Journal of Vertebrate Paleontology 30(2):528–534, March 2010

ARTICLE

THE FIRST EOCARDIIDAE (RODENTIA) IN THE COLHUEHUAPIAN (EARLY MIOCENE) OF BRYN GWYN (NORTHERN CHUBUT, ARGENTINA) AND THE EARLY EVOLUTION OF THE PECULIAR CAVIOID RODENTS

MARÍA E. PÉREZ,[*,1,4] MARÍA G. VUCETICH,[2,4] and ALEJANDRO G. KRAMARZ[3,4]
[1]Museo Paleontológico Egidio Feruglio, Av. Fontana 140, Trelew U9100GYO, Argentina, mperez@mef.org.ar;
[2]Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, División Paleontología Vertebrados, Paseo del Bosque s/n, La Plata B1900FWA, Argentina, vucetich@fcnym.unlp.edu.ar;
[3]Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Sección Paleontología de Vertebrados, Ángel Gallardo 470, 1405 Buenos Aires, Argentina, agkramarz@macn.gov.ar;
[4]CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas)

ABSTRACT—Caviidae and Hydrochoeridae (extant Cavioidea s.s.), probably the most peculiar among rodents, are characterized by their evergrowing double-heart-shaped cheekteeth. They have classically been rooted in Eocardiidae, which ranges from Deseadan to 'Colloncuran' (late Oligocene–middle Miocene) in Patagonia, although in the Deseadan and Colhuehuapian (early Miocene) remains are very scanty. For the Colhuehuapian, only one species coming from the southern cliff of the Colhué Huapi Lake (Gran Barranca, Chubut, Argentina) was known so far. In this paper, the first Colhuehuapian eocardiids from outside Gran Barranca are reported: *Luantus minor*, sp. nov., and *Chubutomys leucoreios*, sp. nov. They are represented by two fragmentary mandibles and a few isolated cheek teeth, from the Trelew Member of the Sarmiento Formation at Bryn Gwyn, lower valley of the Chubut River, Chubut. The new species enlarge the knowledge of eocardiid diversity, and reinforce the hypothesis of a basal dichotomy for the group. *L. minor* represents one of the smallest species of the series *Asteromys* + *Luantus* + *Phanomys* + *Eocardia*, which likely gave rise to modern Cavioidea s.s. *C. leucoreios* pertains to a group of species with precocious hypsodonty and apparently low diversity, but without modern descendant.

INTRODUCTION

Caviomorphs are the most diverse group of rodents, with cuises, maras, and capybaras probably the most peculiar among them. Cuises, maras (Caviidae), and capybaras (Hydrochoeridae) have diverse habits and played the roles in South America of hyraxes, duikers, hippos, jackrabbits, etc. (Mares and Ojeda, 1982). They are characterized, among other features, by their euhypsodont cheek teeth, with a primarily double-heart-shaped occlusal surface. These and other characters suggested their grouping in a single family (Caviidae; Waterhouse, 1839), a single superfamily (Cavioidea; Fischer de Waldheim, 1817:372), or as Cavioidea s.s. (Patterson and Wood, 1982:511); other groups such as Dasyproctidae and Cuniculidae, which have no double-heart cheek teeth, were included in this superfamily.

Caviidae and Hydrochoeridae have been classically rooted in the Family Eocardiidae Ameghino, 1891 (Ameghino, 1893; Landry, 1957:43; Wood and Patterson, 1959:395; Patterson and Wood, 1982:511); eocardiids include cavioids with double-heart-shaped cheek teeth, but retaining primitive characters for the group, such as the persistence of fossettes/ids. Eocardiids are recorded from the Deseadan Land–Mammal Age (SALMA) up to the 'Colloncuran' (late Oligocene–middle Miocene; Patterson and Wood, 1982; Vucetich, 1984) in Patagonia, although in the Deseadan and Colhuehuapian (early Miocene) remains are very scanty. Two species have been recognized for the Deseadan: *Asteromys punctus* Ameghino, 1897, and *Chubutomys simpsoni* Wood and Patterson, 1959. The Colhuehuapian eocardiids were known so far only through a small number of specimens from the southern cliff of the Colhué Huapi Lake (Gran Barranca, Chubut, Argentina; Ameghino, 1900, 1902, 1906; Vucetich et al., in press; Fig. 1) of the protohypsodont species *Luantus initialis* Ameghino, 1902. In this paper, the first remains of eocardiids from Colhuehuapian levels outside the Gran Barranca are reported. They are represented by two fragmentary mandibles and a few isolated cheek teeth that were found in the Trelew Member of the Sarmiento Formation cropping out at Bryn Gwyn, lower valley of the Chubut River, Chubut (Simpson, 1935; Scasso and Bellosi, 2004; Fig. 1). These new remains allow revisiting the hypotheses about the early evolution of this peculiar group of rodents.

MATERIAL AND METHODS

Mandible and dental measurements were taken with a stereomicroscope ZEISS Stemi SV 11. The degree of hypsodonty was measured through the hypsodonty index (H): crown height/anterior transverse diameter (Janis, 1986). H was calculated only in the less worn teeth (not a single unworn tooth is available); it is only an estimate and is expressed in the text as a percentage in relation to other taxa. Height of upper teeth was measured on the lingual side, whereas that of lowers, on the labial side, from top of the crown up to hypoflexus/id base. When necessary, this latter measurement was taken on X-ray images. Dental nomenclature (Fig. 2) follows Candela (1999) and Marivaux et al. (2004).

