

Original article

First complete skull of an octodontoid (Rodentia, Caviomorpha)  
from the Early Miocene of South America and its bearing  
in the early evolution of Octodontoidea<sup>☆</sup>

*Premier crâne complet d'un octodontoïde (Rodentia, Caviomorpha) du Miocène inférieur  
d'Amérique du Sud : apport à l'évolution précoce des Octodontoidea*

Michelle Arnal<sup>\*</sup>, Alejandro G. Kramarz

*Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470,  
C1405DJR Buenos Aires, Argentina*

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**Abstract**

Octodontoidea is the most diverse group of caviomorph rodents. The systematics of most of the fossil representatives has been essentially based upon dental characters. Described here is an almost complete skull with dentition assigned to *Prospaniomys* Ameghino based upon its dental morphology. The specimen comes from the Sarmiento Formation at Pampa de Gan Gan (central Patagonia, Argentina), assigned to the Colhuehuapian SALMA (early Miocene). The most remarkable features are in the posterior portion of the skull, some of them shared with the modern octodontids and interpreted as specialized by previous authors, which contrast with the generalized dental morphology. These combined features were not previously known in other octodontoids. The comparisons with other fossil and extant members of the superfamily suggest that the characters traditionally used to associate *Prospaniomys* with the echimyids are very probably plesiomorphies. *Prospaniomys* would represent an early diverging lineage more closely related to modern octodontids than to echimyids, in which cranial structures evolved more rapidly than dental and mandibular ones.

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*Keywords:* Rodentia; Octodontoidea; *Prospaniomys*; Skull anatomy; Miocene; Patagonia

**Résumé**

Les Octodontoidea sont le groupe le plus diversifié de rongeurs caviomorphes. La systématique de la plupart des représentants fossiles se base essentiellement sur des caractères dentaires. On décrit ici un crâne presque entier, avec sa denture complète, attribué au rongeur caviomorphe *Prospaniomys* Ameghino sur la base de la morphologie dentaire. Le spécimen provient de la Formation Sarmiento à Pampa de Gan Gan (Patagonie Centrale, Argentine), attribuée au Colhuehuapien (Miocène inférieur). Les traits les plus remarquables sont la présence de caractères très spécialisés dans la partie postérieure du crâne, quelques uns partagés avec les octodontidés modernes, contrastant avec la morphologie dentaire généralisée. Cette combinaison de caractères n'était jusqu'à présent pas connue chez d'autres octodontoïdes. La comparaison avec d'autres représentants fossiles et actuels de cette superfamille suggère que les caractères traditionnellement utilisés pour associer *Prospaniomys* aux échimyidés sont très probablement plésiomorphes. *Prospaniomys* pourrait représenter une lignée précocement divergente, plus étroitement reliée aux octodontidés modernes qu'aux échimyidés, et dont les structures crâniennes ont évoluées plus rapidement que celles dentaires et mandibulaires.

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*Mots clés :* Rodentia ; Octodontoidea ; *Prospaniomys* ; Anatomie crânienne ; Miocène ; Patagonie

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<sup>☆</sup> Corresponding editor: Gilles Escarguel.

<sup>\*</sup> Corresponding author.

*E-mail address:* michoarnal@macn.gov.ar (M. Arnal).

## 1. Introduction

Octodontoidea is the most diverse group of caviomorph rodents both in number of species and adaptative forms (Reig, 1986, 1989; Huchon and Douzery, 2001). They are characterized by their derived incisor enamel microstructure (Martin, 1992) and the retention of the DP4/dp4 in the living and most of the fossil species (Wood and Patterson, 1959; Vucetich and Verzi, 1991; Verzi, 1994). The oldest occurrence of this group is in the early Oligocene (Vucetich et al., 2010b; but see Frailey and Campbell, 2004), and by the late Oligocene (Deseadan South American Land Mammal Age, SALMA) the group was widely distributed in Patagonia, Bolivia, and Brazil (Wood, 1949; Wood and Patterson, 1959; Patterson and Pascual, 1968; Patterson and Wood, 1982; Vucetich and Ribeiro, 2003). The extant Octodontoidea are classified in two main groups: Echimyidae (including Myocastorinae) and Octodontidae (including Ctenomyiinae) (Simpson, 1945; Huchon and Douzery, 2001; Honeycutt et al., 2003), with the status of Capromyidae and Abrocomidae still controversial (Glanz and Anderson, 1990; Galewski et al., 2005). All fossil octodontoids older than Chasicosan SALMA (late Miocene) are almost entirely known through dental and mandibular remains, and are traditionally included within the Echimyidae or the Octodontidae (Wood and Patterson, 1959; Patterson and Pascual, 1968; Patterson and Wood, 1982), although their relationships with the modern forms are still controversial (Vucetich and Verzi, 1991; Vucetich and Kramarz, 2003; Carvalho and Salles, 2004).

*Prospaniomys* is an octodontoid rodent described by Ameghino (1902) based on a single mandible with dp4-m1 and the incisor. Further authors referred additional dental materials, including upper cheek teeth (Ameghino, 1904; Patterson and Pascual, 1968; Patterson and Wood, 1982; Kramarz, 2001); new findings confirm these associations (Vucetich et al., 2010a). The only nominal species, *P. priscus*, occurs in levels assigned to the Colhuehuapian SALMA (early Miocene) of Patagonia (Wood and Patterson, 1959; Vucetich et al., 2010a). Based on mandibular and incisor morphology, Ameghino (1902) suggested that *Prospaniomys* was the ancestor of *Spaniomys*. Several authors agreed with Ameghino's proposal, and included both genera into the Echimyidae, as a separate group (Wood and Patterson, 1959) or related with the extant *Myocastor* (Patterson and Pascual, 1968; Patterson and Wood, 1982). Vucetich and Verzi (1991), Vucetich et al. (1993) and Emmons and Vucetich (1998), proposed new relationships within the Echimyidae and removed *Prospaniomys* from the ancestry of *Spaniomys*. Later, Kramarz (2001, 2004) suggested that *Prospaniomys* could be the ancestor of a group including *Spaniomys*. Carvalho and Salles (2004) performed a cladistic analysis in which *Prospaniomys* is placed in an unresolved polytomy within fossil echimyids. Recently, Vucetich et al. (2010a) included *Prospaniomys* in the Adelphomyiinae (Echimyidae).

