Journal of Vertebrate Paleontology 27(3):683–692, September 2007

ARTICLE

ONTOGENY AND DIVERSITY OF THE OLDEST CAPYBARAS (RODENTIA: HYDROCHOERIDAE; LATE MIOCENE OF ARGENTINA)

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ABSTRACT—According to our previous model for interpreting the fossil record of capybaras the cheek teeth grow in width and length throughout life; flexids (especially h.s.i. and h.t.i.) deepen allometrically resulting in diverse occlusal morphologies during ontogeny; in the more derived species the 'onset' of flexid development is pre-displaced, and the relative depth and development rate of the flexids increase. Consequently, we interpreted the different occlusal morphologies found in the fossil record as different ontogenetic stages, leading to a drastic diminution of latest Miocene-Pliocene taxonomic diversity. The analysis of the geologically oldest capybaras, which are from the Arroyo Chasicó Formation (Chasicoan SALMA, late Miocene), is added. This study suggests a single species occurs in this formation that cannot be separated at the genus level from Huayquerian species. In the Arroyo Chasicó species, which is older and theoretically more primitive than that of the Huayquerian, the flexids are shallower as predicted. The analysis supports our model of capybara dental ontogeny and evolution and encourages revision of the whole family according to this model.

INTRODUCTION

Living capybaras are notable among rodents for their large size (100–130 cm body length) and semiaquatic habits. They usually live in groups of about 20 individuals, but colonies up to 100 have been reported (Nowak and Paradiso, 1983). The Hydrochoeridae are first recorded in the Arroyo Chasicó Formation of central Argentina (Chasicoan South American Land Mammal Age, late Miocene; Fig. 1A–D). Capybara remains are relatively common in some late Miocene and Pliocene localities, they decline in the Pleistocene, and today the family is represented by a single genus (*Hydrochoerus*) with two species (Woods and Kilpatrick, 2005).

As for most mammals, fossil capybara taxonomy is based mainly on tooth morphology. Owing to the particularly fragmentary fossil record of capybaras, especially those of Huayquerian age, many taxa are represented by a single specimen, sometimes an isolated tooth. This fact, together with the common practice of using typological criteria for classification, has resulted in a long list of nominal taxa.

In a previous article (Vucetich et al., 2005), we proposed new criteria based on molar ontogenetic growth patterns that permit a better understanding of the fossil record. In short, we proposed that: (1) euhypsodont (= hypselodont) teeth of capybaras grow throughout life in all dimensions, with the peculiar characteristic that the morphology of the occlusal surface becomes more complex with age (i.e., the base of the tooth enlarges and keeps folding throughout life); (2) flex/ids grow in length at different rates (with positive allometry, isometrically, or apparently independently of tooth size), resulting in slightly different occlusal morphologies in relation to tooth size (= ontogenetic stage); consequently, (3) several occlusal morphologies previously thought to pertain to different species or even genera are in fact ontogenetic stages of a single species. Capybara remains from classical localities of Huayquerian age (uppermost Miocene) of central Argentina were recently analyzed within this framework (Vucetich et al., 2005) and their taxonomy was revised accordingly (Table 1).

In this paper we study the oldest capybaras, those found in the Arroyo Chasicó Formation (Buenos Aires Province, Argentina), in order to test whether they follow the proposed model of ontogenetic change and to revise their taxonomy and estimates of diversity.

Institutional Abbreviations—GHUNLPam, Universidad Nacional de La Pampa, Geología Histórica; **MD-CH**, Museo Darwin, Punta Alta, Arroyo Chasicó Collection; **MLP**, Museo de La Plata, La Plata; **MMH**, Museo Municipal de Ciencias Naturales de Monte Hermoso, Monte Hermoso; **MMP**, Museo Municipal de Ciencias Naturales 'L. Scaglia', Mar del Plata; **MPEF**, Museo Paleontológico Egidio Feruglio, Trelew; **SPV-FHC**, Sección Paleontología Vertebrados, Facultad de Humanidades y Ciencias, Montevideo, Uruguay. All of these museums except the last are in Argentina.

METHODS

Nomenclature and Measurements

Tooth nomenclature (Fig. 2A–C) and measurements (Fig. 2D–F) follow Vucetich and colleagues (2005). Abbreviations refer to

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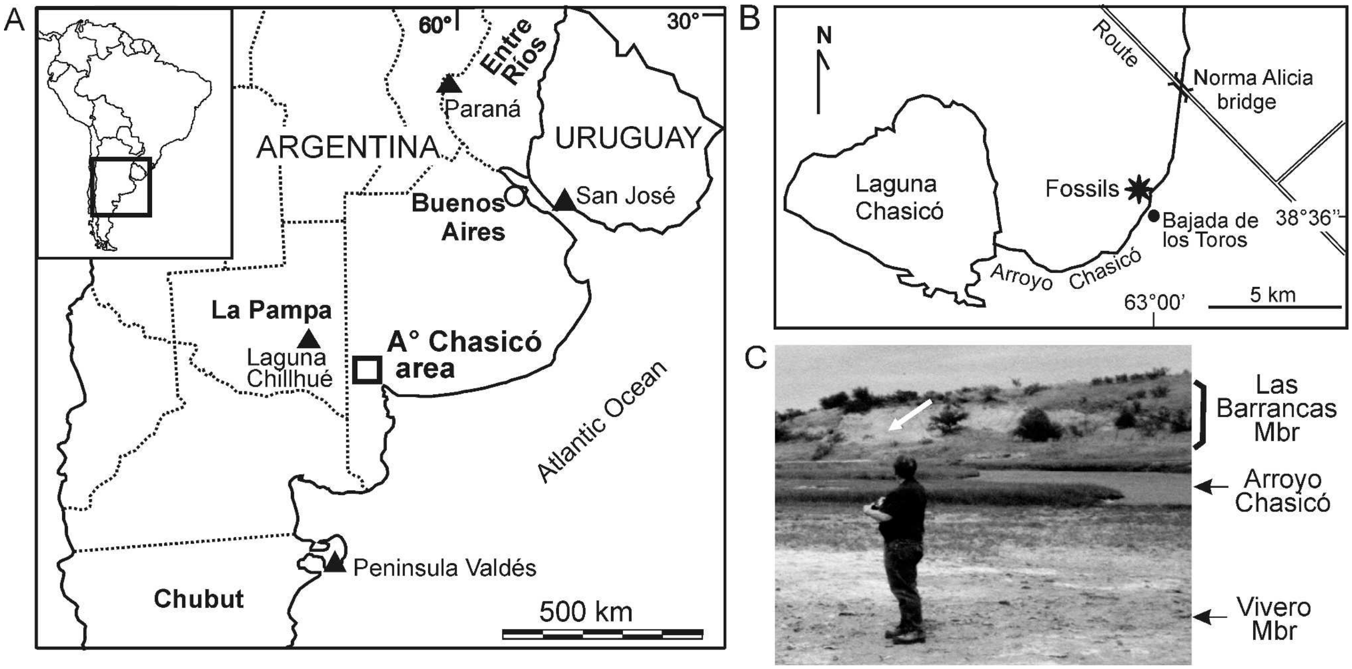

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Epoch	South American Stages/Ages	Lithostratigraphic Units	Hydrochoeridae	Biozones (Verzi et al., in press)	Time (Schultz et al., 2004)
Late Miocene	Huayquerian	Cerro Azul Fm. (Lag. Chillhué)	*Cardiatherium orientalis*	*Chasichimys scagliai*	
	Chasicoan	Arroyo Chasicó Fm. Las Barrancas Mbr.	*Cardiatherium chasicoense*	?	
		Arroyo Chasicó Fm. Vivero Mbr.		*Chasichimys bonaerense*	9.23±0.09

FIGURE 1. **A**, location map with the Argentine Chasicoan and Huayquerian (late Miocene) localities bearing capybaras; **B**, detailed map of the Arroyo Chasicó area with Bajada de los Toros locality; **C**, photograph of the right margin of Bajada de los Toros locality, white arrow points to the fossil-bearing level; **D**, chronological chart of the late Miocene in southern South America.

the Spanish names in order to conform to previous publications on the Hydrochoeridae (e.g., Frailey, 1986).

