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Late Miocene Dasypodidae Gray, 1821 (Xenarthra, Cingulata) from the Toro Negro Formation (Central Andes, Argentina): diversity and chronological and biogeographical implications

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ABSTRACT
Fossil remains herein described are referred to different species of Dasypodidae Gray, 1821 (Mammalia, Xenarthra, Cingulata) and come from the upper levels of the lower member (Late Miocene-Early Pliocene) of the Toro Negro Formation at Quebrada de Las Torrecillas, La Rioja Province, Argentina, where previous vertebrate records only include those of *Pyramiodontherium scillatoyanei* De Iuliis, Ré & Vizcaíno, 2004 (Mammalia, Xenarthra) and *Opisthodactylus* cf. *kirchneri* Noriega, Jordan, Vezzosi & Areta, 2017 (Aves, Rheidae). The remains of Dasypodidae herein presented include *Vetelia ghandii* Esteban & Nasif, 1996, *Chasicotatus peiranoi* Esteban & Nasif, 1996, *Macrochorobates scalabrinii* (Moreno & Mercerat, 1891), *Prozaedyus* sp., and *Paleuphractus argentinus* (Moreno & Mercerat, 1891), and constitute the first records of these species for the Toro Negro Formation, increasing the

mammal diversity for this unit. The association of dasypodids here described shows strong affinities with those described for Late Miocene localities of Northwestern Argentina. Under these evidences, the Dasypodidae here reported for Quebrada de Las Torrecillas site show a characteristic association of taxa from Northwestern Argentina, suggesting a Messinian age (Late Miocene) for the bearing levels of the Toro Negro Formation. In this way, these records support the accurate ages recently proposed for the lower Member of the Toro Negro Formation (i.e., Late Miocene-Early Pliocene).

KEY WORDS
Armadillos,
Neogene,
Northwestern Argentina,
South America.

RÉSUMÉ

Miocène supérieur Dasypodidae Gray, 1821 (Xenarthra, Cingulata) de la Formation Toro Negro (Centre des Andes, Argentine) : diversité et implications chronologiques et biogéographiques.

Les restes fossiles décrits ici se rapportent à différentes espèces de Dasypodidae Gray, 1821 (Mammalia, Xenarthra, Cingulata) et proviennent des niveaux supérieurs du membre inférieur (Miocène supérieur – Pliocène inférieur) de la Formation Toro Negro à Quebrada de Las Torrecillas, Province de La Rioja, Argentine, où les signalements précédents de vertébrés comprennent seulement ceux de *Pyramiodontherium scillatoyanei* De Iuliis, Ré & Vizcaíno, 2004 (Mammalia, Xenarthra) et *Opisthodactylus* cf. *kirchneri* Noriega, Jordan, Vezzosi & Areta, 2017 (Aves, Rheidae). Les restres de Dasypodidae présentés ici incluent *Vetelia ghandii* Esteban & Nasif, 1996, *Chasicotatus peiranoi* Esteban & Nasif, 1996, *Macrochorobates scalabrinii* (Moreno & Mercerat, 1891), *Prozaedyus* sp., et *Paleuphractus argentinus* (Moreno & Mercerat, 1891), et constituent les premiers signalements de ces espèces pour la Formation Toro Negro, augmentant la diversité de mammifères pour cette unité. L'association de dasypodidés décrite ici présente de fortes affinités avec celles décrites pour des localités du Miocène du Nord-Ouest de l'Argentine. Compte tenu de ces éléments, les Dasypodidae rapportés ici pour le site de Quebrada de Las Torrecillas montrent une association caractéristique de taxons du Nord-Ouest de l'Argentine, suggérant un âge Messinien (fin du Miocène supérieur) pour les niveaux comprenant la Formation Toro Negro. Ainsi, ces données soutiennent les âges précis récemment proposés pour le membre inférieur de la Formation de Toro Negro (c'est-à-dire fin du Miocène supérieur – début du Pliocène inférieur).

MOTS CLÉS
Tatous,
Néogène,
Nord-Ouest
de l'Argentine,
Amérique du Sud.

INTRODUCTION

For the greater part of the Cenozoic, South America was an isolated continent, and its mammalian fauna consisted of marsupials, native "ungulates", caviomorph rodents, platyrrhine primates, and xenarthrans. This "splendid isolation" (*sensu* Simpson 1980) ended at the beginning of the Gelasian (2.58 Ma; Pleistocene) with the formation of the Isthmus of Panama that connected South and North America (Woodburne 2010).

In Argentina, pre-Gelasian mammal-bearing rocks occur extensively in Northwestern Argentina (i.e., Catamarca, Tucumán, Jujuy, Salta, Santiago del Estero, and La Rioja provinces). Several localities at Catamarca and Jujuy provinces have Late Miocene-Pliocene outcrops that have been extensively studied geologically and paleontologically, with focus on their fossil mammal content (see Marshall & Patterson 1981; Reguero & Candela 2011; Esteban *et al.* 2014, 2019; Zurita *et al.* 2017; Quiñones *et al.* 2019; Nasif *et al.* 2019; Ercoli *et al.* 2021). By contrast, Neogene mammals from La Rioja Province have remained relatively unexplored compared to others from geographically and coeval nearby units (Chiquimil, Andalhuala, and Corral Quemado Formations, Catamarca Province). Georgieff *et al.* (2004) described fossil mammals collected in the Desencuentro Formation (southeastern of La Rioja Province); Tauber (2005), Brandoni *et al.* (2012), Brandoni & González Ruiz (2021), and Barasoain *et al.* (2022) recorded many taxa from the Salicas Formation (see also Cerdeño & Schmidt 2013), in the northeastern of the province. In turn, De Iuliis *et al.* (2004) and Rodríguez Brizuela & Tauber (2006) described fossil mammals from the Toro Negro Formation, in the northwestern part of the province. In addition, Krapovickas *et al.* (2009), and Krapovickas & Nasif (2011) studied vertebrate tracks and invertebrate traces from the Toro Negro and Vinchina formations.

Focusing on the Toro Negro Formation at La Rioja Province, several genera of Cingulata (Mammalia, Xenarthra), mostly based on isolated osteoderms, have been recorded, i.e., the dasypodids *Proeuphractus limpidus* Ameghino, 1886, *Chorobates villosissimus* Rovereto, 1914, *Paleuphractus* Kraglievich, 1934, and *Doellotatus inornatus* Bordas, 1932; and the glyptodontids *Lomaphorops corallinus* Castellanos, 1931, *Neuryurus* cf. *giganteus* Rovereto, 1914, and cf. *Urotherium* Castellanos, 1926 (see Rodríguez Brizuela & Tauber 2006).

Cingulata (i.e., Dasypodidae Gray, 1821, Peltephilidae, Pampatheriidae, Palaeopeltidae, Glyptodontidae; McKenna & Bell 1997) have a dorsal carapace that covers and protects most part of the animal's body (Engelmann 1985). The carapace consists of articulated individual osteoderms, the dorsal surface of which bears a particular pattern due to the overlying epidermal scales (Holmes & Simpson 1931; Carlini *et al.* 2009; González Ruiz *et al.* 2013). The osteoderms of cingulates are usually abundant in the Cenozoic fossil record and the characters from the dorsal surface, particularly those of

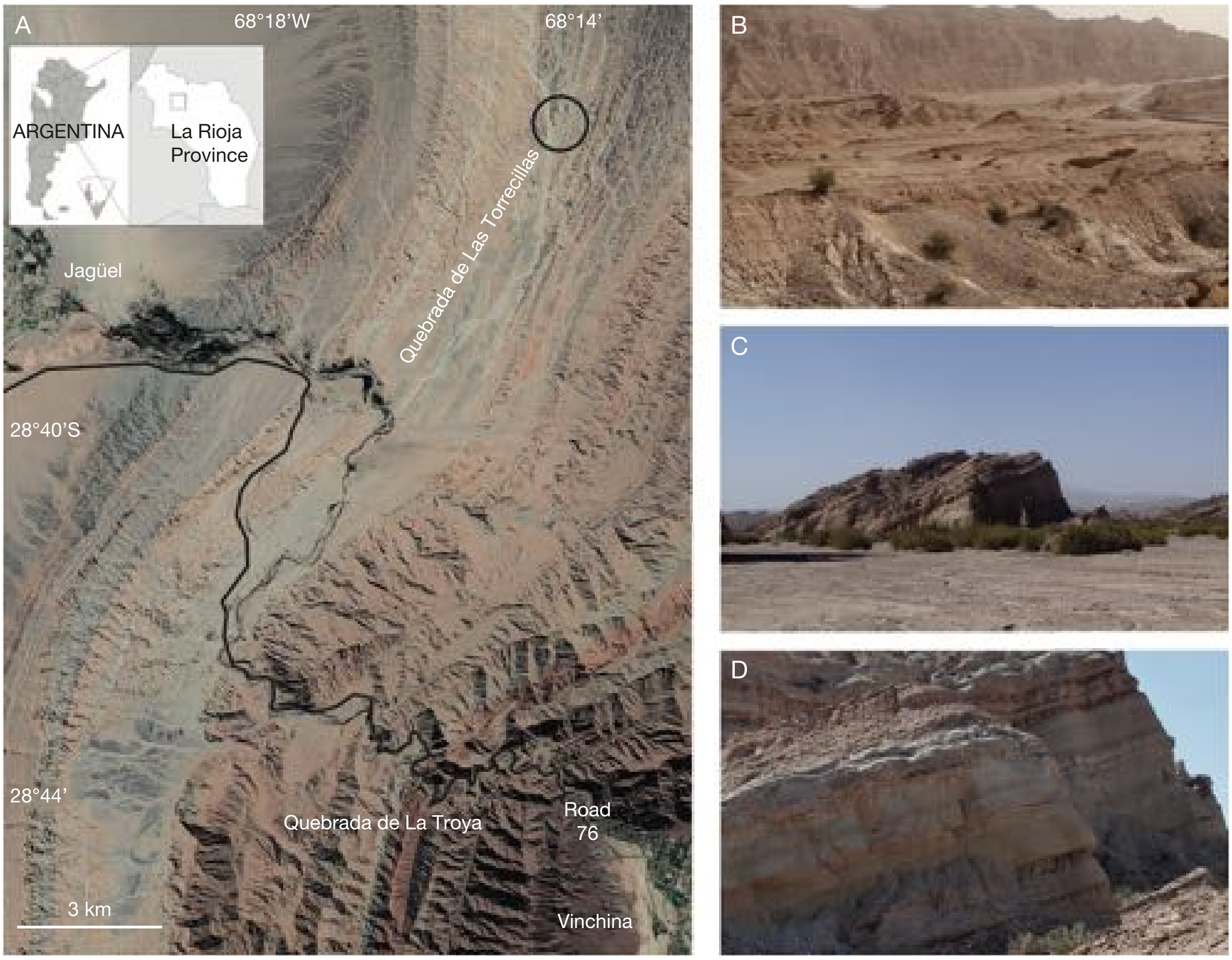

FIG. 1. — **A**, Map showing the study area (**black circle**), La Rioja Province, Argentina; **B**, panoramic view of Toro Negro Formation at road 76 between Vinchina and Jagüel; **C**, panoramic view of Toro Negro Formation at Quebrada de Las Torrecillas; **D**, detail of the lower member of the Toro Negro Formation at Quebrada de Las Torrecillas. Credits: map modified from Google Earth.

the dorsal and caudal carapace, are used for species recognition, especially when the skull and postcranial remains of the animal have not been preserved (Carlini *et al.* 2009; Krmpotic *et al.* 2009; González Ruiz *et al.* 2011, 2017; Zamorano *et al.* 2011; Gaudin & Croft 2015).

