



## New, Late Miocene mammalian assemblage from the Palo Pintado Formation (Northwestern Argentina)

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### ABSTRACT

A new mammalian assemblage from the Late Miocene Palo Pintado Formation in Northwestern Argentina is described. Specimens were exhumed from the lower levels of the unit cropping out at Tonco Valley, Salta Province. The association includes representatives of seven families and three orders: Cingulata (*Macrochorobates*, *Vetelia*, Euphractini gen et sp. indet. a and b), Notoungulata (*Paedotherium*, *Protyotherium*, *Typotheriopsis*), and Rodentia (Caviidae gen et sp. indet. a and b, *Procardiomys*, *Protibrocoma*, *Prolagostomus*, *Lagostomus*). This assemblage, together with stratigraphical information, suggests a Late Miocene age, probably intermediate between Chasicoan and Huayquerian SALMAs for the fossiliferous levels of the Palo Pintado Formation in Tonco Valley. Paleoeological data discernible from the faunal association suggest grassland and marsh communities that developed in the flood-plain setting under a seasonal climate with a conspicuous dry season.

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### 1. Introduction

South American Neogene mammalian assemblages were traditionally known from middle to high latitudes of Argentina (see, e.g., Marshall et al., 1983). Actually, these faunas were the basis of South American biochronology (Pascual et al., 1965, 1966; Marshall et al., 1983) and biostratigraphy (Cione and Tonni, 1995). In recent decades new localities have been discovered in mid-to low latitudes of South America: Northwestern Argentina (Candela et al., 2013; Ortiz et al., 2012; Reguero et al., 2014); Chile (Croft et al., 2004; Croft and Anaya, 2006); Bolivia (Croft et al., 2009, 2011); Perú (Antoine et al., 2016); Brasil (Cozzuol, 2006; Negri et al., 2010); Colombia (Madden et al., 1997) and Venezuela (Sánchez-Villagra et al., 2010). These non-traditional mammalian associations offered new insights on the mammalian evolution in South America and pointed out the necessity to focus the sampling effort in tropical and subtropical latitudes.

The fossiliferous Neogene units of NW Argentina are singular because they include faunal sequences covering several taxonomic groups and recording important biotic events such as the Great American Biotic Interchange and its previous times (Woodburne, 2010; Cione et al., 2015). These mammal-bearing units have been well-studied in three provinces: La Rioja (Toro Negro Fm.), Catamarca (Chiquimil, Corral Quemado and Andalhuala formations), and Jujuy (Maimará and Uquía formations; Butler et al., 1984; Rodríguez-Brizuela and Tauber, 2006; Reguero and Candela, 2008). In Salta

Province, the Payogastilla (Díaz and Malizzia, 1983) and Orán (Russo, 1972) groups cover much of the Neogene and are widely distributed throughout the province. The Palo Pintado Fm. comprises thick deposits of fluvial sediments that crop out in the Calchaquíes Valleys (Fig. 1a).

From a stratigraphical standpoint, this unit is included in the Payogastilla Group which is composed, from bottom to top, by the Quebrada de los Colorados, Angastaco, Palo Pintado and San Felipe formations.

The paleontological content of the Palo Pintado Fm. is extensively mentioned in the literature. Several plant remains were recorded in the basal and medial levels including leaves (Herbst et al., 1987; Anzótegui, 1998, 2006), fruits (Anzótegui et al., 2007a,b), wood (Lutz and Martínez, 2007) and palynomorphs (Anzótegui and Cuadrado, 1996; Acevedo et al., 1997, 1998; Horn, 2014). Invertebrates are represented by bivalves (Morton, 1992; Herbst et al., 2000) and gastropods (Galli et al., 2011). Vertebrates are typified by fishes and turtle scutes (Díaz, 1985, 1987), cranial and postcranial elements of amphibians (Fabrezi et al. in prep) and mandibular remains of caimans (Bona et al., 2014). In the case of mammals, the first reference was made by Starck and Vergani (1996) who reported glyptodontid and toxodontid remains. Posteriorly, Reguero et al. (2014) reported the presence of the pachyrukhine *Paedotherium kakai*. Recently, Armella et al. (2016) reported four dasypodid xenarthrans (*Macroeuphractus*, *Chorobates*, *Chasicotatus*, and *Paraeuphractus*) and a toxodontid notoungulate (*Andinotoxodon*).

