

First record of *Banderomys leanzai* Kramarz, 2005 (Rodentia, Caviomorpha) in Chubut Province, Patagonia (Argentina)

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Abstract: Cephalomyidae was established in the XIX century, and was considered by different authors as a heterogeneous group of hypsodont South American hystricognath rodents. Other authors corroborated this family as a natural group among caviomorphs and recognized some taxa recorded from the Deseadan–Colhuehuapian South American Land Mammals Ages (SALMAs). Among them, *Banderomys leanzai* (the only species of this genus) was, until now, characteristic and exclusive of the locality of Cerro Bandera (early Miocene, Colhuehuapian?, Neuquén Province, Argentina). The aim of this work is to report the first record of *B. leanzai* outside the type locality; the new specimens come from the early Miocene of central Chubut Province (Patagonia, Argentina). This new finding extends the geographical distribution of the species and increases the dental morphology knowledge of *B. leanzai*.

Key words: *Banderomys*, Cephalomyidae, Hystricognathi, early Miocene, South America, Patagonia

Resumen: Primer registro de *Banderomys leanzai* Kramarz (Rodentia, Caviomorpha) en la provincia de Chubut, Patagonia (Argentina). Cephalomyidae fue establecida en el siglo XIX y considerada por diferentes autores como un grupo heterogéneo de roedores hystricognatos sudamericanos con dentición hipsodonte. Otros autores corroboraron a esta familia como un grupo natural dentro de los caviomorfos y reconocieron algunos taxones de las Edades Mamífero Deseadense-Colhuehuapense. Entre ellos, *Banderomys leanzai* (única especie del género) era, hasta el momento, característica y exclusiva de la localidad de Cerro Bandera (Mioceno temprano, Colhuehuapense?, provincia de Neuquén, Argentina). El objetivo de este trabajo es reportar el primer registro de *B. leanzai* fuera de la localidad tipo, los nuevos especímenes son del Mioceno temprano del centro de la provincia de Chubut (Patagonia, Argentina). Este nuevo hallazgo extiende la distribución geográfica de la especie e incrementa el conocimiento de la morfología dentaria de *B. leanzai*.

Palabras clave: *Banderomys*, Cephalomyidae, Hystricognathi, Mioceno temprano, América del Sur, Patagonia

INTRODUCTION

South American hystricognath rodents or Caviomorpha (e.g. viscachas, tuco-tucos, hutias, chinchillas, pacas, capybaras, porcupines) represent one of the most striking groups of the mammal assemblage of the continent (Mares & Ojeda, 1982; Patton *et al.*, 2015). The most ancient caviomorphs are known from the middle Eocene of Peru (Antoine *et al.*, 2012), and for the late Oligocene (i.e. Deseadan SALMA) they were

already highly diversified and widely distributed through South America (Vucetich *et al.*, 2015a). During the late Oligocene, the four superfamilies currently recognized within caviomorph (Chinchilloidea, Caviioidea, Octodontoidea, and Erethizontoidea), were represented by many lineages that are now completely extinct (e.g. cephalomyids, “eocardiids”, acaremyids). Among the latter, Cephalomyidae has been established by Ameghino (1897) on the basis of the Deseadan genus *Cephalomys*, which he considered as a

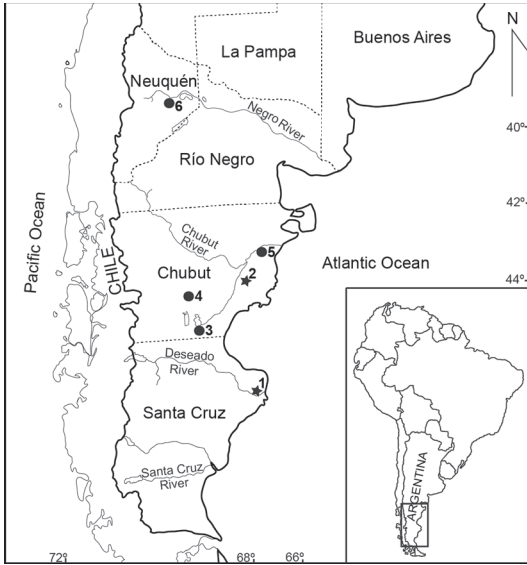


Fig. 1. Location map showing the Deseadan (stars) and Colhuehuapian (circles) Patagonian localities that share caviomorphs with Cerro Bandera locality: 1, La Flecha; 2, Cabeza Blanca; 3, Gran Barranca; 4, La Estrella; 5, Bryn Gwyn; 6, Cerro Bandera

