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ORIGINAL ARTICLE

The Tropics as Reservoir of Otherwise Extinct Mammals: The Case of Rodents from a New Pliocene Faunal Assemblage from Northern Venezuela

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Abstract We report a new vertebrate assemblage from the Pliocene Vergel Member of the San Gregorio Formation in northwestern Venezuela, which includes Crocodylia and Testudines indet., toxodonts, at least four species of xenarthrans of the Dasypodidae, Pamphathiidae, Glyptodontidae and Megatheriidae, and rodents. The last are *Cardiatherium*, cf. *Caviodon* (Hydrochoeridae), *Neoepiblema* (Neoepiblemidae), and what is here described as a new genus of a low-crowned octodontoid. cf. *Caviodon* is the first cardiomyine for northern South America. The rodent assemblage resembles in its ecological composition those of the late Miocene (Huayquerian) from the “Mesopotamian” of Argentina and the Acre region in Brazil, with partially overlapping systematic composition. The stratigraphic position of the San Gregorio Formation and mammals other than caviomorphs suggest a late Pliocene age for these sediments, implying the endurance of rodent taxa beyond their biochron in southern South America.

Keywords Rodentia · Phylogeny · Caviomorpha · Biogeography · Systematics

Introduction

Cenozoic fossil land mammals have an excellent record in the austral part of the South American continent (southern South America, SSA; Pascual et al. 1996; Ortiz-Jaureguizar and Cladera 2006). It was upon this record that South American biochronology and the concept of South American Land Mammal Ages was based. In the last 10 years, biostratigraphy and biochronology of Argentina, in particular, have been greatly improved (Madden et al. 2010) providing a good framework to trace the evolutionary history of mammals (Ortiz-Jaureguizar and Cladera 2006). Several of these improvements have been made upon detailed studies of rodent anatomy and evolution (Vucetich et al. 2005a; Kramarz and Bellosi 2005; Verzi et al. 2008). However, it is evident that the biochronology and main mammalian evolutionary pathways proposed for SSA are not necessarily valid for the entire continent (Pascual et al. 1996; Ortiz-Jaureguizar and Cladera 2006).

The land mammal fossil record of intertropical South America (ISA) is meager and does not reflect the biotic richness that dazzled XIX century explorers such as A. v. Humboldt, C. Darwin, and A. Wallace. The few rich Neogene faunas in ISA (e.g., the middle Miocene of La Venta in Colombia and those of late Miocene in the Acre region; see Kay et al. 1997; Cozzuol 2006; MacFadden 2006) only give a glimpse of this hypothesized past splendor. However, indirect evidence from the SSA fossil record suggests that intertropical mammal diversity was richer than so far recorded (Vucetich and Verzi 2002; Vucetich et al. 2005b). Thus, any new fossil record from

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ISA, and particularly from the northernmost ISA, would provide important evidence to test this hypothesis as well as others about evolutionary trends out of the southern cone.

Here we describe the caviomorph rodents from a new vertebrate assemblage collected in northern Venezuela (Fig. 1), in the San Gregorio Formation referred to the late Cenozoic, and assess their importance in our understanding of South American mammal history.

Institutional abbreviations

FCS, Facultad de Ciencias Sociales, Universidad Nacional del Centro, Buenos Aires, Argentina; MACN, Museo Argentino de Ciencias Naturales “B. Rivadavia”, Buenos Aires, Argentina; MLP, Museo de La Plata, Universidad Nacional de La Plata, Argentina. MMP, Museo Municipal de Ciencias Naturales, Mar del Plata, Buenos Aires, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; SPV-FHC, Sección Paleontología Vertebrados, Departamento de Paleontología, Facultad de Humanidades y Ciencias, Montevideo, Uruguay; UNEFM, Universidad Nacional Experimental Francisco de Miranda, Vertebrate Paleontology Collection, Coro, Venezuela.