Linear measurements of p4–m3 were taken with a stereomicroscope with micrometer eyepiece and included: AP, anteroposterior length; AWa, width of prism Ia; AWb, width of prism Ib; HFEL, length of fundamental external flexid (h.f.e.); HPEL, length of primary external flexid (h.p.e.); HSEL, length of secondary external flexid (h.s.e.); HSIL, length of secondary internal flexid (h.s.i.); HTIL, length of tertiary internal flexid (h.t.i.); MW, middle width; and PW, posterior width (Fig. 2D–F).

The lengths of the flexids with respect to the tooth width were measured linearly on the occlusal surface and expressed as a percent of total tooth width. It is described in the text as the 'depth' of the flexid. Short flexids are 'shallow' and long flexids are 'deep.'

Quantitative Analysis

Only m1 and m2 were considered for the quantitative analysis because they vary less among individuals than p4 and because they are the best represented cheek teeth in the sample of *Cardiatherium patagonicum* on which the proposal of our model was originally based. Isolated m1s and m2s are difficult to differentiate; consequently, they were analyzed together.

The linear measurements of m1 and m2 (Fig. 2) were log-transformed and examined through principal components analysis (PCA) based on a correlation matrix (Bookstein et al., 1985; Legendre and Legendre, 1998). AP was used as a size estimate following Vucetich et al. (2005). In order to test whether *C. chasicoense* follows the proposed model of growth pattern of h.t.i. and h.s.i., HSIL and HTIL versus AP of m1–m2 (Fig. 2) were compared with allometric change of these flexids of the Huayquerian species of the genus analyzed by Vucetich and colleagues (2005).

GEOLOGICAL SETTING

All the remains of Chasicoan capybaras were recovered from the Las Barrancas Member of the Arroyo Chasicó Formation (see below), in southwest Buenos Aires Province, in front of the Bajada de los Toros locality (Fig. 1A–C). This locality is about 500 m downstream from the 'Norma Alicia' bridge over Arroyo Chasicó (IGM 1:50.000 'Estancia Los Chañares' chart N° 3963-10-3; 63° 00′ 00″ W, 38° 36′ 30″ S). The Arroyo Chasicó Formation was formalized by Pascual (1961:63) based on the 'Chasicoense' of Kraglievich (1930) in reference to the sediments cropping out along the margins of Arroyo Chasicó. Fidalgo and Porro (in Bondesio et al., 1980; see also Fidalgo et al., 1987) described

TABLE 1. Revised taxonomy of the Hyayquerian (late Miocene) Hydrochoeridae based on lower cheek tooth morphology.

Systematics sensu Mones, 1991	Stratigraphic and geographic provenance	Revision sensu Vucetich et al., 2005
Anchimys leydi *Anchimys marshi* *Cardiatherium paranense* *Cardiatherium* sp. A *Kiyutherium denticulatum* *Kiyutherium scillatoyanei* *Procardiatherium crassum* *Procardiatherium simplicidens*	Entre Ríos Province; 'conglomerado osífero,' Ituzaingó Formation (Mones, 1991 and references therein)	*Cardiatherium paranense*
?Kiyutherium rosendoi	Catamarca Province; Puerta de Corral Quemado (Bondesio, 1985)	?
Kiyutherium orientalis	San José, Uruguay; Kiyú Formation (Francis and Mones, 1965b)	*Cardiatherium orientalis*
Kiyutherium aff. *orientalis* A	La Pampa Province; Cerro Azul Formation (Pascual and Bondesio, 1982)	
Kiyutherium aff. *orientalis* B	Río Negro Province; Río Negro Formation, capa d (Angulo and Casamiquela, 1982)	*Cardiatherium patagonicum**
Cardiatherium isseli	Río Negro Province; Río Negro Formation, unknown levels (Rovereto, 1914).	*Cardiatherium isseli*
Cardiatherium talicei	San José, Uruguay; San José Formation (Francis and Mones, 1965a)	*Cardiatherium talicei*

*The holotype of *C. patagonicum* comes from Puerto Madryn Formation, Península, Valdés, Chubut Province.

two members for this formation, the lower Vivero Member and the upper Las Barrancas Member (Fig. 1C). Overlying the Arroyo Chasicó Formation are the Pleistocene conglomerates of the Bajada de los Toros Formation and the eolian sands of the Estancia La Aurora Formation (Fidalgo et al., 1979). Zárate and colleagues (2003) and Blasi and colleagues (2004) described four lithofacies (S, F, FSC, and P) for the Arroyo Chasicó Formation. At the base of the profile (S) are very fine sands with escorias interpreted as impact glasses. Overlying are sandy silts (F) with many reworked escorias, laminated mudstones (FSC), and sandy silts and mudstones (P). The whole Arroyo Chasicó Formation represents a fluvial depositional environment of channel bars and areas of flood-plain and overflow with intervals of soil formation (Zárate, 2005). The hydrochoerids studied here were recovered from mudstones and sandy siltstones composing lithofacies association 3 (= facies FSC and P) of Arroyo Chasicó Formation (Zárate pers. comm., July 2005). These sediments were deposited under generally low energy conditions in a swampy environment (Zárate et al., 2007).

The Arroyo Chasicó Formation—stratotype of the Chasicoan Stage—represents the beginning of a new sedimentary cycle generally recognized as 'Araucano' (Doering, 1882; Ameghino, 1889) or an equivalent name (e.g. Araucanense, Estratos Araucanos; Rovereto, 1914), and later as 'Edad de las planicies australes' (Pascual and Bondesio, 1982). This cycle began with the withdrawal of the 'Mar Paranense,' which flooded a widespread surface from northern Patagonia (central Argentina) to northern South America (Ramos, 1999) during the middle to late

