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Source: Acta Palaeontologica Polonica, 59(3) : 517-535

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2012.0063

Late Miocene capybaras from Argentina: Skull anatomy, taxonomy, evolution, and biochronology

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Vucetich, M.G., Deschamps, C.M., Vieytes, E.C., and Montalvo, C.I. 2014. Late Miocene capybaras from Argentina: Skull anatomy, taxonomy, evolution, and biochronology. *Acta Palaeontologica Polonica* 59 (3): 517–535.

Fossil capybaras are morphologically extremely varied, but previous studies have disagreed on whether this diversity reflects intraspecific variation or the existence of multiple species. Here, we review the capybaras from the classic Argentinian Late Miocene localities of Paraná River cliffs ("conglomerado osífero" of the Ituzaingó Formation, Entre Ríos), and Chillhué and Guatraché shallow lakes (Cerro Azul Formation, La Pampa), and perform a morphometric analysis of their upper cheek teeth and the posterior portion of the rostrum. Our results confirm that all of the specimens from the "conglomerado osífero" belong to the single species *Cardiatherium paranense*. In addition, we refer a specimen from Tupungato (Río de los Pozos Formation, Mendoza) to *C. paranense*, thus expanding its geographical range. The material from La Pampa represents a different taxon, and is here preliminary referred to *Cardiatherium* aff. *orientalis*. Our systematic interpretation of Late Miocene capybaras suggests that the early radiation of this group was not as explosive as previously thought, and was likely constrained by the early acquisition of large size, increasing complexity of the cheek teeth, and probably semi-aquatic habits.

Key words: Mammalia, Rodentia, Cavioidea, Hydrochoerinae, anatomy, morphometrics, taxonomy, biostratigraphy, Miocene, Argentina.

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Received 19 June 2012, accepted 18 November 2012, available online 7 December 2012.

Introduction

Capybaras, maras, and guinea pigs (Cavioidea sensu stricto; Patterson and Wood 1982) are among the most divergent lineages within the South American Hystricognathi, and one of the most distinctive lineages among rodents as a whole (Landry 1957, 1999; Mares and Ojeda 1982; Wood 1955). Cavioids sensu stricto are first known from the Late Oligocene, and include the extinct "eocardiids", caviids, and hydrochoerids (following Vucetich and Pérez 2011, we consider Hydrochoeridae to be of family-level rank). Living hydrochoerids are represented by the gigantic, semi-aquatic capybaras (*Hydrochoerus*) and the small rock-dwelling mocos (*Kerodon*), but the family also includes the extinct cardiomyines. Several recent studies (Pérez 2010a, b; Pérez and Vucetich 2011) have advanced our understanding of the early evolution of Cavioidea sensu stricto, but the history of the cavioid crown group (Caviidae + Hydrochoeridae) remains relatively obscure.

Within the crown group, capybaras are particularly interesting owing to their large size, semi-aquatic habits, and their propensity to form large herds (Mones and Ojasti 1986). Capybaras are further characterised by ever-growing cheek teeth with a peculiar occlusal morphology. The latter consists of a complicated pattern of re-entrant folds, and largely forms the basis for the taxonomy of the group. Although the oldest hydrochoerids are known from the Middle Miocene of Patagonia, capybaras first occur in the early Late Miocene of central Argentina (Vucetich and Pérez 2011). By the end of the Miocene, fossil capybaras are recorded in all of South America, but commonly occur in just a small number of formations, including the "conglomerado osífero" of the Ituzaingó Formation (Entre Ríos Province), the Cerro

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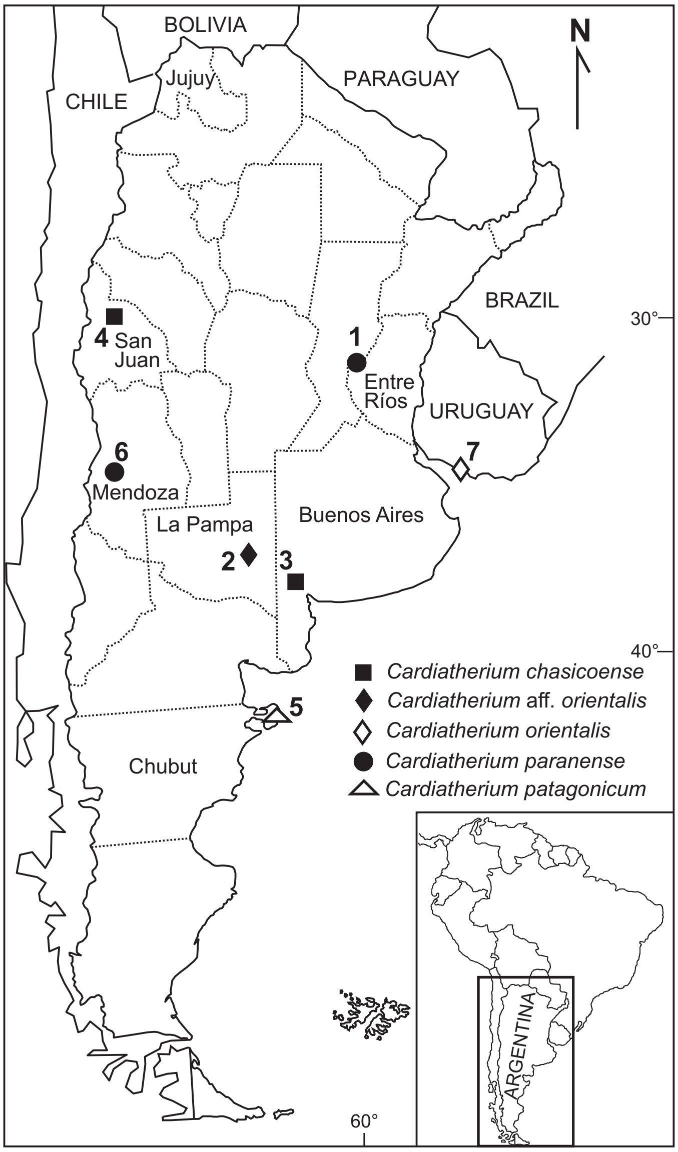


Fig. 1. Map showing the localities mentioned in the text. 1, Paraná, Entre Ríos Province; 2, Laguna Guatraché and Laguna Chillhué, La Pampa Province; 3, Arroyo Chasicó, Buenos Aires Province; 4, Albardón, San Juan Province; 5, Rincón Chico, Chubut Province; 6, Tupungato, Mendoza Province; 7, Barrancas de San Gregorio, San José, Uruguay.

Azul Formation (La Pampa Province), the Arroyo Chasicó Formation (Buenos Aires Province), and the Puerto Madryn Formation (Chubut Province) (Fig. 1; Deschamps et al. 2009 and literature therein). In all of these units, capybaras always occur in levels indicative of an aquatic environment.

Fossil capybaras show a high degree of morphological variation. Previous authors interpreted this variability as reflecting taxonomic diversity, resulting in the description of 23 genera and 59 species grouped in four subfamilies (see Mones 1991 for a systematic review). Most of this diversity is concentrated in the Late Miocene, especially in material from the "conglomerado osífero", from which 10 genera and 18 species have been described. Mones (1991) reviewed the systematics of the capybaras from this unit, and rearranged them into seven genera and 14 species, ranging in size from the small *Anchimys* and *Anchimysops*, somewhat larger than modern rock cavies (*Kerodon*) and guinea pigs (*Cavia*), to the gigantic *Anatochoerus* and *Cardiatherium*, similar in size to living capybaras. Vucetich et al. (2005) provided a very different interpretation of the fossil record of capybaras, and suggested the morphological diversity of the lower teeth from the "conglomerado osífero" to reflect ontogenetic variation within a single species, *Cardiatherium paranense* (Ameghino, 1883a). Subsequently, Vucetich et al. (2012) further suggested that indeed all of the material (skulls and jaws) from this unit belongs to *C. paranense*. However, this hypothesis has not yet been tested.

In this paper, we provide a detailed review of the Late Miocene capybaras from Argentina including evidence from skulls and upper check teeth, thus complementing previous studies which largely focused on the morphology of the mandible and the lower dentition. In addition, we report the results of a morphometric analysis of the rostrum and upper cheek teeth, and briefly discuss the implications of our findings for the generic and suprageneric taxonomy of fossil capybaras.

Institutional abbreviations.—GHUNLPam, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa, Argentina; PVSJ, Instituto y Museo de la Universidad Nacional de San Juan, San Juan, Argentina; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMH-CH, Museo de Monte Hermoso (Chasicó collection), Monte Hermoso, Argentina; MMP, Museo Municipal de Ciencias Naturales "Lorenzo Scaglia", Mar del Plata, Argentina; MPCNP, Museo Provincial de Ciencias Naturales de Paraná, Argentina; MPEF-PV, Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

Other abbreviations.—PC, Principal Component; PCA, Principal Component Analysis; RW, relative warps; SALMA, South American Land Mammal Age.

Historical background

The history of the rich taxonomy of fossil capybaras began with Ameghino (1883a), and continued with the recognition of new taxa throughout the 20th Century (e.g., Kraglievich 1927; Pascual and Bondesio 1961; Francis and Mones 1965a, b). However, few authors (Ameghino 1889; Kraglievich in Kraglievich and Parodi 1940; Mones 1991) have attempted to interpret the evolutionary history of the clade as a whole.

Two main factors favoured the proliferation of nominal taxa, which have mostly been based on differences in size and variations of a peculiar, but monotonous, dental morphology. First, no associated skulls and mandibles were recovered during the first 80 years of research. Consequently, different species were erected based on mandibles and lower teeth on the one hand, and palates and upper teeth on the other. It was only in 1965 that Francis and Mones (1965a) described *Cardiatherium talicei* on the basis of associated skull and mandible fragments including teeth, followed several years later by the description of associated skull and mandible fragments of *Kiyutherium* aff. *orientalis* (Pascual and Bondesio 1982; the skull fragment is currently lost). Secondly, the unusual development of the teeth of capybaras—with tooth size increasing during most of their lives, and allometric growth of some features generating considerable morphological change during ontogeny (Vucetich et al. 2005)—drove specialists to consider different morphologies and sizes as different species. This proliferation of names, together with the fact that taxa were generally only represented by a single specimen (often an isolated tooth), led to the idea that capybaras had a long and poorly recorded history marked by slow evolutionary rates and a general tendency towards an increase in size, as well as an increase in the complexity of the occlusal surface of the cheek teeth (Ameghino 1889; Kraglievich in Kraglievich and Parodi 1940).

A significant milestone in the taxonomic history of capybaras was the description of *Kiyutherium orientalis* Francis and Mones, 1965b from the Late Miocene sediments of Barrancas de San Gregorio, San José, Uruguay (Fig. 1). This record, based on a single mandible, introduced the idea of the existence of another group of capybaras coeval with *Cardiatherium*, characterised by their smaller size and relatively deep flexi. *Kiyutherium* was later recorded at several localities all over South America (e.g., Bondesio 1985a, b; Frailey 1986; Yrigoyen 1993b; Linares 2004). Vucetich et al. (2005) argued that *K. orientalis* was difficult to distinguish from *C. paranense* exclusively on the basis of the occlusal morphology of the lower cheek teeth. Consequently, these authors considered the genus *Kiyutherium* to be a junior synonym of *Cardiatherium*, but refrained from modifying the taxonomic status of the species pending the publication of more comprehensive analyses. The material from the Cerro Azul Formation (Huayquerian South American Land Mammal Age, Late Miocene) is especially interesting in this regard, as it includes several associated skulls and mandibles (Fig. 1: locality 2) assigned to either *Kiyutherium* aff. *orientalis* (Pascual and Bondesio 1982) or *K. orientalis* (Rocha and Montalvo 1999). However, this material has never been studied beyond the occlusal morphology of the lower teeth, and we here for the first time provide a description of the skulls and upper cheek teeth. Another significant specimen studied here is a small skull (MLP 71-VI-16-1) from Tupungato (Mendoza Province; Fig. 1: locality 6), which was first mentioned by Bondesio (1979) without any collection number or systematic assignment. Subsequent studies referred the specimen to either *Kiyutherium* aff. *orientalis* (Bondesio and Vucetich in Yrigoyen 1993b), or *K.* cf. *orientalis* (Yrigoyen 1993a), but without providing any descriptions or illustrations.

