89, right jaw fragment with p4.

La Pampa Province, Conhelló (71 m depth): MACN-Pv 9612, left mandible fragment with p4–m3 and rostrum with both P4.