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### A new early Miocene octodontoid rodent (Hystricognathi, Caviomorpha) from Patagonia (Argentina) and a reassessment of the early evolution of Octodontoidea

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## A NEW EARLY MIOCENE OCTODONTOID RODENT (HYSTRICOGNATHI, CAVIOMORPHA) FROM PATAGONIA (ARGENTINA) AND A REASSESSMENT OF THE EARLY EVOLUTION OF OCTODONTOIDEA

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**ABSTRACT**—A new caviomorph rodent, *Dudumus ruigomezi*, gen. et sp. nov., is described from the Sarmiento Formation, Trelew Member (early Miocene), of the Argentinian Patagonia. This new taxon is represented by upper and lower cheek teeth, mandible, and maxillary remains. It is characterized by retention of deciduous premolar, and low-crowned and terraced lower and upper cheek teeth with well-differentiated cusps, as in *Caviocricetus lucasi*; upper molariforms with the mesolophule and metacone fused with the posterior-most crest, as in *C. lucasi*; lower molars with lingual cusp enlarged and metalophulid II longer in m2 than in m1 and m3, as in *Prospaniomys priscus*; and dp4 with metalophulid I separated from the metaconid and a spur projecting posterolaterally from the posterior wall of metalophulid I, between the protoconid and anteroconid. The incisor enamel microstructure is derived, with the interprismatic matrix perpendicular (at a right angle) to the prisms, as in other octodontoids. A cladistic analysis corroborates that *D. ruigomezi* represents an octodontoid rodent with unusual tooth morphology. This analysis demonstrates that the early evolutionary history of Octodontoidea was characterized by the differentiation of successive lineages that survived until the early or middle Miocene, with no direct relationships with modern Octodontidae and Echimyidae. This analysis also suggests that fossil taxa previously classified as octodontoids are instead more closely related to the other caviomorph rodents.

**SUPPLEMENTAL DATA**—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP).

### INTRODUCTION

Caviomorpha are hystricognath and hystricomorph rodents endemic to Neotropical America. Monophyly of living caviomorphs is supported by morphological and molecular studies (Luckett and Hartenberger, 1993; Adkins et al., 2001, 2003; Huchon and Douzery, 2001; Upham and Patterson, 2012). These rodents are divided into four superfamilies: Erethizontoidea, Octodontoidea, Cavoidea, and Chinchilloidea. The oldest South American rodents are recorded in the late middle Eocene from Contamana, Peru (Antoine et al., 2012). These oldest taxa are not closely related to modern groups of caviomorphs; actually one of these represents a lineage that diverged before the differentiation of the four superfamilies. However, early Oligocene caviomorphs show a higher morphological disparity and have been assigned to some of these superfamilies (Frailey and Campbell, 2004; Vucetich et al., 2010b; Bertrand et al., 2012). Among caviomorph rodents, Octodontoidea is the superfamily with the highest species richness and adaptive diversity (Vucetich and Verzi, 1996; Vucetich and Kramarz, 2003; Vucetich et al., 2010b). Extant Octodontoidea includes the families Octodontidae, Echimyidae, Ctenomyidae, Myocastoridae, Abrocomidae, and Capromyidae (Simpson, 1945; Woods and Kilpatrick, 2005), the first two comprising most of the species. The oldest taxa assigned to Octodontoidea are recorded in the early Oligocene of Patagonia (Vucetich et al., 2010b) and Peru (Frailey and Campbell, 2004) and by the early Miocene (Colhuehuapian South American Land Mammal Age [SALMA]), octodontoids were widely

spread throughout Patagonia (Vucetich and Verzi, 1991, 1996; Vucetich and Kramarz, 2003; Vucetich et al., 2010a). The diversified Colhuehuapian rodent fauna includes primitive as well as highly derived forms (Vucetich and Verzi, 1996), and these small-sized taxa with low-crowned, lophodont to bunolophodont cheek teeth have been traditionally included in this superfamily. Based on their dental morphology, these rodents were assigned to the modern octodontoid families Octodontidae or Echimyidae (Wood and Patterson, 1959; Patterson and Wood, 1982; Vucetich and Verzi, 1991). This traditional classification implies a basal differentiation of these two groups. Nevertheless, in the last 10 years, with the discovery of a larger number of fossil taxa, the concept of a more complex early history of the superfamily was established, challenging the traditional view of a basal dichotomy (Vucetich and Kramarz, 2003; Vucetich and Ribeiro, 2003; Vucetich and Vieytes, 2006; Kramarz et al., 2010; Vucetich et al., 2010a, 2010b). However, only a few studies performed cladistic analyses in order to investigate the phylogenetic relationships of this fossil Octodontoidea (Vucetich and Kramarz, 2003; Carvalho and Salles, 2004). Recently, Antoine et al. (2012) conducted a cladistic analysis that suggested that the early evolution of Caviomorpha is also more complex than the simple differentiation of the main groups usually recognized (Erethizontoidea, Octodontoidea, Cavoidea, and Chinchilloidea), and hypothesized that Octodontoidea was the first of these groups to differentiate. This provides a new scenario for our understanding of the early evolution of caviomorph rodents.

In this paper, we describe a new caviomorph rodent represented by dental, mandibular, and few maxillary remains found in early Miocene levels of the Sarmiento Formation exposed at

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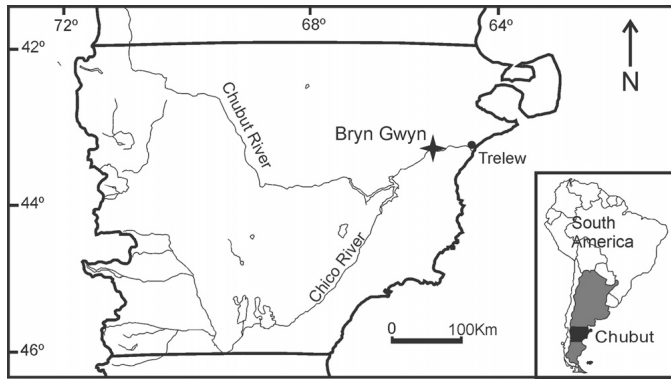


FIGURE 1. Location map showing the area in Chubut Province, Argentina, where the octodontoid *Dudumus ruigomezi*, gen. et sp. nov., was collected.

Bryn Gwyn (Chubut Province, Argentina) (Fig. 1) (Genise and Cladera, 2004; Scasso and Bellosi, 2004). The new taxon has a peculiar dental morphology that provides valuable information about the early evolution of octodontoids. Additionally and based on the new scenario provided by Contamanan rodents, we performed a morphological cladistic analysis in order to elucidate the relationships of the new taxon with other caviomorphs.