All the Late Miocene capybaras—including taxa based on either mandibular or cranial remains—were originally grouped in the subfamily Cardiatheriinae (Kraglievich, 1930), characterised by cheek teeth with united laminae. However, Mones (1975) realised that some capybaras could be distinguished by their “broad snout” and proposed that all the “broad-snouted capybaras” (some cardiatheriines and the hydrochoerine *Hydrochoeropsis* Kraglievich, 1930 from the Pliocene of Jujuy Province, NW Argentina; Fig. 1) should be grouped into a subfamily of their own. This idea was formalised by Mones and Vucetich (in Mones 1991), who erected the subfamily Anatochoerinae to include the “broad-snouted” capybaras from the “conglomerado osífero” (*Anatochoerus* and *Contracavia*) plus *Hydrochoeropsis*, while other skull fragments from this unit, all of them very small in size, were assigned to different genera and species. However, several recent studies have raised doubts as to the validity of this subfamilial arrangement (Prado et al. 1998; Vucetich et al. 2005; Vucetich et al. 2012).

Material and methods

In addition to the specimens reviewed in this study (see Systematic palaeontology section), two other species of the genus *Cardiatherium*, and the living *Hydrochoerus hydrochaeris* were used for comparisons:

(i) *Cardiatherium chasicoense* (Pascual and Bondesio, 1968) is known only from its type locality (Arroyo Chasicó, Buenos Aires Province; Arroyo Chasicó Formation, early Late Miocene; Fig. 1: locality 3), and from Albardón (Loma de las Tapias Formation, San Juan Province; Fig. 1: locality 4; Deschamps et al. 2007, 2009). The only known skull could not be included in this analysis owing to heavy damage. However, the following isolated upper teeth were included: P4 (MMH-CH 86-9-71f; MMH-CH 87-7-49; MMH-CH 88-6-39; MMH-CH 88-6-92f), and M1/M2 (MLP 76-VI-12-98c, MLP 76-VI-12-100, MMP 319, MMP 305a, MMH-CH 88-6-92a, MMH-CH 87-7-104b).

(ii) *Cardiatherium patagonicum* Vucetich, Deschamps, Olivares, and Dozo, 2005 is known from Rincón Chico and La Pastosa (Península Valdés, Chubut Province; uppermost levels of the Puerto Madryn Formation, Late Miocene; Fig. 1: locality 5; Dozo et al. 2010). We included one skull (MPEF-PV 2521) in our analysis, based on photographs (Dozo et al. 2010: fig. 4). In addition, we included the following isolated upper teeth (Vucetich et al. 2005): P4 (MPEF-PV 740/14, MPEF-PV 740/22), and M1/M2 (MPEF-PV 740/13, MPEF-PV 740/15, MPEF-PV 740/16, MPEF-PV 740/23).

(iii) *Hydrochoerus hydrochaeris* (Linnaeus, 1766). Because the Late Miocene material studied here includes specimens potentially representing different ontogenetic stages, we included a range of differently-aged individuals of the living species in order to investigate age-related morphological changes of the palate. This material belongs to the collection of Sección Mastozoología, MLP: MLP 1915, MLP 1918, MLP 1920, MLP 1921; MLP 2030, MLP 2031, MLP 2032, and MLP 2033.

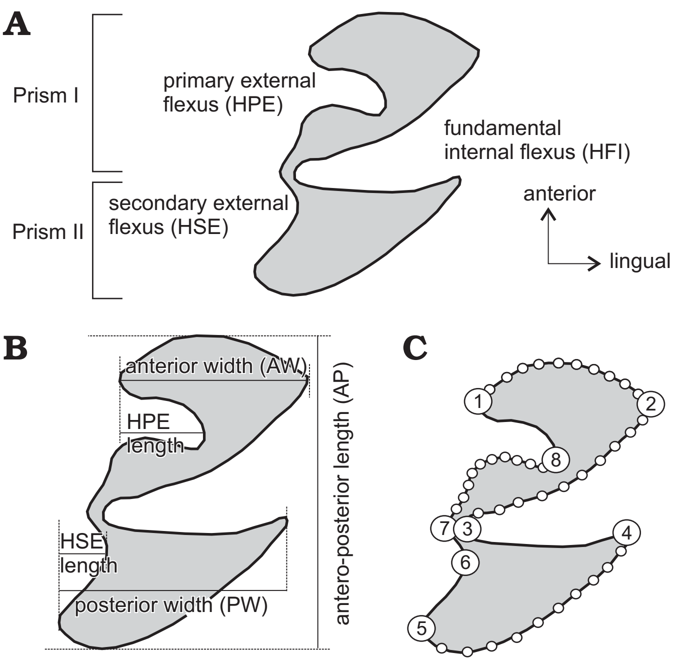


Fig. 2. Tooth nomenclature (**A**), measurements (**B**), and landmarks (1–8)/semilandmarks (small circles) (**C**) on right P4 of *Cardiatherium paranense* (Ameghino, 1883a). 1, labial end of prism I; 2, lingual end of prism I; 3, maximum depth of fundamental internal flexus; 4, lingual end of prism II; 5, labial end of prism II; 6, maximum depth of primary external flexus; 7, labialmost point of isthmus; 8, maximum depth of secondary external flexus.

Differentiation of ontogenetic stages in fossil specimens was crucial for the purpose of this study. The order of tooth eruption and the degree of occlusal wear could not be used in this case, because capybaras are born with the full permanent dentition and even with wear (Mones 1991). Vucetich et al. (2005) showed that, in capybaras, the cheek teeth continue growing in all dimensions, and that their occlusal morphology keeps changing through life (or at least most of it), with size being a good indicator of relative age within a given species. In particular, the difference in size between the apex and the base is conspicuous in juveniles, before gradually decreasing in larger individuals and becoming hardly noticeable above a certain body size. For example, in the M3 of the holotype of *Anchimysops radicei* (MACN 3353), the anteroposterior length is 9.23 mm at the occlusal surface and 12.92 mm at the base of the tooth (40% larger); in MLP 87-XI-1-2, these measurements are 18.79 mm and 19.41 mm (3.3% larger), respectively, whereas in MLP 41-XII-13-161a they are 31.78 mm and 31.99 mm (0.66% larger). In addition to cheek tooth morphology, we identified juvenile specimens based on their relatively small size, the presence of more porous bone even in those areas that later develop into thick compact bone (Currey 1984), the degree of closure of sutures, and mandibular morphology (see Ojasti 1973; Vucetich et al. 2005). All of the small individuals, but none of the larger specimens, showed juvenile characters, thus reinforcing the idea of a size/age relationship within this group.

We used multivariate techniques to analyse the morphology of the rostrum and the upper check teeth, in order to test previous systematic hypotheses (Mones 1975, 1991; Vucetich et al. 2005; Deschamps et al. 2007, 2009). Tooth nomenclature and measurements (Fig. 2A, B) follow Vucetich et al. (2005). We performed a Principal Component Analysis (PCA) based on nine linear measurements of the rostrum (Table 1, Fig. 3) of *Cardiatherium paranense*, *C.* aff. *orientalis*, and *Hydrochoerus hydrochaeris* (all representing a range of ontogenetic stages) as an exploratory analysis of the patterns of morphological variation. Measurements were taken directly on specimens using digital callipers (0.01 mm) and analysed in PAST v. 2.08 (Hammer et al. 2001; Hammer 2007). Because of the small sample size, missing data arising from the inclusion of fragmentary fossil specimens were estimated by data imputation (as implemented in PAST), using

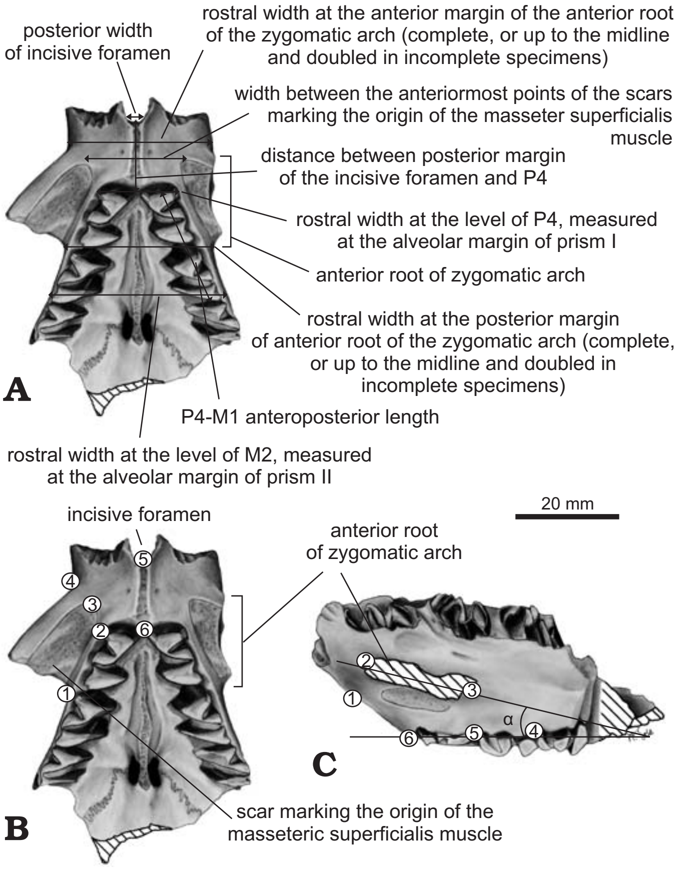


Fig. 3. Late Miocene capybara *Cardiatherium paranense* (Ameghino, 1883a), MLP 87-XI-1-3a, from Paraná River cliffs, Huayquerian SALMA, in ventral (**A**, **B**) and left lateral (**C**, anterior to left) views. **A**. Skull measurements. **B**. Skull landmarks: 1, posterior limit of anterior root of the zygomatic arch; 2, lateralmost point of prism I of P4, measured on the alveolar rim; 3, anteriormost point of scar marking the origin of the masseter superficialis muscle; 4, anterior limit of anterior root of the zygomatic arch; 5, midpoint of posterior margin of incisive foramen; 6, midpoint between both P4s at the level of prism I on the maxillary suture. **C**. Skull landmarks: 1, posterior end of incisive foramen; 2, anterior limit of anterior root of the zygomatic arch; 3, posterior limit of anterior root of the zygomatic arch; 4, point between M1 and M2 on the alveolar plane; 5, point between P4 and M1 on the alveolar plane; 6, point in front of P4 on the alveolar plane; α, angle formed by the anterior root of the zygomatic arch and the alveolar margin of the cheek teeth in lateral view.

Table 1. Skull measurements (in mm) of fossil (*Cardiatherium*) and extant (*Hydrochoerus*) capybaras from Argentina. 1, posterior limit of anterior root of the zygomatic arch; 2, lateralmost point of prism I of P4, measured on the alveolar rim; 3, anteriormost point of scar marking the origin of the masseter superficialis muscle; 4, anterior limit of anterior root of the zygomatic arch; 5, midpoint of posterior margin of incisive foramen; 6, midpoint between both P4s at the level of prism I on the maxillary suture.

Specimen		1	2	3	4	5	6	7	8	9
Cardiatherium paranense	MLP40-XI-15-2	4.00	28.97	20.80	13.12	26.22	32.08	11.12	17.35	18
	MLP41-XII-13-153	3.20	30.70	17.60	12.80	28.00	24.00	11.80	17.78	18
	MLP69-XII-2-19		28.66	19.20	15.60	25.80		14.20	13.92	18
	MLP71-VI-16-1	3.80	22.64	16.00	10.70	21.44	27.40	9.00	12.56	18
	MLP87-XI-1-1	4.46	29.43	24.00	14.68	26.19		17.25	16.35	
	MLP87-XI-1-3	3.32	27.84	20.80	13.66	25.16		15.99	15.45	
	MLP87-XI-1-3a	5.42	32.44	21.60	14.80	29.00		15.70	22.50	18
	MLP87-XI-1-27	8.01	43.72	28.00	19.42	37.70	43.90	22.53	22.31	18
	MACN1049	5.31	29.36	18.00	13.90	26.40		16.12	19.66	18
	MACN1050	5.43	31.30	19.00	14.93	28.30		15.80	20.36	19
	MACN3336	4.76	25.72	19.00	10.79	25.53	32.41	12.50	18.04	
	MACN13469	4.55	32.40	20.00	14.25	28.33	37.50	15.53	20.26	18
Cardiatherium aff. *orientalis*	GUNLPam5236	2.50	13.90	12.80	8.10	15.00		7.20	10.17	25
	GUNLPam2009		23.26	16.00	13.18	23.26	30.49		15.40	24
	GUNLPam5274	2.70	21.84	19.20	12.95	22.15	32.68	16.50	16.79	26
	GUNLPam14452	2.50	25.56	19.20	13.60	25.56	33.81	15.14	17.07	24
	GUNLPam14661	3.00	27.39	19.20	14.88	26.60	35.34	17.42	18.83	25
	GUNLPam27389	3.00	29.05	27.00	17.44	28.25	36.85	18.80	18.29	24
Hydrochoerus hydrochaeris	MLP 1915	8.30	32.20	27.00	23.00	40.60	50.00	24.20	24.00	17
	MLP 1918	8.30	40.00	34.10	23.50	43.20	52.00	19.10	27.20	13
	MLP 1920	9.00	33.60	29.00	23.00	40.10	50.40	20.60	26.00	13
	MLP 1921	10.20	33.10	30.90	24.20	42.00	50.50	21.20	26.30	15
	MLP 2030	8.30	33.90	26.20	21.00	39.40	45.00	18.10	21.70	16
	MLP 2031	10.00	34.50	30.00	24.60	40.00	48.30	15.80	26.50	14
	MLP 2032	5.30	25.00		16.00	30.65	36.50	13.00	20.00	
	MLP 2033	5.00	16.20		11.00	20.20	23.60	9.20	11.60	15

observed values to estimate likely values for the unobserved cases (Schafer and Olsen 1998). All data were standardised to unit variance prior to analysis (Zar 1984). Tooth measurements (Table 2) were not included, because they were not informative for this sample according to a preliminary PCA.

