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Source: Journal of Vertebrate Paleontology, 36(5)

Published By: The Society of Vertebrate Paleontology

URL: <http://www.bioone.org/doi/full/10.1080/02724634.2016.1199557>

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A NEW GENUS OF SIGMODONTINAE (MAMMALIA, RODENTIA, CRICETIDAE) FROM THE PLIOCENE OF CENTRAL ARGENTINA

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ABSTRACT—*Chukimys favaloroi*, new genus and species, is added to the past diversity of sigmodontine rodents, the largest subfamily of Neotropical mammals. It is based on a maxillary with the entire tooth row and both first and second lower molars collected in sediments of the Brochero Formation (Late Pliocene) that crop out in Córdoba Province, Argentina. The new genus represents a small rodent (about 40 g) and has a unique combination of traits, including a zygomatic plate with deeply excavated anterior border and conspicuous zygomatic spine, incisive foramen reaching the level of the protocone of the first upper molar, palate narrow and flat, molars moderately hypsodont, and the first lower molar four-rooted. The new sigmodontine shows similarities with several extant members of the tribes Phyllotini and Reithrodontini, as well as with the extinct *Dankomys vorohuensis* from the Pliocene of Buenos Aires, Argentina. The comparisons performed suggest that *Chukimys* has anatomical features related to omnivory and the incorporation of hard material in its diet. *Chukimys* is the first fossil genus of sigmodontine described from central Argentina and probably represents a new member of the currently monotypic tribe Reithrodontini.

Citation for this article: Barbiere, F., L. E. Cruz, P. E. Ortiz, and U. F. J. Pardiñas. 2016. A new genus of Sigmodontinae (Mammalia, Rodentia, Cricetidae) from the Pliocene of central Argentina. *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2016.1199557.

<http://zoobank.org/urn:lsid:zoobank.org:pub:58195F08-301E-4577-9458-3A0E290B9DE4>

INTRODUCTION

With around 420 species in 86 genera, Sigmodontinae is the second-most speciose clade within Cricetidae and the largest subfamily among living Neotropical mammals (Musser and Carleton, 2005; Patton et al., 2015). In clear contrast, we have poor knowledge about its past diversity and, paradoxically, most of the current inferences on its historical biogeography and origins are based mainly on genetic markers (e.g., Salazar-Bravo et al., 2013; Schenk et al., 2013; Vilela et al., 2014; Parada et al., 2015). The oldest sigmodontines in South America come from Montehermosan (lower Pliocene) beds exposed in southern Buenos Aires Province, Argentina (Reig, 1972, 1978; Pardiñas and Tonni, 1998); a presumed Late Miocene record is controversial (Verzi and Montalvo, 2008; Prevosti and Pardiñas, 2009). The whole diversity for the Pliocene is composed of about 12 known genera, of which six are extinct, and 13 species (Pardiñas et al., 2002, and references therein; Quintana, 2002; Ortiz et al., 2012a). Furthermore, except for †*Pardinamys* and a new taxon cited as aff. *Abrothrix*, both of them from northwestern Argentina (Ortiz et al., 2012a, 2012b), all these forms come from the Atlantic coast of Buenos Aires Province in Argentina. Sigmodontine diversity during the Quaternary is better known, with

numerous extant and extinct species recorded since the Lower and Middle Pleistocene (e.g., Pardiñas et al., 2002; Voglino and Pardiñas, 2005; Pardiñas, 2008; Ortiz et al., 2011). Fortunately, this knowledge is not solely restricted to Argentina. In the past decade, the Quaternary diversity of fossil sigmodontines has been enlarged with descriptions of new extinct genera from northern South America (e.g., *Agathaeromys*; Zijlstra et al., 2010), as well as with rich fossil deposits in several countries (e.g., Ecuador, Costa Rica; see Fejfar et al., 1996; Mora, 2003).

Thus, there is a clear lack of information concerning both the diversity and the geographic distribution of Sigmodontinae during the Pliocene compared with what is known for the Quaternary. For a more detailed understanding of sigmodontine evolution, it is essential to enlarge the knowledge about these ancient Pliocene assemblages. Here, we describe a new genus and species from the Pliocene of Córdoba Province, central Argentina, and based mainly on its morphology, we make some paleoecological inferences.

Institutional Abbreviations—CNP, Colección de Mamíferos del Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina; CNP-E, Colección de Material de Egagrópilas y Afines ‘Elio Massoia’ del Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina; MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; MCNC-PV, Museo Provincial de Ciencias Naturales ‘Dr. Arturo U. Illia,’ Córdoba, Argentina; MMP-M, Museo Municipal de

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Ciencias Naturales y Tradicional ‘Lorenzo Scaglia,’ Mar del Plata, Argentina; **MNHNM**, Museo Nacional de Historia Natural, Montevideo, Uruguay; **MNK**, Colección de Vertebrados del Museo de Historia Natural ‘Noel Kempff Mercado,’ Santa Cruz, Bolivia; **PVL**, Colección de Paleontología de Vertebrados del Instituto Miguel Lillo, Tucumán, Argentina.

MATERIALS AND METHODS

The fossils studied are housed at the MCNC-PV. They consist of a fragment of right maxillary with the entire tooth row and the zygomatic plate (MCNC-PV 298), and isolated first (MNCN-PV 299) and second (lost during preparation) lower molars. All the referred material apparently belongs to the same individual. For the anatomical description, we follow the concepts of Carleton and Musser (1989) and Stepan (1995). Muscle inferences were based on Rinker (1954) and Voss (1988), and the nomenclature of

Reig (1977) was employed for the occlusal surface of the molars. The general taxonomy follows Patton et al. (2015). Measurements were obtained with a micrometer eyepiece on a stereomicroscope. Length and width of upper and lower molars were measured, as well as the minimal breadth of the zygomatic plate. In order to address the number of roots on the lingual side of the first upper molar, a radiograph of the maxillary in lingual view was obtained using a dental X-ray machine (DSJ, Dental San Justo, Argentina) operating at 70 kV and 8 mA; the image was recorded by a digital sensor (Vista Scan, Dürr Dental, Germany) and processed on a computer with the software DBSWIN 5.3.0 (Dürr Dental, Germany). Specimens of several sigmodontines examined for comparison are listed in Appendix 1. The notation used for upper and lower molars is ‘M’ and ‘m,’ respectively.