#### MATERIALS AND METHODS

Dental nomenclature follows Marivaux et al. (2004) and Candela and Rasia (2012) (Fig. 2). Upper deciduous premolar nomenclature follows upper molars nomenclature. Upper- and lowercase letters correspond to upper and lower teeth, respectively.

To study the incisor enamel microstructure, the tooth was embedded in epoxy resin for easier handling. Specimens were ground in longitudinal and cross-sections with sandpaper, polished, and etched for 5–6 seconds with 2 N HCl to create morphological relief. After rinsing and drying, specimens were sputter-coated and examined with scanning electron microscope (SEM) Jeol JSM-T100. The nomenclature of enamel microstructure follows Koenigswald and Sander (1997).

**Institutional Abbreviations**—Studied specimens of extinct and living rodents belong to the following institutions: **AMNH**, American Museum of Natural History, New York, U.S.A.;

**MACN A**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Colección Nacional Ameghino, Buenos Aires, Argentina; **MACN Ma**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Colección Nacional de Mastozoología, Buenos Aires, Argentina; **MACN PV**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Colección Nacional Paleontología de Vertebrados, Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MOZ-PV**, Museo Ol-sacher, Colección Paleovertebrados, Zapala, Argentina; **MPEF-PV**, Museo Paleontológico Egidio Feruglio, Paleontología de Vertebrados, Trelew, Argentina; **YPM PU**, Yale Peabody Museum, New Haven, U.S.A.

#### SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821  
Suborder HYSTRICOGNATHI Tullberg, 1899  
Superfamily OCTODONTOIDEA Waterhouse, 1839  
*DUDUMUS*, gen. nov.

**Type and Only Species**—*Dudumus ruigomezi*, sp. nov.

**Diagnosis**—As for the type and only species.

**Distribution**—Early Miocene of Patagonia.

**Etymology**—The generic name is derived from the latin words ‘dudum’ (long time ago) and ‘mus’ (mouse).

*DUDUMUS RUIGOMEZI*, sp. nov.  
(Figs. 3, 4; Table 1)

**Holotype**—MACN PV CH 2088, right maxillary fragment with DP4–M1.

**Referred Material**—See Appendix 1 in Supplemental Data.

**Stratigraphic and Geographic Provenance**—Trelew Member, Sarmiento Formation (Mendía and Bayarsky, 1981; Scasso and Bellosi, 2004), early Miocene Colhuehuapian SALMA (Flynn and Swisher, 1995). Bryn Gwyn, Chubut Province, Argentina (Fig. 1).

**Diagnosis**—Small octodontoid rodent nearly 15% larger than *Caviocricetus lucasi* and 35% smaller than *Prospaniomys priscus*. DP4/dp4 retained through life. Lower and upper molariforms low crowned, terraced, and with well-differentiated cusps, as in *C. lucasi*. The dp4 with metalophulid I separated from the metaconid in juvenile specimens and a spur projecting posterolingually from the posterior wall of metalophulid I, between the protoconid and anteroconid; lower molars with large lingual cusps and metalophulid II longer in m2 than in m1 and m3, as in *P. priscus*. Dental morphology of upper cheek teeth similar to *C. lucasi*, with anteroposterior diameter longer than transverse one; paracone conspicuously higher than the rest of the tooth; mesolophule present, longer and higher than in *C. lucasi*.

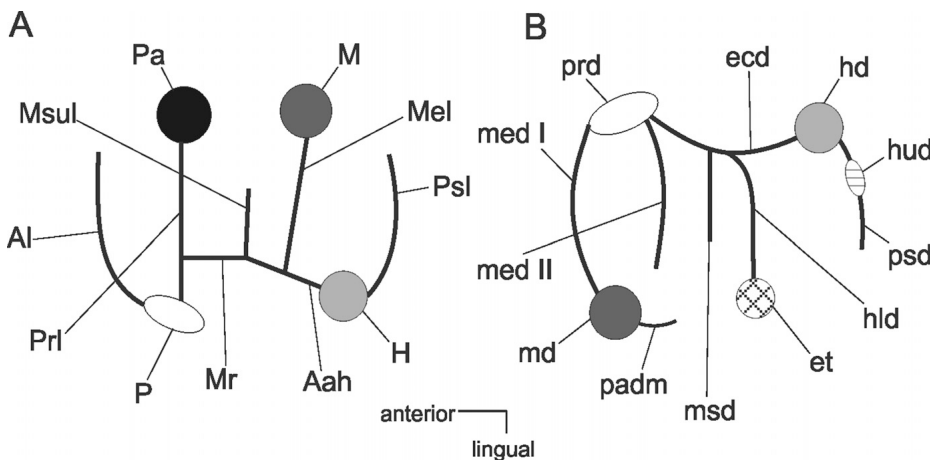


FIGURE 2. Dental nomenclature used for histricognath rodents (modified after Marivaux et al. (2004) and Candela and Rasia (2012)). **A**, upper teeth; **B**, lower teeth. **Abbreviations**: **Aah**, anterior arm of the hypocone; **Al**, anteroloph; **ecd**, ectolophid; **et**, entoconid; **H**, hypocone; **hd**, hypoconid; **hld**, hypoconid; **hud**, hypoconulid; **M**, metacone; **md**, metaconid; **med I**, metalophulid I; **med II**, metalophulid II; **Mel**, metaloph; **Mr**, mure; **msd**, mesolophid; **Msul**, mesolophule; **P**, protocone; **Pa**, paracone; **padm**, posterior arm of the metaconid; **prd**, protoconid; **Prl**, protoloph; **psd**, posterolophid. **Psl**, posteroloph. Anterior to left and lingual below.

