A NEW SPECIES OF *REIGECHIMYS* (RODENTIA, ECHIMYIDAE) FROM THE LATE MIOCENE OF CENTRAL ARGENTINA AND THE EVOLUTIONARY PATTERN OF THE LINEAGE

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Abstract . The genus *Reigechimys* (Rodentia, Echimyidae) was originally described on the basis of two mandibular fragments recovered from Huayquerian (late Miocene) outcrops of the Cerro Azul Formation in La Pampa Province (Argentina). The included species (*R. plesiodon* Verzi *et al*. and *R. octodontiformis* Verzi *et al*.) represent a peculiar lineage characterized by its molar morphology with occlusal simplification that is extreme for the family. New materials recently found at the Cerro Azul Formation allow for a more detailed knowledge of the variation of *Reigechimys* and recognition of a new species, *Reigechimys simplex* sp. nov. characterized by the absence of mesoflexid/fossettid in the m1–2. The morphological changes of *Reigechimys* are described in the context of the turnover exhibited by octodontoid rodents in the Huayquerian of the Cerro Azul Formation. The polarity of changes described for *Reigechimys* is consistent with those of the other lineages. This evolutionary pattern enhances the biochronological interpretation of the Huayquerian in this formation.

Key words. Rodentia. Echimyidae. *Reigechimys*. Late Miocene. Argentina.

Resumen. UNA NUEVA ESPECIE DE *REIGECHIMYS* (RODENTIA, ECHIMYIDAE) DEL MIOCENO TARDÍO DEL CENTRO DE ARGENTINA Y EL PATRÓN EVOLUTIVO DEL LINAJE. *Reigechimys* (Rodentia, Echimyidae) fue descripto inicialmente sobre la base de dos fragmentos mandibulares recuperados de afloramientos de la Formación Cerro Azul en la Provincia de La Pampa (Argentina), asignados al Huayqueriense (Mioceno tardío). Las especies conocidas (*R. plesiodon* Verzi *et al*. y *R. octodontiformis* Verzi *et al*.) representan un linaje singular en esta familia, caracterizado por presentar la mayor simplificación oclusal en sus molares. Nuevos materiales recientemente encontrados en diferentes afloramientos de la Formación Cerro Azul permiten reinterpretar la variabilidad de *Reigechimys* y reconocer una nueva especie, *Reigechimys simplex* sp. nov. caracterizada por la ausencia de mesofléxido/fosétida en los m1–2. La polaridad de los cambios morfológicos de *Reigechimys* es consistente con los cambios descriptos para otros roedores octodontoidea del Huayqueriense de la Formación Cerro Azul. La presencia de *Reigechimys* y su patrón de cambio en varios afloramientos de esta formación provee nueva evidencia para la interpretación biocronológica de los niveles portadores.

Palabras clave. Rodentia. Echimyidae. *Reigechimys*. Mioceno tardío. Argentina.

THE rodents of the family Echimyidae are currently distributed in tropical and subtropical regions of northern South America and Central America, primarily in forested areas (Emmons and Feer, 1997; Galewski *et al*., 2005; Upham and Patterson, 2012). The earliest fossils of the family, from the late Eocene or early Oligocene of Peru (Frailey and Campbell, 2004) and late Oligocene–middle Miocene of Patagonia (Wood and Patterson, 1959; Patterson and Pascual, 1968; Vucetich *et al*., 1993) are related to living clades that inhabit tropical and subtropical forests (Verzi *et al*., 2013). Since the late Miocene arid and cooling trend (Pascual and Ortiz Jaureguizar, 1990; Janis, 1993; Denton, 1999; Arakaki *et al*., 2011), the echimyid record has shown changes in its taxo-

nomic composition that are concurrent with paleoclimatic changes. The species recorded in southern South America since that moment, and until their disappearance from the area, are related to those that currently occupy Chacoan-type open environments in the Cerrado and Caatinga biomes (Reig, 1986; Verzi *et al*., 1995, 2013; Olivares *et al*., 2012; Cartelle, 1999). Among the latter, the species of *Reigechimys* Verzi, Vucetich and Montalvo, 1994 represent a peculiar lineage characterized by their molar morphology which displays an occlusal simplification that is extreme for the family; this morphology mirrors that of the open-habitat dwelling octodontid rodents, but through a different ontogenetic pathway (Verzi *et al*., 1994).

Reigechimys was originally described on the basis of only two mandibular fragments. In this paper we report *Reigechimys* samples recently found at different Huayquerian (late Miocene) outcrops of the Cerro Azul Formation in central Argentina. The new materials allow for a more detailed knowledge of the variation of *Reigechimys*. A new species is recognized, whose molars show clear differences from those of the previously described *Reigechimys plesiodon* Verzi, Vucetich and Montalvo, 1994 and *Reigechimys octodontiformis* Verzi, Vucetich and Montalvo, 1994. The morphological changes of *Reigechimys* are described in the context of the turnover exhibited by octodontoid rodents in the Huayquerian of the Cerro Azul Formation.

GEOLOGICAL SETTING

The central and eastern sectors of La Pampa Province extend across a tectonic block (La Pampa central block) uplifted in the late Miocene and the Macachín tectonic basin (Folguera and Zárate, 2009). Within the domain of the tectonic block, the landscape consists of a structural plain, gently sloping eastward, incised by a series of longitudinal depressions up to 100 m deep, known as transversal valleys. The area under analysis is made up of an upper cover of Neogene continental deposits, grouped into the Cerro Azul Formation of around 100–200 m of thickness that blankets the Precambrian–Mesozoic bedrock, in turn buried by late Quaternary deposits (Fig. 1).

The Cerro Azul Formation consists of brown silts and sandy silts of primary eolian origin (loess deposits), which have been reworked by aqueous agents (loess-like deposits). Paleosol levels and pedogenic features as well as carbonate accumulations including nodules and rhizoconcretions are common throughout the sequence (Folguera and Zárate, 2009). The deposits are discontinuously exposed at scattered locations, generally consisting of reduced outcrops, restricted to the bottom and hills lopes of topographic depressions and the valleys. A detailed description of the geology and stratigraphy of this formation is provided by Linares *et al.* (1980), Goin *et al.* (2000), Visconti (2007) and Folguera and Zárate (2009).

A late Miocene age has been attributed to the Cerro Azul Formation succession (Verzi and Montalvo, 2008; Verzi *et al.*, 2008 and references cited therein) on the basis of its vertebrate fossil content (Chasicoan and Huayquerian SALMA).

The following exposures of the Cerro Azul Formation included *Reigechimys* specimens, Laguna Chillhué, Quehué,

Telén, Loventué, Salinas Grandes de Hidalgo, Puesto Colorado, Estancia Ré, Bajo Giuliani, and Estancia Don Mariano (Fig. 1). The scarce thickness, reduced areal extension and homogeneous aspect of the Cerro Azul Formation exposures, prevent a confident stratigraphic correlation of the outcrops on the basis of lithological criteria. However, five biozones, covering the Chasicoan–late Huayquerian time span (late Miocene), have been recognized for the Cerro Azul Formation, based mainly on the anagenetic pattern of change of the Ctenomyidae rodent *Chasichimys–Xenodontomys* lineage (Verzi *et al.*, 2008). This evolutionary lineage suggests chronological differences among localities, which were later supported by the Octodontidae rodent *Neophanomys* lineage (Verzi *et al.*, 2011).