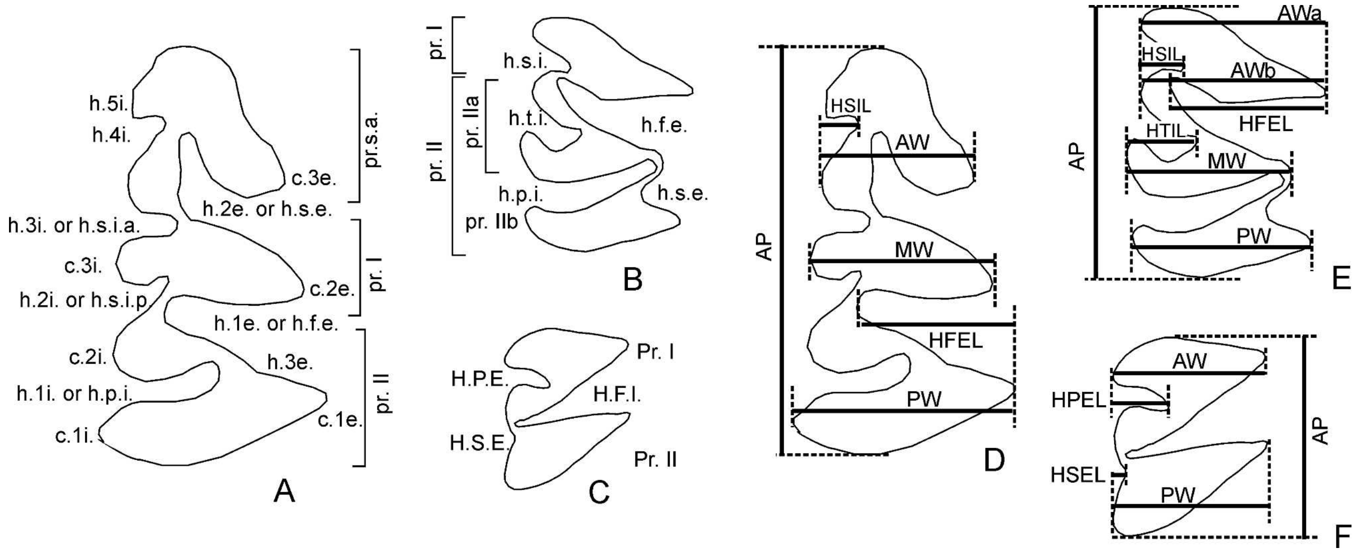


FIGURE 2. Nomenclature (**A**, **B**, **C**) and measurements (**D**, **E**, **F**) of *Cardiatherium chasicoense* teeth. **A** and **D**, right p4; **B** and **E**, right m1 or m2; **C** and **F**, right M1 or M2. **Abbreviations**: **c.1e.–c.3e.**, 1st–3rd external column; **c.1i.–c.3i.**, 1st–3rd internal column; **h.1e.–h.3e.**, 1st–3rd external flexid; **h.1i.–h.5i.**, 1st–5th internal flexid; **h.f.e.**, fundamental external flexid; **H.F.I.**, fundamental internal flexus; **H.P.E.**, primary external flexus; **h.p.i.**, primary internal flexid; **h.s.e.**, secondary external flexid; **H.S.E.**, secondary external flexus; **h.s.i.**, secondary internal flexid; **h.s.i.a.**, secondary anterior internal flexid; **h.s.i.p.**, secondary posterior internal flexid; **h.t.i.**, tertiary internal flexid; **pr.I**, prism I; **pr.II**, prism II; **pr.s.a.**, anterior secondary prism. **Measurements**: **AP**, anteroposterior length; **AW**, anterior width; **AWa**, prism Ia width; **AWb**, prism Ib width; **HFEL**, h.f.e. length; **HPEL**, H.P.E. length; **HSEL**, H.S.E. length; **HSIL**, h.s.i. length; **HTIL**, h.t.i. length; **MW**, middle width; **PW**, posterior width.

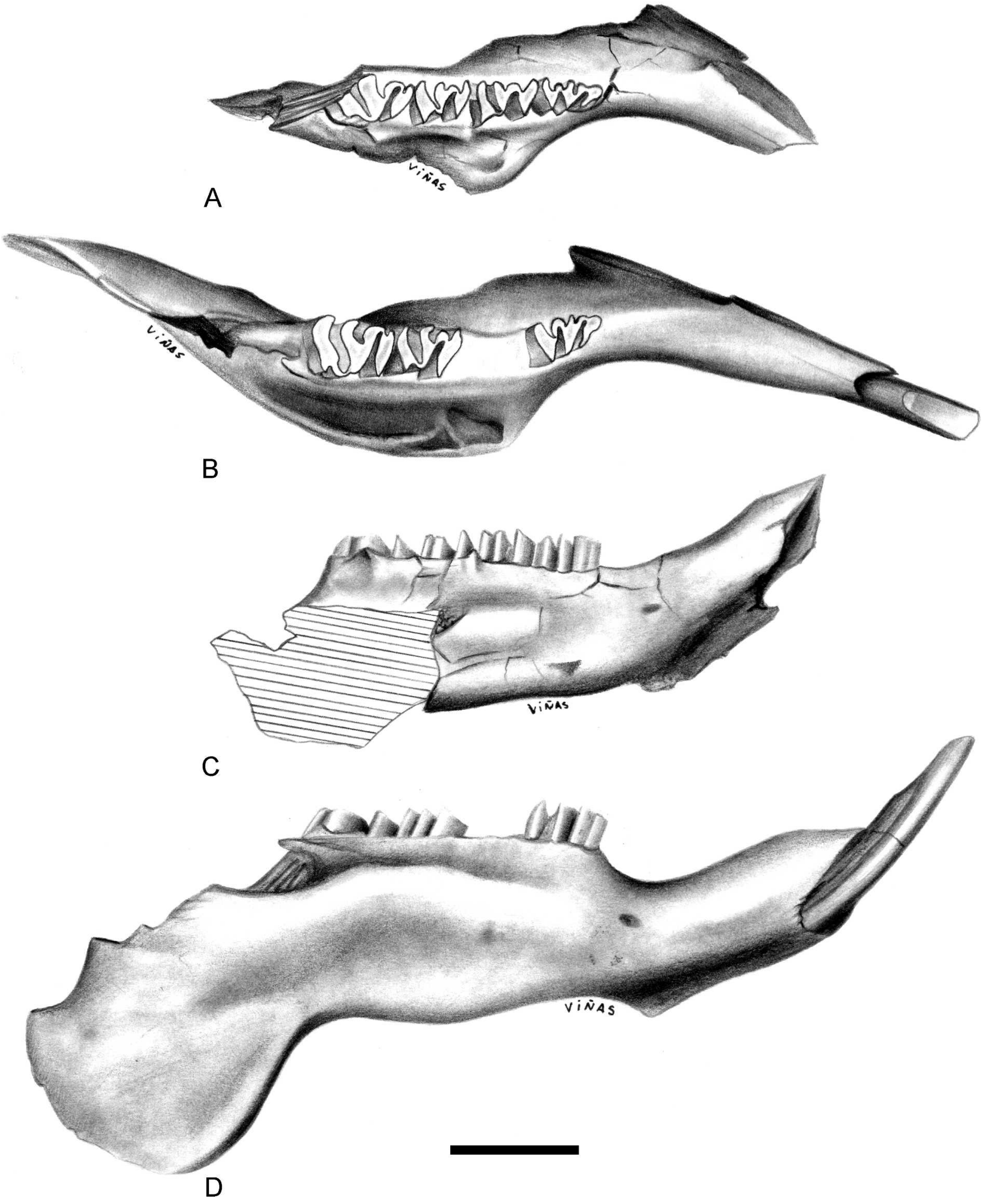


FIGURE 3. Right mandible of *Cardiatherium chasicoense*, new comb, in occlusal (**A**, **B**) and lateral (**C**, **D**) views. **A**, **C**, holotype MMP 300-M; **B**, **D**, MMH-CH 85-4-40. Scale bar equals 2 cm.

Miocene. The regression is coeval with the Quechua diastrophic Phase of the Andean orogeny (Pascual and Bondesio, 1985), and a global climatic amelioration (Janis, 1993). According to Pascual (1984) this withdrawal began around 10.8 Ma. Radiometric analysis of escorias of the basal levels of the Arroyo Chasicó Formation at the type locality yielded a ^{40}Ar/^{39}Ar date of 9.23 ± 0.09 Ma (Schultz et al., 2004). The cuspidate palustrine facies (FSC) at this area would have been deposited after ca. 9 Ma (Zárate, 2005).