We analysed the global morphology of the rostrum and the variation in P4 and M1–2 occlusal shape using geometric morphometric techniques, which offer an effective way of analysing variation in complex structures difficult to describe in terms of linear measurements. Two-dimensional coordinates were captured from two sets of digital images representing the geometry of the rostrum, one with the palate perpendicular to the optical axis of the camera (ventral view), and the other one with the lateral aspect of the rostrum perpendicular to this axis (lateral view). In cases where one side of the rostrum was missing or damaged, we used the mirrored image of the contralateral side. The position of the rostrum and the camera lens plane, as well as distance to the camera lens were standardised following Zelditch et al. (2004). Six type II landmarks located on the palate (Fig. 3B) (Bookstein 1991) were digitised using photographs of *C. paranense*, *C.* aff. *orientalis*, *C. patagonicum*, and *H. hydrochaeris. C. chasicoense* was excluded because the only known skull is extremely fragmentary. Another set of six type II landmarks located on the lateral side of the rostrum (Fig. 3C) was recorded for *C. paranense* and *C.* aff. *orientalis*. *C. patagonicum*, and *H. hydrochaeris* could not be included, because in the available material of these taxa the area of interest is hidden by the zygomatic arch. For the cheek teeth, we recorded eight type II landmarks located on the occlusal surface (Fig. 2C) of *C. paranense*, *C.* aff. *orientalis*, *C. patagonicum*, and *C. chasicoense*, and analysed them separately for P4 and M1–2, respectively. To evaluate the shape of the prisms between these landmarks, we additionally scored 40 semilandmarks, which were evenly distributed in groups of ten between landmarks 1 and 2, 2 and 3, 4 and 5, and 7 and 8 (Fig. 2C). *H. hydrochaeris* was not included in either of these analyses, because in this species the cheek teeth are at a different evolutionary stage in which prisms are already separated at a very early postnatal stage.

In all cases, Cartesian coordinates for each landmark and semilandmark were obtained using TPSDIG, version 2.12 (Rohlf 2008). The effects of translation, rotation and scaling of the landmark and semilandmark configuration were removed using generalised Procrustes analysis (GPA; Rohlf 1990; Rohlf and Slice 1990; Mitteroecker and Gunz 2009). Semilandmarks were slid to minimise the variation tangential to the curve using the "minimum bending energy" crite-

Table 2. Tooth measurements (in mm) of the upper cheek teeth of fossil (*Cardiatherium*) and extant (*Hydrochoerus*) capybaras from Argentina. Abbreviations: AP, anteroposterior length; AW, anterior width; HPEL, primary external flexus length; HSEL, secondary esternal flexus length; PW, posterior width.

Specimen		P4					M1					M2					M3	
		AP	AW	HPEL	HSEL	PW	AP	AW	HPEL	HSEL	PW	AP	AW	HPEL	HSEL	PW	AP	AW
Cardiatherium paranense	MACN 1049	9.50	6.20	33.00	1.40	8.00												
	MACN 1050	9.90	6.10	4.60	2.30	9.00	8.60	7.50	4.50	1.20	9.00							
	MACN 3336						7.20										20.13	
	MACN 3353																9.23	
	MACN 13434	12.00	8.20	5.70	2.00	9.70	11.00	8.70	6.00	2.00	9.70							
	MACN 13465	9.20	6.30	4.20	1.20	7.30	8.10	7.40	4.50	1.00	7.40	8.10	6.20	4.60	1.00	7.20		
	MACN 13469	9.00	6.00	4.00	1.00	7.10	8.40	7.00	4.00	1.00	7.30	7.60	7.00	4.00	1.30	7.60	25.58	7.46
	MLP 40-XI-15-2	8.00	4.96	1.76	1.60	9.44	7.20	7.04	2.40	0.64	7.68	6.40	7.20	1.92	0.96	7.84	20.00	6.88
	MLP 41-XII-13-1																29.12	8.16
	MLP 41-XII-13-153	8.32	6.08	3.52	1.60	7.36	7.84	6.88	4.00	1.60	7.52	7.20	7.52	4.16	1.92	7.68		7.20
	MLP 41-XII-13-161																37.58	10.72
	MLP 41-XII-13-161a																32.41	10.72
	MLP 41-XII-13-171																21.12	6.56
	MLP 41-XII-13-233						9.76	8.16	4.00	0.96	9.12							
	MLP 41-XII-13-233a	8.48	6.40	2.72	1.60	7.20												
	MLP 41-XII-13-291																32.80	8.00
	MLP 52-X-5-75a																26.40	7.20
	MLP 69-XII-2-19	7.50	4.59	2.04	1.02	4.89	6.63	4.89	2.24	0.71	5.50							
	MLP 71-VI-16-1	6.08	4.64	1.92	0.96	4.64	5.12	4.96	2.56	0.96	4.64	4.96	5.44	2.40	1.76	5.44	12.69	5.93
	MLP 87-XI-1-1	9.60	7.04	2.88	1.44	8.00	8.00	7.68	3.36	0.96	7.68							
	MLP 87-XI-1-2																18.72	6.88
	MLP 87-XI-1-3	8.16	6.08	3.04	1.76	7.36	7.20	6.40	3.20	1.12	7.20							
	MLP 87-XI-1-3a	11.04	8.00	5.12	1.60	8.80	9.60	8.64	4.16	1.44	8.80	8.00	8.32	4.16	2.24	8.96		
	MLP 87-XI-1-27	11.68	7.36	3.84	1.92	7.68	9.92	6.40	4.00	0.64	8.56	9.12	6.40	4.00	0.96	7.20	27.20	7.36
Cardiatherium aff. *orientalis*	GHUNLPam 139						5.60	5.44	2.40	0.80	6.08	5.60	5.92	2.56	1.12	5.92	6.88	
	GHUNLPam 5236	5.28	3.36	1.92	0.80	4.16	4.48	4.00	1.76		4.32							
	GHUNLPam 5274	7.36	5.28	2.72	1.28	5.76	5.92	5.92	2.72	1.28	6.72	7.68	6.40	2.88	0.88	6.56	18.77	6.19
	GHUNLPam 8978	4.80	3.04	1.44	0.48	3.68	4.00	3.36	1.60									
	GHUNLPam 14452	8.80	5.76	2.56	2.08	7.52	7.68	6.88	3.04	1.28	7.84	6.72	7.52	3.36	1.60	7.68	20.44	7.60
	GHUNLPam 14661	9.76	5.28	2.88	1.60	6.72	8.32	6.72	3.52	0.96	6.56	8.16	6.72	3.68	1.44	6.40	20.75	7.17
	GHUNLPam 14985	9.23	6.42	2.81	1.09	7.83	8.92	7.20	2.97	0.62								
	GHUNLPam 21572																	8.48
	GHUNLPam 27389	9.28	5.76	2.72	1.44	7.20	7.36	7.04	3.36	0.96	7.04						21.53	7.74
Hydrochoerus hydrochaeris	MLP 1915	0	0	0	0	0	9.396	9.083	6.264	5.168	9.709	9.553	9.239	5.324	5.011	0	38.84	9.553
	MLP 1918	14.09	9.40	7.52	6.26	12.06	11.28	10.81	7.20	5.79	11.28	12.06	11.28	7.05	7.05	14.09	0	0
	MLP 1920	14.09	9.40	6.58	6.26	10.96	10.34	10.02	5.95	5.48	10.96	10.02	9.08	5.48	5.01	10.96	37.27	10.34
	MLP 1921	13.00	8.46	6.11	5.64	10.49	10.02	10.18	5.79	5.17	10.96	10.49	10.18	6.26	5.64	12.68	38.52	10.81
	MLP 2031	13.47	9.87	7.05	6.26	11.43	10.49	10.49	6.11	5.95	11.28						38.05	10.65
	MLP 2032						7.83	7.20	3.76	4.23	8.14	7.67	7.20	3.45	3.76	7.99	29.60	8.14
	MLP 2033	5.95	3.60	1.88	2.35	4.70	5.01	4.54	2.04	2.19	5.01	5.01	4.38	2.04	2.19	4.70	18.17	5.17

rion (Bookstein 1997; Gunz et al. 2005; Perez et al. 2006). We performed Principal Component analyses to summarise the major trends in shape variation in a low-dimensional morphospace, using TPSRELW version 1.46 (Rohlf 2008). Shape differences were described by means of deformation grids (Bookstein 1989; Monteiro and dos Reis 1999; Zelditch et al. 2004).

Geological setting

The material described in this paper was derived from three separate localities and formations including: (i) the "conglomerado osífero" ("bonebed conglomerate" sensu Behrensmeyer 1991; Rogers et al. 2007), a fluvial, sandy conglomerate at the base of the Ituzaingó Formation (Herbst 2000), exposed along the cliffs of the Paraná River near Paraná City, Entre Ríos Province. The "conglomerado osífero" is also called "Mesopotamiense", and was assigned to the Huayquerian South American Land Mammal Age (SALMA), Late Miocene (Cione et al. 2000), based on its mammalian content and the age of the underline marine Paraná Formation; (ii) the Río de los Pozos Formation, an alluvial unit associated with semi-permanent water courses (Milana and Zambrano 1996) exposed at Tupungato, Mendoza Province. This formation is likely no younger than 5.8 Ma, and no older than 8.2–7.4 Ma, or Late Miocene, based on interpretations of the stratigraphic sequence and absolute dating of the over- and underlying units (Chiaramonte et al. 2000; Irigoyen et al. 1995); (iii) the Cerro Azul Formation, consisting of massive, brown-reddish, sandy silt with loessic erosion (Linares et al. 1980), exposed at Laguna Chillhué and Laguna Guatraché, La Pampa Province. At these localities, aeolian and lacustrine deposits are intercalated (Verzi et al. 2008) and have been referred to the Huayquerian SALMA, Late Miocene (Verzi et al. 2008), based on their mammalian fauna.

Systematic palaeontology

Order Rodentia Bowdich**,** 1821
Suborder Hystricognathi Tullberg, 1899
Family Hydrochoeridae Gray, 1825
Subfamily Hydrochoerinae Gray, 1825

Emended diagnosis.—Hydrochoerids with cheek teeth with deep re-entrant folds, with two new re-entrant folds on m1–3, one lingual (tertiary internal flexid), and one labial (secondary external flexus); labial re-entrant folds on P4–M2 dissimilar in length, with the primary external flexus being long and the secondary external flexus being very short; M3 with many thin laminae; paraoccipital apophyses robust, very long, and laterally compressed.

Remarks.—This taxon corresponds to Hydrochoeridae of previous authors (e.g., Mones 1991). Only those hydrochoerids sharing the characters above are here considered to be capybaras.

Genus *Cardiatherium* Ameghino, 1883b

Type species: *Cardiatherium doeringi* Ameghino, 1883b; Paraná River cliffs, Huayquerian SALMA.

1883 *Hydrochoerus*; Ameghino1883a: 104, nec Brisson, 1762.
1883 *Cardiatherium*; Ameghino 1883b: 270–274.
1885 *Procardiatherium*; Ameghino 1885: 55–59.
1885 *Contracavia*; Burmeister 1885: 158–159.
1885 *Cardiodon*; Ameghino 1885: 64–65, nec Owen, 1841.
1886 *Plexochoerus*; Ameghino1886: 58.
1886 *Anchimys*; Ameghino 1886: 71–72.
1891 *Eucardiodon*; Ameghino 1891: 247.
1940 *Anchimysops*; Kraglievich 1940: 322–323, nec Kraglievich, 1927: 597.
1965 *Kiyutherium*; Francis and Mones 1965b: 47.
1991 *Anatochoerus*; Vucetich and Mones in Mones, 1991: 32.

Diagnosis.—Medium to large-sized capybaras; cheek teeth with prisms united on the labial side in the upper ones, and on the lingual side in the lowers; M3 with 8 to 10 prisms; rostrum transversely broad in ventral view, with a straight and well-exposed premaxillary-maxillary suture; rostrum anterior to the anterior root of the zygomatic arch as wide or wider than immediately posterior to it.