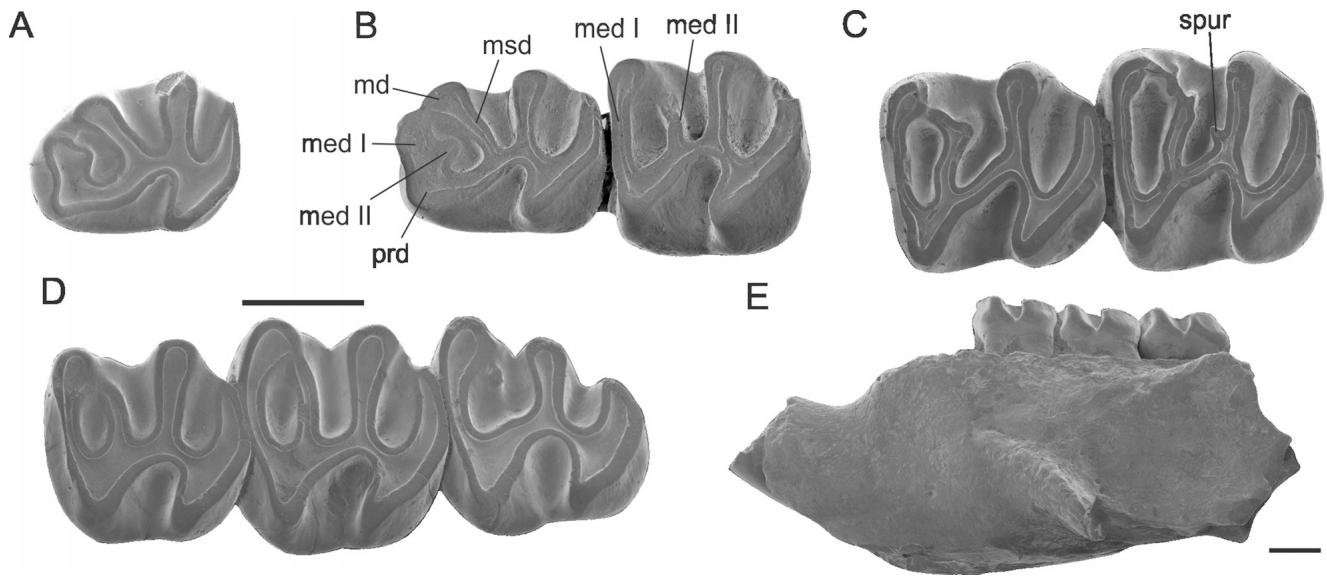


FIGURE 3. Lower cheek teeth of the octodontoid *Dudumus ruigomezi*, gen. et sp. nov. (early Miocene of Chubut Province, Argentina). **A**, MACN PV CH 2042, left dp4; **B**, MACN PV CH 2022, left dp4 and m1; **C**, MACN PV CH 2040, left m1–m2; **D**, MACN PV CH 2021, right mandible with m1–m3; **E**, MACN PV CH 2020, left mandible with m1–m3. Anterior to left. All scale bars equal 1 mm.

**Etymology**—In honor of Eduardo A. Ruigomez, Collection Manager of the MEF and lifelong friend of one of the authors (A.G.K.).

### Description

**Lower Dentition**—The dp4 is similar to that of *Prospaniomys priscus*, with four main lophids and the metalophulid II reduced or absent (Fig. 3A, B). The metalophulid I unites the protoconid with the anteroconid. Nevertheless, only in some adult specimens does this crest reach the metaconid (Fig. 3B), delimiting an anterofossettid, whereas it is always defined in *P. priscus*. A small spur, here interpreted as the metalophulid II, projects from the posterior wall of metalophulid I between the protoconid and anteroconid (Fig. 3A, B). The ectolophid extends from the posterior border of the protoconid to the base of the labial end of the anterior arm of the hypoconid. The mesolophid is well developed and turns forward to reach the metaconid (Fig. 3A, B). The hypolophid extends lingually from the point where the ectolophid joins the anterior arm of the hypoconid, and reaches the entoconid; it is the most internally projected lophid. The posterior border of the tooth is formed by the posterolophid; this crest is short, anteriorly concave, and at the midline of the tooth it has an inflection point that would probably correspond to the hypoconulid (Fig. 3A, B). All flexids are wide and shallow, the mesoflexid being the broadest and the hypoflexid the deepest.

The molars have small depressions on the labial portion of the anterior and posterior walls that resemble cingulids, as in *P. priscus*, but less developed. The m2 is larger than m1 and m3 (Fig. 3D; Table 1). The lophids are more transverse than in *P. priscus*. Unlike dp4, the metalophulid I merges the protoconid and metaconid (Fig. 3B–D); this crest can be straight or somewhat convex, and in most specimens it is anteriorly oblique because of the anterior position of the metaconid in relation to the protoconid. The entoconid is slightly anterior to the hypoconid. The metalophulid II is longer in m2 than in m1, so that in m2 its lingual end contacts the posterolabial slope of the metaconid and delimits a small and shallow anterofossettid (Fig. 3B–D). In most m3s the metalophulid II is absent; but in MACN PV CH

2047 it is present, and in MACN PV CH 2021 (Fig. 3D) a cusp can be observed in the antero- + mesoflexid, attached to the posterolabial slope of the metaconid, which is interpreted as a remnant of the metalophulid II. Unlike dp4, the hypoconulid is not

TABLE 1. Dental measurements (mm) of lower and upper cheek teeth of *Dudumus ruigomezi*, gen. et sp. nov.

Teeth	Dimension	Specimen					
		2084	2088	2092	2099	2108	2119
DP4	apl	1.78	1.66	—	1.70	—	—
	T	1.54	1.66	—	1.76	—	—
	h	0.88	0.98	—	1.00	—	—
M1	apl	1.62	1.82	1.68	1.92	1.94	—
	T	1.98	1.96	1.88	1.98	2.22	—
	h	1.06	1.08	0.86	1.36	0.94	—
M2	apl	—	—	1.76	—	2.06	—
	T	—	—	1.96	—	2.34	—
	h	—	—	0.82	—	0.68	—
M3	apl	—	—	—	—	—	1.96
	T	—	—	—	—	—	2.20
	h	—	—	—	—	—	1.28
		2020	2021	2022	2024	2030	2031
dp4	apl	—	—	1.94	1.90	—	1.98
	T	—	—	1.40	—	—	1.38
	h	—	—	0.82	0.84	—	0.70
m1	apl	1.88	1.88	1.88	1.98	1.92	1.92
	T	1.82	1.78	1.82	—	1.90	1.78
	h	0.88	0.84	0.92	0.98	0.90	1.00
m2	apl	2.02	2.00	—	2.02	2.08	2.02
	T	1.96	1.98	—	—	2.18	2.02
	h	0.96	0.90	—	1.20	0.90	1.02
m3	apl	1.92	1.96	—	—	—	—
	T	1.70	1.96	—	—	—	—
	h	0.98	0.72	—	—	—	—

All specimen numbers refer to the MACN PV CH. **Abbreviations:** **apl**, anteroposterior length; **h**, height of the crown (measured at the level of the protocone/id); **T**, transverse width (measured at the level of the hypoflex/id).

individualized. In older specimens, the posteroflexid closes, forming a posterior fossettid, whereas the mesoflexid and the hypoflexid remain open.

Lower incisors are little compressed, with the anterior face forming a straight angle lingually and a curved border labially. They are long and their posterior end is located at the base of the coronoid apophysis of the mandible, behind the m3.

