

Unexpected primitive rodents in the Quaternary of Argentina

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Abstract

This article describes the first fossils recorded in the Hernandarias Formation (Pleistocene) in Entre Ríos province (eastern Argentina). They are represented by three teeth assigned to the caviomorph rodents (Rodentia, Mammalia) *Aenigmys diamantensis* gen. et sp. nov. and *Eumysops*. To establish the phylogenetic affinities of the two most enigmatic teeth, their enamel microstructure was studied. *Aenigmys diamantensis* is considered the most primitive taxon of a clade formed by Dinomyidae–Neoepiblemidae–Heptaxodontidae. Evidence of the close relationships among these families also is presented herein. The new fossils reinforce previous hypotheses about the survival of primitive Brazilian taxa after their extinction in the Pampas and Patagonia of southern South America. They also show that the diversity of caviomorph rodents during the Quaternary was greater than supposed and that an important Quaternary extinction, not previously detected, affected several lineages. With the available evidence, it is not possible to determine if these rodents indicate a warm pulse or a particular biogeographic situation in Entre Ríos.

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1. Introduction

Living caviomorph rodents are grouped into 13 families widely, though unequally, distributed in South America. In the Brazilian subregion (Hershkovitz, 1958) the brachy- to protohypsodont genera of the families Erethizontidae, Dasyproctidae, Agoutidae, and Echimyidae are dominant, together with a few euhypsodont genera of the families Dinomyidae, Caviidae, and Hydrochoeridae and the protohypsodont *Myocastor*.

In contrast, the caviomorph fauna from the southern part of the continent, Hershkovitz's (1958) Patagonian subregion, is dominated by euhypsodont taxa (*sensu* Mones, 1982) of the families Caviidae, Octodontidae, Abrocomidae, Chinchillidae, and Hydrochoeridae, as well as

Myocastor. This familial composition was established during the Ensenadan (Early–Middle Pleistocene) after the extinction of the echimyid *Eumysops*, whereas the current generic composition was attained during the Lujanian (Late Pleistocene) with the extinction of the hydrochoerid *Neochoerus*.

However, several brachy- and protohypsodont taxa recently have been found in the Ensenadan of different localities of Buenos Aires province, which apparently partly contradicts this faunal evolution scheme. The Brazilian affinities of these taxa and their episodic record suggest higher caviomorph diversity during the Quaternary, as well as southern migration of 'Brazilian' faunas during warmer or more temperate pulses. Some of these records belong to surprisingly primitive taxa, of whose existence, until recently, we had no evidence (Vucetich et al., 1997; Vucetich and Verzi, 1998, 1999, 2002).

In this article, we describe the first Quaternary rodents from the city of Diamante (Fig. 1) (Entre Ríos province) that certify the survival of very primitive caviomorphs into this

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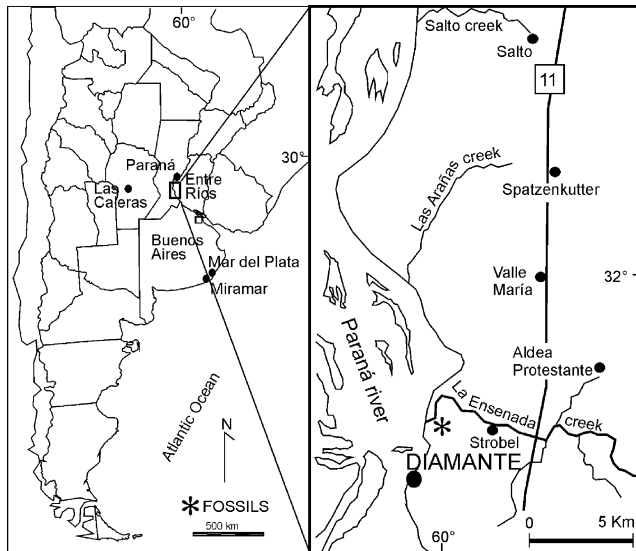


Fig. 1. Location map.

period and provide a new perspective on this group for the Quaternary as well as the Late Tertiary.