A biochronologic and biostratigraphic scheme for the late

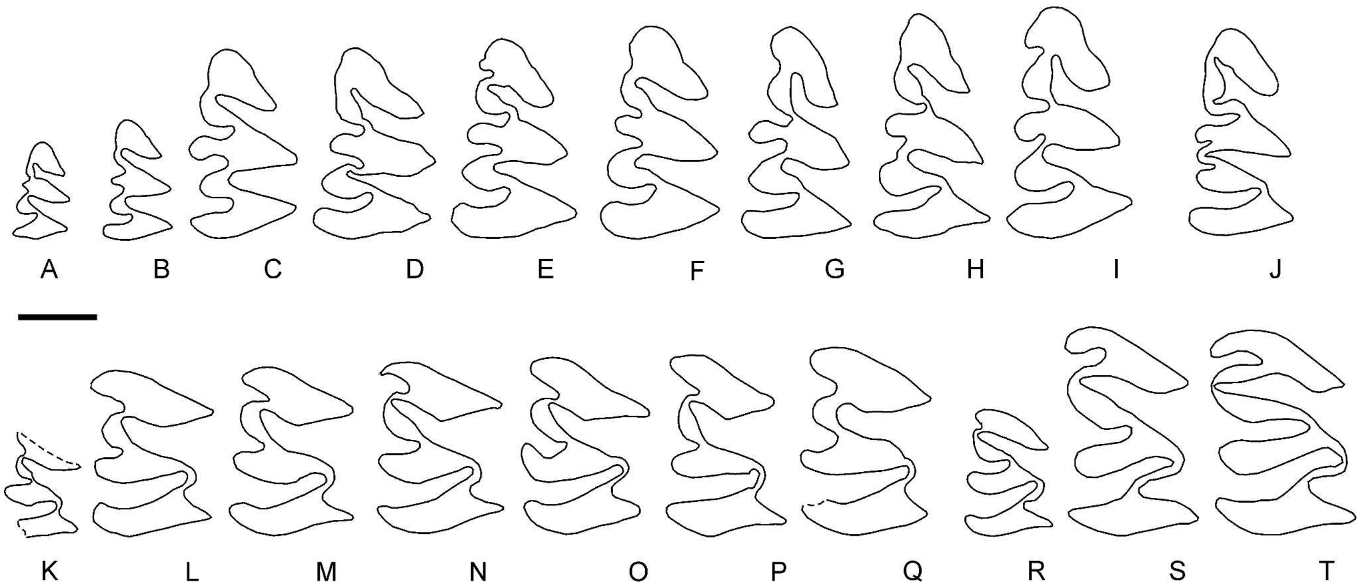


FIGURE 4. Right (or left, reversed) p4 (**A**–**J**) and m1/2 (**K**–**T**) of *Cardiatherium chasicoense* (**A**–**I**, **K**–**Q**), *C. orientalis* (**R**), *C. paranense* (**S**), and *C. patagonicum* (**J**, **T**). **A**, MMH-CH 83-3-60; **B**, MD-CH-06-235-1; **C**, MMP 300-M (holotype); **D**, MMH-CH 88-6-92e (reversed); **E**, MMH-CH 86-9-71b (reversed); **F**, MMH-CH 85-4-40; **G**, MMH-CH 86-9-118c (reversed); **H**, MMH-CH 88-6-71 (reversed); **I**, MLP 60-VI-18-37 (reversed, type of *Procardiatherium dubium*); **J**, MPEF 740/9 (reversed); **K**, MMH-CH 86-9-71c; **L**, MMP 300-M (m1, holotype); **M**, MMP 300-M (m2, holotype); **N**, MMH-CH 88-6-43; **O**, MLP 68-VIII-29-1 (reversed, m2); **P**, MMH-CH 85-4-40; **Q**, MMH-CH 87-7-104a (reversed); **R**, SPV-FHC-27-XI-64-20 (holotype of *Kiyutherium orientalis*); **S**, MLP 40-XI-15-1 (neotype); **T**, MPEF 740/24. Scale bar equals 5 mm.

Miocene of central Argentina recently has been proposed on the basis of an anagenetic sequence of octodontid rodents from the Vivero Member of the Arroyo Chasicó Formation and different localities of the Cerro Azul Formation, La Pampa Province (Verzi et al., 2004, in press; Montalvo et al., 2005). In this scheme, the oldest biozone is the *Chasichimys bonaerense* Zone from the Vivero Member, followed by the *Chasichimys scagliai* Zone in Laguna Chillhué (La Pampa), and, finally, the biozones of the Late Huayquerian based on the genus *Xenodontomys*. The Chasicoan capybaras were found in the upper levels of the Las Barrancas Member (= FSC facies) overlying the *Chasichimys bonaerense* Zone. *C. orientalis* was found in the *Chasichimys scagliai* Zone (Fig. 1D). In the upper biozones of the Huayquerian, no capybaras have been found.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOGNATHI Tullberg, 1899
Family HYDROCHOERIDAE Gill, 1872
Genus *CARDIATHERIUM* Ameghino, 1883

Emended Diagnosis—Hydrochoerids with prisms of cheek teeth undivided in adults; flexids variably developed according to ontogeny; M3 composed of 6–11 prisms.

Type Species—*Cardiatherium doeringi* Ameghino, 1883.

Included Species—*C. paranense* (including *C. doeringi*), *C. patagonicum*, *C. orientalis*, and *C. chasicoense* (see Table 1).

Age and Distribution—Late Miocene (Chasicoan and Huayquerian SALMAs) of Argentina, Brazil, Peru, Uruguay, Venezuela.

CARDIATHERIUM CHASICOENSE new combination
(Figs. 3–6, Table 2)

Procardiatherium chasicoense Pascual and Bondesio, 1968:238, pl. 1 (figs. A–J).

?*Cardiatherium dubium* Pascual and Bondesio, 1968:244, 247, 249–250, pl. 1 (fig. K).

Procardiatherium dubium (Pascual and Bondesio) Mones, 1984:5.

Procardiatherium sp. Bondesio, Laza, Scillato-Yané, Tonni, and Vucetich, 1980:110; Mones, 1991:25.

Holotype—MMP 300-M, fragment of right mandible with p4–m3 (Fig. 3A, C).

Revised Diagnosis—p4 with h.p.i up to 50% of total width (up to 70% in *C. patagonicum*, and 60% in *C. orientalis* and *C. paranense*); h.2i. and h.3i. nearly similar in depth (this character is rarely present in *C. paranense* and *C. patagonicum*); m1–2 with h.s.i. only up to 17% of the total width and h.t.i. up to 31% (up to 34% and 50%, respectively, in *C. paranense*, and 50% and 75% in *C. patagonicum*); anterior prism of m3 cordiform (heart-shaped); P4–M2 with H.P.E. less than 50% of the transverse diameter of anterior lobe, making the posterior lobe of Pr.I much smaller than the anterior one and than those of *C. patagonicum* (the most derived species of the genus); Pr.II somewhat labially and posteriorly projected, unlike in *C. patagonicum* in which it is anteroposteriorly thin; M3 with only six laminae (7–8 in *C. paranense* and *C. orientalis*, 10–11 in *C. patagonicum*).