Institutional Abbreviations—**MPEF-PV**, Museo Paleontológico Egidio Feruglio-Paleontología de Vertebrados, Trelew; **MLP**, Museo de La Plata, La Plata; **MACN A**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" Colección Nacional Ameghino; **MACN Pv**, Museo Argentino de

*Corresponding author.

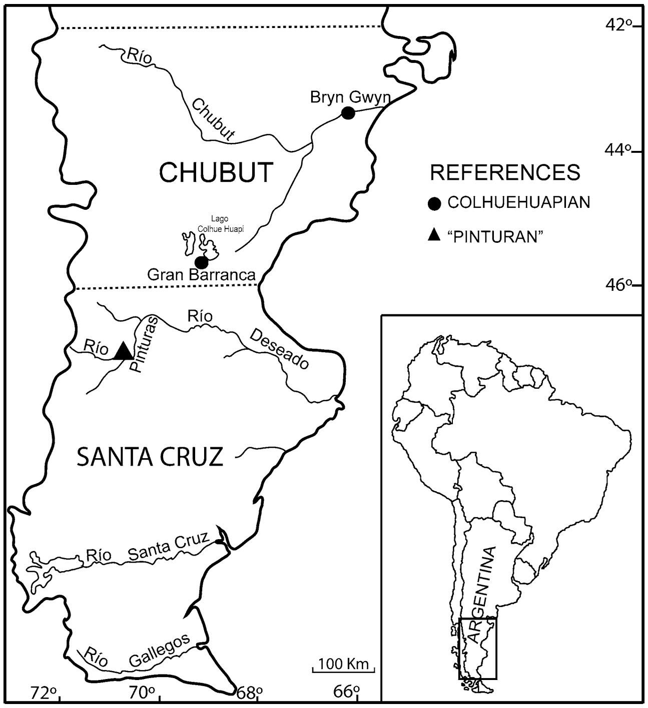

FIGURE 1. Location map of Bryn Gwyn and Gran Barranca localities, Chubut province, Argentina.

Ciencias Naturales "Bernardino Rivadavia" Colección Nacional de Paleovertebrados; **AMNH**, American Museum of Natural History.

Anatomical Abbreviations—**APL**, anteroposterior length; **AW**, anterior width; **PW**, posterior width; **hH**, hypoflexid height; **h**, hypoflexid.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOGNATHI Tullberg, 1899
Superfamily CAVIOIDEA Fischer de Waldheim, 1817:372
Family EOCARDIIDAE Ameghino, 1891
Genus *LUANTUS* Ameghino, 1899

Eocardia Ameghino, 1887:65–66 (in part)

Included Species—*Luantus initialis* Ameghino, 1902, Colhuehuapian; *Luantus propheticus* Ameghino, 1899, 'Pinturan,' *Luantus toldensis* Kramarz, 2006, Santacrucian? Wood and Patterson (1959) considered *Luantus gracilis* (Ameghino, 1906) as the smallest species of *Luantus*. However, Kramarz (2006) interpreted that the lectotype of this species (an isolated upper cheek tooth) is a Dp4 of *Eocardia*.

LUANTUS MINOR, sp. nov.
(Fig. 3A–J, Table 1)

Holotype—MPEF-PV 5007, a fragment of right mandible with m1–2 moderately worn (Fig. 3A, B).

Referred Material—MPEF-PV 1154a, an isolated left lower molar (m2?) (Fig. 3C–F); MPEF-PV 5028, an isolated right M3 of an adult (Fig. 3G–H); MPEF-PV 1154b, an isolated right upper cheek tooth of a juvenile (DP4?) (Fig. 3I–J).

Diagnosis—Smallest species of *Luantus*; mesofossettid persistent, but small and subcircular; hypoflexid wide and less penetrating than in the other species of the genus; crowns of cheek teeth about 5% lower than in *Luantus propheticus*, 27% lower than in and *L. toldensis*, but about 60% higher than in *Luantus initialis.*