Geographic and stratigraphic range.—South America; Late Miocene–Early Pliocene.

Cardiatherium paranense (Ameghino, 1883a) Francis and Mones, 1965a

Figs. 4, 5.

1883 *Hydrochoerus paranensis*; Ameghino 1883a: 104–105.
1883 *Cardiatherium Doeringi*; Ameghino 1883b: 270–274.
1885 *Contracavia matercula*; Burmeister 1885: 158–159.
1885 *Cardiatherium petrosum*; Ameghino 1885: 50–51.
1885 *Cardiatherium denticulatum*; Ameghino 1885: 51.
1885 *Cardiatherium minutum*; Ameghino 1885: 54.
1885 *Procardiatherium simplicidens*; Ameghino 1885: 55–58.
1885 *Procardiatherium crassum*; Ameghino 1885: 58–59.
1885 *Cardiodon Marshii*; Ameghino 1885: 61–64.
1885 *Cardiodon*? *Leidyi*; Ameghino 1885: 64–65.
1886 *Plexochoerus paranensis* (Ameghino, 1885); Ameghino 1886: 58.
1886 *Anchimys Leidyii* (Ameghino, 1885); Ameghino 1886: 72–74.
1889 *Plexochoerus adluis*; Ameghino 1889: 252–253.
1889 *Plexochoerus lynchi*; Ameghino 1889: 910.
1891 *Eucardiodon affinis*; Ameghino 1891: 247.
1891 *Procardiotherium denticulatum* (Ameghino); Ameghino 1891: 248.
1891 *Eucardiodon marshi*; Ameghino 1889: 249.
1927 *Procardiotherium septemlaminatus*; Kraglievich 1927: 597.
1927 ?*Procardiotherium octolaminatus*; Kraglievich 1927: 598.
1934 *Procardiotherium septemlaminatus*; Kraglievich 1934: 83–84.
1934 *Cardiotherium* sp.; Rusconi 1934: 180.
1940 *Anchimysops radicei*; Kraglievich 1934: 322.
1940 ?*Anchimysops dubius*; Kraglievich 1934: 323–324.
1940 *Procardiotherium* (*Eocardiotherium*) *septemlaminatus*; Kraglievic 1940: 326–329.
1945 *Plexochoerus paranensis* (Ameghino); L. Kraglievich in Kraglievich 1945: 453–454.

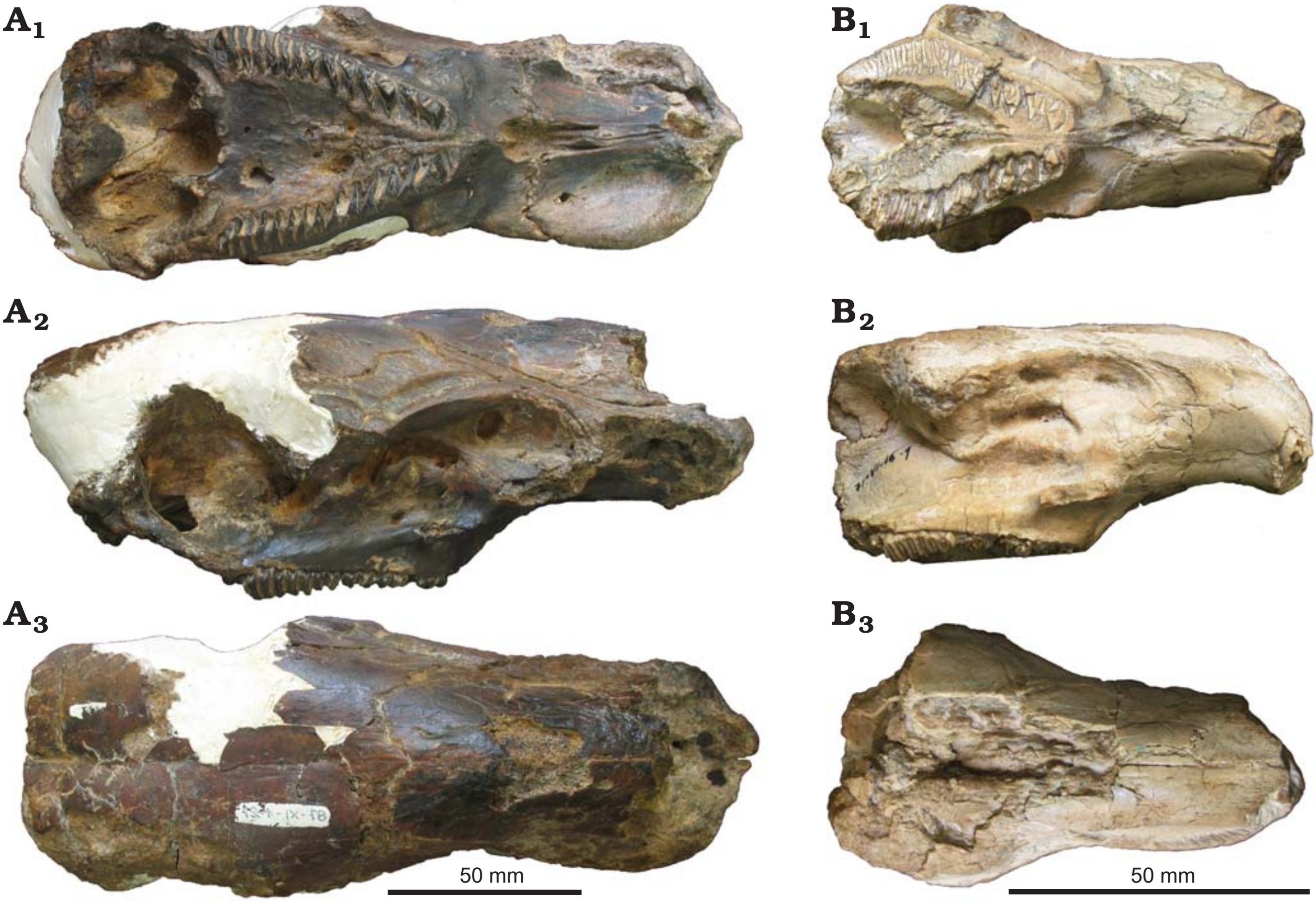


Fig. 4. Late Miocene capybara *Cardiatherium paranense* (Ameghino, 1883a). **A**. MLP 87-XI-1-27, holotype of *Anatochoerus inusitatus* Vucetich and Mones in Mones, 1991, Río Paraná cliffs. **B**. MLP 71-VI-16-1, juvenile specimen, Tupungato. In ventral (A_1, B_1), lateral (A_2, B_2), and dorsal (A_3, B_3) views.

1945 *Plexochoerus petrosus* (Ameghino); L. Kraglievich in Kraglievich 1945: 455.
1945 *Cardiotherium rothi*; Kraglievich 1945: 456.
1961 *Plexochoerus* sp.; Pascual and Bondesio 1961: 106.
1965 *Cardiatherium lynchi* (Ameghino); Francis and Mones 1965a: 31.
1965 *Cardiatherium paranensis* (Ameghino); Francis and Mones 1965a: 30.
1965 *Cardiatherium rothi*; Francis and Mones 1965a: 27.
1965 *Cardiatherium adluis* (Ameghino); Francis and Mones 1965a: 31.
1979 *Eucardiodon* cf. *marshi*; Mones and Castiglioni 1979: 80–81.
1984 *Anchimys marshi* (Ameghino); Mones 1984: 3.
1984 *Kiyutherium denticulatum* (Ameghino); Mones 1984: 4.
1984 *Procardiatherium matercula* (Burmeister); Mones 1984: 5.
1985 *Kiyutherium scillatoyanei*; Bondesio 1985a: 276.
1986 *Procardiatherium* (*Eocardiotherium*) *septemlaminatum*; Mones 1986: 204.
1991 *Cardiatherium* sp. A (Pascual and Bondesio); Mones 1991: 31.
1991 *Anatochoerus inusitatus*; Vucetich and Mones in Mones, 1991: 32.
1991 *Contracavia minuta* (Ameghino); Mones 1991: 35.
1993 *Kiyutherium* aff. *orientalis*; Yrigoyen 1993b; nec Pascual and Bondesio, 1985.

For further details regarding changes and modifications to this systematic list, see Mones (1991).

Neotype: MLP 40-XI-15-1 designated by Mones (1991), right mandibular fragment with p4–m3 (see Mones 1991; Vucetich et al. 2005: fig. 9E). The holotype, currently lost, was an isolated and fragmentary M3, the only cranial material so far assigned to this species.

Type specimens of synonymised species: *Anatochoerus inusitatus* Vucetic and Mones in Mones, 1991, MLP 87-XI-1-27, incomplete skull with both P4–M3; *Anchimys leydi* (Ameghino, 1885), MLP 73-I-10-5, anterior fragment of mandible with both incisors and right p4 alveolus; *Anchimys marshii* (Ameghino, 1885), MLP 73-I-10-7, right mandible with i, p4–m3; ?*Anchimysops dubius* Kraglievich, 1934, MACN 9055, right M3; *Anchimysops radicei* Kraglievich, 1934, MACN 3353, right M3; *Cardiatherium denticulatum* Ameghino, 1885, MPCNP? (lost specimen, cast MLP M-27), isolated right m1 or m2; *Cardiatherium doeringi* Ameghino, 1883b, MLP 73-I-10-11, fragment of left mandible with p4–m1; *Cardiatherium minutum* Ameghino, 1885, MLP 69-XII-2-19, anterior left palatal fragment with anterior root of the zygomatic arch and P4–M1; *Cardiatherium petrosum* Ameghino, 1885, MLP 69-XII-2-16, fragment of left mandible with i, p4–m1; *Cardiotherium rothi* Francis and Mones, 1965a, MACN unknown number (lost specimen), right M3; *Contracavia matercula* Burmeister, 1885, MACN 1049, anterior fragment of palate with anterior root of the zygomatic arch and both P4; *Contracavia matercula* Burmeister, 1885, MACN 1050, anterior fragment of palate with anterior root of the zygomatic arch, both P4, and anterior prisms of both M1; *Eucardiodon affinis* Ameghino, 1891, MACN 5890, fragment of right mandible with the base of incisor and m1–2; *Kiyutherium scillatoyanei* Bondesio, 1985a, MLP 78-II-27-1, fragment of right mandible with p4–m3; *Plexochoerus adluis* Ameghino, 1889, unknown repository (lost specimen), left M3 (Ameghino 1889: pl. 79: 4, 4a); *Plexochoerus lynchi* Ameghino 1889, unknown repository (lost specimen), palatal fragment with both M1–3 (Ameghino 1889: pl. 79: 6, 13); *Procardiatherium crassum* Ameghino, 1885, unknown repository (lost specimen, cast

MLP M-22), left p4; *Procardiatherium octolaminatum* Kraglievich, 1927, MACN 8934, M3 and part of the skull including the left parietal and frontal; *Procardiotherium* (*Eocardiotherium*) *septemlaminatum* Kraglievich, 1927, MACN 3336, incomplete skull with both P4–M3; *Procardiatherium simplicidens* Ameghino, 1885, MLP 73-I-10-8, fragment of left mandible with p4–m2.

Referred material.—MACN 13434, anterior fragment of palate with anterior root of the zygomatic arch, both P4 and right M1; MACN 13465, fragment of palate with left P4–M3 and right M1–2; MACN 13469, anterior fragment of palate with anterior root of the zygomatic arch, right P4–M2 and left P4–M3; MLP 40-XI-15-2, anterior fragment of palate with anterior root of the zygomatic arch, right P4–M2 and left P4–M3; MLP 41-XII-13-1, isolated M3; MLP 41-XII-13-153, right anterior fragment of palate with anterior root of the zygomatic arch and P4–M3; MLP 41-XII-13-161, isolated M3; MLP 41-XII-13-161a, isolated M3; MLP 41-XII-13-171, isolated M3; MLP 41-XII-13-233, isolated M1 or M2; MLP 41-XII-13-233a, isolated M2?; MLP 41-XII-13-291, isolated M3; MLP 52-X-5-75a, isolated M3; MLP 71-VI-16-1, anterior portion of skull with complete dentition, albeit somewhat damaged (Fig. 4B; see Historical background); MLP 87-XI-1-1, anterior fragment of palate with anterior root of the zygomatic arch, both P4 and left M1; MLP 87-XI-1-2, isolated M3; MLP 87-XI-1-3, anterior fragment of palate with anterior root of the zygomatic arch, left P4 and both M1; MLP 87-XI-1-3a, anterior fragment of palate with anterior root of the zygomatic arch and both P4–M2. For material not included in this analysis (mandibles and lower teeth), see Vucetich et al. (2005).