Among cingulates, Dasypodidae is the most diversified group, including Dasypodinae, Euphractinae, Tolypeutinae, and Chlamyphorinae, and it is the only group with extant representatives (Abba & Vizcaíno 2011; Gibb *et al.* 2016; Feijó *et al.* 2019; Barasoain *et al.* 2020a). Additionally, Dasypodidae also represents the most ancient group of xenarthrans, with the oldest records coming from the early Eocene of Brazil (i.e., *Riostegotherium yanei* Oliveira & Bergqvist, 1998), and reaching North America during the GABI (Great American Biotic Interchange) (Woodburne 2010; Feng *et al.* 2017).

The aim of this contribution is to analyze and describe a new collection of osteoderms belonging to the dorsal carapace of Dasypodidae from the Neogene deposits of the Toro Negro Formation, and discuss their systematic assignment and geographical and chronological significance.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Toro Negro Formation (Turner 1964), outcropping at La Rioja Province, Argentina (Fig. 1), comprises one of the best represented Neogene sequences identified within the Central Andes (Ciccioli *et al.* 2020). This unit, deposited during the Late Miocene to the Pleistocene (Rodríguez Brizuela & Tauber 2006; Amidon *et al.* 2016; Ciccioli *et al.* 2018, 2020), was divided into two informal members (lower and upper, see Ramos 1970; De Iuliis *et al.* 2004; Rodríguez Brizuela & Tauber 2006; Ciccioli *et al.* 2018; Chiesa *et al.* 2019).

Most of the described fossil vertebrates from the Toro Negro Formation were collected from the lower member at Quebrada de La Troya site, in the proximity of the road between the localities of Vinchina and Jagüel (see Rodríguez Brizuela & Tauber 2006; Tambussi *et al.* 2021) (Fig. 1A, B). The dasypodid remains herein described come from the upper levels of the lower member of the Toro Negro Formation at Quebrada de Las Torrecillas, where previous vertebrate records in the area include those of *Pyramiodontherium scillatoyanei* De Iuliis,

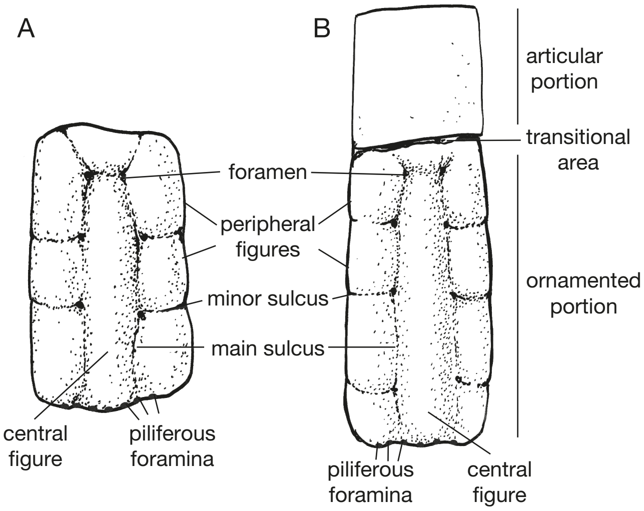

Fig. 2. — Morphology of osteoderms for the dorsal carapace: **A**, fixed osteoderm; **B**, mobile osteoderm.

Ré & Vizcaíno, 2004 (Mammalia, Xenarthra, Megatheriinae) and *Opisthodactylus* cf. *kirchneri* Noriega, Jordan, Vezzosi & Areta, 2017 (Aves, Rheidae) (28°36'S, 68°14'W) (see Ramos 1970; De Iuliis *et al.* 2004; Tambussi *et al.* 2021) (Fig. 1A, C).

The lower member of the Toro Negro Formation is mainly composed of sandstones, mudstones (reddish in color alternating with greenish interstratified beds), muddy intra-formational breccias and extra-formational conglomerates, and contains several tuff layers (Ramos 1970; Ciccioli & Marenssi 2012; Ciccioli *et al.* 2018; Chiesa *et al.* 2019) (Fig. 1D). The upper member presents a low-relief basal unconformity and is mainly composed of cobble conglomerates and coarse-grained sandstones (Ciccioli & Marenssi 2012; Ciccioli *et al.* 2018; Chiesa *et al.* 2019).

For the levels bearing *Py. scillatoyanei*, based on data from Tabutt *et al.* (1989), De Iuliis *et al.* (2004) estimated an age between 3.11 and 3.04 Ma (Piazencian, Late Pliocene). However, many different ages for the lower member of the Toro Negro Formation were proposed: Ciccioli *et al.* (2005) indicated an age of 8.6 ± 0.3 Ma and 6.8 ± 0.2 Ma (Late Miocene) for the middle-upper levels of the member; Amidon *et al.* (2016) indicated an age of *c.* 6.87 to 4.95 Ma (Messinian-Zanclean; see also Ciccioli *et al.* 2020); and Ciccioli *et al.* (2018) mentioned ages of 6.64 ± 0.1 Ma and 5.40 ± 0.12 Ma for levels at Quebrada del Yeso. Considering the most accurate proposed ages (see Ciccioli *et al.* 2005, 2018, 2020; Amidon *et al.* 2016) a Messinian-Zanclean age (Late Miocene-Early Pliocene) is herein considered for the lower member of the Toro Negro Formation.

MATERIAL AND METHODS

The specimens here analyzed include several fossil remains belonging to distinct specimens of Neogene Dasypodidae. All remains were collected during field work at Quebrada de Las Torrecillas, in the area where remains of *Py. scillatoyanei* and *O.* cf. *kirchneri* were collected (28°36'S, 68°14'W). The systematic scheme proposed by McKenna & Bell (1997), Gardner (2005), and Delsuc *et al.* 2012 (but see Delsuc *et al.* 2016; Mitchell *et al.* 2016; Gibb *et al.* 2016) is partially followed. The adopted terminology for describing osteoderm morphology (i.e., central figure, peripheral figures, foramina; see Fig. 2) follows that applied by Scillato-Yané (1982), Carlini *et al.* (2014), Castro *et al.* (2014), and Barasoain *et al.* (2021). For chronological purposes, we follow the International Chronostratigraphic Chart (Cohen *et al.* 2013; International Commission on Stratigraphy 2022). Anatomical measurements of the described osteoderms were obtained by using a 0.02 mm resolution digital calliper. Images were taken using a Nikon D5200 camera with a Nikon AF-S Micro-Nikkor 105 mm 1:2.8G ED lens, in a light box with fluorescent tubes.

Abbreviations

Institutional abbreviation

CRILAR-Pv Departamento de Geociencias, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica, Anillaco, La Rioja, Argentina.

Other abbreviation

GABI Great American Biotic Interchange.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order XENARTHRA Cope, 1889
Suborder CINGULATA Illiger, 1811
Family Dasypodidae Gray, 1821
Subfamily Tolypeutinae Gray, 1865
Tribe Priodontini Gray, 1873

Genus *Vetelia* Ameghino, 1891

Type species. — *Vetelia puncta* Ameghino, 1891.

Vetelia gandhii Esteban & Nasif, 1996
(Fig. 3A-F; Table 1)

Vetelia puncta Esteban & Nasif, 1996: 329.

Material referred. — CRILAR-Pv 116, one isolated fixed osteoderm; CRILAR-Pv 117, one fixed osteoderm associated with a fragment of an osteoderm from the right lateral border of the carapace; and CRILAR-Pv 118, an association of seven broken osteoderms interpreted as belonging to a juvenile.

Geographic and stratigraphic provenance. — Quebrada de Las Torrecillas (28°36'S, 68°14'W), La Rioja Province, Argentina (Fig. 1). Upper levels of the lower member of the Toro Negro Formation (Messinian-Zanclean; Late Miocene-Early Pliocene).

Description

Fixed and lateral osteoderms. The size of fixed osteoderms is similar to that of the extant *Priodontes maximus* (Kerr, 1792).

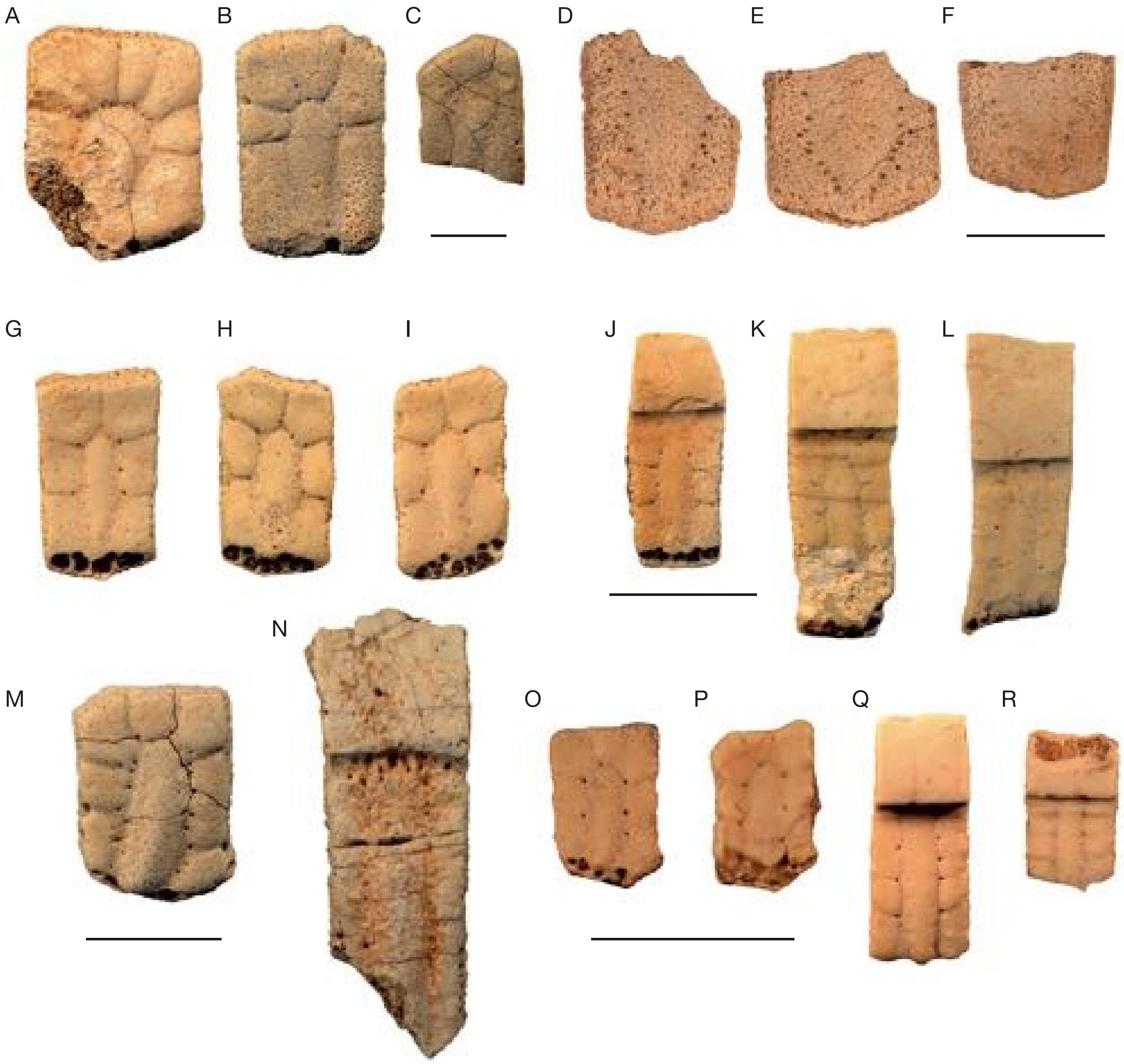

Fig. 3. — Dasypodidae from the Toro Negro Formation at Quebrada de Las Torrecillas, La Rioja Province, Argentina: **A**-**F**, *Vetelia gandhii* Esteban & Nasif, 1996 (CRILAR-Pv 116; CRILAR-Pv 117; CRILAR-Pv 118); **G**-**L**, *Chasicotatus peiranoi* Esteban & Nasif, 1996 (CRILAR-Pv 119); **M**, **N**, *Macrochorobates scalabrinii* (Moreno & Mercerat, 1891) (CRILAR-Pv 120); **O**-**R**, *Prozaedyus* sp. (CRILAR-Pv 121). Scale bars: 1 cm.