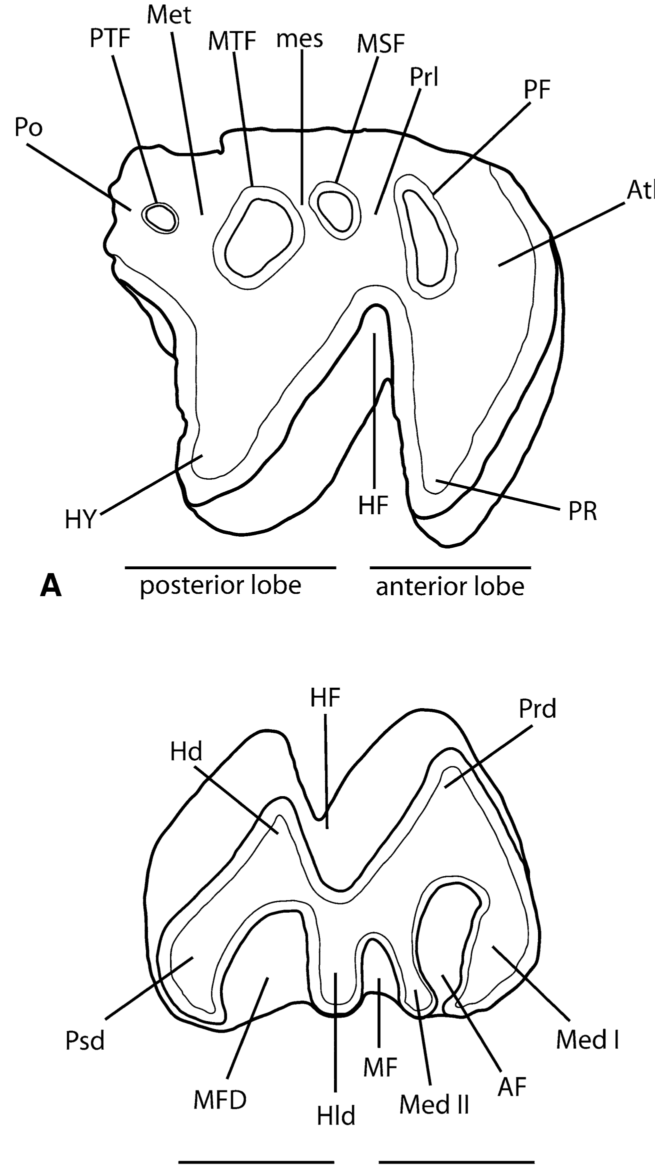

FIGURE 2. Occlusal dental morphology of upper and lower teeth and related nomenclature (Candela, 1999; Marivaux et al., 2004). **A**, Upper molars: *Luantus minor* sp. nov., MPEF PV 5028, right M3 in occlusal and lingual views. **Abbreviations**: **Atl**, anteroloph; **HF**, hypoflexus; **HY**, hypocone; **mes**, mesolophule; **Met**, metaloph; **MSF**, mesoflexus or mesofossette; **MTF**, metaflexus or metafossette; **PF**, paraflexus or parafossette; **Po**, posteroloph; **PR**, protocone; **Prl**, protoloph; **PTF**, posterofossette. **B**, Lower molars: *Luantus minor* sp. nov., MPEF PV 1154a, left m2? in occlusal view. **Abbreviations**: **AF**, anterofossetid; **Hd**, hypoconid; **HF**, hypoflexid; **Hld**, hypolophid; **Med I**, metalophulid I; **Med II**, metalophulid II; **MF**, mesoflexiid or mesofossettid; **MFD**, metaflexid or metafossettid; **Prd**, protoconid; **Psd**, posterolophid.

Etymology—*minor*: in reference to the smallest size species of the genus.

Occurrence—Bryn Gwyn, southern cliff of the Chubut River, Chubut Province (Fig. 1), Trelew Member of the Sarmiento Formation; Colhuehuapian SALMA (early Miocene).

