A primitive cephalomyid hystricognath rodent from the early Miocene of northern Patagonia, Argentina

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A new genus and species, *Banderomys leanzai*, from the Cerro Bandera Formation (early Miocene?) of Neuquén province, Argentina, is described. It is known through a mandibular fragment with two molars and several isolated cheek teeth. With wear the upper molars develop a bilobate pattern, whereas the lowers molars attain a trilophodont one. *Banderomys* is referred to the Cephalomyidae because it has an "asymmetric" dental pattern as other members of the family, but it is less hypsodont, and therefore it is more primitive than any other contemporary or older cephalomyids so far known. A phylogenetic analysis suggests that the relationships between the Cephalomyidae and the Cavioidea are closer than what was traditionally assumed. The cephalomyids would have radiated in pre-Deseadan times, from an ancestor with a dentition very close to that of *Banderomys*, and reached their main diversity during the Deseadan–Colhuehuapian lapse, when they constituted the dominant hypsodont rodent group in South America.

Key words: Rodentia, Hystricognathi, Cephalomyidae, Cerro Bandera Formation, Miocene, Neuquén province, Patagonia.

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Introduction

The Cephalomyidae was originally established by Ameghino (1897) as the basal stock of the Hystricomorpha. Later authors considered *Cephalomys* Ameghino, 1897 (Deseadan SALMA) and its allies as ancestral or mere collateral branches of different hypsodont groups (Loomis 1914; Miller and Gidley 1918; Kraglievich 1940; Simpson 1945; Landry 1957). Wood and Patterson (1959) and Patterson and Wood (1982) rejected the validity of the Cephalomyidae, whereas Vucetich (1985) accepted them as a heterogeneous group of hypsodont genera related to the Chinchillidae. Recent discoveries of fossil rodents related to *Cephalomys* (Vucetich 1985, 1989; Kramarz 2001a) from Deseadan (late Oligocene) and Colhuehuapian (early Miocene) levels, have helped to enlarge our knowledge about the diversity and evolution of the Cephalomyidae, and the recognition of these South American extinct hystricognaths as a natural group with well-defined dental characteristics (Kramarz 2001a).

In this contribution I describe a new genus and species of hystricognath rodents related to *Cephalomys*, which is represented by a single mandibular fragment with two molars and many isolated lower and upper cheek teeth. These remains were discovered in the Cerro Bandera Formation, Neuquén Province, Argentina (Fig. 1), assigned to the Colhuehuapian SALMA (Leanza and Hugo 1997; Kramarz et al. 2001). This record brings new information about the early evolution of the family, and is the first one in non-traditional Patagonian localities of this age.

Abbreviations.—SALMA, South American Land Mammal Age; M/m, upper/lower molar; DP/dp, upper/lower deciduous premolar; P/p, upper/lower premolar.

Institutional abbreviations.—MACN, Museo Argentino de Ciencias Naturales "B. Rivadavia", Buenos Aires, Argentina; MLP, Museo de La Plata, Argentina; PV-MOZ, Paleontología de Vertebrados, Museo Juan A. Olsacher, Zapala, Neuquén, Argentina; PVPH, Paleontología de Vertebrados, Museo Carmen Funes, Plaza Huincul, Neuquén, Argentina.

Geological setting

The Cerro Bandera Formation (Leanza and Hugo 1997) is a Miocene continental succession 45 m thick, exposed in isolated areas at the NE of Barda Negra, South of Cerro Bandera, NW of Sierra del Portezuelo and at the NW slope of Cerro Bayo Mesa, Neuquén Province, Northwest Patagonia (Argentina) (Fig. 1). This unit conforms the relicts of an old sedimentary filling developed in small local valleys excavated on Late Cretaceous (Neuquén Group) and Paleocene (Roca Formation) rocks. This paleotopography was attributed by Uliana (1978) and Leanza and Hugo (1997) to a process of uplift and erosion related to the diastrophic Pehuenchan phase (late Oligocene) (Yrigoyen 1979). The sequence is composed of alternated primary and reworked pyroclastic deposits, with several pedogenized and bentonitic levels, and epiclastic sandstones in the upper section (Fig. 2). The origin of these depos-

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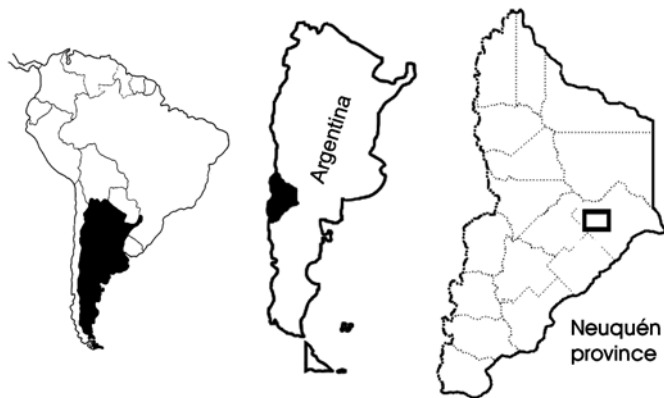
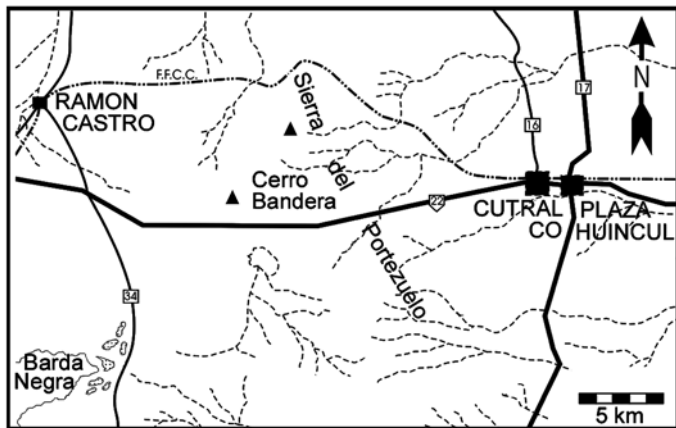http://app.pan.pl/acta50/app50-249.pdf

Fig. 1. Location map showing fossil localities (triangles) of the Cerro Bandera Formation in Neuquén Province, North Patagonia, Argentina.

its would be associated with a fluvial environment of moderate energy, with lacustrine deposits (bentonites) confined in the central areas of the paleovalleys, and soil development in the topographically higher areas (Leanza and Hugo 1997; Kramarz et al. in press). The Cerro Bandera Formation is overlain by younger Neogene sediments (Collón Cura or Bayo Mesa Formations).

