

Paleobiology of the basal hydrochoerine *Cardiomys* Ameghino, 1885 (Rodentia, Caviomorpha, late Miocene, South America) as inferred from its postcranial anatomy

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Abstract.—Extinct Hydrochoerinae traditionally included within ‘Cardiomyinae’ (Cavioidea, Caviidae) are caviomorph rodents well represented in the late Miocene to late Pliocene of Argentina, but their paleobiology has received little scientific attention. The postcranium of these rodents is poorly known and has not been considered in morphofunctional or systematic studies. Here, we provide the first description of the postcranium of the basal hydrochoerine *Cardiomys* Ameghino, 1885, based on a well-preserved specimen from the late Miocene of Central Argentina, and evaluate its paleobiological and systematic implications. A morphofunctional study and a character mapping analysis were performed. We concluded that most of its postcranial features are neither adaptations to a specialized cursoriality, as in some extant cavioids, nor major modifications associated with swimming, as in extant capybaras. *Cardiomys* exhibits several features (high humeral distal articular surface, perforated olecranon fossa, proximal portion of radius cranially located with respect to the ulna, subrectangular-shaped radial head with flattened ulnar facet, calcaneocuboid joint distally located with respect to the astragalonavicular joint) that allow us to interpret it as an ambulatory caviid. Among cavioids, some features of *Cardiomys* are more similar to those of *Hydrochoerus* Brisson, 1762 (lateral coronoid process reduced, humeral capitular tail well differentiated, capitular tail facet of the radial head well developed and relatively short craniodistally, plantar process of the navicular massive and short). Other postcranial features (relatively longer and more gracile third metatarsal and phalanges, straight caudal border of the ulna) suggest that *Cardiomys* would have been a generalized hydrochoerine, as also indicated by its dental and cranial characters.

Introduction

Extinct Hydrochoerinae (Caviidae, Cavioidea; sensu Madozzo-Jaén and Pérez, 2017) known as ‘cardiomyines’ encompass medium-sized caviomorph rodents, mainly characterized by ever-growing teeth, p4 composed of three prisms, P4–M2 and m1–m3 formed by two heart-shaped prisms with accessory flexi/ids, M3 multiprismatic, and a broad palate (Vucetich et al., 2011; Pérez et al., 2014). They are first known from the middle Miocene of Patagonia (Vucetich and Pérez, 2011), reaching their greatest taxonomic diversity during the late Miocene–late Pliocene of Argentina (Rovereto, 1914; Kraglievich, 1927, 1940; Pascual, 1961; Pascual and Bondesio, 1963; Pascual et al., 1966; Vucetich et al., 2011), with additional reports from the Neogene of Bolivia (Anaya and MacFadden, 1995), Venezuela (Vucetich et al., 2010), and Brazil (Kerber et al., 2017). Late Miocene and Pliocene ‘cardiomyines’ are represented by several species included in the genera *Cardiomys*, *Caviodon* Ameghino, 1885 (including *Lelongia* Kraglievich, 1930b), *Procardiomys* Pascual, 1961, and *Xenocardia* Pascual and

Bondesio, 1963, all of which are known from abundant cranial and dental remains. Traditionally, these genera were included within the subfamily Cardiomyinae of Caviidae (Rovereto, 1914; Pascual, 1961; Pascual et al., 1966; Mones, 1986; McKenna and Bell, 1997). Later, the cardiomyines were considered Hydrochoeridae (e.g., Vucetich and Pérez, 2011; Vucetich et al., 2011). More recently, cladistic analyses (Madozzo-Jaén and Pérez, 2017; Pérez et al., 2017b) recovered *Caviodon*, *Cardiomys*, *Xenocardia*, and *Procardiomys* as basal Hydrochoerinae within the family Caviidae, but the monophyly of ‘Cardiomyinae’ (as originally defined) was not recognized. The postcranial anatomy of ‘cardiomyines’ is poorly known and their paleobiology was scarcely scrutinized. Only a few fragmentary postcranial bones of *Caviodon cuyano* Vucetich et al., 2011 (Pliocene of Mendoza Province) have been described (Vucetich et al., 2011). Moreover, the postcranium of these rodents was not used as source of characters either in systematic analyses or to infer probable locomotor behavior.

In this contribution, we present the first description of postcranial remains of *Cardiomys*. The specimen studied comes

from the Chasicó Formation (late Miocene, Buenos Aires Province, Argentina) and represents the ‘cardiomyine’ with the most completely preserved postcranium known. We evaluate it from a paleobiological point of view and discuss the systematic implications of its postcranial features.