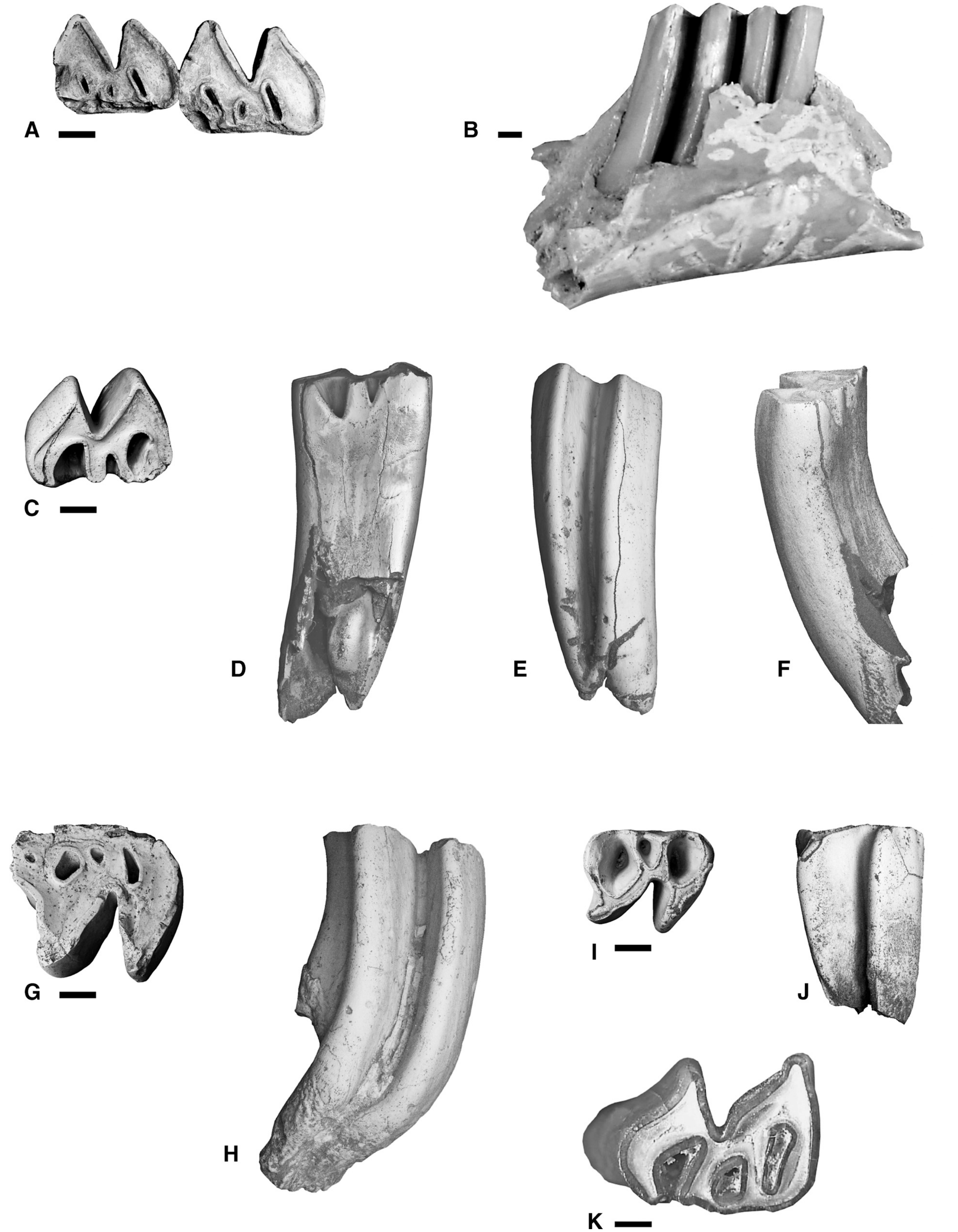

FIGURE 3. *Luantus minor*, sp. nov., from the Colhuehuapian Gaiman Locality. **A**, **B**, MPEF PV 5007, *L. minor*, sp. nov., right m1–m2 in occlusal and labial views. **C**–**F**, MPEF PV 1154a, left m2? in occlusal, labial, lingual, and posterior views. **G**, **H**, MPEF PV 5028, right M3 in occlusal and lingual views. **I**, **J**, MPEF PV 1154b, right upper cheek tooth in occlusal and lingual views. *Luantus initialis* from the Colhuehuapian Gran Barranca Locality. **K**, MLP 93–11-18–28, m2? Scale bar equals 1 mm.

TABLE 1. Dental measurements of several protohypsodont eocardiids, in mm.

		APL	AW	PW	hH	H
Luantus minor, sp. nov.						
MPEF-PV 5007 (holotype)	m1	3.4	2.8	2.7		
	m2	4.2	3.2	3.1	6.3	1.97
MPEF-PV 1154 a	m2?	4.1	2.9	2.5	8.9	3.06
MPEF-PV 1154 b	DP4?	3.5	2.3	2.6		
MPEF-PV 5028	M3	8.5	4.3	4.2		
Chubutomys leucoreios, sp. nov.						
MPEF-PV 1153 (holotype)	p4	3.1	1.8	2.5		
	m1	4.1	3.1	3	4	1.29
	m2	4.8	3.7	3.5	9	2.43
	m3	4.5	3.7	2.8		
Chubutomys simpsoni						
AMNH 29557 (holotype)	m1	3.3	2.5	2.6	6.8	2.72
	m2	3.5	2.6	2.5		
Luantus initialis						
MACN A 52164 (lectotype)	m1	5	3.9	4.1		
MLP 93–11-18–28	m2?	5.69	4.7	3.9	9	1.91
Luantus propheticus						
MACN A 2018 (holotype)	p4	4.2	2.5	3.3		
	m1	4.3	4.0	3.7		
	m2	5.1	4.5	4.5		
	m3	5.5	4.5	4.0		
MACN Pv SC3985	m2?	5	4.5	4.3	14.5	3.22
Luantus toldensis						
MACN Pv SC2574 (holotype)	m2?	5.5	4.3	4.2	18.1	4.21

The dental measurements for *L. propheticus* were taken from an isolated molar from the Pinturas Formation with similar stage of wear to the MPEF PV 1154a. **Abbreviations**: **APL**, anteroposterior length; **AW**, anterior width; **PW**, posterior width; **hH**, hypoflexid height; **H**, hypsodonty index.

Description—The type specimen (MPEF-PV 5007) is a fragment of right mandible with m1–2 moderately worn. The cheek teeth are high crowned but rooted (protohypsodont; Mones, 1982); X-ray analysis showed that the hypoflexid of m1 closes approximately at two thirds of the crown height, whereas that of m2 closes almost at the base of the crown. Crowns are at least 60% higher than in *L. initialis*, and approximately 5% and 27% lower than in *L. propheticus* and *L. toldensis*, respectively. There are no enamel discontinuities on the exposed crowns. The anterior and posterior walls are convex, whereas the lingual one and those forming the hypoflexid are straight. The hypoflexid is triangular, wide, and less penetrating than in the other species of the genus; it has no cement, at least in this stage of wear. Both m1 and m2 have three small lingual fossettids, forming a tetralophodont occlusal pattern (Fig. 3A). The antero- and metafossettid are narrow and elongate, and the mesofossettid is smaller, subcircular, less persistent than in *L. initialis* and *L. propheticus*, and is placed slightly anterior to the tip of the hypoflexid. The m1 is conspicuously smaller than m2.

The mandible fragment (Fig. 3B) is quite incomplete, only the area of the m1–2 is preserved. On the labial side, the massetteric crest is at 26° with respect to the alveolar margin, it is thin and the notch for the insertion of the tendon of the *pars infraorbitalis masseter medialis* muscle (Woods and Howland, 1979) is smooth, and is placed under m1. On the lingual side, the alveolus for the incisor extends up to the posterior part of the m2.

The other lower tooth herein referred to this species corresponds to an isolated m2? (MPEF-PV 1154a). In this molar the lingual flexi are still open, indicating that it belongs to an individual younger than the holotype. In this stage of wear, the metalophulid II is thin and already extends up to the labial wall of the molar (Fig. 3C). The antero- and metaflexid are wide and deep (Fig. 3C, D), whereas the mesoflexid is smaller and shallower. The hypoflexid has no cement (Fig. E). The enamel surrounds the whole tooth, except at the base of the posterolingual wall (Fig. 3F); this condition cannot be observed in the holotype because all molars are inserted in their alveoli.