Fossil mammals were recovered from both bentonitic and pedogenized tuffs (Fig. 2). Colhuehuapian SALMA (early Miocene) is inferred for this unit because of the presence of *Cramauchenia normalis* (Litopterna), *Proadinotherium* cf. *P. muensteri* (Notoungulata), *Eosteiromys* sp., and *Caviocricetus lucasi* (Rodentia), plus a species of *Protypotherium* (Notoungulata) with more primitive dentition than those known from the Santacrucian Age (Kramarz et al. 2001).

Systematic paleontology

Order Rodentia Bowdich, 1821
Suborder Hystricognathi Tullberg, 1899
Family Cephalomyidae Ameghino, 1897
Genus *Banderomys* nov.

Type species: *Banderomys leanzai* sp. nov.

Etymology.—In relation to Cerro Bandera Formation, the unit in which all the material was recovered.

Stratigraphical and geographic distribution.—Colhuehuapian SALMA (early Miocene, Flynn and Swisher 1995); Neuquén Province, Argentina.

Diagnosis.—A cephalomyid slightly larger than *Cephalomys arcidens*, with protohypsodont 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 crown. Worn upper molars with rounded labial fossettes, the mesofossette is the largest and most persistent, as in *Cephalomys*; hypoflexus extends only half way across the crown. Lower molars are tetralophodont during early and moderate stages of wear, lingual end of the mesolophid connected with the posterolabial slope of the metaconid. The
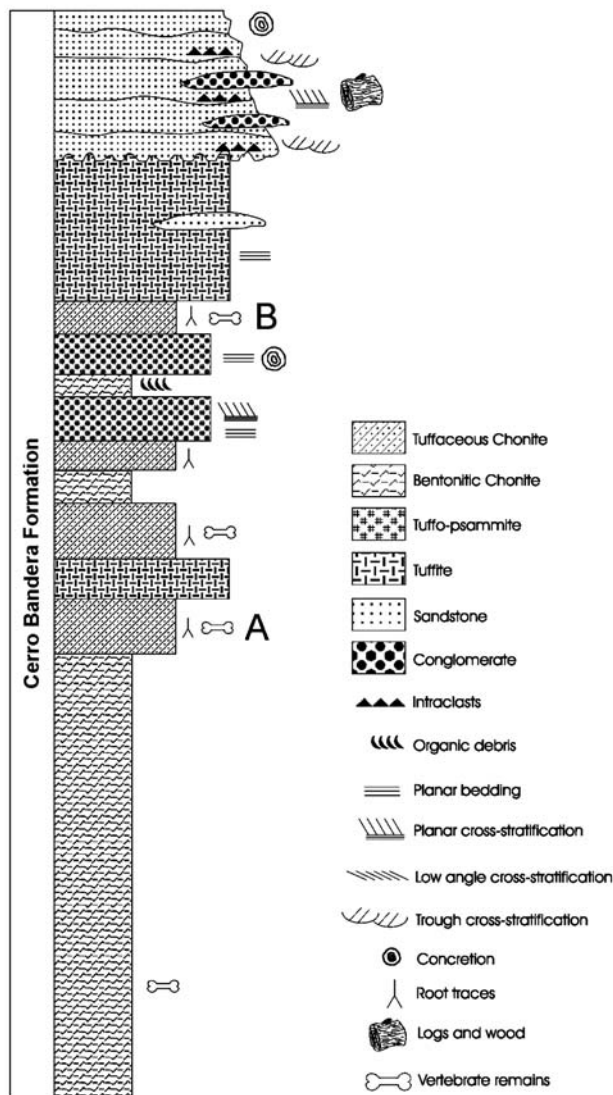