Materials and methods

The new specimen of *Cardiomyis* (MLP 29-IX-3-19) described here is represented by an isolated right M3 and associated postcranial remains. Molar morphology of this specimen was compared with specimens of *Caviodon*, *Cardiomyis*, *Xenocardia*, and *Procardiomyis* by direct observation or by comparison with published data (Ameghino, 1885; Rovereto, 1914; Kraglievich, 1930b; Pascual, 1961; Pascual et al., 1966; Vucetich et al., 2011; Pérez et al., 2014). The postcranial elements of specimen MLP 29-IX-3-19 were compared with the postcranium of the type specimen of *Caviodon cuyano* from the Aisol Formation (Pliocene, Mendoza Province), based on descriptions and illustrations provided by Vucetich et al. (2011). We also compared the postcranial remains with extant species of all main lineages of Cavoioidea (Supplemental Data 1). Dental nomenclature follows that of Pérez et al. (2014). The osteological nomenclature follows that used by Candela and Picasso (2008) and the International Committee on Veterinary Gross Anatomical Nomenclature (2005). Most of the postcranial characters of cavioids used in the comparisons have been previously discussed by Candela and Picasso (2008) and García-Esponda and Candela (2016). The myological nomenclature and muscular system are based on Woods (1972) and García-Esponda and Candela (2010). Locomotor habits and substrate preferences of present-day species follow Candela et al. (2017).

Four linear measurements were taken from photographs of the studied material using ImageJ 1.50i software (Schneider et al., 2012). The variables measured were navicular body length, plantar process of the navicular length, third metatarsal (Mt III) length, and Mt III width. Two indices were calculated: (1) plantar process of the navicular length/navicular body length, and (2) Mt III length/width. Each box plot was created in R software 3.1.5 (R Development Core Team, 2015).

Part of the morphological variation observed among cavioids was coded in six characters. Only those characters considered informative in the context of our taxon sample were included in the character mapping. Character state definitions are provided in Supplemental Data 2, and the resultant data matrix is provided as a TNT script in Supplemental Data 3. The evolution of these characters was mapped on the composite molecular-morphological phylogeny of Cavoioidea provided by Madozzo-Jaén and Pérez (2017), which was simplified to living taxa and the extinct *Cardiomyis*. Cladistic mapping was done with TNT 1.5 (Goloboff and Catalano, 2016). Four discrete character states were considered unordered whereas the remaining two characters were coded as continuous (Goloboff et al., 2006), using the mean value for each terminal taxa.

Repositories and institutional abbreviations.—The studied specimens are housed in the following collections: Museo de La Plata (MLP), La Plata, Argentina; Museo de Ciencias Naturales

‘Bernardino Rivadavia’ (MACN), Buenos Aires, Argentina; zoological collection of Museo de Ciencias Naturales ‘P. Antonio Scasso’ (MPS-Z), San Nicolás, Argentina; Centro Nacional Patagónico (CNP), Puerto Madryn, Argentina; mammal collection of Museo Municipal de Ciencias Naturales ‘Lorenzo Scaglia’ (MMPMa), Mar del Plata, Argentina; American Museum of Natural History (AMNH), New York, New York, USA; Yale Peabody Museum of Natural History (YPM), New Haven, Connecticut, USA.

Systematic paleontology

Order Rodentia Bowditch, 1821
 Suborder Hystricomorpha Brandt, 1855
 Superfamily Cavoioidea (Fischer von Waldheim, 1817)
 Kraglievich, 1930a
 Family Caviidae Fischer von Waldheim, 1817
 Subfamily Hydrochoerinae (Gray, 1825) Gill, 1872; Weber,
 1928 sensu Kraglievich, 1930a
 Genus *Cardiomyis* Ameghino, 1885

Type species.—*Cardiomyis cavinus* Ameghino, 1885, ‘Mesopotamiense’ (lower member of Ituzaingó Formation, late Miocene), Entre Ríos Province, northeast Argentina.

Cardiomyis leufuensis Pérez, Deschamps, and Vucetich, 2017

Occurrence.—Chasicó Locality, southwest Buenos Aires Province (Argentina); Arroyo Chasicó Formation, Chasicóan Stage/Age, late Miocene (see Tonni et al., 1998; Cione and Tonni, 2005; Zárate et al., 2007).

Description.—The M3 has four prisms separated by deep lingual flexi (Fig. 1). The first prism is the most anteroposteriorly compressed of all prisms; it displays a convex anterior border and a labial superficial flexus (sulcus). The second and third prisms are heart-shaped. The second prism has two labial flexi, somewhat deeper than that of the first prism. The third prism is anteroposteriorly wider than the second and displays a labial superficial sulcus on its anterior labial border. The fourth prism is labiolingually narrower than the other prisms and shows a posterior prolongation. Enamel is thicker on the lingual border of the prisms than on the labial side. This tooth would correspond to an adult individual because the diameters of its base and occlusal surfaces are approximately equal (Vucetich et al., 2011).

In general appearance, the distal portion of the humerus (Fig. 2.2) is similar to that of other cavioids. The olecranon fossa is perforated. The entepicondyle is moderately developed, showing an expansion similar to that of *Hydrochoerus* (Fig. 2.1) and *Dasyprocta* Illiger, 1811, but relatively larger than in caviines and dolichotines (Fig. 2.3) and smaller than that of *Cuniculus* Brisson, 1762. The distal articular surface of the humerus is relatively higher proximodistally than that of *Cuniculus*, similar to that of *Hydrochoerus*, and lower than that of Caviinae, Dolichotinae, and *Dasyprocta*. The capitular tail has a degree of differentiation similar to that of *Hydrochoerus*; compared to other cavioids, it is more lateromedially extended and differentiated from the capitulum. The trochlea is steeply