The fossils studied were found in exposed sediments along the right margin looking downstream of Los Sauces River, a fluvial course that dissects a valley within the mountain system of

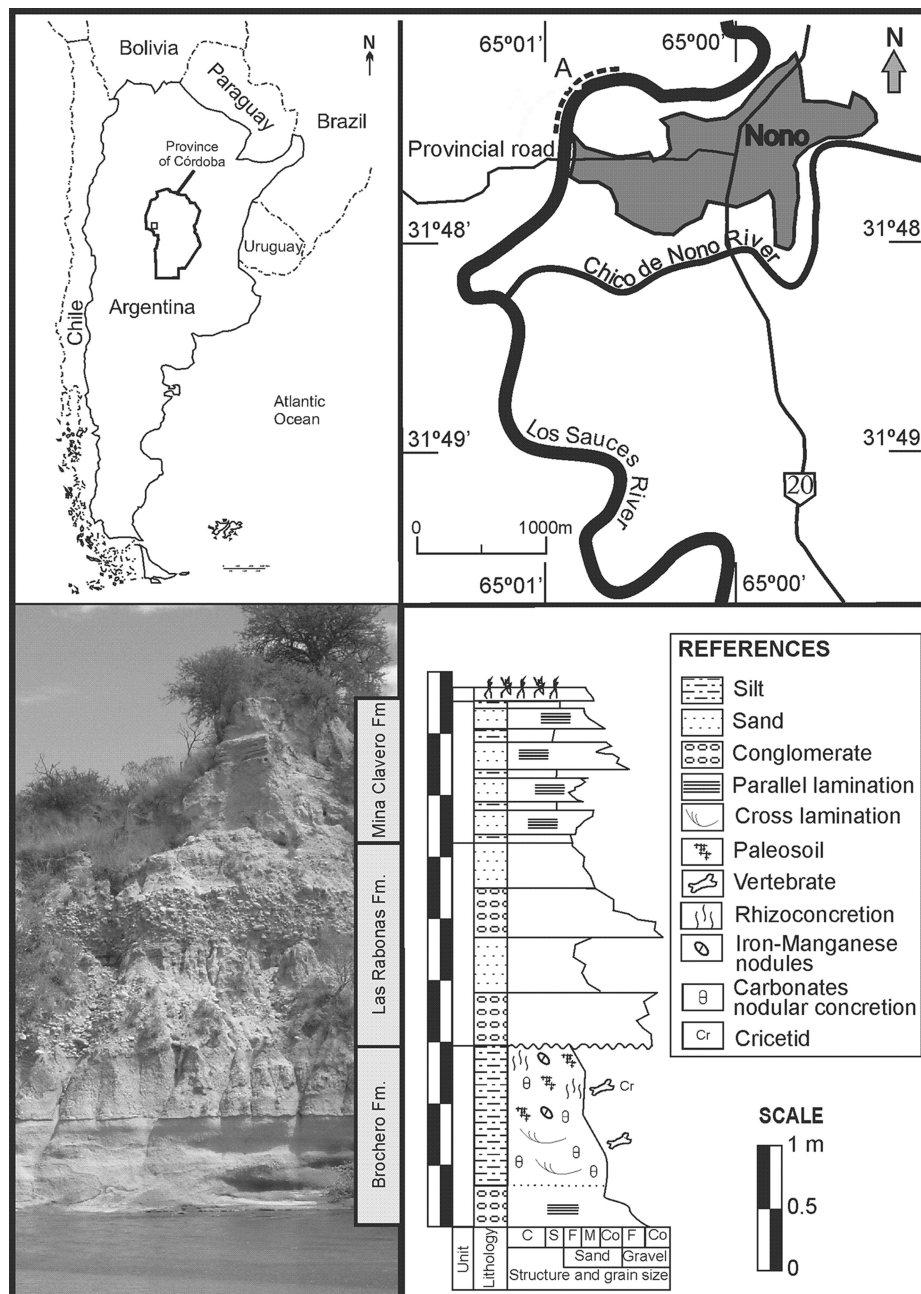


FIGURE 1. Geographic and stratigraphic provenances of the sigmodontine rodent described in this paper: the province of Córdoba in central Argentina (top, left); location of the bearing sediments along the right margin of Los Sauces River (A) in the vicinity of Nono (top, right); exposed sediments in a cliff of Los Sauces River, showing the main stratigraphic units (bottom, left); schematic stratigraphic profile (bottom, right).

Sierras Grandes in central-western Córdoba, Argentina (Fig. 1). The river cliffs expose about 10 m of outcrop and are composed, from bottom to top, of deposits that belong to the Brochero, Las Rabonas, and Mina Clavero formations (sensu Bonalumi et al., 1999). The studied materials come from the upper level of the Brochero Formation, approximately 1 m from the base of the unit (Fig. 1) and are attributed to the Late Pliocene.

This unit is clearly a fluvial sedimentary level without significant lamination but including very small clasts and very slightly hinted ripple marks, which probably correspond to a secondary flood zone, evidenced by a paleotopography with floodplain and paleosols. In the same bed, several other vertebrates (e.g., anurans, snakes, lizards; Cruz et al., 2014) were also obtained, including the cricetid rodent *Abrothrix magnus*, which was previously recorded in the Vorohuean (Piacenzian) deposits exposed in the Atlantic coast of Buenos Aires Province (Reig, 1987; Tonni et al., 1992; Teta et al., 2014). Additional mammals recovered in the same unit, but from lower levels, are the hydrocherid rodent *Phugatherium* cf. *P. novum* and the armadillo *Doellotatus* cf. *D. chapadmalensis* (Cruz et al., 2013, 2014); both taxa are also recorded in

the Chapadmalalan (late Zanclean–early Piacenzian). Therefore, although our knowledge is still limited, we are confident in referring the Brochero Formation to the Zanclean–Piacenzian interval (5.3 to 2.6 Ma).

RESULTS

The most remarkable anatomical feature of MCNC-PV 298 is the morphology of the zygomatic plate (Fig. 2). This structure is characterized by (1) a large upper spinous process also called zygomatic spine (sensu Steppan, 1995:30), associated with a strong excavation in the ventral body of its anterior border; (2) a poorly expressed area of insertion of the anterior deep masseter muscle; and (3) an inferior border of the spinous process running from the body of the zygomatic plate and forming a ‘twist’ in the junction with the anterior border. Broadly similar zygomatic plates are found in a few extant and extinct sigmodontines, including representatives of most of the recognized clades (e.g., Akodontini, Euneomyini, Phyllotini, and Reithrodontini). We conducted a complete survey and figured known examples on a recent phylogeny of