Fig. 2. Reconstructed profile of the Cerro Bandera Formation (modified from Kramarz et al. in press). Fossil localities: A, Cerro Bandera; B, Sierra del Portezuelo Norte.
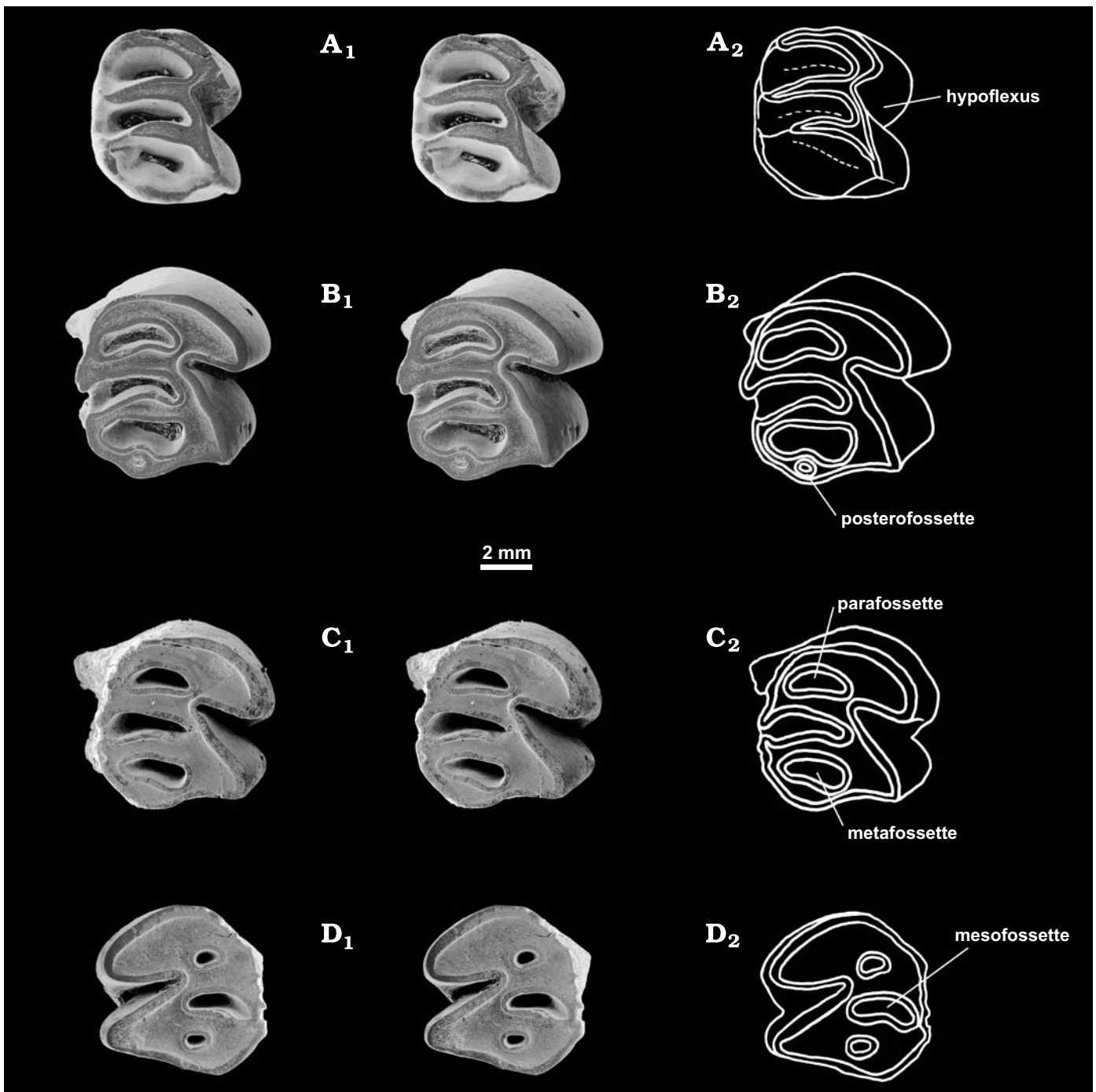
Fig. 3. *Banderomys leanzai* gen. et sp. nov., upper dentition. **A**. Right M1 or M2 (PV 6832 MOZ), stereophotographs (A$_1$) and diagramatic sketch (A$_2$). **B**. Right M1 or M2 (PV 6833 MOZ), stereophotographs (B$_1$) and diagramatic sketch (B$_2$). **C**. Right M1 or M2 (PVPH 363), stereophotograph (C$_1$) and diagramatic sketch (C$_2$). **D**. Left M1 or M2 (PVPH 364), stereophotograph (D$_1$) and diagramatic sketch (D$_2$). All in occlusal view, anterior is up.

anterofossettid is the smallest and most ephemeral lingual flexid and with wear the occlusal pattern turns trilophodont.

Banderomys leanzai sp. nov.

Figs. 3–6.

Holotype: PVPH 367 (Figs. 5A, 6), left mandibular fragment with m1 and m2 and the alveoli for the incisor and p4.