In this contribution, we describe an almost complete skull with the whole dentition referable to *Prospaniomys* based upon its dental morphology; it is the first skull known for this genus

and the best preserved Miocene octodontoid skull known so far. This specimen was collected during a MACN-SUNY expedition during the eighties, led by J.G. Fleagle and M.F. Soria. It comes from Colhuehuapian levels of the Sarmiento Formation exposed at Pampa de Gan Gan, near the cerro Sacanana, in Chubut Province, Argentina (Rusconi, 1935; Feruglio, 1949; Fleagle and Bown, 1983) (Fig. 1). It is herein compared with representatives of the previously recognized main groups of echimyid and octodontid rodents, and preliminary considerations on the phylogenetic meaning of the cranial characters are provided. The study of this material supplies relevant additional information for the genus *Prospaniomys*, and allows comparisons of cranial features with other octodontoids, besides the already known dental features. This information is relevant for further phylogenetic studies in order to elucidate the relationships among this and other basal octodontoids and the better known modern forms, as well as the principal features of the early evolution of these rodents.

## 2. Systematic paleontology

Teeth of the upper dentition are indicated by upper case letters. Cranial nomenclature follows Van der Klaauw (1931), Woods and Howland (1979), and Wible et al. (2005), unless specified in the text. Tooth nomenclature follows Marivaux et al. (2004). The fossil and extant material studied in this work is listed in Appendix A.

Order RODENTIA Bowdich, 1821

Suborder HYSTRICOGNATHI Tullberg, 1899

Superfamily OCTODONTOIDEA Waterhouse, 1839

Genus *Prospaniomys* Ameghino, 1902

**Type and only species:** *Prospaniomys priscus* Ameghino, 1902.

**Occurrence:** Sarmiento Formation, Chubut Province, Argentina. Colhuehuapian SALMA (early Miocene).

*Prospaniomys* cf. *P. priscus*

Figs. 2–4

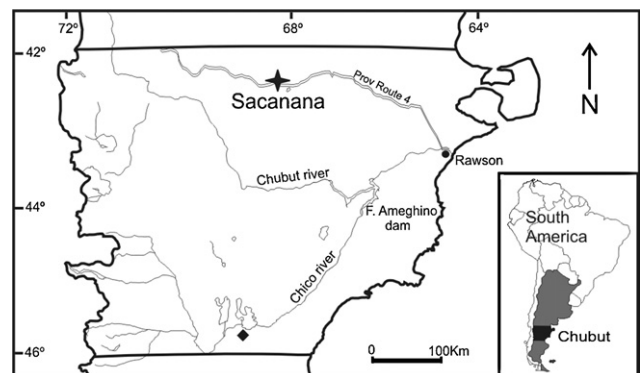


Fig. 1. Map of Chubut province, Argentina, showing the location of Sacanana (★), at Pampa de Gan Gan, where MACN PV CH 1913 was collected, and Gran Barranca (◆).