group of caviomorph with generalized characters that originated the others South American hystricognath rodents. Other authors considered cephalomyids as a heterogeneous group that includes hypsodont forms (*Cephalomys*, *Litodontomys* Loomis, 1914; *Cephalomyopsis* Vucetich, 1985) with an enigmatic status, and uncertain phylogenetic relationships (Ameghino, 1897; Loomis, 1914; Simpson, 1945; Lavocat, 1976; Wood & Patterson, 1959; Patterson & Wood, 1982; Vucetich, 1985). Later, Kramarz described two new genera (*Soriamys* Kramarz, 2001 and *Banderomys* Kramarz, 2005) and performed a phylogenetic analysis that corroborated the monophyly of the family Cephalomyidae, recorded from the Deseadan–Colhuehuapian SALMAs (late Oligocene–early Miocene). During the last years only one new species (*Cephalomys ceciae* Vucetich *et al.*, 2015b) from the Deseadan of Patagonia was described. Some doubtful records for the Santacrucian (early Miocene; Chinchas Formation, San Juan, Argentina; López *et al.*, 2011) and the Laventan SALMAs (middle Miocene; Quebrada Honda, Bolivia; Croft *et al.*, 2011) were recognized but they need further revision. Cephalomyids have a wide geographical distribution with reports of records from the Bolivian localities of Salla (Lavocat, 1976) and Lacayani (Vucetich, 1989), and from

the Argentinean provinces of Chubut, Santa Cruz, Neuquén, and Corrientes (Ameghino, 1897; Wood & Patterson, 1959; Bond *et al.*, 1998; Kramarz, 2001, 2005).

Banderomys leanzai Kramarz (2005), the only species of this genus, was originally described from Cerro Bandera (Neuquén province, Argentina; Fig. 1), initially considered early Miocene in age (Colhuehuapian? SALMA, but see Kramarz *et al.*, 2011, 2013, 2015). *B. leanzai* is currently represented by scarce registers, including a poorly preserved mandible fragment, and some isolated teeth. Here, we report the first specimens of *B. leanzai* outside Cerro Bandera coming from a new locality in Chubut Province (Fig. 1). In addition, new dental material unknown for this species until now, provide a more complete knowledge of *Banderomys* enlarging the morphological information to future phylogenetic analysis.

MATERIALS AND METHODS

Institutional abbreviations

MOZ-PV, Museo Provincial de Ciencias Naturales “Dr. Prof. Juan A. Olsacher” Zapala, Neuquén, Argentina; **MPEF-PV**, Museo Paleontológico Egidio Feruglio – Paleontología de Vertebrados, Trelew, Chubut, Argentina; **PVPH**, Museo Municipal Carmen Funes, Plaza Huincul, Neuquén, Argentina.

Dental nomenclature and abbreviations

Dental nomenclature used here follows Arnal & Vucetich (2015). Upper tooth abbreviations: Al, anteroloph; Hf, hypoflexus; Ms, mesolophule; Msf, mesoflexus/mesofossette; Mt, metaflexus/metafossette; Mel, metaloph; Pf, paraflexus/parafossette; Prl, protoloph; Psl, posteroloph. Lower tooth abbreviations: af, anteroflexid/anterofossettid; hld, hypolophid; med I, metalophulid I; med II, metalophulid II; msf, mesoflexid/mesofossettid; mt, metaflexid/metafossettid; psd, posterolophid.

Material for comparison

For taxonomic determination, we conducted an extensive bibliographic revision, and the new specimens were compared with materials housed at PVPH and MOZ-PV, listed in Supplementary Data. The measurements of the new specimens were obtained using a digital caliper with an accuracy of 0.01mm (Table 1).

Table 1. Dental measurements of *Banderomys leanzai* from La Estrella. Abbr.: **AW**, anterior maximum preserved width; **L**, total preserved length; **PW**, posterior maximum preserved width. Measurements in mm.