**Mandible**—A small mental foramen is located lateral and anterior to the dp4, dorsoventrally aligned with a well-developed mental process. No specimen preserved the complete diastema; however, in MACN PV CH 2020 (Fig. 3E) its posterior portion is well depressed compared with the alveolar border. The notch for the tendon of the masseter medialis pars infraorbitalis is antero-posteriorly short and shallow, and it is located at the level of m1 or dp4–m1 limit (Fig. 3E). This notch continues posteroverentrally with a well-developed masseteric crest (Fig. 3E). The masseteric fossa is shallow and the groove forming its anterodorsally limit is moderately deep. The coronoid apophysis rises at the level of the m3 (Fig. 3E) and delimits a lateral retromolar fossa. The symphysis is long, extending posteriorly almost up to the level of m1.

**Upper Dentition**—Upper cheek teeth are terraced, with labial cusp of upper molars higher than the remaining structures of the occlusal surface (Vucetich and Verzi, 1996); additionally, there is a slightly unilateral hypsodonty as in *Caviocricetus lucasi* (Fig. 4A); cusps are conspicuous, specially the paracone (Fig. 4B); anteroposterior diameter longer than the transverse one (Table 1).

The DP4 is rounded in outline and smaller than M1 and M2 (Fig. 4C, E; Table 1). The protocone is rounded or compressed labiolingually, and obliquely oriented. The anteroloph is short, not reaching the paracone, but longer than in *C. lucasi*. Some specimens show a small depression on the anterior side of the anteroloph, located close to the protocone and near the base of the crown, as in *Prospaniomys priscus*, but less developed. The protoloph is generally straight and obliquely oriented (Fig. 4C, E). Nevertheless, some specimens have the labial portion of the crest curve, only the lingual portion being straight and oblique. The mure arises from the lingual end of the protoloph and is usually anterolabially posterolingually oblique. The third crest in position is here interpreted as the mesolophule; it is short and posteriorly oriented; in some specimens this crest does not contact the lingual slope of the metacone (Fig. 4E), whereas in others it does (Fig. 4C). The fourth crest in position is interpreted here as composed by the posteroloph and the metaloph, as in *C. lucasi* (Vucetich and Verzi, 1996) because in little worn specimens this crest is formed by a lingual short portion extending from the hypocone that would be the posteroloph, and by a longer labial portion that would be the metaloph because it bears labially the metacone (Fig. 4). This posteroloph + metaloph is anteriorly concave. The mesoflexus is the widest flexus, whereas the hypoflexus is the deepest valley and is anteriorly oriented.

The molars are similar in structure to the premolar but more quadrangular in occlusal outline (Fig. 4C–E). The M2 is larger than M1 (Table 1). The anteroloph and the protoloph are less

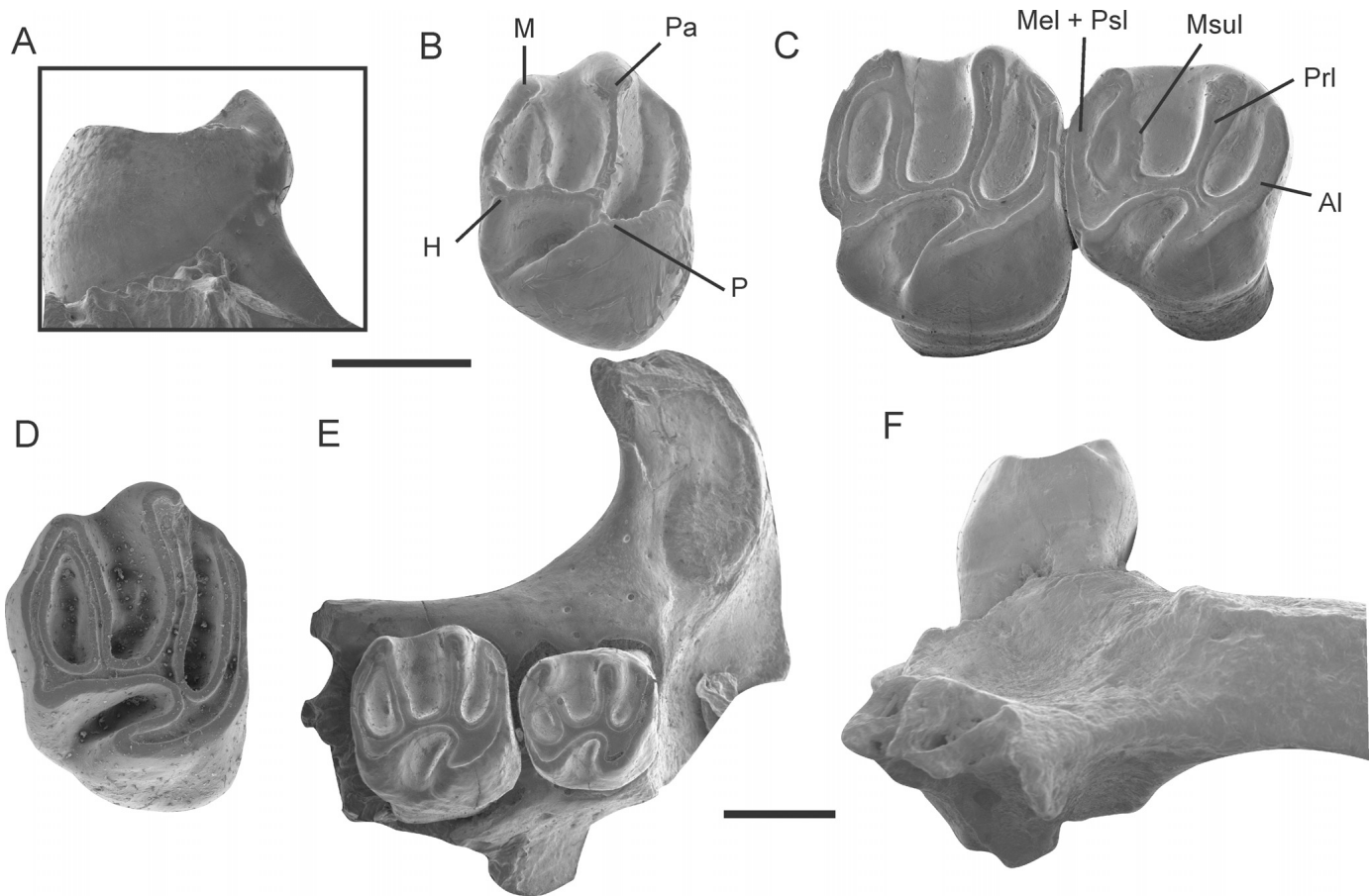


FIGURE 4. Upper cheek teeth of the octodontoid *Dudumus ruigomezi*, gen. et sp. nov. (early Miocene of Chubut Province, Argentina). **A**, MACN PV CH 2125 showing the terraced morphology; **B**, MACN PV CH 2133, right upper molar; **C**, MACN PV CH 2099, left maxillary fragment with DP4 and M1 (reversed); **D**, MACN PV CH 2119, right M3; **E**, MACN PV CH 2088 (holotype), right maxillary fragment with DP4 and M1; **F**, MACN PV CH 2109, right maxillary fragment with DP4. Anterior to right. All scale bars equal 1 mm.