In this contribution, we describe the mammalian remains collected by our team in several field expeditions to Tonco Valley in 2014–2016. The aim of this paper is to give a compressive report of the

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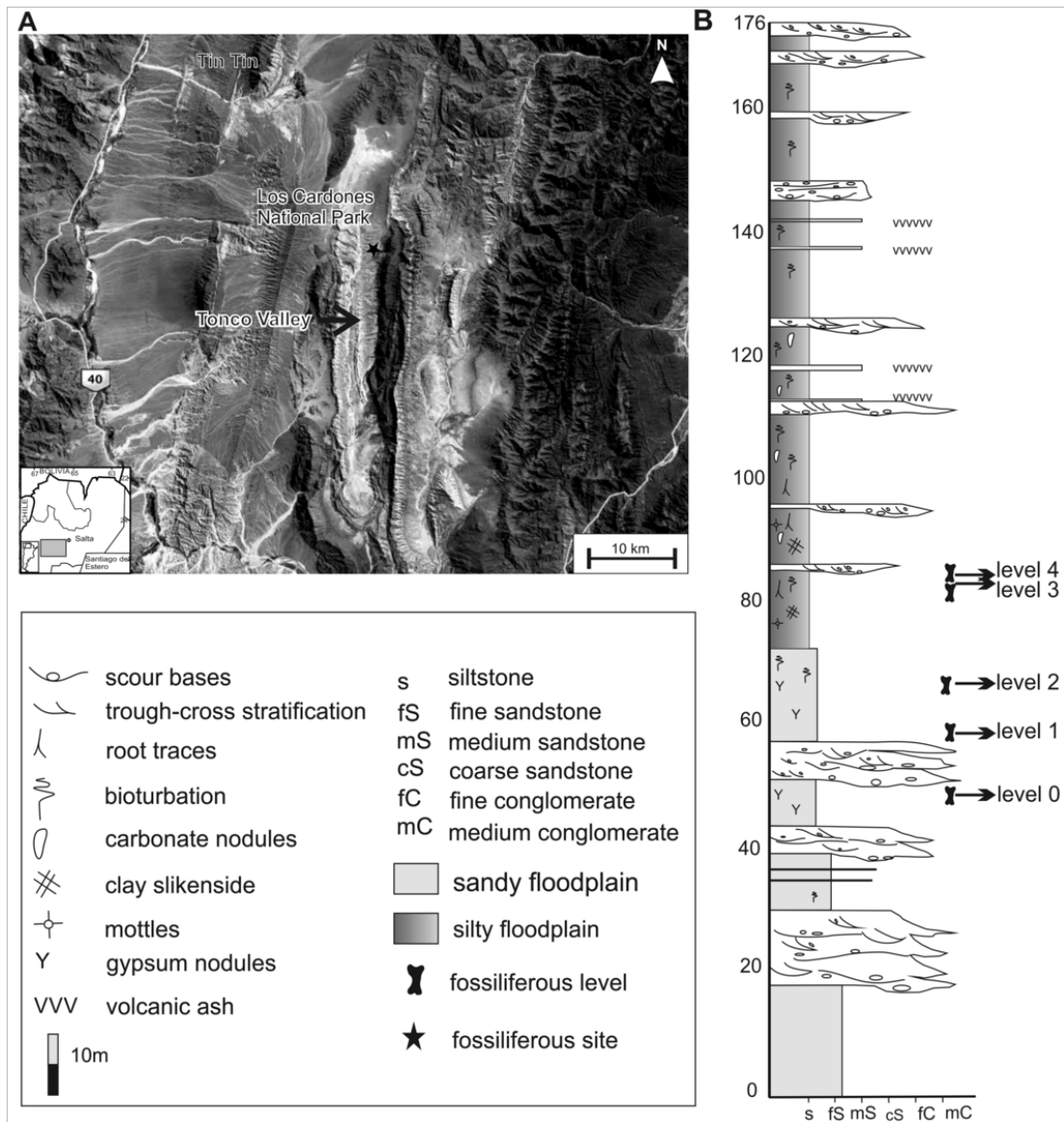


Fig. 1. A. Satelital image showing the location of the study area in Argentina. B. Sedimentary log of the Palo Pintado Formation in the Tonco Valley with the location of the fossiliferous levels mentioned in the text.

mammalian assemblage of the Palo Pintado Fm. at Tonco Valley with comments on its biochronological importance and the paleoenvironmental conditions developed during the late Miocene in the Central Andes.