We provisionally refer to this species two isolated upper cheek teeth. MPEF-PV 5028 is an M3; it has two lobes with equal transverse diameter, but the posterior one has a short but conspicuous posterior projection, which does not form a true third lobe (Fig. 3G). The labial wall is straight; the hypoflexus is triangular, with cement from the base up to two thirds of its height, consistent in being the most worn specimen of the sample (Fig. 3H). The occlusal pattern is pentalophodont; the parafossette is narrow and elongate, whereas the metafossette is round; both of them are deep. The meso- and posterofossette are very small, shallow, and subcircular. The enamel is continuous around the crown, but it is interrupted at the base of the anterior labial wall. In *L. propheticus* and *L. toldensis*, the enamel is interrupted on the anterolabial and posterolabial corners of the upper molars and on the anterolingual and posterolingual corners of the lowers. *L. initialis* was known only through the holotype, in which the molars are inserted in the mandible and their bases are not exposed, but new specimens of this species (Fig. 3K, Table 1; Vucetich, et al., in press) coming from Gran Barranca (Fig. 1) show that the enamel is continuous in the crown of the upper and lower molars.

The other specimen (MPEF-PV 1154 b; Fig. 3I, J) is an almost unworn DP4?, bilobed and tetralophodont tooth. The hypoflexus penetrates transversally up to the middle of the crown; it is wide and its apex is quite rounded. The transverse diameter of the anterior lobe is greater than that of the posterior one. It has a wide paraflexus, which is separated from the hypoflexus by the posterior arm of the protocone. The area of the protocone is transversally elongate and very narrow. The posterior lobe has a deep and very wide metaflexus that occupies a large part of the lobe. The mesoflexus is also deep, but smaller than the other two, and posterior to the hypoflexus. The area of the hypocone is very narrow, elongate and directed backward. The enamel is continuous around the preserved crown; it has no cement.

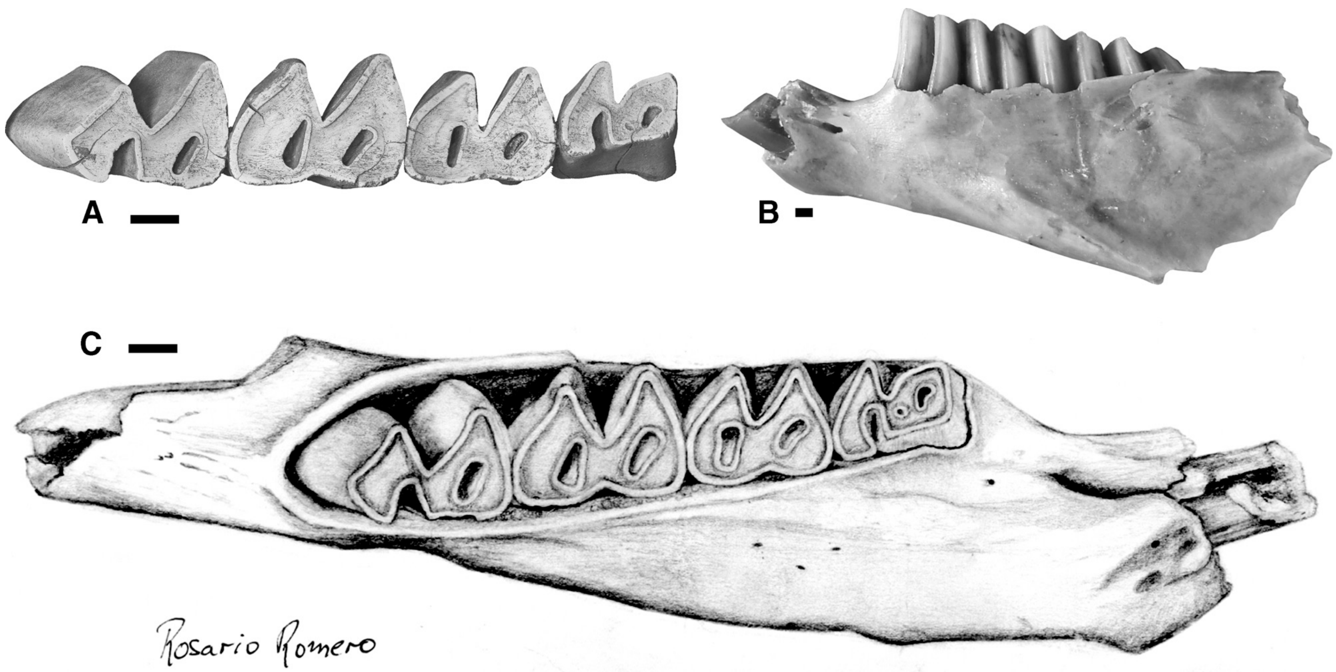

FIGURE 4. *Chubutomys leucoreios*, sp. nov., from the Colhuehuapian Gaiman locality. **A**, **B**, MPEF PV 1153, holotype, left p4–m3 in occlusal and labial views. **C**, MPEF PV 1153, holotype, illustration of left mandible. Scale bar equals 1 mm.

Genus *CHUBUTOMYS* Wood and Patterson, 1959

Included Species—*Chubutomys simpsoni* Wood and Patterson, 1959, Deseadan.

CHUBUTOMYS LEUCOREIOS, sp. nov.
(Fig. 4A–C, Table 1)

Holotype—MPEF-PV 1153, a left mandible fragment of an adult young specimen, with p4–m3 and broken incisor (Fig. 4A–C).

Occurrence—Bryn Gwyn, southern cliff of the Chubut River, Chubut Province (Fig. 1), Trelew Member of the Sarmiento Formation; Colhuehuapian SALMA (early Miocene).