The fixed osteoderm CRILAR-Pv 116 (Fig. 3A) is thick, wide, and has a pentagonal outline, and probably belongs to the more dorsal region of the carapace. In turn, the fixed osteoderm CRILAR-Pv 117 (Fig. 3B) is thinner and narrower than CRILAR-Pv 116 and has a sub-rectangular in outline, so it probably occupied a more lateral position within the carapace. The whole dorsal surface of the osteoderms is full of small foramina. In lateral view, osteoderms have a constant thickness from the anterior to the posterior margin.

The ornamentation pattern of the dorsal surface is composed by a wide and slightly convex central figure, and a variable number (4-5) of minor peripheral figures restricted to the anterior half of the osteoderm. The central figure is sub-elliptical, and is delimited by a main sulcus containing several small dorsal foramina, which are more numerous in the proximal area. Towards the posterior margin of the osteoderm, this sulcus becomes progressively shallower until disappearing, so that the central figure becomes unified with the remaining dorsal surface of the osteoderm. The peripheral figures, anteriorly placed, are sub-pentagonal, and delimited by minor sulci. Contrary to the main sulcus, these sulci have no dorsal foramina and are much deeper.

In the posterior margin, there is a variable number of large piliferous foramina, posteriorly oriented and arranged into a single row. Osteoderm CRILAR-Pv 116 has just one foramen, while osteoderm CRILAR-Pv 117 has a row of three piliferous foramina. There are no foramina at the lateral margins of the fixed osteoderms. By contrast, there are two piliferous foramina in the external margin of the preserved fragment of the osteoderm from the right lateral border of the carapace (Fig. 3C).

Juvenile osteoderms. These osteoderms (CRILAR-Pv 118; Fig. 3D-F) are of similar shape to those of fixed osteoderms of adult individuals, but can be recognized as belonging to juvenile stage due to several features, such as a much smaller size (Table 1); undeveloped central and peripheral figures and very punctuate dorsal and ventral surfaces. The same morphological differences have been reported for juveniles of other cingulate groups such as glyptodonts (see Luna & Krapovickas 2011; Zurita *et al.* 2011; Luna *et al.* 2018). Additionally, these osteoderms have a series of conspicuous dorsal foramina which correspond with the location of the main sulcus in osteoderms belonging to adult individuals.

Remarks

Vetelia includes *V. puncta*, *V. perforata* Scillato-Yané, 1977, and *V. ghandii*. The analyzed specimens are assigned to *V. ghandii* for having large and scarce piliferous foramina (1-3) at the posterior margin. In *V. perforata* foramina are much smaller and numerous (6-14) (see Scillato-Yané 1977, 1982; Barasoain *et al.* 2021). In turn, *V. puncta* osteoderms develop several small piliferous foramina at the posterior margin (Ameghino 1891), several dorsal foramina in both main and minor sulci, and smaller piliferous foramina are present at the anterior and lateral margins of the osteoderm, which are absent in *V. ghandii* (see Esteban & Nasif 1996; Barasoain *et al.* 2021).

Subfamily Euphractinae Pocock, 1924
Tribe Eutatini Bordas, 1933

Genus *Chasicotatus* Scillato-Yané, 1979

Type species. — *Chasicotatus ameghinoi* Scillato-Yané, 1979.

Chasicotatus peiranoi Esteban & Nasif, 1996
(Fig. 3G-L; Table 1)

Chasicotatus peiranoi Esteban & Nasif, 1996: 330.

Material referred. — CRILAR-Pv 119, an association of six fixed osteoderms and three complete plus three broken mobile osteoderms.

Geographic and stratigraphic provenance. — Quebrada de Las Torrecillas (28°36'37"S, 68°14'14"W), La Rioja Province, Argentina (Fig. 1). Upper levels of the lower member of the Toro Negro Formation (Messinian-Zanclean; Late Miocene-Early Pliocene).

Description

Fixed osteoderms. Osteoderms (Fig. 3G-I) are sub-rectangular in outline, slightly longer than wide (see Table 1). In lateral view, the thickness progressively increases towards the posterior margin. The dorsal surface of the osteoderms is mostly smooth and foramina are scarce.

The ornamentation pattern of the dorsal surface includes a well-developed central figure and a set of 6-7 peripheral figures. The central figure is rounded in section and elongated. It occupies more than two thirds of the anteroposterior total length of the osteoderms, extending to the posterior margin, where it becomes narrower. It is delimited by a main sulcus in which many small foramina are placed. Though in some osteoderms the central figure deviates slightly towards the lateral margin, in most cases it is straight. Peripheral figures are slightly convex in section, and develop very variable contours, ranging from hexagonal and pentagonal to rectangular. In all osteoderms, there are 2 peripheral figures at either side of the central figure. Instead, anteriorly to the central figure there are 2 to 3 peripheral figures, depending on the osteoderm. All peripheral figures are delimitated by sulci, which are shallower than the main sulcus. Along these sulci there are small foramina, though they are more scarce than in the main sulcus. Additionally, large dorsal foramina are placed at the boundary between main and minor sulci.

At the posterior margin, there is a double row of piliferous foramina. The lower row includes the largest foramina, varying from 4 to 7 in number. These foramina have a great anteroposterior development and are dorsally oriented. In turn, the upper row includes much smaller foramina intercalated between the large foramina of the first row, placed in the upper half of the septum that separates them. There are no foramina at the anterior and lateral margins.

Mobile osteoderms. Osteoderms (Fig. 3J-L) are rectangular in outline, much longer than wider (see Table 1). The articular portion represents approximately one third of the total length, and is separated from the ornamented portion by a great transitional area with a flat and unornamented surface. In turn, the ornamented portion includes a central figure and a set of peripheral figures.

The central figure is rounded in section and elongated. It extends straightly from the transitional area to the posterior margin of the osteoderms, extending the entire length of the ornamented portion, while maintaining an approximately constant width. At either side of the central figure there are 3-4 peripheral figures. All figures are delimited by sulci. The main sulcus, which delimits the central figure, is deeper and wider than the sulci that delimit the peripheral figures. As in fixed osteoderms, there are large foramina placed at the boundary between the main and minor sulci.

At the posterior margin, there is a double row of piliferous foramina. The lower and largest row includes 5 to 7 foramina, less dorsally oriented than those of fixed osteoderms. In turn, the upper row is composed by much smaller intercalated foramina, which are more scarce than in fixed osteoderms. Some osteoderms also develop small piliferous foramina in the distal area of the lateral margins.

Remarks

Chasicotatus includes *C. ameghinoi*, *C. powelli* Scillato-Yané, Krmpotic & Esteban, 2010, *C. spinozai* Scillato-Yané, Krmpotic & Esteban, 2010 and *C. peiranoi*. The analyzed

TABLE 1. — Measurements (in mm) of the described osteoderms.

Taxa	Fixed osteoderms Length	Fixed osteoderms Width	Mobile osteoderms Length	Mobile osteoderms Width
Vetelia ghandii Esteban & Nasif, 1996 (adult)	22.81-26.67	16.66-24.23	–	–
V. ghandii (juvenile)	14.72	10.55-12.51	–	–
Chasicotatus peiranoi Esteban & Nasif, 1996	11.36-14.31	9.13-9.41	20.15-27.85	8.71-9.73
Macrochorobates scalabrinii (Moreno & Mercerat, 1891)	16.38	11.43	41.81	12.57
Prozaedyus sp.	8.87-9.16	6.11-6.85	15.21	6.23
Paleuphractus argentinus (Moreno & Mercerat, 1891)	10.57-14.28	9.51-10.23	16.36-24.28	7.27-8.96

material is assigned to *C. peiranoi* as it bears a double row of piliferous foramina at the posterior margin of the osteoderms (see Esteban & Nasif 1996; Scillato-Yané *et al.* 2010). It differs from *C. spinozai* as the latter develops much smaller piliferous foramina, while *C. powelli* develops more conspicuous foramina at the dorsal surface of the osteoderms (see Scillato-Yané *et al.* 2010). In turn, *C. ameghinoi* develops just one row of piliferous foramina at the posterior margin of the osteoderms (see Esteban & Nasif 1996; Scillato-Yané *et al.* 2010).

Tribe EUPHRACTINI Pocock, 1924

Genus *Macrochorobates* Scillato-Yané, 1980

TYPE SPECIES.— *Proeuphractus scalabrinii* Moreno & Mercerat, 1891.

Macrochorobates scalabrinii (Moreno & Mercerat, 1891) (Fig. 3M, N; Table 1)

Proeuphractus scalabrinii – Moreno & Mercerat, 1891: 226.

MATERIAL REFERRED. — CRILAR-Pv 120, an association of one fixed osteoderm and one complete, plus one broken mobile osteoderm.

GEOGRAPHIC AND STRATIGRAPHIC PROVENANCE. — Quebrada de Las Torrecillas (28°36'37"S, 68°14'14"W), La Rioja Province, Argentina (Fig. 1). Upper levels of the lower member of the Toro Negro Formation (Messinian-Zanclean; Late Miocene-Early Pliocene).

DESCRIPTION

Fixed osteoderm. This osteoderm (Fig. 3M) is sub-rectangular in outline, longer than wide (Table 1). Its entire dorsal surface is covered with small foramina. In lateral view, it maintains a constant width from the anterior to the posterior margin.

The ornamentation pattern of the dorsal surface is composed by a large central figure surrounded both laterally and anteriorly by a set of 7 minor peripheral figures. The central figure is keeled in section and sub-elliptical. It is very extended posteriorly, extending beyond the posterior margin of the osteoderm. The central figure is much more elevated than the peripheral figures, and its height progressively increases towards the posterior margin. The central figure is delimited by a main sulcus in which there are several large dorsal foramina. The peripheral figures have a convex surface and develop very variable irregular contours from slightly oval to pentagonal. Their size is variable, as some figures are double the size of others. At each lateral of the central figure there are 3 peripheral figures, while one is placed anteriorly, between the central figure and the anterior margin of the osteoderm. All peripheral figures are delimited by shallow sulci, in which there are no dorsal foramina as also occurs in the main sulcus.

At the posterior margin, there is a single row of 6 posteriorly oriented piliferous foramina of variable size. Additionally, there are several foramina along the entire length of the lateral margins. Among these, the 2 foramina placed in a posterior position are much larger than the others.

Mobile osteoderm. This osteoderm (Fig. 3N) is broken posteriorly so that the posterior margin is absent. It is rectangular in outline, much longer than wider (Table 1). The articular portion represents approximately one third of the osteoderm total length. The transitional area is short but develops a roughed surface.

The ornamented portion includes a wide and elongated central figure, keeled in section, which extends straightly from the transitional area to the posterior margin, while maintaining a constant width. At either side, there is an elongated and undivided figure, which extends parallel to the central figure. The central figure is more elevated, and separated from the lateral figures by a wide but shallow sulcus. Along this sulcus there are a few small dorsal foramina which are randomly distributed, some of them cluster together.

Along the entire length of the lateral margins there is a single row of several small foramina, which become larger towards the posterior margin. The posterior margin is not preserved.

REMARKS

Macrochorobates includes *M. chapalmalensis* (Ameghino, 1908) and *M. scalabrinii*. The analyzed materials are assigned to *M. scalabrinii* for having piliferous foramina at the lateral margins of both fixed and mobile osteoderms, which are absent in *M. chapalmalensis* (see Contreras *et al.* 2013), and less convex peripheral figures of fixed osteoderms than *M. chapalmalensis* (see Scillato-Yané 1982).

Genus *Prozaedyus* Ameghino, 1891

TYPE SPECIES. — *Euphractus proximus* Ameghino, 1887.

Prozaedyus sp.
(Fig. 3O-R; Table 1)

Prozaedyus Ameghino, 1891: 295.

Material referred. — CRILAR-Pv 121, two complete plus one broken fixed osteoderms and one complete plus two broken mobile osteoderms.