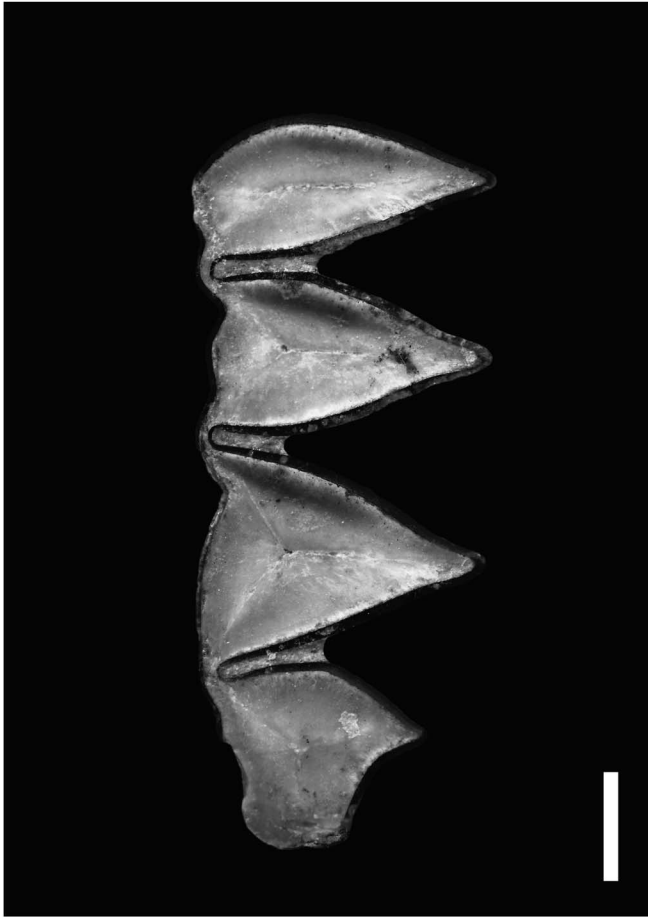


Figure 1. MLP 29-IX-3-19, right upper third molar of *Cardiomys leufuensis* in occlusal view. Scale bar = 2 mm.

angled. The lateral lip of the trochlea is well developed on the caudal facet of the articular surface, but cranially it ends abruptly.

As in other cavioids, the proximal extremity of the radius (Fig. 2.5) articulates cranially with respect to the ulna. The proximal articular surface of the radius is subquadrangular, being wide lateromedially and short craniocaudally. Among cavioids, this configuration is also seen in *Cuniculus*, Caviinae, and *Hydrochoerus* (Fig. 2.4), whereas in Dolichotinae (Fig. 2.6) and *Dasyprocta*, this articular surface is less lateromedially extended. The proximal articular surface has three distinct facets: a central facet, the fovea; a medial facet, the trochlear facet; and a lateral facet, the capitular tail facet. The fovea is the main facet of the radial head, articulating with the capitulum of the humerus. It has a somewhat triangular outline, resembling that of *Hydrochoerus*. The trochlear facet has a steep inclination from lateral to medial, showing a similar development to that of Caviinae and Dolichotinae but greater than that of *Cuniculus* and *Dasyprocta*. The fovea and the trochlear facet are separated by a crest, which ends in a spine, the capitular eminence, on the cranial border of the head of the radius. The capitular tail facet lies on the lateral side of the radial head, articulating with the capitular tail of the humerus when the elbow is flexed. This facet has an inclination from medial to lateral and is separated from the fovea by a crest. As in *Hydrochoerus*, the capitular tail facet

is well differentiated from the fovea and to a greater degree than in caviines (in Dolichotinae, this facet is not differentiated from the fovea). In addition, the most lateral portion of the radial head is craniocaudally shorter with respect to the rest of the articular surface. This narrowing is similar to, although not as pronounced as, that of *Hydrochoerus* but greater than that of Caviinae. Although the ulnar facet is poorly preserved, it is relatively flat.

The ulna (Fig. 2.8) is not completely preserved, but it can be noticed that the olecranon process is as long as the trochlear notch, a condition also observed in other cavioids (with the exception of *Dasyprocta*, in which the olecranon process is relatively shorter). The medial coronoid process is well differentiated, but the lateral coronoid process is very reduced (Fig. 2.8). The latter condition is close to that of *Hydrochoerus* and *Cuniculus*, in which this process is absent, and differs from that of caviines, dolichotines (Fig. 2.9), and *Dasyprocta*, all of which have a well-developed lateral coronoid process. The radial notch is wide, as in other cavioids, reflecting a broad anterior contact with the radius. As in *Cuniculus* and *Dasyprocta*, this notch is represented by a single facet. On the contrary, in *Hydrochoerus*, dolichotines, and caviines, the radial notch is composed of two separated facets for articulation with the radius. As in most Caviioidea, the caudal border of the proximal portion of the ulna is straight. This contrasts with the condition observed in *Hydrochoerus*, in which the caudal border is more concave, as a consequence of its caudally oriented olecranon. As observed in most cavioids, the lateral surface of the ulnar shaft has a shallow fossa (area of origin of the m. abductor pollicis longus), which extends proximally to the level of the radial notch.