We use CICYTTP-PV-M to refer to the Centro de Investigaciones Científicas y de Transferencia de Tecnología a la Producción de Diamante–CONICET, Paleontología de Vertebrados.

2. Geology and biochronology

The stratigraphic sequence at Diamante is composed of the most ancient ‘Pampean’ formations that outcrop in southwestern Entre Ríos. They form the Punta Gorda Group, which can be divided into several units, such as the regionally recognized Alvear and Hernandarias formations (Iriando, 1980). These sediments traditionally have been regarded as Pleistocene in age (Iriando, 1980, 1996, 1999; Bidegain, 1991). Bidegain (1991) believed the Hernandarias Formation was deposited during the Olduvai event (~1.8 Ma), whereas Iriando (1996) thought it was deposited after the Jaramillo event (~0.98 Ma). In either case, the Hernandarias Formation would be Pleistocene in age.

In Diamante, the Pleistocene silts of the Pampean formations discontinuously overlie the marine and/or estuarine green clays of the Paraná Formation, which has been assigned to the Late Miocene (Aceñolaza, 2000) or Pliocene (Bidegain, 1991).

The rodents described herein were collected from the base of Unit 4 in the following sequence (Fig. 2):

1. Gray and light green clays, 6.5–7 m, plastic with abundant reddish limonite spots. Calcareous levels separate this unit from the overlying greenish clayey–

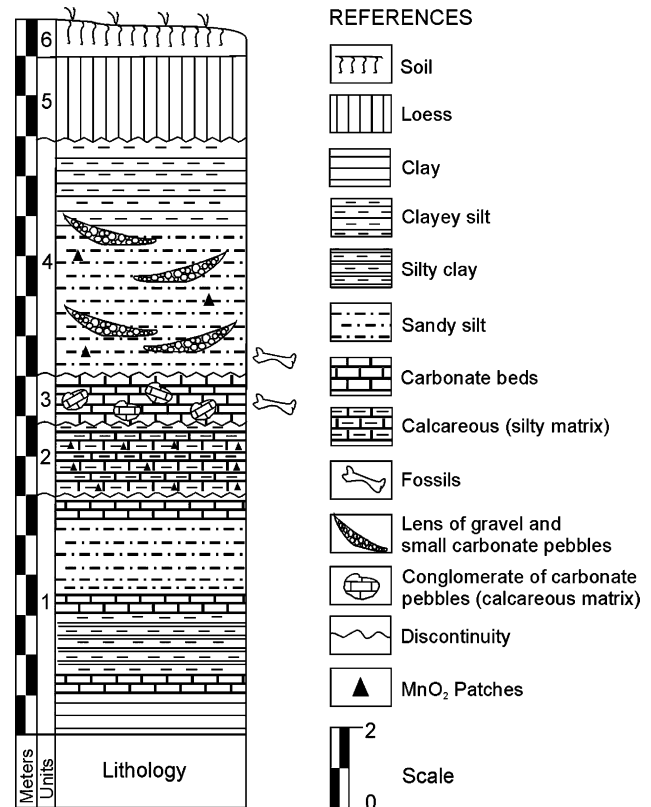


Fig. 2. Stratigraphic profile.

sandy silts. Unit 1 belongs to marine and/or estuarine levels of the Paraná Formation.

2. Overlying the calcareous level at the top of Unit 1, 2–3 m of very light grayish green silts with high calcium carbonate content in discontinuous horizontal and vertical veins form a network with abundant MnO₂ nodules. It correlates with the lower part of the Punta Gorda Group (= Alvear Formation, typically represented somewhat farther north of Diamante) and appears of aeolian genesis, deposited in lacustrine or palustrine environments (Iriando, 1980).
3. Conglomerate of carbonate pebbles, 0.6–1 m, derived from the erosion of the preceding unit, cemented by carbonate matrix. This well-defined and strong carbonate floor forms a discontinuity as a ridge on the profile of the cliff, clearly limiting the beginning of the overlying level.
4. Clayey silt, 4.5–6 m, partly sandy, light brown to pink and reddish brown; some sections are loessoid and massive, forming a slope of approximately 50–60° of rounded or somewhat conical erosion microforms. It has MnO₂ nodules and gypsum and intercalates with other sections with more vertical slopes that are composed of lenses or poorly defined levels of gravel and small calcium carbonate clasts in a coarse sand matrix. This unit corresponds to the upper part of the Punta Gorda Group (= Hernandarias Formation, which is more typically recognized north of Paraná City).