Differential diagnosis.—Portion of rostrum anterior to the anterior margin of the zygomatic root wider than in *C.* aff. *orientalis* Pascual and Bondesio, 1965b and *C. patagonicum* Vucetich, Deschamps, Olivares, and Dozo, 2005; palate at the level of M3 wider than in *C.* aff. *orientalis* and *C. patagonicum*; attachment areas for masseter superficialis muscle anteriorly convergent; angle formed by anterior root of the zygomatic arch and alveolar plane smaller than 20° in lateral view; distance between base of the incisive foramen and middle point between both P4s shorter than in *C.* aff. *orientalis*; broad incisive foramen; base of P4 projected lateral to the occlusal surface in ventral view, thus forming a conspicuous bulge immediately dorsal to the anterior margin of the anterior root of the zygomatic arch; cheek teeth with flexi/flexids deeper than in *C. chasicoense* (Pascual and Bondesio, 1968); lower cheek teeth with secondary internal flexid and tertiary internal flexid shallower than in *C. patagonicum*.

Description

Skull.—The description of the skull is mostly based on MLP 87-XI-1-27, the holotype of *Anatochoerus inusitatus*, because it is the most complete (Figs. 4A, 5). This specimen, originally described by Vucetich and Mones (in Mones 1991), is marked by peculiar roll-shaped expansions located at the anterior part of the rostrum involving the dorsolateral margin of the premaxilla and a short anterolateral portion of the maxilla, which led to the description of the genus *Anatochoerus* and its own subfamily Anatochoerinae (see Mones 1991). The porous appearance of the bone forming these protuberances is different from the rest of the skull, changing transitionally within the premaxillae and maxillae. Work is in progress to determine whether these structures are normal or represent a pathological condition. The premaxillae are absent in all other specimens from the "conglomerado osífero", except for MACN 3336 (holotype of *Cardiatherium septemlaminatum*), in which the ventromedial portions of these bones have been preserved. The specimen from Tupungato (MLP 71-VI-16-1, described below) lacks such expansions (Fig. 4B), but it should be noted that it is a juvenile.

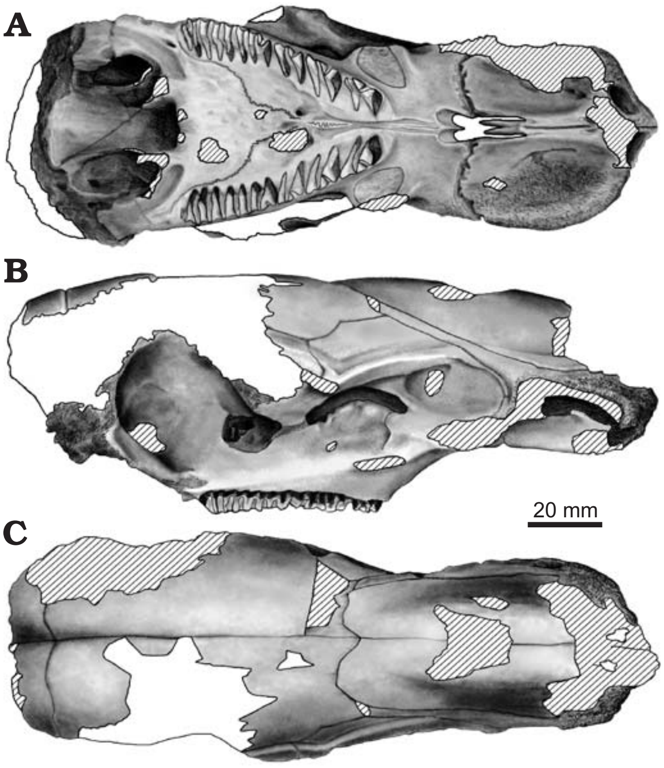


Fig. 5. Late Miocene capybara *Cardiatherium paranense* (Ameghino, 1883a), MLP 87-XI-1-27, holotype of *Anatochoerus inusitatus* Vucetich and Mones in Mones, 1991 from Paraná River cliffs, Huayquerian SALMA, in ventral (**A**), lateral (**B**), and dorsal (**C**) views.

In ventral view, the palate is relatively flat (as opposed to concave in *H. hydrochaeris*), and the tooth rows are conspicuously divergent, with M3 being approximately in line with P4–M2. The length of the diastema located between the anterior margin of the alveolus of P4 and the posterior margin of the alveolus of I1 exceeds the combined length of P4–M3, and is comparatively much longer than in *H. hydrochaeris*. In the juvenile MLP 71-VI-16-1, the diastema is 3.2% longer than P4–M3 (diastema: 32 mm; P4–M3: 31 mm), which increases to 27% in the largest available specimen, MLP 87-XI-1-27 (75 mm and 59 mm, respectively). This demonstrates the lengthening of the rostrum with age, which is also seen in *H. hydrochaeris*, although in the modern species the diastema is always shorter than the combined length of P4–

M3 (25.1/37.2 mm in the juvenile MLP 2033, and 67.9/79.3 mm in the adult MLP 2031). The rostrum is wider than in any other hydrochoerine, and almost doubles in width both anterior and posterior to the anterior root of the zygomatic arch, relative to its width at the level of prism I of P4 (Fig. 5A). This relative increase in rostral width—at least along the posteriormost part of the diastema—is related to the lateral projection of the base of P4 relative to both its own occlusal surface and the rest of the upper dentition (e.g., MLP 87-XI-1-3a, MLP 87-XI-1-3, MLP 41-XII-13-153, MACN 13468), which forms a conspicuous bulge immediately dorsal to the anterior margin of the anterior root of the zygomatic arch (Figs. 4A$_1$, 5A). By contrast, the base of P4 is not so conspicuous and is completely located above the anterior root of the zygomatic arch in *H. hydrochaeris*. Both the width of the rostrum and the degree of outward protrusion of P4 seem to increase with age, although this is not certain owing to the incompleteness of the available material.

The incisive foramen is sub-rectangular in outline and equidistant between P4 and the incisors, with the premaxillary portion of the premaxillary septum being divided into two rami; the foramen is large, but looks narrow transversely when compared with the wide diastema. The transversely oriented premaxillary-maxillary suture crosses the incisive foramen at its midpoint and is broadly exposed on the wide palate. The suture is mostly straight, but turns anteriorly near the lateral border of the rostrum. The base of the zygomatic arch is oriented posterolaterally (MLP 87-XI-1-3a; Fig. 3C), rather than laterally as in *H. hydrochaeris*, and bears the origin of the masseter superficialis muscle. The muscle scars are oval, run parallel to the dental series, and converge anteriorly (Fig. 5A). They begin on the posterior margin of the anterior root of the zygomatic arch (corresponding to the level of prisms I/II of P4), and extend up to half the distance between the base of the incisive foramen and the anterior margin of the alveolus of P4, but never beyond the anterior margin of the anterior root of the zygomatic arch. In other specimens, these scars begin at the level of the posterior border of P4 (MLP 87-XI-1-3a; Fig. 3A, B).

The suture between the maxilla and the palatine originates from the alveolar margin next to prism V of M3, and then abruptly turns medially at the level of prism II, before turning again and running anteriorly to the base of the palatine foramen (Figs. 4A$_1$, 5A). Thus, the anterior portion of the palatine is reduced to one third of its posterior width, which results in the maxilla forming a relatively large part of the palate. By contrast, the palatines are V-shaped in *H. hydrochaeris*, and the maxillary-palatine suture diverges from the alveolar margin gradually at the level of prism X of M3. The large palatal foramina (MLP 87-XI-1-3a, MACN 13469) are located at the level of M2 and extend anteriorly, before merging with each other at the level of P4. The mesopterygoid fossa is wide and has a straight anterior margin reaching the last prism of M3. In other specimens (e.g., MACN 3336), the fossa is deeper and reaches the antepenultimate prism (note that the number of prisms increases with size/age). Between the mesopterygoid fossa and M3, there is a conspicuous sulcus.

In dorsal view (Fig. 5C), the ascending apophyses of the premaxillae are slightly convergent posteriorly, whereas they are parallel in *Hydrochoerus hydrochaeris*. The naso-frontal suture is concave anteriorly, instead of almost straight as in *H. hydrochaeris*, and extends posteriorly beyond the fronto-premaxillary suture, with the frontals protruding as a wedge between the posteriormost portions of the nasals. The maxilla is broadly exposed on the skull roof, dorsal to the posterior portion of the rostral masseteric fossa, and is limited anterodorsally by the ascending apophysis of the premaxilla, posterodorsally by the frontal, and posteriorly by the lacrimal. The fronto-parietal suture is almost straight. The skull roof is depressed medially along the posterior portions of the frontals and the interparietal suture. In MACN 8934, the single specimen in which the posteriormost part of the skull is preserved, this depression does not continue posteriorly beyond the anterior portions of the parietals. The latter narrow posteriorly to form temporal fossae separated by a plane area without a sagittal crest, as in *H. hydrochaeris*.

In lateral view, the nasals are domed, facing mostly laterally and forming roughly half of the height of the rostrum in lateral view (Fig. 5B). At their centre, the nasals form a gibbous prominence. The masseteric fossa is short anteroposteriorly, with an anterodorsally oriented dorsal border (as opposed to being slightly anteroventral as in *H. hydrochaeris*) (Fig. 5B), and does not extend anteriorly beyond the anteriorly convex portion of the premaxillary-maxillary suture. The dorsal root of the antorbital bar is located ventral to the level of the dorsalmost portion of the masseteric fossa. The anterior root of the zygomatic arch is inclined anterodorsally-posteroventrally with respect to the alveolar plane, at an angle of less than 20º (Fig. 5B). Dorsal to the roots of M1–2, and posterior to the protuberance formed by P4, there is a large and ventrally concave foramen representing the most anterior part of the nasolacrimal canal, which runs between P4 and M1 and opens into the nasal cavity.

MLP 69-XII-2-19 (holotype of *Cardiatherium minutum*) is a left anterior skull fragment preserving P4–M1 and the anterior root of the zygomatic arch. It is markedly smaller than MLP 87-XI-1-27 (Tables 1 and 2). According to Mones (1991), the rostrum of this specimen is not as broad as that of MLP 87-XI-1-27, but our new data demonstrate that it is also rather wide. The scar marking the origin of the masseter superficialis muscle also resembles that of MLP 87-XI-1-27 in its orientation and shape, but is deeper and has clearly defined margins. This is the only specimen that preserves a small portion of the zygomatic arch. The latter is dorsoventrally compressed near the base, in the area of the origin of the masseter superficialis muscle, before becoming laterally compressed further anteriorly. This condition is also seen in other Plio-Pleistocene genera (e.g., "*Chapalmatherium*", *Neochoerus* Hay, 1926), but not in *H. hydrochaeris*, in which the zygomatic arch remains dorsoventrally compressed up to the antorbital bar.

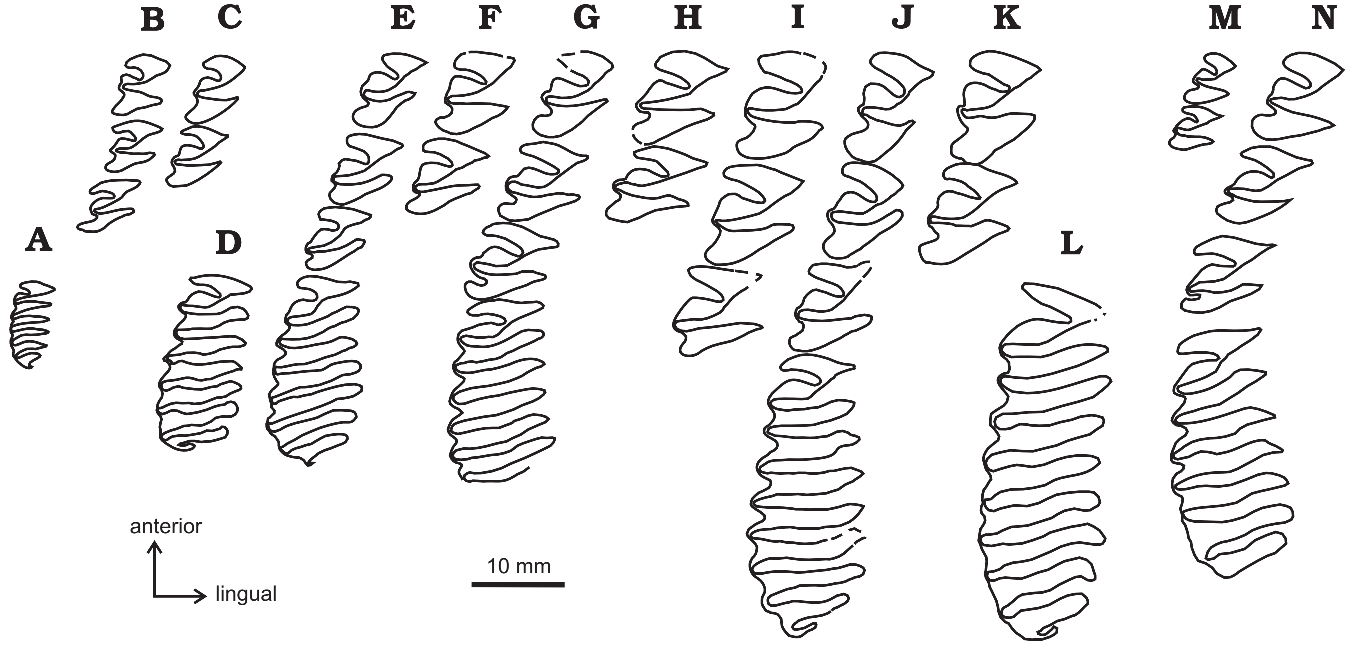


Fig. 6. Occlusal view of the right upper teeth of Late Miocene capybaras *Cardiatherium paranense* (Ameghino, 1883a) (**A**–**L**) and *C*. aff. *orientalis* (**M**, **N**). C–E, H, N, reversed. **A**. MACN 3353, M3. **B**. MLP 71-VI-16-1, P4–M2. **C**. MLP 69-XII-2-19, P4–M1. **D**. MLP 87-XI-1-2, M3. **E**. MLP 40-XI-15-2, P4–M3. **F**. MLP 87-XI-1-3, P4–M1. **G**. MLP 41-XII-13-153, P4–M3. **H**. MLP 87-XI-1-1, P4–M1. **I**. MLP 87-XI-1-3a, P4–M2. **J**. MLP 87-XI-1-27, P4–M3. **K**. MACN 13434, P4–M1. **L**. MLP 41-XII-13-161, M3. **M**. GHUNLPam 5236, P4–M1. **N**. GHUNLPam 14452, P4–M3.