Specimens	L	AW	PW
MPEF-PV 10996a M1or M2	3.14	3.11	2.89
MPEF-PV 10996b M1 or M2	3.21	3.23	3.04
MPEF-PV 10996c M1 or M2	3.09	3.24	3.05
MPEF-PV 10996d m1 or m2	3.97	2.68	2.26
MPEF-PV 10996e m3	4.59	3.99	3.52

GEOLOGICAL SETTING

Fossil material described here proceed from “La Estrella” (S 44°35’36.60”; W 69° 5’47.90”), named after its proximity (around 3 km in west-east direction) to the homonymous ranch, is located in the western part of the Meseta del Canquel, central Chubut Province, Argentina (Fig. 1) (see also Novo *et al.*, 2017: figure 1). The rocks bearing the herein reported teeth belong to the Sarmiento Formation. The section characterizes by around 18 m of a monotonous succession of mostly massive, fine tuffs, ranging in color from pinkish grey, in the lower section, to greyish, in the top. The fossiliferous section overlies basalts cropping out in the middle section of Meseta del Canquel (e.g. Scarritt Pocket), indicating a post-Deseadan age (Marshall *et al.*, 1986; Vucetich *et al.*, 2014), and underlies a basalt located toward the top of Meseta del Canquel, assigned by Marshall *et al.* (1986) to the lower Miocene. This stratigraphic position and similarities in lithological features recognized in La Estrella as well as in Gran Barranca (Spalletti & Mazzoni, 1979) allow assigning the study section to the Colhué Huapí Member.

The fossil mammal assemblage at La Estrella, is represented by caviomorph rodents (*Perimys*, *Banderomys*, *Eosteiomys*), plathyrrhine primates (*Mazzonicebus almendrae*; Novo *et al.*, 2017), xenarthrans (Dasypodinae, Glyptodontidae), Notungulata (Hegetotheriidae, Interatheriidae), and marsupials (Paucituberculata, Sparassodonta). Until now, *Banderomys* was exclusive from Cerro Bandera locality, considered early Miocene in age (Colhuehuapian?) by Kramarz (2005). However, Kramarz *et al.* (2011, 2013, 2015) questioned the age of Cerro Banderas due to the discovery

of additional caviomorphs (e.g. *Leucocephalos*, *Cephalomys*) that are only present in the older Deseadan SALMA and suggested that “... the Cerro Bandera assemblage would represent a transitional association between the typical Deseadan and Colhuehuapian faunas, corresponding to a pre-Colhuehuapian age, not recorded elsewhere in South America” (Kramarz *et al.*, 2011: 189). The presence of *M. almendrae*, *Perimys* and *Eosteiomys* at La Estrella and the absence of typical Deseadan taxa, suggests an age not older than the Colhuehuapian for this locality.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821

Suborder HYSTRICOGNATHI Tullberg, 1899

Family CEPHALOMYIDAE Ameghino, 1897

Genus *Banderomys* Kramarz, 2005

Banderomys leanzai Kramarz, 2005

Holotype. PVPH 367, left mandibular fragment with m1and m2 and the alveoli for the incisor and p4 (Kramarz, 2005: figs. 5A, 6).

Hypodigm. The new material described here MPEF-PV 10966a-e and the material listed in Kramarz 2005 (p. 251). MPEF-PV 10966a, left M1 or M2; MPEF-PV 10966b, right M1 or M2; MPEF-PV 10966c, right M1 or M2; MPEF-PV 10966d, left m1 or m2; MPEF-PV 10966e, right m3.

Geographic and stratigraphic provenance.

The new specimens come from La Estrella locality (Sarmiento Formation, Chubut Province, Argentina). All the material listed in Kramarz, 2005 (p. 252) come from Northwest of Sierra del Portezuelo Norte (Confluencia Department) and Cerro Bandera (Zapala Department), Cerro Bandera Formation, Neuquén Province, Argentina; pre-Colhuehuapian? – Colhuehuapian SALMA (early Miocene, Flynn & Swisher, 1995).

Diagnosis (from Kramarz, 2005: 250-251).

cephalomyid slightly larger than *Cephalomys arcidens*, with protohypodont cheek teeth, lower crowned than in *Cephalomys*; unilateral hypsodonty in the uppers. Cement absent. Unworn or little worn upper molars with pentalophodont or tetralophodont occlusal pattern; the labial flexi are wide and transverse, and the hypoflexus extends less than half way across the occlusal surface. Worn upper molars with rounded labi-

al fossettes; the mesofossette is the largest and most persistent, as in *Cephalomys*; hypoflexus extends only half way across the occlusal surface. Lower molars are tetralophodont during early and moderate stages of wear; lingual end of the metalophulid II connected with the postero-labial slope of the metaconid. The anterofossettid is the smallest and most ephemeral lingual flexid, and with wear the occlusal pattern turns trilophodont.