5. Overlying discontinuously, 1.5–2 m of clayey loessoid silts, massive, dusty, very light brown to yellowish, with abundant subspherical or ramified calcium carbonate scattered in the matrix (Tezanos Pinto Formation); it is considered Late Lujanian.
6. Soil (1 m) developed from Unit 5.

As we stated, the age of the bearing sediments, though controversial in its precision, can be attributed to the Pleistocene (Bidegain, 1991, 1996, 1999). Thus far, fossils are not known from the Hernandarias Formation, and those described herein do not supply biochronological information. However, *Toxodon* remains referable to *T. gracilis* (Notoungulata, Toxodontidae; M. Bond, pers. comm.) have been recorded in the underlying conglomerate (level 3, Fig. 2). *T. gracilis* has been recorded only in the Bonaerian of Buenos Aires province (Bond, 1999), in support of Iriando's (1996, 1999) age assignment.

3. Systematic paleontology

Order Rodentia Bowdich, 1821
 Suborder Hystricognathi Tulberg, 1899
 Infraorder Cavimorpha Wood and Patterson, 1959
 Family uncertain
Aenigmys gen. nov.

Type species: Aenigmys diamantensis sp. nov.

Diagnosis: Medium-sized cavimorph rodent; protohypodont with cement in the flexids, trilophodont lower molars with the central lophid unusually wide; posterolophid attached to the rest of the tooth by a narrow isthmus; presence of isolated pillars in the hypoflexid; enamel band irregular in thickness with bulbous portions; presence of longitudinal crests in the enamel–dentine junction.

Geographical and temporal distribution: Pleistocene of Entre Ríos province.

Name derivation: From the Latin *aenigma* = enigma and the Greek *mys* = rat, in reference to its unusual gross morphology.

Aenigmys diamantensis sp. nov.

(Fig. 3a–c)

Holotype: CICyTTP-PV-M-1-17, an isolated left lower molar (m3?).

Geographic provenance: The material was found at the cliff on the left bank of La Ensenada Creek, 300 m north of its outlet into the Paraná River, Diamante, Entre Ríos province, Argentina (32°40'S–60°38'W). The cliff stands along the coastal road from the harbor of Diamante to the village of Strobel (Fig. 1).

Diagnosis: As for the genus.

Name derivation: In reference to its geographic provenance, Diamante.

Description. It is a relatively large tooth, similar in size to that of species of *Dasyprocta*, corresponding to a 4.5 kg animal. Remains of cement block the view of the basal portion of the lingual wall. It is high crowned, longer than wide, and thus rectangular in outline. The anterior wall is mainly flat, whereas the posterior is very curved. The hypoflexid reaches the base of the crown, but the internal flexids are shallow. The occlusal surface is very simplified. The hypoflexid penetrates posteriorly, has a sinuous anterior wall, and widens at its end. The posteroflexid runs anterolabially, and its end opposes the end of the hypoflexid. A very thin dentine isthmus separates these flexids, and the posterolophid is almost separated from the anterior part of the tooth. This character is likely the beginning of lamination. The anteroflexid barely penetrates, and the cleft behind it, of uncertain homologies, is interpreted as the remnant of another lingual flexid. In this way, a very wide central lophid is determined. On the lateral external wall, there are two enamel pillars in the hypoflexid that do not reach the occlusal surface in this stage of wear. The sinuosity of the anterior wall of the hypoflexid may result from the presence of a third pillar higher than the other two, which would be already incorporated into the anterior wall of the hypoflexid by wear. The enamel is somewhat irregular in thickness, very thin in some areas and very thick in others, especially in the posteroflexid; in some sections, it abruptly thickens, acquiring a bulbous shape (Table 1).