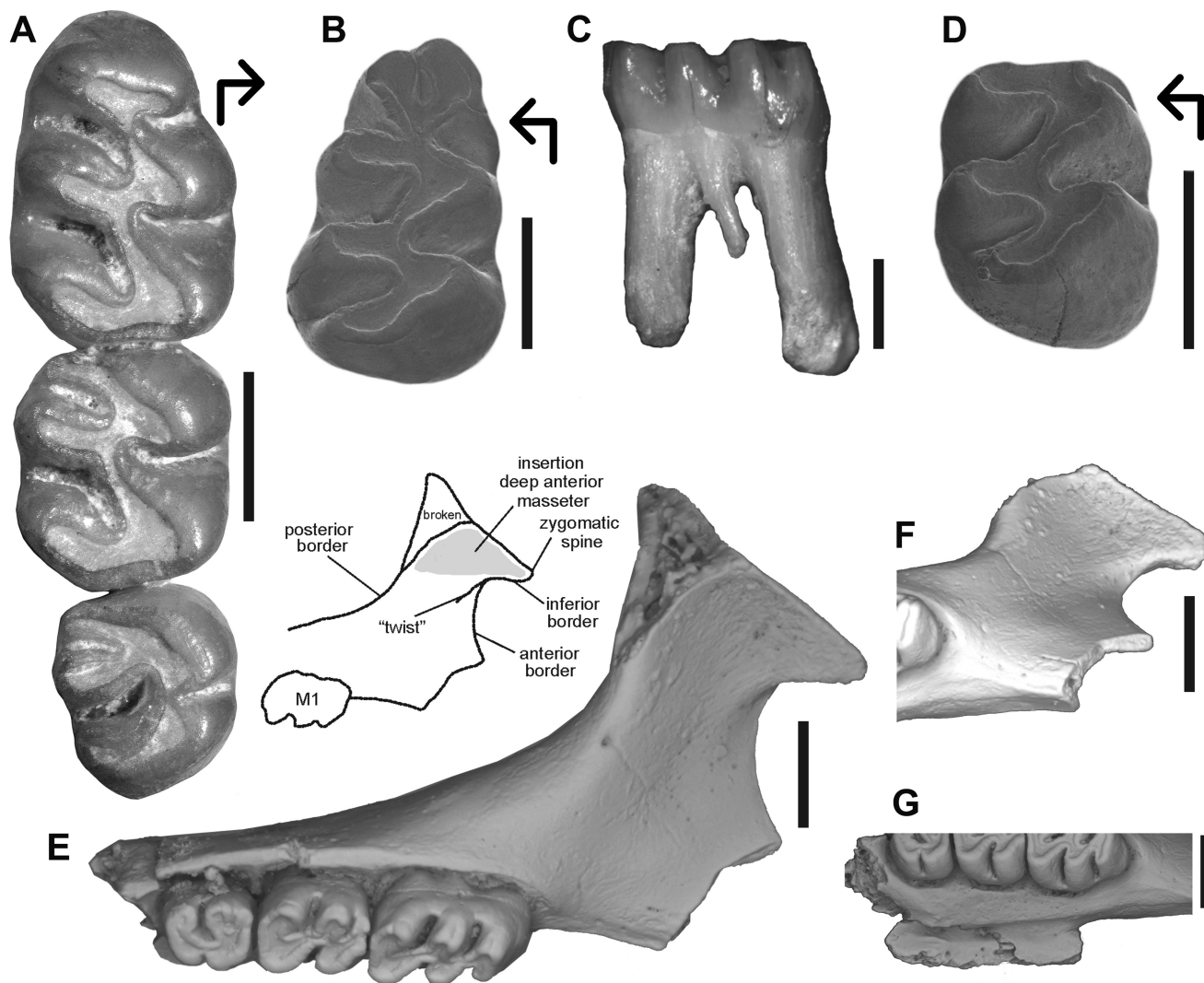


FIGURE 2. *Chukimys favaloroi*, new genus and species, MCNC-PV 298 (holotype) and MCNC-PV 299 (paratype). **A**, right M1–3 of MCNC-PV 298 in occlusal view; **B**, right m1 of MCNC-PV 299 in occlusal view; **C**, right m1 of MCNC-PV 299 in lingual view; **D**, right m2 in occlusal view (material loss); **E**, right maxillary of MCNC-PV 298 in lateral view and schematic diagram to indicate main anatomical features; **F**, anterior portion of the maxillary of MCNC-PV 298 in ventral view; **G**, detail of the bony palate of MCNC-PV 298 in ventral view. Arrows indicate anterolingual side. Scale bars equal 1 mm (A–D) and 2 mm (E–G).