Description and comparison

The new specimens consist in isolated lower and upper teeth (Figs. 2, 3). The entire sample is assigned here to *Banderomys leanzai*, because the teeth share the combination of dental characters in the diagnosis for this species. Regarding general characteristics, the molari-forms are protohypodont, with crowns lower than *Cephalomys*, lack cement, and the enamel is continuous around the entire crown. The lower and upper dental series show an asymmetrical pattern, and with moderate wear, the occlusal surface becomes tetralophodont (Figs. 2A, B and see Kramarz, 2005). The upper molars have three roots, a large lingually and two smaller labially, like in *Cephalomys* and *Soriamys*. None of the lower molars preserved the roots in the new sample from Chubut.

Upper molars. Among the upper teeth in the new sample, there are three M1 or M2 (Figs. 2A–C and 3A–C); all of them show unilateral hypodonty. The MPEF-PV 10966a is a left M1 or M2 (Figs. 2A, 3A) with moderate stage of wear, the tooth appears to be tetralophodont but the posterior portion is broken and this cannot be corroborated. The hypoflexus is transversely short, V-shaped, and antero-posteriorly oriented, with the tip next to the paraflexus. The paraflexus and mesoflexus remain open, being the latter the deepest. These flexi are long and straight, wider labially, extending over the middle of the occlusal surface, and their lingual tips are slightly rounded. The only closed labial flexus is forming the metafossette, the anterior margin is relatively straight, and the lingual border is rounded. The postero-labial angle of the tooth is slightly broken and it is impossible to determine whether the posterofossette is present, although in this stage of wear, is usually present in the specimens from Cerro Bandera. The anterior margin of the anteroloph is straight and curved posteriorly at the lingual extreme. Thus, the protocone area is acute, while the hypocone area is more rounded

and slightly more labial than the former. The anteroloph and protoloph are relatively straight; the mesolophule is curved postero-labially, and is probably joined to the metaloph.

The MPEF-PV 10966b is a right M1 or M2 (Figs. 2B, 3B) a little more worn than MPEF-PV 10966a; at this stage of wear it is clearly tetralophodont with the three labial fossettes completely close, and the posterofossette is absent. The hypoflexus is longer than in MPEF-PV 10966a, transversely extending almost up to the middle portion of the occlusal surface. It is V-shaped with the lingual tip acute, near the parafossette. The fossettes are transversely elongated, especially the mesofossette. The anteroloph is curved, protoloph and mesolophule are relatively straight, and the posteroloph present a widening at its labial end. In this stage of wear, the protocone and hypocone areas are more triangular in outline than in MPEF-PV 10966a, and they are mesio-distally aligned.

MPEF-PV 10966c is a right M1 or M2 (Figs. 2C, 3C), showing a more advanced stage of wear even than MPEF-PV 10966b; it is broken with the posterior and labial portions missing. The hypoflexus is longer than in the other upper teeth of the sample. It is quadrangular at the labial extreme. It is slightly oblique, and almost contacts the parafossette. Only the lingual portion of the parafossette and the mesofossette are preserved, and they are rounded. The protocone area is rounded.

Lower molars. The lower teeth are represented by a m1 or m2 and the first m3 reported for *B. leanzai* (Figs. 2D–E, 3D–E). MPEF-PV 10966d is a left m1 or m2 (Figs. 2D, 3D) and it is badly damaged, with the entire lingual and postero-labial portion lost. The hypoflexid is wide and V-shaped, and is very close to the metafossettid. The preserved anterior margin of the metalophulid I is straight, while the posterior wall of the tooth appears to be oblique, typical of *B. leanzai* lower teeth. There is only a small vestige of the anterofossettid, almost lost due to wear. The preserved labial portion of the mesofossettid and metafossettid are rounded. The protoconid and hypoconid area are acute and mesio-distally aligned.