Diagnosis—Size 25% larger, crowns of cheek teeth about 30% lower, and hypoflexid less penetrating than in the type species *C. simpsoni*.

Etymology—From Greek *leucos* = white, *oreios* = mountain inhabitant; in reference to the locality name (Bryn Gwyn = *Loma Blanca* = White Hill).

Description—Cheek teeth are protohypsodont and bilobed. The p4–m1 length is shorter than that of m2–m3 (Wood and Patterson, 1959:370), as in *L. initialis* and *L. propheticus*. The metaflexid is open both in p4 and m3 (Fig. 4A). In addition, the base of m3—exposed through a break in the mandible—is still open, and is wider than the occlusal surface, and the p4 is conical in lateral view (Fig. 4B). These facts indicate that the specimen is a young adult. X-ray showed that the hypoflexid closes at half the preserved height of the crown in p4 and m1, but almost at the base of the crown in m2. The hypoflexid of p4 and m2 extends transversally up to about half the crown, whereas in m1 and m3 it is slightly longer.

The lobes of p4 are very different in form and size. The anterior lobe is sub-quadrangular in cross-section with its anterior margin straight and transverse, and the postero-labial wall convex. It has a kidney-shaped anterofossettid, and a small, subcircular, and very shallow mesofossetid. The metalophulid II is narrow (Fig. 4A, C). The posterior lobe is wider than the anterior, triangular in outline with the anterior wall straight and the posterior one convex; the metaflexid is elongated, wider and deeper than the fossettids of the anterior lobe. The lingual wall of the tooth is straight.

In m1–m3 there is no mesofossettid; hence, only the antero- and metafossettid are seen, resulting in a trilophodont occlusal surface (Fig. 4A, C).

The m1 is larger than p4. The anterior and posterior walls are convex, whereas those forming the hypoflexid are straight; the lingual wall has a slight inflection opposed to the hypoflexid. Both lobes are approximately similar in shape, although the anterior one is transversally a little larger. The fossetids are narrow, elongate, and deep. The anterofossetid is anterolabial-posterolingually oriented, whereas the metafossetid is transverse. The m2 is similar to m1 but larger. There is a slight constriction on the posterior lobe in the area of the hypoconid and the inflection on the labial wall is much deeper than in m1.

The m3 (Fig. 4A, C) is smaller than m2. The anterior lobe is similar to that of m1–2. Contrarily, the posterior lobe is irregular in shape, and smaller than the anterior one; the metaflexid is still open. The lingual wall is straight. Despite little wear, this molar has no mesofossettid (not even a minute one as in p4), neither a discernable metalophulid II.

The horizontal ramus is slender. The preserved part of the diastema is concave, and the symphysis rises at an angle of 49° with respect to the dental series; the posterior union of the symphysis is not particularly heavy; a very small and elongated mental foramen is located anterior to p4 in laterodorsal position. The masseteric crest is conspicuous but thin, oblique backwards and downwards, at 25° with respect to the occlusal surface; the notch for the insertion of the *masseter medialis pars anterior* muscle is very smooth and below m1. The incisor (Fig. 4B, C) is slender, with the anteroposterior lenght much larger than the transverse one, and extends up to the posterior part of the m2; the anterior wall is slightly convex.

Remarks—*Chubutomys leucoreios*, sp. nov., shares with *Chubutomys simpsoni*, the type and, up to now, single species of the genus, the absence of mesofossettid (at least since already very early stages of wear), associated to high-crowned cheek teeth, and lack of cement. *C. leucoreios*, sp. nov., differs from *C. simpsoni* in its larger size, the hypoflexid less penetrating, and lower crowned cheek teeth.

It must be noted that *C. simpsoni* is known only by the holotype, which is a fragmentary mandible with m1–2, not m2–3 as interpreted by Wood and Patterson (1959).

Chubutomys leucoreios, sp. nov., differs from other protohypsodont eocardiids such as *Asteromys punctus*, *Luantus initialis*, *Luantus minor*, sp. nov., and *L. propheticus* in that these latter retain the mesofosetid during most of their life.

DISCUSSION AND CONCLUSIONS

Within their constraining heart-shape occlusal outline, Cavioidea s.s. display a great degree of variation in tooth morphology due to both individual and ontogenetic causes. This usually makes difficult the recognition of species limits in the fossil record (Contreras, 1964; Quintana, 1998; Vucetich et al., 2005; Kramarz, 2006). In the case of the eocardiids, the gradual closure of the fossettes/ids characteristic of protohypsodont teeth adds additional complications. On the other hand, the Deseadan to 'Pinturan' (late Oligocene–early Miocene; see Kramarz and Bellosi, 2005, for a discussion about the 'Pinturan') eocardiids, except for *L. propheticus* (Kramarz, 2006), are known through very scarce material that not only precludes a good understanding of the limits of the different taxa, but also of their ontogenetic variation and morphological diversity. In this context, we have been very conservative in the systematic assignment of the new fossils. We referred all the material with a persistent mesofossette/id to *Luantus*, and, in spite of the lack of association among lower and upper teeth, to only one species because in all of them the mesofossette/id is very small and rounded, and they match in size. On the contrary, the most complete specimen, MPEF-PV 1153, is the most complete material, and is assigned to *Chubutomys* because it does not display the mesofossettid in m1–m3, in spite of being a young adult specimen, with the m3 base still open.