Superfamily Octodontoidea Waterhouse, 1839

Family Echimyidae Gray, 1825

Eumysops Ameghino, 1888

(Fig. 4)

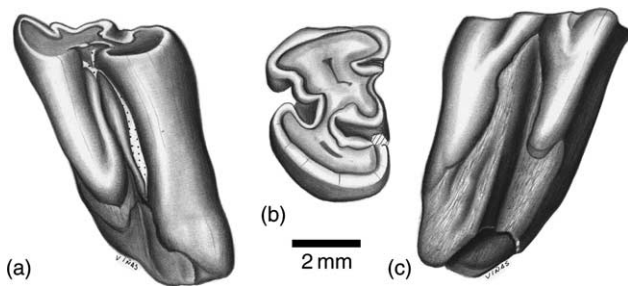


Fig. 3. Left m3? of *Aenigmys diamantensis* gen. et sp. nov. (CICyTTP-PV-M-1-17). (a) Labial view, (b) occlusal view, (c) lingual view.

Table 1

Measurements in mm of *Aenigmys diamantensis* CICyTTP-PV-M-1-17

Anteroposterior diameter	4.95
Anterior transverse diameter	3.85
Posterior transverse diameter	3.55
Crown height on the protoconid	7.40
Crown height on the metaconid	5.44

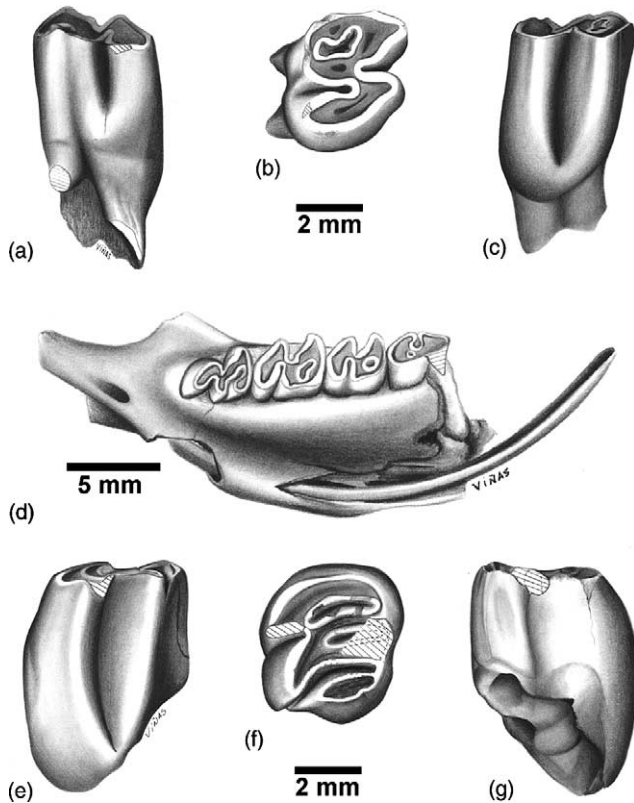


Fig. 4. Right m1 or m2 of *Eumysops* sp. (CICyTTP-PV-M-1-18). (a) Lingual view, (b) occlusal view, (c) labial view. (d) Left mandible of *Eumysops* sp. (MLP 91-IV-5-190, Chapadmalalan) and left M of *Eumysops* (CICyTTP-PV-M-1-19), (e) lingual view, (f) occlusal view, (g) labial view.

Material: CICyTTP-PV-M-1-18, an isolated right lower m1 or m2; CICyTTP-PV-M-1-19, an isolated left upper molar.

Provenance: As for CICyTTP-PV-M-1-17.

Description: CICyTTP-PV-M-1-18 is a protohypsodont molar with a slight unilateral hypsodonty and an occlusal surface somewhat longer than wide. The anterior side is straight, whereas the posterior is sinuous. The anterofossettid is closed, large, and kidney shaped with an anterior concavity; the posteroflexid is open, penetrates more than half the occlusal surface, and labially extends up to near the base. The lingual opening is very wide. The hypoflexid is mainly transverse, penetrating up to almost half the occlusal surface; its posterior wall is essentially transverse

and short, whereas the anterior wall is long and very oblique. The labial opening of this flexid is very wide. The hypoconid is notably more labial than the protoconid, so the posterior lobe is slightly narrower than the anterior (Table 2).

