

A NEW SPECIES OF CARDIOMYINAE (RODENTIA, HYDROCHOERIDAE) FROM WESTERN ARGENTINA. ITS AGE AND CONSIDERATIONS ON ONTOGENY AND DIVERSITY OF THE SUBFAMILY



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Abstract. A new Cardiomyinae rodent (Hydrochoeridae) from Arroyo Seco de la Frazada, Mendoza Province, Argentina, is described. The new species, *Caviodon cuyano* sp. nov., is distinguished by its greater robustness, deeper fissures, and greater number of prisms in M3, which are derived characters within the context of Hydrochoeridae evolution. An assessment of the species of *Caviodon* Ameghino showed that tooth growth is allometric and occlusal morphology becomes more complex during ontogeny, as in hydrochoerines. The true diversity of this genus, when tooth postnatal ontogeny is considered, may be less than heretofore estimated. The fossil-bearing levels, the middle section of the Aisol Formation, have been considered no older than Huayquerian in age (late Miocene). The evolutionary stage of the new species suggests that the age of these sediments could be even younger, no older than early Pliocene and possibly up to late Pliocene.

Key words. Rodents. Cardiomyinae. Argentina. Ontogeny. Diversity.

Resumen. UNA NUEVA ESPECIE DE CARDIOMYINAE (RODENTIA, HYDROCHOERIDAE) DEL OESTE DE ARGENTINA. SU EDAD Y CONSIDERACIONES SOBRE ONTOGENIA Y DIVERSIDAD DE LA SUBFAMILIA. Se describe un nuevo roedor Cardiomyinae (Hydrochoeridae) proveniente de Arroyo Seco de la Frazada, provincia de Mendoza, Argentina. La nueva especie, *Caviodon cuyano* sp. nov., se distingue por su mayor robustez, mayor profundidad de las hendiduras y mayor número de prismas en el M3, caracteres considerados derivados en el contexto de la evolución de la Familia Hydrochoeridae. Una evaluación de las especies de *Caviodon* Ameghino permitió constatar que los dientes crecen alométricamente y la morfología oclusal se hace más compleja durante la ontogenia, como en los hidroquerinos. La diversidad de este género podría ser menor que la estimada hasta ahora, cuando se tiene en cuenta la ontogenia dentaria postnatal. Los niveles portadores, sección media de la Formación Aisol, fueron considerados no más antiguos que huayquerienses (Mioceno tardío). El estado evolutivo de la nueva especie sugiere que la edad de los sedimentos portadores podría ser más reciente, correspondiente al Plioceno temprano o incluso al Plioceno tardío.

Palabras Clave. Roedores. Cardiomyinae. Argentina. Ontogenia. Diversidad.

THE Subfamily Cardiomyinae Kraglievich, 1930, comprises middle- to large-sized extinct cavioids with euhyposodont cheek-teeth, P4-M2 and m1-m3 formed by two heart-shaped prisms with an accessory fissure on each one, external in uppers and internal in lowers, M3 formed by five to seven prisms, and broad palate. They are known mainly from the late Miocene–late Pliocene of central Argentina (Rovereto, 1914; Kraglievich, 1940; Pascual, 1961; Pascual and Bondesio, 1963; Pascual *et al.*, 1966), although they have also been reported from Bolivia (Anaya and MacFadden, 1995) and recently from Venezuela (Vucetich *et al.*, 2010). This subfamily includes the genera *Cardiomys* Ameghino,

1885, and *Caviodon* Ameghino, 1885 (including *Lelongia* Kraglievich, 1930), with numerous nominal species, and the monotypic *Procardiomys* Pascual, 1961, and *Xenocardia* Pascual and Bondesio, 1963.

Cardiomyines have been traditionally related to the Caviidae (Rovereto, 1914; Mones, 1986; MacKenna and Bell, 1997). Their dental morphology resembles that of hydrochoerid hydrochoerines; hence they have been sometimes mistaken for the latter (Pascual, 1961; see Deschamps *et al.*, 2009). Recently, Vucetich *et al.* (2005; in press), Vucetich and Deschamps (in press), and Pérez (2010a,b) considered the Cardiomyinae as the sister group of Hydrochoerinae

and grouped them together in the Family Hydrochoeridae. Neontological papers dealing with the relationships of the crown group Cavoioidea (*sensu* Pérez, 2010b) did not take cardiomyines into account (Rowe and Honeycutt, 2002; Opazo, 2005; Woods and Kilpatrick, 2005). The group remains quite obscure because cardiomyines have not been revisited since the original descriptions of genera and species. Consequently, their systematics, the boundaries of each species, their geographic and temporal distribution, and their relationships with other rodents are in need of an in-depth revision.

The aim of this paper is to describe a new cardiomyine found in the Aisol Formation, Mendoza Province (Fig. 1). This material is particularly interesting because it includes associated skull, mandible, and postcranium, and also because it extends the geographical distribution of the genus southward within the Andean region. Although a complete revision of the subfamily lies beyond the scope of this paper, the new remains allow a revision of some systematic and paleobiological aspects of this interesting but neglected group of rodents.

LOCALITY AND GEOLOGICAL SETTING

The fossil-bearing site of Arroyo Seco de la Frazada is located about 35 km south of the town of San Rafael, Mendoza Province, Argentina (Fig. 1.2). The sediments form a long cliff stretching along about 10 km from the mentioned locality southward to Cerro Aisol (González Díaz, 1972). The stratigraphic section exposed at Arroyo Seco de la Frazada represents the type section of the Aisol Formation (González Díaz, 1972). In addition, this unit crops out in separate small basins over the Bloque de San Rafael, mainly associated to the Atuel and Diamante rivers (Dessanti, 1954, 1956; González Díaz, 1972; Sepúlveda *et al.*, 2001, 2007).

Recently, the Aisol Formation was informally divided into three sections (Forasiepi *et al.*, 2011). In the studied area, the lower section (LS) is approximately 15 m thick. It consists of medium- to fine-grained sandstones with fine interbedded levels of siltstone (Fig. 1.3). Fossil wood and vertebrate remains have been found in different parts of the section. The vertebrate association includes an Anura frog, Testudininae turtles, Phorusrhacidae birds, and diverse mammals (*i.e.*, Xenarthra, Notoungulata, Litopterna, and Rodentia) and has been assigned to the middle Miocene (Soria, 1983; Forasiepi *et al.*, 2011).

The middle section (MS), where the cardiomyine comes from, is 8.50 m thick. It consists of fine-grained, well-sorted,

pebbly, lithic sandstones (Fig. 1.3). Fine levels of mudstone are interbedded in the sandstones and become thicker towards the upper part of the section. Fossil vertebrates have been collected from the lower part and include the cardiomyine described here, the Sparassocynidae *Hesperocynus dolgopola* (Reig, 1958), an unidentified species of the Heterotheridae *Tremacyllus* Ameghino, 1891, and the rodents Dolichotinae indet., Abrocomidae indet., and Ctenomyidae indet. The vertebrate association suggests that the MS sediments are younger than those of the LS and no older than late Miocene Huayquerian South American Land Mammal Age (SALMA) (Forasiepi *et al.*, 2009, 2011).