Dental abbreviations

Tooth nomenclature for Hydrochoeridae (Fig. 2) follows Vucetich et al. (2005a), and abbreviations refer to the Spanish names in order to conform to previous publications on this clade (e.g., Frailey 1986). Abbreviations. H.P.E., primary external flexus; H.S.E., secondary external flexus; h.t.i., tertiary internal flexid; h.p.i., primary internal flexid; h.s.e., secondary external flexid

Geological setting

The fossil material was collected from localities in Falcón State in northwestern Venezuela (Fig. 1). This savanna-like region contains the Neogene Urumaco trench, which has yielded a high vertebrate diversity (Sánchez-Villagra and Aguilera 2006; Johnson et al. 2009). The paleoenvironment based on palynofloras from the Urumaco Formation suggests a continuum of the Amazonian forest into northwestern Venezuela during the Miocene (Jaramillo et al. 2010). The Urumaco fauna includes marginal marine, freshwater, and continental vertebrates (Sánchez-Villagra and Aguilera 2006; Aguilera et al. 2010). The latest Miocene-early Pliocene Codore Formation flora replaced the Amazonian palynoflora with xerophyte vegetation; this happened during the major environmental change related to the collapse of the Urumaco delta during the late Miocene, which is correlated with a major uplift of the northern

Andes and the eastward changing hydrographic course of a paleo-Orinoco River (Díaz de Gamero 1996; Quiróz and Jaramillo 2010). From the Codore Formation only few faunal specimens from the El Jebe Member, such as, glyptodontid xenarthrans (Carlini et al. 2008) and grassy wetlands birds Ciconiidae (Walsh and Sánchez 2008), have been recovered. This underlines the Vergel Member of the San Gregorio Formation, representing sedimentary accumulation in alluvial fans (Quiróz and Jaramillo 2010), in which the aquatic paleoenvironment in a tropical wetland with meandering channels and inundate savanna, form the characteristic paleosoil where the specimens were collected (Fig. 3). Vergel is the lowest member of three of the San Gregorio Formation, and it is composed of approximately 85% limestones, 5% sandstones, and 10% conglomerates, encompassing 350 m at the type section (Ministerio de Energía y Minas 1997). Until recently, the only paleontological study of this formation had dealt with molluscs, crustaceans, and foraminiferans from the overlying marine Cocuiza Member (Hambalek et al. 1994; Aguilera et al. 2010; Mihaljević et al. in press), the middle portion of the formation, a 80 m thick section characterized by the presence of numerous conspicuous fossil beds separated by siltstones. The age of the San Gregorio Formation is estimated to be of late Pliocene to early Pleistocene age based on stratigraphical position as well as the limited palynological information (Hambalek et al. 1994; Ministerio de Energía y Minas 1997).

The vertebrate fauna from the San Gregorio Formation (Table 1) is restricted until now to the Vergel Member and is currently under study. It includes Crocodylia and Testudines indet. and among mammals besides rodents, there are toxodonts and at least four species of xenarthrans (Dasypodidae, Pamphathiidae, Glyptodontidae, and Megatheriidae). Among the glyptodontids from this formation are osteoderms of a species aff. *Boreostemma codorensis* as well as remains of Pamphathiidae aff. *Holmesina floridanus*, the latter a species from the Blancan (Pliocene) of North America. The specimens here described are deposited at the UNEFM and were discovered, all in the same stratigraphic layer, in a diameter of about 50 meters around the coordinates N 11° 17' 52.9"; W 70° 14' 08.7".

Systematic paleontology

Rodentia Bowdich, 1821

Hystricognathi Tullberg, 1899

Cavioidea Fischer de Waldheim, 1817

Hydrochoeridae Gill, 1872

Cardiatherium Ameghino, 1883

Cardiatherium sp.



Fig. 1 Map of South America indicating localities mentioned in the text.

Material: UNEFM-VF-50, posterior fragment of right m1 or m2; UNEFM-VF-51, right M1 or M2. UNEFM-VF-52 two very fragmentary dental remains.

Description and comparisons: These teeth are referred to *Cardiatherium* because the laminae are joined to each other by the lingual side in the lower tooth and the labial in the upper, even in the largest specimen (Fig. 2a–d, f, g; Vucetich et al. 2005a; Deschamps et al. 2007). In the species of *Cardiatherium*, the laminae are joined to each other through life. Contrarily, in the other genera of the family, as in the early to middle Pliocene *Phugatherium*, laminae are separated already in young individuals (Fig. 2e; unpublished data).