The remains from Laguna Chillhué (Pascual and Bondesio, 1982; Montalvo *et al.*, 1995) were recovered from the lower levels of the Cerro Azul Formation, recently interpreted as fluvial facies (Deschamps *et al.*, 2013). From the same levels, Verzi *et al.* (2008) defined the Biozone of *Chasichimys scagliai* (late Chasicoan or early Huayquerian?, late Miocene). The remains from Quehué come from fluvial facies of the Cerro Azul Formation. These levels also yielded fossil remains of the Octodontidae *Neophanomys pristinus* Verzi, Vieytes and Montalvo 2011. The Cerro Azul Formation in Telén was interpreted as a loess deposit with two similar and slightly developed paleosols; the Huayquerian assemblage recovered from this locality was dealt with by Montalvo *et al.* (2008). The outcrops of Loventué consist of loess deposits with slightly developed paleosols (Montalvo *et al.*, 2002). The Cerro Azul Formation in Salinas Grandes de Hidalgo has similar characteristics to the exposures of Laguna Chillhué. Their basal levels were interpreted as lacustrine (Goin *et al.*, 2000), but new studies suggest a fluvial origin for these deposits (M. Zárate, pers. com.). The fossil assemblage was classically assigned to the Huayquerian (Pascual and Bocchino, 1963; Pascual *et al.*, 1965; Zetti, 1972; Campbell and Tonni, 1980; Goin and Montalvo, 1988; Verzi *et al.*, 1994; Vizcaíno and Fariña, 1999; Goin *et al.*, 2000; Cerdeño and Montalvo, 2001, 2002; Urrutia *et al.*, 2008, Cenizo *et al.*, 2012; Olivares *et al.*, 2012; Vezzosi, 2012). The outcrops of Puesto Colorado, Estancia Ré, Bajo Giuliani and Estancia Don Mariano are similar to each other with a reduced thickness (siltstones showing evidence of pedogenesis and diagenesis). Verzi *et al.* (2008) defined the Biozone of "*Chasichimys* morphotype a"
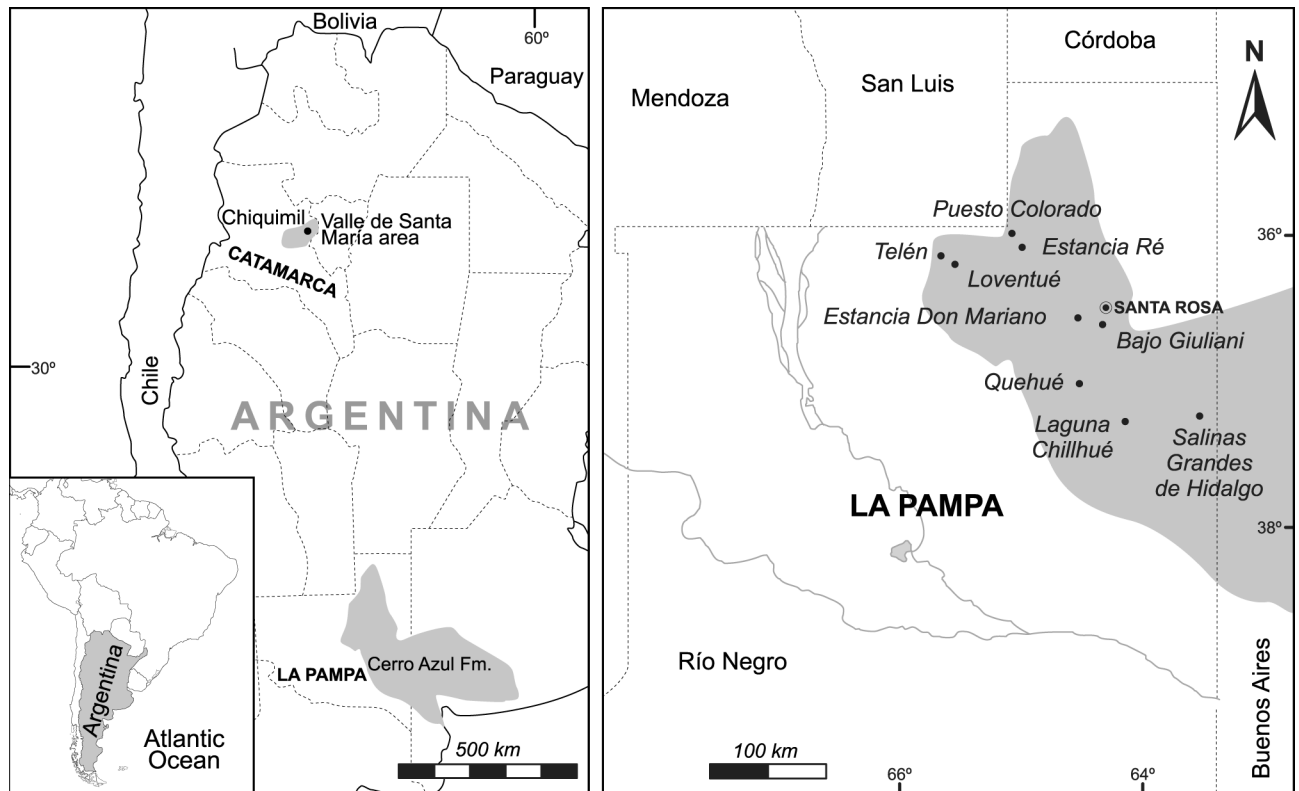
Figure 1. Geographic location of the late Miocene deposits of Cerro Azul Formation and Valle de Santa María.

(late Huayquerian, late Miocene) in the middle levels of Bajo Giuliani, where remains of *N. pristinus* were also found (Verzi *et al*., 2011). The holotype of this species comes from Estancia Don Mariano (Verzi *et al*., 2011).

MATERIAL AND METHODS

The studied specimens belong to the paleontological collections of the following institutions: **GHUNLPam**, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, La Pampa, Argentina; **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina.

Nomenclature used (Figs. 2.1–2) follows the proposal of Marivaux *et al*. (2004). Over each specimen, length of the dental series available, antero-posterior length (AP), anterior width (AW) and posterior width (PW) of each molariform (Fig. 2.3), were measured using a micrometer ocular in a binocular Leica MS5 microscope. Dental series of all specimens were drawn with the camera lucida of the same microscope. The photographs were taken with a digital camera Leica DFC 295 connected to a stereomicroscope Leica M50.

Ontogeny analysis was based on characters from the occlusal morphology of the lower cheek teeth, because they are the most abundant remains, which are comparable with the holotype specimens of known species. The closing sequence of flexids and fossettids permanence were especially taken into account in this analysis. Distinctive and qualitative features of upper cheek teeth were also described and illustrated.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOMORPHA Brandt, 1855
Infraorder HYSTRICOGNATHI Tullberg, 1899
Superfamily OCTODONTOIDEA Waterhouse, 1839
Family ECHIMYIDAE Gray, 1825

Genus ***Reigechimys*** Verzi, Vucetich and Montalvo, 1994

Type species. *Reigechimys octodontiformis* Verzi, Vucetich and Montalvo, 1994; original designation; Cerro Azul Formation, Huayquerian, late Miocene; La Pampa Province, Argentina.

Included species. The type species; *Reigechimys plesiodon* Verzi, Vucetich and Montalvo, 1994; *Reigechimys simplex* sp. nov.