Hypodigm—The holotype; MLP 60-VI-18-37, left p4 (holotype of ?*Cardiatherium dubium*); MMP 305a-M, right M1/M2; MMP 305b-M, left M1/M2; MMP 305c-M, right P4; MMP 306-M, fragment of right m3; MMP 306 bis-M, fragment of right m1/m2; MMP 307-M, right m3; MMP 308-M, right m1/m2; MMP 319-M, right M1/M2, and left incisor; MMP 574-M, fragment of right M3; MMP 583-M, right p4; MLP 55-IV-28-15, fragment of left m2, fragment of right mandible with partial m2 and complete m3; MLP 60-VI-18-39, right p4; MLP 55-IV-28-23, right P4?; MLP 60-VI-18-40, left M3; MLP 60-VI-18-45, fragment of left M3; MLP 68-VIII-29-1, fragment of left mandible with p4–m2. Additions to the hypodigm: MMP 979-M, left mandible with damaged p4–m2; MMH-CH 85-4-40, almost complete right mandible with i1, p4, m1, and m3; MMH-CH 88-6-71, pair of mandibles of a single individual with left i1–m2 and right m1; MMH-CH 86-9-71b, left p4.

Description

New materials from the Arroyo Chasicó Formation allow us to expand the original description of the species made by Pascual and Bondesio (1968).

Mandible—The mandible coincides mostly with the original description, but two new mandibles (MMH-CH 85-4-40, Fig. 3B, D; MMH-CH 88-6-71), more complete than the holotype, allow a better description of some characters. Pascual and Bondesio (1968) described the masseteric fossa of the holotype as wide and uniformly extended anteroposteriorly, lacking a clear separation between the anterior and posterior fossae, as in '*P. simplicidens*,' '*Eucardiodon marshii*,' and '*Anchimys leidyi*,' all of these now regarded as juvenile specimens of *C. paranense* (Vucetich et al., 2005). In the new mandibles (which are also larger than the holotype) the masseteric fossa is clearly divided into anterior and a posterior fossae. On the external surface, there is a triangular surface between both (Fig. 3B). This morphology of the masseteric area is also seen in large specimens of *Cardiatherium paranense*. Hence, the shape of the masseteric fossa of the holotype described by Pascual and Bondesio (1968) is a consequence of its juvenile condition (see Fig. 3A, C). The juvenile condition of the holotype can also be seen in the position of the posterior margin of the symphysis; it is positioned anterior of p4 in the holotype, but is below the midpoint of p4 in larger (adult) specimens such as MMH-CH 85-4-40 (Fig. 3C). In addition, the mandible projects superiorly anterior of p4 in the holotype, the anterior portion of the symphysis being much higher than the level of the occlusal surfaces of the cheek teeth (Fig. 3C); in adults, this portion of the mandible descends immediately in front of p4, and the anterior portion of the symphysis is level with the cheek teeth (Fig. 3D; see Vucetich et al., 2005).

Teeth—The size range of the available material is not as great as in *C. paranensis* and *C. patagonicum*, but four new small specimens, two right p4 (MMH-CH 83-3-60 and MD 06-235-1; Fig. 4A–B), one right m1/m2 (MMH-CH 86-9-71c; Fig. 4K), and one right M3 (MD-CH-06-107/1; Fig. 6N) allow a better understanding of ontogenetic change in cheek tooth morphology as well as better comparisons with other species of *Cardiatherium*.

The p4 (Fig. 4A–I) has three prisms, the pr.s.a. being the most variable. All the flexids are shallower than in the other species of the genus (Fig. 4A–I vs. 4J); h.p.i. penetrates up to 50% the total width in *C. chasicoense*, less than in *C. patagonicum* (70%) or *C. paranense* and *C. orientalis* (60%). The h.4i. is variably developed from deep to shallow or even absent, especially in small specimens (Fig. 4E–G). The h.3i. is similar in depth to the h.2i; consequently, c.3i. is at the middle of an almost symmetric Pr.I. The h.2e. can be transverse (especially in small specimens), oblique or directed straight forward (Fig. 4G). Rarely, a small h.sn.i. can be present (Fig. 4H).

The m1–2 (Fig. 4K–Q) are similar in shape. The h.s.i. and h.t.i. are very shallow as compared to *C. orientalis* (Fig. 4R), *C. paranensis* (Fig. 4S), and *C. patagonicum* (Fig. 4T). Both h.s.i. and h.t.i. display little variation with increasing AP (Fig. 8), unlike the other species in which these flexids increase markedly with size (Vucetich et al., 2005). Even in the largest specimens of *C. chasicoense*, the h.s.i. reaches only up to 17 %, and the h.t.i. 31% of the total width, whereas these values are 33% and 52% in *C. paranense*, 19% and 52% in *C. orientalis*, and 46% and 78% in *C. patagonicum*, respectively.

In m3 (Fig. 5A–F), pr.I is cordiform, similar to that of m1–2, and has a short h.s.i.; this contrasts with the condition in *C. orientalis* (Fig. 5G), *C. paranensis* (Fig. 5H–L) and *C. patagonicum* (Fig. 5M–N) in which pr.I of m3 is semilunar with an h.s.i. that deepens with size (= age). The h.t.i. extends only up to one third of the tooth width, maintaining the triangular shape of pr.IIa. The h.p.i. deepens with size, and in large specimens (Fig. 5D–F) it bifurcates.

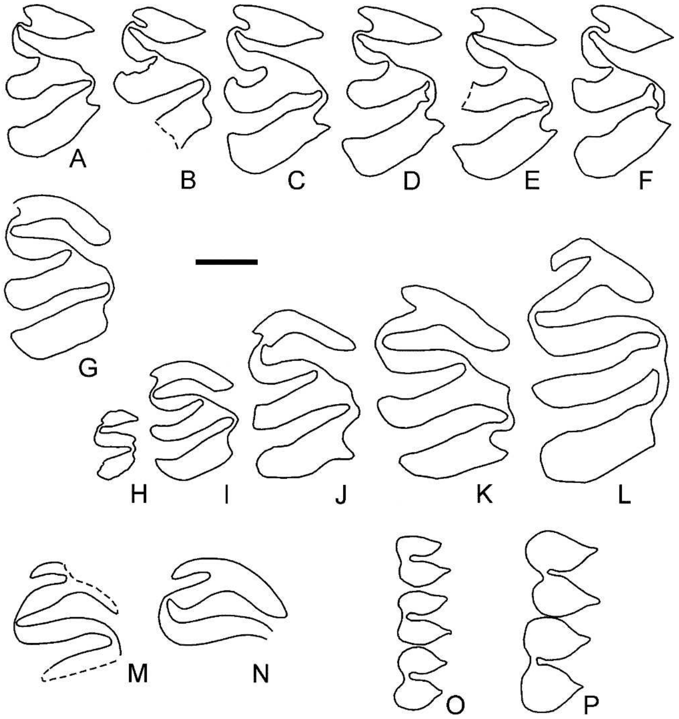


FIGURE 5. Right m3 (or left reversed) of *Cardiatherium chasicoense* (**A**–**F**), *C. orientalis* (**G**), *C. paranense* (**H**–**L**), and *C. patagonicum* (**M**, **N**); right m1–3 of *Eocardia* (**O**); and right m2–3 of *Dolichotis* (**P**). Anterior to toward the top of the page. **A**, MMH-CH 88-6-41; **B**, MMP 300-M (holotype); **C**, MMH-CH 85-4-40; **D**, MMH-CH 88-6-71 (reversed); **E**, MMH-CH 88-6-92b (reversed); **F**, MLP 55-IV-28-15; **G**, SPV-FHC-27-XI-64-20 (holotype of *Kiyutherium orientalis*); **H**, MLP 73-I-10-7; **I**, MLP 61-VI-8-1 (reversed); **J**, MLP 78-II-27-1; **K**, MLP 61-VI-8-2; **L**, MLP 40-XI-15-1 (neotype of *C. paranense*); **M**, MPEF 740/20; **N**, MPEF 740/7; **O**, MLP 15-217; **P**, MLP 247. Scale bar equals 5 mm.