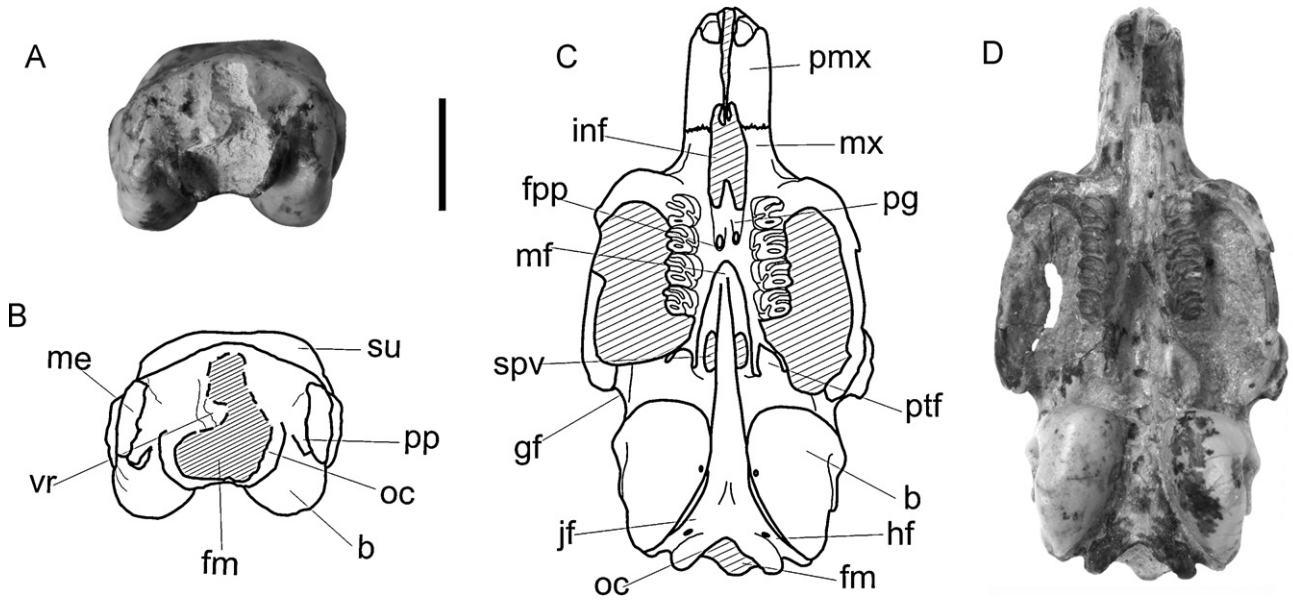


Fig. 2. *Prospaniomys* cf. *P. priscus*, MACN Pv CH1913. **A, B.** Posterior view of the skull. **C, D.** Ventral view of the skull. Abbreviations: b: bulla; fm: foramen magnum; fpp: foramen postpalatine; gf: glenoid fossa; hf: hypoglossal foramen; inf: incisive foramen; jf: jugular foramen; mf: mesoptergoid fossa; me: mastoid exposure; mx: maxilla; oc: occipital condyle; pg: palatal grooves; pmx: premaxillary; pp: paraoccipital process; ptf: pterygoid fossa; spv: sphenopalatine vacuity; su: supraoccipital; vr: vertical ridge. Striped area: fill with sediment. Scale bar: 10 mm.

**Referred material:** MACN Pv CH1913, an almost complete skull with complete dentition.

**Occurrence:** Sarmiento Formation exposed at Pampa de Gan Gan, Chubut Province, Argentina. Colhuehuapian SALMA (early Miocene).

**Description**

**Dentition:** The specimen MACN Pv CH1913 has preserved the complete dentition, except the distal ends of both incisors. The incisors are delicate and semi-circular in cross section (Fig. 2(C–D)). The anterior enameled face is curved. The

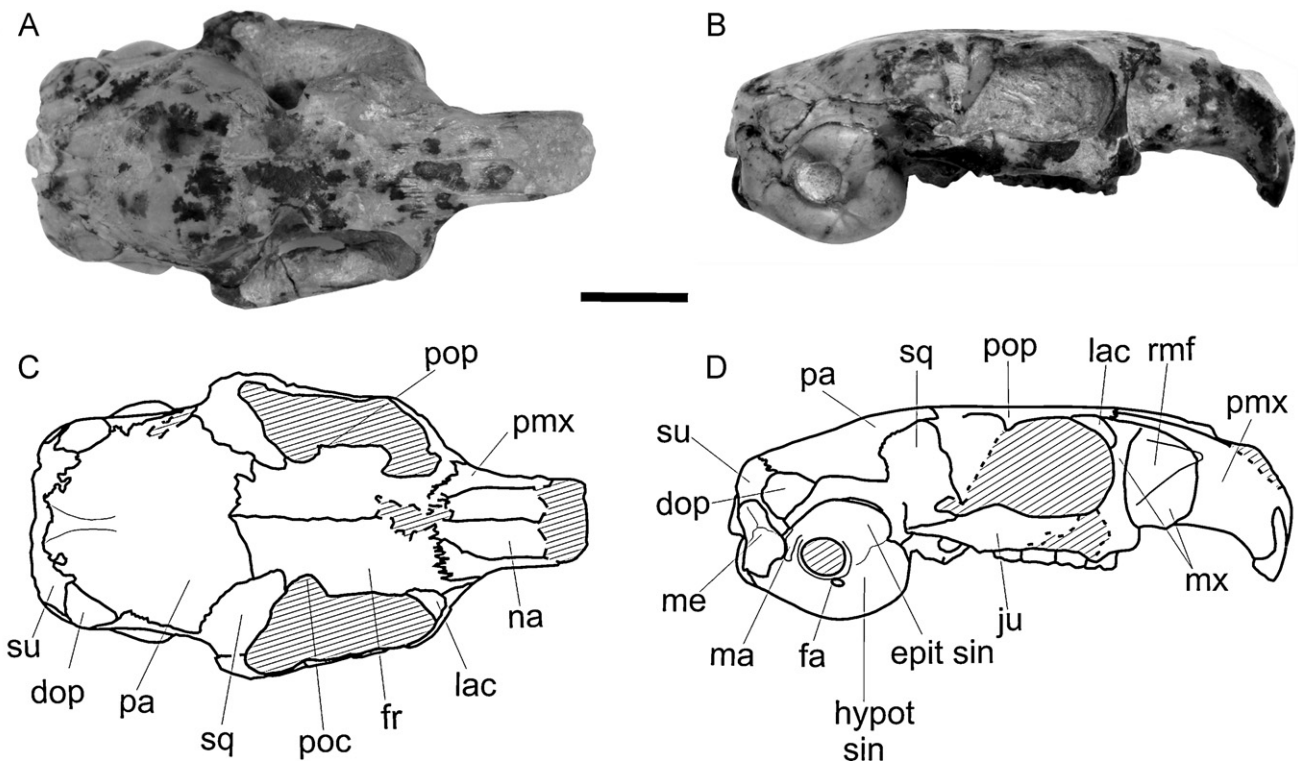


Fig. 3. *Prospaniomys* cf. *P. priscus* MACN Pv CH1913. **A, C.** Dorsal view of the skull. **B, D.** Lateral view of the skull. Abbreviations: dep: dorsal exposition of the petrosal bone; epit sin: epitympanic sinus; fa: accessory foramen; fr: frontal; hypot sin: hypotympanic sinus; lac: lacrimal; ju: jugal; ma: mastoid apophysis; me: mastoid exposure; mx: maxilla; na: nasal; pa: parietal; pmx: premaxilla; poc: postorbital constriction; pop: postorbital process; rmf: rostral masseteric fossa; sq: squamosal; su: supraoccipital. Striped area: fill with sediment. Scale bar: 10 mm.