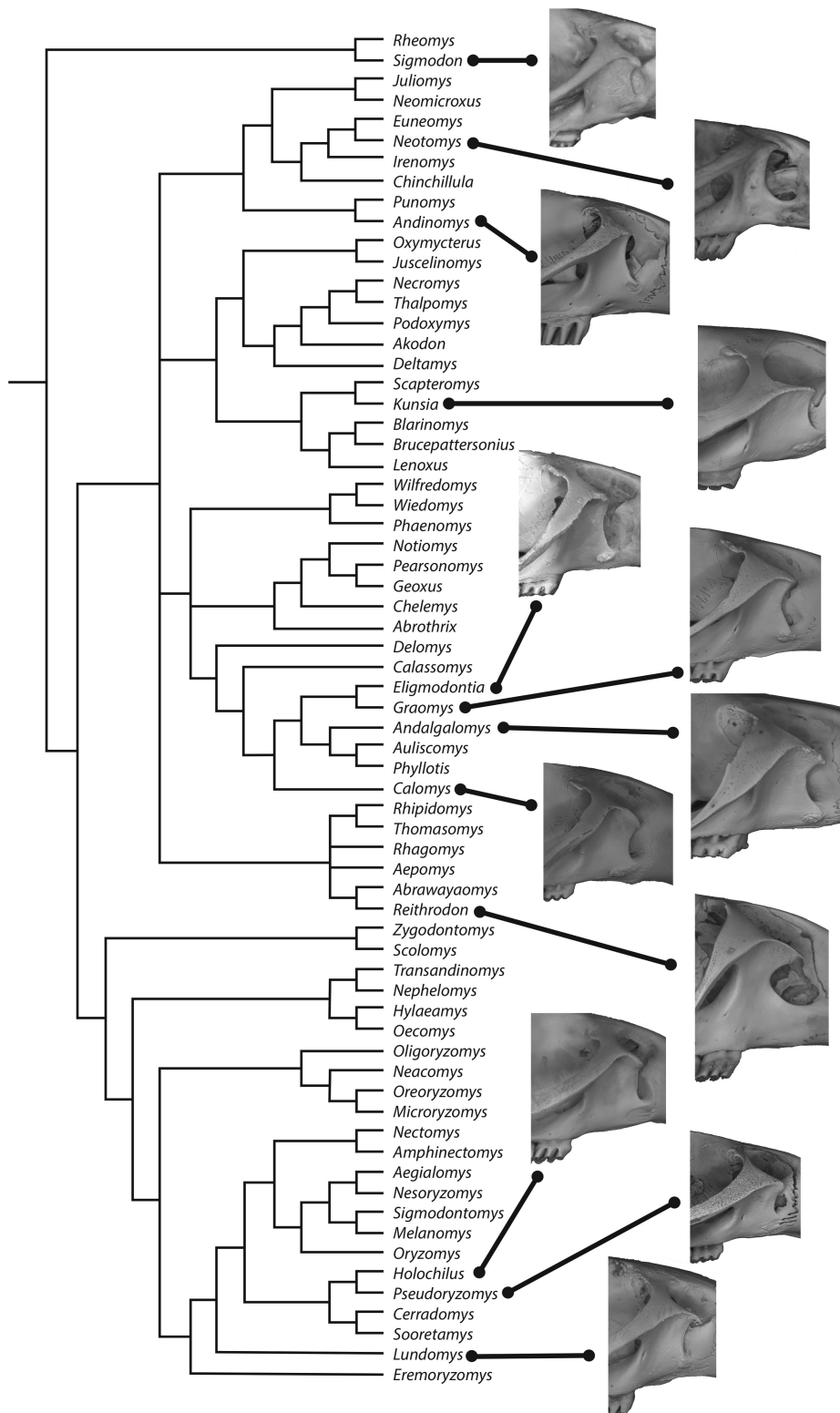


FIGURE 3. The diversity of living sigmodontine rodents that have zygomatic plates with zygomatic spines or acute upper corners mapped onto a recent phylogeny of the subfamily (after Parada et al., 2013, with modifications).

the subfamily in order to facilitate the following comparative section (Fig. 3).

In spite of having a concave anterior border and a moderately acute upper corner, the akodontine *Kunsia* clearly differs from MCNC-PV 298 by the general morphology of its zygomatic plate—with the antorbital bridge lying well below the dorsal surface of the rostrum—associated with complex hypsodont molars. *Andinomys*,

the Oryzomyini *Holochilus*, *Lundomys*, *Pseudoryzomys*, and the Sigmodontini *Sigmodon* have a slightly concave anterior border of the zygomatic plate and a short zygomatic spine, partially bent as a 'hook', and the same is true for †*Tafimys* (cf. Ortiz et al., 2000). This general morphology departs from what is observed in MCNC-PV 298, which shows a distinctly concave anterior border and a strongly developed and broad spinous process. Furthermore, and excepting

Pseudoryzomys, the molars of these taxa are highly hypsodont and laminated with a planate coronal surface, contrasting with those of MCNC-PV 298, characterized by a moderate hypsodonty and terraced surface.

The Phyllotini *Calomys* and *Eligmodontia* have a slightly excavated anterior border of the zygomatic plate and weakly developed acute upper corner, the expression of these features being much more reduced in these genera than in MCNC-PV 298. As for the molars, the occlusal surface of the upper ones is similar to what is observed in the specimen described here: simplified molars lacking a mesoloph, and an extended anteroloph on M2 and M3 almost divided into two lobes. Nevertheless, *Calomys* and *Eligmodontia* can be easily ruled out because of their bunodont and brachyodont molars. Two additional phyllotines, *Andalgalomys* and *Graomys*, have a concave anterior border of the zygomatic plate and broad zygomatic spines—as developed as in MCNC-PV 298 in *Andalgalomys*, less so in *Graomys* (Fig. 4A, B, E, F). Contrasting with the flat and uncomplicated palate exhibited by the MCNC-PV 298, the bony palate of *Graomys* is characterized by a more abundant development of foramina and furrows. In *Andalgalomys*, the palate is uncomplicated, although widely fenestrated by the disproportionate development of the anterior palatal foramen, clearly departing from the observed condition in the MCNC-PV 298. The fossil remains share some features with *Graomys* and *Andalgalomys* in molar morphology, including moderately hypsodont teeth, M3 with a tendency to division into two lobes, and the presence of an anteromedian flexid, and a central fossetid in the procingulum of the m1. However, noteworthy differences are also patent: whereas the anteroloph in M2 and M3 of MCNC-PV 298 are well developed, these structures are reduced in *Andalgalomys* and *Graomys*. In addition, median mures are clearly less oblique in MCNC-PV 298 compared with those of the mentioned phyllotines.

The shape of the zygomatic plate in the Euneomyini *Neotomys* and the Reithrodontini *Reithrodon* is very similar to that in MCNC-PV 298, with both genera characterized by a well-excavated anterior border and a strongly developed zygomatic spine. Nevertheless, whereas *Reithrodon* shows a spine as developed as in MCNC-PV 298, in *Neotomys* this structure does not reach the same expression. Furthermore, *Reithrodon* is one of the two sigmodontines that shares with MCNC-PV 298 a poorly developed area of insertion of the anterior deep masseter muscle and a ‘twist’ in the junction between the inferior border of the zygomatic spine and the anterior border of the zygomatic plate (Fig. 4C, D, G). At the same time and contrasting with the MCNC-PV 298, *Neotomys* and *Reithrodon* have strongly hypsodont and laminated simplified molars.

The extinct *Dankomys vorohuensis* Reig, 1994 (Fig. 5), is certainly the most similar taxon to MCNC-PV 298 that we observed with respect to both the general morphology of the zygomatic plate and the molars. *Dankomys vorohuensis* was described as a species of the genus †*Dankomys*, which is a member of Akodontini according to Reig (1978). However, it is fair to say that *D. vorohuensis* displays distinct morphological differences with respect to the type species of the genus, *Dankomys simpsoni* Reig, 1978, from Chapadmalalan deposits. Indeed, in the current treatment of sigmodontine taxonomy, it is hard to justify assignment of both forms to the same genus. *Dankomys vorohuensis* has a strongly excavated anterior border and also exhibits a poorly developed area of insertion of the anterior deep masseter. However, the spinous process in *D. vorohuensis* is not as prominent as in MCNC-PV 298 and its inferior border does not produce a perceptible ‘twist.’ Minor differences can also be seen in the development of the incisive foramen, which extends more posteriorly in *D. vorohuensis* and ends in a more rounded shape. Molars are very similar when MCNC-PV 298 and MCNC-PV 299 and the holotype of *D. vorohuensis* are compared and differences in wear are taken into account.

The comparisons presented above lead to the conclusion that the studied remains from the Pliocene of Córdoba have a unique combination of anatomical features within the sigmodontine radiation. To our best understanding, the mosaic produced by a specialized zygomatic plate morphology and a generalized molar pattern deserves the recognition of a new genus and species, as follows.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821

Family CRICETIDAE Fischer, 1817

Subfamily SIGMODONTINAE Wagner, 1843

†*CHUKIMYS*, gen. nov.