Hypodigm: The holotype and the following specimens: PVPH 363, right isolated M1 or M2; PVPH 364, left isolated M1 or M2; PVPH 365, isolated right M3; PVPH 366, isolated right m1 or m2; PVPH 368, isolated right m1 or m2; PVPH 369, isolated right p4; PVPH 370, 13 isolated upper molars; PVPH 448, 4 isolated lower molars; PV 6832 MOZ, isolated right M1 or M2; PV 6833 MOZ, isolated right M1 or M2; PV 6834 MOZ, isolated right DP4; PV 6835 MOZ, isolated right m1 or m2; PV 6836 MOZ, isolated right m1 or m2; PV 6837 MOZ, 4 isolated upper molars; PV 6838 MOZ, 3 isolated upper molars.
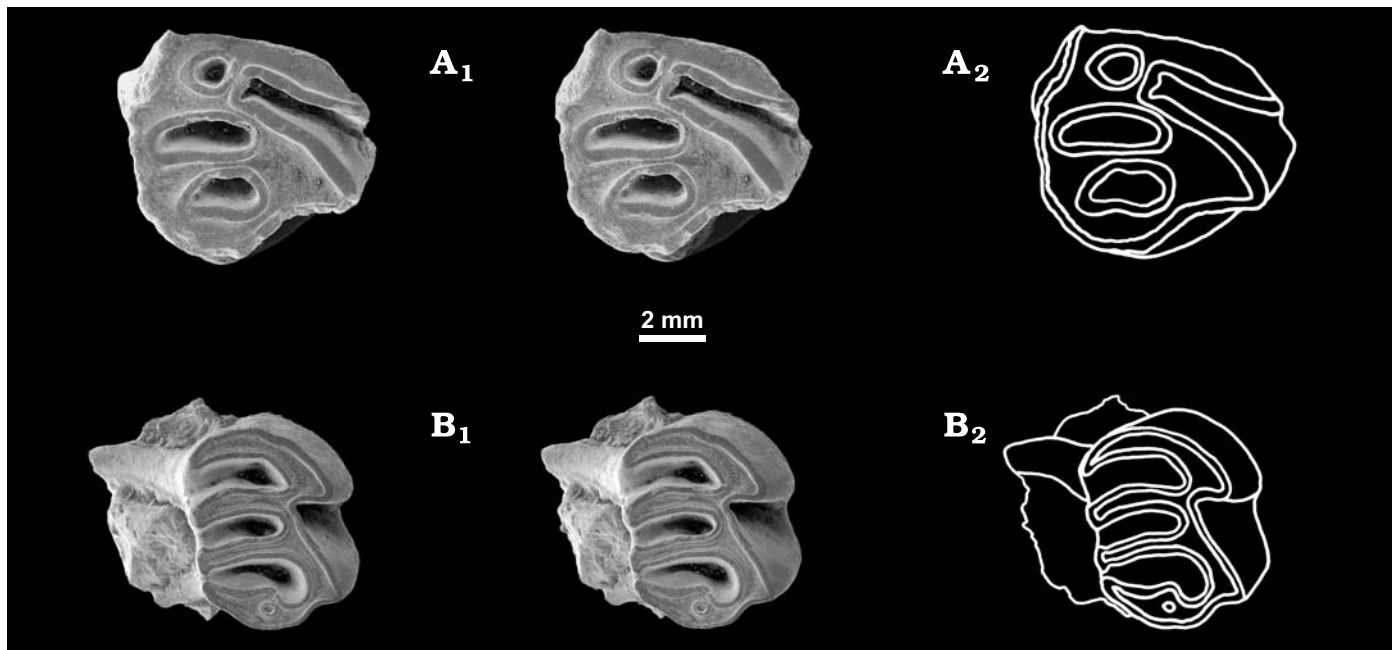
Fig. 4. *Banderomys leanzai* gen. et sp. nov., upper dentition. **A**. Incomplete right M3 (PVPH 365), stereophotographs (A$_1$) and diagrammatic sketch (A$_2$). **B**. Right DP4 (PV 6834 MOZ), stereophotographs (B$_1$) and diagrammatic sketch (B$_2$). All in occlusal view, anterior is up.

Etymology.—In acknowledgement to Dr. Héctor Leanza for his studies on the geology and biostratigraphy of Neuquén Basin.

Geographic provenance.—PVPH 363–370 and 448 come from Northwest of the Sierra del Portezuelo Norte (Confluencia Department, Neuquén Province, Fig. 1); PV 6832 MOZ–PV 6838 MOZ come from Cerro Bandera (Zapala Department, Neuquén province, Fig. 1).

Stratigraphic provenance and age.—All the materials derive from the Cerro Bandera Formation, Colhuehuapian SALMA (Leanza and Hugo 1997; Kramarz et al. 2001), early Miocene.

Diagnosis.—As for the genus.

Description and comparisons

The cheek teeth of *Banderomys leanzai* are protohypsodont (*sensu* Mones 1982), lower crowned than in *Cephalomys*; the uppers have conspicuous unilateral hypsodonty. The enamel covering does not present discontinuities.

The upper dentition (Figs. 3 and 4) is known only through isolated cheek teeth. Unworn or little worn upper molars are longer than wider (Fig. 3A, B, Table 1). At this stage of wear the labial flexi are large and sub-equal; the hypoflexus penetrates less than half way across the crown, as in *Cephalomys* and *Soriamys* Kramarz, 2001a (Colhuehuapian SALMA). Some molars have a minute ephemeral posterofossette, determining an initial pentalophodont occlusal pattern (Fig. 3B), in opposition to *Cephalomys*. The variable presence of such a fossette would depend on the position of the molar in the tooth row, as in the protohypsodont eocardiid *Luantus*

propheticus, from the early Miocene "*couches à Astrapothericulus*" (Ameghino 1900–1902, 1906). When present, the posterofossette is not located on the posterolabial corner of the tooth—the usual position in most of the pentalophodont Hystricognathi—but is located slightly more lingually on the posterior margin.

With wear the main labial flexi become rounded fossettes; the mesofossette is the largest one, and all persist until final stages of wear (Fig. 3C, D). The oblique hypoflexus penetrates opposite to the parafossette nearly half way across the crown, insinuating a bilobed pattern. On the contrary, in *Cephalomys* and *Soriamys* all the fossettes become worn away; the mesofossette is the more persistent one, and the hypoflexus is more penetrating, transverse and opposite to the protoloph. Thus the occlusal surfaces attain a well-defined simplified bilobed pattern.

The M3 (Fig. 4A) is differentiable in its robust posterolabial root and shows a posterolabial extension less developed

Table 1. Statistics of dental measurements (in mm) for *Banderomys leanzai* gen. et sp. nov. Abbreviations: APL, anteroposterior length; n, number of specimens; TRW, transverse width; SD, standard deviation.