Wood and Patterson (1959) divided the Family Eocardiidae into two subfamilies, implying an early dichotomy. Based on dental morphology, these authors established the Luantinae represented by *Asteromys* and *Luantus*, and Eocardiinae by *Chubutomys*, *Phanomys*, *Eocardia*, and *Schistomys*. Such characters as the metalophulid II (metalophid sensu Wood and Patterson, 1959) retained or not, presence/absence of cement, degree of hypsodonty, and persistent or ephemeral fossettes/ids were considered as relevant for distinguishing subfamilies (Wood and Patterson, 1959). The inclusion of *Chubutomys* within the 'eocardiines' followed the presence of high crown, more penetrating hypoflexid, and more ephemeral fossettids than in 'luantines' (thus resembling the Santacrucian euhypsodont *Eocardia*). In turn, *Asteromys* was interpreted as the most primitive member of a phyletic line formed by this genus and *Luantus*, defined by relatively lower crowned cheek teeth, more persistent fossettes/ids, hypoflex/id penetrating up to half of the oclusal surface, absence of cement, and metalophulid II lost in m2–m3 of later forms as *L. propheticus*.

Kramarz (2006) objected to this scheme. On the one hand, he stated that some of the characters used by Wood and Patterson had dubious systematic value, such as the structure of the metalophulid II (mesolophid for Kramarz) in view of the high variation seen in *Luantus*. In this genus (especially in *L. propheticus*, the best known species), the metalophulid II can be either present, reduced, or absent.

On the other hand, Kramarz (2006:775) stated that *L. toldensis* shares with Santacrucian eocardiids those characters that Wood and Patterson considered exclusive of the 'eocardiines,' and in addition they share the presence of cement, which is absent in *Chubutomys*. On this basis, Kramarz (2006) interpreted that "... *Asteromys*, *L. initialis*, *L. propheticus*, and *L. toldensis* represent an evolutionary series of increasing hypsodonty and related characters that leads to the euhypsodont dental pattern of *Eocardia.* The apical occlusal configuration of each species of this evolutionary series mimics the basal configurations of its ancestors." Consequently, Kramarz (2006) considered *Luantus* as the structural ancestor closest to *Phanomys* (and, implicitly, through this to later euhypsodont eocardiids), and interpreted *Chubutomys* as a member of an early hypsodont radiation of the family not directly related to Santacrucian eocardiids. Thus, Kramarz maintained the idea of a basal dichotomy for the eocadiids, although the relationships among genera proposed by him are quite different from those proposed by Wood and Patterson (1959).

The material here described is better understood under Kramarz's proposal. In this context, in the *Chubutomys* group, hypsodonty would be acquired earlier, cement would not be acquired, or would be only in very old individuals (no old individuals of *Chubutomys* are known), and the trilophodont pattern could be due to the fusion of metalophulid II to the hypolophid, with the consequent early disappearance of the mesofossetid. On the contrary in the clade *Asteromys* + *Luantus* + *Phanomys* + *Eocardia*, hypsodonty is more gradually acquired, cement is progressively acquired following increasing hypsodonty (but earlier than in *Chubutomys* in relation to the degree of hypsodonty and ontogenetic stage, if *Chubutomys* eventually acquired it), and the trilophodont pattern observed in many specimens of *Luantus* results from the reduction of the metalophulid II and the consequent merging of antero- and mesofossetids. Notwithstanding, it has to be considered that the evolutionary series proposed by Kramarz (2006) is founded on the basis of the increasing hypsodonty degree and the development of associated characters (e.g., occlusal simplification, increasing enamel discontinuities, cement gradually present in earlier ontogenetic stages). This series assumes that the evolutionary history of hypsodonty occurred progressively and irreversible. The evidence supplied by *Chubutomys leucoreios*, sp. nov., suggests that at least in this lineage, the evolution of hypsodonty could have been the opposite way, because the Deseadan species has a higher crown and larger enamel discontinuities than that of the Colhuehuapian *C. leucoreios*, sp. nov. An alternative hypothesis would be that both species referred to *Chubutomys* do not represent a phyletic line but are members of a group of eocardiids with precocious hypsodonty, extremely early disappearance of the mesofossettid, and lack of cement. *Chubutomys*—only known through these two species—would have been more rich and complex than so far supposed.

The levels in which these new species have been found–the Trelew Member of the Sarmiento Formation—were considered slightly younger than the Colhué Huapi Member (Gran Barranca) where *L. initialis* has been found (Simpson, 1935). However, Vucetich et al. (in press) considered that the differences between both localities are more related to environmental than temporal causes. The new species here described does not supply clear evidence to resolve this matter.

ACKNOWLEDGMENTS

We thank Carolina Vieytes (MLP) for her valuable comments about this research, and Cecilia Deschamps (MLP) for improving the English version; Jaime Groizard (ALUAR) for his technical work in the MEB, the curators Eduardo Ruigómez (MPEF) and Marcelo Reguero (MLP) for access to material under their care, Rosario Romero (MPEF) for illustration of *C. leucoreios*, sp. nov., specimen, and the technicians of MPEF for their laboratory work.

LITERATURE CITED

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia austral y depositados en el Museo de La Plata. Boletín del Museo de La Plata 1:1–26 (del apartado). Buenos Aires.

Ameghino, F. 1891. Caracteres diagnósticos de cincuenta especies nuevas de mamíferos fósiles argentinos. Revista Argentina de Historia Natural 1:129–167.

Ameghino, F. 1893. Les mammifères fossils de la Patagonie australe (notes par E. Trouessart). Revue Scientifique 51:13–17.

Ameghino, F. 1897. La Argentina a través de las últimas épocas geológicas. P. E. Coni, Buenos Aires.