Geographic and stratigraphic provenance. — Quebrada de Las Torrecillas (28°36'37"S, 68°14'14"W), La Rioja Province, Argentina (Fig. 1). Upper levels of the lower member of the Toro Negro Formation (Messinian-Zanclean; Late Miocene-Early Pliocene).

Description

Fixed osteoderms. These osteoderms (Fig. 3O, P) are subrectangular in outline, longer than wide (Table 1). The dorsal surface is smooth and small foramina are scarce to absent. Osteoderms maintain a constant thickness from the anterior to the posterior margin.

The ornamentation pattern includes a narrow and elongated central figure which extends to the posterior margin being rounded in section. It can be straight or slightly deviated toward the external lateral margin, and is a bit more elevated towards its posterior margin. It is laterally and anteriorly surrounded by 7-8 peripheral figures which vary from polygonal to elliptical. These figures have similar sizes, except for the one placed anteriorly to the central figure, which is much smaller than the others. The central figure is delimited by a shallow main sulcus, while even shallower minor sulci delimite peripheral figures. Noticeable dorsal foramina are placed at the boundary between minor sulci and main sulcus.

At the posterior margin there is a single row of four small piliferous foramina. All are similar in size and posteriorly oriented. At the distal area of the external lateral margin there are 2-3 small foramina.

Mobile osteoderms. These osteoderms (Fig. 3Q, R) are rectangular in outline, much longer than wide (see Table 1). The length of the ornamented portion is twice that of the articular portion. The articular portion is more elevated than the ornamented portion, and both are separated by a flat and extremely short transitional area.

The ornamentation pattern includes a straight, elongated, and nearly flat central figure surrounded on each side by 4-5 peripheral figures. Its length extends across the entire ornamented portion, from the transitional area to the posterior margin. Along the surface of the central figure there are several small foramina, always placed next to the lateral boundary of the figure. These foramina are absent in the rest of the dorsal surface of the osteoderm. Peripheral figures are sub-rectangular and have similar sizes, except for those placed closer to the posterior margin, which are the largest. The main sulcus, which delimites the central figure, is deeper than in fixed osteoderms. Contrarily, the minor sulci that delimitate peripheral figures are shallow, as in fixed osteoderms. Several prominent dorsal foramina are observable at the junction between main and minor sulci.

Only one osteoderm preserves its posterior margin, where there is a single row of five posteriorly oriented piliferous foramina, larger than those of fixed osteoderms. At the posterior area of the external lateral margin there are 2 small foramina.

Remarks

Prozaedyus includes *Pr. proximus* (Ameghino, 1887), *Pr. exilis* (Ameghino, 1887), *Pr. impressus* Ameghino, 1897 (synonym of *Pr. planus*, *sensu* Loomis, 1914), *Pr. Tenuissimus* Ameghino, 1897, *Pr. humilis* Ameghino, 1902, and *Pr. scillatoyanei* Barasoain, Contreras, Tomassini & Zurita, 2020. The recovered osteoderms are assigned to *Prozaedyus* sp. for being smaller than other Euphractinae, having a narrow central figure and a single row of piliferous foramina at the osteoderms posterior margin plus small foramina at the distal half of the external lateral margin (see Croft *et al.* 2009; Barasoain *et al.* 2020b). Since main diagnostic characters among *Prozaedyus* species are given by cranial features (see Barasoain *et al.* 2020b), the preserved specimens preclude a determination at the species level. *Prozaedyus* differs from *Chasicotatus* and other Eutatini armadillos in having much smaller piliferous foramina (Scillato-Yané 1982; Scillato-Yané *et al.* 2010). It differs from *Proeuphractus* Ameghino, 1886 in being smaller and not having large foramina along both lateral margins (Perea & Scillato-Yané 1995). It differs from *Chorobates* Reig, 1958 in not having an elevated and keeled central figure (Carlini & Scillato-Yané 1996).

Genus *Paleuphractus* Kraglievich, 1934

Type species. — *Dasypus argentinus* Moreno & Mercerat, 1891.

Paleuphractus argentinus (Moreno & Mercerat, 1891)
(Fig. 4; Table 1)

Dasypus argentinus – Moreno & Mercerat, 1891: 227.

Material referred. — CRILAR-Pv 122, several associated elements, including 15 fixed osteoderms, nine mobile osteoderms, one nuchal osteoderm and seven osteoderms of the carapace borders, plus several broken postcranial elements.

Geographic and stratigraphic provenance. — Quebrada de Las Torrecillas (28°36'37"S, 68°14'14"W), La Rioja Province, Argentina (Fig. 1). Upper levels of the lower member of the Toro Negro Formation (Messinian-Zanclean; Late Miocene-Early Pliocene).

Description

Nuchal osteoderm. A single osteoderm (Fig. 4A) of the nuchal bands was recovered. As in mobile osteoderms (see below), it is divided into an articular and an ornamented portion. However, it is smaller and has a very reduced articular portion in relation to osteoderms of the mobile bands. It has a rectangular outline. The ornamentation includes flat and poorly developed central and lateral figures, which are only partially delimited by shallow sulci. At the posterior margin

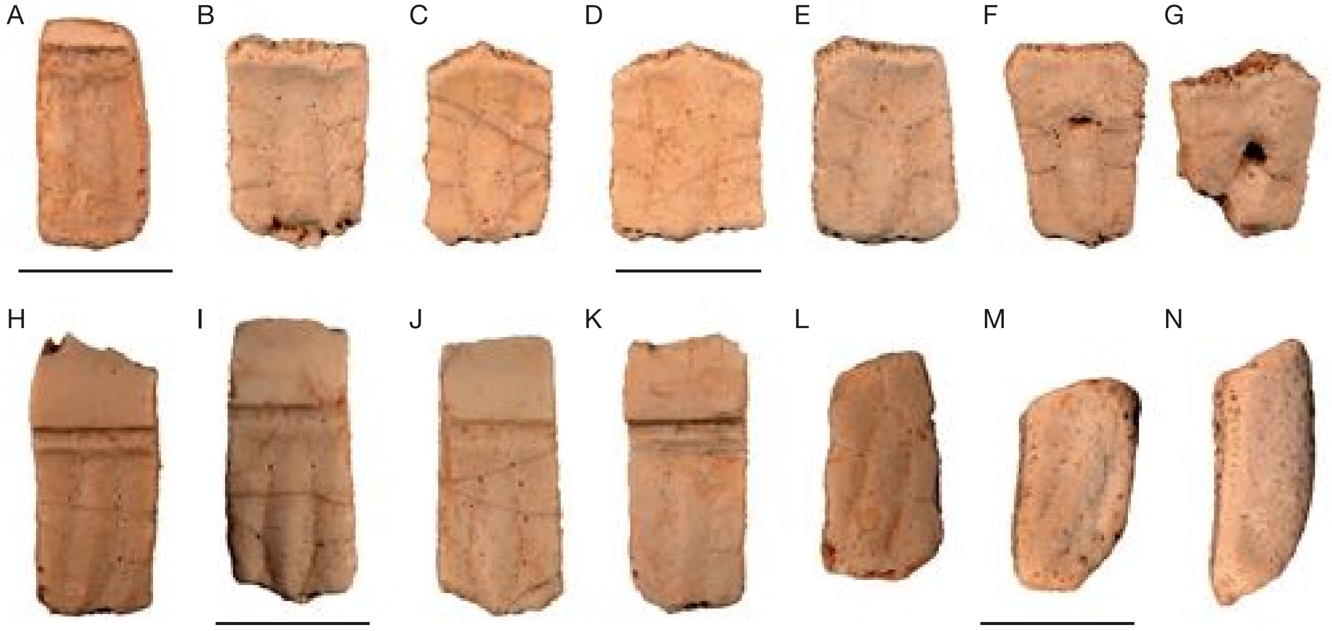

Fig. 4. — Dasypodidae from the Toro Negro Formation at Quebrada de Las Torrecillas, La Rioja Province, Argentina: **A**-**N**, *Paleuphractus argentinus* (Moreno & Mercerat, 1891) (CRILAR-Pv 122). Scale bars: 1 cm.

there is a single row of 6 piliferous foramina but, contrary to the osteoderms of the mobile bands, there are 3 to 4 much larger foramina at the lateral margins.

Fixed osteoderms

These osteoderms (Fig. 4B-G) can be either rectangular or pentagonal in outline, and are slightly longer than wide (Table 1). The entire dorsal surface is covered by very small foramina, very abundant in some osteoderms while practically absent in others. All osteoderms have a constant thickness from the anterior to posterior margin.

The ornamentation pattern includes a wide and subelliptical central figure surrounded laterally and anteriorly by a variable number of peripheral figures. It extends posteriorly to reach the posterior margin, and deviates slightly toward the external lateral margin of the osteoderm. Towards the posterior margin it widens progressively, occupying more than one third of the osteoderm width. It is delimited by a shallow main sulcus. Anteriorly, this sulcus becomes shallower and disappears, so that the central figure merges with the dorsal surface. In lateral view, the central figure progressively increases its elevation until reaching the posterior margin, where it is much more elevated than the peripheral figures. Peripheral figures vary from 5 to 8, being seven in most cases. These figures are delimited by such shallow sulci and their limits are often diffuse or mostly indistinguishable. Some osteoderms develop large dorsal foramina at all the boundaries between main and minor sulci, while in others they are only present at some boundary or absent.

Two of the fixed osteoderms have a particular morphology, including a deep cavity placed at the anterior limit of the central figure (Fig. 4F, G). Such cavities are related to the presence of odoriferous glands, which are present in the pelvic shield of many euphractine armadillos (Scillato-Yané 1982, Redford & Wetzel 1985). This structure has not been previously described for *Pal. argentinus*.

At the posterior margin, there are several small piliferous foramina, arranged in an irregular row. These foramina are variable in both number (5-10) and size, as some are twice the size of others, and are arranged in a zig-zag row. Although the lateral margins do not bear foramina, the row of piliferous foramina may extend slightly towards the more distal area of the external lateral margin.

Mobile osteoderms

These osteoderms (Fig. 4H-K) are rectangular, longer than wide (Table 1). The articular portion represents less than one third of the total length. The transitional area is flat and unornamented. Some osteoderms develop a transverse ridge at the end of the transitional area, delimiting it from the ornamented portion.

The ornamentation pattern is composed by a central figure surrounded by 2 elongated and undivided lateral figures. The central figure is rounded to slightly keeled in section and sub-elliptical, and extends to the posterior margin. In some osteoderms it is straight, while in others it deviates slightly towards the external lateral margin. In contrast to the condition in fixed osteoderms, it gets much narrower towards the posterior margin. The central figure is delimited by a main sulcus, along which there are several dorsal foramina. Towards the anterior area of the ornamented portion, this sulcus becomes progressively shallower, so that the central figure merges with the dorsal surface. Lateral figures are parallel to the central figure. In some cases, some of these peripheral figures are subdivided by shallow sulci.

At the posterior margin there is a single row of 4 to 7 piliferous foramina, much smaller than those of fixed osteoderms. Also, in contrast to those of fixed osteoderms, these foramina are arranged into a straight line. In those osteoderms in which the central figure is slightly deviated, there are 2 to 3 piliferous foramina in the more ventral area of the external lateral margin.

Osteoderms of the marginal rows. These osteoderms (Fig. 4L-N) belong to the most lateral rows of the dorsal carapace. They are more elongated than regular osteoderms, and develop an irregular wedge shape. This is a representative morphology of both fossil and extant euphractine armadillos, which usually develop serrated lateral carapace borders (see Scillato-Yané 1982; Krmpotic *et al.* 2009).

Ornamentation is nearly or entirely absent, although some osteoderms have poorly developed central and peripheral figures. Some osteoderms of the lateral area develop more similar morphologies to those of other carapace areas, having a single row of piliferous foramina at the posterior margin which is absent in those belonging to the carapace border.