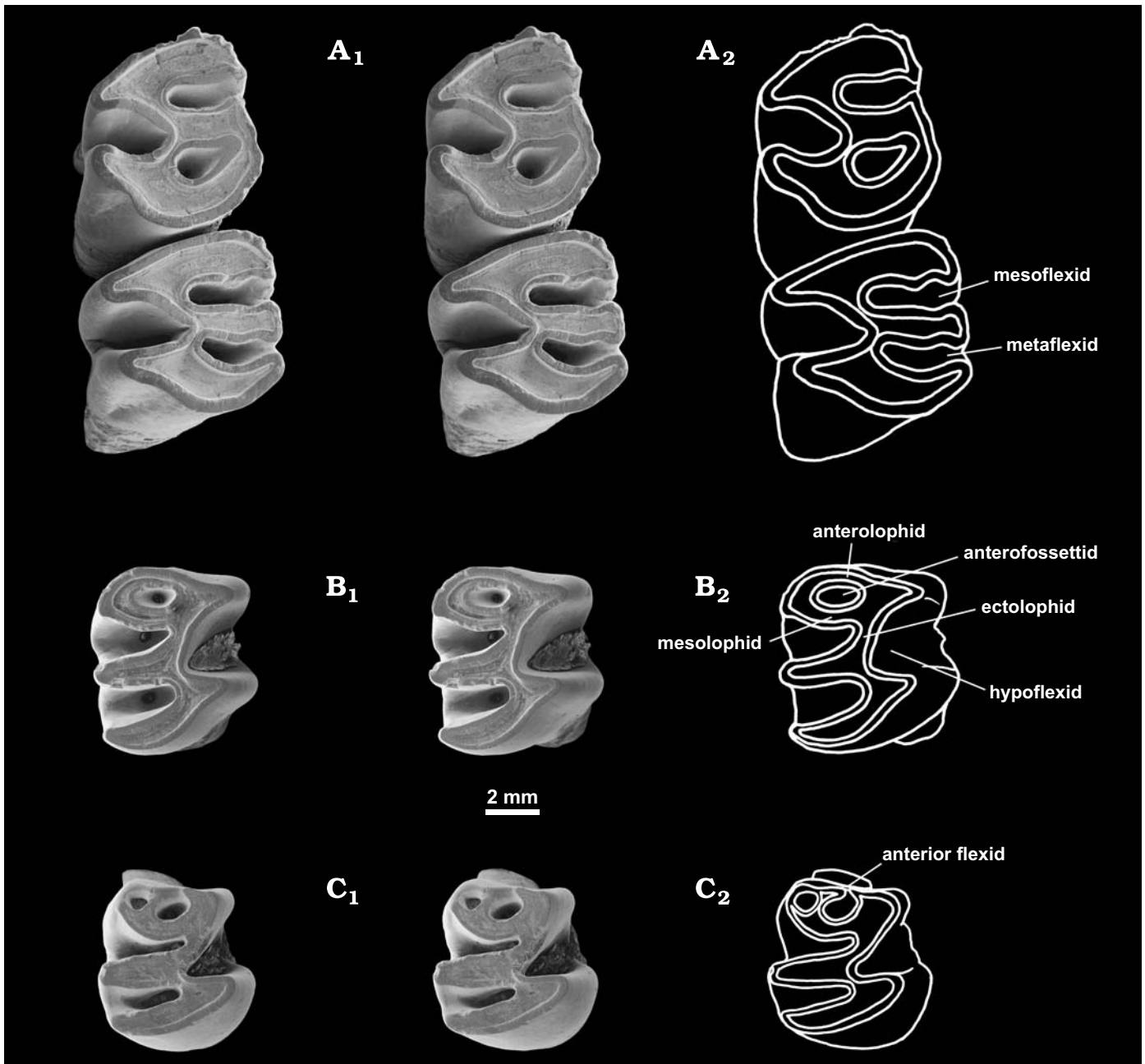|		DP4	M1 or M2	M3	p4	m1	m2	m1 or m2
n		2	10	1	1	2	2	5
APL	mean	3.275	3.59	3.95	3.25	3.65	3.65	3.8
	range	0.05	0.4	0	0	0.2	0	0.65
	SD	0.035	0.126	–	–	0.141	0	0.262
TRW	mean	2.45	3.35	3.25	3	3.35	3.275	3.54
	range	0.5	0.65	0	0	0	0.55	0.7
	SD	0.354	0.236	–	–	0	0.389	0.288

Fig. 5. *Banderomys leanzai* gen. et sp. nov., lower dentition. **A**. Left m1–m2 (PVPH 367, holotype), stereophotographs (A$_1$) and diagrammatic sketch (A$_2$). **B**. Right m1 or m2 (PVPH 366), stereophotographs (B$_1$) and diagrammatic sketch (B$_2$). **C**. Right p4 (PVPH 369), tentatively assigned, stereophotographs (C$_1$) and diagrammatic sketch (C$_2$). All in occlusal view, anterior is up.

than in *Soriamys* and *Eoviscaccia* Vucetich, 1989 (Deseadan and Colhuehuapian SALMA).

The only available DP4 (Fig. 4B) is lower crowned and narrower than the molars (Table 1), but has a pentalophodont occlusal pattern. No permanent upper premolar is known.

The lower molars are tetralophodont during initial and moderate stages of wear (Fig. 5B). The anterior margin of the molars is slightly convex, as in *Cephalomys*, but not as much as in *Soriamys*. The mesolophid extends from the protoconid, as in *Soriamys*, not from the ectolophid as in *Cephalomys*, and its lingual end curves forward to contact the

posterolabial slope of the metaconid. The mesostylid is indistinguishable. The anterolophid and the mesolophid delimit a small anterofossettid that is less ephemeral than in *Soriamys*. The anterofossettid is worn away in advanced stages and the molar acquires a trilophodont occlusal pattern (Fig. 5A) as in *Soriamys*, but the crests are less oblique. The mesoflexid of m1 and m2 remains open until more advanced stages of wear than the metaflexid, as in *Cephalomys*, but in the latter the metafossettid is also ephemeral and with wear the teeth attain an eight-shaped occlusal pattern. Three-crested molars are also present during unworn or little worn stages in the early

lagostomine *Eoviscaccia*, but such pattern is attained by the simple reduction of the mesolophid (Kramarz 2001b), in contrast with the Cephalomyidae. The base of the posterior wall of the hypoconid is slightly concave, thus the inflection of the posterolabial wall of the tooth is well marked in very worn teeth (see the m1 of the holotype, Fig. 5A) and much less conspicuous in unworn or little worn teeth (Fig. 5B).