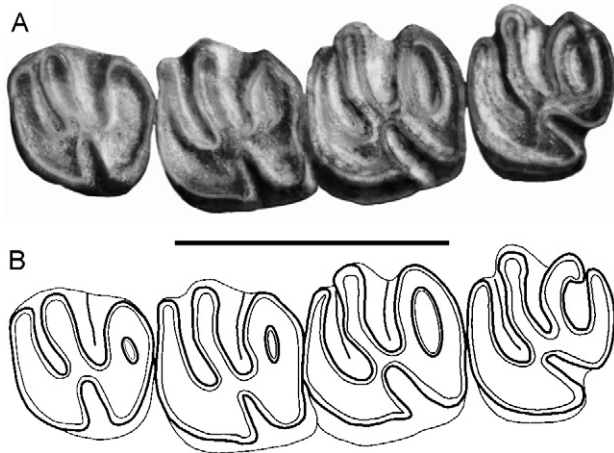


Fig. 4. *Prospaniomys* cf. *P. priscus*, MACN Pv CH1913. A. Upper cheek teeth in occlusal view. B. Diagram of the upper cheek teeth. Anterior to left. Scale bar: 5 mm.

incisors are short, with the base located dorsal and slightly anterior to the ventral root of the zygoma. The preserved portions of the incisors suggest that they are not proodonts (*sensu* Landry, 1957; Fig. 3(B, D)).

The cheek teeth show rather intense wear, indicating that it was an adult specimen (Fig. 4). They are proportionally large in comparison with the size of the skull and are implanted nearly perpendicular with respect to the palatal plane. All the cheek teeth are brachyodont and tetralophodont, and have sub-quadrangular contour as in *Protacaremys*, *Acarechimys*, *Platypittamys*, and the acaremyids. The M2 is slightly larger than the remaining teeth (Table 1). The labial cusps, specially the paracone, are recognized by a marked thickening and elevation of the labial ends of the corresponding crests, thus the occlusal surfaces are somewhat concave. The crests are narrow, separated by wide and relatively deep valleys as in *Protacaremys* and *Acarechimys*. The molars have the protocone area enlarged, forming a nearly right anterolingual corner, and is somewhat posteriorly elongated, forming a sharp posterior projection in M1 and M2. The area of the hypocone is rounded and smaller than that of the protocone. The anteroloph departs

directly from the protocone and forms almost the entire anterior margin of the tooth, but does not reach the labial margin; it is rather convex, especially the lingual portion. The protoloph is the largest crest and extends from the junction of the posterior arm of the protocone and the mure to the paracone. The labial portion of the protoloph is almost transverse, but the lingual portion is oblique, aligned with the hypoflexus; this inflection is more evident in M2 and M3. The protoloph remains isolated from the anteroloph until very advanced stages of wear. The metaloph departs from the junction of the mure and the anterior arm of the hypocone and extends up to the metacone; it is convex in all molars. The posteroloph forms the posterior margin connecting the hypocone and the metacone, enclosing a posterior fossette. The mesoflexus is the widest and deepest valley; the posterior fossette is the smallest and most ephemeral, and the anterior flexus is the most penetrating valley (nearly two thirds of the width of the occlusal surface). The hypoflexus is very compressed and penetrates obliquely (posterolingual-anterolabial), opposed to the protoloph nearly one-third of the width of the occlusal surface. The M3 has the hypocone more labially located, thus the two posterior transverse lophs are shorter than in M1 and M2.

The anterior cheek tooth is DP4, as in *Protacaremys*, *Acarechimys*, *Stichomys* and *Spaniomys*, since it is more worn than the following teeth (Fig. 4). The morphology is essentially as in M1 and M2, but the inflection of the protoloph is much less marked, and the hypoflexus is slightly less oblique. Because it is more worn than the molars, the anteroflexus and posterofossette are almost worn away. The anterior wall of the anteroloph shows a small depression located close to the protocone and near the base of the crown. This feature only occurs in the right premolar; probably in the left one it was already worn away.

**Skull:** The skull is very well preserved, with no evidences of significant *post-mortem* deformation. Only the anterior portion of the nasals and premaxillaries and some minor parts of the basicranium are missing. The skull is small-sized, similar to *Acaremys*, *Sciameys*, the octodontid *Octodontomys* and the echimyid *Euryzygomatomys*, relatively long, and low (Table 2). The skull roof is flat and with straight, parallel borders at the level of the nasal and frontal bones, wider at the level of the parietals. The bulla is large and rounded in lateral view.

The anterior portion of the nasal bones are incomplete, but at least the preserved part indicates that the nasals are wide, forming almost the entire dorsal portion of the snout.

Table 1  
Dental measurements (mm) of MACN Pv CH1913.

DML		10.9
DP4	APL	2.60
	aw	2.50
	pw	2.25
M1	APL	2.65
	aw	2.65
	pw	2.45
M2	APL	2.80
	aw	2.85
	pw	2.40
M3	APL	2.55
	aw	2.80
	pw	1.90

APL: anteroposterior length; aw: anterior width; DML: DP4-M3 length; pw: posterior width.

Table 2  
Cranial measurements (cm) of MACN Pv CH1913.