In P4 (Fig. 6A–D) the H.P.E. penetrates up to 38% the total width, whereas in *C. orientalis* (Fig. 6E) it is up to 55%, and *C. patagonicum* (Fig. 6F) it is about 60%. In addition, this flexus extends backward, dividing the Pr.I into a large anterior portion and a very small posterior one, rather like a neck that joins Pr.II. In *C. patagonicum* the H.P.E. is transverse to the AP axis, and thus the posterior part is proportionally larger than in *C. chasicoense*; in *C. orientalis* it is intermediate (Fig. 6E–F). Pr.II is anteroposteriorly thicker in *C. chasicoense* than in *C. patagonicum* (Fig. 6A–D, F) and the portion behind the H.S.E. is somewhat labially and posteriorly projected as in *C. orientalis* (Fig. 6E) but shallower. In *C. patagonicum* H.S.E. is even deeper and Pr.II is very curved, almost semilunar.

In M1 and M2 (Fig. 6G–L) both prisms are anteroposteriorly narrower than in P4, and in Pr.II the labial and posterior margins extend less than in P4. Both H.P.E. and H.S.E. are as in P4. *C. patagonicum* has deeper H.S.E. and H.P.E. and Pr.II is narrow and semilunar, as in P4. The upper M1 and M2 of *C. paranense* and *C. orientalis* are still under study.

M3 (Fig. 6N–O) has six laminae, the first one with H.P.E. and the last one short; *C. orientalis* has 7–8 laminae, and *C. patagonicum* has ten (Fig. 6P). The M3 referred to *C. paranense* has been lost (see Mones, 1991:27). The flexi deepen with age but even in large specimens (Fig. 6O) they are not as deep as in *C. patagonicum* (Fig. 6P). Each lamina is cordiform and anteroposteriorly thicker than in the other species of the genus.

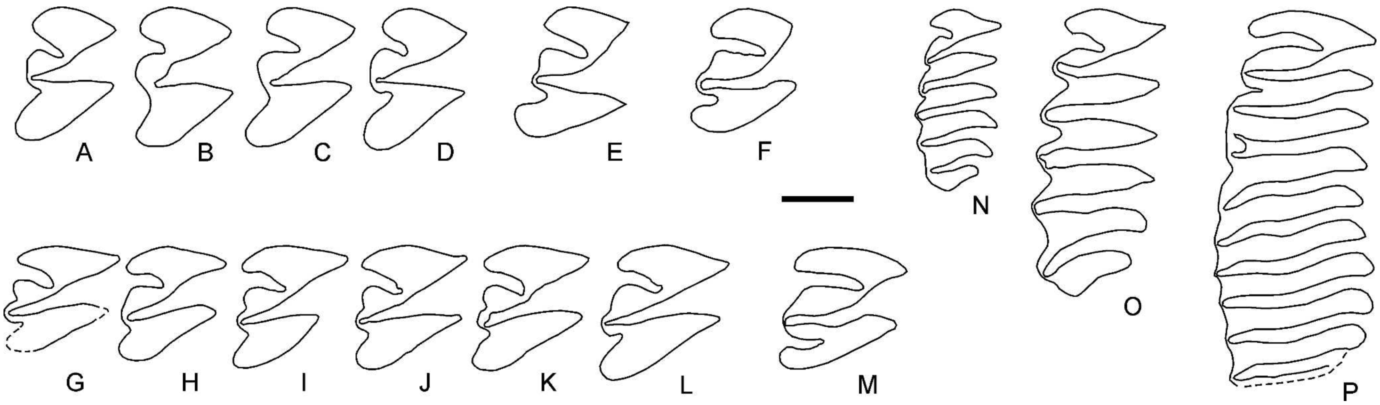
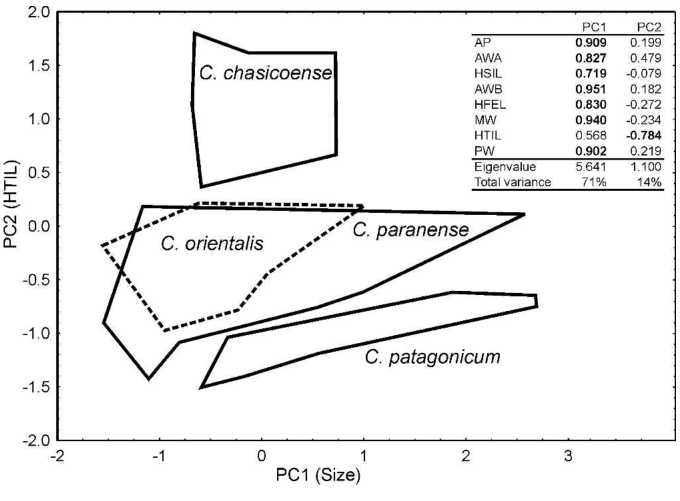


FIGURE 6. Occlusal view of right (or left reversed) P4 (**A**–**F**), M1/M2 (**G**–**M**), and M3 (**N**–**P**) of *Cardiatherium chasicoense* (**A**–**D**, **G**–**L**, **N**–**O**), *C. orientalis* (**E**), and *C. patagonicum* (**F**, **M**, **P**). **A**, MMH-CH 88-6-92f; **B**, MMH-CH 88-6-39; **C**, MMH-CH 87-7-49 (reversed); **D**, MMH-CH 86-9-71f (reversed); **E**, GHUNLPam 14452 (reversed); **F**, MPEF 740/22 (reversed); **G**, MLP 71-II-26-1; **H**, MMH-CH 87-7-104b; **I**, MMP 319; **J**, MMH-CH 88-6-92a; **K**, MLP 76-VI-12-98c (reversed); **L**, MMP 305a; **M**, MPEF 740/23; **N**, MD-CH-06-107/1; **O**, MMP 979-M (reversed); **P**, MPEF 740/18. Scale bar equals 5 mm.

Quantitative Analysis

Multivariate Analysis—A principal components analysis (PCA) of eight linear measurements of m1/m2 of *C. patagonicum*, *C. paranense*, *C. orientalis* and *C. chasicoense* was performed for the size range in which variables increase linearly (Fig. 7). The first principal component (PC) axis reflects mainly size because variables had high positive loadings (Fig. 7, Table 2; Lessa and Stein, 1992). In PC2, h.t.i. length (HTIL), loads highest, clearly discriminating *C. chasicoense* and *C. patagonicum* from *C. orientalis* and *C. paranense*. This distribution along PC2 matches a chronological distribution of the species from oldest (positive scores) to youngest (negative scores).

Regression Analysis—Bearing in mind the proposal of Vucetich et al. (2005), we compared the scaling of HTIL and HSIL vs. AP. In *C. chasicoense* these variables did not meet the assumptions of the regression analysis (e.g. homoscedasticity) because the sample is biased toward large size (Table 2). Consequently, we plotted the raw data and obtained a trendline through least-squares. We compared the results with the regression lines of the other species of the genus (Fig. 8).