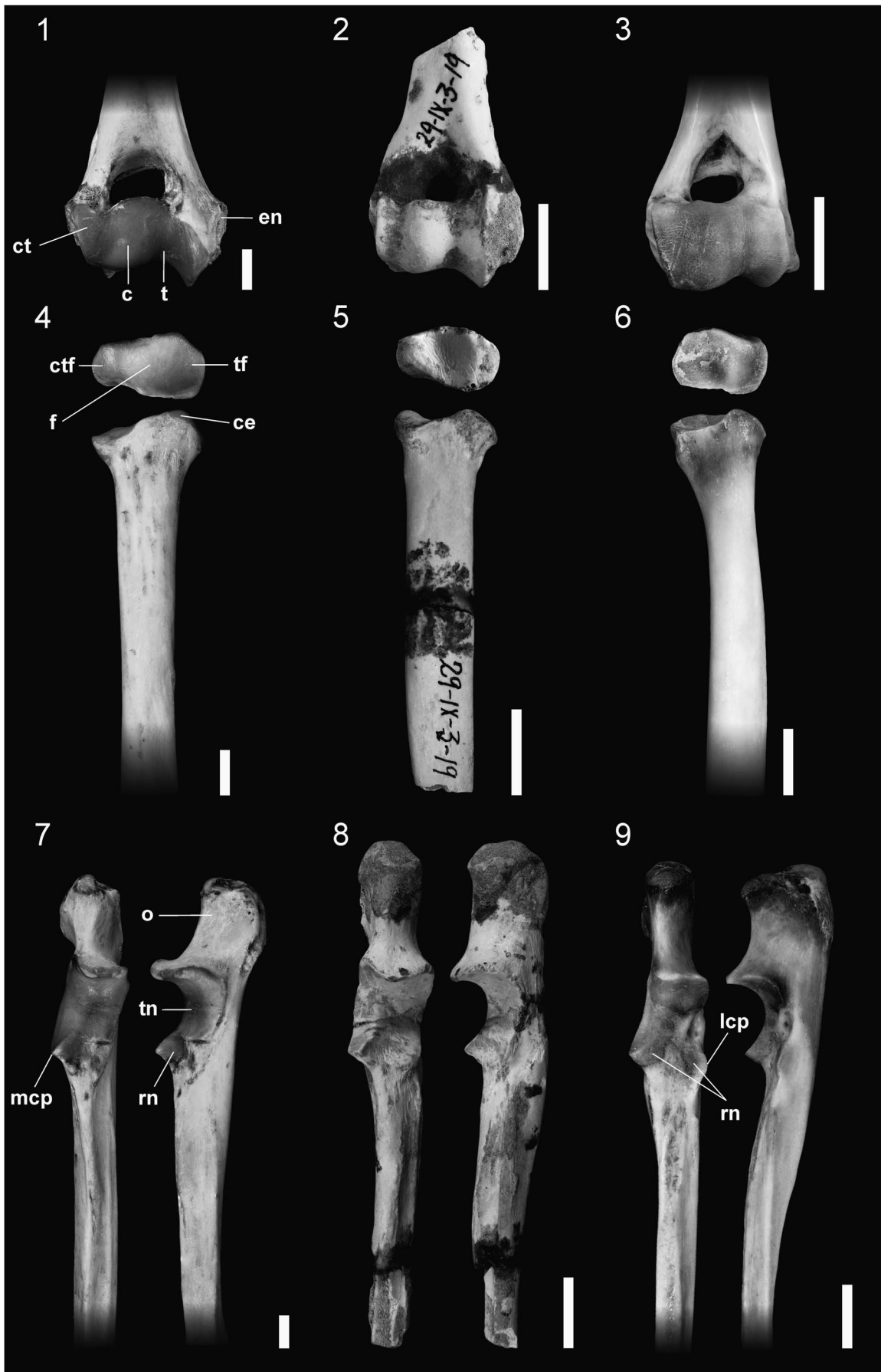
Bones of the left manus are only represented by the pisiform (which is similar in shape to that of the other cavioids) and a fragmentary proximal end of the fourth metacarpal.

Only a small portion of the left ischium is preserved. This portion comprises the cranial part of the body of the ischium, including part of the acetabulum. It also includes the cranial portion of the lesser sciatic notch. The ischiadic spine and the pulley where the tendon of m. obturator internus slides are similar to those of *Hydrochoerus*.

Only the distal portion of the right fibula is preserved. The articular facet for the tibia and astragalus, and the sulci for the mm. peronei are similar to those of *Hydrochoerus*.

The ectal facet of the calcaneus (Fig. 3.2) is somewhat obliquely oriented with respect to the longitudinal axis of the bone, facing distally. The sustentaculum bears a subcircular and flat facet that is obliquely oriented and faces dorsodistally. The tuber calcanei is not preserved. The peroneal tubercle is short and indistinct, as in other cavioids. The cuboid facet is concave in dorsoventral direction, facing medially, similar to that of *Hydrochoerus*. As in other cavioids, this facet is far distally located with respect to the sustentaculum.

The navicular is poorly preserved, represented by two portions: a part of the navicular body (Fig. 3.2) and the plantar process (Fig. 3.5). The facet for the astragalus head is less lateromedially extended than in *Hydrochoerus* (Fig. 3.1), similar to that of *Dolichotis* Desmarest, 1820 (Fig. 3.3). The preserved portion of the body is relatively proximodistally longer than that of *Hydrochoerus*. The plantar process is similar



to that of *Hydrochoerus*, being wider and relatively shorter than that of caviines, dolichotines, and *Dasyprocta* (Figs. 3.4, 3.6, 4.1).