CICyTTP-PV-M-1-19 is a tetralophodont quadrangular upper molar, with marked unilateral hypsodonty. The walls are globose, and the stage of closure of the flexi and the lack of roots suggest that it is a scarcely worn juvenile specimen. The anteroloph is long, gently curved, and joined to the paracone by its labial end. The protoloph is slightly anterolabial–posterolingually oblique. It is connected to the hypocone, but the connection to the protocone is still weak because the mure is scarcely developed. The mesoloph is slightly oblique backward and slightly widened at its labial end. The posterior loph (postero- or meta- plus posteroloph) is short, and at this stage of wear, it is still disconnected from the hypocone, but it is connected to the third loph, so the posteroflexus is closed labially but open to the posterior side. The anterofossette is closed and very elongate. The labial region of the mesoflexus is broken, so it cannot be determined whether it was already closed. In this stage of wear, the hypocone is somewhat more labial than the protocone. The posterior wall has a cleft all along its height. It may be an M3 because of the opening of the metaflexid toward the posterior wall, the vertical cleft on the posterior wall, and the lack of an interdental wear facet. Notwithstanding, it also may be an M1 or M2, because it belongs to a juvenile (Table 3).

4. Enamel microstructure

The enamel microstructure of the caviomorph cheek teeth appears to be a useful and reliable tool to solve some systematic problems (Vieytes et al., 2001; Verzi et al., 2004; Vieytes, 2003) and consequently offers new evidence to test systematic hypotheses based on macromorphological characters. Because of the systematic uncertainties posed by these materials, an analysis of the enamel microstructure was carried out in the two cheek teeth, CICyTTP-PV-M-1-17 (*Aenigmys diamantensis*) and CICyTTP-PV-M-1-19 (*Eumysops*), that are most problematic.

The teeth were embedded in polyester resin and then sectioned longitudinally and transversally. Subsequently,

Table 2

Measurements in mm of *Eumysops* sp. CICyTTP-PV-M-1-18 compared with Chapadmalalan specimens with similar occlusal morphology

	CICyTTP-PV-M-1-17	MLP 91-IV-5-190	MLP 62-VII-27-77	MLP 91-IV-5-224	MLP 62-VII-27-96
Anteroposterior diameter	3.84	3.36	3.17	3.17	3.05
Anterior transverse diameter	3.36	3.04	3.35	2.50	2.80
Posterior transverse diameter	3.20	2.56	3.05	2.74	2.56
Crown height on the protoconid	5.44				
Crown height on the metaconid	3.68			5.49	3.59
Height of the metastriid	2.40			2.13	closed
Height of the posterostriid	4.00			4.51	2.13

Table 3
Measurements in mm of *Eumysops* sp. CICyTTP-PV-M-1-19

Anteroposterior diameter	3.84
Anterior transverse diameter	3.84
Posterior transverse diameter	3.04
Crown height on the protocone	5.76
Crown height on the paracone	2.4

the specimens were polished with sandpaper and grinding powder. The sections were etched with 10% HCl for approximately 4–6 s. After rinsing and drying, the specimens were coated with gold and examined with a scanning electron microscope (SEM) Jeol JSM-T100.

4.1. Enamel microstructure of *CICyTTP-PV-M-1-17* (*Aenigmys diamantensis*)

Most of the molar is surrounded by a thick enamel layer that ranges between 250 and 330 μm , though in some areas the enamel layer is very thin, near 100 μm . Both in the leading and trailing edges, the *schmelzmuster* (pattern of