I tentatively refer to this species one isolated p4 (Fig. 5C). It is rather smaller than m1 of the holotype (Table 1), but the distance between the roots agrees with that of the alveoli of the p4. The central portion of the anterolophid is unworn even in this stage of wear, suggesting that a superficial anterior flexid was present on the anterior wall of the tooth. Such flexid is also present in primitive octodontoids, in *Cephalomys*, *Asteromys* Ameghino, 1897 (Deseadan SALMA), and in juvenile specimens of *Scotamys* Loomis, 1914 (Deseadan SALMA), *Eoviscaccia*, and *Luantus*, and is considered a primitive character for the Hystricognathi (Vucetich and Kramarz 2003). As in the molars, the lingual end of the mesolophid curves forward to contact the metaconid. The occlusal pattern of the p4 differs from that of the molars by having a small anteroposterior crest between the mesolophid and the anterolophid that crosses the anterofossetid. The hypoconid does not present the posterior concavity observed in the lower molars.

A portion of the mandible is preserved in the holotype (Fig. 6). The preserved part of the diastema is slightly concave, nearly as in *Cephalomys* and *Soriamys*, but the symphysis is comparatively higher. The mental foramen is not present on the preserved part of the jaw. The masseteric crest is very prominent and there is not a differentiable scar for the *M. masseter medialis pars infraorbitalis* (*sensu* Woods and Howland 1979), as in *Platypittamys* Wood, 1949 (Deseadan SALMA). The posterior part of the alveolus for the incisor is incomplete but it surely extended posteriorly at least up to a point below the m3, and therefore it was longer than in *Soriamys*. The labial wall of the mandible is preserved back to the level of the posterior root of the m2, and it shows no evidence of the beginning of the coronoid process, suggesting that it was reduced as in the cavioiids, *Cepha-*

Fig. 6. *Banderomys leanzai* gen. et sp. nov. Left mandibular fragment in lateral view (PVPH 367, holotype).

lomys, *Soriamys*, *Perimys* Ameghino, 1887 (Colhuehuapian to Santacrucian SALMA), and *Prolagostomus* Ameghino, 1887 (Santacrucian to Friasian SALMA), or displaced posteriorly as in the extant chinchillid *Lagidium*.

The affinities of *Banderomys leanzai*

In a preliminary examination we interpreted that *Banderomys* could be related to the eocardiids (Kramarz et al. 2001) by having upper worn molars with a bilobed occlusal pattern with small rounded fossettes restricted to the labial portion of the teeth. However, this pattern is also present, at least temporarily, in other unrelated primitive hypsodont Hystricognathi (e.g., *Soriamys*, *Eoviscaccia*, *Scotamys*). Further, *Banderomys* lacks the characteristic reduction of the mesofossette and mesofossettid of the eocardiids (Wood and Patterson 1959), present in the more primitive known eocardiid *Asteromys*.

Cheek teeth of *Banderomys* have nearly the same size and the same height of the crowns as *Australoprocta* Kramarz, 1998, a primitive dasyproctid from the Colhuehuapian beds of Chubut province. With the exception of these general dental features, *Australoprocta* clearly differs from *Banderomys* by having persistent and more compressed fossettes and fossettids, and a figure S shaped occlusal pattern in advanced stages of wear. Possibly *Banderomys* would play a similar ecological role to *Australoprocta*, but there is really no evidence supporting phylogenetic affinity between *Banderomys* and the dasyproctids.

As far as it is known, *Banderomys* does not present features that suggest any affinities with the Octodontoidea. With the exception of its latest members, this superfamily is characterised mainly by primitive characters, at least from the dental point of view. The only derived character is the presence of a multiserial right-angle incisor enamel microstructure (Martin 1992), but this condition is still not testable in *Banderomys*. Moreover, *Banderomys* shows a much more advanced hypsodonty than all the known Oligocene and early Miocene octodontoids.

The more conspicuous dental feature of *Banderomys* is that, with wear, the upper molars attain a not fully developed bilobed configuration whereas the lowers become trilophodont by the fusion of the anterolophid with the mesolophid. Therefore, the occlusal pattern of the lower molars does not mirror that of the uppers (asymmetric dental pattern). Such transformations are also observed during middle stages of wear in *Cephalomys* and early stages in *Soriamys*. The Cephalomyidae were recognised as a monophyletic group (Kramarz 2001a), characterised by such asymmetry between the occlusal morphology of the upper and lower cheek teeth. *Soriamys*, *Cephalomyopsis* Vucetich, 1985 (Colhuehuapian SALMA), and probably also *Litodontomys* Loomis, 1914 (Deseadan SALMA), may be considered part of this clade. On the other hand, *Perimys* (Colhuehuapian–Santacrucian
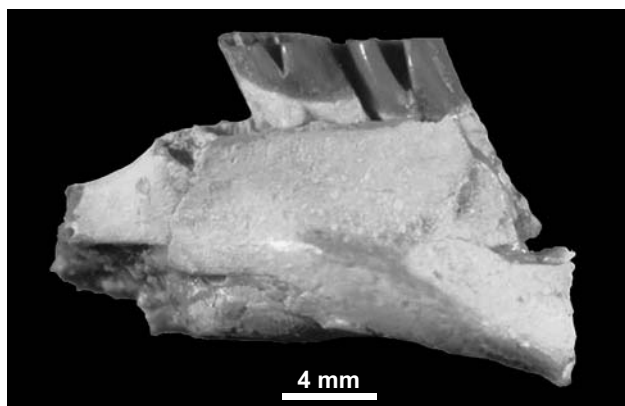
Table 2. List of characters and character definition used in the phylogenetic analysis.