2. Materials and methods

The fossil specimens described below are housed in the Vertebrate Paleontology collections of the Instituto de Bio y Geociencias del NOA (IBIGEO-CONICET), Salta Province, Argentina. Measurements were made to the nearest 0–1 mm using a digital caliper. In the descriptions, upper tooth loci are indicated by upper-case letters (e.g. I1, P2, M1) and lower tooth loci by lower-case letters (e.g. i1, p2, m1). The terminology adopted for Cingulata osteoderms follows Krmpotic et al. (2009). Dental terminology for Notoungulata follows Cerdeño and Montalvo (2001) and Reguero et al. (2014). The dental and mandibular terminology for caviomorph rodents follows Pérez

et al. (2014) and Croft et al. (2011). Biochronologic terms and concepts used in the text follow Woodburne (2004).

2.1. Anatomical abbreviations

**al**, anterior lobe; **ap**, anterior projection; **c**, cement; **cap**, caudal portion; **cf**, central figure; **crp**, cranial portion; **esf**, external surface foramina; **hfe**, fundamental external flexid; **hsi**, Secondary internal flexid; **hpi**, Primary internal flexid; **L**, total length; **Lal**, length of the anterior lobe; **Lpl**, length of the posterior lobe; **pef**, peripheral figure; **pf**, piliferous foramina; **pl**, posterior lobe; **td**, transverse depression; **W**, total width; **Wpl**, width of the posterior lobe.

2.2. Biochronologic abbreviations and definitions

**Ma**, Megannum; one million years in the radioisotopic time scale (e.g., 10 Ma refers to the ten million year point on the time scale).

**Mammal Ages**, biochronologic units that make up the basic chronologic system used to describe the age and succession of events in mammalian evolution (Woodburne, 2004). Mammal ages are typically assemblage chrons, although some have been interval chrons or lineage chrons. When mammal ages are defined on the base of immigrant taxa, their limits are the first appearance datum of such taxa (see Woodburne, 2004). **SALMAs**, South American Land Mammal Age; see Pascual et al. (1965), Simpson (1971), Patterson and Pascual (1972), Marshall et al. (1983).

### 3. Geology and stratigraphy

The Tonco Valley is located some 150 km southwest of Salta City (Fig. 1). The northern end of this valley is included within the protected area known as Parque Nacional Los Cardones. We worked on several creeks located at 25°22'24.55"S and 65°54'55.33"W (Fig. 1a).

The mammalian remains described here come from the lower section of the Palo Pintado Fm. (Fig. 1b). In the Tonco Valley, this unit has a partial thickness of 176 m, the basal contact is transitional with the Angastaco Formation and the upper contact is an erosional unconformity with Quaternary sediments. It consists of fine to medium conglomerate and fine-grained sandstone to siltstone strata (Fig. 1b). The conglomeratic levels form lenticular to shallow lenticular beds with normal grading and trough – cross stratification suggesting high energy shallow channels. On the other hand, the fine-grained sediments consist of light brown siltstones to sandy siltstones with mottles, millimeter-scale nodules of gypsum and carbonate, bioturbation features, sporadically interbedded thin layers of medium-coarse sandstones.

The characteristics of the sedimentary deposits suggest an anastomosing fluvial system in which the main channels scours through thick cohesive floodplain (Díaz, 1985, 1987; del Papa et al. in prep.).

Fossiliferous levels numbered 0, 1, 2, and 3 located within the fine-grained floodplain setting. From level 0 to 3, all findings were made on flooding plains, and each deposit has an average thickness of 4 m. Level 4 corresponds to a high lenticular conglomeritic channel deposit immediately above level 3 (Fig. 1b).