Cranial length	4.84
Diastema length	1.21
Rostrum width immediately anterior to the inferior root of the zygoma	0.81
Palatal length	1.89
Palatal width at the level of DP4	0.36
Bulla length	1.35
Maximum bulla width	0.75
Skull height immediately posterior to the glenoid fossa	1.17
Skull width immediately posterior to the glenoid fossa	1.87

Posteriorly, the nasals taper gradually between the ascending processes of the premaxillaries, reaching the level of the DP4 and the dorsal root of the zygoma (Fig. 3(A, C)). The premaxillaries occupy the anterior half of the lateral wall of the rostrum. The vertical part of the premaxillary-maxillary suture is slightly concave to the rear. The ascending processes of the premaxillaries are as long as the nasals; they extend along the dorsolateral wall of the rostrum to the base of the dorsal root of the zygoma (Fig. 3). The rostral masseteric fossa is similar to that present in *Octodontomys*, *Octomys*, *Euryzygomatomys*, and *Echimys*, mainly formed by the maxillary and secondarily by the premaxillary (Fig. 3(B, D)); it is rather deep, subtriangular, with its anterior vertex more acute than the posterior. Dorsally, it is limited by a faint rim of the premaxillary and ventrally by the conspicuous tuberosity of the base of the incisor.

The frontal bones are narrow and almost flat. The anterior portion does not penetrate between the nasal and premaxillary, and barely between the premaxillary and maxillary (Fig. 3(A, C)). The suture with the nasals and the premaxillaries is strongly crenulated. The suture with the parietals is slightly concave to the front and little crenulated. The lateral edge of the frontal is straight and forms a prominent supraorbital margin, which continues anteriorly with the posterior margin of the dorsal root of the zygoma (Fig. 3(A, C)). Posteriorly, the supraorbital margin ends in a well-developed postorbital process; behind this process the frontals narrow abruptly, forming a very conspicuous postorbital constriction (Fig. 3(A, C)). Behind the constriction, there is a faint temporal line, which curves posteroventrally following the parietal-squamosal suture. *Myocastor* also has a postorbital constriction, but it is less pronounced and the posterior temporal line is represented by a much prominent, straight shelf overhanging the postorbital portion of the squamosal. A postorbital constriction also occurs in *Spaniomys*, but no available specimen preserves its posterior part, preventing a complete comparison of this structure.

The infraorbital foramen is large, as wide as high. The dorsal root of the zygoma is located at level of the DP4 and the posterior portions of the premaxillaries and nasals. On the posterior portion of the root there are a set of irregular, barely observable sutures that should correspond to the lacrimal bone (Fig. 3(B, D)); according to these sutures, the lacrimal bone would be well exposed on the outer surface, much more than in other studied taxa. This bone is limited anteriorly and ventrally by the maxillary, and dorsally by the frontal, extending over the anteriormost part of the supraorbital margin, very near to the posterior margin of the premaxillaries (Fig. 3(D)). The vertical ramus of the zygoma is robust, although somewhat constrained in its central portion (Fig. 3(B, D)). Unlike the taxa included in the comparisons, the ventral root is located above DP4, almost vertically aligned with the dorsal root (Fig. 3(B, D)). In ventral view, the ventral root projects laterally, forming an arch that continues with the horizontal ramus of the zygoma (Fig. 2(C, D)). The masseteric tuberosity (for the origin of the superficial masseter muscle *sensu* Woods and Howland, 1979) is low and laterally short. A shallow depression for the origin of the lateral masseter muscle extends almost up to the level of M3, as in

*Echimys*, *Euryzygomatomys*, *Kannabateomys*, *Octomys*, and *Octodontomys*. The horizontal ramus of the zygoma is straight and slightly divergent in ventral view (Fig. 2(C, D)). In lateral view the horizontal ramus is low and nearly straight. It is formed mainly by the jugal, which is excluded from the vertical ramus. The squamosal-jugal suture is long, nearly horizontal (Fig. 3(B, D)). The paraorbital process (Verzi, 1994) is small, formed mainly by the jugal and by a small portion of the squamosal, as in *Sciomyss*, *Echimys*, *Octomys*, and *Octodontomys*. The jugal fossa (for the origin of the posterior masseter muscle *sensu* Woods and Howland, 1979) is short and shallow, exposed only in ventral view (Fig. 2(D)). The zygomatic portion of the squamosal is short.

The anterior margin of the orbit is rounded; posteriorly it is widely open, only limited by the postorbital process of the frontal and the paraorbital process of the jugal (Fig. 3(B, D)). Except for a small part of the intraorbital portions of the frontal and squamosal, the intraorbital structures are not discernible. This portion of the skull is still embedded in an extremely hard matrix that could not be removed with mechanical or chemical techniques. The intraorbital portion of the squamosal is short; its anteriormost part is high and the suture with the intraorbital portion of the frontal is almost vertical and reaches the posterior margin of the orbital constriction (Fig. 3(D)). The postorbital portion of the squamosal is somewhat convex. Behind the posterior root of the zygoma, the squamosal narrows abruptly, becoming a thin stripe between the parietal and the auditory bulla (Fig. 3(B, D)). In this section the suture with the parietal is somewhat elevated. The posterior-most portion of the squamosal behind the level of the *meatus acusticus externus* (MAE) is even narrower and posteroventrally oblique (Fig. 3(B, D)), as in *Octomys*.

In dorsal view, the parietal region is the widest of the skull roof. The anterior portion of the parietals is slightly vaulted, flattening gradually to the back. The weak temporal lines do not contact in the midline and form a poorly developed sagittal area (Fig. 3(C)). The suture with the supraoccipital is very crenulated and sinuous along the entire length. There is a subtriangular ossification between the posterior portion of the squamosal, the posterolateral margin of the parietal, and the lateral process of the supraoccipital (Fig. 3(A, C)). This ossification is part of the dorsal exposition of the petrosal bone, which is isolated by the overlying squamosal; it is also present in the living Octodontidae.