Remarks

Paleuphractus is monotypic, with *Pal. argentinus* being the only recognized species. The material here analyzed can be assigned to *Pal. argentinus* based on a low central figure, mobile osteoderms with undivided lateral figures, and small piliferous foramina located on the posterior and external lateral margins (see Scillato-Yané 1982). It differs from *Paraeuphractus* Scillato-Yané, 1975 in developing dorsal foramina at the intersections between the main sulcus and the minor sulci of fixed osteoderms (Rodríguez Brizuela & Tauber, 2006), and from *Chorobates* and *Macrochorobates* in being smaller, having a less elevated and deviated central figure in both fixed and mobile osteoderms, and developing undivided lateral figures in mobile osteoderms (Scillato-Yané 1982). It differs from *Proeuphractus* in having much smaller piliferous foramina at both the posterior and lateral margins (Perea & Scillato-Yané 1995).

DISCUSSION

The known diversity of fossil vertebrates from the lower member of the Toro Negro Formation mainly consists of mammals and birds (see Arcucci *et al.* 1999; De Iuliis *et al.* 2004; Rodríguez Brizuela & Tauber 2006, Krapovickas *et al.* 2009; Tambussi *et al.* 2021). Until the present contribution, mammals from this formation are represented by the xenarthrans *Pyramiodontherium scillatoyanei*, cf. *Plesiomegatherium* Roth, 1911, "*Xyophorus*" aff. *bondesioi* Scillato-Yané, 1979, and cf. *Proscelidodon* Bordas, 1935 (Folivora); *Proeuphractus limpidus*, *Chorobates villosissimus*, *Paleuphractus* sp., *Doellotatus inornatus*, *Lomaphorops corallinus*, *Neuryurus* cf. *giganteus*, and cf. *Urotherium* sp. (Cingulata); the rodents *Abrocoma* Waterhouse, 1837, *Protabrocoma* Kraglievich, 1927, *Propediolagus* Ortega, 1963; and the litoptern *Eoauchenia* Ameghino, 1887 (see De Iuliis *et al.* 2004; Rodríguez Brizuela & Tauber 2006; Krapovickas *et al.* 2009). Among them, only *Py. scillatoyanei* was recovered from the area of Quebrada de Las Torrecillas, whereas the other taxa were recovered from sediments in proximity to the road between the localities of Vinchina and Jagüel (see Rodríguez Brizuela & Tauber 2006). The cingulates here reported, i.e., *Vetelia ghandi*, *Chasicotatus peiranoi*, *Macrochorobates scalabrinii*, *Prozaedyus* sp., and *Paleuphractus argentinus*, constitute the first records of these species for the Toro Negro Formation increasing the mammal diversity for this unit. Regarding Dasypodidae from the Toro Negro Formation, diversity is increased to 8 genera, which is the richest diversity recorded for La Rioja Province, and the second richest in northwestern Argentina, following that of the Late Miocene-Early Pliocene of Catamarca Province (see Esteban *et al.* 2014).

Vetelia includes large-sized armadillos traditionally included within Euphractinae. However, most recent analyses including more complete specimens suggest their inclusion within Tolypeutinae (see Barasoain *et al.* 2021). Though the genus has a wide latitudinal distribution in Argentina (i.e., Santa Cruz, Chubut, Neuquén, Río Negro, Buenos Aires, La Pampa, La Rioja, San Juan, and Catamarca provinces), records of *V. ghandii* are restricted to Late Miocene localities of Catamarca and San Juan provinces (González Ruiz *et al.* 2014; Barasoain *et al.* 2021). The records from Catamarca Province include its type specimen, coming from the subsequences IIb and IIc of Playa del Zorro Alloformation from the Cajon Valley (Late Miocene; see Esteban & Nasif 1996). In San Juan Province, *V. ghandii* is recorded from two distinct Neogene deposits. One belongs to the Loma de Las Tapias Formation, with an estimated age of 9 Ma (Late Miocene; Contreras & Baraldo 2011). The other belongs to unnamed levels outcropping at Los Berros locality, with an inferred Late Miocene age according to Contreras *et al.* (2019) (see Ciancio *et al.* 2006; González Ruiz *et al.* 2014; Barasoain *et al.* 2021). In this framework, this work extends the distribution of *V. ghandii* to La Rioja Province.

Chasicotatus includes medium- to small-sized armadillos, and is recorded in several Late Miocene deposits of Argentina, and is among the more geographically widespread of Eutatini (Euphractinae) (see Scillato-Yané *et al.* 2010). After the type species *C. ameghinoi*, *C. peiranoi* has the second largest distribution within the genus, with records coming from Catamarca, Buenos Aires, and San Juan provinces (Esteban & Nasif 1996; Deschamps 2005; Ciancio *et al.* 2006). In Catamarca Province, *Chasicotatus peiranoi* is described for the subsequences IIb and IIc of Playa del Zorro Alloformation from the Cajon Valley (Esteban & Nasif 1996). According to the stratigraphic scheme proposed by Bossi *et al.* (1993), fossil-bearing levels are correlated with the Late Miocene deposits of the Chiquimil (Tortonian-Messinian) and Andalhuala (Messinian-Zanclean) Formations from the Santa María Valley (Catamarca Province, see Esteban *et al.* 2014). In Buenos Aires Province, *C. peiranoi* is recorded from the "Relleno Sanitario" quarry, southwestern Buenos Aires Province, for which a Late Miocene age is inferred based on faunal correlations (see Deschamps 2005). In turn, the the oldest records come from Loma de Las Tapias

Formation (*c.* 9 Ma, Contreras & Baraldo 2011). The current work extends the distribution of *C. peiranoi* to La Rioja Province, Argentina. These records suggest a great affinity of this taxon with the Subandean region of western Argentina, where it is often found in association with other taxa, such as *V. ghandii*, with a more restricted distribution (see above).

Macrochorobates scalabrinii is a medium-to large-sized Euphractini (Euphractinae) armadillo known from several Late Miocene deposits over a wide latitudinal range in Argentina. In the Pampean Region, it is known from the Cerro Azul Formation of La Pampa Province (see Esteban *et al.* 2001; Urrutia *et al.* 2008; Montalvo *et al.* 2019), and the "Epecuén Formation" (see Scillato-Yané 1980, 1982) of Buenos Aires Province. In this respect, Goin *et al.* (2000) considered that the latter should be included within the Cerro Azul Formation since there are no significant lithostratigraphic or faunistic differences. Additionally, the presence of *M. scalabrinii* was also noted in a still unnamed unit overlying the Arroyo Chasicó Formation (see Tonni *et al.* 1998). Based on this evidence, the biozone of *M. scalabrinii* was proposed (Tonni *et al.* 1998; Cione & Tonni 2005) as an indicator of a Huayquerian Stage/Age (Tortonian-Messinian) of the Pampean Region, though it was not supported by further analyses (see Verzi *et al.* 2004, 2008; Urrutia *et al.* 2008).

Other records of *M. scalabrinii* belong to the Cuyo and Northwest regions. In San Juan Province, it is recorded for the depositional sequences 5 to 6 of Las Flores Formation (Iglesia Group, see Contreras *et al.* 2013), which have an estimated age of 6.9 to 6.3 Ma (Late Miocene), according to the geological scheme proposed by Ré *et al.* (2003). In Tucumán Province, it is mentioned by Castellanos (1947) and Scillato-Yané (1980, 1982) for the "Araucanian", without further detail. In turn, records from Catamarca Province come from several Late Miocene-Early Pliocene sites (i.e., Entre Ríos, Puerta de Corral Quemado, Villavil) within the Chiquimil and Andalhuala Formations (see Marshall & Patterson 1981; Bossi *et al.* 1987; Esteban & Nasif 1996; Esteban *et al.* 2014), with an estimated age of 8.7-3.66 Ma (Late Miocene-Early Pliocene; Reguero & Candela 2011; Esteban *et al.* 2014; Bonini *et al.* 2017). The northernmost records of *M. scalabrinii* come from Middle-Late Miocene deposits outcropping at the Calahoyo Basin in Jujuy Province (Quiñones *et al.* 2019). In La Rioja Province, it was known, prior to the current contribution, from the Salicas Formation (Messinian, Late Miocene) (Tauber 2005; Brandoni *et al.* 2012).

Prozaedyus includes several species of small-sized euphractine armadillos, and has a relatively much larger biochron than other euphractines, with records ranging from the late Oligocene to the Late Miocene, and mainly restricted to Patagonian areas (Croft *et al.* 2009, 2016; Vizcaíno *et al.* 2012; Barasoain *et al.* 2020b). Though Patagonian records are well characterized and have been widely studied (Scott 1903; Gaudin & Wible 2006; Vizcaíno *et al.* 2012; Fernicola & Vizcaíno 2019), Late Miocene records from extra-Patagonian areas are very fragmentary, scarce, and little studied. To date, the only recognized species for the Late Miocene was *Pr. scillatoyanei* from Loma de Las Tapias Formation (*c.* 9 Ma, Contreras & Baraldo 2011), San Juan Province, Argentina (see Barasoain *et al.* 2020b). In this context, the records here analyzed extend the Late Miocene distribution of *Prozaedyus* to La Rioja Province, supporting the idea that this taxon would have persisted until the Late Miocene in Northwestern Argentina.

Paleuphractus argentinus, the only recognized species within the genus, is a medium-sized Euphractini (Euphractinae) known from Late Miocene deposits of Catamarca and La Rioja provinces. Its type specimen comes from the "Araucanian" of Puerta del Corral Quemado, in Catamarca Province (see Moreno & Mercerat 1891; Kraglievich 1934). Later on, it was mentioned for the same locality by Marshall & Patterson (1981). Esteban & Nasif (1996) recorded *Paleuphractus* sp. for the subsequences IIb and IIc of Playa del Zorro Alloformation (Late Miocene; see Bossi *et al.* 1993). Esteban *et al.* (2014) recorded *Pal. argentinus* for the Chiquimil and Andalhuala Formations and established the Association Biozone of *Proeuphractus limpidus-Paleuphractus argentinus-Chasicotatus ameghinoi*, with type locality in Puerta del Corral Quemado, estimated at between 8.7 Ma and 7.14 Ma in age (Late Miocene; see Esteban *et al.* 2014 and references therein).

In La Rioja Province, *Pal. argentinus* is recorded for the Desencuentro Formation (Georgieff *et al.* 2004). These deposits have an estimated age of 7.4 Ma (Late Miocene; see Reynolds 1987). In turn, Rodríguez Brizuela & Tauber (2006) recorded *Paleuphractus* sp. from the lower member of the Toro Negro Formation, at its type section of the Quebrada de La Troya site. Given that the more complete materials here analyzed establish the presence of *Pal. argentinus* in the Quebrada de Las Torrecillas site of the Toro Negro Formation, the record reported by Rodríguez Brizuela & Tauber (2006) for this formation may also belong to this species. *Paleuphractus argentinus* is considered to be rare (Esteban *et al.* 2014), have a very restricted chronological and geographical distribution and, according to Scillato-Yané (1982), exclusive to the Subandean region.

CONCLUSIONS

The deposits of the Toro Negro Formation are geographical and chronologically extensive, and belong to one of the largest Neogene sequences in the world (Ramos 1970, 1999; Rodríguez Brizuela & Tauber 2006). The estimated age of its lower member varies from the Messinian age (Late Miocene) to the Piazencian age (Late Pliocene) (De Iuliis *et al.* 2004; Rodríguez Brizuela & Tauber 2006; Amidon *et al.* 2016; Ciccioli *et al.* 2018, 2020).

The association of Dasypodidae here described shows strong affinities with those described for Late Miocene localities of Northwestern Argentina, such as Loma de Las Tapias Formation in San Juan Province, and Playa del Zorro Aloformation, and Chiquimil and Andalhuala formations in Catamarca Province. Considering the records herein presented, *V. ghandii*, *Pal. argentinus*, and possibly *C. peiranoi* represent endemic species of Dasypodidae recorded during the Late Miocene of Northwestern Argentina. Regarding *Prozaedyus*, the record here presented extend the Late Miocene distribution of the genus to La Rioja Province, supporting the idea that this taxon would have persisted until the Late Miocene in Northwestern Argentina. In turn, *M. scalabrinii* is, among the recovered species, the only one recorded from both Late Miocene and Early Pliocene deposits.