The preserved portion of the cuboid indicates that, as in other cavioids, the dorsal face of this bone is smaller than the ectocuneiform (Fig. 3.2). The calcaneo-cuboid facet of the cuboid is also similar to that of other cavioids. The plantar process of this bone is robust (Fig. 3.5), similar to that of *Hydrochoerus* (Fig. 3.4) and caviines but somewhat more robust than that of *Dolichotis* (Fig. 3.6).

The ectocuneiform shows the typical plantar extension observed in other cavioids. Its dorsal surface has a subrectangular outline, being relatively proximodistally longer than that of *Hydrochoerus* but shorter than that of *Dolichotis* (Fig. 3.1–3.3).

The third metatarsal (Fig. 3.2) is relatively more gracile and elongated than that of *Hydrochoerus* (Fig. 3.1) and *Cuniculus* but more robust than that of *Dolichotis* (Fig. 3.3), *Cavia* Pallas, 1766, and *Galea* Meyen, 1833 (Fig. 4.2).

The preserved proximal portions of the second and fourth metatarsals (Fig. 3.2) are morphologically similar but slenderer than those of *Hydrochoerus* (Fig. 3.1). The proximal and middle phalanges of the third digit and the middle phalanx of the fourth digit are slenderer than those of *Hydrochoerus* and morphologically similar to those of *Caviodon*.

Materials.—MLP 29-IX-3-19, right M3, distal ends of both humeri, proximal portions of both ulnae, right radius without its distal end, proximal portion of the left radius, left pisiform, proximal end of the left fourth metacarpal, portion of the left ischium, distal end of the right fibula, right calcaneus and partially preserved right navicular, right ectocuneiform, poorly preserved right cuboid, right Mt III, proximal portions of right Mt II and Mt IV, right proximal and middle phalanges of the third digit and middle phalanx of the fourth digit of the pes.

Remarks.—Specimen MLP 29-IX-3-19 is referred to *Cardiomys* because its M3 has four prisms, which are relatively anteroposteriorly wider and present relatively more superficial labial flexi (= sulci) than those of *Caviodon* and *Xenocardia* species (Pascual et al., 1966; Vucetich et al., 2010; Vucetich et al., 2011). Therefore, we excluded assignment to *Caviodon australis* Ameghino, 1888 (Montehermosan, early Pliocene; Rovereto, 1914) and *Caviodon pozzi* Kraglievich, 1927 (Chapadmalalan, late Pliocene) as both species have M3 with more prisms and much more penetrating fissures. *Xenocardia* (Chasicooan?) was also eliminated as it also has more penetrating labial flexi and more delicate prisms (Vucetich et al., 2010). Specimen MLP 29-IX-3-19 also differs from the type of *Procardiomys martinoi* Pascual, 1961 because the latter has an M3 with three lobes and a well-developed posterior projection (Pérez et al., 2014). The M3 of the type of *Cardiomys ameghinorum* Rovereto, 1914 has four prisms and one posterior projection (a fifth