The small individual from Tupungato (MLP 71-VI-16-1; Fig. 4B) is here considered to be extremely young because of its size and the porous condition of the bone in some areas. In this specimen, the maxillo-palatine suture is completely open, although it should be noted that even in adult individuals of *H. hydrochaeris* the number of open sutures may be high (Wilson and Sánchez-Villagra 2009). MLP 71-VI-16-1 shares with the specimens from the "conglomerado osífero" a wide rostrum, large incisive foramina, a laterally displaced socket of P4 located immediately dorsal to the anterior root of the zygomatic arch, laterally facing nasals forming almost half of the height of the rostrum in lateral view, and markedly divergent tooth rows. It differs from MLP 87-XI-1-27 in having a masseteric fossa extending anteriorly beyond the premaxillary-maxillary suture (Fig. $4B_2$), as well as the lack of rostral protuberances. This is the only specimen preserving a large portion of the lacrimal, which is a very large bone occupying the anterodorsal part of the orbit. The lacrimal foramen is located far ventrally.

Upper dentition (Fig. 6A–L).—Incisors: Only MLP 71-VI-16-1 preserves small, extra-alveolar fragments of both incisors (Fig. $4B_2$). Unlike in *H. hydrochaeris*, the latter lack a longitudinal furrow and are subtriangular in cross section, with their anteroposterior diameter exceeding their transverse one.

P4: Like M1–2, P4 comprises two prisms separated lingually by the fundamental internal flexus. Labially, each prism shows an additional flexus, the primary external flexus in prism I, and the secondary external flexus in prism II. The primary external flexus is oriented posterolingually and extends along more than 50% of the total transverse width of prism I in the largest specimens. The secondary external flexus is shallower than the primary one, V-shaped, and extends beyond the end of the fundamental internal flexus (Fig. 6I–K). The first prism of P4 is transversely narrow, and the labial margin of its posterior portion (prism Ib) bears an incipient flexus in some specimens. This feature does not seem to be size-related. Prism II is wider transversely than prism I, and longer anteroposteriorly than the second prisms of the molars, which tend to be laminar.

M1–2: The anterior two molars resemble each other, and differ from P4 in their anteroposteriorly somewhat shorter, but transversely wider, prism I. As in P4, prism Ib shows a slight flexus on the labial margin in some specimens. Prism II is almost laminar. In the largest specimens, the primary external flexus extends along more than 50% of the total transverse width of prism I.

M3: The number of prisms increases with size, ranging from six plus a little incipient last prism in the smallest specimen (MACN 3353, holotype of *Anchimysops radicei*; Fig. 6A), to seven plus an incipient last one in MLP 87-XI-1-2 and MLP 40-XI-15-2 (Fig. 6D, E), to eight with an incipient last one in MLP 87-XI-1-27 (Fig. 6J, holotype of *Anatochoerus inusitatus*), and finally nine plus an incipient last one in MLP 41-XII-13-161a and MLP 41-XII-13-161, the largest complete specimen (Fig. 6L). The number of prisms seems to become stable at ten, since the latter two specimens have the same number despite differing in size (see Table 2). Prism I is heart-shaped as in the other cheek teeth, with the primary external flexus being deeper than the other external flexi. The rest of the prisms are laminar with a labial flexus, except for the ninth. The two last prisms are narrow transversely.

Geographic and stratigraphic range.—All of the specimens except MLP 71-VI-16-1 come from the "conglomerado osífero" ("bonebed conglomerate" sensu Behrensmeyer 1991; Rogers et al. 2007), exposed at the cliffs of the Paraná River near Paraná City, Entre Ríos Province; Huayquerian South American Land Mammal Age (SALMA), Late Miocene (Cione et al. 2000). MLP 71-VI-16-1 comes from the Río de los Pozos Formation, exposed at Tupungato, Mendoza Province (Fig. 1: locality 6), estimated to be no younger than 5.8 Ma and no older than 8.2-7.4 Ma, Late Miocene (Chiaramonte et al. 2000; Irigoyen et al. 1995).

Cardiatherium aff. *orientalis* Pascual and Bondesio, 1982

Fig. 7.

1982 *Kiyutherium* aff. *orientalis*; Pascual and Bondesio 1982: 20; nec Pascual and Bondesio 1985: 135.
1999 *Kiyutherium orientalis*; Rocha and Montalvo 1999: 284.
2005 *Kiyutherium orientalis*; Vucetich et al. 2005: 260.

Material.—GHUNLPam 139, extremely damaged skull fragment with both M1–3; GHUNLPam 2009, skull fragment with both P4–M3; GHUNLPam 5236, anterior fragment of palate of a juvenile specimen with anterior root of the zygomatic arch, both P4 and left M1; GHUNLPam 5274; skull with both P4–M3, rostrum, right orbital area and damaged skull roof; GHUNLPam 8978, small fragment of palate with left M1–2; GHUNLPam 14452, palate with both P4–M3 and posterior portion of rostrum; GHUNLPam 14661, distorted skull with both P4–M3; GHUNLPam 14985, damaged rostrum with right incisor, right P4–M2 and left P4; GHUNLPam 27389, skull with both P4–M3, incisors, a left mandible fragment with p4–m3, and six cervical vertebrae articulated to skull; MLP 62-XII-4-17, left mandible fragment with p4–m3 and palatal fragment with left P4–M3 and right P4–M1 (the palatal fragment is currently lost). For mandibular remains, see Rocha and Montalvo (1999) and Vucetich et al. (2005). All specimens from Laguna Chillhué apart from GHUNLPam 139, 14985, and 27389, which are from Laguna Guatraché, La Pampa Province; lacustrine levels of the Cerro Azul Formation, Late Miocene.

Differential diagnosis.—No diagnosis can be provided given the present state of knowledge of *C. orientalis* Francis and Mones, 1965b. The occlusal morphology of the lower teeth is similar to that of *C. paranense* and the type of *C. orientalis* (Vucetich et al. 2005; Deschamps et al. 2007, 2009). However, some characters allow the differentiation of the taxon from the Cerro Azul Formation from *C. chasicoense* (Pascual and Bondesio, 1968), *C. paranense* (Ameghino, 1883a), and *C. patagonicum* Vucetich, Deschamps, Olivares, and Dozo, 2005. Concerning potential morphological similarities with *C. orientalis*, the present specimens will need to be compared with as yet unpublished material from the type locality of the species in Uruguay.

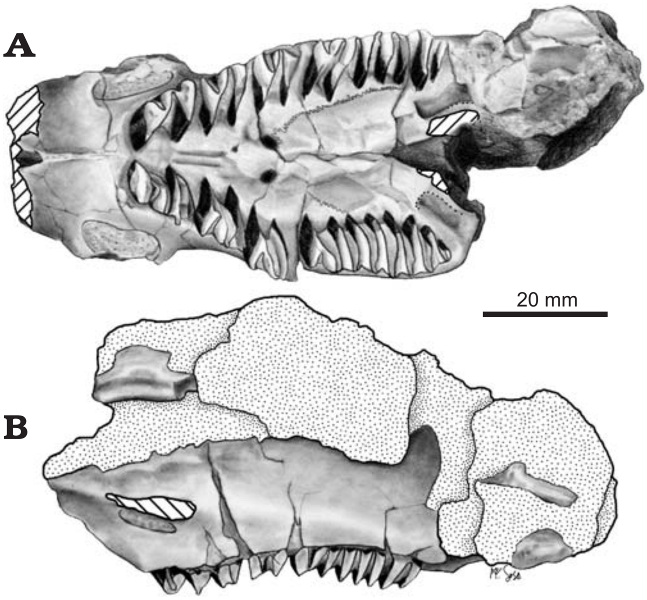


Fig. 7. Late Miocene capybara *Cardiatherium* aff. *orientalis* Pascual and Bondesio, 1982, GHUNLPam 14452 from Laguna Chillhué, Huayquerian SALMA, in ventral (**A**) and lateral (**B**) views (anterior to the left). Dotted area, sediment.

Description

Skull.—The state of preservation of the skulls from the Cerro Azul Formation is generally poor, but they preserve the palatal region. None of the specimens has a snout with roll-shaped expansions, as seen in MLP 87-XI-1-27. The length of the diastema exceeds the combined length of P4–M3, especially in larger specimens (44.2/41.5 mm in GHUNLPam 5274, 6.5% longer; 58/53 mm in GHUNLPam 27389, 9.5% longer). The zygomatic arch is not preserved in any of the skulls.

Compared with *H. hydrochaeris*, the rostrum is wide transversely both anterior and posterior to the anterior root of the zygomatic arch, but not as wide as in *C. paranensis*. The bottom of the P4 alveolus is located further dorsally than in *Cardiatherium paranense*, and does not extend laterally beyond the occlusal surface of the tooth. The incisive foramen is long, but slender. The premaxillary-maxillary suture is straight and crosses the incisive foramen near its posterior border, rather than its centre as in *C. paranense*. The scar marking the origin of the masseter superficialis muscle begins at the posterior margin of the anterior root of the zygomatic arch, between prisms I and II of P4. It extends up to half the distance between the posterior margin of the incisive foramen and the anterior margin of P4, without extending anteriorly beyond the anterior margin of the anterior root of the zygomatic arch. The muscle scars are oval in shape, narrower than in *C. paranense*, and parallel to the maxillary symphysis. The palate is not as wide as in *C. paranense* because M3 does not follow the oblique orientation of P4–M2, and instead is oriented slightly medially towards the sagittal plane. The maxillo-palatine suture diverges from the alveolar margin at the level of prism III of M3, before gently curving towards the base of the small palatine foramina. Thus, the palatine occupies a larger area of the palate than in *C. paranense*. The anterior margin of the mesopterygoid fossa is deeper than in *C. paranense*, reaching the fourth prism from the last of M3.

The dorsal margin of the masseteric fossa appears to be more horizontally oriented than in *C. paranense*, thus more closely resembling that of *Hydrochoerus hydrochaeris*. The anterior root of the zygomatic arch is inclined anterodorsally-posteroventrally with respect to the alveolar plane, at an angle greater than 20º. The posterior portion of the skull is preserved, but damaged, in GHUNLPam 27389. The temporal fossa is large and there is a moderately developed sagittal crest, unlike in *Hydrochoerus* and *Neochoerus* in which the latter is absent. The posterior wall of the skull is proportionally narrower than in *Hydrochoerus*, although this feature may be exaggerated as the posterior portion of the skull has been deformed by slight lateral compression. The paroccipital process is robust, laterally compressed, and long (the preserved fragment is more than 30 mm), extending well ventral to the ventral border of the bulla. These features of the paroccipital process characterise capybaras, and are also found in *Hydrochoerus*, *C. patagonicum* Vucetich, Deschamps, Olivares, and Dozo, 2005, and "*Chapalmatherium*" *novum* Ameghino, 1908. By contrast, the paroccipital process is slender and scarcely extends beyond the ventral border of the bulla in *Kerodon* and in other large cavioids such as *Dolichotis*. Both bullae have been partially preserved in this specimen, and contribute new data to those originally provided by Mones (1974). The bulla is more spherical and larger than in *C. patagonicum* (Dozo et al. 2010: fig. 4), *Neochoerus* (Deschamps 1998), and *H. hydrochaeris* (Linnaeus, 1766). The epitympanic sinus is large, and the external acoustic meatus appears to be doubled, as also seen in other hydrochoerids, with the inferior portion being enlarged anteroposteriorly.