The auditory bulla is formed by the ectotympanic, as in extant rodents (Van der Klaauw, 1931). It is very large, much longer than wide (Table 2), ending at the posterior margin of the skull, strongly resembling that of the extant Octodontidae (Fig. 2(C, D)). The MAE is located nearly at the anteroposterior center of the bulla; it is large, subcircular, limited by a low anteroventral ridge as in the extant Octodontidae. Like in *Acaremys*, *Sciomyss*, *Octodontomys*, and *Octomys* a conspicuous accessory foramen is located ventral to the MAE, separated by the anteroventral ridge (Fig. 3(B, D)). There is an inflated epitympanic sinus (Van der Klaauw, 1931) located dorsal and anterior to the MAE, more differentiable from the hypotympanic sinus (Van der Klaauw,

1931) than in *Octodontomys*, and less than in *Tympanoctomys*. The hypotympanic sinus is also inflated, especially at its anterior portion as in *Octomys* and *Octodontomys*. The bulla contacts the squamosal along most of its length, except a small, narrow gap in the anterior part of the epitympanic sinus, which very probably corresponds to the postglenoid foramen. There is a small stylomastoid foramen appressed between the posterior margin of the MAE and the mastoid apophysis (*sensu Verzi, 1994*). The mastoid apophysis, formed by the ectotympanic is short, robust and its tip is somewhat posteriorly oriented, as in *Octomys* (Fig. 3(B, D)); it departs from the posterodorsal rear of the bulla and ends at the level of the center of the MAE, between the mastoid exposure and the MAE. In ventral view, the bulla is nearly almond-shaped, wider anteriorly than posteriorly (Fig. 2(C, D); Table 2). The medial wall is more convex than the external one. There is a small foramen on the medial wall near the contact with the basioccipital (Fig. 2(C, D)). The homology of this structure is still uncertain.

The mastoid exposure is large and inflated, slightly less than *Octomys* and *Octodontomys*, and is closely associated to the posterior portion of the bulla. It forms the posterolateral aspect of the skull, and thus is well exposed in lateral and posterior views (Figs. 2(A, B), 3(B, D)). It extends dorsally higher than the epitympanic sinus, penetrating between what are here interpreted as the lateral process of the supraoccipital and the exoccipital, excluding the latter from the lateral wall of the skull (Fig. 3(B, D)).

The occipital region is low and relatively wide (Fig. 2(A, B)). As in other adult caviomorphs, the occipitals bones are fused, forming a single occipital bone; nevertheless, we identify the basioccipital, supraoccipital and exoccipital bones according to their position in the skull. The foramen magnum is large, wider than high (Fig. 2(A, B)); although it is incomplete, the preserved part of the dorsal margin suggests that it has a nearly trapezoidal contour, wider dorsally than ventrally. The supraoccipital forms the posterior part of the skull roof (Fig. 3(A, C)). In this region, the supraoccipital shows a small anterior projection penetrating between the parietal and the dorsal exposition of the petrosal bone. The lateral process of the supraoccipital separates the squamosal from the mastoid exposure (Fig. 3(B, D)); as in the extant octodontids, it is narrow and short, reaching the dorsal margin of the bulla. Contrarily, in the Echimyidae and Myocastoridae, the lateral process of the supraoccipital is longer, reaching the ventral margin of the MAE. The occipital plane is not completely preserved, however there is a prominent medial portion suggesting the presence of a vertical ridge on the supraoccipital's midline (Fig. 2(A, B)). The occipital condyles are high and compressed; they are well separated and somewhat diverging dorsally. The preserved portion of the paraoccipital processes is robust, anteroposteriorly compressed, diverging ventrally and attached along to the posterior face of the bulla, as in extant Octodontidae (Woods, 1984).

The diastema is slightly longer than the cheek teeth series (Fig. 2(C, D); Table 2). In lateral view it is almost plane, but higher than the interdental portion of the palate (Fig. 3(B, D)).

The maxillary fossae (*sensu Woods and Howland, 1979*) are very shallow. The incisive foramina open into a large, elongated post-incisive fossa (*sensu Candela, 2000*). This fossa continues posteriorly with the very deep palatal grooves (*sensu Carvalho and Salles, 2004*), which extend posteriorly to the level of the M1 (Fig. 2(C, D)), as in *Octomys*, *Spaniomys*, *Stichomys*, and *Euryzygomatomys*. The grooves are separated by a medial keel, less developed than in *Stichomys*. The posterior nares open between the anterior half of the M2, delimiting a triangular mesopterygoid fossa (Fig. 2(C, D)). The interdental portion of the palate is transversely wider than the width of the molars, and anteroposteriorly shorter than in all the compared taxa. The tooth rows are almost parallel (Fig. 2(C, D)). The posterior palatine foramina are conspicuous and located between the M1s, in the posterior end of the palatal grooves. The maxillary-palatine suture is not observable. The sphenopalatine vacuities are present; they are large and ovoid as in *Acaremys*, *Octomys*, *Octodontomys*, *Tympanoctomys* and *Euryzygomatomys*. The pterygoid forks posteriorly to form the entopterygoid and the ectopterygoid crests (*sensu Wible et al., 2005*), delimiting a small pterygoid fossa (Fig. 2(C, D)). These crests are incomplete, but the preserved parts indicate that they are short, robust, and did not contact the tympanic bulla. The presphenoid and the basisphenoid are badly preserved. The basisphenoid-basioccipital suture is not discernible. The basioccipital is triangular, relatively broad in spite of the large size of the bullae; the anterior portion bears a tiny medial keel (Fig. 2(C)). There is a long fissure between the bulla and the basioccipital along the posterior two-thirds of the length of the bulla; this structure would correspond, at least partially, to the jugular foramen (Fig. 2(C, D)). A large, rounded hypoglossal foramen is located at the base of the occipital condyle.