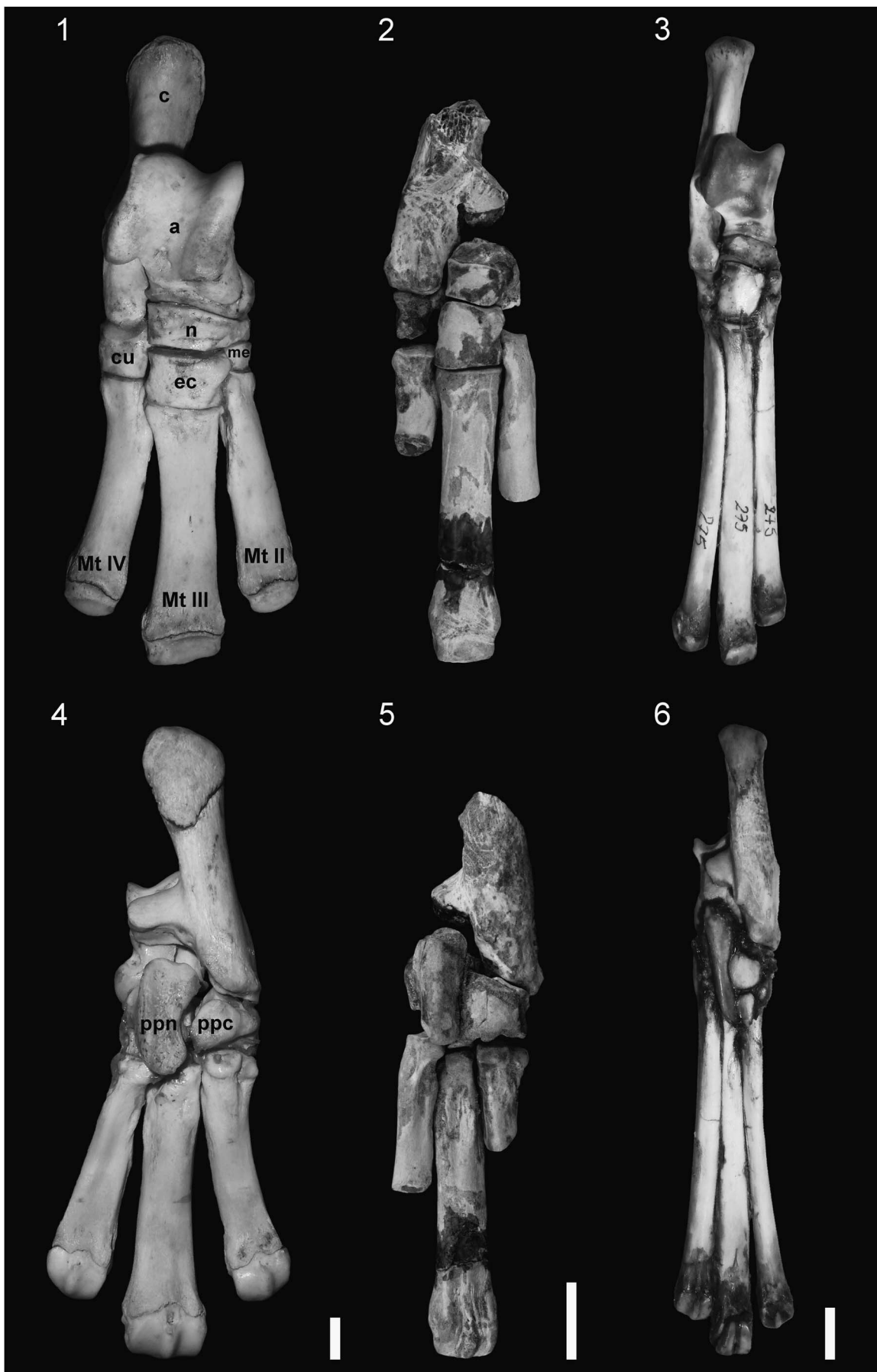
small lobe) that is well differentiated from the last prism by a lingual flexus. Specimen MLP 29-IX-3-19 differs from the type of this species because the fourth prism of M3 is narrower than the third and the posterior projection is continuous with the fourth prism. The M3 of the specimen MLP 29-IX-3-19 is very similar in size and general morphology (number and relative size of prisms, depth of labial flexi) to that of the type of *Cardiomys leufuensis*, but differs from it in the morphology of the second prism, which has two labial flexi in MLP 29-IX-3-19 and a straight labial side in *C. leufuensis* (Pérez et al., 2017a, fig. 6F). Besides this difference, all other shared features support the specific assignment of the MLP 29-IX-3-19 to *C. leufuensis*.

Discussion

Systematic considerations on the postcranial features.—The phylogeny of Caviioidea has been based on molecular, cranial, and dental data while postcranial features have not been analyzed from a systematic point of view. Our study indicates that many postcranial features of *Cardiomys* are shared with other analyzed cavioids (proximal portion of radius cranially located with respect to the ulna, olecranon fossa perforated, distal articular humeral surface relatively high, radial head lateromedially extended and posteriorly flattened, distal portion of calcaneus extended, dorsal face of cuboid smaller than that of ectocuneiform). Character mapping (Fig. 5) indicates that the extreme reduction of the lateral coronoid process of the ulna (character state 3¹), presence of a greatly differentiated capitular tail of the humerus (character state 5²), shortening of the Mt III (character 1), and shortening of the plantar process of the navicular (character 2) would be potential synapomorphies of Hydrochoerinae, in the context of Caviioidea. Thus, these characters support *Cardiomys* as within Hydrochoerinae, in agreement with phylogenetic hypothesis based on other morphological characters. Optimization of robustness of Mt III (character 1) shows that dolichotines have a more slender Mt III than the remaining cavioids, whereas the Hydrochoerinae display the most robust Mt III in the context of this group. Within the Hydrochoerinae, Mt III of *Cardiomys* is less robust than that of *Hydrochoerus*, closer to the ancestral condition of this clade. In the phylogenetic context of cavioids, the well-differentiated and craniodistally narrow capitular tail facet of the radius (character state 6²) is a feature only present in *Cardiomys* and *Hydrochoerus*. However, ambiguous optimization of this feature at the node of the clade that contains Dolichotinae and Hydrochoerinae precludes us from inferring whether this feature could be a potential synapomorphy of Hydrochoerinae. Chasicooan hydrochoerines have been recognized as critical to understanding the early evolution of the group because they display dental features that anticipate the derived dentition of modern capybaras (Pérez et al., 2014). In agreement with this, some postcranial features of *Cardiomys* seem to be more generalized than those of modern capybaras (relatively more

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Figure 2. (1–3) Cranial view of right humeri. (4–6) Proximal and cranial views of right radii. (7–9) Cranial and lateral views of left ulnae. (1, 4, 7) *Hydrochoerus hydrochaeris* (MPS-Z 142); (2, 5, 8) *Cardiomys leufuensis* (MLP 29-IX-3-19); (3, 6, 9) *Dolichotis patagonum* (MLP 249). Views 1, 3, and 4 are mirrored. c = capitulum; ce = capitular eminence; ct = capitular tail; ctf = capitular tail facet; en = entepicondyle; f = fovea; lcp = lateral coronoid process; mcp = medial coronoid process; o = olecranon; rn = radial notch; t = trochlea; tf = trochlear facet; tn = trochlear notch. Scale bars = 10 mm.