Character 1. Angular process extends more ventrally than the mental keel
    0 = no 1 = yes

Character 2. Height of the condyle
    0 = high 1 = low

Character 3. Discontinuity between the masseteric crest and the tubercle for the insertion of the M. masseter medialis pars infraorbitalis
    0 = absent 1 = present

Character 4. Location of the tubercle for insertion of the tendon of the pars maxilomandibularis
    0 = posterior to the level of m1 1 = at the level of m1 2 = anterior to the level of m1

Character 5. Length of the diastema
    0 = shorter than the tooth row 1 = equal or longer than the tooth row

Character 6. Concavity of the diastema
    0 = concave 1 = plane, diastema almost at the same height of the alveolar line

Character 7. Mental foramen (non additive)
    0 = present, lateral 1 = present, dorsolateral 2 = absent

Character 8. Coronoid procces
    0 = high, starting at the level of the m2 1 = reduced (and/or posteriorly displaced)

Character 9. Degree of hypsodonty
    0 = brachyodont 1 = protohypsodont 2 = euhypsodont

Character 10. Cement
    0 = absent 1 = present

Character 11. Asymmetric pattern of the upper and lower teeth
    0 = absent 1 = present

Character 12. Lamination of the dental morphology
    0 = absent 1 = cheek teeth composed by subtriangular lobes 2 = cheek teeth composed by rectangular laminae

Character 13. Incisor enamel microstructure (after Martin, 1992)
    0 = multiserial, acute angular 1 = multiserial, right angular

Character 14. Posterior extension of the lower incisors
    0 = up to below the m3 or more 1 = up to below the m2 2 = up to the m1

Character 15. Fusion of the mesolophid with the anterlophid
    0 = no 1 = yes

Character 16. Reduction of the mesolophid
    0 = complete 1 = reduced

Character 17. Mesoflexid remains opened
    0 = no 1 = yes

Character 18. Dental replacement
    0 = normal replacement 1 = deciduous premolars retained

Character 19. Penetration degree of the hypoflexus in upper molars (in adults)
    0 = hypoflexus does not extends more than half way across crowns
    1 = hypoflexus extends more than half way across crowns
    2 = hypoflexus crosses completely the crowns

Character 20. Direction of the penetration of the hypoflexus
    0 = obliquely, opposed to the parafossete 1 = transversally, opposed to the protoloph

Character 21. Width of the hypoflexus (non additive)
    0 = normal 1 = compressed 2 = very thick

Character 22. Third lamina or lobe in M3
    0 = absent 1 = present

SALMA) and probably *Scotamys* (Deseadan SALMA) represent a distinct lineage, more closely related to the Chinchillidae (Kramarz 2001a) by their symmetrical laminar dental pattern.

The extant genus *Abrocoma* also has an asymmetrical dental pattern, but its relationships with the octodontoids (Ellerman 1940; Simpson 1945; Landry 1957; Patterson and Wood 1982; Carleton 1984; Parent 1980; Reig 1986; Martin 1992; Huchon and Douzery 2001) or with the chinchilloids (Glanz and Anderson 1990; Kramarz 2001a), are still controversial.

A cladistic analysis was performed in order to determine the affinities of *Banderomys*. The criterion of maximum parsimony was followed using the NONA program (Goloboff 1993). Node support was assessed using Relative Bremmer Support values calculated by searching suboptimal trees up to 4 extra steps with mult* 100 (40 sub optimal trees were found).

The analysis included *Cephalomys* and *Soriamys* (Cephalomyidae), *Perimys* (Neoepiblemidae), Lagostominae (*Lagostomus* plus *Eoviscaccia*), the protohypsodont eocardiid *Luantus*, *Abrocoma*, *Octodontomys* (Octodontidae), *Proechimys* (Echimyidae), and the primitive octodontoid *Platypittamys*. The Erethizontidae *Steiromys* Ameghino, 1887 (Santacrucian SALMA) were selected as the outgroup because of previous hypotheses suggesting that the erethizontids represent an independent radiation of South American hystricognaths (Sarich and Cronin 1980; Woods and Hermanson 1985; Bugge 1985; Bryant and McKenna 1995).

Only mandibular and dental characters were evaluated, as they are the only ones that can be tested in *Banderomys*. Characters of the occlusal morphology (characters 15, 16, 17, and 20) were evaluated in the Lagostominae through inference of those observed in *Eoviscaccia*; these characters were evaluated in *Perimys* in juvenile specimens (see Kramarz 2002). Character states are listed in Table 2. For character 9, degree of hypsodonty, three states have been determined (brachyodont, protohypsodont and euhypsodont, following Mones 1982) in order to not overweight this feature. Therefore, same state was assigned to *Luantus*, *Cephalomys*, and *Banderomys*, even taking into account that they have positively different degrees of hypsodonty. Characters 7 (location of the mental foramen) and 21 (width of the hypoflexus) were treated as unordered multi-state characters because I could not deduce *a priori* the transformation series. The data matrix is shown in Table 3.

Results and conclusions

Two most parsimonious trees were obtained by exhaustive searching, with length = 53, ci = 54, and ri = 62; the strict consensus tree is shown in Fig. 7. *Banderomys* groups with the cephalomyids *Cephalomys* and *Soriamys* by sharing 3 apomorphies: asymmetric pattern of the upper and lower teeth (character 11), fusion of the mesolophid with the anter-

Table 3. Taxon-character matrix employed for assessing the phylogenetic relationship of *Banderomys leanzai* sp. nov. with eleven selected taxa all belonging to the Hystricognathi. Characters and character definition are listed in Table 2. Missing or unknown characters are represented by "?".