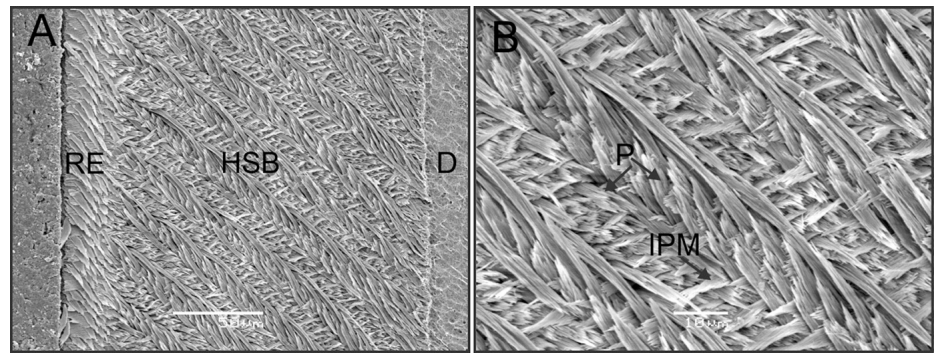


FIGURE 5. Scanning electron microscope micrographs of the lower incisor enamel in longitudinal section of the octodontoid *Dudumus ruigomezi*, gen. et sp. nov. (early Miocene of Chubut Province, Argentina). **A**, general view; **B**, detail of **A** showing the IMP running at right angle to the prisms. **Abbreviations:** RE, radial enamel; D, dentine; HSB, Hunter-Schreger bands.

oblique than in DP4, and the protocone is always labiolingually compressed and anterolabially-posterolingually oriented (Fig. 4C–E). The paracone is larger than in DP4. The mesolophule is longer and higher than in DP4 and than in molars of *C. lucasi*; consequently, the posterior fossette is more laterally elongated instead of subcircular as in *C. lucasi*. Thus, the mesolophule merges with the metacone in earlier stages of wear than in *C. lucasi* (Fig. 4C, E). In M3, the hypocone is more labially placed than the protocone (Fig. 4D).

Additionally, structures of uncertain homologies are present in some lower and upper molariforms. For example, m2 of MACN PV CH 2043 has a spur anterolingually oblique in the anterolabial end of the hypolophid (Fig. 3C). In MACN PV CH 2096, a left DP4, there is a conspicuous cusp in the mesoflexus, near the posterior border of the protoloph. In MACN PV CH 2097, a right DP4, the labial end of the protoloph continues posteriorly into a lingually oblique spur.

**Skull**—The only preserved parts of the skull are small portions of the maxillaries. The ventral root of the zygomatic arch arises at the level of the anterior border of the DP4 slightly oblique anteriorly, but immediately turns back forming a semicircle (Fig. 4E). Ventrally, there is a conspicuous masseteric tuberosity (Fig. 4E). Posteriorly, there is an accessory foramen of uncertain homologies in most specimens. Lateral to the masseteric tuberosity is a shallow depression for the insertion of the lateral masseter. There is no groove for the passage of the infraorbital nerve on the dorsal view of the ventral root. The maxillary fossa in front of DP4 is deep (Fig. 4F).

**The Incisor Enamel of *Dudumus ruigomezi*, gen. et sp. nov.**—The lower incisor schmelzmuster of *Dudumus ruigomezi* is two-layered (Fig. 5A). The inner multiserial Hunter-Schreger band (HSB) comprises four or five prisms, the plate-like IMP runs at right angles to the long axes of the prism, and the HSB inclination is 40° (Fig. 5B). Transition zones between the HSB are well developed. In the external portion, prisms incline 60° apically. Enamel thickness is 200 μm and the thin external radial enamel occupies 12% of the total enamel. Prism-less enamel (PLEX) is missing (Fig. 5A). The incisor enamel microstructure of *D. ruigomezi* agrees with that observed in modern octodontoids and most fossil taxa assigned to Octodontoidea (Martin, 1992).

#### PHYLOGENETIC ANALYSIS

In order to assess the phylogenetic relationships of the new species within Octodontoidea, a cladistic analysis was performed. This analysis also aims at informing the early evolution of the superfamily by improving the taxon and character sampling in relation to previous analyses (Vucetich and Kramarz, 2003; Arnal and Pérez, 2013). The data matrix is composed of 31 taxa and 106 morphological characters. The character list and data

matrix are provided in Appendices 2 and 3 in Supplemental Data. The identification of upper deciduous and permanent premolars was based on the identification of primary homologies (de Pinna, 1991; Rieppel, 1994). Taxa included in the phylogenetic analysis are listed in Appendix 4 in Supplemental Data. The hystricognath *Bugtimys zafarullahi* (early Oligocene of Pakistan), the ‘phiomorphs’ *Phiomys andrewsi* (late Eocene–early Oligocene of Africa) and *Metaphiomys schaubi* (early Oligocene of Africa), *Canaanimys maquiensis* and *Cachiyacuy contamanensis* (middle Eocene of Peru), the chinchilloid *Garridomys curunuquem* (early Miocene of Patagonia), the extant dasyproctid *Dasyprocta azarae*, and the erethizontids *Eosteiomys homogenidens* and *Steiomys detentus* (early Miocene of Patagonia) were used as outgroup taxa. The Asian species and the ‘phiomorphs’ are the sister group of Caviomorpha (Hoffstetter and Lavocat, 1970; Nedbal et al., 1994; Marivaux et al., 2004; Antoine et al., 2012). *Canaanimys maquiensis* was recently described as the earliest diverging caviomorph, and *C. contamanensis* as a basal form within the sister group of Octodontoidea (Antoine et al., 2012). The erethizontids were proposed as the sister group of Caviida (Octodontoidea + Cavoidea + Chinchilloidea) (Bryant and McKenna, 1995) or as included (with Cavoidea) in the sister clade of Octodontoidea (with Chinchilloidea) (Nedbal et al., 1994; Adkins et al., 2001; Antoine et al., 2012; Upham and Patterson, 2012; Fabre et al., 2012). *Dasyprocta azarae* is a representative of Cavoidea s.l. (Pérez, 2010), and *G. curunuquem* is a recently described chinchilloid closely related to Chinchillidae (Kramarz et al., 2013). Morphological variation within Octodontoidea is represented by fossil and living echimyids, fossil and living octodontids, and other fossil octodontoids of still controversial affinities. *Bugtimys zafarullahi* was used to root the recovered most parsimonious trees (MPTs).