	PC1	PC2
AP	**0.909**	0.199
AWA	**0.827**	0.479
HSIL	**0.719**	-0.079
AWB	**0.951**	0.182
HFEL	**0.830**	-0.272
MW	**0.940**	-0.234
HTIL	0.568	**-0.784**
PW	**0.902**	0.219
Eigenvalue	5.641	1.100
Total variance	71%	14%

FIGURE 7. Plot of scores and factor loadings of PC1 and PC2 of m1/m2 linear measurements. Polygons represent the ranges of variation of species analyzed. Loadings > 0.7 are in bold. Abbreviations as in Fig. 2.

The HTIL of *C. chasicoense* seems to behave differently from the other species with respect to increasing size. In the smallest specimen, HTIL shows values similar to those of the other species at similar size, but in the rest, HTIL is comparatively shorter than in the other species. Thus in *C. chasicoense*, h.t.i shows little change with increasing size, at least within the range of the available sample. Likewise, HSIL shows little change with increasing size, but values are within the range of those of *C. paranense*, *C. orientalis* and *C. patagonicum* of similar size (Fig. 8).

DISCUSSION

Our studies show that all the hydrochoerids found in the Arroyo Chasicó Formation belong to a single species. '?*C. dubium*' was based on a single specimen, and the characters used to distinguish it from '*P.*' *chasicoense* (h.4i., h.2e. directed straight forward) are, in fact, also present, but differently combined, within the new sample (see Description). The original sample of '*P.*' *chasicoense* was too small (five specimens including the holotype of ?*C. dubium*; Pascual and Bondesio, 1968) to notice the p4 variability. On the other hand, and in the present state of the knowledge, this species cannot be separated at the genus level from younger species of Huayquerian Age (uppermost Miocene). Some characters used to define the genus *Procardiatherium* (e.g., h.3i. similar in depth to h.2i. of p4, and consequently, c.3i. at the middle of an almost symmetric Pr.I.; see Ameghino, 1885) are, in fact, observed in young specimens of *Cardiatherium paranense* and in some specimens of *C. patagonicum* (Vucetich et al., 2005; fig. 5D, G). In the case of the holotype of *Procardiatherium chasicoense*, the shape and depth of the masseteric fossa reflect only differences in ontogenetic stage (it is shallow in juveniles and deep in adults) rather than different character states. This is supported by other juvenile characters (Vucetich et al., 2005) such as the relatively anterior position of the posterior part of the symphysis with respect to p4 (Fig. 3A, B), and the upward projection of the mandibular diastema (Fig. 3C, D). Although *C. chasicoense* displays some characters that differ from other late Miocene species (cordiform lobes, shallower flexi/ids, cordiform Pr.I of m3, fewer prisms in M3) it is more parsimonious to consider it a primitive species of the same genus (see below) than generically distinct. In addition, the cheek tooth morphology differs more dramatically between late Miocene and Pliocene-Recent species (extreme depth of flexi/ids dividing lobes, and multiplication of laminae of the M3) than between *C. chasicoense* and other species of *Cardiatherium*. The

TABLE 2. Dental measurements of *Cardiatherium chasicoense*, new. comb.

Cardiatherium chasicoense	p4							
	AP	AWa	HSIL	AWb	HFEL	MW	HTIL	PW
MMH-CH 83-3-60	6.42	2.30	0.03	2.40	2.50	3.20		3.80
MD 06-235-1 7.04	7.04	2.60	0.05	2.70	2.80	3.60		4.08
MMP 300-M Type	11.04	3.84	2.72	4.16	4.64	6.24		6.08
MMH-CH 88-6-92c	11.20	4.64	0.80	4.72	3.20	6.08		6.24
MLP 68-VIII-29-1	11.36							
MLP 60-VI-18-39	11.52							
MMH-CH 88-6-92e	11.84	5.12	0.048	5.20	4.32	6.24		7.20
MMH-CH 86-9-71b	12.16	4.80	1.12	4.96	4.16	6.40		7.68
MMH-CH 88-6-45	12.16	4.64	0.24	4.80	4.00	6.24		6.56
MMH-CH 85-4-40	12.16	4.80	0.32	4.96	4.16	6.08		6.88
MLP 60-VI-18-38b	12.32	4.16	0.48	5.28	4.00	6.24		7.20
MMH-CH 86-0-118c	12.64	3.84	0.64	4.00	4.16	5.92		6.56
MLP 60-VI-18-38a	12.96	4.96	0.32	5.28	4.48	6.40		6.40
MMH-CH 88-6-71	13.44	4.32	16.80	4.48	3.52	5.92		6.96
MLP 76-VI-12-98a		4.64		4.32	3.84	5.76		6.56
MLP 76-VI-12-98b	13.60	4.64	0.64	4.96	3.52	5.60		7.20
MLP 60-VI-18-37	13.76	4.80	1.44	5.28	3.36	6.88		7.36
	m1 or m2							
MMH-CH 86-9-71c	6.08	3.44	0.64	3.44	2.96	3.36	1.60	
MMP 300-M m1 Type	9.60	7.20	1.28	6.40	4.00	5.60	1.60	6.72
MMP 300-M m2 Type	9.60	6.72	1.60	6.40	4.32	5.76	1.76	6.88
MMP 308-M	9.92	6.72	0.72	6.24	5.28	5.60	1.28	7.04
MMH-CH 88-6-71 m1	10.24	7.04	1.36	6.56	6.08	5.60	2.08	7.36
MMH-CH 88-6-43	10.40	7.52	1.60	7.36	6.72	6.24	2.56	7.60
MMH-CH 88-6-92d	10.40		1.12			5.92	1.84	7.52
MMH-CH 87-7-104a	11.52	7.68	1.28	7.36	6.08	6.80	1.84	7.52
MMH-CH 88-6-71 m2	10.56	7.20	1.44	6.56	5.60	5.60	1.60	7.04
MMH-CH 88-6-40	10.56	7.52	0.96	6.56	5.60	5.76	2.08	7.20
MMH-CH 88-6-92g	10.72	7.52	1.12	7.36	6.88	6.40	2.56	7.84
MLP 68-VIII-29-1 m1	10.72	6.72	0.96	6.40	3.84	5.60	2.24	6.56
MLP 68-VIII-29-1 m2	10.72	6.56	1.12	6.40	4.32	5.28	2.88	6.40
MMH-CH 85-4-67	10.88	7.36	0.64	6.88	5.76	6.24	1.92	7.60
MMH-CH 85-4-40	10.88	7.68	1.52	7.20	6.24	6.56	2.72	7.52
MMH-CH 87-7-68		7.36	1.44	7.36	7.04	6.24	2.40	
MMP 306 b-M						5.92	1.60	
	m3							
MMP 300-M Type		6.24	2.24	7.04	6.08	8.00	3.84	
MMH-CH 85-4-40	14.08	7.52	1.92	8.16	7.36	8.64	3.68	8.96
MMH-CH 88-6-41	14.08	6.08	1.92	7.52	6.72	8.32	3.52	8.96
MMH-CH 88-6-71	14.88	7.04	1.76	7.36	6.88	8.00	3.68	9.44
MLP 55-IV-28-15	14.88	7.68	2.08	8.00	7.20	8.48	3.52	8.80
MMH-CH 88-6-92b	15.52	7.68	1.44	8.32	7.68	8.48	4.32	9.44
MMP 285-M		7.04	1.44	7.68			4.00	
MMP 307-M			1.28	7.52	7.04	8.00	3.20	8.32
MMP 306-M						8.48	3.48	9.12

	P4				
	AP	AW	HPEL	HSEL	PW
MMP 319-M	8.00	7.20	2.72	1.44	7.68
MMP 305 c-M	8.64	7.20	2.40	1.12	7.52
	M1 or 2				
MMP 319-M	8.16	7.68	2.88	1.60	8.32
MMP 305 b-M	8.48	6.72	2.72	1.28	7.68
MMP 305 a-M	9.28	7.20	3.04	1.44	8.00
	M3				
MD-CH-06-107/1	12.75	5.10			
MLP 60-VI-18-40	19.36	8.00			
MLP 71-II-26-1	19.20	7.20			
MMP 979-M	20.16	7.36			

discovery of additional specimens, especially skull and/or postcranianal remains, will permit testing this proposal against new evidence.