Distribution. *Reigechimys* is recorded in Huayquerian (upper late Miocene) deposits of central Argentina (Fig. 1). The speci-
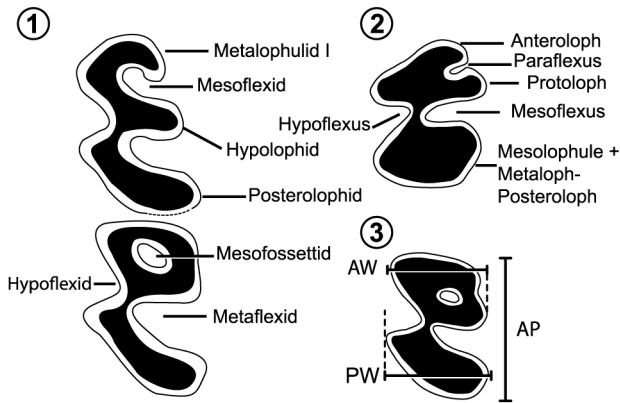
Figure 2. Echimyidae tooth nomenclature and measurements (following Marivaux *et al.*, 2004). **1,** Dp4–m1 of GHUNLPam 22971; **2,** DP4 of GHUNLPam 19053. **3,** m1 of GHUNLPam 9459. Abbreviations: **AW,** anterior width; **PW,** posterior width; **AP,** anteroposterior length.

men MACN 8369 from the Araucanian (late Miocene) of Catamarca ("*Plataeomys*" *in schedis*) could be related to this genus (Verzi *et al.*, 1994).

Revised diagnosis. Echimyid similar in size to *Thrichomys*. Protohypsodont cheek teeth (*sensu* Mones, 1982) with a transitory figure-eight shaped occlusal surface; Dp4 trilophodont in juveniles, with an occasional spur behind the first lophid, both limiting an ephemeral fossettid in the anterior lobe; m1–m3 with persistent hypoflexid/fossettid, metaflexid/fossettid less so, and mesoflexid/fossettid more ephemeral or absent. Posterolophid broad. Upper molars with only hypo- and mesoflexus/fossette; para- and metaflexus/fossette absent. Incisor slender and high. Mandible with masseteric crest

barely projected outward because the presence of a shallow masseteric fossa.

Reigechimys simplex sp. nov.
Figures 3, 4.1 and 4.4, Tables 1–2

2011. *Reigechimys octodontiformis* Verzi, Vieytes and Montalvo.

Etymology. *Simplex*, simple, indicating that the occlusal morphology is more simplified than in the other species.

Diagnosis. Enamel design in the occlusal surface of molars more simplified than that of the remaining species of the genus. Juvenile m1–m2 without mesoflexid/fossetid; the figure-eight-shaped occlusal surface of these molars persists to the ontogenetic stage in which Dp4 has a small metafossetid. Lingual tip of the anterior lobe of m1–m2 antero-posteriorly narrower than in the other species of the genus.

Holotype. GHUNLPam 4634, left mandibular fragment with intra–alveolar portion of the incisor, Dp4 alveolus, m1–2, and erupting m3 (Figs. 3–4).

Hypodigm. The holotype, and GHUNLPam 2182, left mandibular fragment with intra-alveolar incisor and Dp4–m1; GHUNLPam 2194, right mandibular fragment with intra-alveolar incisor and Dp4, and m1–m2; GHUNLPam 2975, left mandibular fragment with Dp4–m2; GHUNLPam 5712, right mandibular fragment with incisor, broken Dp4–m1 and m2–m3; GHUNLPam 8119, left mandibular fragment with Dp4–m2; GHUNLPam 14064, right mandibular fragment with incisor, broken Dp4 and m1–m3; GHUNLPam 14065, left mandibular fragment with m2; GHUNLPam 14580, right mandibular fragment with intra-alveolar incisor and Dp4–m2; GHUNLPam 19139,

Figure 3. *Reigechimys simplex* sp. nov. 1–2, GHUNLPam 4634 (holotype), left mandibular fragment with intra-alveolar portion of the incisor, Dp4 alveolus, m1–2, and erupting m3; **1,** labial view, **2,** occlusal view; **3,** GHUNLPam 14580, right mandibular fragment with intra-alveolar incisor and Dp4–m2, occlusal view; **4,** GHUNLPam 5712, right mandibular fragment with incisor, broken Dp4–m1 and m2–3, occlusal view; **5,** GHUNLPam 14064, right mandibular fragment with incisor, broken Dp4 and m1–m3, occlusal view; **6,** GHUNLPam 19053, right DP4, occlusal view; **7,** GHUNLPam 14068, fragment of left maxilla with DP4–M1, occlusal view; **8,** GHUNLPam 359, fragment of right maxilla with M1–M3, occlusal view. Scale bar= 2 mm.

TABLE 1 - Measurements (in mm) of lower molars of **Reigechimys/** *Medidas (en mm) de los molares inferiores de* **Reigechimys.**

	R. plesiodon		R. octodontiformis		R. simplex *sp. nov.*									
	N	Mean	N	Mean	4634	2182	2194	14580	8119	19139	5712	14064	2975	5916
i AP	9	2.22	15	3.05	1.80	1.80	1.80					1.80		2.40
i PW	10	2.22	15	2.29	1.50	1.20	1.20	1.50			1.50	1.20		1.50
dp4-m3			3	10.50								9.90		
dp4-m2	9	7.90	9	8.28					8.85	7.65		7.05	7.35	
dp4-m1	9	5.33	16	6.00		5.55			5.85	4.95		4.35	4.80	
m1-m3	5	8.19	4	7.91					5.40		8.55	7.65		9.00
m1-m2	14	5.38	12	5.88	4.80		5.85	6.15			5.10	4.95	4.95	5.85
m2-m3	6	5.63	4	5.33							6.00	5.40		6.00
dp4 AP	13	2.56	17	3.48		2.70		2.70	2.40				2.40	
dp4 AW	13	1.63	18	2.52		1.35		1.35	1.35				1.35	
dp4 PW	13	2.03	18	2.84		2.10		2.10	1.80			1.95	1.65	
m1 AP	23	2.56	21	3.42	2.70	2.85	3.00	3.00	2.25		2.55	2.25	2.25	2.85
m1 AW	22	2.14	21	3.03	1.95	2.10	2.25	2.25	2.10		2.40	2.25	2.10	2.25
m1 PW	23	2.27	21	3.15	1.95	2.10	2.25	2.25	2.25		2.40	2.10	2.40	2.55
m2 AP	22	2.80	15	3.49	2.55		3.00	2.70			3.15	2.70	2.55	3.30
m2 AW	22	2.43	15	3.11	1.80		2.25	2.10	2.25		2.55	2.55	2.70	2.25
m2 PW	21	2.44	14	3.12	1.80		1.95	2.10	2.25		2.40	2.85	2.70	2.70
m3 AP	8	2.91	5	2.78	1.05					3.00	2.85	2.70		2.70
m3 AW	8	2.21	5	2.48	1.35					1.65	2.10	2.55		2.10
m3 PW	7	1.95	5	2.22						1.80	1.80	1.80		1.95

Abbreviations: **AW,** anterior width; **PW,** posterior width; **AP,** antero-posterior length.

right m3; GHUNLPam 359, fragment of right maxilla with M1–M3; GHUNLPam 5542 and 22682, right M1 or M2; GHUNLPam 8867, fragment of right maxilla with DP4–M2; GHUNLPam 14068, fragment of left maxilla with DP4–M1; GHUNLPam 19053, right DP4; GHUNLPam 5916, left mandibular fragment with m1–m3 (Fig. 4).