### 3. Discussion and conclusions

The general characters of the dentitions of the specimen MACN Pv CH1913 (brachyodont, barely cuspidate cheek teeth with four transverse crests separated by wide and deep valleys) are shared with most of the Oligocene–early Miocene octodontoids (e.g., *Eosallamys*, *Eospina*, *Eosachacui*, *Platypittamys*, *Prospaniomys*, *Protacaremys*, *Acarechimys*, *Galileomys*). However, MACN Pv CH1913 differs from the Peruvian Santa Rosa octodontoids, *Platypittamys*, *Galileomys*, and other acaremyids by the retention of the deciduous premolars, and from all the acaremyids because the molars do not acquire an eight-shaped occlusal pattern. It differs from *Protacaremys* and the species of *Acarechimys* by the larger size, by having cheek teeth with less evident unilateral hypsodonty, the anterior valley open on the labial side even in advanced stages of wear, and the protoloph with a conspicuous inflection. Additionally, the upper molars of the MACN Pv CH1913 differ from those of *Protacaremys* in having less markedly right anterolingual angle (but more than in *Acarechimys*), more curved and transverse protoloph, and broader mesoflexus. On the other hand, MACN Pv CH1913 agrees with specimens positively referred to *Prospaniomys* in size, degree of hypsodonty, and general

morphology of the cheek teeth. Additionally, it also agrees in having the anteroflexus remaining open labially, even in advanced stages of wear, labial portion of the anteroloph straight and parallel to the protoloph, anterior and lingual margin of the molars forming a nearly right angle, protoloph differentiated in a transverse labial portion and an oblique lingual portion aligned with the hypoflexus, and DP4 with a faint depression on the anterior face of the anteroloph. These characters justify the assignment to the genus *Prospaniomys*. Nevertheless, MACN Pv CH1913 hardly differs from those referred to *Prospaniomys priscus* from Gran Barranca (Fig. 1) by the larger area of the protocone and the more marked obliquity of the lingual portion of the protoloph. Such differences do not justify a generic distinction of the MACN Pv CH1913, although the possibility of a specific separation should be explored.

Concerning the relationships of *Prospaniomys*, Ameghino (1902) remarked that the dentition was similar to that of *Protacaremys*, but interpreted *Prospaniomys* as the ancestor of *Spaniomys*, based upon the morphology of the mandible and the incisors, and included them within his family Echinomyidae, a heterogeneous group including several taxa currently classified as echimyids, octodontids, dasyproctids, and dinomyids. Wood and Patterson (1959) classified all the fossil octodontoids within the Echinomyidae or the Octodontidae, according to the cheek teeth morphology. The authors agreed with Ameghino in the ancestor–descendant relationship of *Prospaniomys* and *Spaniomys*, but interpreted both genera as representing a distinct lineage named “*Spaniomys* Group” within the Echinomyidae. Patterson and Pascual (1968), followed by Patterson and Wood (1982), interpreted the “*Spaniomys* Group” as ancestral to *Myocastor*, and classified these genera within the echimyid subfamily Myocastorinae. Vucetich and Verzi (1991) interpreted *Prospaniomys* as probably related to *Protacaremys*, *Acarechimys*, *Platypittamys*, and other Deseadan octodontoids, excluding *Prospaniomys* as potential ancestor of *Spaniomys*. This last interpretation was followed by Vucetich et al. (1993) and Emmons and Vucetich (1998). However, Kramarz (2001, 2004) proposed *Prospaniomys* as ancestral to the lineage formed by *Spaniomys*, *Maruchito*, and *Callistomys*, separated from *Protacaremys* and the adelphomyines (i.e., *Adelphomys*, *Prostichomys*, *Stichomys*). More recently, Vucetich et al. (2010a) included *Prospaniomys* within Echinomyidae, subfamily Adelphomyinae, although the relationships of this rodent with other octodontoids are still controversial.

The original assignment of *Prospaniomys* to the Echinomyidae proposed by Wood and Patterson (1959) is essentially based on dental features. However, most of these characters are also shared with basal members of other caviomorph superfamilies, and they are likely to be the primitive conditions for octodontoids (Wood, 1981; Frailey and Campbell, 2004). Consequently, the dental features of *Prospaniomys* suggest a basal position among the octodontoids and do not provide evidences of phylogenetic affinities with any particular group of echimyids.

Except for the presence of a marked postorbital constriction of the frontals shared with *Spaniomys* and *Myocastor*, the

comparison of the cranial features of *Prospaniomys* (represented by the MACN Pv CH1913) reveals that most of the characters are consistently shared with both the echimyids and octodontids included in the analysis (Fig. 5). As interpreted for the dentition, the general morphology of the skull of *Prospaniomys* should represent a generalized pattern for the Octodontoidea.

However, the auditory region of the MACN Pv CH1913 (Figs. 2 and 3) shows characters that are considered specialized in modern octodontids (Verzi, 1994) and abrocomids (Glanz and Anderson, 1990). Particularly, the conspicuous enlargement of the auditory bulla, the development of the epitympanic sinus and its probably associated dorsal exposition of the petrosal bone, and the extensive exposure of the mastoid strongly resembles those of *Octodontomys* (Fig. 5(D–F)), *Octomys* (Fig. 5(G–I)), and *Tympanoctomys*. Likewise, the shape and extension of the paraoccipital processes are also characteristic of modern octodontids (Woods, 1984). These features have been previously interpreted as synapomorphies of Octodontidae (Verzi, 1994). Additionally, other features, such as the reduction of the length of the lateral process of the supraoccipital and the posterodorsal interruption of the peripheral ridge of the MAE, are also shared with modern octodontids (Fig. 5(D–I)), although the systematic significance of these characters has not yet been evaluated. Although the definitive elucidation of the relationships of *Prospaniomys* is pending a detailed and extensive cladistic analysis (which should include the remaining octodontoids with still uncertain systematic position), the available evidence suggests that *Prospaniomys* could represent an early diverging lineage more closely related to the modern octodontids than to the echimyids and other extinct octodontoids.