The age of the Palo Pintado Fm. is constrained between  $8.8 \pm 0.5$  Ma (Carrapa et al., 2012) and  $5.27 \pm 0.28$  Ma (U/Pb, zircon) (Coutand et al., 2006) based on dating volcanic ashes from the base and top of this formation.

### 4. Systematic paleontology

Order Cingulata Illiger, 1811.

Family Dasypodidae Bonaparte, 1838.

Subfamily Euphractinae Pocock, 1924.

Tribe Euphractini Simpson, 1945.

Genus *Macrochorobates* Scillato-Yané, 1980.

*Macrochorobates* sp.

(Fig. 2a–b).

**Referred material.** IBIGEO-P33, an almost complete fixed osteoderm; IBIGEO-P37, a fragmentary movable osteoderm.

**Measurements.** IBIGEO-P 33,  $16.4 \times 13.3$  mm.

**Occurrence.** Level 2.

**Description.** The ornamentation of the fixed osteoderm is composed by a central figure highly elevated and deviated to the external margin. It is surrounded by eight peripheral and inflated figures. External surface foramina are visible at the intersection between the lateral and longitudinal sulci. Two piliferous foramina can be observed along the posterior margin on each side of the central figure. The preserved portion of the movable osteoderm shows an obliquely oriented

central figure that is triangular in section and progressively elevated toward the posterior margin.

**Comments.** The morphology of the Palo Pintado specimens is similar to that of *M. scalabrini* but smaller in size. Additionally, the fragmentary movable osteoderm has the distal portion with a notably elevated central figure that had been mentioned for *M. chapalmalensis* (Scillato Yané, 1982).

Genus *Vetelia* Ameghino 1891.

*Vetelia* cf. *V. gandhii* Esteban and Nasif 1996.

(Fig. 2c–e).

**Referred material.** IBIGEO-P40, 14 complete fixed osteoderms, two complete movable osteoderms, several fragments of fixed and movable osteoderms and postcranial elements belonging to the same individual (not described here).

**Measurements.** Largest movable osteoderm,  $38.7 \times 16.5$  mm; largest fixed osteoderm,  $26.6 \times 20$  mm.

**Occurrence.** Level 0.

**Description.** Large euphractine; Fixed osteoderms are quadrangular, sub-pentagonal to sub-hexagonal in shape with the ornamentation formed by a central lageniform figure surrounded and completely enclosed by three to six inflated peripheral figures. All figures are convex and delimited by sulci. These sulci are softly defined in some osteoderms in which the central and peripheral figures are less delimited. The central figure is elongated, non-elevated with respect to the lateral ones; it occupies the posterior two-thirds of the osteoderm and is slightly oriented towards the postero-lateral corner of the osteoderm. Four small peripheral figures are located anterior and lateral to the central figure, while two elongated peripheral figures are located postero-lateral to it. Several small foramina of the external surface are placed at the intersection of the external border and the lateral sulci. Piliferous foramina are located at the intersection between the radial sulci and the outer contour and in the posterior edge of the osteoderms. One fixed osteoderm corresponds to the margin of the dorsal shield and has a distal conical prominence (Fig. 2c). Movable osteoderms have cranial and caudal portions separated by a transverse depression. This depression is punctured by numerous small foramina and lack crenulations. The cranial portion is elevated and key-shaped. It occupies slightly more than one-third of the total length of the osteoderms, lacks ornamentation but bears numerous and very small foramina. The caudal portion is ornamented by an elongated central figure with two single peripheral figures. The central figure is directed to the postero-lateral end as in fixed osteoderms. Small external surface foramina are placed in the sulci at the anterior end of the caudal portion. One noticeable piliferous foramen is found at the end of the central figure and a few smaller ones, on the posterior edge of the osteoderm.

**Comments.** The genus *Vetelia* is characterized by its large size, movable osteoderms with elongated central figure and undivided peripheral figures, fixed osteoderms with a sub-elliptic central figure, enclosed by three to six peripheral figures with one to three piliferous foramina and small foramina at the corner of the sulci. The specimen IBIGEO-P40 is similar to *V. gandhii* in that the peripheral figures of fixed osteoderms are elevated respect to the central one. Additionally, the conical prominence of the marginal osteoderm is a feature previously mentioned for *V. gandhii* (Esteban and Nasif, 1996).