The upper section (US) is 5.6 m thick and is covered by recent dunes. The US consists mostly of sandstones, firmly cemented at the base and more friable in the rest of the column. A thin cineritic bed is interbedded in the middle part of the US. At present, no fossil remains have been collected from this section.

MATERIALS AND METHODS

Materials. The new materials here reported consist of associated skull, mandible fragments, and some postcranial remains (see details below), housed in the MHNSR–PV. A comparative morphological study was made using the following holotypes of cardiomyine species: *Caviodon bravardii* Kraglievich, 1927, MACN Pv 4495, left M3, from Paraná, Entre Ríos; *Cardiomys cavinus* Ameghino 1885, MACN Pv 4593, right mandible with m1–m3, from Paraná, Entre Ríos; *Caviodon pozzii* Kraglievich, 1927, MACN Pv 6915, right mandible fragment with p4–m2, from Chapadmalal, Buenos Aires; *Cardiomys ameghinorum* Rovereto, 1914, MACN Pv 8538, mandible with p4–m3, from Huayquerías, Mendoza; *Caviodon (Lelongia) paranensis* Kraglievich, 1930, MACN Pv 13471, right M3, from Paraná, Entre Ríos; *Xenocardia diversidens* Pascual and Bondesio 1963, MLP 57-XII-23-5, skull fragment with damaged right and left P4–M3, from Huachipampa, San Juan; *Procardiomys martinoi* Pascual, 1961, MMP 471 (M), skull fragment with right and left P4–M3 and mandible fragment with p4–m3, from Arroyo Chasicó, Buenos Aires.

Other referred materials were studied: MACN Pv 8246, skull without rostrum, with right and left P4–M3 partially damaged of *Cardiomys ameghinorum*, from Catamarca; MACN Pv 14841, left mandible fragment with m1–m2, undetermined material, from Farola Monte Hermoso, Buenos Aires, here referred to *C. pozzii*; MLP 55-IV-28-11, partial skull with right P4, M2–M3 and left P4–M3 of *Cardiomys*

sp., from Arroyo Chasicó, Buenos Aires; MLP 87-XI-1-8, left mandible fragment with i, p4–m2 of *Cardiomyinae*, from Paraná, Entre Ríos; MMP 525-M, skull with right P4–M3 and left M1–M3, undetermined material, from Chapadmalal, Buenos Aires, here referred to *C. pozzii*; PVL 3275, palate with right and left P4–M3 of *Cardiomyis* sp., from El Molle, Catamarca; PVL 3281, right hemimandible with p4 of *Cardiomyinae*, from Quebrada de Caspinchango, Catamarca; PVL 3297, left hemimandible with broken p4

and m1 of *Cardiomyinae* from Quebrada de Caspinchango, Catamarca; PVL 3304, skull with very damaged right and left P4–M3 of *Cardiomyis* sp. from El Molle, Catamarca; PVL 3309, left hemimandible with broken p4–m3, undetermined material here referred to *Caviodon* sp., from Tío Punco, Catamarca; PVL 3310, skull fragment of *Cardiomyis* sp. from Catamarca.

Institutional Abbreviations. MACN Pv, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Ver-

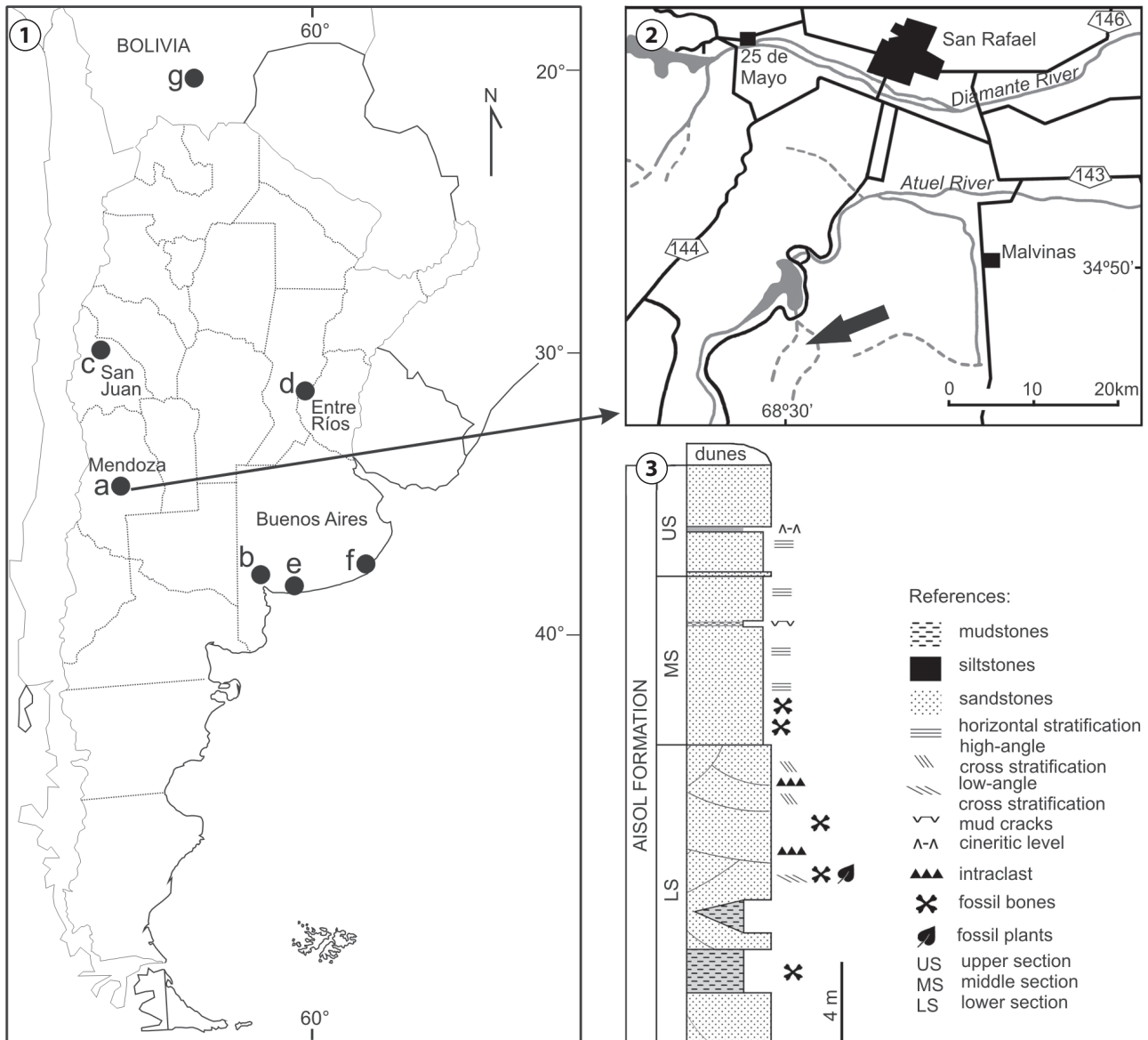


Figure 1. 1, Map of South America showing localities bearing cardiomyines mentioned in the text / mapa de América del Sur mostrando las localidades portadoras de cardiominos mencionadas en el texto. a, Arroyo Seco de la Frazada; b, Arroyo Chasicó; c, Loma del Camello; d, Paraná; e, Farola Monte Hermoso; f, Chapadmalal; g, Inchasi. 2, Geographical setting of Arroyo Seco de la Frazada, Mendoza Province, Argentina/ ubicación geográfica de Arroyo Seco de la Frazada, provincia de Mendoza, Argentina. 3, Stratigraphic column of the Aisol Formation in the area of Arroyo Seco de la Frazada (modified from Forasiepi et al., 2011)/ columna estratigráfica de la Formación Aisol en el área de Arroyo Seco de la Frazada (modificado de Forasiepi et al., 2011).

tebrate Paleontology collection, Buenos Aires, Argentina; **MHNSR–PV**, Museo de Historia Natural de San Rafael, Vertebrate Paleontology collection, San Rafael, Mendoza, Argentina; **MMP**, Museo de Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia”, Buenos Aires, Argentina; **PVL**, Paleontología Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina.