Type Species—†*Chukimys favaloroi*, new genus and species.

Included Species—Only the type species.

Diagnosis—As for the type and only species.

Distribution—Recorded only in western Córdoba Province, Argentina (Chapadmalalan–Vorohuean).

Etymology—The name highlights the conspicuous zygomatic spine that characterize the new entity described hereby combining *chuki* the Quechua word for ‘arrow’ and *mys* from the Greek, for ‘mouse.’

†*CHUKIMYS FAVALOROI*, gen. et sp. nov.

(Fig. 2)

Holotype—MCNC-PV 298, a fragment of right maxillary with zygomatic plate, the M1–3 and the associated portion of the bony palate.

Paratype—MCNC-PV 299, a right m1.

Etymology—This species is dedicated to physician René Gerónimo Favaloro (1923–2000), the Argentinean cardiac surgeon who first invented the coronary artery bypass surgery in 1967. Favaloro gave his life in defense of the ideals in a country that still needs examples like him.

Type Locality and Stratigraphy—Right margin of Los Sauces River (31°47′30″S, 65°00′58″W, 860 m), about 1.5 km west-northwest of Nono, San Alberto Department, Córdoba Province, Argentina. The type locality had been called ‘Paso de río arriba’ according to Castellanos (1942:34). The remains were collected from upper levels of the Brochero Formation (Chapadmalalan–Vorohuean).

Diagnosis—A small sigmodontine rodent (length of maxillary tooth row = 4.75 mm) similar in size to the extant phyllotine *Andalgalomys pearsoni* (Myers, 1977), showing a unique combination of characters that includes a zygomatic plate with strongly excavated anterior border and a conspicuous zygomatic spine in the upper corner, poorly developed area of insertion of the anterior deep masseter, and a ‘twist’ present in the junction between the inferior border of the zygomatic spine and the anterior border of the zygomatic plate; incisive foramen reaching the protocone of M1; palate narrow and flat; molars moderately hypsodont; procingulum of m1 with linguallly displaced antero-median flexus infolded to form a lake; and m1 four-rooted.

Measurements—M1: length = 2.05 mm, width = 1.5 mm; M2: length = 1.5 mm, width = 1.3 mm; M3: length = 1.25 mm, width = 1.15 mm; length of upper tooth row (alveolar) = 4.75 mm; m1: length = 2.25 mm, width = 1.5 mm; m2 (measured from a photograph): length = 1.26 mm, width = 1.26 mm; width of the zygomatic plate at the plate’s narrowest point = 2.25 mm.

Description—Upper molars are moderately hypsodont and terraced (sensu Hershkovitz, 1962), except for a flat M3. They have a simplified occlusal design without mesoloph and with the main cusps arranged in opposite pattern; the enamel is thick.

The M1 is oval in outline (Fig. 2A). Flexi meet at the midline. The mesoflexus is deeper than the paraflexus and both have their ends curved posteriorly, whereas the proto- and hypoflexus are

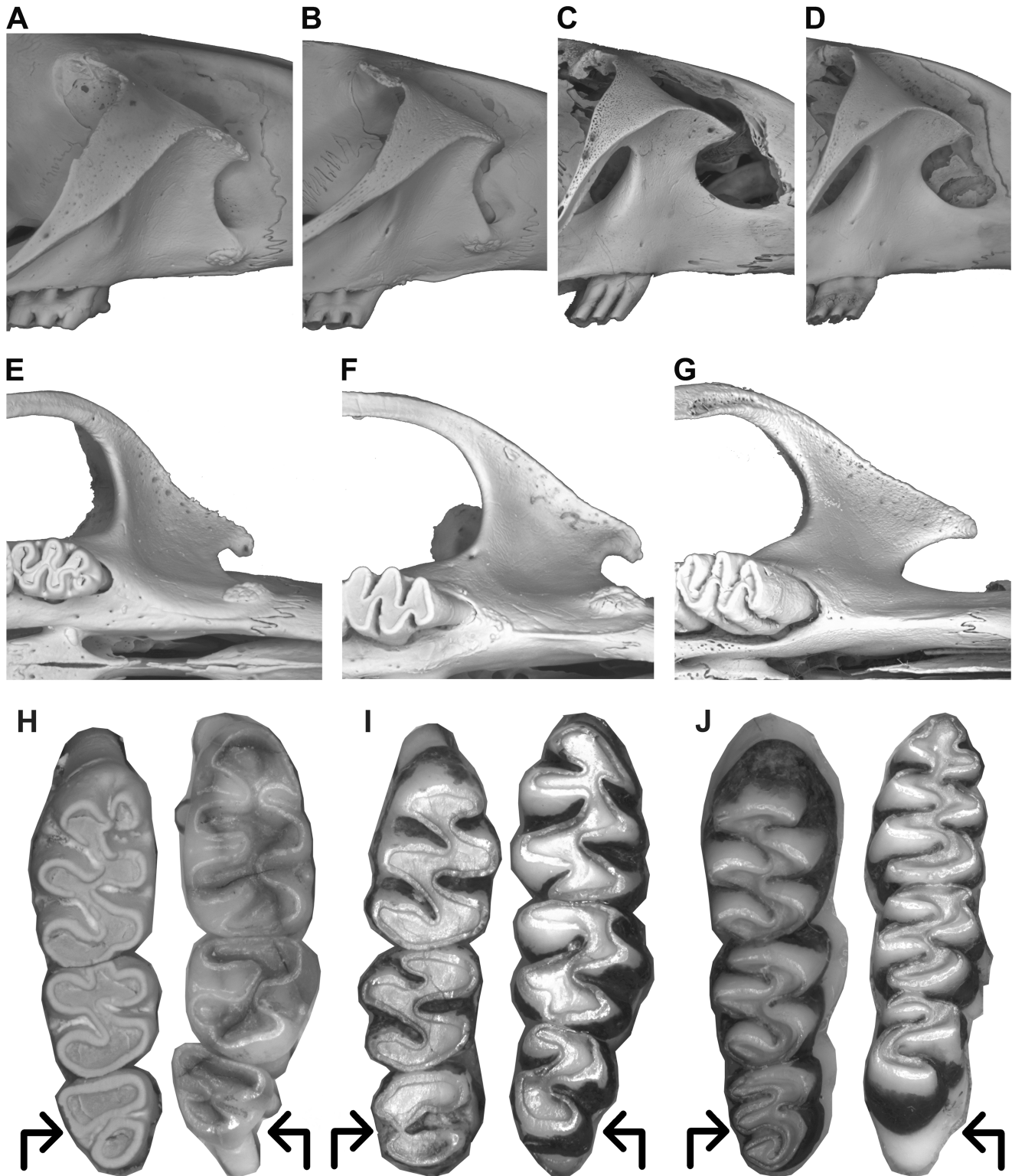


FIGURE 4. Zygomatic plates (A–G) and upper and lower tooth rows (H–J) of sigmodontine rodents in A–D, lateral and E–J, occlusal views. A, E, H, *Andalgalmys roigi*, CNP 2398; B, F, I, *Graomys griseoflavus*, CNP 4087; C, *Reithrodon auritus*, CNP-E 489-1, a young individual; D, G, *R. auritus*, CNP-E 489-2, an adult individual; J, *R. auritus*, CNP 3988. Arrows indicate anterolingual side.