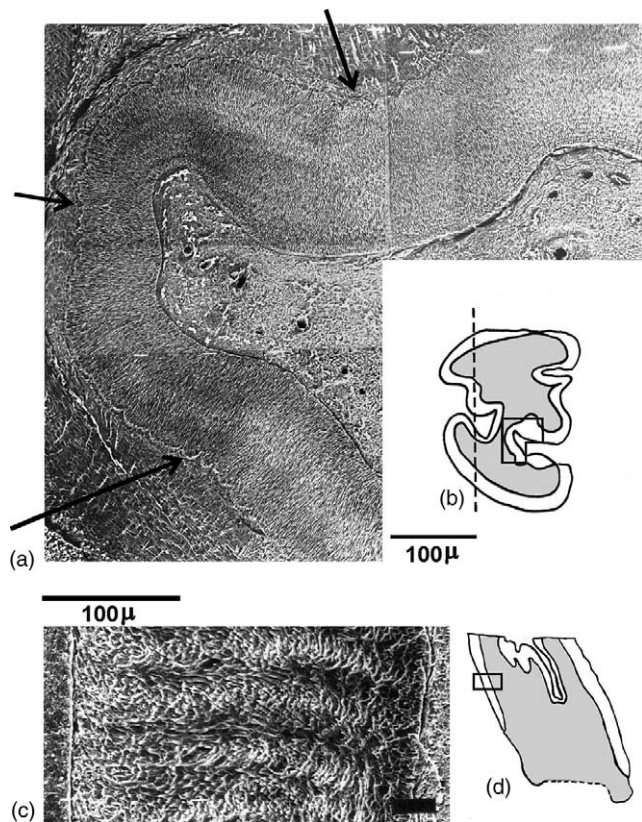


Fig. 5. SEM micrographs of *Aenigmys diamantensis* gen. et sp. nov. (CICyTTP-PV-M-1-17). (a) Detail of the posteroflexus, with arrows showing the longitudinal crests; (b) sketch of the occlusal view showing the area of the micrograph and the plane of the longitudinal section of the micrograph in c (dashed line); (c) *schmelzmuster* with HSB in longitudinal section; (d) sketch of longitudinal section of the tooth showing the area of the micrograph.

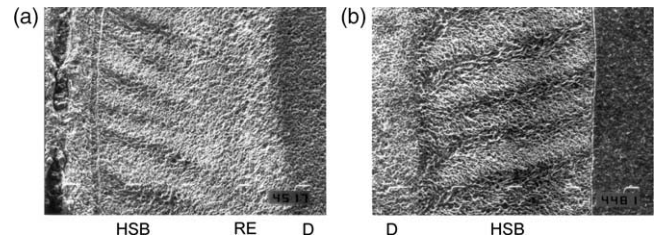


Fig. 6. SEM micrograph showing (a) trailing edge and (b) leading edge of the upper molar of *Eumysops* CICyTTP-PV-M-1-19. D, dentine; HSB, Hunter–Schreger bands; RE, radial enamel.

distribution of the different enamel types) is formed almost exclusively by Hunter–Schreger bands (HSB) (Fig. 5a–c). In a few areas, a thin internal zone of radial enamel (RE) is present but irregular and discontinuous. The HSB do not show inclination with respect to the dentine–enamel border (EDJ) and are 5 prisms wide. The interprismatic matrix (IPM) is perpendicular to the prisms in the internal zone of the enamel, but toward the external zone, it is acute to almost parallel to the prisms, as in most caviomorphs.

In the labial end of the posteroflexid and the lingual end of the hypoflexid (though less developed), there is a very particular feature: The EDJ is not even as in most mammals but shows longitudinal crests (Fig. 5a). These crests are seen in transverse section, parallel to each other and extending from the occlusal surface to the base of the crown, and are separated by narrow dentine valleys. Each crest is between 25 and 35 μm wide, though their size and shape are variable. Some crests are high and separated by deep valleys, whereas others are wider and shallow. The EDJ is even in the rest of the molar.

4.2. Enamel microstructure of *CICyTTP-PV-M-1-19* (*Eumysops*)

The enamel varies between 200 and 260 μm in thickness. The *schmelzmuster* of the trailing edge is formed by a layer of thin internal RE that occupies 20% of the band and one external layer of HSB (Fig. 6a). The leading edge is formed only by HSB (Fig. 6b). The HSB are inclined 20–25° and are 5–6 prisms wide. In both the leading and trailing edges, the HSB are gently curved toward the dentine, convex to the occlusal surface. The IPM is at a right angle in the most internal zone of the enamel band, near the dentine; toward the external zone, the angle decreases.