Nomenclature and measurements (Fig. 2). Tooth nomenclature is simplified from that used for hydrochoerines (Mones,

1991; Vucetich *et al.*, 2005) because the teeth of cardiomyines have fewer fissures. Abbreviations for dental structures refer to the Spanish names in order to conform to previous publications (Frailey, 1986). Following the common use in cardiomyines, hypoflexus/hypoflexid is used instead of fundamental external fissure (H.F.E./ h.f.e.) of hydrochoerines. Upper and lower case letters refer to upper and lower teeth, respectively: **H.P.E.**, primary external fissure; **h.p.i.**, primary internal fissure; **H.S.E.**, secondary external fissure; **h.s.i.**, secondary internal fissure; **Hy**, hypoflexus; **hyd**, hypoflexid; **h.2e.**, secondary external fissure; **h.5i.**, fifth internal fissure; **pr.I**, prism I; **pr. II**, prism II; **pr.s.a.**, supernumerary anterior prism; **Pr.I–VII**, prism I–VII of upper teeth.

Dental measurements (Tab. 1): **AP**, anteroposterior length; **AW**, anterior width; **HPEL**, H.P.E. length; **HPIL**, h.p.i. length; **HSEL**, H.S.E./h.s.e. length; **HSIL**, h.s.i. length; **Hdyl**, hypoflexid length; **MW**, middle width, pr.I width of p4; **PW**, posterior width.

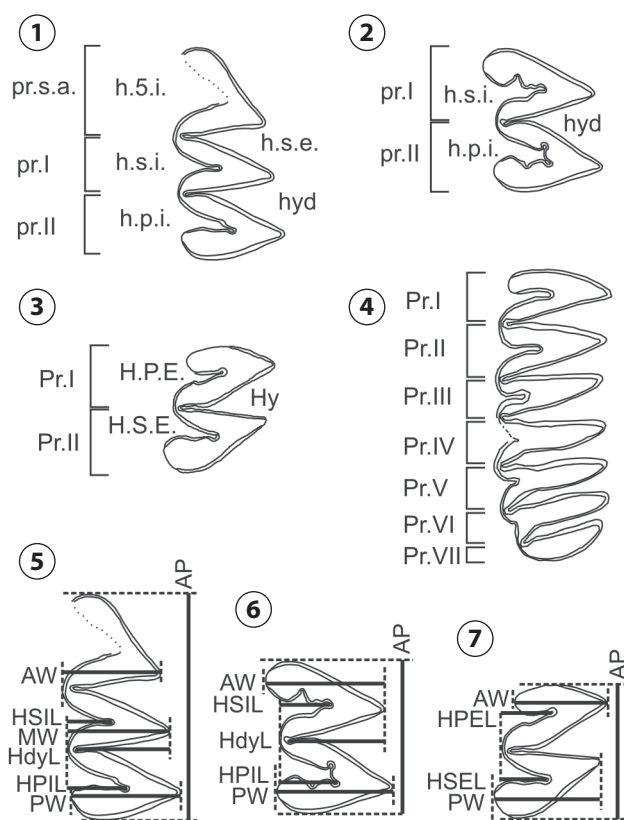


Figure 2. Tooth nomenclature and measurements/ *nomenclatura y medidas dentarias*. **1, 5**, right p4/ p4 derecho; **2, 6**, right m1/ m1 derecho; **3, 7**, right P4/ P4 derecho; **4**, right M3/ M3 derecho. **1–4**, Nomenclature/ *nomenclatura*. **H.P.E.**, primary external fissure/ *hendidura primaria externa*; **h.p.i.**, primary internal fissure/ *hendidura primaria interna*; **H.S.E.**, secondary external fissure/ *hendidura secundaria externa*; **h.s.i.**, secondary internal fissure/ *hendidura secundaria interna*; **Hy**, hypoflexus/ *hypoflexo*; **hyd**, hypoflexid/ *hypoflexido*; **h.2e.**, secondary external fissure/ *hendidura secundaria externa*; **h.5i.**, fifth internal fissure/ *quinta hendidura interna*; **pr.s.a.**, supernumerary anterior prism/ *prisma supernumerario anterior*; **pr.I**, prism I/ *prisma I*; **pr. II**, prism II/ *prisma II*; **Pr.I–VII**, prism I–VII of upper teeth/ *prisma I–VII de los dientes superiores*. **5–7**, Measurements/ *Medidas*. **AP**, anteroposterior length/ *diámetro anteroposterior*; **AW**, anterior width/ *diámetro transverso anterior*; **HPEL**, H.P.E. length/ *profundidad de H.P.E.*; **HPIL**, h.p.i. length/ *profundidad de h.p.i.*; **HSEL**, H.S.E./h.s.e. length/ *profundidad de H.S.E./h.s.e.*; **HSIL**, h.s.i. length/ *profundidad de H.S.I./h.s.i.*; **Hdyl**, hypoflexid length/ *profundidad del hipoflexido*; **MW**, middle width/ *diámetro transverso medio*; **PW**, posterior width/ *diámetro transverso posterior*.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821

Suborder HYSTRICOMORPHA Brandt, 1855

Infraorder HYSTRICOGNATHI Tullberg, 1899

Superfamily CAVIOIDEA (Gray, 1821) Kraglievich, 1930

Family HYDROCHOERIDAE (Gray, 1825) Gill, 1872

Subfamily CARDIOMYINAE Kraglievich, 1930

Genus *Caviodon* Ameghino, 1885

Type species. *Caviodon multiplicatus* Ameghino, 1885.

Caviodon cuyano sp. nov.

Figures 3–5, Table 1

Derivation of name. *Cuyano* in reference to Cuyo, the historical and geographical area in western Argentina that includes the Province of Mendoza, where this specimen was found.

Diagnosis. Very large and robust Cardiomyinae, about 20% larger than *Caviodon pozzii*; wide cheek-teeth, with very deep accessory fissures penetrating more than half of the width of the occlusal surface, and with conspicuous irregularities in the enamel band; M3 with seven prisms and a rudiment of an eighth one; posterior portion of M3 lingually bended, so that the last three prisms become closer to each other than the rest, especially at their lingual ends; very wide skull roof; wide palate with mesopterygoid fossa subcircular in outline.