The MPEF-PV 10966e is a right m3 with moderate wear (Figs. 2E, 3E). It is assigned to a m3 due to the short posterior lophid and lack of wear facet on the posterior wall. Metalophulid I and II are connected at the lingual extreme, defining a small and boomerang-shaped anterofossettid. This fossettid is the first one formed, and

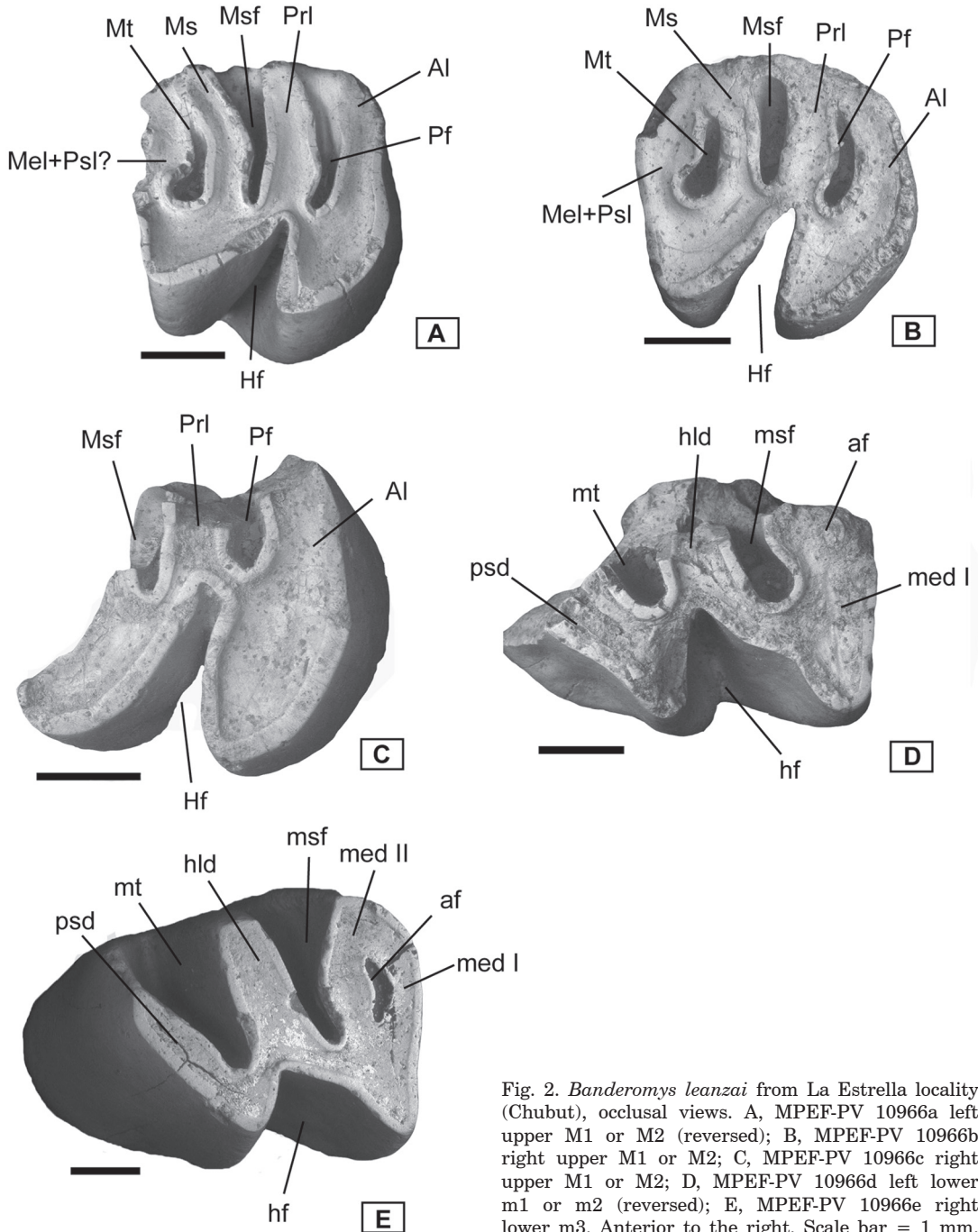


Fig. 2. *Banderomys leanzai* from La Estrella locality (Chubut), occlusal views. A, MPEF-PV 10966a left upper M1 or M2 (reversed); B, MPEF-PV 10966b right upper M1 or M2; C, MPEF-PV 10966c right upper M1 or M2; D, MPEF-PV 10966d left lower m1 or m2 (reversed); E, MPEF-PV 10966e right lower m3. Anterior to the right. Scale bar = 1 mm.