5. Discussion and conclusions

5.1. Relationships of the studied taxa

5.1.1. *Aenigmys diamantensis*

The external morphology of *Aenigmys* makes the assignment of this genus to any of the suprageneric groups (clusters) of caviomorphs difficult. However, the enamel

microstructure offers several characters that suggest possible relationships.

The longitudinal crests in the EDJ are an infrequent feature among mammals. Two types of crests have been described for human beings and the Litopterna *Miguelsoria parayirunhor* (Oliveira et al., 2001), but they are different from those of *Aenigmys* because they vary in size, shape, frequency, and distribution.

Similar crests to those of *Aenigmys diamantensis* have been found in several genera of the families Dinomyidae (*Simplimus*, *Isostilomys*, *Telicomys*, *Tetrastilus*, *Diaphoromys*, *Pentastylomys*, and *Dinomys*), Neoepiblemidae (*Neoepiblema*, *Euphilus*, and *Phoberomys*), and Heptaxodontidae (*Amblyrhiza*) (Vieytes, 2003). The crests observed in these genera are higher, but the shape, diameter, and frequency are similar to those of *Aenigmys*.

Systematics and relationships among Dinomyidae, Neoepiblemidae, and Heptaxodontidae are quite confusing, which results in a plethora of contradictory systematic proposals. For example, McKenna and Bell (1998) separate these families into different superfamilies; Mones (1986) does not deal with Heptaxodontidae but includes Dinomyidae and Neoepiblemidae within the Chinchilloidea; Woods (1982) includes Dinomyidae among the Caviioidea and Heptaxodontidae among the Octodontoidea; and Simpson (1945) gathers these rodents into two families of the Superfamily Caviioidea.

Thus, the presence of this kind of crest in the EDJ supports the hypothesis that these taxa could be related, regardless of the superfamily in which they are included. Likewise, it suggests that *Aenigmys* might be related to these families.

The presence in *Aenigmys* of a simple *schmelzmuster*, primitive for caviomorphs (Vucetich et al., 2001), does not contradict these hypothesized relationships. It matches an underived macromorphology that points to primitive membership in the hypothesized lineage. Within each caviomorph lineage studied thus far (Vieytes, 2003), the taxa with primitive features in their dental morphology have simple *schmelzmuster*, exclusively or dominantly with HSB (Vieytes et al., 2001; Vucetich et al., 2001; Verzi et al., 2002; Verzi et al., 2004).

Some macromorphological characters support the hypothesized relationship with Dinomyidae. In several Dinomyidae, the enamel layer has small thickenings in some sections (Frailey, 1986, Fig. 21D), as in *Aenigmys*. Another interesting character is the presence of pillars in the hypoflexid of *Aenigmys*; pillars aligned with a crest are also frequent among Dinomyidae (Vucetich, 1984, Lam V j; Frailey, 1986).

In Dinomyidae, as well as in Neoepiblemidae and Heptaxodontidae, cheek teeth are laminar, euhypsodont, or protohypsodont but always very high crowned. In this sense, the dental morphology of *Aenigmys*, protohypsodont and very weakly laminated, would be primitive for the group.

Even accepting the proposed relationships, it is impossible to determine with the available data to which of these

families *Aenigmys diamantensis* is most closely related. Given that this taxon presents many primitive dental characters (protohypsodonty, weak lamination, lower and more localized crests in the EDJ, prevailing HSB), it could be a late representative of an early offshoot. Regardless, *Aenigmys diamantensis* offers a fascinating perspective on the phylogeny of these poorly understood rodent families with laminated teeth, the evolution of which likely was much more complex than previously supposed.

5.1.2. *Eumysops*

The taxon *Eumysops* displays high morphological diversity, is poorly known from a systematic standpoint, and requires a deep revision to understand its actual systematic diversity and relationships (Kraglievich, 1965; Vucetich and Verzi, 1995). This morphological diversity is mainly expressed in the cheek teeth, which have a varied hypsodonty degree and occlusal morphology.