Under these evidences, the Dasypodidae here reported for Quebrada de Las Torrecillas site show a characteristic association of taxa from Northwestern Argentina, suggesting a Messinian age (Late Miocene) for the bearing levels of the Toro Negro Formation. This way, these records support the most accurate proposed ages for the lower member of the Toro Negro Formation, i.e., Late Miocene-Early Pliocene (Amidon *et al.* 2016; Ciccioli *et al.* 2018, 2020).

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REFERENCES

Abba A. M. & Vizcaíno S. F. 2011. — Distribución de los armadillos (Xenarthra: Dasypodidae) en la provincia de Buenos Aires, Argentina. *Mastozoología Neotropical* 18 (2): 185-206.

Ameghino F. 1886. — Contribuciones al conocimiento de los mamíferos fósiles de los terrenos terciarios antiguos del Paraná. *Boletín de la Academia Nacional de Ciencias (Córdoba)* 9: 5-228.

Ameghino F. 1887. — Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de la Patagonia austral y depositados en el Museo de La Plata. *Boletín del Museo de la Plata* 1: 5-26.

Ameghino F. 1891. — Mamíferos y aves fósiles argentinas. *Revista Argentina de Historia Natural* 1: 240-288.

Ameghino F. 1897. — Mamíferos cretáceos de la Argentina. Segunda contribución al conocimiento de la fauna mastológica de las capas con restos de *Pyrotherium*. *Boletín Instituto Geográfico Argentino* 18: 431-521.

Ameghino F. 1902. — Notas sobre algunos mamíferos fósiles, nuevos o poco conocidos del valle de Tarija. *Anales del Museo Nacional de Buenos Aires* 3: 255-261.

Ameghino F. 1908 — Las formaciones sedimentarias de la región litoral de Mar del Plata y Chapadmalal. *Anales del Museo Nacional de Buenos Aires* 10: 343-428.

Amidon W. A., Ciccioli P. L., Marenssi S. A., Limarino C. O., Burch Fisher G., Burbank D. & Kylander-Clark A. 2016. — U-Pb ages of detrital and volcanic zircons of the Toro Negro Formation, northwestern Argentina: age, provenance and sedimentation rates. *Journal of South American Earth Sciences* 70: 237-250. https://doi.org/10.1016/j.jsames.2016.05.013

Arcucci A. B., Tambussi C. T., Pardiñas U. F. J. & Petrulevicius J. F. 1999. — Nuevos registros de vertebrados en el Terciario superior del noroeste de La Rioja, Argentina. *Ameghiniana* 36: 95-96.

Barasoain D., Tomassini R. L., Zurita A. E., Montalvo C. I. & Superina M. 2020a. — A new fairy armadillo (Cingulata, Chlamyphorinae) from the upper Miocene of Argentina: first fossil record of the most enigmatic Xenarthra. *Journal of Vertebrate Paleontology* 39 (5): e1716778.

Barasoain D., Contreras V. H., Tomassini R. L.& Zurita A. E. 2020b. — A new pygmy armadillo (Cingulata, Euphractinae) from the late Miocene of Andean Argentina reveals an unexpected evolutionary history of the singular *Prozaedyus* lineage. *Journal of South American Earth Sciences* 100: 102589. https://doi.org/10.1016/j.jsames.2020.102589

Barasoain D., González Ruiz L. R., Tomassini R. L., Zurita A. E., Contreras V. H. & Montalvo C. I. 2021. — First phylogenetic analysis of the Miocene armadillo *Vetelia* reveals novel affinities with Tolypeutinae. *Acta Paleontológica Polónica* 66: 2791-2797

Barasoain D., González Ruiz L. R. & Brandoni D. 2022. — About the diversity of Dasypodidae (Xenarthra, Cingulata) along the Late Miocene of northwestern Argentina: The case of the Salicas Formation. *Journal of South American Earth Sciences* 120: 104105. https://doi.org/10.1016/j.jsames.2022.104105

Bonini R. A., Georgieff S. M. &Candela A. M. 2017. — Stratigraphy, geochronology, and paleoenvironments of Miocene - Pliocene boundary of San Fernando, Belén (Catamarca, northwest of Argentina). *Journal of South American Earth Sciences* 79: 459-471. https://doi.org/10.1016/j.jsames.2017.08.020

Bordas A. F. 1932. — Proposición de un nuevo género para *Eutatus inornatus*. *Physis* 11: 167-168.

Bordas A. F. 1933. — Notas sobre los Eutatinae nueva subfamilia extinguida de Dasypodidae. *Anales del Museo Argentino de Ciencias Naturales, Buenos Aires* 37: 583-614.

Bordas A. F. 1935. — Observaciones sobre los géneros «*Scelidodon*» Amegh. y "*Proscelidodon*" n.g. *Physis* 19: 484-491.

Bossi G., Muruaga C., Sanagua J., Hernando A. & Ahumada A. 1993. — *Geología y Estratigrafía de la Cuenca Neógena Santa María-Hualfín (Dptos. Santa María y Belén), Provincia de Catamarca*. XII Congreso Geológico Argentino y II Congreso de Exploración de Hidrocarburos, Mendoza 2: 156-165.

Bossi G. E., Ovejero R. & Strecker M. 1987. — *Correlación entre los perfiles del Terciario superior en la Puerta de Corral Quemado-Hualfín y de Entre Ríos (Chiquimil). Provincia de Catamarca, Argentina*. X Congreso Geológico Argentino, Tucumán 2: 117-120.

Brandoni D., Schmidt G. I., Candela A., Noriega J. I., Brunetto E. & Fiorelli L. E. 2012. — Mammals from the Salicas Formation (Late Miocene), La Rioja Province, northwestern Argentina: Paleobiogeography, age, and paleoenvironment. *Ameghiniana* 49 (3): 375-387. https://doi.org/10.5710/AMGH.v49i3(467)

Brandoni D. & González Ruiz L. R. 2021. — New remains of Glyptodontidae (Mammalia, Xenarthra) from the Salicas Formation (late Miocene, Messinian), La Rioja Province, Argentina. *Journal of South American Earth Sciences*105: 102952. https://doi.org/10.1016/j.jsames.2020.102952

Carlini A. A. & Scillato-Yané G. J. 1996. — *Chorobates recens* (Xenarthra, Dasypodidae) y un análisis de la filogenia de los Euphractini. *Revista del Museo de La Plata* 9: 225-238.

Carlini A. A., Ciancio M. R., Flynn J. J., Scillato-Yané G. J. & Wyss A. R. 2009. — The phylogenetic and biostratigraphic significance of new armadillos (Mammalia, Xenarthra, Dasypodidae, Euphractinae) from the Tinguiririca n (Early Oligocene) of Chile. *Journal of Systematic Palaeontology* 7 (4): 489-503. https://doi.org/10.1017/S1477201908002708

Carlini A. A., Castro M. C., Madden R. H. & Scillato-Yané G. J. 2014. — A new species of Dasypodidae (Xenarthra: Cingulata) from the late Miocene of northwestern South America: implications in the Dasypodini phylogeny and diversity. *Historical Biology* 26 (6): 728-736. https://doi.org/10.1080/08912963.2013.840832

Castellanos A. 1926. — Sobre un nuevo gliptodóntido chapadmalense. "*Urotherium simplex*" y las formas afines. *Anales del Museo Nacional de Historia Natural de Buenos Aires "Bernardino Rivadavia"* 34: 263-278.

Castellanos A. 1931. — Nuevos géneros de gliptodontes en relación con su filogenia. *Physis* 11: 99-100.

Castellanos A. 1947. — Nuevos restos de coraza de los géneros "*Proeuphractus*" y "*Macroeuphractus*" Ameghino descubiertos en el "Araucanense" del Valle de Yocavil (provincias de Catamarca y Tucumán). *Publicaciones del Instituto de Fisiografía y Geología (Facultad de Ciencias Matemáticas, Físico-químicas y Naturales. Universidad Nacional del Litoral)* 32: 1-44.

Castro M. C., Carlini A. A., Sánchez R. & Sánchez-Villagra M. R. 2014. — A new Dasypodini armadillo (Xenarthra: Cingulata) from San Gregorio Formation, Pliocene of Venezuela: affinities and biogeographic interpretations. *Naturwissenschaften* 101: 77-86. https://doi.org/10.1007/s00114-013-1131-5

Cerdeño E. & Schmidt G. I. 2013. — Milk molars or extra premolars in Mesotheriinae (Mesotheriidae, Notoungulata): new insights into an old controversy. *Geobios* 46 (3): 195-202. https://doi.org/10.1016/j.geobios.2012.10.014

Ciancio M. R., Krmpotic C. M., Soibelzon E. & Urrutia J. J. 2006. — Los Dasypodoidea (Mammalia, Xenarthra) de la Formación Lomas de las Tapias, San Juan, Argentina. Implicancias paleobiogeográficas. *Ameghiniana, Suplemento Resúmenes* 43: 4R.

Ciccioli P. L. & Marenssi S. A. 2012. — Paleoambientes sedimentarios de la Formación Toro Negro (Neógeno), antepaís fracturado andino, noroeste argentino. *Andean Geology* 39 (3): 406-440. https://doi.org/10.5027/andgeoV39n3-a04

Ciccioli P. L., Limarino C. O. & Marenssi S. A. 2005. — Nuevas edades radimétricas para la Formación Toro Negro en la Sierra de Los Colorados, Sierras Pampeanas Noroccidentales, provincia de La Rioja. *Revista de la Asociación Geológica Argentina* 60: 251-254.

Ciccioli P. L., Marenssi S. A., Amidon W. H., Limarino C. O. & Kylander-Clark A. 2018. — Alluvial to lacustrine sedimentation in an endorheic basin during the Mio-Pliocene: the Toro Negro Formation, Central Andes of Argentina. *Journal of South American Earth Sciences* 84: 69-87. https://doi.org/10.1016/j.jsames.2018.03.011

Ciccioli P. L., Ré G. H., Amidon W. H., Marenssi S. A. & Limarino C. O. 2020. — Cronología depositacional del Miembro Inferior de la Formación Toro Negro (Mioceno-Plioceno), antepaís andino, La Rioja. *Revista de la Asociación Geológica Argentina* 77: 475-489

Cione A. L. & Tonni E. P. 2005. — Bioestratigrafía basada en mamíferos del Cenozoico superior de la provincia de Buenos Aires, Argentina, *in* de Barrio R. E., Etcheverry R. O., Caballé M. F. & Llambias E. (eds), *Geología y Recursos Minerales de la Provincia de Buenos Aires*. Relatorio del XVI Congreso Geológico Argentino, La Plata: 183-200.

Chiesa J., Bonini R., Colombi C., Brandoni D., Basaez A., Tauber A., Prevosti F. J., Olivares I., Lucero N. & Forasiepi A. M. 2019. — Estratigrafía, paleontología y paleoambientes del Plioceno de la región Cuyo de Argentina (San Luis, Mendoza, San Juan y La Rioja), *in* Nasif N., Esteban G., Chiesa J., Zurita A. & Georgieff S. (eds), *Mioceno al Pleistoceno del Centro y Norte de Argentina*. Opera Lilloana 52: 287-347.

Cohen K. M., Finney S. C., Gibbard P. L. & Fan J. X. 2013. — The ICS international chronostratigraphic chart. *Episodes* 36 (3): 199-204. https://doi.org/10.18814/epiiugs/2013/v36i3/002

Contreras V. H. & Baraldo J. A. 2011. — Calibration of the Chasicoan-Huayquerian stages boundary (Neogene), San Juan, western Argentina, *in* Salfity J. A. & Marquillas R. A. (eds), *Cenozoic Geology of the Central Andes of Argentina*. SCS Publisher, Salta: 111-121.