Upper teeth (Fig. 6M, N).—Incisors: Only the largest specimen (GHUNLPam 27389) preserves the incisors. They are subcircular rather than subtriangular in cross section and lack a longitudinal furrow.

P4: The premolar resembles that of *C. paranense*, but in the juvenile specimen both the primary and secondary external flexi are shallower. The labial flexus of prism Ib is very shallow.

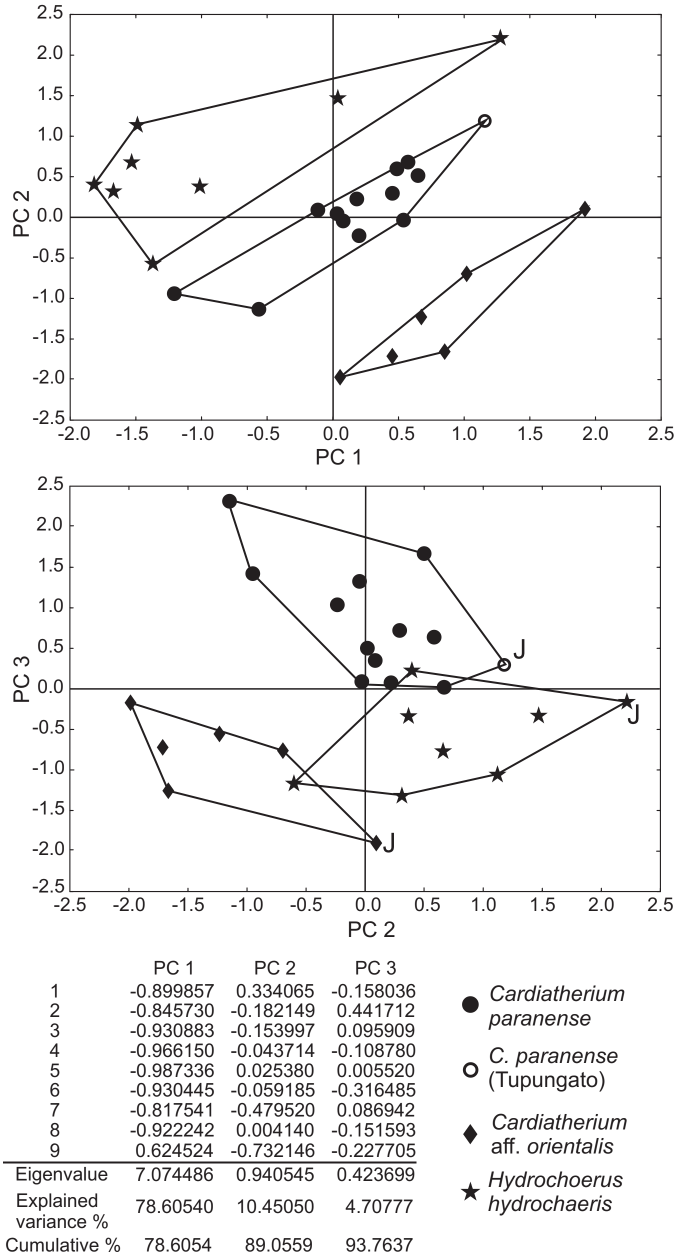
M1–2: These molars differ from those of *C. paranense* in lacking a labial flexus on prism Ib. The primary external flexus extends along up to 50% of the total transverse width of prism I, whereas the secondary external flexus is shorter, especially in the young specimen (GHUNLPam 5236).

M3: The third molar differs from that of *C. paranense* in comprising seven prisms, plus an incipient last one (the left M3 of GHUNLPam 14452 lacks this incipient prism; Fig. 6N). Only prisms II to VI have labial flexi. The transverse width of the prisms increases up to prism IV, whereas prisms VI to VIII decrease in size.

Morphometric analysis

Rostral morphology

Linear measurements.—The first three components account for 93.7% of the total variance (PCI: 78.6%, PCII: 10.45% and PCIII: 4.7%). PCI represents size for all variables except for the angle of the anterior root of the zygomatic arch (Fig. 8), as shown by a regression of PC 1 on size ($p < 0.001$; $R^2 = 0.955$). By contrast, PCII and PCIII are independent from size ($p = 0.307$; $R^2 = 0.041$). Within each species, individuals



	PC 1	PC 2	PC 3
1	-0.899857	0.334065	-0.158036
2	-0.845730	-0.182149	0.441712
3	-0.930883	-0.153997	0.095909
4	-0.966150	-0.043714	-0.108780
5	-0.987336	0.025380	0.005520
6	-0.930445	-0.059185	-0.316485
7	-0.817541	-0.479520	0.086942
8	-0.922242	0.004140	-0.151593
9	0.624524	-0.732146	-0.227705
Eigenvalue	7.074486	0.940545	0.423699
Explained variance %	78.60540	10.45050	4.70777
Cumulative %	78.6054	89.0559	93.7637

Fig. 8. Scatterplot and axis scores of the first two PCs (**A**) and the second and third PC (**B**) of the Principal Component Analysis of the linear rostral measurements of "fossil (*Cardiatherium*) and extant (*Hydrochoerus*) capybaras from Argentina, illustrated in Fig. 2. J, juvenile.

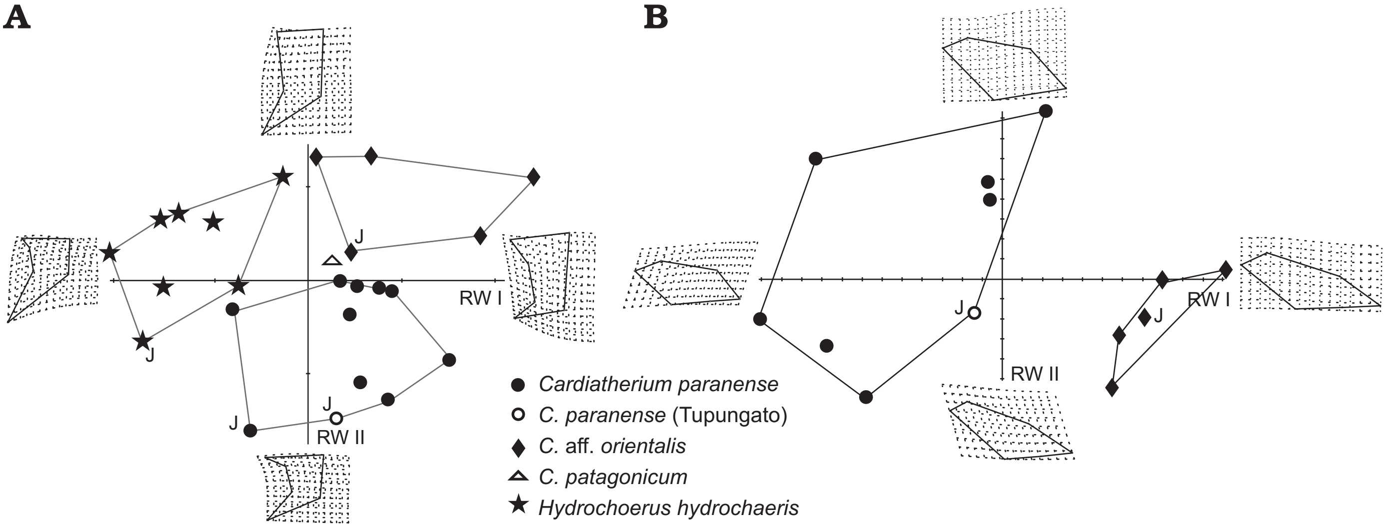


Fig. 9. First two relative warps (RWs) of the geometric morphometric analyses of the posterior region of the rostrum of fossil (*Cardiatherium*) and extant (*Hydrochoerus*) capybaras from Argentina, in ventral (**A**) and lateral (**B**) views. J, juvenile.

are also arranged according to size, with the smaller specimens tending to have more positive values (Fig. 8A). PCII mostly summarises variation in the angle of the anterior root of the zygomatic arch with the alveolar plane, the distance from the posterior border of the incisive foramen to P4, and the posterior width of the incisive foramen. Finally, the variables with the highest loadings for PCIII are the anterior width of the rostrum and the rostral diameter at the level of M2 (palatal width; Fig. 8B), with *C. paranense* tending towards positive values (wide rostrum and palate), whereas *C.* aff. *orientalis* and *H. hydrochaeris* tend towards the opposite (narrower snouts and palates).

Geometric morphometrics exploratory analysis.—The first two relative warps (RW) of the shape analysis of the rostrum in ventral view account for 76% (RWI: 50% and RWII: 26%) of the total variation (Fig. 9A). *Hydrochoerus hydrochaeris* occupies the negative range of RWI, while the remaining species are arranged in a gradient from near zero in the case of *C. paranense* to positive values for *C.* aff. *orientalis.* The single specimen of *C. patagonicum* falls out close to the mean value. MLP 71-VI-16-1 (the juvenile from Tupungato) is closer the specimens from the "conglomerado osífero" than to any of the other species. RWI reflects, from negative to positive values (Fig. 9A), (i) gradual lengthening of the distance between the posterior margin of the incisive foramen and the middle point between both P4s; (ii) a more posterior origin of the masseter superficialis muscle; (iii) displacement of the posterior limit of the anterior root of the zygomatic arch both anteriorly and towards the midline of the rostrum; and (iv) an increase of the distance between the lateralmost point of prism I of P4 (landmark 2) and the anterior limit of anterior root of the zygomatic arch (landmark 4). The fossil species are separated along RWII, with *C. paranense* tending towards negative values, and *C.* aff. *orientalis* towards positive ones. *H. hydrochaeris* occupies positive and intermediate values, except for the juvenile, which shows negative values owing to its relatively wide rostrum. The main shape changes (from positive to negative scores) represented by RWII are related to (i) a gradual increase in the distance between the anterior limit of the anterior root of the zygomatic arch and the middle point of the posterior margin of the incisive foramen; and (ii) anteroposterior shortening of this portion of the rostrum. Thus, *C.* aff. *orientalis* is characterised by a relatively long and narrow posterior portion of the snout, whereas the same area is shorter and wider in *C. paranense*.

In the analysis of the lateral view of the rostrum (Fig. 9B), the first two RWs account for 72% of the total variation (RWI: 56%, RWII: 16%). Along RWI, *C. paranense* is positioned towards the negative values, and *C.* aff. *orientalis* toward the positive ones. The landmarks that vary most in position are those marking the anterior and posterior margins of the anterior root of the zygomatic arch and the posteriormost point of the incisive foramen, indicating lengthening of the posterior area of the diastema and greater inclination of the anterior root of the zygomatic arch in *C.* aff. *orientalis*. The juvenile specimen from Tupungato falls out close to the specimens from the "conglomerado osífero". In terms of RWII, *C. paranense* is widely distributed across most of the morphospace, whereas *C.* aff. *orientalis* is restricted to the right-lower quadrant owing to its relatively long snout.