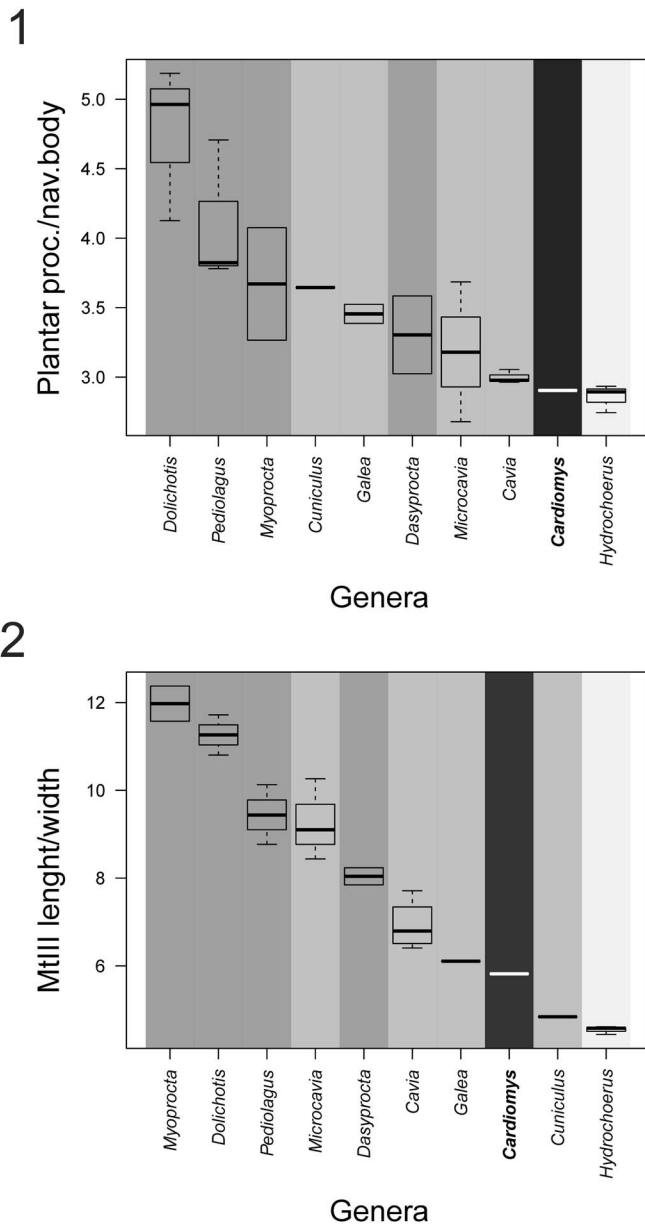


Figure 4. Box plots of morphological indices of the pes in cavioid rodents. (1) Plantar process of the navicular length/navicular body length index; (2) third metatarsal length/width index. Dark grey = cursorial; middle grey = ambulatory; light grey = swimming; black = unknown (see Candela et al., 2017).

gracile and longer Mt III and phalanges and straight caudal border of the ulna). The presence of a single radial notch of the ulna (character 4⁰) in *Cardiomys* would be a reversion to the plesiomorphic condition present in *Cuniculus*. A phylogenetic study based on wider taxon and character sampling could test whether the common features of *Cardiomys* and *Hydrochoerus* are synapomorphies of hydrochoerines and whether postcranial characters support *Cardiomys* as a basal hydrochoerine.

Paleobiology based on postcranial features.—The elbow joint of *Cardiomys* displays several features that indicate a relatively

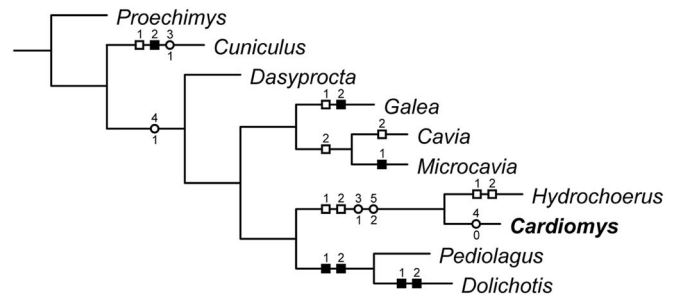


Figure 5. Mapping of six anatomical characters, as reconstructed using parsimony, onto the phylogeny of Caviioidea modified from Madozo-Jaén and Pérez (2017). Only unambiguous character state optimizations are shown. For discrete characters (circles), numbers above branches indicate character number whereas those below are character states. For continuous characters, closed/open squares indicate an increase/decrease of the measurements (see Supplemental Data 3 for characters and character states).