Holotype. MHNSR-PV 1101, large part of a deformed skull with posterior part of the rostrum, part of the roof, left and

right P4–M3, right zygomatic arch, and right bulla; fragments of both hemimandibles with left p4, m2–m3 and right p4–m3, a small portion of the atlas, a damaged fragment of the sacrum; fragments of both femora, left fabella, some phalanges, and sesamoid bones.

Geographic provenance. Arroyo Seco de la Frazada (S34° 53'57.3"–W68°28'52.6"), San Rafael Department, Mendoza Province, Argentina (Fig. 1.1–2).

Stratigraphic provenance. Lower part of the middle section of the Aisol Formation (Fig. 1.3).

Description

Skull (Fig. 3.1, 3, 5). MHNSR-PV 1101 is much flattened dorsoventrally and the preserved portion of the rostrum is slightly twisted to the right. Sutures are hardly visible because the bone is very cracked. The skull roof and the palate are very wide, and the zygomatic arches are strongly convex. These characters make the skull of *C. cuyano* sp. nov. more robust than those of other cardiomyines such as *C. pozzii* (Fig. 3.2, 4, 6).

The ventral zygomatic root is placed above P4. It is dorsoventrally thin, anteroposteriorly narrow, and projects laterally at a straight angle, as in the living cavioid *Kerodon* Cuvier, 1825. In contrast, in living hydrochoerines the anterior zygomatic root is wider anteroposteriorly and directed laterally and backwards. This is also observed in fossil hydrochoerines, in which the beginning of the arch is anteroposteriorly wide and posterolaterally directed. The fossa for insertion of the lateral masseteric muscle is large and ventrally oriented. The dorsal root is placed above the anterior lobe of M3. The antorbital bar is oriented in an anterodorsal-posteroventral direction. The horizontal portion of the zygomatic arch is high, especially below the antorbital bar, and proportionally longer than in *Hydrochoerus* (Brisson, 1762). The squamosal seems to reach anteriorly up to the middle of the horizontal ramus. The ventral border of the horizontal portion is well below the occlusal surface of cheek-teeth, but this could be exaggerated because of the flattening of the skull. The zygomatic arch is very convex giving the skull a subcircular aspect in ventral view, but this could also be exaggerated by deformation. Medially, the zygomatic arch is occupied by a deep and elongated fossa, proportionally longer than in *Hydrochoerus*. The orbit is large. The postorbital apophysis is broken, but its base is anteroposteriorly wide.

The posterior half of the palate is formed mostly by the palatine. This bone is transversely wide and extends anteriorly up to the anterior lobe of M2. The mesopterygoid fossa is very wide and semicircular, occupying 66% of the palate

width at the level of the last prism of M3 and extending up to Pr.V of M3. Several palatine foramina open in the maxillary portion of the palate from the level of P4 up to the palatine. The pterygoid fossae are internal to the dental series and placed more posteriorly with respect to M3 than in *Hydrochoerus*. In this character, MHNSR-PV 1101 is more similar to *Kerodon*. The bulla is small and subspherical.

Mandible (Fig. 3.7). Mandibular remains are very fragmentary. The left hemimandible preserves the origin of the angular process, which arises below m2/m3. The horizontal crest is only partially preserved. It seems to be robust and is located on the dorsal half of the mandibular ramus. The anterior portion of this crest, corresponding to the notch for insertion of the tendon of the *masseter medialis pars infraorbitalis* muscle (Pérez, 2010a,b) is placed below the posterior portion of the alveolus of p4 and the alveolus of m1, as in other cardiomyines.

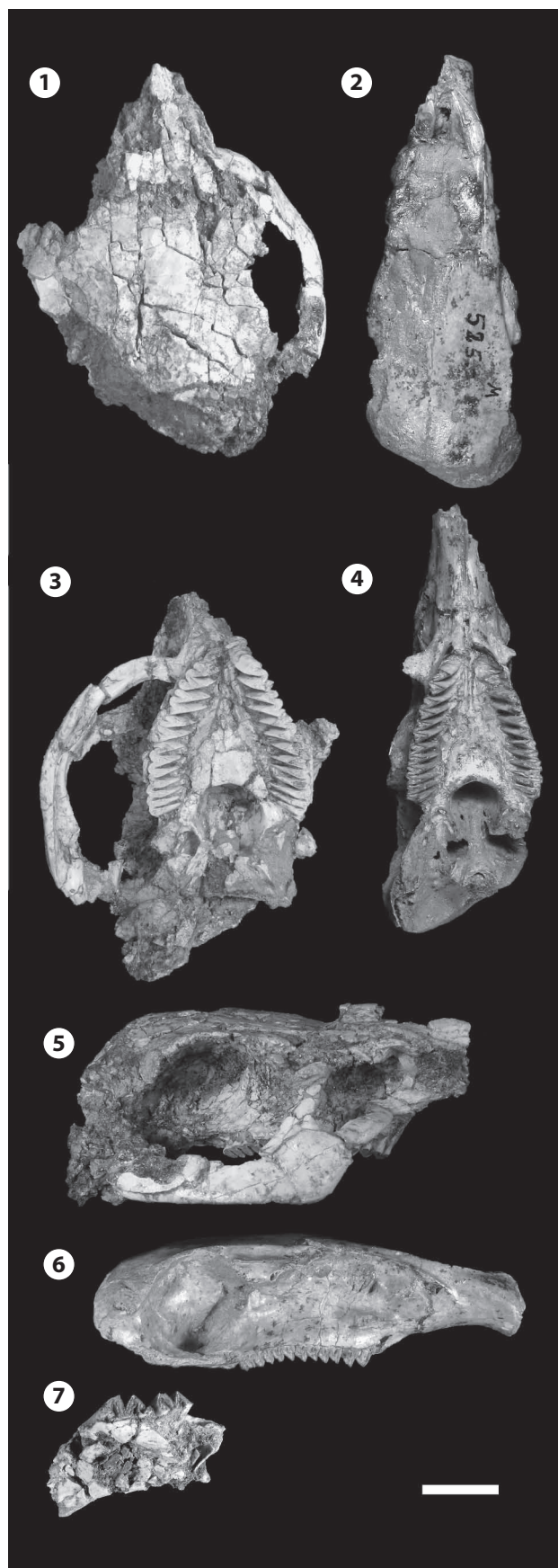
Upper teeth (Figs. 2; 4.1). P4 has two prisms, each one with one external fissure, H.P.E./H.S.E., which makes them heart-shaped. The anterior wall of Pr.I is somewhat convex. Fissures extend up to half the width of the occlusal surface, H.P.E. points to the internal apex, but H.S.E. points slightly backwards. The hypoflexus is lingually wide and narrows outward, becoming funnel-shaped. Enamel is interrupted on the anterior and posterior labial walls.

M1 and M2 are very similar in morphology. They have two prisms like P4, but the anterior wall of Pr.I is straight. The external fissures and the hypoflexus are as in P4. The anterior prism is slightly more slender than the posterior one. Enamel is also interrupted as in P4.

M3 has seven prisms united at the labial margin. The first two are heart-shaped with a fissure that extends up to 45% and 40%, respectively, across the prism; the third one is intermediate with a less penetrating fissure (up to 25%). Prisms IV to VII are laminar and their fissures are only slightly marked. Left M3 has a minute eighth lobe placed at the postero-labial angle. The posterior portion of the tooth bends slightly inward so that the three most posterior prisms are closer to each other, especially at their lingual tips. Enamel is interrupted on the anterior labial wall of the first prism.