The lower molar (UNEFM-VF-50, Fig. 2a) is probably a juvenile as its base is visibly larger than the apex (Table 2; see Vucetich et al. 2005a). Taking this into account, the h.s.e. (Fig. 2a) is proportionally deeper (about 25% of the transversal length of the lamina) than in the other species of the genus (Fig. 2b–d) at the same size (= ontogenetic stage; see Vucetich et al. 2005a), and the h.p.i. is also comparatively deep (Vucetich et al. 2005a; Deschamps et al. 2007).

The upper molar (UNEFM-VF-51, Fig. 2f) is larger than the lower and probably represents an adult. The anterior face is straight and the posterior lobe is notably shorter than the anterior one. The H.P.E. (Fig. 2f) penetrates up to half the width of the lobe. The H.S.E. is posteriorly directed and penetrates up to one-third of the

width of the lobe, more than in the other species (compare Fig. 2f, g) with the exception of *Cardiatherium patagonicum* (Fig. 2h).

Comments: In their scheme of the evolutionary history of the capybaras, Vucetich et al. (2005a) and Deschamps et al. (2007, 2009) consider that this group has never been really diverse. Moreover, these authors have proposed the existence of only one species for each locality and level. The high diversity reported in the fossil record of this group, both in morphology and size, is not related to a high taxonomic diversity but instead to a high degree of ontogenetic change (Vucetich et al. 2005a). Following this scheme, we consider that all the material from the San Gregorio Formation probably pertains to only one species. Although the material is too scanty and fragmentary for a more accurate species assignment, some of the characters (relative depth of the fissures in the lower molar and difference in size between lobes, and relative depth and direction of the fissures of the upper molar) suggest this species is different from, and maybe somewhat more derived (especially the relative depth of fissures) than, those recognized for the late Miocene of southern South America (Vucetich et al. 2005a; Deschamps et al. 2007).

Capybaras have been recently classified as Caviidae taking into account neontological data (Woods and Kilpatrick 2005). However, work in progress based on paleontological evidence (Pérez 2010) strongly suggests

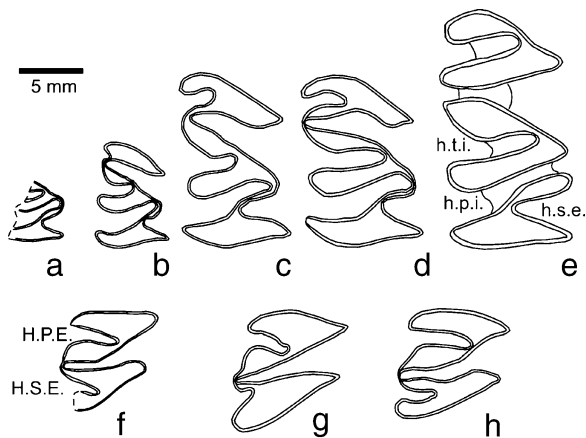


Fig. 2 Cheek teeth of selected Hydrochoeridae. **a**, *Cardiatherium* sp., UNEFM-VF-50 (posterior fragment of right m1 or m2); **b**, *Cardiatherium orientalis*, SPV-FHC-27-XI-60-20 (m1); **c**, *Cardiatherium paranense*, MLP 40-XI-15-1 (m1); **d**, *Cardiatherium patagonicum*, MPEF 740/24 (m1 or 2); **e**, *Phugatherium novum*, FCS-92-V-15/3 (m1); **f**, *Cardiatherium* sp., UNEFM-VF-51 (right M1 or M2); **g**, *Cardiatherium chasicoense*, MMP 305a (M1 or M2); **h**, *Cardiatherium patagonicum*, MPEF 740/23 (M1 or M2). Abbreviations. H.P.E., primary external flexus; H.S.E., secondary external flexus; h.t.i., tertiary internal flexid; h.p.i., primary internal flexid; h.s.e., secondary external flexid.

that the Caviioidea *sensu stricto* (i.e., cavioids with heart-shaped cheek teeth; Patterson and Wood 1982) are in need of systematic revision, and that capybaras belong to a different clade than caviids (both caviines and dolichotines). Because of this, we prefer to refer to the classical clade Hydrochoeridae for the capybaras.