Distribution. The holotype, GHUNLPam 4634, and the rest of the sample except for GHUNLPam 5916 come from Bajo Giuliani (36°42′40.39″S–64°16′59.89″W; *Chasichimys* morphotype a Zone, Verzi *et al.*, 2008); GHUNLPam 5916 comes from Estancia Don Mariano (36°41′S–64°27′W; Toay Department), La Pampa Province, central Argentina; Cerro Azul Formation, Huayquerian, upper late Miocene (Goin *et al.*, 2000; Verzi *et al.*, 2008, 2011) (Fig. 1).

Description. The mandible is morphologically similar to that of *R. octodontiformis*. The posterior margin of the symphysis forms a step in front of Dp4. The incisor is narrow and high; its enamel-covered surface is straight or slightly curved and the enamel extends over the labial surface.

The molariforms are protohypsodont, with figure-eight-shaped occlusal surface as early as the earliest ontogenetic stages (GHUNLPam 4634), up to advanced stages. In the juvenile GHUNLPam 2182, Dp4 is trilophodont. The m1–m2 lack the mesoflexid/fossetid throughout the sample, even in the youngest specimen GHUNLPam 4634 in which m2 is scarcely worn and m3 is erupting. In adult, non-senile stages (GHUNLPam 8119, 14580), the lingual side of the first lobe of these molars is longer antero-posteriorly than that of the second lobe, but this difference is less marked than in the two other species. There is a mesofossettid in the m3 of GHUNL-

TABLE 2 - Measurements (in mm) of upper molars of Reigechimys */Medidas (en mm) de los molares superiores de* Reigechimys.

	R. plesiodon		R. octodontiformis		R. simplex *sp. nov.*				
	N	Mean	N	Mean	359	8867	14608	19053	19053
DP4-m3	1	10.05							
DP4-M2	1	7.80	2	7.28		7.05			
DP4-M1	2	6.70	2	4.80		4.35	4.65		
M1-M3	1	7.65			8.25				
M1-M2	1	5.25	4	4.95	5.70	4.95			
M2-M3	1	4.95			5.55				
DP4 AP							2.25	2.40	2.40
DP4 AW							2.25	1.95	1.95
DP4 PW	2	4.95	2	2.03		1.95	2.25	1.80	1.80
M1 AP	2	4.95	5	2.37	2.70	2.25	2.40		
M1 AW	2	4.95	4	2.18	2.85	1.95	2.25		
M1 PW	2	4.95	4	2.25	2.85	1.65	2.10		
M2 AP	1	2.55	4	2.55	2.85	2.70			
M2 AW			3	2.48	3.15	2.25			
M2 PW			3	2.10	2.25	1.80			
M3AP	1	2.25							
M3 AW	1	2.25	1		2.25				
M3 PW	1	1.50							

Abbreviations: **AW,** anterior width; **PW,** posterior width; **AP,** antero-posterior length.

Pam 5712 and 19139.

The DP4 of the juvenile GHUNLPam 19053 bears a shallow paraflexus and mesoflexus, which is open labially. The mesoflexus is transient in M1–M2; GHUNLPam 14068 has only a mesofossette on the labial side, while the specimen GHUNLPam 8867 has no labial fossette and only one hypo-fossette. In the M1 of GHUNLPam 359, the meso- and hypofossette form a large central fossette.

Reigechimys octodontiformis Verzi, Vucetich and Montalvo, 1994
Fig. 4.2 and 4.4, Tables 1–2

Revised diagnosis. Dp4 trilophodont with small mesolophid (or metalophulid II?) spur. Lower molars with mesoflexid more ephemeral than that of *R. plesiodon*. Mesoflexid transformed into mesofossettid in m1 and replaced by mesofossettid in m2 during early ontogenetic stages. Mesofossettid of m1 absent when metaflexid begins to close.

Holotype. MLP 65-VII-29-107, right mandibular fragment bearing the incisor and Dp4–m3.

Referred material. The holotype and GHUNLPam 88, left mandibular fragment with Dp4–m1; GHUNLPam 6996, right mandibular fragment with intra-alveolar incisor and Dp4-m2; GHUNLPam 93, fragment of right maxilla with DP4-M2. All these specimens were recovered from Salinas Grandes de Hidalgo. GHUNLPam 6406 and 14261, left mandibular fragments with intra-alveolar incisor and m1–m2; GHUNLPam 14262, left mandibular fragment with intra-alveolar incisor, Dp4 and broken m1–m2; GHUNLPam 14263, right mandibular fragment with m2; GHUNLPam 22601 and 22973, left mandibular fragments with intra-alveolar incisor and Dp4–m2; GHUNLPam 22602, left mandibular fragment with intra-alveolar incisor, Dp4 and m1; GHUNLPam 22604, left m1 or m2; GHUNLPam 22964, left mandibular fragment with intra-alveolar incisor, Dp4 alveolus and m1–m3; GHUNLPam 22965, right mandibular

fragment with intra-alveolar incisor, Dp4–m1 and broken m2; GHUNLPam 22966, left mandibular fragment with intra-alveolar incisor, Dp4, and m1–m3; GHUNLPam 22968 and 22970, left mandibular fragments with intra-alveolar incisor and Dp4–m3; GHUNLPam 22969, left mandibular fragment with intra-alveolar incisor, Dp4–m2 and m3 alveolus; GHUNLPam 22971, left mandibular fragment with Dp4–m1; GHUNLPam 22972, left mandibular fragment with Dp4–m2; GHUNLPam 22974, left mandibular fragment with intra-alveolar incisor and m2–m3; GHUNLPam 22975, right mandibular fragment with intra-alveolar incisor and Dp4–m2; GHUNLPam 22976, left mandibular fragment with broken Dp4; GHUNLPam 22967, fragment of right and left maxilla with M1–M2; GHUNLPam 4283, fragment of left maxilla with M1–M2. All these specimens were recovered from Estancia Ré; GHUNLPam 6642, right mandibular fragment with Dp4–m1; GHUNLPam 6643, 14115 and 14118, left mandibular fragments with Dp4–m1; GHUNLPam 14114, right mandibular fragment with intra-alveolar incisor and m1–2; GHUNLPam 14116, right mandibular fragment with intra-alveolar incisor and broken Dp4–m1; GHUNLPam 14117, fragment of left maxilla with M1–M2. All these specimens were recovered from Puesto Colorado (Fig. 4.2 and 4.4).

Distribution. Salinas Grandes de Hidalgo (37°13′S–63°36′W), Estancia Ré (36°0.7′25.9″S–64°59′73.6″W) and Puesto Colorado (36°10′27″S–64°59′47″W), La Pampa Province, central Argentina; Cerro Azul Formation, Huayquerian, upper late Miocene (Fig. 1).

Description. The collected maxillaries correspond to adult individuals, whose molars present a mesofossette. Their morphology is similar to that of the two other species of the genus. Most remains of this species (N = 21) belong to the sample from Estancia Ré. Juvenile specimens have a trilophodont Dp4, with a small mesolophid spur (absent in GHUNLPam

22971). The mesoflexid is more ephemeral than in *R. plesiodon*; it is closing or transformed into mesofossettid in the m1, and represented by a small mesofossettid in the m2 of the youngest specimens. In m1, the mesofossettid disappears before the metaflexid begins to close. As a consequence of this closure sequence of the flexids, the occlusal morphology with two lobes separated by hypo- and metaflexid lasts longer during ontogeny than in *R. plesiodon*.

Reigechimys plesiodon Verzi, Vucetich and Montalvo, 1994
Fig. 4.3–4, Tables 1, 2

Revised diagnosis. Juvenile with anterofossettid in Dp4 and mesoflexid in m1–m3. Mesofossettid present in m1 with the metaflexid near to closing.