The molar CICyTTP-PV-M-1-18 is within the size range of the large species of *Eumysops*, and its morphological pattern (posteroflexid much deeper than the anteroflexid, posterolophid with marked sinuosity, and hypoconid more lingual than the metaconid) is poorly represented in the material from the Pliocene of the coastal region of Buenos Aires province, where this taxon is best known. Only four specimens in the collection of the Museo de La Plata, found in upper Chapadmalalan levels (mid-Pliocene) between Miramar and Mar del Plata (Fig. 1), show these features (Fig. 4d). The molar CICyTTP-PV-M-1-18 is somewhat larger than these specimens (see Table 2); therefore, it would represent a different species.

The molar CICyTTP-PV-M-1-19 would correspond to the upper dentition of the species represented by molar CICyTTP-PV-M-1-18, but it differs from the *Eumysops* of the Pampean region in that the opening of the posteroflexid toward the posterior wall is longer.

All eumysopines studied by Vieytes (2003) show only HSB or a *schmelzmuster* formed by two types of enamel, through the addition of an inner layer of RE, that may be confined to the trailing edge as in *Eumysops* or occur on both the trailing and leading edges. Genera of other subfamilies show other *schmelzmuster* (Vieytes, 2003). Consequently, the enamel microstructure does not rule out assignment of CICyTTP-PV-M-1-19 to *Eumysops*.

5.2. Quaternary diversity and biogeography

Recently, Vucetich and Verzi (2002) proposed that the diversity of Quaternary caviomorphs must have been much higher than previously expected, especially in low latitudes. This hypothesis was based on a new genus and species of a primitive dasyproctid found in the Pleistocene of Argentina, as well as on the presence of the echimyid *Dicolpomys* in the Quaternary of Brazil and Argentina (Vucetich and Verzi, 1999), both of which represent extinct lineages of Brazilian stock. We assume that the record of Pleistocene Brazilian

caviomorphs in Argentina, associated with interglacial periods, represents marginal distributions of these taxa. Thus, it becomes evident that they represent a depauperized sample of unrecorded greater diversity of Quaternary caviomorphs in the northern part of the continent.

The rodents here described also support the idea of greater Quaternary diversity, because they show the Pleistocene survival of more lineages without modern representation. *Aenigmys* is especially remarkable in this sense, in that it represents a lineage hitherto unknown. The absence of potential ancestors of *Aenigmys* in the rich Neogene records of the Patagonian and Pampean regions suggests that this lineage may have inhabited the north of the continent, as is the case of living Dasyproctidae, Erethizontidae, and Primates (Candela, 2000; Vucetich and Verzi, 2002). However, they would have been rare and/or lived in very restricted areas. It must be taken into account that neither in the Late Miocene ('Mesopotamian') of Paraná (approximately 40 km north of Diamante), where dinomyids and neopiblemids were abundant and diverse, nor in the Late Miocene of Acre, Brazil, where protohypsodont dinomyids and neopiblemids were still living (Frailey, 1986, Fig. 21A; Sant' Anna, 1994; Negri, 1998), have related taxa been found. *Eumysops* was known only in Pliocene levels from the provinces of Buenos Aires and Córdoba (Las Caleras, Fig. 1; Tauber, 2000); its youngest record is of Sanandresian age (Late Pliocene). Citations for the Late Miocene are dubious (Montalvo et al., 1996; Vucetich and Verzi, 1995; Vucetich and Verzi in Cione et al., 2000; Table 2).

The fossils here described supply more proof of the survival of mammals with primitive dental characters into the Quaternary. With the available data, it cannot be known whether the record of these rodents in Diamante reflects a southern migration caused by a warm pulse, as has been suggested for other Brazilian rodents of the Pleistocene of Buenos Aires province, or a particular biogeographic circumstance of the Entre Ríos region (Noriega et al., 2001).

The record of these caviomorphs opens a new perspective on the Quaternary rodent fauna of South America, especially with regard to their diversity, the survival of primitive genera during the Quaternary, and the occurrence of a significant extinction phenomenon of small- and medium-sized mammals during this period. This extinction event caused the disappearance of entire lineages such as those represented by *Dicolpomys*, *Eumysops*, *Plesiaguti*, and *Aenigmys*. *Eumysops* and *Dicolpomys* likely represent lineages that originated during the Late Miocene (Vucetich and Verzi, 1996), whereas the other two genera probably belong to older groups.

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