*Prospaniomys* exhibit a peculiar combination of generalized dental features and characters of the auditory region that are derived in octodontids, which is unique among the octodontoids. Similarly, *Acarechimys*, the cranial morphology of which is almost entirely unknown, has dental features essentially as generalized as in *Prospaniomys*, but exhibits some derived mandibular characters suggesting octodontid affinities (Verzi, 2002). If such octodontid affinities are correct, this pattern suggests that the cranial and mandibular specializations typifying the modern octodontids would have developed earlier than the dental ones during the evolution of this group. The acaremyids were originally interpreted as primitive octodontids (Wood, 1949; Wood and Patterson, 1959) by sharing a figure-eight-shaped cheek teeth pattern, but Vucetich and Kramarz (2003) concluded that acaremyids are an early radiation of the Octodontoidea in which this dental pattern evolved independently. Thus, the octodontids are certainly recorded since the Chasicosan SALMA (late Miocene) (Verzi, 1999; Verzi et al., 1999), although they would have diverged from the echimyids in older times. The recognition of primitive octodontids in pre-Chasicosan faunas is probably hampered by the fact that the record of pre-Chasicosan octodontoids is mostly represented by dental remains, in which octodontid features are still not developed.

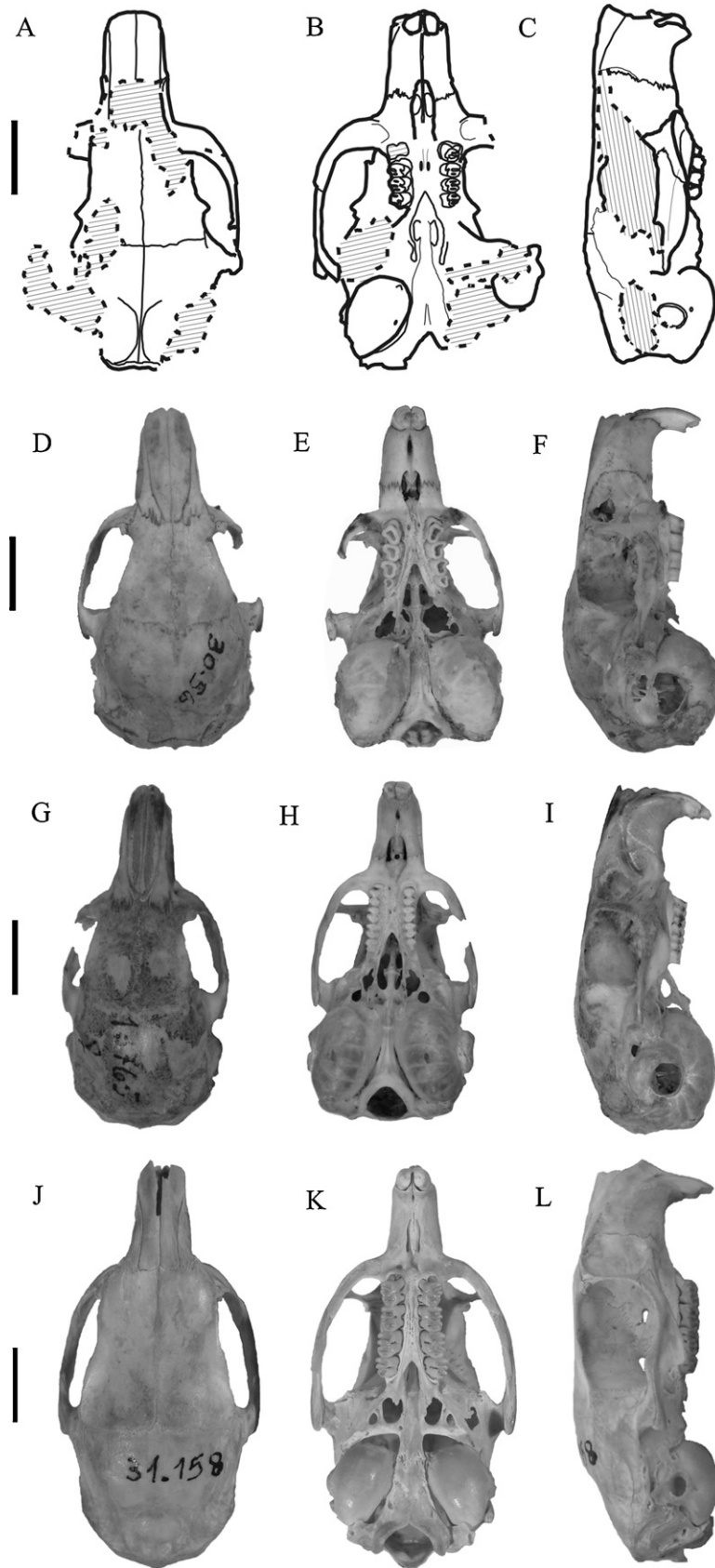


Fig. 5. Skulls of compared octodontoid rodents. **A–C.** *Acaremys murinus* (MACN A 10095), skull partially preserved with right and left P4-M3. **D–F.** *Octodontomys* (MACN Ma 30.56), complete skull with the dentition. **G–I.** *Octomys* (MACN Ma 13765), complete skull with the dentition. **J–L.** *Echimys* (Ma 31.158), complete skull with the dentition. A, D, G, J: dorsal view; B, E, H, K: ventral view; C, F, I, L: lateral view; Striped area: fill with sediment. Scale bar: 10 mm.



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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.geobios.2010.12.003](https://doi.org/10.1016/j.geobios.2010.12.003).

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