P4–M2 series diverge with an angle of about 55°, but M3s change direction and become almost parallel to each other. This arrangement is very similar to that observed in hydrochoerines.

There is a single fragment of upper incisor, triangular in section, with equal anteroposterior and transverse diameters of 6.1 mm. The occlusal surface is strongly concave.



Lower teeth (Fig. 4.2). The p4 has three prisms, the anterior one is the largest and the middle one is the smallest. Internal fissures (h.5i., h.s.i., and h.p.i.) are deep, extending up to more than half the width of the prism in the first and third ones, and a bit less than half in the middle prism. Enamel is interrupted on the posterior lingual wall.

The external fissures (h.s.i. and h.p.i.) of m1–m2 are wide, deep, and at the middle of the prism (Fig. 4.2), dividing the latter into similarly-sized anterior and posterior portions. The margins of the fissures are irregular, with small ramifications or bifurcations. This characteristic is also present in some specimens of hydrochoerines, both living (Mones, 1991) and fossil, *i.e.*, *Cardiatherium patagonicum* (see Vucetich *et al.*, 2005) and *C. chasicoense* (see Deschamps *et al.*, 2007). Individuals of other species of *Caviodon* show very slight enamel irregularities (see Discussion). The hypoflexid is also deep, funnel-shaped. The anterior wall of these teeth is straight, while the posterior one is convex. Enamel is interrupted on the anterior and posterior lingual walls.

The m3 is larger than the other two molars and similar in morphology, but its anterior and posterior walls are convex. Enamel is interrupted as in m1–m2.

Postcranium (Fig. 5). Few and fragmentary postcranial elements are known. They are represented by a small portion of the atlas, a fragmentary sacrum, both femora, medial fabella from the left knee joint, proximal phalanges of digit III (left and right hindfeet), proximal phalanx of digit IV (left hindfoot), intermediate phalanx of digit III (left hindfoot), intermediate phalanx of digit IV (left hindfoot), and three sesamoid bones from the metatarsal-phalangeal articulation (probably left hindlimb).

The sacrum (Fig. 5.1) is fragmentary and incomplete, only the dorso-lateral aspect is accessible because it is still embedded in the sediment. The extremely fragmented condition of this material precluded further removal of sediment. In the median sacral crest, the first spinous process is incomplete and the second and third processes are known by their bases. The *pars lateralis* presents thickened outer margins, thus determining more defined sacral grooves than those of the living *Hydrochoerus*. The sacral articular tubercles are small and poorly preserved but present, unlike

Figure 3. 1, 3, 5, 7, *Caviodon cuyano* sp. nov. MHNSR-PV 1101. 1, skull in dorsal view/ *cráneo en vista dorsal*; 3, skull in ventral view/ *cráneo en vista ventral*; 5, skull in lateral view/ *cráneo en vista lateral*; 7, mandible fragment in lingual view/ *fragmento mandibular en vista lingual*. 2, 4, 6, *Caviodon pozzii* MMP 525-M. 2, skull in dorsal view/ *cráneo en vista dorsal*; 4, skull in ventral view/ *cráneo en vista ventral*; 6, skull in lateral view/ *cráneo en vista lateral*. Scale/ *escala*= 20 mm.

in *Hydrochoerus*. The dorsal sacral foramina are apparently small, and obliterated by sediment. Very fragmented parts of the ilion, crushed and distorted, articulate with the anterior part of the sacrum.

The right femur (Fig. 5.2–3) is known only by the middle part of the diaphysis, the head, and additional small fragments. The left femur is better preserved but incomplete; the greater trochanter and distal epiphysis are missing. Both femoral condyles are preserved as separate fragments. The femur is medium- to large-sized for a rodent, about 70% of

the size of the femur of *Hydrochoerus* (Fig. 5.3). Although the bone is somewhat diagenetically flattened, its robustness seems to have been similar to that of *Hydrochoerus*. The lesser trochanter is less defined and protuberant than in *Hydrochoerus*. The femoral head is hemispherical, its original inclination with respect to the diaphysis cannot be assessed with certainty as it has been reconstructed and glued to the neck. The neck is relatively more slender than in *Hydrochoerus*. The third trochanter is robust and seems to be more proximally located than in *Hydrochoerus* (the lack of the distal portion precludes a more accurate estimation of its position).

The condyles are similar to those of *Hydrochoerus* and they are as robust as in the latter genus. The *sulcus popliteus* on the lateral epicondyle is deeper and more extended posteriorly than in *Hydrochoerus*. The patellar surface and the intercondyloid fossa are not preserved.

The phalanges (Fig. 5.4–5) are morphologically similar to those of *Hydrochoerus*, but smaller and more slender. Both the fabella from the knee joint (Fig. 5.6) and the autopodial sesamoids (Fig. 5.7) are similar to those of *Hydrochoerus* but smaller.

DISCUSSION

The new species described here is referred to the genus *Caviodon* because of the very deep accessory fissures and the M3 with more than six prisms, while it differs from *Cardiomys*, *Procardiomys*, and *Xenocardia* in various features.

In *Cardiomys*, the prisms are subtriangular to heart-shaped, with the anteroposterior diameter proportionally longer than in *Caviodon*, the accessory fissures are very shallow, and M3 has four to five prisms. Species of this genus are widely distributed, especially in the late Miocene–early Pliocene (Chasicuan to Montehermosan) of central Argentina both in the Pampean and Andean regions. For the middle Miocene, Kraglievich (1930) tentatively referred two species to *Cardiomys*, *C. andinus* Kraglievich, 1930 and *C. hue-mulensis* Kraglievich, 1930, each based on an isolated tooth. These species have very dubious status and their *Cardiomyinae* affinities are also uncertain (Vucetich, 1984), *Procardiomys* is known exclusively through the species *P. martinoi* from Arroyo Chasicó, Arroyo Chasicó Formation (late Miocene, Chasicuan), Buenos Aires Province (Fig. 1.1). It is characterized by its M3 with lesser number of prisms, P4–M2 with only H.S.E., lower molars with a single fissure of uncertain homology, opposed to the hypoflexus, and p4 with two well developed prisms and only a rudimentary third one.