Holotype. GHUNLPam 306, left mandibular fragment bearing m1–m2.

Referred material. The holotype and GHUNLPam 8770, left mandibular fragment with m1–m2, recovered from Laguna Chillhué; GHUNLPam 6263, right mandibular fragment with intra-alveolar incisor and m1–m3; GHUNLPam 6264, isolated left m1–m2; GHUNLPam 6343, 8972 and 27269, left mandibular fragments with m1–m3; GHUNLPam 6471 and 8473, left mandibular fragments with Dp4–m1; GHUNLPam 6474 and 9459, right mandibular fragments with Dp4–m2; GHUNLPam 6477, left Dp4; GHUNLPam 8087, right mandibular fragment with intra-alveolar incisor and Dp4–m1; GHUNLPam 8386, right m1 or m2; GHUNLPam 8495, right mandibular fragment with intra-alveolar incisor and Dp4–m2; GHUNLPam 8556, left Dp4; GHUNLPam 9458, 21675 and 27432, left mandibular fragments with Dp4–m2; GHUNLPam 9617, left mandibular fragment with incisor and m1–m3; GHUNLPam 9618, right mandibular fragment with intra-alveolar incisor and m1; GHUNLPam 12917, right mandibular fragment with intra-

Figure 4. Occlusal morphology of *Reigechimys*. **1,** lower cheek-teeth of *R. simplex* sp. nov.; **a,** GHUNLPam 4634; **b,** GHUNLPam 2182; **c,** GHUNLPam 2194 reversed; **d,** GHUNLPam 14580 reversed; **e,** GHUNLPam 8119; **f,** GHUNLPam 19139 reversed; **g,** GHUNLPam 5712 reversed; **h,** GHUNLPam 14064 reversed; **i,** GHUNLPam 2975; **2,** lower cheek-teeth of *R. octodontiformis*; **a,** GHUNLPam 22972; **b,** GHUNLPam 22971; **c,** GHUNLPam 22975 reversed; **d,** GHUNLPam 22601; **e,** GHUNLPam 22973; **f,** GHUNLPam 22965 reversed; **g,** GHUNLPam 14261; **h,** GHUNLPam 22970; **i,** GHUNLPam 22966; **j,** GHUNLPam 22969; **k,** GHUNLPam 22968; **l,** GHUNLPam 22964; **m,** GHUNLPam 22974; **3,** Lower cheek-teeth of *R. plesiodon*; **a,** GHUNLPam 27268; **b,** GHUNLPam 9617; **c,** GHUNLPam 27432; **d,** GHUNLPam 9459 reversed; **e,** GHUNLPam 6474 reversed; **f,** GHUNLPam 8495 reversed; **g,** GHUNLPam 8437 reversed; **h,** GHUNLPam 9458; **i,** GHUNLPam 6263 reversed; **j,** GHUNLPam 14472 reversed; **k,** GHUNLPam 8972; **l,** GHUNLPam 21675; **m,** GHUNLPam 27270 reversed; **n,** GHUNLPam 27269; **4,** Upper cheek-teeth; **a,** GHUNLPam 19053; **b,** GHUNLPam 14068; **c,** GHUNLPam 8867 reversed; **d,** GHUNLPam 359 reversed. **e,** GHUNLPam 22967; **f,** GHUNLPam 4283. **g,** GHUNLPam 12888 reversed; **h,** GHUNLPam 18488 reversed; **i,** GHUNLPam 18523 reversed. Scale bar= 1 mm.
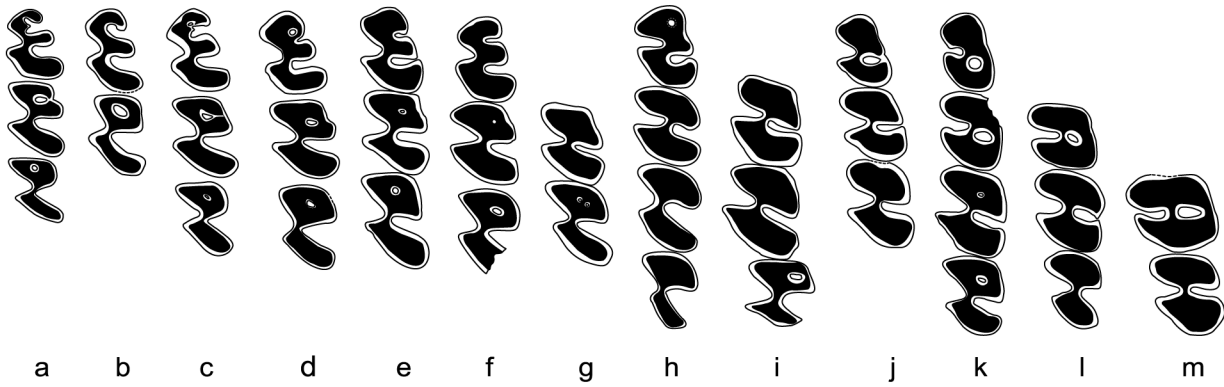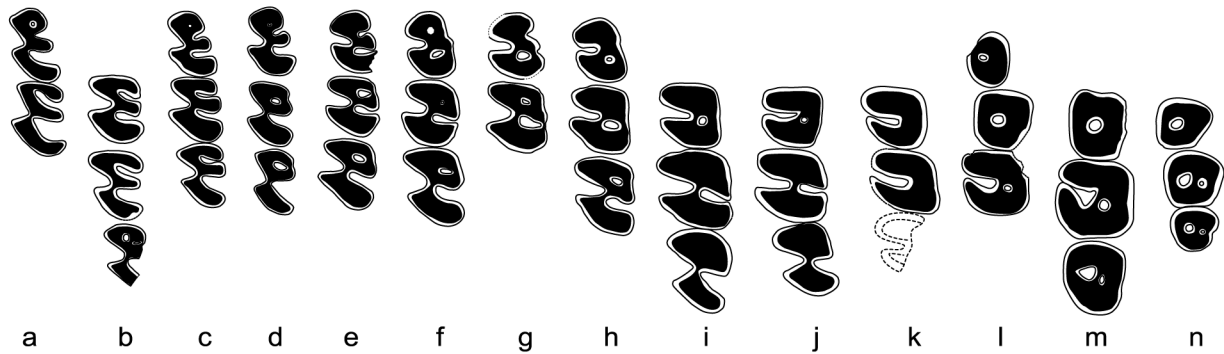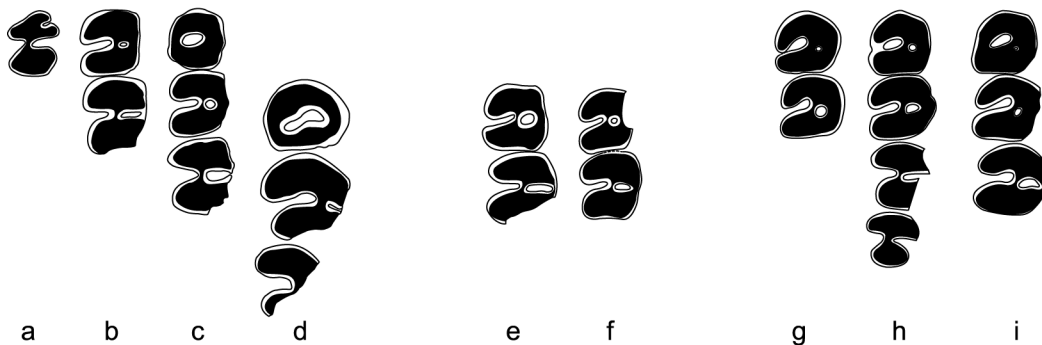
① *R. simplex*