transverse. Anterior and median mures are slightly oblique, the anterior mure being ‘strangulated.’ The procingulum is anteroposteriorly compressed, slightly oblique, with its labial half anterior to the lingual one, and lacks an anteromedian

flexus. The protocone and hypocone are subtriangular, the former slightly larger and more labially disposed than the latter. The paraloph and metaloph are subequal in size. There is no indication of a posteroloph. The M1 seems to have five roots,

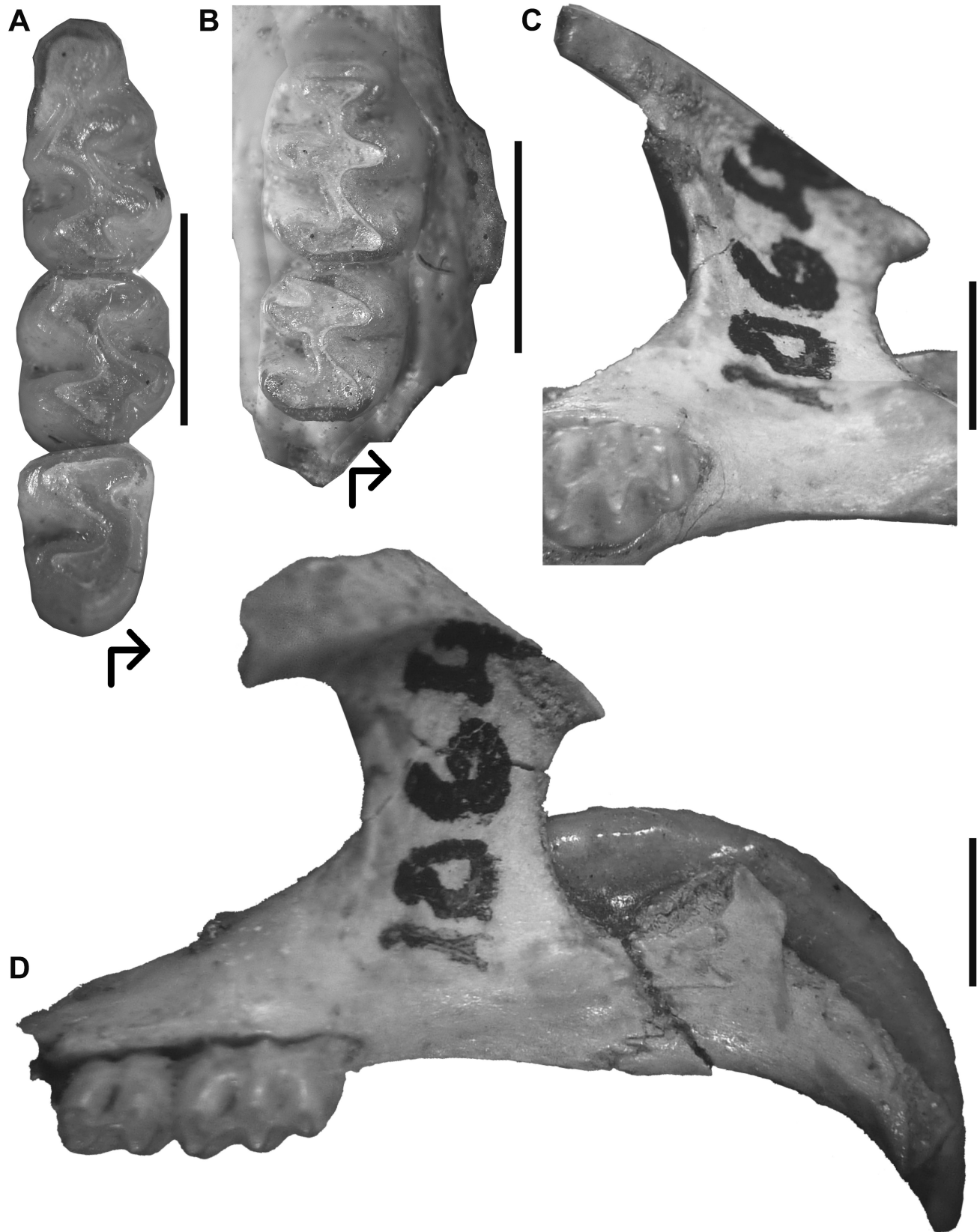


FIGURE 5. *Dankomys vorohuensis*, based on its holotype (Buenos Aires, 1 km south of Punta Lobería; MMP-M 1064). **A**, right m1–3 in occlusal view; **B**, right maxillary in ventral view with M1–2 and portion of bony palate; **C**, anterior portion of right maxillary in ventral view; **D**, right maxillary in lateral view. Arrows indicate anterolingual side. Scale bars equal 2 mm.

three of which can be easily seen directly from the material: an anterior one under the procingulum, a posterolabial one under the metacone, and an accessory root under the paracone. The X-ray view reveals that what seems to be a single lingual root lying under both the protocone and hypocone is in fact two fused roots originating from a common base.

The M2 is subrectangular in outline, with flexi meeting at the midline (Fig. 2A). The anteroloph is well developed. The hypoflexus and paraflexus are transverse, whereas the mesoflexus is shifted posteriorly. Median mure is slightly oblique, and the same is true for the paraloph and metaloph. The hypocone is slightly larger than the protocone, and the posteroloph is absent.

The M3 is about 80% of the length of M2. It has four well-developed cusps and transverse lophs (Fig. 2A). The anteroflexus is penetrating and flanked anteriorly by a thin anteroloph of same extension as the paraloph. This molar is almost divided in two lobes by the meeting of a short hypoflexus and a deeply penetrating and anteriorly shifted mesoflexus.