it would be rapidly lost with more wear. The hypolophid is wide and straight, and is as long as the metalophulids. The posterolophid is the shortest lophid with an antero-posteriorly oblique orientation, so the trigonid is much longer than the talonid. The area of the protoconid is more la-

bial than the hypoconid area. The mesoflexid is funnel shaped and large, extending beyond the middle of the occlusal surface. Its labial extreme is rounded and slightly curved anteriorly. The metaflexid also extends beyond the middle of the tooth, almost reaching the hypoflexid. It is

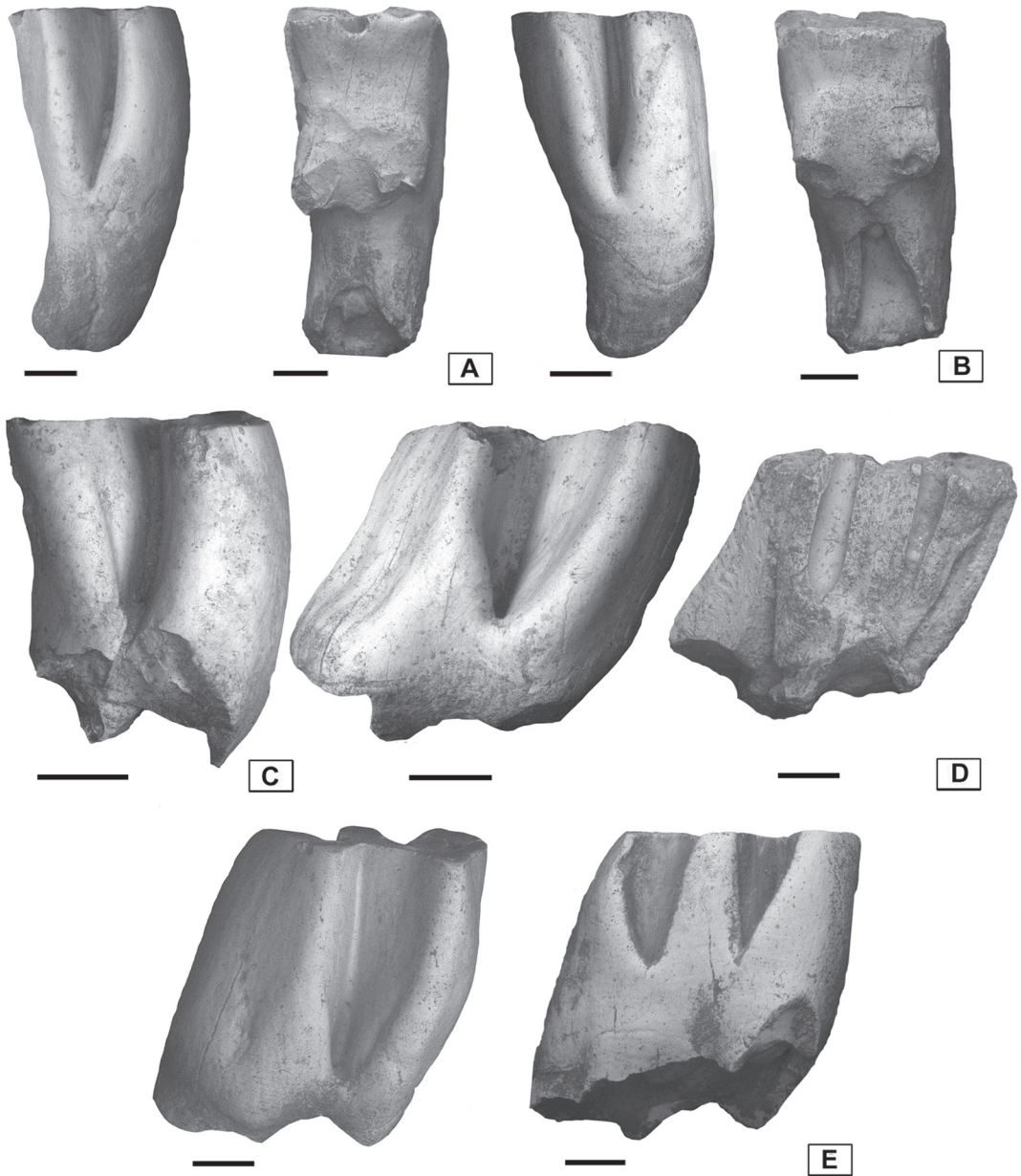


Fig. 3. *Banderomys leanzai* A, MPEF-PV 10966a lingual (reversed) and labial view; B, MPEF-PV 10966b lingual and labial (reversed) view; C, MPEF-PV 10966c lingual view; D, MPEF-PV 10966d labial (reversed) and lingual view; E, MPEF-PV 10966e labial and lingual (reversed) view. Anterior to the right. Scale bar = 1 mm.