Caviodon Ameghino, 1885
cf. *Caviodon*

Material: UNEFM-VF-53, left M1 or M2 (Fig. 4a).

Description and comparisons: This is a very small (Table 2) bilobed tooth; each lobe is heart shaped with a

fissure on the labial side. The fissures are equal in depth, reaching approximately 25% of the lobes' width. The fissure of the anterior lobe is narrow, whereas that of the posterior one is wide and triangular in shape. The posterolabial angle of the tooth projects far laterally. The anterior face of the anterior lobe is slightly convex but the posterior face is straight. The anterior face of the posterior lobe is straight, but the posterior face is slightly sinuous. It is not possible to establish with this single tooth if it corresponds to an adult individual of a small species or a young individual of a large one, as the ontogeny of cardiomyines is almost unknown. The characters described above are similar to those of *Caviodon australis* from the Montehermosan (early Pliocene) in that both fissures penetrate about 25% of the lobes length (Rovereto 1914; Fig. 4b), but in *C. australis* lobes are more triangular. *Caviodon pozzi* from the Chapadmalalan has much more penetrating fissures (Kraglievich 1927). The San Gregorio specimen (UNEFM-VF-53) shares with *Xenocardia* (Chasicoan?; Fig. 4c) delicate lobes and the 25% penetrating fissures. *Cardiomys* (Chasicoan—Huayquerian; Fig 4d, e) has wider lobes and less penetrating fissures. *Procardiomys* Pascual, 1961, has a different structure.

Comments: Cardiomyines have been usually considered caviids, but Vucetich and Deschamps (2010) considered them hydrochoeriids. Several genera have been described for the cardiomyines: *Caviodon*, *Xenocardia*, *Cardiomys* (Fig. 4b–e), and *Procardiomys* (the small *Parodimys*, probably represents a juvenile of some of the other genera). However, it must be taken into account that cardiomyine taxonomy needs revision. New criteria based on ontogenetic morphological change used to revise different cavioids have produced surprising results that lead to a drastic reduction of diversity and a better definition of the different genera and species (Vucetich et al. 2005a; Deschamps et al. 2007; Pérez et al. 2010).



Fig. 3 Paleosols containing the rodent fossil teeth described in this work. Urumaco region, San Gregorio Formation. Detail shows toxodont tooth in situ and the strong diagenesis in a fossil long bone.

Table 1 Mammals from the San Gregorio Formation

- Pampatheriidae aff. *Holmesina floridanus*.
- Glyptodontidae: Glyptodontidae indet.; aff. *Boreostemma codorensis*
- Megatheriidae indet.
- Toxodontia indet.
- Hydrochoeridae: *Cardiatherium* sp.; cf. *Caviodon*
- Neopiblemidae: *Neopiblema* sp.
- Octodontoidea?: *Marisela gregoriana* gen. et sp. nov.

The tooth here described is the first cardiomyine for northern South America. Frailey (1986) mentioned two cardiomyine taxa for the late Miocene of the Rio Acre region fauna based upon two isolated teeth, but none of them is a cardiomyine. Genus and species indeterminate A of Frailey (1986), although a caviid, does not have a fissure in each lobe characteristic of this subfamily but only one opposed to the hypoflexus, while Genus and species indeterminate B of Frailey (1986) is not a caviid, but probably a neopiblemide (see Frailey 1986: figs. 13.A and 13.B, respectively).

Chinchilloidea Kraglievich, 1940
 Neopiblemidae Kraglievich, 1926
Neopiblema (Ameghino, 1886)
Neopiblema sp.

Material: UNEFM-VF-54, fragment of cheek teeth heavily eroded.

Description and comparisons: This tooth fragment displays three laminae separated by a layer of cement as thick as the lamina (Fig. 5a, b). This character is diagnostic for Neopiblemidae. It has at least a fourth lamina, because there is cement behind the last enamel layer indicating it could be a p4 or M3. This tooth is

within the size of *Neopiblema horridula*, a relatively small neopiblemid.