Character / taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Steiromys	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platypittamys	0	0	0	?	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cephalomys	1	1	0	2	0	1	1	1	1	0	1	1	0	0	1	0	1	0	1	1	0	?
Banderomys	?	?	0	1	?	1	?	1	1	0	1	1	?	0	1	0	1	0	0	0	0	0
Soriamys	1	1	0	2	1	1	1	1	1	1	1	1	?	1	1	0	1	0	1	1	2	1
Lagostominae	0	0	?	1	1	0	2	1	2	0	0	2	0	0	0	1	0	0	2	0	1	1
Perimys	0	0	0	0	1	0	0	1	2	1	0	2	0	2	0	1	0	0	1	0	2	1
Luantus	1	?	0	1	0	1	1	1	1	?	0	1	0	1	0	?	0	0	1	1	0	1
Proechimys	0	0	0	1	0	0	2	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0
Abrocoma	0	0	1	2	1	0	2	0	2	1	1	2	1	0	?	?	1	1	0	1	2	1
Octodontomys	0	0	1	2	0	0	2	0	2	0	0	0	1	0	?	1	1	0	?	0	0

lophid (character 15) and the mesoflexid remaining open (character 17). However, *Banderomys* is more plesiomorphic than the remaining cephalomyids by having a primitive condition of the scar for insertion of the tendon of the *M. masseter medialis pars infraorbitalis* (character 4), hypoflexus penetrating only half way across the crown (character 19), oblique and opposite to the paraflexus (character 20). Moreover, *Banderomys* is even less hypsodont than *Cephalomys*: the cheek teeth are lower crowned, the enamel layer is continuous and occlusal simplification occurs comparatively later during ontogeny. Nevertheless, the presence of an asymmetrical dental pattern, at least during advanced stages of wear, clearly reveals its affinities with the cephalomyids. On the other hand, the affinities of *Abrocoma* with the chinchillids or with the cephalomyids is not supported in the present analysis, but it clusters with *Octodontomys* by sharing the discontinuity between the masseteric crest and the tubercle for the insertion of the *M. masseter medialis pars infraorbitalis* (character 3), the anterior location of this tubercle (character 4), the euhypsodont condition (character 9) and mesoflexid remaining open (character 17); the latter feature and the asymmetric dental pattern (character 11) would be convergent with that of the cephalomyids.

The relationships of *Cephalomys* and its allies vary depending on studies (see Wood and Patterson 1959). Landry (1957) included the cephalomyids within the Chinchilloidea, and at present this is the more accepted position (Vucetich 1985, 1989; Dozo 1995; Vucetich et al. 1999; Kramarz 2001a). In the current analysis the cephalomyids are excluded from the Chinchilloidea and are grouped with the eocardiid *Luantus* by sharing the angular process extended more ventrally than the mental keel (character 1) and the diastema almost at the same height as the alveolar line (character 6). Moreover, *Soriamys* and *Cephalomys* share with *Luantus* some suggestive dental characters, as the transverse penetration of the hypoflexus (character 20) and the development of an anterior derivation of the ectolophid in the dp4 (Kramarz 2001a). These results are in agreement with Kra-

glievich's proposal (1940), followed by Simpson (1945) and McKenna and Bell (1997). However, I must admit that these results must be taken cautiously and more evidence is necessary to define the nesting of the Cephalomyidae within the Cavioidea, as well as to resolve the relationships of the Chinchilloidea with the Octodontoidea and Cavioidea.

The record of the Cephalomyidae is characterised by the coexistence of species at very different evolutionary stages: the Cephalomyidae indet. described by Vucetich (1989) (very probably allied to *Cephalomyopsis hypselodontus*), from the Deseadan SALMA of Patagonia and Bolivia, has euhypsodont cheek teeth, and therefore is much more derived than its contemporaneous *Cephalomys* and *Litodontomys*. Likewise, *Banderomys* is more primitive than its Colhuehuapian allies *Soriamys* and *Cephalomyopsis*. This pattern suggests that the family would have its main radiation during pre-Deseadan times. Such radiation would have occurred from an ancestor with a dentition structurally very close to that of *Banderomys*, which gave rise to the main
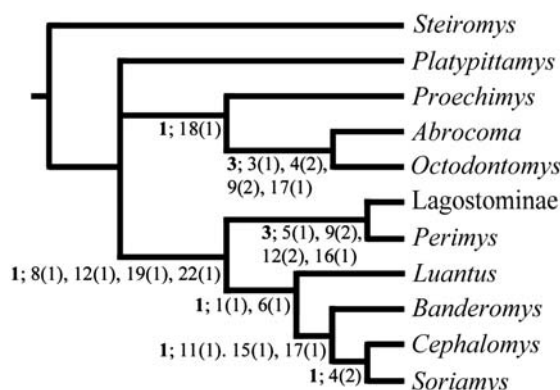

Fig. 7. Strict consensus from two most parsimonious trees obtained by exhaustive searching, with length = 53, ci = 54, and ri = 62. Numbers in boldface are Relative Bremmer Support index, calculated by searching suboptimal trees up to 4 extra steps with the command mult* 100 (40 suboptimal trees were found). Normal numbers are apomorphies corresponding to characters listed in Table 2; character states are enclosed in parentheses.

group of high-crowned hystricognath rodents during the Deseadan–Colhuehuapian lapse. In fact, *Cephalomys* is the most abundant rodent of the Deseadan record of Patagonia (Vucetich 1986), *Soriamys* is the most abundant hypsodont rodent, at least at the Colhuehuapian Gaiman locality (Chubut province), and *Banderomys* is the more abundant rodent so far known at Cerro Bandera Formation.

Frailey (1980) reported the record of *Cephalomys*, or some related genus (Vucetich 1985), in Santacrucian sediments of Bolivia; however no cephalomyid is recorded at the rich Patagonian localities of this age or younger. This suggests that cephalomyids would have declined after the Colhuehuapian, coinciding with the adaptive radiation of other South American high-crowned hystricognath rodents, such as the caviids, dasyproctids and, to a lesser extent, the chinchillids.

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