The data matrix was analyzed using TNT 1.1 (Goloboff et al., 2008a, 2008b) followed by TBR branch swapping algorithm (holding 10 trees per replicate). We used equally weighted parsimony to minimize the number of postulated evolutionary transformations. Eighteen characters were treated as ordered (see Appendix 2, Supplemental Data), either because they contain nested state sets or because they represent multistate characters with one of the states being absent. The robustness of the obtained MPTs was calculated with both absolute and relative Bremer support.

The parsimony analysis resulted in two MPTs of 381 steps, with a consistency index of 0.378 and a retention index of 0.523, found in 125 out of the 1000 replicates. The strict consensus tree is shown in Figure 6. In both MPTs, *Dudumus ruigomezi* is nested within the clade including the late diverging echimyids and octodontids and almost all fossil taxa traditionally included in Octodontoidea. Within this clade (Octodontoid lineage; Fig. 6), *D. ruigomezi* appears as the sister group of the clade formed by *Plesiacaerchimys koenigswaldi* and *Caviocricetus lucasi*. This

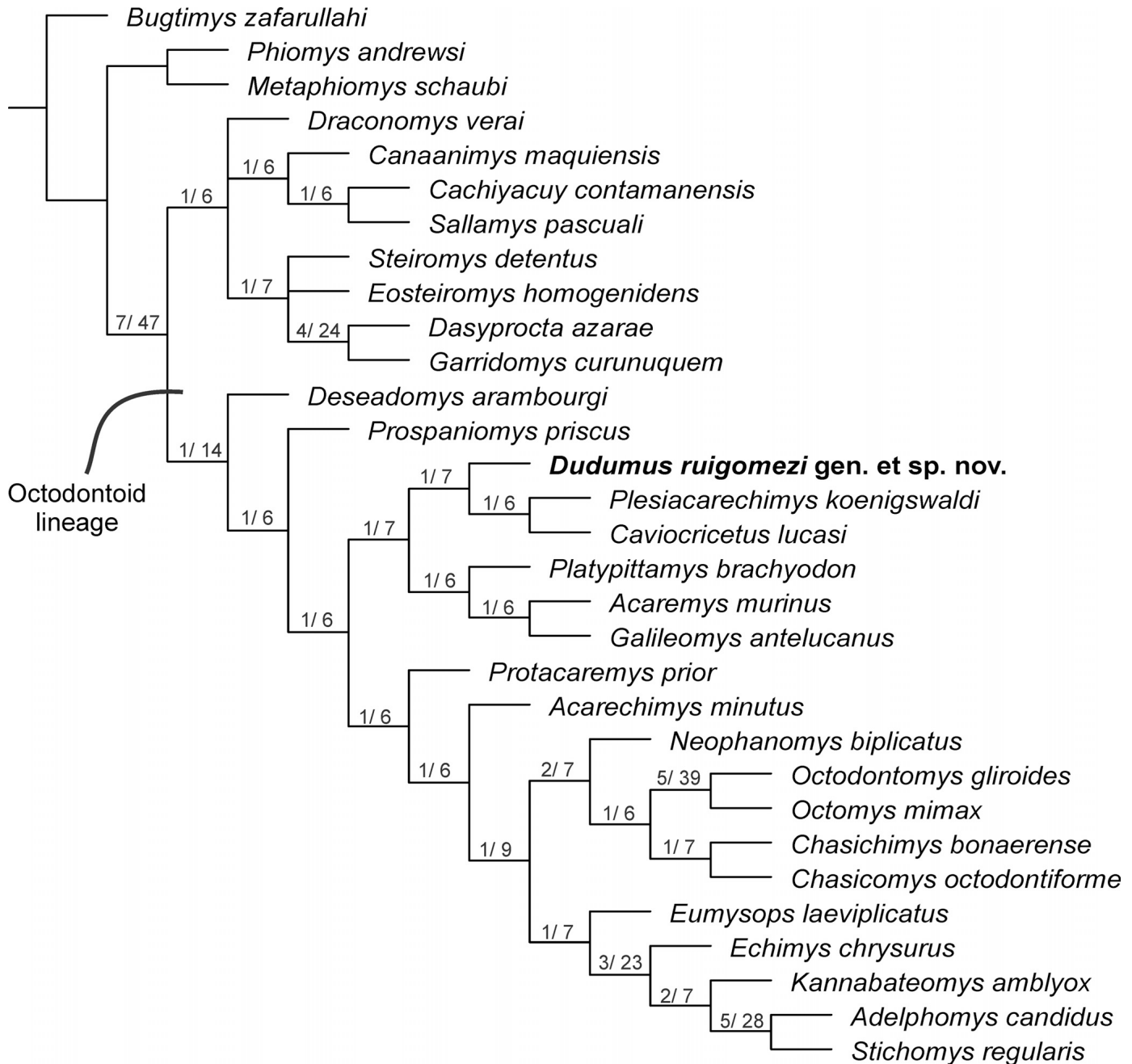


FIGURE 6. Strict consensus of the two most parsimonious trees (tree length = 381 steps; consistency index = 0.378; retention index = 0.523) resulting from a cladistic analysis of 31 taxa and 106 characters showing the phylogenetic position of *Dudumus ruigomezi*, gen. et sp. nov., and depicting octodontoid and caviomorph relationships. Numbers above nodes separated by slash are absolute and relative Bremer support values.

relationship is supported by three synapomorphies: presence of mesolophule on M1–M3 (character 36[0]), metaloph indistinct on M1–M3 (character 38[2]), and a high position of the notch for the masseter muscle pars infraorbitalis at the middle of the mandible (character 100[1]).

The octodontoid lineage (Fig. 6) is characterized by five synapomorphies: mesodont cheek teeth (character 3[1]), absence of metaloph in P4 (character 19[1]), absence of mesolophule on M1–M3 (character 36[1]), metaloph lingually joined to the anterior arm of the hypocone on M1–M3 (character 38[0]), and anterior face of lower incisors forming a right-angled lingual border and a curved labial one (character 94[1]). *Deseadomys*

*arambourgi* and *Prospaniomys priscus* are the earliest divergent taxa, and are excluded from the clade that includes the remaining Octodontoidea by the absence of three synapomorphies: lingually aligned protocone and hypocone on M1 and M2 (character 40[1]), and laterally compressed upper (character 52[0]) and lower incisors (character 93[0]).