Comments: We refer this tooth to *Neopiblema* because its size is similar to the species of this genus. Neopiblemidae *sensu stricto* have been recorded for the late Miocene. Two genera are known for this period: *Neopiblema* (= *Euphyllus*) including medium sized individuals, and *Phoberomys* (= *Dabbenea*) including gigantic individuals, and several species have been described for each genus (see Sánchez-Villagra et al. 2003 and Candela 2005 for phylogenetic and systematic discussions). *Perimys*, a putative early—middle Miocene neopiblemid, has been mentioned for the “Mesopotamiense” but its actual presence is uncertain (Candela 2005).

It has been pointed out that the teeth in euhypsodont rodents (and also other mammals) keep growing in all dimensions during the animal’s lifetime or at least during a long period, and also that in species with multilaminar cheek teeth laminae can be added in postnatal development (e.g., Vucetich et al. 2005a). This condition makes it difficult to distinguish juveniles from adults of the same taxon when dealing with isolated teeth. Thus, we consider that differences in size among late Miocene neopiblemids could represent only specific differences, or even only ontogenetic differences in a single species in spite of previous systematic arrangements (Negri and Ferigolo 1999; Candela 2005).

Table 2 Tooth dimensions (in mm) of rodent specimens. AP anteroposterior length; AW anterior width; PW posterior width; c-b crown base

Taxon	AP	AW	PW	c-b
<i>Cardiatherium</i> sp.				
UNEFM-VF-50 m1 or m2			4.99	5.40
UNEFM-VF-51 M1 or M2	7.95	6.83	7.14	
cf. <i>Caviodon</i>				
UNEFM-VF-53	4.59			
<i>Neopiblema</i> sp.				
UNEFM-VP-54	7.44	3.57	4.48	
<i>Marisela gregoriana</i>				
UNEFM-VF-55 M1	3.36	3.06	2.65	
UNEFM-VF-55 M2	3.36	2.95	2.34	

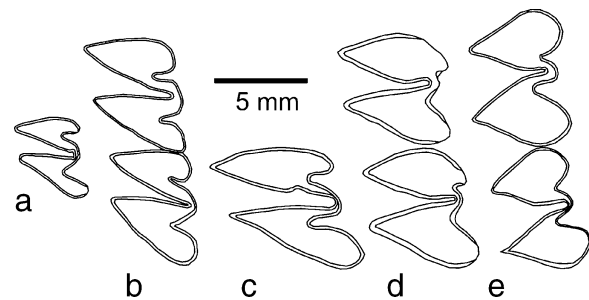


Fig. 4 Cheek tooth comparison among Cardiomyinae. **a**, cf. *Caviodon*, UNEFM-VF-53 (left M1 or M2); **b**, *Caviodon australis*, MACN 7326 (left M1-2); **c**, *Xenocardia diversidens* MLP 57-XII-23-5 (left M2); **d**, *Cardiomys* sp., MLP 55-IV-28-11 (M1-2 left); **e**, *Cardiomys ameghinorum*, MACN 8247 (left M1-2).

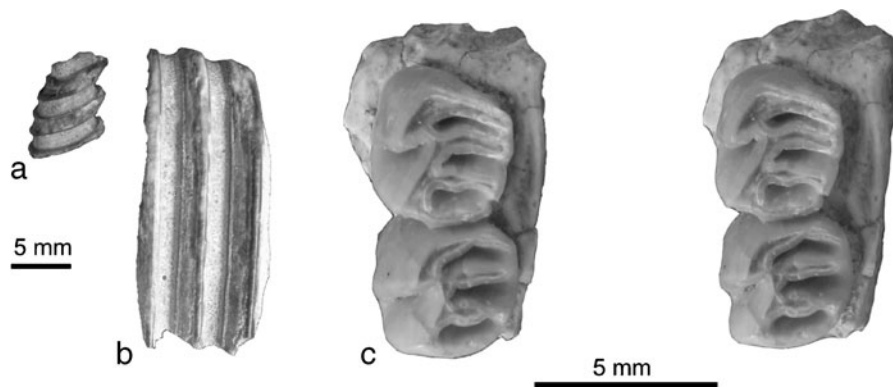


Fig. 5 **a–b**, *Neopiblema* sp. UNEFM-VF-54, **a**, occlusal view; **b**, lateral view; **c**, *Marisela gregoriana* gen. et sp. nov. (holotype, UNEFM-VF-55), stereo-pair of M1-M2 in occlusal view.