transversal, with a rounded labial extreme and triangular outline. The mesoflexid is the last flexid to become a fossettid, but it seems that this is slightly variable between the specimens from Cerro Bandera. The hypoflexid is short and wide, with a V-shape outline and antero-posteriorly oblique. It does not pass the middle of the tooth and is markedly shorter than the lingual flexid.

DISCUSSION AND CONCLUSIONS

The family Cephalomyidae is an enigmatic group of caviomorph rodents, from a taxonomic and phylogenetic point of view. They are recorded from Deseadan to Colhuehuapian SALMAs, in middle (Bolivia) and high latitudes (Patagonia, Argentina) of South America (Ameghino, 1897;

Loomis, 1914; Wood & Patterson, 1959; Lavocat, 1976; Patterson & Wood, 1982; Vucetich, 1985, 1989; Kramarz, 2001, 2005). Frailey (1981) mentioned the presence of *Cephalomys* for the middle Miocene of Quebrada Honda (Bolivia), but we have not seen this material.

The cephalomyids known from Colhuehuapian localities in Patagonia (Fig. 1) come from Bryn Gwyn (*Soriamys gaimanensis*, *Cephalomyopsis hypselodontus*), Gan Gan (*S. ganganensis*), and Gran Barranca (cephalomyid indet.) in Chubut Province, and Cerro Bandera (*Banderomys leanzai*) in Neuquén Province (Vucetich, 1985; Kramarz, 2001, 2005; Vucetich et al., 2010).

Here we report the first specimens assigned to *Banderomys leanzai* outside of its type locality in a Colhuehuapian locality (La Estrella, Fig. 1; Novo et al., 2017) of Chubut Province. The age of La Estrella locality is supported by the sedimentological data (see Geological Setting above) and mammal assemblage, especially by the presence of *Mazonicebus almendrae*, *Perimys* and *Eosteiomys* which are not found in older SALMAs. This new record enlarges the geographical distribution of *B. leanzai* for the Colhuehuapian SALMA.

Most genera of caviomorph rodents found in Cerro Bandera are present in other pre-Deseadan to “Colloncuran” localities of Argentina, Bolivia, and Chile.

Eosteiomys? (see Vucetich et al., 2010), *Caviocricetus*, *Galileomys*, and *Eoviscaccia* from Cerro Bandera, are also recorded in Gran Barranca and Bryn Gwyn localities in Chubut Province (Colhuehuapian SALMA; Vucetich et al., 2010). *Eosteiomys* is also found in the Pinturas Formation (Santa Cruz Province, Argentina; Kramarz, 2004). *Eoviscaccia* is also recorded in some Deseadan localities such as Cabeza Blanca (Chubut Province, Argentina) and Lacayani (Bolivia) (Vucetich, 1989), and in the Tinguirirican locality of Chile (Bertrand et al., 2012), whereas *Galileomys* is found in Cañadon del Tordillo (“Colloncuran” SALMA, Neuquén Province; Vucetich & Kramarz, 2003) and Pinturas Formation (Kramarz, 2004). *Leucokephalos* (exclusive of the Deseadan age; Vucetich et al., 2015b) come from Cabeza Blanca. *Cephalomys* is found in several Deseadan localities of Argentina and Bolivia, the best knowns are La Flecha (Santa Cruz Province, Argentina; Loomis, 1914) and Cabeza Blanca (Wood & Patterson, 1959). *Banderomys* is now recorded in La Estrella locality and in this context, *Doryperimys* and *Garridomys* (Kramarz et al.,

2013, 2015) are the only exclusive caviomorph rodents of Cerro Bandera Formation. If an earlier age is corroborated for Cerro Bandera, the biochron of this species would encompass a pre-Colhuehuapian to Colhuehuapian age.

Cephalomyids are poorly known, excepting *Cephalomys*; and thus, more collection efforts are needed in order to find more and more complete material that allow to shed light to this intriguing caviomorph family.

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