Ameghino, F. 1899. Sinopsis geológico-paleontológica. Suplemento (Adiciones y correcciones). Imprenta La Libertad, La Plata.

Ameghino, F. 1900. L'âge des formations sédimentaires de Patagonie. Anales de la Sociedad Científica Argentina, Buenos Aires 50:109–130; 145–165, 209–229.

Ameghino, F. 1902. Première contribution à la connaissance de la faune mammalogique des couches à Colpodon. Boletin de la Academia Nacional de Ciencias de Córdoba 17:71–138.

Ameghino, F. 1906. Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie avec um parallèle entre leurs faunes mammalogiques et celles de l'ancien continent. Anales del Museo Nacional de Historia Natural de Buenos Aires 15:1–568.

Bowdich, T.E. 1821. An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travelers. J. Smith, Paris, 115 pp.

Contreras, J. 1964. Datos acerca de la variación intrapoblacional de la morfología de los molares de entidades de los géneros *Galea* y *Microcavia* (Rodentia, Caviidae). Ameghiniana 3:235–255.

Candela, A. M. 1999. The evolution of the molar pattern of the Erethizontidae (Rodentia, Hystricognathi) and the validity *Parasteiromys* Ameghino, 1904. Palaeovertebrata 28:53–73.

Fischer de Waldheim, G. 1817. Adversaria zoologica. Mémoires de la Société Impériale des Naturalistes de Moscou 5:357–428.

Janis, C. M. 1986. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference; pp. 367–387 in D. E. Russell, J. Santoro, and Sigogneau-Russell (eds.), Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology, Paris 1986. Mèmoires du Museum National d'Histoire Naturelle, Paris (serie C) 53:367–387.

Kraglievich, L. 1930. Diagnosis osteológico-dentaria de los géneros vivientes de la subfamilia Caviinae. Anales del Museo Nacional de Historia Natural de Buenos Aires 36:59–95.

Kramarz, A. G. 2006. Eocardiids (Rodentia, Hystricognathi) from the Pinturas Formation, late early Miocene of Patagonia, Argentina. Journal of Vertebrate Paleontology 26:770–778.

Kramarz, A. G., and E. S. Bellosi. 2005. Hystricognath rodents from the Pinturas Formation, early–middle Miocene of Patagonia, biostratigraphic and paleoenvironmental implications. Journal of South American Earth Sciences 18:199–212.

Landry, S. O. 1957. The Interrelationships of the New and Old World Hystricomorph Rodents. University of California Publications in Zoology 56:1–118.

Mares, M. A., and R. A. Ojeda. 1982. Patterns of diversity and adaptation in South American hystricognath rodents; in M. A. Mares and H. Genoways (eds.), Mammalian Biology in South America. Special Publication Pymatuning Laboratory of Ecology 6:393–432.

Marivaux, L., M. Vianey-Liaud, and J. J. Jaeger. 2004. High-level phylogeny of early Tertiary rodents: dental evidence. Zoological Journal of the Linnean Society 142:105–134.

Mones, A. M. 1982. An equivocal nomenclature: what means hypsodonty? Paläontologische Zeitschrift 56:107–111.

Patterson, B., and A. E. Wood. 1982. Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. Bulletin of the Museum of Comparative Zoology 149:370–543.

Quintana, C. A. 1998. Relaciones filogenéticas de roedores Caviinae (Caviomorpha, Caviidae), de América del Sur. Boletín de la Real Sociedad Española de Historia Natural (Sección Biología) 94:125–134.

Scasso, R. A., and E. S. Bellosi. 2004. Cenozoic continental and marine trace fossils at the Bryn Gwyn Paleontological Park, Chubut; in R. A. Scasso and E. S. Bellosi (eds.), Bryn Gwyn Guidebook, First International Congress on Ichnology, April 19–23. Museo Paleontológico Egidio Feruglio, Trelew, Argentina, 19 pp.

Simpson, G. G. 1935. Early and Middle Tertiary geology of the Gaiman Region, Chubut, Argentina. American Museum Novitates 775:1–29.

Tullberg, T. 1899. Uber das System der Nagethiere: eine phylogenetische Studie. Nova Acta Regiae Societatis Scientiarium Upsaliensis 3:1–514.

Vucetich, M. G. 1984. Los roedores de la Edad Friasense (Mioceno medio) de Patagonia. Revista del Museo de La Plata (nueva serie, Paleontología) 8:47–126.

Vucetich, M. G., A. G. Kramarz, and A. M. Candela. In press. Colhuehuapian rodents from Gran Barranca and other Patagonian localities: the state of the art; in R. H. Madden, A. A. Carlini, M. G. Vucetich, and R. F. Kay (eds.), The Paleontology of Gran Barranca: Evolution and Environmental Change Through the Middle Cenozoic of Patagonia. University of Cambridge Press, Cambridge, U.K.

Vucetich, M. G., C. M. Deschamps, A. I. Olivares, and M. T. Dozo. 2005. Capybaras, Size, shape, and time: a model kit. Acta Paleontologica Polonica 50:259–272.

Waterhouse, G. E. 1839. Observations on the Rodentia, with a view to point out the groups, as indicated by the structure of the crania in this order of Mammals. Magazine of Natural History 3:90–96.

Wood, A. E., and B. Patterson. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. Bulletin of the Museum of Comparative Zoology 120:280–428.

Woods, C. A., and E. B. Howland. 1979. Adaptive radiation of capromyid rodents: anatomy of the masticatory apparatus. Journal of Mammalogy 60:95–116.

Submitted February 8, 2009; accepted June 10, 2009.