Octodontoidea Waterhouse, 1839

Octodontoidea?

Marisela gen. nov.

Type species: *Marisela gregoriana* sp. nov.

Etymology: Referring to the second feminine character of Rómulo Gallegos' popular romance "Doña Bárbara".

Diagnosis: As in the type and only species.

Marisela gregoriana gen. et sp. nov.

Holotype: UNEFM-VF-55, left M1-M2 of a young individual.

Etymology: In reference to the San Gregorio Formation where the holotype was found.

Diagnosis: A medium size caviomorph, with tetralophodont M1-2 displaying conspicuous unilateral hypsodonty; lophs made by several isolated portions when young and retaining bulbous aspect at least with moderately wear; anterolingual corner rectangular in shape; occlusal surface concave after some wear.

Description: UNEFM-VF-55 is a juvenile, with the labial portion of the posteroloph of M2 still without wear (Figs. 5C, 6a-d). Crowns are subquadrangular in outline and moderately high, with a conspicuous unilateral hypsodonty (Fig. 6b-d); both M1-2 have four crests. As M2 has so little wear it still shows important structural details (Fig. 5c). The area of the mure is formed by two distinct portions. The anterior one is partially connected to the protocone, whereas the posterior one does so to the hypocone. The anteroloph is formed by at least two portions; the labial extreme of this loph is slightly damaged obscuring if there is a third isolated portion. The protoloph is formed by a long portion joining labially the still unworn and relatively small paracone, and lingually to the anterior portion of the mure. The third loph, here interpreted as the metaloph, is formed by a thick and relatively short central

portion joined labially to the large metacone through a thin crest, and lingually to the posterior portion of the mure. The posteroloph is much curved and bears a cuspule near its labial end. All these details are already lost in M1 due to the greater wear; only the bulbous aspect of some lophs remains. In the area of the protocone, anterior and lingual walls contact forming a rectangular angle, as in some echimyids such as living dactylomyines and extinct adelphomyines.

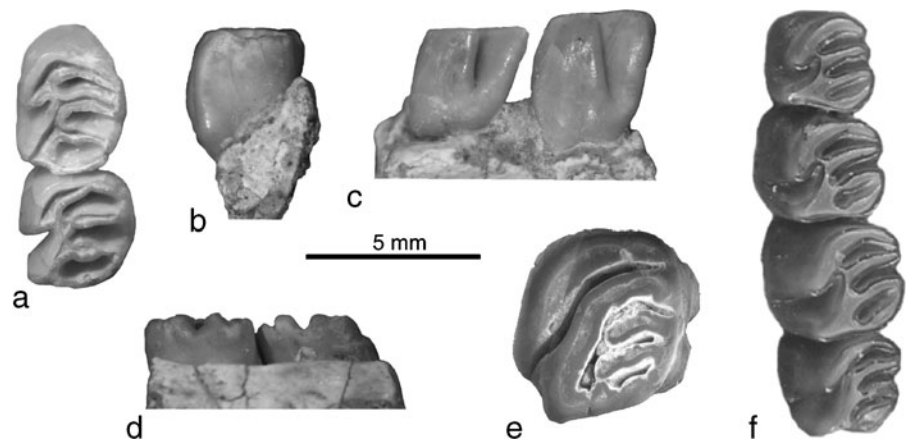
Comparisons: *M. gregoriana* resembles the Dasyproctidae *Plesiaguti totoi* (Ensenadan) (Fig. 6e), as well as the living dasyproctids, in the bulbous aspect of lophs, but it has only four crests instead of the five of dasyproctids. *M. gregoriana* also resembles the Echimyidae "*Eumysops*" *parodii* ("Mesopotamiense")—known only through the holotype—in their tetralophodont and quadrangular molars, but differs especially in that "*E.*" *parodii* is slightly smaller, has narrower fossettes, straighter walls, and curved contact between the anterior and lingual walls (Fig. 6f; see Olivares 2009 for an accurate description). As the holotype of "*E.*" *parodii* is an individual older than that of *M. gregoriana* (M3 is already worn), it is not possible to establish if lophs are also formed by isolated portions, but in this stage of wear lophs do not have the bulbous aspect of the M1 of *M. gregoriana*. Some Erethizontidae, as *Eosteioromys* (Colhuehuapian), can also display a multiplicity of bulbous structures on the occlusal surface.