Xenocardia is known exclusively by its species *X. diver-*

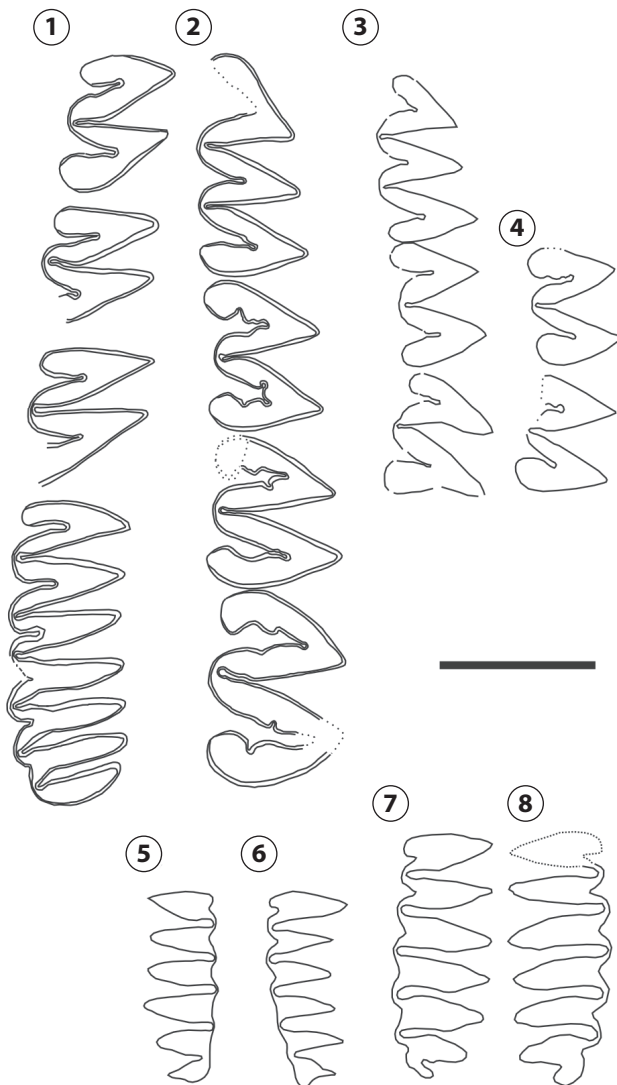


Figure 4. Dental series in occlusal (1–5 and 7) and basal (6 and 8) surfaces/ superficies oclusal (1–5 y 7) y basal (6 y 8) de las series dentarias. 1–2, *Caviodon cuyano* sp. nov. MHNSR-PV 1101. 1, right P4–M3/ P4–M3 derechos; 2, right p4–m3/ p4–m3 derechos. 3, *C. pozzii*, MACN Pv 6915, holotype, right p4–m3/ holotipo p4–m2 derechos. 4, *Caviodon* sp. MACN Pv 14841, right m1–m2/ m1–m2 derechos. 5–6, *C. bravardi*, MACN Pv 4495, holotype, left M3/ holotipo, M3 izquierdo. 7–8, *C. (L.) paranense*, MACN Pv 13471, holotype, right M3/ holotipo, M3 derecho. Scale/ escala = 10 mm.

sidens from Loma del Camello, Huachipampa Formation (late Miocene, Chasicohan?), San Juan Province (Fig. 1.1). It is characterized by the first prism of its M1–M2 being much narrower anteroposteriorly than the posterior prism, whereas in the P4 the first one is much thicker anteroposteriorly than the posterior and has no H.P.E. External accessory fissures are deeper than in *Cardiomyis*, reaching about 25–30% of the width of the prisms. M3 has six prisms; the first five are lanceolate and the sixth is labiolingually shorter and anteroposteriorly thicker.

For the genus *Caviodon*, several nominal species have been described coming from “Mesopotamian” (Huayquerian, late Miocene), Montehermosan (early Pliocene), and Chapadmalalan (late Pliocene) levels (see Mones, 1986). Species of this genus are based on single isolated cheek-teeth or incomplete mandibular and palatal fragments, which

render comparison among species a complex issue. A similar circumstance occurs in hydrochoerid “cardiatheriines”, for which numerous species have been described based on non-comparable remains (see Mones, 1991), a situation that has been partially resolved through ontogenetic studies (Vucetich *et al.*, 2005).

C. multiplicatus, the type species of *Caviodon*, is based on a fragment of right M3 found near the city of Paraná, in the “conglomerado osífero” of the Ituzaingó Formation (“Mesopotamian”, Huayquerian, late Miocene; Fig. 1.1). Originally, Ameghino (1885) interpreted this tooth fragment as a p4. Two other species from the “conglomerado osífero”, *C. bravardi* and *C. (L.) paranense*, have also been described, each one based on an isolated M3. These three nominal species are small and their fissures are very shallow (see Ontogeny).