a   b   c   d   e   f   g   h   i

② *R. octodontiformis*

a   b   c   d   e   f   g   h   i   j   k   l   m
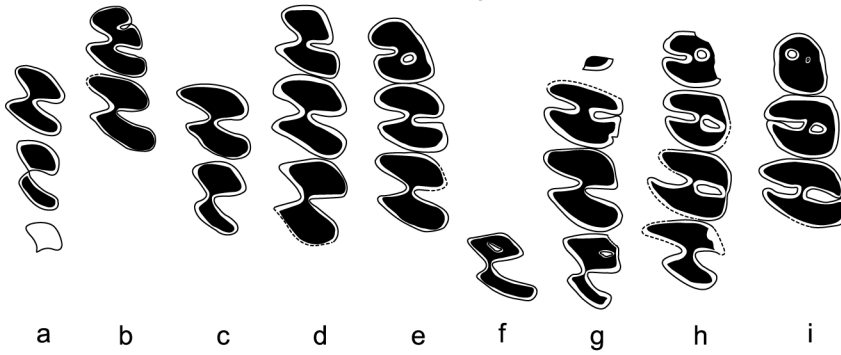
③ *R. plesiodon*

a   b   c   d   e   f   g   h   i   j   k   l   m   n

④ *R. simplex*   *R. octodontiformis*   *R. plesiodon*

a   b   c   d   e   f   g   h   i

alveolar incisor, broken m1 and m2–m3; GHUNLPam 14472, right mandibular fragment with intra-alveolar incisor, broken Dp4 and m1–3; GHUNLPam 18488 and 18705, right mandibular fragments with Dp4–m1; GHUNLPam 18519, left mandibular fragment with m1–m2; GHUNLPam 18522, left mandibular fragment with m1–m2; GHUNLPam 18532, right m1 or m2; GHUNLPam 18641, isolated m1–m3; GHUNLPam 18758, left mandibular fragment with m1–m3; GHUNLPam 21670 and 22734, right mandibular fragments with m2; GHUNLPam 27268, left mandibular fragment with incisor and Dp4–m1; GHUNLPam 27270, right mandibular fragment m1–m3; GHUNLPam 27271, right mandibular fragment with m1; GHUNLPam 27431, left mandibular fragment with broken m1 and m2–m3; GHUNLPam 27433, left mandibular fragment with intra-alveolar incisor and m1–m3; GHUNLPam 12888, fragment of right maxilla with DP4–M1; GHUNLPam 18523, fragment of right and left maxilla with Dp4–M2. All these specimens were recovered from Telén. GHUNLPam 9185, right mandibular fragment with intra-alveolar incisor and m1–m3; GHUNLPam 9186, right mandibular fragment with m1–m3; GHUNLPam 9189, right DP4. All these specimens were recovered from Loventué. GHUNLPam 8148, right mandibular fragment with m1–m2; GHUNLPam 9675, left m1 or m2, recovered from Quehué (Figs. 4.3–4).

Distribution. Laguna Chillhué (37°24′18″S–64°13′01″W; *Chasichimys scagliai* Zone, Huayquerian, Verzi *et al.*, 2008); Quehué (37°15′S–64°32′W); Telén (36°15′S–65°30′W) and Loventué (36°16′S–65°10′W), La Pampa Province, central Argentina; Cerro Azul Formation, Huayquerian, upper late Miocene (Goin *et al.*, 2000; Verzi *et al.*, 2008, 2011) (Fig. 1).

Description. The sample from Telén yielded most of the remains of this species (N= 37). Juvenile specimens present Dp4 with hypo- and postero-lophids, and an anterior lobe
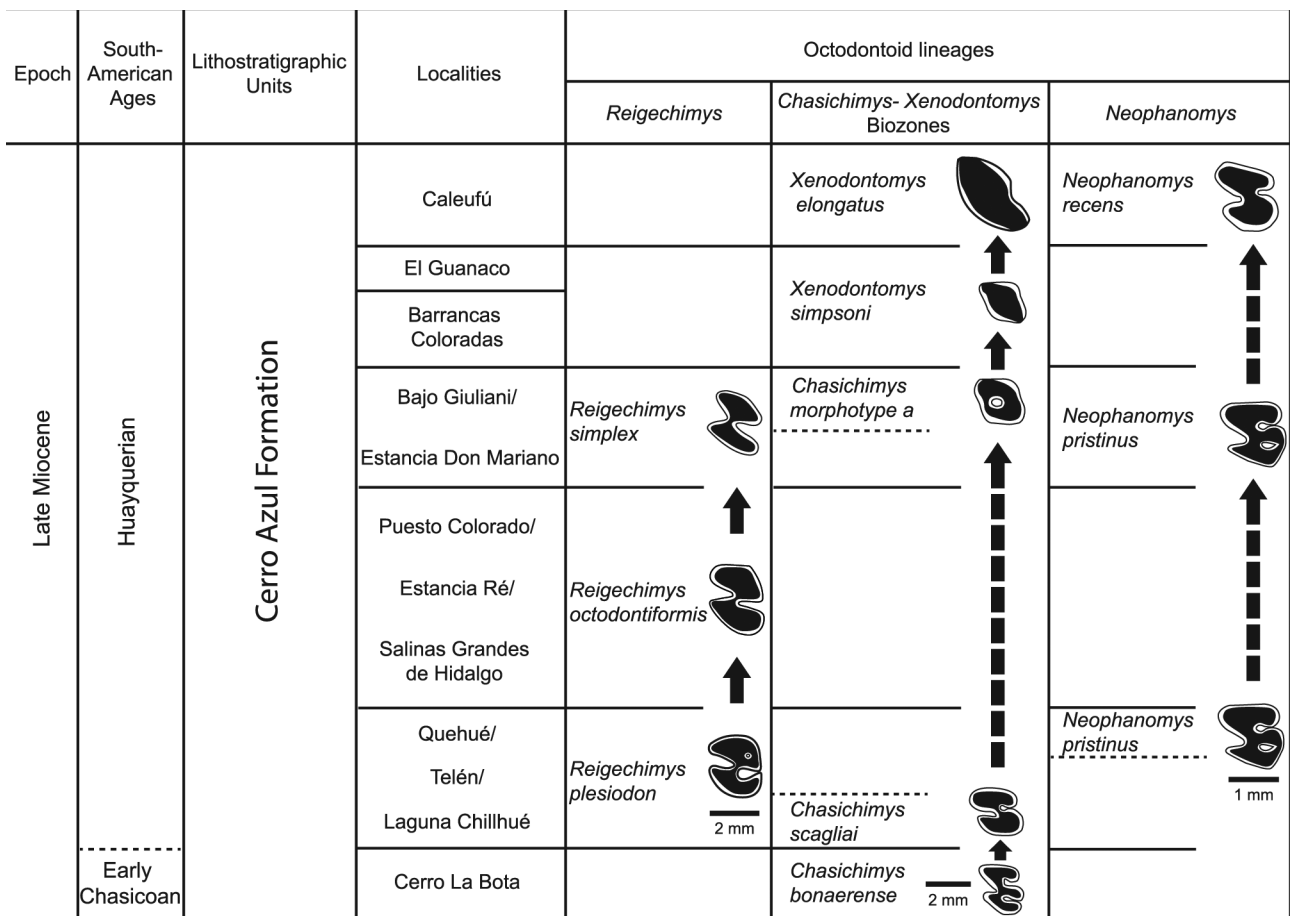

Figure 5. Stratigraphic distribution of octodontoid lineages from the Late Miocene of central Argentina. Localities separated by bars are considered as putatively synchronous in the biochronological hierarchy. Stratigraphic scheme follows Verzi *et al.* (2008) and Verzi *et al.* (2011).

with variably developed anterofossettid; individuals with less wear have mesoflexid in m1–m2. The latter transforms into a fossettid much earlier than the metaflexid, which is a characteristic of this genus. However, in *R. plesiodon* the closing of these flexids is less asynchronous than in the two other species, and the mesofossettid persists in m1 with nearly-closed metaflexid. The most worn molars (GHUNLPam 21675, 27269, and 27270) show subquadrangular occlusal surface and possess both meta- and hypofossettid, or only the latter. Recovered maxillaries correspond to adult specimens whose molars present mesofossette and a narrow hypoflexus; this morphology is similar to that of *R. simplex* and *R. plesiodon*.