The Acaemyidae (the clade including *Acaemys murinus*, *Galileomys antelucanus*, and *Platypittamys brachyodon*) is recovered as a monophyletic group, in accordance with previous analyses (Vucetich and Kramarz, 2003; Arnal, 2012; Arnal and Pérez, 2013). Acaemyids appear as the sister clade of the group including *D. ruigomezi*. In general terms, most Bremer indices are low



( $B = 1$ ) in those nodes involving fossil octodontoids not related to modern species (Fig. 6).

In addition, the analysis also supports the monophyly of Echimyidae including the early Pliocene to early Pleistocene *Eumysops laeviplicatus* as the earliest diverging echimyid, the extant *Echimyus chrysurus* and *Kannabateomys amblyox*, and the Santacrucian *Adelphomys candidus* and *Stichomys regularis* (Fig. 6), corroborating the traditional classification of both fossil taxa as echimyids (Wood and Patterson, 1959; Patterson and Pascual, 1968; Patterson and Wood, 1982; Kramarz, 2004). Nodes grouping echimyids show the highest support of the analysis (Fig. 6). Nevertheless, unlike previous proposals (Wood and Patterson, 1959; Patterson and Pascual, 1968; Patterson and Wood, 1982; Kramarz, 2004), the Deseadan *Deseadomys arambourgi* and the Colhuehuapian *Protacaremys prior* and *Prospaniomys priscus* do not group with the latter clade (Fig. 6). The monophyly of Octodontidae is also recovered, because the late Miocene *Neophanomys biplicatus* appears as the sister taxon of the clade formed by the late Miocene *Chasichimys bonaerense* + *Chasicomys octodontiforme* and the clade including living Octodontidae (*Octodontomys gliroides* + *Octomys mimax*) in both MPTs (Fig. 6). The node clustering living octodontids shows the highest support within this family ( $B = 5$ ).

These results show that the remaining caviomorph taxa included in this analysis (representatives of the other three superfamilies and the recently described Contamanan rodents) represent an evolutionary lineage independent from Octodontoidea (Fig. 6). This lineage is characterized by the presence of the metaloph joined lingually to the posteroloph on DP4 (character 9[1]), a strong mesostyle on DP4 (character 11[2]), a hypocone more labially placed related to the protocone on M3 (character 45[0]), and an entoconid aligned to the hypoconid on m1–m3 (character 81[0]). The most striking aspect of these results is the position of *Sallamys pascuali* and *Draconomys verai*. The latter was interpreted as belonging to Octodontoidea (Vucetich et al., 2010b; Antoine et al., 2012). According to our results, this taxon is more closely related to the Contamana rodents, and the erethizontids, cavioids, and chinchilloids included in this analysis (Fig. 6). *Sallamys pascuali* was described as an octodontoid more closely related to Echimyidae than to Octodontidae (Hoffstetter and Lavocat, 1970; Patterson and Wood, 1982; Antoine et al., 2012). However, our results suggest that *S. pascuali* is a caviomorph more closely related to the Contamanan *Cachiyacuy contamanensis* (Fig. 6).

Concerning the Contamana rodents, *Cachiyacuy contamanensis* was placed closely related to the clade including Cavoidea, Erethizontidae, and Chinchilloidea, which is essentially in accordance with the proposal of Antoine et al. (2012). However, our results suggest that *Canaanimys maquiensis*, originally interpreted as the sister group of all the remaining caviomorph groups (Antoine et al., 2012), is also related to this latter clade (Fig. 6). A broader caviomorph sampling may improve these results, but this is beyond the scope of this work.

## DISCUSSION

### Higher-Level Taxonomic Assignment of *Dudumus ruigomezi*

The systematic relationships of the extant Octodontoidea are controversial despite the large amount of previous work on this issue (Nedbal et al., 1994; Huchon and Douzery, 2001; Woods and Kilpatrick, 2005; Candela and Rasia, 2012; Upham and Patterson, 2012). The systematics of the superfamily including fossils taxa (particularly those from the Oligocene to the middle Miocene) is also poorly known and still under debate, owing to the absence of comprehensive phylogenetic studies including fossil and living representatives of this superfamily. Thus, there is not a phylogenetic definition of Octodontoidea establishing the extension of crown and stem groups. Therefore, we prefer to preserve

the traditional concept of the superfamily proposed by Simpson (1945), but including those taxa described in the last decades. Namely, within Octodontoidea are included all taxa more closely related to modern octodontids than to chinchillids, caviids, or erethizontids. Under this concept, and based on the topology recovered from our phylogenetic analysis, *Dudumus ruigomezi* belongs to Octodontoidea. Further, our results do not support the alleged affiliation of *Sallamys pascuali* and *Draconomys verai* with octodontoids. Consequently, and in order to preserve the monophyly of Octodontoidea, these taxa should be excluded from this superfamily.

Given the results obtained in this analysis, the traditional classification of octodontoids into families does not allow an appropriate representation of monophyletic entities when fossil taxa are included. The taxon sampling scheme presented here is far from being complete, and in future analyses the inclusion of more fossil and extant octodontoids taxa is expected to formalize a better definition of Octodontoidea and of the main groups traditionally included within it.

### Comments on the Early Octodontoid Evolution

The pentalophodonty is largely accepted as the ancestral condition for the upper molars of caviomorphs (Hoffstetter and Lavocat, 1970; Jaeger, 1989; Vucetich and Verzi, 1994; Candela, 1999; Antoine et al., 2012). In fact, most erethizontids and the basal-most members of Cavoidea and Chinchilloidea show a five-crested occlusal design. However, almost all caviomorphs with lophodont cheek teeth attributed to Octodontoidea have tetralophodont upper molars (Wood and Patterson, 1959; Patterson and Wood, 1982). *Caviocricetus lucasi*, *Sallamys pascuali*, *Draconomys verai*, and *Plesiacaechimys koenigswaldi*, with presumed primitive dental features, were proposed to be representatives of different lineages within a basal octodontoid stock (Vucetich and Vieytes, 2006; Vucetich et al., 2010b). Among putative basal octodontoids, only *P. koenigswaldi* and *D. verai* have pentalophodont patterns. The result of our cladistic analysis suggests that the basal-most member of Octodontoidea present tetralophodont upper dental pattern with reduced mesolophule (*Deseadomys arambourgi* and *Prospaniomys priscus*). The Deseadan occurrence of *D. arambourgi* and *Platypittamys brachyodon* indicates that such occlusal pattern already was present among octodontoids by the late Oligocene. Under the evolutionary context supported by our cladistic analysis, the mesolophule present in *D. ruigomezi* and *C. lucasi*, and the pentalophodont occlusal pattern existing in *P. koenigswaldi* are not homologous to that characterizing the basal-most forms of the remaining caviomorph groups, and would represent a secondary modification derived from the tetralophodont octodontoid pattern. *Draconomys verai* and *S. pascuali* (the latter with variably reduced mesolophule and metaloph) are here interpreted as non-octodontoids caviomorphs.