Discussion

The new remains of caviomorph fossils described here provide interesting data about the late Neogene diversity in northernmost South America, and the geographical and temporal distribution of several lineages, and add new evidence about "the tropics as cradle or museum" of biodiversity.

The rodent assemblage from the San Gregorio Formation resembles those of the late Miocene (Huay-

Fig. 6 Cheek tooth comparison among selected caviomorphs. **a–d**, *Marisela gregoriana* gen. et sp. nov., holotype UNEFM-VF-55 (left M1–M2). **a**, occlusal view; **b**, M2 posterior view; **c**, M1–M2 lingual view; **d**, labial view. **e**, *Plesiaguti toti* MLP 92-IV-29-82 (left M1 or M2); **f**, “*Eumysops*” *parodii*, MLP 41-XII-13-242 (left P4–M3).



querian Age) from the “Mesopotamiense” of central Argentina (Entre Ríos; Cione et al. 2000; Fig. 1) and the Acre region (Brazil; Frailey 1986; Sant’Anna 1994), both in ecological types and, although partially, systematic composition. These three faunas share *Cardiatherium* and *Neoepiblema*, while cardiomyines have been truthfully reported only for the “Mesopotamiense”. The low-crowned *M. gregoriana* resembles morphologically the echimyid “*Eumysops*” *parodii*. The presence of *Cardiatherium* suggests an aquatic environment for the rodent localities of the San Gregorio Formation, because living capybaras inhabit areas around ponds, lakes, rivers, marshes, and swamps, using water primarily as refuge, and fossil capybaras have always been found in water-related settings (Deschamps et al. 2007). Likewise, *Neoepiblema* (and/or *Phoberomys*) comes from the Ituzaingó, Solimoes, and Urumaco formations, which are also water-related sediments. In addition, neither *Neoepiblema* nor *Phoberomys* have been found in the rich late Miocene eolian deposits of western Argentina. The presence of crocodiles supports this paleoenvironmental reconstruction.

The stratigraphic position of the San Gregorio Formation suggests a late Pliocene age for these sediments. If this were correct, it would imply the endurance of most of these genera beyond their biochron in southern South America. *Cardiatherium* and *Neoepiblema* have not been recorded beyond the late Miocene, while the cardiomyines are recorded only up to the early Pliocene.

Previous work based on discoveries in southern Brazil and northern Argentina, and extrapolations of what past distributions and diversity patterns must have been, suggested a much greater diversity of Miocene-Pleistocene caviomorphs in ISA than the one known today (Vucetich and Verzi 2002; Vucetich et al. 2005b; Hadler et al. 2008). This diversity would be hidden by Quaternary extinctions

together with the already mentioned scanty record. These authors also proposed that ISA served as a reservoir for rodent taxa that had already become extinct in southern South America. The Pliocene San Gregorio assemblage is relevant in this regard, as it supports both hypotheses.

On the one hand, *Marisela gregoriana* represents a lineage not yet recorded in SSA and thus would be a case similar to that of the echimyid *Ricardomys longidens*, the Dasyproctidae Dasyproctinae, and the Erethizontidae Erethizontinae (Vucetich et al., unpublished information), that is, old lineages always restricted to ISA. On the other hand, *Cardiatherium* and *Neoepiblema* are typical cases of taxa with a wider geographical distribution that survived in the tropics beyond their extinction in the south. This survival would be related to the persistence of fluvial environments under warm conditions. This constitutes then another example of the tropics as “cradle and museums” of biodiversity (Jablonski et al. 2006). In sum, this assemblage represents an example of the great but poorly known extinct biodiversity in species and anatomical features that the exploration of vertebrates in northern Neotropics can reveal (Head et al. 2009).

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