Caviodon australis (Ameghino, 1888) is recorded at Faro-

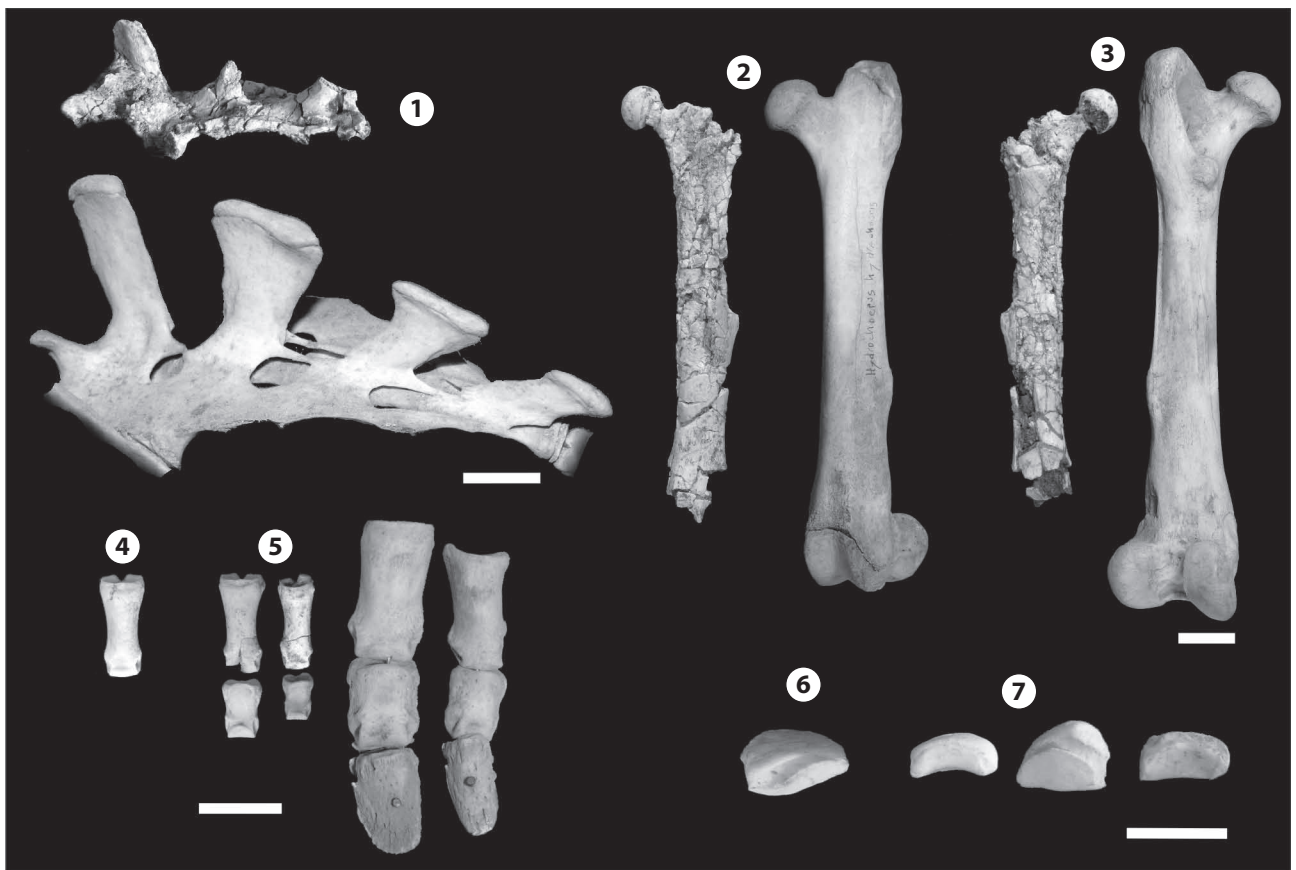


Figure 5. Postcranial elements of *Caviodon cuyano* sp. nov. (top in 1 and left in 2,3,5) compared to *Hydrochoerus hydrochaeris* (bottom in 1 and right in 2,3,5)/ elementos postcraneanos de *Caviodon cuyano* sp. nov. (arriba en 1 e izquierda en 2,3,5) comparados con *Hydrochoerus hydrochaeris* (abajo en 1 y derecha en 2,3,5). **1**, Sacrum in dorso-lateral view, left side/ sacro en vista dorso-lateral del lado izquierdo. **2**, Left femur, anterior view/ fémur izquierdo, vista anterior. **3**, Idem, posterior view/ idem, vista posterior. **4–5**, Hindfoot phalanges/ falanges de miembro posterior. **4**, Proximal phalanx of right third digit of *C. cuyano* sp. nov./ falange proximal de dedo 3 derecho de *C. cuyano* sp. nov. **5**, Proximal and middle phalanges of left third and fourth digits/ falanges proximales y medias de dedos 3 y 4 izquierdos. **6–7**, Sesamoid bones of *C. cuyano* sp. nov./ huesos sesamoideos de *C. cuyano* sp. nov.; **6**, Medial fabella (left knee joint)/ fabela medial (rodilla izquierda); **7**, Autopodial sesamoids/ sesamoideos del autopodio. Scale/ escala 1–5= 20 mm; 6–7= 10 mm.

la Monte Hermoso (Fig. 1.1), Monte Hermoso Formation (Montehermosan, early Pliocene), Buenos Aires Province. This species could have reached a size similar to that of *C. cuyano* sp. nov., but its accessory fissures are shallower, penetrating up to 20% of the width of the tooth, and M3 has only six prisms, of which the first five are lanceolate and the sixth is short and anteroposteriorly thick. An interesting material found at the same locality is a right mandible fragment with m1–m2 (MACN Pv 14841, “hermosense” in schedis) equivalent in size to *C. australis*. In this specimen the fissures are deeper than those expected for the lower teeth of *C. australis*, judging from those in the upper teeth of the holotype

and referred material (Rovereto, 1914), extending across almost half of the occlusal surface, similar to *C. pozzii* (see below). The fissures are placed in the middle of the prisms, as in *C. pozzii*, but the h.p.i. is directed slightly backwards, and the h.s.i. of both m1 and m2 shows only subtle enamel irregularities (Fig. 4.2). The systematic value of the h.p.i. differences cannot be assessed yet, but they may indicate either morphological variation within *C. australis*, morphological variation within *C. pozzii* sp. nov.—in this case, the species would be recorded already in the Montehermosan—, or even the presence of a second species in the Monte Hermoso Formation, different from the one already described.

TABLE 1 - Dental measurements of *Caviodon cuyano* sp. nov., holotypes of the other species of the genus, and referred materials (see Materials and Abbreviations for details)/ medidas dentarias de *Caviodon cuyano* sp. nov., holotipos de otras especies del género y materiales referidos (ver detalles en Materials and Abbreviations)

| <i>p4</i> | AP | AW | MW | PW | HSEL | HydL | HSIL | HPIL |
|---------------------|-------|------|------|------|------|------|------|------|
| MHNSR-PV 1101 right | 14.24 | 6.08 | 6.56 | 7.04 | 5.92 | 6.52 | 2.88 | 2.88 |
| MHNSR-PV 1101 left | | | 6.56 | 6.8 | | 6.08 | 3.04 | 3.68 |
| MACN 6915 | 10.35 | 4.80 | 5.10 | 5.25 | 4.50 | 4.95 | 2.40 | 2.40 |
| <i>m1</i> | AP | AW | PW | HydL | HSIL | HPIL | | |
| MHNSR-PV 1101 right | 9.76 | 7.04 | 7.20 | 6.08 | 3.52 | 3.84 | | |
| MACN 6915 | 7.50 | 5.25 | 5.10 | 4.80 | 2.40 | 2.55 | | |
| MACN 14841 | 7.50 | 4.95 | 5.40 | 5.10 | 2.10 | 2.10 | | |
| <i>m2</i> | AP | AW | PW | HydL | HSIL | HPIL | | |
| MHNSR-PV 1101 right | 9.60 | 7.68 | 8.08 | 7.20 | 6.00 | 4.80 | | |
| MHNSR-PV 1101 left | 9.44 | 7.36 | 8.32 | 6.88 | 4.16 | 4.80 | | |
| MACN 6915 | 7.80 | 6.00 | 6.00 | 5.10 | | 2.85 | | |
| MACN 14841 | 7.50 | 5.55 | 5.55 | 5.25 | 2.25 | 2.25 | | |
| <i>m3</i> | AP | AW | PW | HydL | HSIL | HPIL | | |
| MHNSR-PV 1101 right | 12.00 | 7.84 | 8.04 | 8.16 | 5.76 | 6.88 | | |
| MHNSR-PV 1101 left | 11.68 | 8.00 | 7.84 | 7.36 | 5.76 | 5.92 | | |
| <i>P4</i> | AP | AW | PW | HPEL | HSEL | | | |
| MHNSR-PV 1101 right | 8.96 | 5.76 | 7.20 | 2.56 | 3.84 | | | |
| MHNSR-PV 1101 left | 9.28 | 5.76 | 7.52 | 2.40 | 4.00 | | | |
| MMP 525-M | 7.36 | 5.12 | 6.24 | 2.56 | 2.56 | | | |
| <i>M1</i> | AP | AW | PW | HPEL | HSEL | | | |
| MHNSR-PV 1101 right | 7.36 | 6.72 | 7.36 | 2.88 | 4.00 | | | |
| MHNSR-PV 1101 left | 7.84 | 6.40 | 8.00 | 2.56 | 3.36 | | | |
| MMP 525-M | 5.92 | 5.44 | 6.08 | 1.76 | 1.92 | | | |
| <i>M2</i> | AP | AW | PW | HPEL | HSEL | | | |
| MHNSR-PV 1101 right | 8.00 | 6.72 | 8.16 | 2.72 | 4.00 | | | |
| MHNSR-PV 1101 left | 8.48 | 6.72 | 8.32 | 2.56 | 4.32 | | | |
| MMP 525-M | 6.40 | 5.44 | 5.76 | 1.76 | 2.08 | | | |
| <i>M3</i> | AP | AW | | | | | | |
| MHNSR-PV 1101 right | 19.56 | 7.74 | | | | | | |
| MMP 525-M | 14.45 | 5.42 | | | | | | |
| MACN 4495 | 10.50 | 3.61 | | | | | | |
| MACN 13471 | 13.42 | 4.99 | | | | | | |