high stability and restricted rotational movements, as are observed in other cavioid rodents. A high humeral distal surface and a steeply angled trochlea, which contacts with the medially extended trochlear facet of the radius, restrict mediolateral mobility and increase stability at the elbow joint during flexion-extension (Argot, 2001; Sargis, 2002; Candela and Picasso, 2008; Abello and Candela, 2010). The markedly differentiated humeral capitular tail, which contacts with the laterally extended capitular tail facet of the radius during the flexion, also maximizes the stability at the humeroradial joint. The subrectangular radial head with a flattened caudal ulnar facet restricts the arc through which the radius may be rotated and prevents supination (Taylor, 1974; Szalay and Sargis, 2001). The cranially located radial head with respect to the ulna also leads to a severe restriction of supination, indicating that the radius is more efficient in incurring loads at the humeroradial joint during locomotion (Jenkins, 1973; Argot, 2001; Sargis, 2002; Schmitt, 2003). These features would be effective for resisting mediolateral forces at the elbow joint, maximizing the stability of the humeroradial, radioulnar, and humeroulnar joints and restricting rotational movements. A perforated fossa and a relatively long olecranon (the attachment site for the m. triceps brachii) are features compatible with a strong extension of the forearm, which could be advantageous for digging or swimming (Hildebrand, 1985; Samuels and Van Valkenburgh, 2008). The orientation of the olecranon process with respect to the ulnar shaft has been related to the effectiveness of the lever arm of the triceps muscle, the primary extensor of the elbow joint, maximizing the action of this muscle at certain joint angles (Van Valkenburgh, 1987; Drapeau, 2004; Fujiwara, 2009). Therefore, the straight caudal border of the olecranon of *Cardiomys* suggests that this genus would have had a lower elbow joint angle during the stance phase of locomotion than *Hydrochoerus*, having a more crouched position of its forelimbs (Fujiwara, 2009). In addition, the caudally oriented olecranon of *Hydrochoerus* may represent a consequence of its larger body size, a condition that was also observed in other groups of mammals (e.g., Van Valkenburgh, 1987; Drapeau, 2004).

Figure 3. Right feet in (1–3) dorsal and (4–6) plantar views. (1, 4) *Hydrochoerus hydrochaeris* (MPS-Z 142); (2, 5) *Cardiomys leufuensis* (MLP 29-IX-3-19); (3, 6) *Dolichotis patagonum* (MLP 249). a = astragalus; c = calcaneus; cu = cuboid; ec = ectocuneiform; me = mesocuneiform; Mt II–IV = second to fourth metatarsals; n = navicular; ppc = plantar process of the cuboid; ppn = plantar process of the navicular. Scale bars = 10 mm.

As in other cavioid rodents, the configuration of the ectal, sustentacular, and cuboid facets of the calcaneus indicates relatively high stabilization of the foot, restricting mediolateral movements and emphasizing flexion-extension. Likewise, the calcaneocuboid joint is more distally located with respect to the astragalonavicular joint, further restricting mediolateral movements (Candela and Picasso, 2008; Candela et al., 2017).

According to García-Esponda and Candela (2016), the hind limb of the capybara differs from that of other semiaquatic rodents (see Samuels and Van Valkenburgh, 2008) in exhibiting a lower pes index, which could be related with an increment of the out-force generated by the foot during swimming. *Cardiomyis* displays relatively longer and slenderer ectocuneiform, metatarsal III, and phalanges with respect to those of *Hydrochoerus* (Fig. 4). These features indicate that *Cardiomyis* would have had a longer and more gracile foot than extant capybaras. Therefore, the pes of *Cardiomyis* would not have reached the degree of swimming specialization exhibited by *Hydrochoerus*. In turn, *Cardiomyis* would have had a shorter foot with respect to the cursorially adapted *Dolichotis* and *Dasyprocta*. This feature suggests that running adaptations were absent in *Cardiomyis*.

In summary, in the context of the Caviioidea, the postcranial features of *Cardiomyis* are interpreted neither as adaptations to highly specialized cursoriality, such as those of *Dolichotis* (Candela and Picasso, 2008; García-Esponda and Candela, 2010), nor as specializations to an aquatic mode of life. *Cardiomyis* exhibits several features shared with other cavioids that allow us to consider it as a generalized ambulatory species.

Considering the morphology and relative size of the pes of the extinct hydrochoerines *Cardiomyis* and *Phugatherium* Ameghino, 1887 (= *Protohydrochoerus* Rovereto, 1914, a large cursorial hydrochoerine from the late Miocene–early Pliocene of Argentina; Kraglievich, 1940), the shortening of the pes appears to be an acquisition of the more recent genus *Hydrochoerus*. Therefore, the origin of a semiaquatic lifestyle in capybaras is likely a recent (Pleistocene) adaptation in the context of the evolutionary history of Hydrochoerinae. Thus, we hypothesize that the morphology of *Cardiomyis* represents an ancestral postcranial pattern of hydrochoerines.

Conclusions and final remarks

Features of *Cardiomyis* are more similar to *Hydrochoerus* than to any other Caviioidea, which seems to be compatible with the phylogenetic information provided by dental and cranial data (e.g., Pérez et al., 2017b). Our results indicate that *Cardiomyis* can be considered an ambulatory rodent. Like the dental structure, the postcranial features of these rodents show a more generalized morphology than extant capybaras. As recently proposed by García-Esponda and Candela (2016), adaptations to semiaquatic habits would have occurred more recently in the evolution of the *Hydrochoerus* lineage.

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.f8h7h>.

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