Further, this analysis supports previous hypotheses suggesting that many octodontoid lineages diverged before the differentiation of modern echimyids and octodontids (Vucetich and Kramarz, 2003; Vucetich and Ribeiro, 2003; Vucetich and Vieytes, 2006; Arnal, 2012). Among these fossil lineages, those represented by *Acaremys murinus* would have experienced a significant radiation: the Acaremyidae (Vucetich and Kramarz, 2003; Arnal and Pérez, 2013), as well as the clade including *D. ruigomezi*, characterized by having a secondary development of mesolophule (Fig. 6).

Contrasting these phylogenetic results with the known chronological distribution of the studied taxa suggests that Octodontoidea would have differentiated from other caviomorphs clades in pre-Contamana times. The Echimyidae-Octodontidae dichotomy was not a phylogenetically basal event in the Octodontoidea history, although the close relationship of *Adelphomys*



*candidus* and *Stichomys regularis* with modern echimyids (*Echimyus chrysurus*, *Kannabateomys amblyox*, and *Eumysops laeviplicatus*) suggests that echimyids would have diverged from octodontids at least in early Miocene times (Santacrucian SALMA). *Eodelphomys almeidacomposi*, from the Santa Rosa fauna (Peru), was described as an adelphomyinae octodontoid (Frailey and Campbell, 2004). If this relationship is confirmed, the Echimyidae-Octodontidae dichotomy should be traced back to early Oligocene times.

**Evolution of the Incisor Enamel Microstructure**—The incisor schmelzmuster of rodents has generally two layers, an internal portion (portio interna, PI) formed by Hunter-Schreger bands (HSB), and an external one (portio externa, PE) formed by radial enamel (RE) (Koenigswald and Clemens, 1992). The characteristic type of HSB in incisors of hystricognath rodents is multiserial with thick bands formed by three to eight prisms. There are three basic subtypes of multiserial HSB, depending on the interprismatic matrix (IPM) orientation. The IPM may run parallel, at acute angles, or at right angle with respect to the prisms. The latter is considered to be the most derived by biomechanical considerations and evolutionary occurrence (Martin, 1992, 1993, 1994a, 2004). Among caviomorph rodents, the first two subtypes are present in Cavoidea, Chinchilloidea, and Erethizontoidea, whereas most taxa previously assigned to Octodontoidea have the most derived subtype, which was considered so far the only synapomorphy of the superfamily (Martin, 1992). However, a transitional stage between acute and rectangular subtypes was described for several Deseadan to Colloncuran caviomorphs (Martin, 1994b; Vucetich and Vieytes, 2006; Vucetich et al., 2010b). In this subtype, the angle of the IPM is higher than 45°, up to 70°, in the upper incisors, and reaches 90° only in some sectors of the lower incisors (60° to 90°). This subtype was interpreted as the condition from which the typical octodontoid IPM arrangement would have been derived (Vucetich and Vieytes, 2006).

The incisor enamel microstructure of the herein interpreted as basal-most octodontoids (*D. arambourgi* and *P. priscus*) is still unknown. Nevertheless, other basal octodontoids already showed the IPM at right angle that typifies the superfamily (*D. ruigomezi*, *P. prior*, *Acarechimys minutus*, and acaremyids); thus, the transitional subtype of *Caviocricetus lucasi* and *Plesiacarechimys koenigswaldi* represents a reversion to the ancestral condition based on the results of this phylogenetic analysis.

On the other hand, the incisor enamel microstructure of basal-most members of the non-octodontoid lineage here analyzed (i.e., the Contamana rodents and *Draconomys verai*) is still unknown. However, our results suggest that the multiserial HSB with IPM in an acute angle of the non-octodontoid lineage would have also derived from the transitional stage; thus, the transitional subtype observed in *Sallamys pascuali* (here interpreted a non-octodontoid caviomorph) represents a pleisiomorphy. These hypotheses oppose previous proposals (Martin 1992, 1993, 1994a). Nevertheless, more information on the incisor enamel microstructure of basal octodontoids and early caviomorphs (e.g., Contamanan rodents) is still needed for an accurate understanding of the evolution of this feature.

## CONCLUSIONS

The new taxon here described from early Miocene beds of Patagonia is a small caviomorph rodent with low crowned, bunolophodont cheek teeth. *Dudumus ruigomezi* is part of a large caviomorph radiation that includes modern octodontids and echimyids, the Octodontoidea. Other fossil taxa previously classified as octodontoids are here interpreted as related to the lineage leading to erethizontids, cavioids, and chinchilloids (*Draconomys verai*), or as related to Contamanan rodents (i.e., *Sallamys pascuali* and *Draconomys verai*). The Octodontoidea represents the earliest of the caviomorph superfamilies to differ-

entiate, as proposed by Antoine et al. (2012). Such differentiation involved an early reduction of the ancestral pentalophodont occlusal pattern of the upper molars by the loss of the mesolophule. However, *D. ruigomezi* shows a secondary loph acquisition equivalent to a mesolophule in the upper cheek teeth and of terraced occlusal surfaces, which are unusual features of caviomorphs shared with *C. lucasi*.

Octodontoidea has been characterized by having a derived enamel microstructure with the IPM at right angles with respect to the prisms (Martin, 1993, 1994a). We support this hypothesis within a cladistic context. Nevertheless, the enamel microstructure of the basal-most octodontoids is still unknown and the transitional subtype appears as a reacquisition in *Caviocricetus lucasi* and *Plesiacarechimys koenigswaldi*, in opposition to the proposal of Vucetich and Vieytes (2006). In addition, the evolutionary pathway of enamel microstructure in non-octodontoids caviomorphs deduced from our analysis also does not agree with previous proposals (Martin, 1993, 1994a). Both evolutionary hypotheses must be revised with additional information and in a much broader taxonomic context.

In the traditional view of octodontoid systematics, the fossil forms are attributed to some of the groups with extant representatives. We conclude that the early evolutionary history of Octodontoidea (as here defined) was characterized by differentiation of successive lineages that survived until the early or middle Miocene, with no direct relationships with the main modern groups; consequently, they can be classified neither as Echimyidae nor as Octodontidae. *Dudumus ruigomezi* would be allied to *Plesiacarechimys koenigswaldi*, *Caviocricetus lucasi*, and the acaremyids, which together constitute the most diversified among these early octodontoid radiations. This clade probably deserves a formal suprageneric designation, but a formal classification of fossil Octodontoidea is still pending an exhaustive revision of their affinities with extant taxa.

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