Contreras V. H., Tomassini R. L., Pérez M. A. & Oliva C. 2013. — *Macrochorobates scalabrinii* (Moreno & Mercerat) (Cingulata, Dasypodidae) en el Mioceno tardío de la provincia de San Juan (Argentina). Implicancias biocronoestratigráficas y paleobiogeográficas. *Revista Brasileira de Paleontologia* 16 (2): 309-318. https://doi.org/10.4072/rbp.2013.2.11

Contreras V. H., Bracco A. I. & Baraldo J. A. 2019. — Estratigrafía, bioestratigrafía y cronología del Mioceno superior de la provincia de San Juan (Argentina), *in* Nasif N., Esteban G., Chiesa J., Zurita A. & Georgieff S. (eds), *Mioceno al Pleistoceno del Centro y Norte de Argentina*. Opera Lilloana 52: 177-206.

Cope E. D. 1889. — The Edentata of North America. *The American Naturalist* 23 (272): 657-664. https://doi.org/10.1086/274985

Croft D. A., Anaya F., Auerbach D., Garzione C. & MacFadden B. J. 2009. — New data on Miocene neotropical provinciality from Cerdas, Bolivia. *Journal of Mammalian Evolution* 16: 175-198. https://doi.org/10.1007/s10914-009-9115-0

Croft D. A., Carlini A. A., Ciancio M. R., Brandoni D., Drew N. E., Engelman R. K. & Anaya F. 2016. — New mammal faunal data from Cerdas, Bolivia, a middle-latitude Neotropical site that chronicles the end of the Middle Miocene Climatic Optimum in South America. *Journal of Vertebrate Paleontology* 36 (5): e1163574. https://doi.org/10.1080/02724634.2016.1163574

De Iuliis G., Ré G. H. & Vizcaíno S. F. 2004. — The Toro Negro Megatheriine (Mammalia, Xenarthra): a new species of *Pyramiodontherium* and a review of *Plesiomegatherium*. *Journal of Vertebrate Paleontology* 24 (1): 214-227. https://doi.org/10.1671/17.1

Delsuc F., Superina M., Tilak M. K., Douzery E. J. & Hassanin A. 2012. — Molecular phylogenetics unveils the ancient evolutionary origins of the enigmatic fairy armadillos. *Molecular Phylogenetics and Evolution* 62 (2): 673-680. https://doi.org/10.1016/j.ympev.2011.11.008

Delsuc F., Gibb G. C., Kuch M., Billet G., Hautier L., Southon J., Rouillard J., Fernicola J. C., Vizcaíno S. F. & MacPhee R. D. E. 2016. — The phylogenetic affinities of the extinct glyptodonts. *Current Biology* 26 (4):141-156. https://doi.org/10.1016/j.cub.2016.01.039

Deschamps C. M. 2005. — Late Cenozoic mammal bio-chronostratigraphy in southwestern Buenos Aires province, Argentina. *Ameghiniana* 42: 733-750.

Engelmann G. F. 1985. — The Phylogeny of the Xenarthra, *in* Montgomery G. G. (ed.), *Ecology of Armadillos, Sloths, and Vermilinguas*. Smithsonian Institution Press, Washington and London: 51-64.

Ercoli M. D., Álvarez A., Verzi D. H., Ulberich J. P. V., Quiñones S. I., Constantini O. E. & Zurita A. E. 2021. — A new mammalian assemblage for Guanaco Formation (northwestern Argentina), and the description of a new genus of New World porcupine. *Journal of South American Earth Sciences* 110: 103389. https://doi.org/10.1016/j.jsames.2021.103389

Esteban G. I. & Nasif N. L. 1996. — Nuevos Dasypodidae (Mammalia, Xenarthra) del Mioceno tardío del Valle del Cajón, Catamarca, Argentina. *Ameghiniana* 33 (3): 327-334.

Esteban G. I., Nasif N. L. & Montalvo C. I. 2001. — Nuevos registros de Dasypodidae (Xenarthra) del Mioceno tardío de la provincia de La Pampa, Argentina. *Revista Española de Paleontología* 16 (1): 77-87.

Esteban G., Nasif N. & Georgieff S. 2014. — Cronobioestratigrafía del Mioceno tardío - Plioceno temprano, Puerta de Corral Quemado y Villavil, provincia de Catamarca, Argentina. *Acta Geológica Lilloana* 26 (2): 165-192.

Esteban G., Georgieff S. M., Nasif N., Ibánez L. & Bonini R. 2019. — Marco estratigráfico, paleontología de vertebrados y paleoambientes del Plioceno de Catamarca, Tucumán y Santiago del Estero, Argentina, *in* Nasif N., Esteban G., Chiesa J., Zurita A. & Georgieff S. (eds), *Mioceno al Pleistoceno del Centro y Norte de Argentina*. *Opera Lilloana* 52 (11): 348-366.

FEIJÓ A., VILELA J. F., CHENG J., SCHETINO M. A. A., COIMBRA R. T., BONVICINO C. R., SANTOS F. R., PATTERSON B. D. & CORDEIRO-ESTRELA P. 2019. — Phylogeny and molecular species delimitation of long-nosed armadillos (*Dasypus*: Cingulata) supports morphology-based taxonomy. *Zoological Journal of the Linnean Society* 186 (3): 813-825. https://doi.org/10.1093/zoolinnean/zly091

FENG X., ANACLETO T. C. S. & PAPEŞ M. 2017. — Climatic similarity of extant and extinct *Dasypus* armadillos. *Journal of Mammalian Evolution* 24: 193-206. https://doi.org/10.1007/s10914-016-9336-y

FERNICOLA J. C. & VIZCAÍNO S. F. 2019. — Cingulates (Mammalia, Xenarthra) of the Santa Cruz Formation (Early-Middle Miocene) from the río Santa Cruz, Argentine, Patagonia. *Publicación Electrónica de la Asociación Paleontológica Argentina* 19 (2): 85-101. https://doi.org/10.5710/PEAPA.14.10.2019.291

GARDNER A. L. 2005. — Order Cingulata, *in* WILSON D. E. & REEDER D. M. (eds), *Mammal Species of the World: A Taxonomic and Geographic Reference*. The Johns Hopkins University Press, Baltimore: 94-99.

GAUDIN T. J. & CROFT D. A. 2015. — Paleogene Xenarthra and the evolution of South American mammals. *Journal of Mammalogy* 96 (4): 622-634. https://doi.org/10.1093/jmammal/gyv073

GAUDIN T. J. & WIBLE J. R. 2006. — The phylogeny of living and extinct armadillos (Mammalia, Xenarthra, Cingulata): a craniodental analysis, *in* CARRANO M. T., GAUDIN T. J., BLOB R. W. & WIBLE J. R. (eds), *Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds and Reptiles*. University of Chicago Press, Chicago: 153-198.

GEORGIEFF S., HERBST R., ESTEBAN G. & NASIF N. 2004. — Análisis paleoambiental y registro paleontólogico de la Formación Desencuentro (Mioceno superior), Alto de San Nicolás, La Rioja, Argentina. *Ameghiniana* 41 (1): 45-56.

GIBB G. C., CONDAMINE F. L., KUCH M., ENK J., MORAES-BARROS N., SUPERINA M., POINAR H. N. & DELSUC F. 2016. — Shotgun Mitogenomics Provides a Reference Phylogenetic Framework and Timescale for Living Xenarthrans. *Molecular Biology and Evolution* 33 (3): 621-642. https://doi.org/10.1093/molbev/msv250

GOIN F. J., MONTALVO C. I. & VISCONTI G. 2000. — Los marsupiales (Mammalia) del Mioceno superior de la Formación Cerro Azul (Provincia de La Pampa, Argentina). *Estudios Geológicos* 56: 101-126. https://doi.org/10.3989/egeol.00561-2158

GONZÁLEZ-RUIZ L. R., ZURITA A. E, SCILLATO-YANÉ G. J., ZAMORANO M. & TEJEDOR M. F. 2011. — Un nuevo Glyptodontidae (Mammalia, Xenarthra, Cingulata) del Mioceno de Patagonia (Argentina) y comentarios acerca de la sistemática de los gliptodontes del SALMA "Friasense". *Revista Mexicana de Ciencias Geológicas* 28: 566-579.

GONZÁLEZ-RUIZ L. R., GÓIS F., CIANCIO M. R. & SCILLATO-YANÉ G. J. 2013. — Los Peltephilidae (Mammalia, Xenarthra) de La Formación Collón Curá (SALMA Colloncurense, Mioceno Medio), Argentina. *Revista Brasileira de Paleontologia* 16 (2): 319-330. https://doi.org/10.4072/rbp.2013.2.12

GONZÁLEZ-RUIZ L. R., GÓIS F., SCILLATO-YANÉ G. J., OLIVA C., CONTRERAS V. & ESTEBAN G. 2014. — *New records of* Vetelia *Ameghino (Mammalia, Xenarthra, Dasypodidae) in the Miocene of Argentina: anatomical and paleogeographic implications*. 74th International Palaentological Congress, Mendoza: 722.

GONZÁLEZ-RUIZ L. R., REATO A., CANO M. & MARTÍNEZ O. 2017. — Old and new specimens of a poorly known glyptodont from Patagonia and their biochronological implications. *Acta Palaeontologica Polonica* 62 (1): 181-194. https://doi.org/10.4202/app.00280.2016

GRAY J. E. 1821. — On the natural arrangement of vertebrose animal. *London Medical Repository* 15: 296-310.

GRAY J. E. 1865. — Revision of the genera and species of entomophagous Edentata, founded on the examination of the specimens in the British Museum. *Proceedings of the Zoological Society of London* 33 (1): 359-386. https://doi.org/10.1111/j.1469-7998.1865.tb02351.x

GRAY J. E. 1873. — *Hand-list on the Edentata, Pachydermata and Ruminantia in the British Museum*. British Museum (Natural History), London, 174 p.

HOLMES W. W. & SIMPSON G. G. 1931. — Pleistocene exploration and fossil Edentates in Florida. *Bulletin of the American Museum of Natural History* 59 (7): 383-418. http://hdl.handle.net/2246/347

ILLIGER C. 1811. — *Prodromus Systematis Mammalium et Avium; Additis Terminis Zoographicis Utriusque Classis, Eorumque Versione Germanica*. C. Salfeld, Berlin: xviii + 302 p.

INTERNATIONAL COMMISSION ON STRATIGRAPHIC 2022. — *International Chronostratigraphic Chart*. Available at the following address: www.stratigraphy.org

KERR R. 1792. — *The Animal Kingdom or Zoological System, of the Celebrated Sir Charles Linnaeus. Class I. Mammalia A*. Edinburgh Press, Edinburgh, 400 p.

KRAGLIEVICH L. 1927. — Nota preliminar sobre nuevos géneros y especies de la fauna argentina. *Physis* 8: 591-598.

KRAGLIEVICH J. L. 1934. — *La antigüedad Plioceno de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que le precedieron y sucedieron*. Imprenta El Siglo Ilustrado, Montevideo, 136 p.

KRAPOVICKAS V., CICCIOLI P. L., MÁNGANO M. G., MARSICANO C. A. & LIMARINO C. O. 2009. — Paleobiology and paleoecology of an arid-semiarid Miocene South American ichnofauna in anastomosed fluvial deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology* 284 (3-4): 129-152. https://doi.org/10.1016/j.palaeo.2009.09.015

KRAPOVICKAS V. & NASIF N. L. 2011. — Ichnologic evidence of dinomyids (Rodentia: Caviomorpha) in the Late Oligocene Vinchina Formation, Argentina. *Paleontología Electrónica* (SVP) 14.2.12A: 1-13

KRMPOTIC C. M., CIANCIO M. R., BARBEITO C., MARIO R. C. & CARLINI A. A. 2009. — Osteoderm morphology in recent and fossil euphractine xenarthrans. *Acta Zoologica* 90 (4): 339-351. https://doi.org/10.1111/j.1463-6395.2008.00359.x

LINNAEUS C. 1758. — *Systema Naturae*. 10e edition. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, v. 1: Regnum animale*. Laurentius Salvius, Stockholm: 10 i-ii + 1-824.