DISCUSSION AND CONCLUSIONS

A clear turnover is recorded among octodontoid rodents in the late Miocene Chasicoan–Huayquerian interval of the Cerro Azul Formation. This is indicated by the increasing richness of euhypsodont species (*sensu* Mones, 1982) and the decline of brachy- to protohypsodont ones (Verzi, 1999; Verzi and Montalvo, 2008; Verzi *et al.*, 2008, 2011). The echimyid richness also decreases as part of the decline of protohypsodont octodontoids. However, unlike the octodontids involved in this turnover, echimyids never acquired euhypsodonty. Beyond this, *Reigechimys* shows that at least some species of this family also underwent some changes in their molar morphology before their local or complete extinction. In *Reigechimys*, these changes involve primarily a reduction of the ontogenetic persistence of the mesoflexid/fossettid in m1–m2, from *R. plesiodon* through *R. octodontiformis*, to absence of this flexid/fossettid in *R. simplex*. As a result, *Reigechimys* is one of the echimyids with the most simplified molar occlusal pattern. Interestingly, it shares this dental characteristic with *Dicolpomys fossor* Winge, 1887, from the late Pleistocene–Holocene of Minas Gerais and Rio Grande do Sul (Brazil; Hadler *et al.*, 2008), and with MACN 8369, a specimen from the late Miocene of Catamarca (Verzi *et al.*, 1994). The relationships of these taxa with *Reigechimys* have not been explored yet.

Given that the evolutionary pattern and the distribution of *Reigechimys* only partially overlap those of *Chasichimys-Xenodontomys* and *Neophanomys* lineages in the Cerro Azul Formation, *Reigechimys* enhances the biochronological interpretation of the Huayquerian in this formation (Fig. 5). The polarity of changes in *Reigechimys* is consistent with those of

the other lineages, thus providing additional support to the biochronological proposals based on the evolution of octodontoid rodents (Verzi, 1999; Verzi and Montalvo, 2008; Verzi *et al.*, 2008, 2011; Deschamps *et al.*, 2012).

REFERENCES

Arakaki, M., Christin, P.A., Nyffeler, R., Lendel, A., Eggli, U., Ogburn, R.M., Spriggs, E., Moore, M.J. and Edwards, E.J. 2011. Contemporaneous and recent radiations of the world's major succulent plant lineages. *Proceedings of the National Academy of Sciences* 108: 8379–8384.

Bowdich, T.E. 1821. *An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travelers*. J. Smith, Paris, 115 p.

Brandt, J.F. 1855. Beiträge zur nähern Kenntniss der Säugethiere Russlands. *Mémoire de l'Académie impériale des Sciences, St. Petersburg, Physique, Mathématique, et Naturalistique, Séries 6*, 9: 1–365.

Campbell, K. and Tonni, E. 1980. A new genus of teratorn from the Huayquerian of Argentina (Aves, Teratornithidae). *Contributions in Sciences* 330: 59–68.

Cartelle, C. 1999. Pleistocene Mammals of the Cerrado and Caatinga of Brazil. In: J.F. Eisemberg, and K.H. Redford, (Eds.), *Mammals of the Neotropics. The Central Neotropics*. The University of Chicago Press, Chicago and London, p. 27–46.

Cenizo, M.M., Tambussi, C.P. and Montalvo, C.I. 2012. Late Miocene continental birds from the Cerro Azul Formation in the Pampean región (central–southern Argentina). *Alcheringa* 36: 47–68.

Cerdeño, E. and Montalvo, C.I. 2001. Los Mesotheriinae (Mesotheriidae, Notoungulata) del Mioceno superior de La Pampa, Argentina. *Revista Española de Paleontología* 16: 63–75.

Cerdeño, E. and Montalvo, C.I. 2002. Los Hegetotheriinae (Hegetotheriidae, Notoungulata) del Mioceno superior de la Provincia de La Pampa, Argentina. *Revista del Museo Argentino de Ciencias Naturales* 4: 35–43.

Denton, G.H. 1999. Cenozoic climate change. In: T.G. Bromage, and F. Schrenk (Eds.), *African Biogeography Climate Change & Human Evolution*. Oxford University Press, New York. p. 94–114.

Deschamps, C.M., Vucetich, M.G., Verzi, D.H., and Olivares, A.I., 2012. Biostratigraphy and correlation of the Monte Hermoso Formation (early Pliocene, Argentina), the evidence from caviomorph rodents. *Journal of South American Earth Sciences* 35: 1–9.

Deschamps, C.M., Vucetich, M.G., Montalvo, C.I. and Zárate, M.A. 2013. Capybaras (Rodentia, Hydrochoeridae, Hydrochoerinae) and their bearing in the calibration of the late Miocene–Pliocene sequences of South America. *Journal of South American Earth Sciences* 48: 145–158.

Emmons, L. and Feer, F. 1997. *Neotropical Rainforest Mammals. A Field Guide*, 2nd edition. The University of Chicago Press, Chicago and London, 185–244.

Folguera, A. and Zárate, M. 2009. La sedimentación neógena continental en el sector extra-andino, Argentina central. *Revista de la Asociación Geológica Argentina* 64: 692–712.

Frailey, C.D. and Campbell, K.E. 2004. Paleogene rodents from the Amazonian Peru, the Santa Rosa local fauna. In: K.E. Campbell (Ed.), *The Paleogene Mammalian Fauna of Santa Rosa, Amazonian Peru*. Natural History Museum of Los Angeles County, Science Series 40, p. 61–69.

Galewski, T., Mauffrey J.F., Leite, Y.L.R., Patton J.L. and Douzery, E.J.P. 2005. Ecomorphological diversification among South American spiny rats (Rodentia; Echimyidae) a phylogenetic and chronological approach. *Molecular Phylogenetics and Evolution* 34: 60–615.

Goin, F. and Montalvo, C.I. 1988. Revisión sistemática y reconocimiento de una nueva especie del género *Thylatheridium* Reig (Marsupialia,

Didelphidae). *Ameghiniana* 25: 161–167.

Goin, F., Montalvo, C.I. and Visconti, G. 2000. Los Marsupiales (Mammalia) del Mioceno Superior de la Formación Cerro Azul (Provincia de La Pampa, Argentina). *Estudios Geológicos* 56: 101–126.

Gray, J.E. 1825. Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. *Annals of philosophy*, n.s. 10: 337–344.