Caviodon pozzii is the most conspicuous and easily identifiable species of the genus. It is based on the anterior part of a right hemimandible with p4–m2 (MACN Pv 6915) from the Chapadmalal Formation (Chapadmalalan, late Pliocene), Chapadmalal (Fig. 1.1), Buenos Aires Province. The holotype is the only material formally referred to *C. pozzii*, but a skull found in the Chapadmalal Formation (MMP 525-M; in front of Baliza Caniu, levels III to V; Fig. 3.2,4,6), in the same levels as the holotype of *C. pozzii*, matches the size and occlusal morphology of the type specimen, and can be assigned confidently to this species. This assignment permits a more complete comparison with *C. cuyano* sp. nov. Internal fissures in *C. pozzii* are deep but shallower than in *C. cuyano* sp. nov. Enamel irregularities are slight, not as conspicuous as in *C. cuyano* sp. nov. The accessory fissures are placed in the center of each prism dividing it into two almost equal portions, and they are directed toward the apex of the prism. The skull of *C. pozzii* is much narrower, the P4–M3 series are less divergent, hence the palate is narrower, and the mesopterygoid is semielliptical instead of semicircular as in *C. cuyano* sp. nov. (Fig. 3.4). In addition, *C. pozzii* is smaller and its M3 has fewer prisms than that of *C. cuyano* sp. nov.

Isolated teeth found in Inchasi, Bolivia, have been assigned to *Caviodon* sp. (Anaya and MacFadden, 1995, p. 110–111, fig. 16). The illustration provided shows these are a lower molar (m1 or m2) and an upper one (P4, M1, or M2) very similar to those of *C. pozzii* because of the depth of the accessory fissures, general morphology of prisms with curved walls, very slight enamel irregularities, and transverse orientation of h.p.i. The fossil-bearing levels of this material were assigned to the Chapadmalalan s.s. *sensu* Cione and Tonni (2001).

TOOTH ONTOGENY, SYSTEMATICS, AND DIVERSITY

The holotypes of *Caviodon bravardi* (MACN Pv 4495) and *Caviodon (Lelongia) paranensis* (MACN Pv 13471), two very small isolated M3 (see Tab. 1), are especially interesting because they allow some inferences about aspects of postnatal tooth ontogeny among cardiomyines. The difference in size observed between the base and the occlusal surface of both teeth indicates a juvenile condition, as in other euhyposodont rodents such as hydrochoerines (Vucetich *et al.*, 2005) or the chinchilloid *Perimys* Ameghino, 1887 (Kramarz, 2002). *C. bravardi* is the smallest (Tab. 1; Fig. 4.5–6), and the external fissures in Pr.I and Pr.II are subtly marked, but they are deeper at the base of the tooth (Fig. 4.5). It has six prisms

in occlusal view (Fig. 4.5), with the last one shorter than the others. However, the base of this tooth shows the rudiment of a seventh prism (Fig. 4.6). *C. (L.) paranensis* (MACN Pv 13471; Fig. 4.7–8) has six prisms and a very small seventh one, although more developed than the seventh prism seen in the molar base of *C. bravardi*. At the base of the tooth of *C. (L.) paranensis*, this seventh prism is a little larger and the fissures are more evident than on the occlusal surface (Fig. 4.7–8). This shows that in cardiomyines the final occlusal configuration is acquired during postnatal ontogeny and tooth size could be indicative of the age of the specimen, as in hydrochoerines (Vucetich *et al.*, 2005). It also suggests that *C. bravardi* and *C. (L.) paranensis* may correspond to successive ontogenetic stages of a single species. Thus, it is possible that the true species diversity of *Caviodon* may be lower than supposed, at least in the “conglomerado osífero”.

In this context, it is possible that the differentiation of the genus *Caviodon*, and probably also *Xenocardia*, would be associated with ontogenetic differences such as predisplacement of the onset of accessory fissures. In *Cardiomys*, the accessory fissures are hardly developed even in adult (=large) individuals. It should be taken into account that the deepening of fissures, like the multiplication of the number of prisms in M3, is a general trend within Hydrochoeridae (Vucetich *et al.*, 2005; Deschamps *et al.*, 2007).

AGE OF THE AISOL FORMATION

The MS of the Aisol Formation has been assigned to the late Miocene (Huayquerian SALMA) or considered even younger on the basis of the mammal record (Forasiepi *et al.*, 2009, 2011). The presence of *C. cuyano* sp. nov. in this section of the Aisol Formation contributes new information to this discussion. According to the depth of the accessory fissures and the number of prisms in the M3, *C. pozzii* is the most specialized cardiomyine known. It comes from upper Chapadmalalan levels (late Pliocene), as do the materials from Inchasi, also with deep fissures. However, the presence of the mandible MACN Pv 14841 in the Monte Hermoso Formation suggests that the genus *Caviodon* was already represented by species with deep accessory fissures in the early Pliocene. Dental features in *C. cuyano* sp. nov. are even more specialized than in *C. pozzii*. Based on the current stratigraphic distribution of *C. pozzii*, we would not expect to find a taxon with the specializations of *C. cuyano* sp. nov. in levels older than the Montehermosan. Furthermore, the dental specializations of *C. cuyano* sp. nov. compared with *C. pozzii* and within the context of hydrochoerid evolution, suggest that the MS of the

Aisol Formation might be even younger. This chronological suggestion matches with the presence of a Ctenomyidae aff. *Eucelophorus* Ameghino, 1908 (D. Verzi, com. pers. 2011), which is hitherto known from Pliocene to Pleistocene deposits (*i.e.*, Montehermosan to Ensenadan SALMAs; Rovereto, 1914; Verzi *et al.*, 2004; Verzi, 2008). In this case, the biochron of the marsupial *Hesperocynus dolgopolae* (Reig, 1958), recorded so far in the late Miocene, would stretch to the Pliocene. Other mammalian remains (*e.g.*, *Tremacyllus*, Ameghino, 1891, Dolichotinae indet., and Abrocomidae indet.) do not contribute to elucidate the age of this section, but at least they do not contradict the idea of a Pliocene age.

CONCLUSION

Caviodon cuyano sp. nov. is the largest known cardiomyine. It shares with *C. pozzii* cheek-teeth with deep accessory fissures located at the center of each prism. However, it differs from this species in its wider cheek-teeth, deeper fissures with strong enamel irregularities, M3 with one more prism, and the semi-circular outline of the mesopterygoid fossa. Furthermore, its wider cranial roof and wider palate give *C. cuyano* sp. nov. a more robust aspect.

Caviodon cuyano sp. nov. extends the geographical distribution of the genus southward within the Andean region. Its outstanding robustness suggests that it may represent an endemic lineage for this area.

Our results show that, as in hydrochoerines, the occlusal morphology of cardiomyines is completed during postnatal ontogeny, with allometric growth of the prisms and fissures. Hence, the dental morphology of adults differs from that of juveniles. Consequently, the use of tooth size and morphology to define cardiomyine species should be approached with caution. A thorough revision of the group is necessary in order to elucidate which morphologies belong to different ontogenetic stages of a single species, and which actually represent different species.

Given this ontogenetic variation, the true diversity of cardiomyines may have been less than previously assumed, as illustrated by the materials from the “conglomerado osífero” discussed above.

The evolutionary stage of *C. cuyano* sp. nov. suggests that the age of the MS of the Aisol Formation could be younger than previously supposed, no older than early Pliocene and possibly up to late Pliocene.

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