LOOMIS F. B. 1914. — *The Deseado Formation of Patagonia*. The Rumford Press, Concord, New Hampshire, 232 p.

LUNA C. A. & KRAPOVICKAS J. M. 2011. — Primer registro de un ejemplar juvenil de *Glyptodon* sp. (Cingulata, Glyptodontidae) del Cuaternario de la provincia de Córdoba, Argentina. *Mastozoología Neotropical* 18: 135-141.

LUNA C. A., CERDA I. A., ZURITA A. E., GONZÁLEZ R., PRIETO M. C., MOTHÉ D. & AVILLA L. S. 2018. — Distinguishing Quaternary glyptodontine cingulates in South America: how informative are juvenile specimens?. *Acta Palaeontologica Polonica* 63 (1): 59-170. https://doi.org/10.4202/app.00409.2017

MARSHALL G. L. & PATTERSON B. 1981. — Geology and geochronology of the mammal-bearing Tertiary of the Valle de Santa María and Río Corral Quemado, Catamarca Province, Argentina. *Fieldiana Geology* 9: 1-80.

MCKENNA M. C. & BELL S. K. 1997. — *Classification of Mammals Above the Species Level*. Columbia University Press, New York, 640 p.

MITCHELL K. J., SCANFERLA A., SOIBELZON E., BONINI R., OCHOA J. & COOPER A. 2016. — Ancient DNA from the extinct South America giant glyptodont *Doedicurus* sp. (Xenarthra: Glyptodontidae) reveals that glyptodonts evolved from armadillos. *Molecular Ecology* 25 (4): 3499-3508. https://doi.org/10.1111/mec.13695

Montalvo C. I., Tomassini R. L., Sostillo R., Cerdeño E., Verzi D. H., Visconti G., Folguera A. & Schmidt G. I. 2019. — A chasicoan (late Miocene) vertebrate assemblage from Cerro Azul Formation, central Argentina. Geomorphological and biochronological considerations. *Journal of South American Earth Sciences* 95: 102218. https://doi.org/10.1016/j.jsames.2019.102218

Moreno F. P. & Mercerat A. 1891. — Exploración arqueológica de la Provincia de Catamarca: paleontología. *Revista del Museo de La Plata* 1: 222-236.

Nasif N., Esteban G., Georgieff S. M., Ibáñez L. & Spagnuolo C. M. 2019. — Biocronoestratigrafía y paleoambientes del Mioceno tardío de Catamarca, Tucumán y Santiago del Estero, Argentina, *in* Nasif N., Esteban G., Chiesa J., Zurita A. & Georgieff S. (eds), *Mioceno al Pleistoceno del Centro y Norte de Argentina*. *Opera Lilloana* 52: 229-3250.

Noriega J. I., Jordan E. A., Vezzosi R. I. & Areta J. I. 2017. — A new species of *Opisthodactylus* Ameghino, 1891 (Aves, Rheidae), from the late Miocene of northwestern Argentina, with implications for the paleobiogeography and phylogeny of rheas. *Journal of Vertebrate Paleontology* 37 (1): e1278005. https://doi.org/10.1080/02724634.2017.1278005

Oliveira É. V. & Bergqvist L. P. 1998. — A new Paleocene armadillo (Mammalia, Dasypodoidea) from the Itaboraí basin, Brazil. *Publicación Electrónica de la Asociación Paleontológica Argentina* 5: 35-40.

Ortega E. J. H. 1963. — Dos nuevos Caviidae de la region de Chapadmalal. Datos complementarios a las diagnosis de otros Caviinae poco conocidos. *Ameghiniana* 3: 21-28.

Perea D. & Scillato-Yané G. J. 1995. — *Proephractus limpidus* Ameghino, 1886 (Xenarthra, Dasypodidae, Euphractini): Osteología comparada del cráneo y elementos de la coraza asociados (Neógeno del Uruguay). *Boletín de la Real Sociedad Española de Historia Natural, Sección geológica* 90: 125-130.

Pocock R. I. 1924. — The external characters of the South American edentates. *Proceedings of the Zoological Society of London* 94 (4): 983-1031. https://doi.org/10.1111/j.1096-3642.1924.tb03325.x

Quiñones S. I., Miño-Boilini A. R, Zurita A. E., Contreras S. A., Luna C. A., Candela A. M., Camacho M., Ercoli M. D., Solís N. & Brandoni D. 2019. — New records of Neogene Xenarthra (Mammalia) from eastern Puna (Argentina): diversity and biochronology. *Journal of Paleontology* 93: 1258-1275. https://doi.org/10.1017/jpa.2019.64

Ramos V. A. 1970. — Estratigrafía y estructura del Terciario en la Sierra de los Colorados (Provincia de La Rioja), República Argentina. *Revista de la Asociación Geológica Argentina* 25: 359-382.

Ramos V. A. 1999. — Los depósitos sinorogénicos terciarios de la región andina. *Geología Argentina* 29: 651-682.

Ré G., Jordan T. E. & Kelley S. 2003. — Cronología y paleogeografía del Terciario de la cuenca intermontana de Iglesia septentrional, Andes de San Juan, Argentina. *Revista Asociación Geológica Argentina* 58 (1): 31-48.

Redford K. H. & Wetzel R. M. 1985. — Euphractus sexcinctus. *Mammalian Species* 252: 1-4

Reguero M. A. & Candela A. M. 2011. — Late Cenozoic mammals from the Northwest of Argentina, *in* Salfity J. A. & Marquillas R. A. (eds), *Cenozoic Geology of the Central Andes of Argentina*. SCS Publisher, Salta: 411-426.

Reig O. A. 1958. — Notas para una actualización del conocimiento de la fauna de la Formación Chapadmalal. I. Lista faunística preliminar. *Acta Geológica Lilloana* 11: 241-253.

Reynolds J. H. 1987. — *Chronology of Neogene Tectonics in the Central Andean (27º - 33ºS) of Western Argentina, Based on the Magnetic Polarity Stratigraphy of Foreland Basin Sediments*. PhD Thesis, Dartmouth College, 353 p.

Rodríguez Brizuela R. & Tauber A. 2006. — Estratigrafía y mamíferos fósiles de la Formación Toro Negro (Neógeno), Departamento Vinchina, noreste de la provincia de La Rioja. *Ameghiniana* 43: 257-272.

Roth S. 1911. — Un nuevo género de la familia Megatheriidae. *Revista del Museo de La Plata* 18: 7-21.

Rovereto C. 1914. — Los estratos araucanos y sus fósiles. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 25: 1-250.

Scillato-Yané G. J. 1975. — Nuevo género de Dasypodidae (Edentata, Xenarthra) del Plioceno de Catamarca (Argentina). Algunas consideraciones filogenéticas y zoogeográficas sobre los Euphractini, *in I Congreso Argentino de Paleontología y Bioestratigrafía, Tucumán 1974*. *Actas* 2: 449-461.

Scillato-Yané G. J. 1977. —Notas sobre los Dasypodidae (Mammalia, Edentata) del Plioceno del territorio argentino I. Los restos de edad Chasiquense (Plioceno inferior) del sur de la Provincia de Buenos Aires. *Ameghiniana* 14: 133-144.

Scillato-Yané G. J. 1980. — *Catálogo de los Dasypodidae fósiles (Mammalia, Edentata) de la República Argentina*. II Congreso Argentino de Paleontología y Bioestratigrafía y I Congreso Latinoamericano de Paleontología, Buenos Aires 1978, Actas: 7-36.

Scillato-Yané G. J. 1982. — *Los Dasypodidae (Mammalia: Edentata) del Plioceno y Pleistoceno de Argentina*. PhD Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 127 p.

Scillato-Yané G. J., Krmpotic C. M. & Esteban G. I. 2010. — Las especies del género *Chasicotatus* Scillato-Yané (Eutatini, Dasypodidae). *Revista Mexicana de Ciencias Geológicas* 27: 43-55.

Scott W. B. 1903. — Mammalia of the Santa Cruz Beds. Volume V, paleontology. Part I, Edentata. 1. Dasypoda, *in* Scott W. B. (ed.), *Reports of the Princeton University Expeditions to Patagonia, 1896-1899*. Princeton University, Stuttgart: 1-106.

Simpson G. G. 1980. — *Splendid Isolation: The Curious History of South American Mammals*. Yale University Press, New Haven: 266 p.

Tabbutt K. D., Naeser Ch. W., Jordan T. E. & Cerveny P. F. 1989. — New fission-track New fission-track ages of Mio-Pliocene tuffs in the Sierras Pampeanas and Precordillera of Argentina. *Revista de la Asociación Geológica Argentina* 44: 408-419.

Tambussi C. P., Degrange F. J., Ciccioli P. L. & Prevosti F. 2021. — Avian remains from the Toro Negro Formation (Neogene), Central Andes of Argentina. *Journal of South American Earth Sciences* 105: 102988. https://doi.org/10.1016/j.jsames.2020.102988

Tauber A. A. 2005. — Mamíferos fósiles y edad de la Formación Salicas (Mioceno tardío) de la sierra de Velasco, La Rioja, Argentina. *Ameghiniana* 42 (2): 443-460.

Tonni E., Scillato-Yané G. J., Cione A. & Carlini A. 1998. — *Bioestratigrafía del Mioceno continental en el curso inferior del Arroyo Chasicó, provincia de Buenos Aires*. Congreso Argentino de Paleontología y Bioestratigrafia, Bahía Blanca: 135.

Turner J. C. M. 1964. — Descripción geológica de la Hoja 15c. Vinchina (Provincia de La Rioja). *Boletín Dirección Nacional de Geología y Minería* 100: 81.

Urrutia J. J., Montalvo C. I. & 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, Deschamps C. M. & Tonni E. P. 2004. — Biostratigraphic and palaeoclimatic meaning of the Middle Pleistocene South American rodent *Ctenomys kraglievichi* (Caviomorpha, Octodontidae). *Palaeogeography, Palaeoclimatology, Palaeoecology* 212 (3-4): 315-329. https://doi.org/10.1016/S0031-0182(04)00328-1

Verzi D. H., Deschamps C. M. & Montalvo C. I. 2008. — Biostratigraphy and biochronology of the Late Miocene of central Argentina: evidence from rodents and taphonomy. *Geobios* 41 (1): 145-155. https://doi.org/10.1016/j.geobios.2006.09.005

Vizcaíno S. F., Fernicola J. C. & Bargo M. S. 2012. — Paleobiology of santacrucian glyptodonts and armadillos (Xenarthra, Cingulata). *in* Vizcaíno S. F., Kay R. F. & Bargo M. S. (eds), *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press, New York: 194-215.

Waterhouse G. R. 1837. — Characters of new species of the genus *Mus*, from the collection of Mr. Darwin. *Proceedings of the Zoological Society of London* 1837: 15-21.

Woodburne M. 2010. — The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. *Journal of Mammalian Evolution* 17: 245-264. https://doi.org/10.1007/s10914-010-9144-8

Zamorano M., Scillato-Yané G., Gonzalez-Ruiz L. R. & Zurita A. E. 2011. — Revisión de los géneros *Nopachtus* Ameghino y *Phlyctaenopyga* Cabrera (Xenarthra, Glyptodontidae, Hoplophorinae) del Mioceno tardío y Plioceno de Argentina. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 13: 59-68.

Zurita A. E., Oliva C., Dondas A., Soibelzon E. & Isla F. I. 2011. — El registro más completo de un Hoplophorini (Xenarthra: Glyptodontidae) para los Pisos/Edades Chapadmalalense-Marplatense (Plioceno tardío-Pleistoceno temprano). *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 13: 69-75.

Zurita A. E., Camacho M., Miño-Boilini A. R., Candela A. M., Cuadrelli F., Krmpotic C. M. & Solís N. 2017. — Xenarthra (Mammalia) from a new late Neogene fossiliferous locality in northwestern Argentina. *Journal of South American Earth Sciences* 80: 229-236. https://doi.org/10.1016/j.jsames.2017.09.023

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