The m1 is oval in outline, with flat surface, the main cusps alternate, and lophids transverse (Fig. 2B). The procingulum is well developed, fan-shaped, with an anteromedian flexid lingually displaced and infolded to form a central enamel ring; the anterolabial conulid is larger than the anterolingual one. A thin anterolabial cingulum—no more than an enamel ridge at this wear stage—partially closes the protoflexid. The anterior murid, placed in the midline, is narrow and very short. The protoconid and hypoconid are subtriangular, the former slightly larger and more labially displaced than the latter. This cusp, slightly compressed anteroposteriorly, shows an enamel spur in its anterior border. The median murid is oblique to the main axis of the tooth because the hypoflexid is posteriorly directed and the apex of the entoflexid is anteriorly shifted. The ento- and hypoflexid meet at the midline. A well-developed, slightly oblique posterolophid is present. The tooth has four roots, two main ones in anterior and posterior locations and two accessory labial and lingual tiny roots in the middle (Fig. 2C).

The m2 is square in outline and has a trilophodont pattern (Fig. 2D). Its morphology is very similar to the comparable portion of the m1. The protoflexid is very short, delimited anteriorly by a strong anterolabial cingulum. The lophids are slightly oblique, and the cusps are alternate. The entoflexid, anteriorly directed, and the hypoflexid, posteriorly directed, flank an oblique median murid. As in the m1, the posteroflexid is well developed and delimited posteriorly by a posterolophid smaller in extension to the entolophid and metalophid.

The general morphology of the zygomatic plate (Fig. 2E, F) was described above. The zygomatic spine is slightly broken in its end, which prevents an estimate of its full length. The posterior margin of the body of the plate is anterior to the alveolus of M1 (Fig. 2E). The posterior end of the incisive foramen reaches the anterior level of the protocone of M1 and seems to be acute in shape (Fig. 2G). The palate is narrow (sensu Hershkovitz, 1962), and its total length cannot be appreciated due to the fragmentary condition of the material. A tiny anterior palatal foramen can be seen at the level of the M2.

Comparisons—In spite of their strong resemblance (see above and Figs. 2, 5), *Chukimys favaloroi* and *Dankomys vorohuensis* show several differences that support that they belong to two separate species. *Chukimys favaloroi* has smaller molars than *D. vorohuensis* (cf. Reig, 1994). Also, *C. favaloroi* has an acute posterior end of the incisive foramen, whereas in *D. vorohuensis* it is more rounded. In addition, the former has a more prominent zygomatic spine than the latter. The two species also differ in the morphology and proportions of the M2. *Chukimys favaloroi* has a subrectangular M2 (length: 1.5 mm, width: 1.3 mm) with a well-developed paraflexus, whereas the M2 in *D. vorohuensis* is square in outline (length: 1.5 mm, width: 1.5 mm) and its paraflexus is smaller. In the m1, the anterolabial cingulum extends backwards in *D.*

vorohuensis, whereas it has a more labial extension in *C. favaloroi*. Other differences such as the lack of 'twist' in the zygomatic plate of *D. vorohuensis*, in contrast with the presence of this trait in *C. favaloroi*, can be attributed to ontogenetic variation.

DISCUSSION

Tribal Affiliation—As is true for most of the fossil sigmodontines, morphological data at hand are insufficient to support a tribal allocation with confidence. *Chukimys* could be included in Phyllotini because it has a molar occlusal morphology typical of several members of this tribe, characterized by a simplified occlusal trilophodont pattern, lacking mesoloph, squared M2, and moderately short M3. However, the new genus described here shares with the unique extant Reithrodontini both the 'twist' in the zygomatic plate and the slightly excavated area of insertion of the anterior deep masseter. Because *Reithrodontomys* also has simplified molars, the hypothesis that *Chukimys* is an extinct member of Reithrodontini—although with less hypsodont teeth—cannot be discarded. A refined phylogenetic analysis is needed to test the two advanced hypotheses. Several efforts have been made—from morphological or combined evidence—to clarify the relationships among Phyllotini and, with minor extension, Sigmodontinae (e.g., Steppan, 1995; Salazar-Bravo et al., 2013; Pardiñas et al., 2014; Carrizo and Catalano, 2015). Unfortunately, the more complex analyses performed to date excluded fossil taxa (cf. Carrizo and Catalano, 2015), which were explicitly assessed in more limited taxonomic approaches (e.g., Steppan and Pardiñas, 1998; Ortiz et al., 2000).

Taxonomic Implications—The description of *Chukimys* improves the known Pliocene diversity of Sigmodontinae. To date, few extinct Pliocene representatives of this group of mammals have been recorded, including the genera *Cholomys* Reig, 1980, *Dankomys* Reig, 1978, *Panchomys* Pardiñas, 1997, and *Pardinamys* Ortiz, Jayat, and Steppan, 2012 (Pardiñas et al., 2002; Ortiz et al., 2012a). The erection of *Chukimys* is refreshing in connection with a previously known supposed akodontine, *Dankomys vorohuensis* Reig, 1994. *Chukimys* is clearly different from *Dankomys simpsoni*, the type species of this genus. Among several anatomical features, *D. simpsoni* is characterized by a broad zygomatic plate with the upper corner rounded and the anterior border flat (cf. Reig, 1978:fig. 3), departing deeply from the zygomatic spine present in *Chukimys* and its strongly excavated anterior border. However, this is not the case of the second species assigned to *Dankomys*, *D. vorohuensis* (see above). Our perception is that the hypothesis advanced by Reig in his doctoral dissertation regarding the generic position of *D. vorohuensis* (i.e., the allocation of *D. vorohuensis* in *Dankomys*; Reig, 1972) was formulated under the practice of the systematic paradigm widespread in the 1960s that constructed genera and species containing ample morphological variation (cf. Hershkovitz, 1966). Unfortunately, A. M. Báez and C. Quintana decided to publish several unrevised aspects of Reig (1972) in a posthumous contribution (Reig, 1994), cementing by this action a genus *Dankomys* composed of two very different species. However, *D. vorohuensis* is neither a *Dankomys* nor an Akodontini. Our hypothesis is that *D. vorohuensis* represents an additional species of *Chukimys*, a result that will be presented in a forthcoming paper dealing with a revision of the genus *Dankomys*.

Biostratigraphic Implications—*Chukimys* was found in association with *Abrothrix magnus* Reig, 1987, an Echimyidae, gen. et sp. indet., and other vertebrates, such as anurans (*Rhinella* cf. *R. arenarum* and *R. cf. R. spinulosa*, Bufonidae), snakes ('Colubridae,' indet), and lizards (Iguanidae, Teiidae, and Tropiduriinae; Brizuela and Cruz, 2013; Cruz et al., 2014). From the same formation but in a lower level the rodent *Phugatherium* cf. *P. novum* (Caviidae) and the cingulates *Doellotatus* cf. *D. chapadmalensis* (Dasypodidae), *Phlyctaenophya* sp.