Occlusal morphology of the upper cheek teeth

In the analysis of the occlusal morphology of P4 (Fig. 10A), the first two RWs account for 56% (RWI: 35.5% and RWII: 20.5%) of the total variation. Species are separated mostly along RWI, with *C. patagonicum* and *C. paranense* tending towards negative values, *C.* aff. *orientalis* occupying an intermediate position overlapping with that of *C. paranense*, and *C. chasicoense* tending towards positive values. The juvenile specimens MLP 71-VI-16-1 (*C. paranense*, Tupunga-

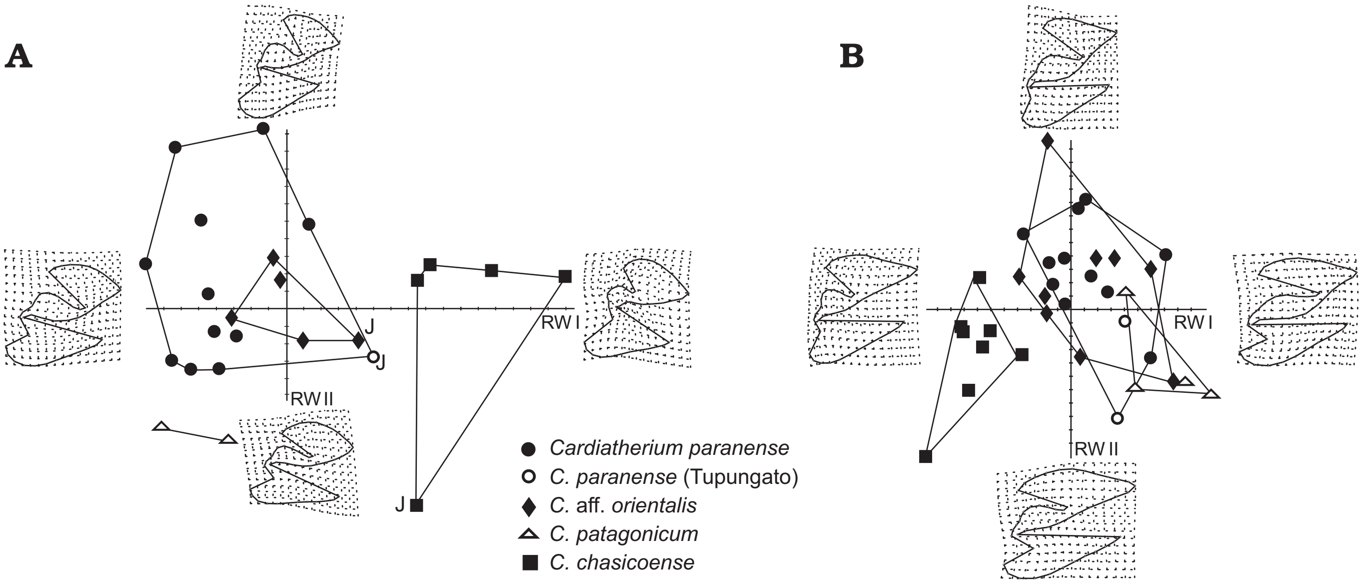


Fig. 10. First two relative warps (RWs) of the geometric morphometric analyses of the upper cheek teeth of fossil capybaras from Argentina, in occlusal view. **A**. P4. **B**. M1–2. J, juvenile.

to) and GHULNPam 5236 (*C.* aff. *orientalis*) fall out close to the distribution of *C. chasicoense*. We interpret this position as a result of their juvenile condition, since the tooth morphology of juveniles resembles that of adults of more archaic species (Deschamps et al. 2007). Along RWI, from positive to negative values, both the primary and secondary external flexi become deeper (Fig. 2A), with the former being the longer of the two. As the primary external flexus deepens, prism I widens transversely in its posterior portion and gradually acquires a straighter anterior margin, while prism II also widens transversely, but rotates slightly anteriorly. The location of the juveniles in the right lower quadrant is explained by the incipient development of the primary and secondary external flexi during the early stages of ontogeny (Vucetich et al. 2005). Towards the negative values of RWII the molars widen, with the posterior part of prism I becoming stretched transversely and its anterior margin straightening even more than indicated by RWI. The labial angle of prism I rotates posteriorly, and all the prisms narrow anteroposteriorly. *C. paranense* is located mostly within the positive and intermediate range of values, whereas *C. patagonicum* falls withing the negative range. Except for the juvenile specimen of *C. chasicoense*, both the latter and *C.* aff. *orientalis* occupy an intermediate position.

In the analysis of M1 and M2 (Fig. 10B), the first two RWs account for 48.61% (RWI: 25.7% and RWII: 23%) of the variation. The ranges of *C. paranense*, *C.* aff. *orientalis* and *C. patagonicum* largely overlap, and only *C. chasicoense* can be clearly distinguished. The partial overlap of *C. patagonicum* with some of the other taxa is probably due to the juvenile condition of the available specimens. Previous studies (Vieytes and Deschamps 2007) including lower molars of both juvenile and adult specimens showed clear morphological differentiation of this species from the other members of the genus.

Concluding remarks

Species taxonomy.—The capybaras from the Late Miocene, traditionally assigned to several genera and species on the basis of lower cheek tooth morphology, were recently gathered into the single genus *Cardiatherium*, which now includes *C. chasicoense*, *C. paranense*, *C. orientalis*, and *C. patagonicum* (Vucetich et al. 2005; Deschamps et al. 2007, 2009). The oldest species, *C. chasicoense* from the earliest Late Miocene, is known from the provinces of Buenos Aires and San Juan (Deschamps et al. 2007, 2009). *C. patagonicum*, the most derived species with regards to its dental morphology, comes from Península Valdés, Chubut Province (Vucetich et al. 2005), and represents the southernmost record of any capybara. Finally, *C. paranense* is known from the provinces of Entre Ríos and Mendoza (this paper), whereas *C. orientalis* is found in Uruguay (Francis and Mones 1965b). The material from La Pampa Province could represent a fifth species, here referred to *Cardiatherium* aff. *orientalis* (*C. orientalis* in previous papers; e.g., Rocha and Montalvo 1999; Vucetich et al. 2005). Any definitive identification of these specimens must await the description of additional material of *C. orientalis* (see also Mones 1991: 17). Other Late Miocene species are known exclusively from their holotypes (fragmentary mandibles), and have not yet been revised. These include "*Kiyutherium*?" *rosendoi* Bondesio, 1985b (unknown levels exposed at Puerta de Corral Quemado, Catamarca Province), which may be synonymous with *C. paranense* (Deschamps et al. 2007), and *Cardiatherium isseli* Rovereto, 1914 (uncertain levels of the Río Negro Formation, Río Negro Province).

C. paranense and *C. orientalis* were described based mostly on size and the morphology of their lower teeth, without taking into account the effects of ontogeny. According to Vucetich et al. (2005), these species (as well as *C.* aff. *ori-*

entalis) cannot be clearly separated based on just the lower teeth and mandibles, whereas *C. chasicoense* and *C. patagonicum* are undoubtedly different (Deschamps et al. 2007, 2009). In agreement with this, we found that *C. paranense* and *C.* aff. *orientalis* overlap in the morphology of their upper teeth, whereas *C. chasicoense* and, in part, *C. patagonicum* show different morphologies (Fig. 10), with the P4 being more reliable than the molars for species recognition. By contrast, the cranial material studied here does provide new data corroborating the differentiation of *C. paranense* from *C.* aff. *orientalis*.

Our RW analysis of rostral shape demonstrates that the differences between specimens mainly reflect changes in the position of the origin of the masseter superficialis muscle, the distance between the incisive foramen and P4, and the inclination of the anterior root of the zygomatic arch. All the specimens from the "conglomerado osífero", as well as the specimen from Tupungato, share a unique combination of characters (relatively wide snout; short distance between the incisive foramen and P4; little inclination of the anterior root of the zygomatic arch; wide incisive foramen; and marked lateral projection of the alveolus of P4), uniting them into a single species. Given that all of the lower teeth and mandibular fragments from the "conglomerado osífero" have been assigned to *C. paranense* (Vucetich et al. 2005), we suggest that the cranial material described here also belongs to this species (as suggested by Vucetich et al. 2012), with the specimen from Tupungato likely representing a juvenile individual. By contrast, *C.* aff. *orientalis* is characterised by a narrower snout, a longer distance between the incisive foramen and P4, a higher degree of inclination of the anterior root of the zygomatic arch, and a narrower incisive foramen, resulting in an overall more gracile rostral architecture. However, a more detailed assessment of the status of this taxon and it phylogenetic relationships will have to await the description of further material of *C. orientalis*.

In our PCA of the linear measurements (Fig. 8), different specimens are arranged in the morphospace according to their size, suggesting that (i) at least part of the morphological variation is related to ontogenetic change, and (ii) that "*Anatochoerus*", "*Contracavia*", and "*Anchimysops*" form part of a single ontogenetic sequence representing *C. paranense*. These results eliminate any record of small-sized species of capybaras from the Late Miocene of Argentina, with all of the small specimens described so far representing young individuals instead. This implies that large size may have been acquired early during the evolutionary history of the group, and reinforces the idea that the early radiation of capybaras was not as explosive as previously thought (see Mones 1991). Instead, it is likely that this radiation would have been constrained by an early acquisition of large size, increasing complexity of cheek teeth, and probably semi-aquatic habits (Vucetich et al. 2012).

Suprageneric taxonomy.—Our results substantially modify the contents of the capybara lineage. Thus, the Cardiatherinae, formerly thought to include *Anchimys*, *Anchimysops*, *Procardiatherium*, *Cardiatherium*, *Kiyutherium*, and *Phugatherium* (Mones 1991), should likely be reduced to the single genus *Cardiatherium*, with the Pliocene *Phugatherium* likely being a senior synonym of the protohydrochoerine *Chapalmatherium* (=*Protohydrochoerus*) (Vucetich et al. 2005, 2012). Equally, the taxa formerly included in the "Anatochoerinae" (*Anatochoerus* and *Contracavia*, but not *Hydrochoeropsis*, which has not been included in this study but is probably more closely related to *Hydrochoerus*; personal observations MGV and CMD), are likely also junior synonyms of *Cardiatherium paranense*, making Anatochoerinae superfluous. Taken together, our findings therefore emphasise the need for a thorough revision of the classical suprageneric arrangement of capybaras (see also Prado et al. 1998; Vucetich et al. 2005).

Biogeography, palaeoenvironments, and biostratigraphy.—From a biogeographic point of view, the assignment of the specimen from Tupungato to *Cardiatherium paranense* expands the geographic distribution of this species (Fig. 1), which so far had only been known only from the Paraná River cliffs, Entre Ríos Province. This larger geographic distribution recollects that of *C. chasicoense* (Deschamps et al. 2009), and is in accordance with the wide geographic range of the living species. Like all fossil capybaras found to date (Deschamps et al. 2009), the specimen from Tupungato occurred in water-related sediments, thus reinforcing the idea that the semi-aquatic habits of modern capybaras were also typical of their fossil representatives (Pascual and Bondesio 1981; Vucetich et al. 2012). In addition, the stratigraphic position of the specimen from Tupungato may help to constrain the age of the Late Miocene "conglomerado osífero". The Río de los Pozos Formation, which yielded the Tupungato specimen, has been estimated to be younger than 5.8 Ma, and no older than 8.2-7.4 Ma (see above). Given that the earlier Chasicoan SALMA ends around 7 Ma (Deschamps et al. 2009), the "conglomerado osífero" is likely to have been deposited during a short episode between 7 and 5.8 Ma.

Cardiatherium aff. *orientalis* was found at Laguna Chillhué, where the Late Miocene biozone of *Chasichimys scagliai* was defined on the basis of the *Chasichimys*–*Xenodontomys* octodontoid rodent lineage, with an upper age limit of about 6.02 Ma (Verzi et al. 2008). Thus, *C.* aff. *orientalis* could have been coeval with *C. paranense*. Another species of *Cardiatherium*, *C. talicei* Francis and Mones, 1965a, is based on a fragmentary mandible and skull from Uruguay, and differs from the holotype of *C. orientalis* (see Francis and Mones 1965b: 52) mainly in its larger size and deeper tooth flexids. Future analysis may establish whether these differences represent ontogenetic stages of a single species, or the presence of genuinely different taxa. *Cardiatherium* has not been recorded from the Plio-Pleistocene sequence of Argentina, where capybaras are represented by other genera characterised by a rather different and more derived dental morphology and other characters. By contrast, *C. talicei* has been considered as either Montehermosan (Early Pliocene; Mones 1991, and references there in) or even Ensenadan (Early Pleistocene; Bossi et al. 2009) in age, thus making it the only occurrence of the genus younger than the Late Miocene.

Finally, another fossil capybara specimen consisting of a single m1 or m2 was found together with the holotype of *C. orientalis* in the Kiyú Formation (currently Kiyú lithofacies of the Camacho Formation sensu Sprechmann et al. 2000 = San Pedro Member of the Camacho Formation sensu Perea and Martínez 2005). Originally attributed to *Eucardiodon* cf. *marshi* (Ameghino, 1891) by Mones and Castiglioni (1979), the specimen was later synonymised with *Anchimys marshii* (Mones 1991), which in turn has been suggested to be a potential juvenile of *C. paranense* (Vucetich et al. 2005). However, since the latter cannot be distinguished from *C. orientalis* on the basis of their lower teeth alone, it is more likely that *A. marshii* instead represents a juvenile *C. orientalis*.

Acknowledgements

We thank Alejandro Kramarz (MACN), Ricardo Martínez (PVSJ), Alejandro Dondas (MMP), and the late Vicente Di Martino (MMH) for access to material, Alicia Álvarez and Cecilia Morgan (both Facultad de Ciencias Naturales y Museo de La Plata, Argentina) for comments on the manuscript and for help with photographs. Manuel Sosa (Facultad de Ciencias Naturales y Museo de La Plata) produced the drawings. Alvaros Mones (Augsburg, Germany) and Andrés Rinderknecht (Museo Nacional de Historia Natural, Montevideo, Uruguay) provided useful comments on this manuscript. Special thanks to the editor Felix Marx (National Museum of Nature and Science, Tsukuba, Japan) for his generous help with the final version. This paper was partially supported by grants UNLP 11/568, and CONICET PIP 0270, and Facultad de Ciencias Exactas y Naturales, UNLPam to C.I.M.

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