Considering the general tendency in cheek teeth development of euhypsodont cavioids from simple and bilobed (lower Miocene *Eocardia* and the living *Dolichotis*; Fig. 5O, P) to multilaminar (*Hydrochoerus*), the morphology present in *C. chasicoense* turns out to be more primitive than that of *C. paranense*, *C. orientalis* and *C. patagonicum*. All the flexi/ids of *C. chasicoense* are shallower than those of the other species of the genus. The h.t.i. is especially enlightening in this sense. This flexid, a novelty for the Superfamily Cavioidea (Vucetich et al., 2005), is the one that grows most in the remaining species of the genus. In the contrary, it stops growing or at least slows its growth in *C.*

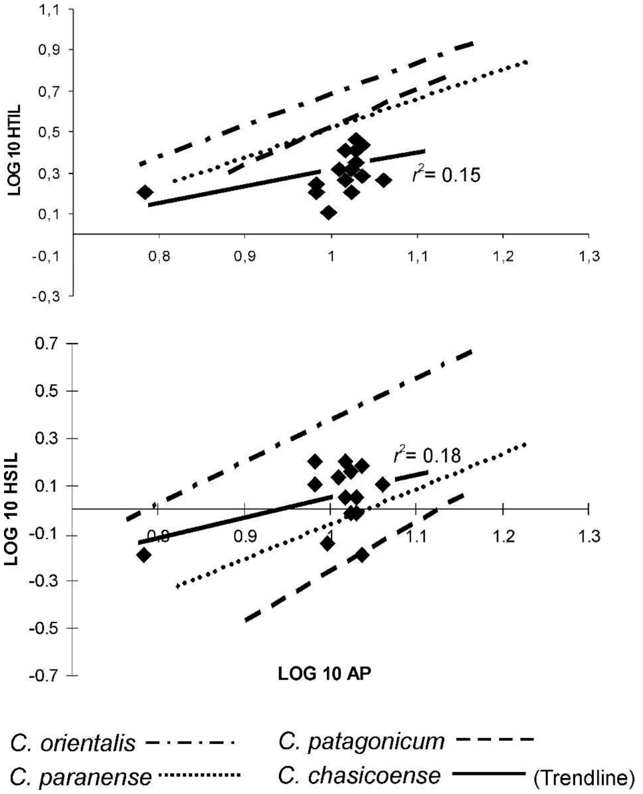


FIGURE 8. Model II regressions (of log-transformed data) of tertiary internal flexid length (HTIL; above) and secondary internal flexid length (HSIL; below) on antero-posterior length (AP) for Huayquerian hydrochoerids (modified from Vucetich et al., 2005). Raw data (diamonds) for *Cardiatherium chasicoense* are included.

chasicoense. Such a growth pattern is expected based on our model of ontogenetic change for a species older than those previously analyzed. The primitive condition of the cheek teeth of *C. chasicoense* is also seen in the shape of the anterior prism of m3. This prism is similar to those of m1–2 (Fig. 5A–F vs. Fig. 4L–Q; see also Fig. 3A, B), equivalent to the condition seen in *Eocardia* and *Dolichotis* (Fig. 5O, P). Whereas in the other species of the genus this prism is semilunar (Fig. 5G–N vs. Fig. 4R–T), different from that of m1–2.

Modern capybaras inhabit areas around ponds, lakes, rivers, marshes and swamps, using water primarily as refuge (Nowak and Paradiso, 1983). The geographic distribution of late Miocene capybaras is scattered, restricted to certain localities. All the lithological fossil bearing units have been interpreted as deposited in water-related settings. The unit that produces *C. chasicoense* is a swampy environment (Zárate et al., in press). Similarly, *C. orientalis* from Laguna Chillhué (La Pampa Province) is found in lacustrine levels of the Cerro Azul Formation (Montalvo et al., 2005). The 'conglomerado osífero' at the base of the Ituzaingó Formation (Entre Ríos Province) in which *C. paranense* is found is a discontinuous fluvial deposit formed by sands and conglomerates that filled the previously irregular topography of the Paraná Formation (Herbst, 2000). *C. patagonicum* is found in levels deposited in a freshwater channel, not far from the sea (Cione et al., 2005:36). All these environments would have been quite propitious for capybaras. This fact may explain their absence from other rich fossil-bearing sites of this age of La Pampa and southwest Buenos Aires provinces; these depositional environments are mostly eolian, probably unsuitable for capybaras.

The revision of the family with our new approach (Vucetich et al., 2005) sheds light on the supposed high diversity of capybaras; instead of demonstrating the high specific diversity suggested by typological criteria used in the classical systematics, we interpret capybaras as exhibiting high morphological and ontogenetic intraspecific diversity. This results in the recognition of only one species at each locality and thus low local taxonomic diversity. (analyses in progress suggest this is also valid for the 'conglomerado osífero'; see Vucetich et al., 2005). According to our proposal, the species of *Cardiatherium* probably represent different evolutionary stages from the most primitive—*C. chasicoense*—to the most derived—*C. patagonicum*—with *C. paranense* and *C. orientalis* being intermediate; this trend continues in the Pliocene with another genus (i.e., *Phugatherium* = *Chapalmatherium*; Vucetich et al., 2005). The relationships among these taxa have yet to be analyzed within the context of the whole family, however. Although there is not a single stratigraphic sequence with different levels to test this, it is now recognized that species do not occur together in the same levels (or locality). The species within the new systematic framework may turn out quite useful for biocorrelation, especially in some late Miocene localities of Argentina, which are far from being completely understood from a biostratigraphic point of view. In this sense, the capybaras suggest that the Las Barrancas Member of the Arroyo Chasicó Formation is older than the sediments of the Cerro Azul Formation cropping out at Laguna Chillhué, which, according to the record of octodontoid rodents, could be considered coeval (see Verzi, 1999; Fig. 1D).

We consider that our proposal of tooth growth pattern (Vucetich et al., 2005) provides a useful basic framework to study Chasicoan and Huayquerian capybaras. Both the related cardiomyines of the late Miocene—their putative sister group (Vucetich et al., 2005)—and their Pliocene descendants will be studied within this framework in order to understand the systematics and the evolutionary patterns of the whole group.

ACKNOWLEDGMENTS

We thank Dr. D. Verzi for fruitful comments; V. Di Martino (director of the MMH), A. Dondas (MMP), M. Reguero (MLP), and T. Manera (MD) for access to material under their care. C. Montalvo and J. Urrutia kindly lent us unpublished materials. UNLP 11/N442 and CONICET PIP 5242 grants supported this research. Two anonymous reviewers provided thorough comments for improvements to the manuscript.

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Submitted December 18, 2006; accepted February 15, 2007.