(Glyptodontidae), and a Panochthidae, gen. et sp. indet. were recovered (Cruz et al., 2013, 2014). These taxa are recorded for the Vorohuean and Chapadmalalan in the more continuous and detailed paleontological record of southeastern Buenos Aires Province (Reig, 1987; Tonni et al., 1992), suggesting this temporal range for the sediments. Nevertheless, if the hypothesis of congeneric status between *Chukimys favaloroi* and *Dankomys vorohuensis* is correct, this evidence, plus the record of *Abrothrix magnus*, points to a Vorohuean time for the deposition of the upper level of Brochero Formation. In this context, *Chukimys* would be a valuable stratigraphic indicator of the Vorohuean in association with *Abrothrix magnus*. Furthermore, this result could indicate an environmental and climatic continuity between the Buenos Aires and Córdoba provinces during the late Pliocene. Preliminarily, the analysis of the faunal list shows that elements typical of arid and colder conditions of Chapadmalalan age (e.g., *Doellotatus*; Prado et al., 1998) are recorded in the lower part of the Brochero Formation. Supporting these inferences, it is possible that *Phugatherium*, recovered from these units, was a cursorial (not semiaquatic) taxon, such as other Miocene-Pliocene hydrochoerids (Kraglievich, 1940; García Esponda and Candela, 2015), and therefore not necessarily associated with humid environments characterized by perpetual water bodies, such as those inhabited by the extant capybara. On the contrary, those taxa indicators of more humid conditions and of Vorohuean age (e.g., Echimyidae) are restricted to the upper levels of this stratigraphic unit. These paleoclimatic inferences are also supported by sedimentological data: the upper level of the Brochero Formation has a paleotopography defining an area of alluvial fans and mud flows and further development of paleosols.

Paleoecological Inferences—The anterior deep masseter, a fundamental muscle in mastication, originates in the upper portion of the zygomatic plate (Voss, 1988). Studies conducted on *Sigmodon*, which shows a zygomatic spine (Rinker, 1954), contrasted with those carried out in *Ichthyomys*, which lacks this structure (Voss, 1988), suggest that the spinous process is involved in the attachment of the anterior deep masseter. The zygomatic spine provides a mechanical advantage by extending the distance between the areas of origin and insertion of the anterior deep masseter and thus increasing its strength (Hiimae, 1971).

From a morphofunctional point of view, the anterior deep masseter is involved in the two cycles of mastication, the ingestive cycle—when gnawing at the incisor—and the masticatory cycle—when chewing at the molars (Hiimae, 1971). Therefore, it is tempting to propose that in mainly herbivorous genera such as *Neotomys* (Ortiz and Jayat, 2015) or *Reithrodon* (Scaglia et al., 1982; Pearson, 1988), which exhibit strongly hypsodont molars, the development of a spinous process is associated with the need for strength in order to grind fibrous vegetative material during the masticatory cycle. On the other hand, in omnivorous genera such as *Graomys*, which incorporates hard material such as seeds in their diet (Giannoni et al., 2005) and have moderately hypsodont molars, the development of a spinous process provides strength to crush these resistant materials during the ingestive cycle. *Chukimys* does not exhibit features of typically herbivorous taxa, which mostly bear hypsodont and simplified molars. On the contrary, their moderately hypsodont and terraced molars point to an omnivorous diet. In addition, the well-developed zygomatic spine would then suggest that it incorporated hard material in its diet.

CONCLUSION

Here, we add a new extinct genus, *Chukimys*, to the known assemblage of Pliocene sigmodontines, until now restricted to animals from Pampean region and northwestern Argentina. This new rodent increases the taxonomical and morphological

diversity of ancient sigmodontines in South America. Particularly, *Chukimys* is interesting in the combination of a specialized zygomatic plate, characterized by a conspicuous zygomatic spine, with moderately hypsodont simplified molars. This discovery reminds us that much is still waiting to be learned about the ancient radiation of this diverse group of rodents and represents a call for attention about the limits of the current phylogenies.

ACKNOWLEDGMENTS

We thank C. A. Carignano, J. C. Fernicola, and J. Kaluza for field assistance, H. N. Aragón and P. González for the radiographic view, and P. Teta for his input to this project in an initial stage. Access to several collections or loans was provided by the curators D. Flores (MACN), E. González (MNHM), F. Scaglia and A. Dondas (MMP-M), J. Powell (PVL), and N. Rocha (MNK). CONICET grant PIP 2011-164 to F. Prevosti and Agencia grant PICT 2012-1054 to L.E.C. and PICT 2014-1039 to U.F. J.P. supported this research.

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Submitted December 18, 2015; revisions received March 3, 2016;

accepted March 10, 2016.

Handling editor: Thomas Martin.

APPENDIX 1. Specimens examined. All from Argentina unless indicated otherwise.

Andalgalomys roigi—Catamarca, Nueva California (CNP 2397, 2398).
Andinomys edax—Jujuy, Humahuaca (CNP 5401); Salta, Valle Encantado (CNP-E 809).
Calomys callidus—Entre Ríos, Ea. Santa Ana de Carpinchorí (CNP 1650).
†*Dankomys vorohuensis*—Buenos Aires, 1 km south of Punta Lobería (upper Pliocene; MMP-M 1064).
†*Dankomys simpsoni*—Buenos Aires, Atlantic cliffs between Mar del Plata and Miramar (upper Pliocene; MMP-M 1153).
Eligmodontia typus—Chubut, Puerto Lobos (CNP 1156).
Graomys chacoensis—Formosa, Reserva Natural El Bagual (CNP 3706).
Graomys griseoflavus—Mendoza, Mendoza (CNP 4087); Chubut, Bahía Cracker (CNP 3443); Piedra Grande (CNP 3444); La Pampa, Pichi Mahuida (CNP 3684, 3699, 3790, 3822).

Holochilus chacarius—Chaco, Selvas del Río de Oro (CNP 3982).
Kunsia tomentosus—Santa Cruz, Parque Nacional Noel Kempff Mercado, Bolivia (MNK 2078).
Lundomys molitor—Canelones, Bañados Tropas Viejas, Uruguay (MNHNM 735).
Neotomys ebriosus—Salta, San Antonio de los Cobres (CNP 3639, 3640).
Pseudoryzomys simplex—Santa Fe, Berna (CNP 543, 547); Formosa, Reserva Natural El Bagual (CNP 606, 622).
Reithrodon auritus—Santa Cruz, Ea. La Julia (CNP-E 489), Cajón del río Oro (CNP 3739, 3803); Neuquén, Piedra del Aguila (CNP 3353); Chubut, Cabo Raso (CNP 3465).
Sigmodon sp.—Venezuela (MACN unnumbered).
†*Tafimys powelli*—Tucumán, La Angostura (late Pleistocene; PVL 5450).