Hadler, P., Verzi, D.H., Vucetich, M.G., Ferigolo, J. and Ribeiro, A.M. 2008. Caviomorphs (Mammalia, Rodentia) from the Holocene of Rio Grande do Sul State, Brazil, systematics and paleoenvironmental context. *Revista Brasileira de Paleontologia* 11: 97–116.

Janis, C.M. 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology and Systematics* 24: 467–500.

Linares, E., Llambías, E. and Latorre, C. 1980. Geología de la Provincia de la Pampa, República Argentina y Geocronología de sus rocas metamórficas y eruptivas. *Revista de la Asociación Geológica Argentina* 35: 87–146.

Marivaux, L., Vianey-Liaud, M. and Jaeger, J.J. 2004. High-level phylogeny of early Tertiary rodents, dental evidence. *Zoological Journal of the Linnean Society* 142: 105–134.

Mones, A. 1982. An equivocal nomenclature: What means hypsodonty?. *Paláontologisches Zeitschrift* 56: 107–111.

Montalvo, C.I., Melchor, R.N., Visconti, G. and Cerdeño, E. 2008. Vertebrate taphonomy in loess–paleosol deposits, a case study from the Late Miocene of central Argentina. *Geobios* 41: 133–143.

Montalvo, C.I., Verzi, D.H. and Visconti, G. 2002. Hallazgo de un pequeño Octodontoidea (Rodentia, Caviomorpha) en Loventué, La Pampa (Formación Cerro Azul, Mioceno tardío). *7as Jornadas Pampeanas de Ciencias Naturales*, (Santa Rosa), *Actas*, p. 157–158.

Montalvo, C.I., Visconti, G., Pugener, L. and Cardonatto, M.C. 1995. Mamíferos huayquerienses (Mioceno tardío) de la Laguna Chillhué (Provincia de La Pampa). *4as Jornadas Geológicas y Geofísicas Bonaerenses*, *Actas* 1: 73–79.

Olivares, A.I., Verzi, D.H., Vucetich M.G. and Montalvo, C.I. 2012. Phylogenetic affinities of the late Miocene echimyid *Pampamys* and the age of *Thrichomys* (Rodentia, Hystricognathi). *Journal of Mammalogy* 93: 76–86.

Pascual, R. and Bocchino, A. 1963. Un nuevo Borhyaeninae (Marsupialia) del Plioceno medio de Hidalgo (La Pampa). *Ameghiniana* 3: 97–107.

Pascual, R. and Bondesio, P. 1982. Un roedor Cardiatheriinae (Hydrochoeridae) de la Edad Huayqueriense (Mioceno tardío) de La Pampa. Sumario de los ambientes terrestres en la Argentina durante el Mioceno. *Ameghiniana* 19: 19–35.

Pascual, R. and Ortiz Jaureguizar, E. 1990. Evolving climates and mammals faunas in Cenozoic South America. *Journal of Human Evolution* 19: 23–60.

Pascual, R., Pisano, J. and Ortega, E. 1965. Un nuevo Octodontidae (Rodentia, Caviomorpha) de la Formación Epecuén (Plioceno medio) de Hidalgo (Provincia de La Pampa). *Ameghiniana* 4: 19–30.

Patterson, B. and Pascual, R. 1968. New echimyid rodents from the Oligocene of Patagonia, and a synopsis of the family. *Museum of Comparative Zoology, Breviora* 301: 1–14.

Reig, O.A. 1986. Diversity patterns and differentiation of high Andean rodents. In: F. Vuilleumier, and M. Monasterio (Eds.), *High altitude tropical biogeography*. Oxford University Press, p. 404–439.

Tullberg, T. 1899. Uber das system der Nagetiere. Eine phylogenetische studie. *Nova Acta Regiae Societatis Scientiarium Upsaliensis* 18: 1–514.

Upham, N.S. and Patterson, B.D. 2012. Diversification and biogeography of the Neotropical caviomorph lineage Octodontoidea (Rodentia, Hystricognathi). *Molecular Phylogenetics and Evolution* 63: 417–429.

Urrutia, J.J., Montalvo, C.I. and Scillato Yané, G.J. 2008. Dasypodidae (Xenarthra, Cingulata) de la Formación Cerro Azul (Mioceno tardío) de la Provincia de La Pampa, Argentina. *Ameghiniana* 45: 289–302.

Verzi, D.H. 1999. The dental evidence on the differentiation of the ctenomyine rodents (Caviomorpha, Octodontidae, Ctenomyinae). *Acta Theriologica* 44: 263–282.

Verzi, D.H. and Montalvo, C.I. 2008. The oldest South American Cricetidae (Rodentia) and Mustelidae (Carnivora), Late Miocene faunal turnover in central Argentina and the Great American Biotic Interchange. *Palaeogeography, Palaeoclimatology, Palaeoecology* 267: 284–291.

Verzi, D.H., Montalvo, C.I. and Deschamps, C.M. 2008. Biochronology and Biostratigraphy of the Upper Miocene of central Argentina, evidence from rodents and taphonomy. *Geobios* 41: 145–155.

Verzi, D.H., Olivares, A.I. and Morgan, C.C. 2013. Phylogeny, evolutionary patterns and timescale of South American octodontoid rodents. The importance of recognising morphological differentiation in the fossil record. *Acta Palaeontologica Polonica*. doi, http,//dx.doi.org/10.4202/app.2012.0135.

Verzi, D.H., Vieytes, E.C. and Montalvo, C.I. 2011. Dental evolution in *Neophanomys* (Rodentia, Octodontidae) from the Late Miocene of central Argentina. *Geobios* 44: 621–633.

Verzi, D.H., Vucetich, M.G. and Montalvo, C.I. 1994. Octodontid-like Echimyidae (Rodentia), an Upper Miocene episode in the radiation of the family. *Palaeovertebrata* 23: 199–210.

Verzi, D.H., Vucetich, M.G. and Montalvo, C.I. 1995. Un nuevo Eumysopinae (Rodentia, Echimyidae) del Mioceno tardío de la Provincia de La Pampa y consideraciones sobre la historia de la subfamilia. *Ameghiniana* 32: 191–195.

Vezzosi, R.I. 2012. First record of *Procariama simplex* Rovereto, 1914 (Phorusrhacidae, Psilopterinae) in the Cerro Azul Formation (upper Miocene) of La Pampa Province; remarks on its anatomy, palaeogeography and chronological range. *Alcheringa* 36: 157–169.

Visconti, G. 2007. [*Sedimentología de la Formación Cerro Azul (Mioceno Superior) de la Provincia de La Pampa*. Thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, 203 p. Unplublished].

Vizcaíno, S.F. and Fariña, R. 1999. On the flight capabilities and distribution of the giant Miocene bird *Argentavis magníficens* (Teratornithidae). *Lethaia* 32: 271–278.

Vucetich, M.G., Mazzoni, M.M. and Pardiñas, U.F.J. 1993. Los roedores de la Formación Collón Cura (Mioceno Medio) y la Ignimbrita Pilcaniyeu, Cañadón del Tordillo, Neuquén. *Ameghiniana* 30: 361–381.

Waterhouse, G.E. 1839. Observations of the Rodentia, with a view to point out the groups, as indicated by the structure of the crania, in this order of Mammals. *Magazine of Natural History*, n.s. 3: 90–96.

Winge, H.1887. Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. E Museo Lundii, Lund (1),1–200.

Wood, A.E. and Patterson, B. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bulletin of the Museum of Comparative Zoology* 120: 281–428.

Zetti, J. 1972. Observaciones sobre los Pachyrukhinae (Notoungulata) del Plioceno argentino. *Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata* 2: 41–52.