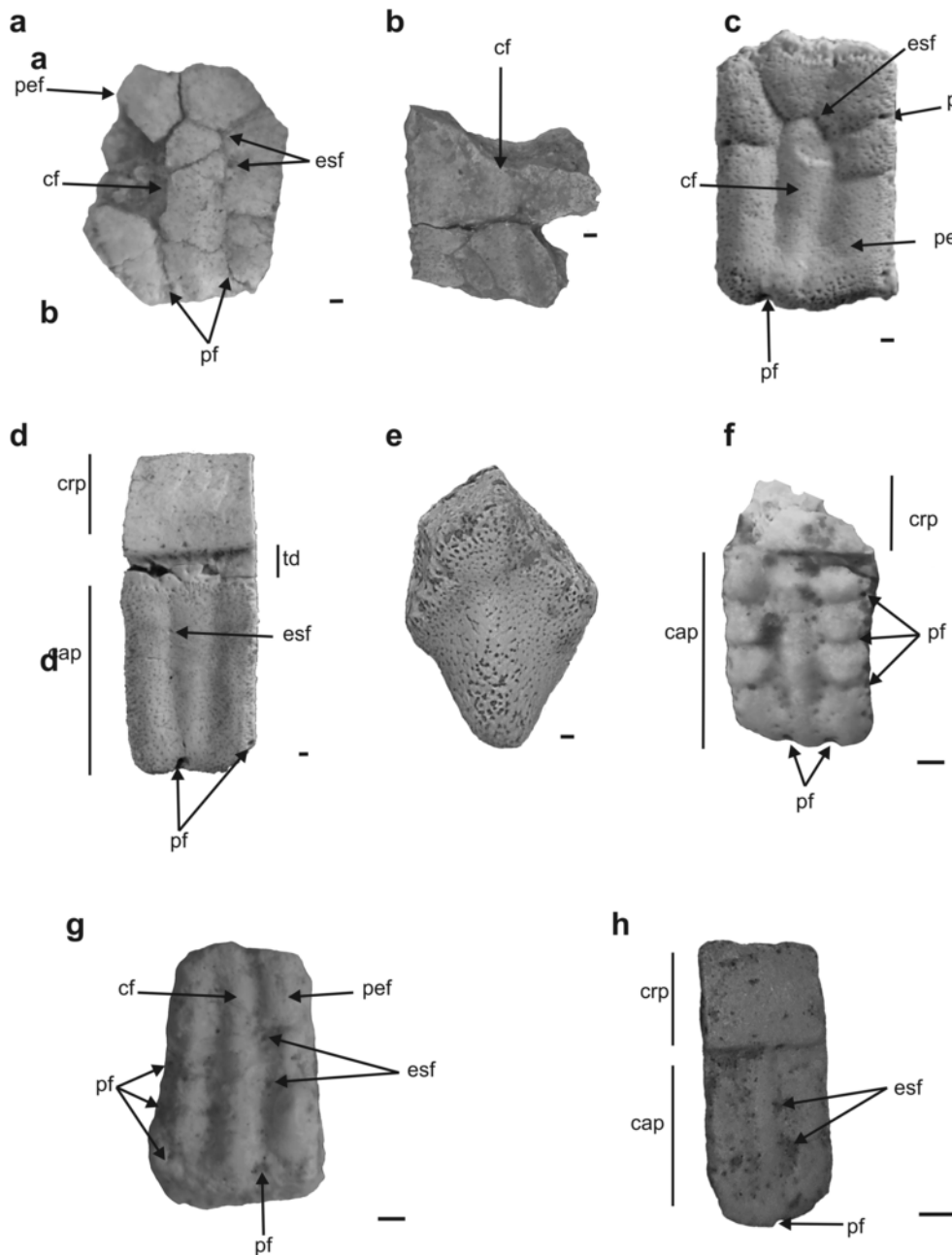
Gen et sp. indet A.

(Fig. 2f).

**Referred material.** IBIGEO-P34, a fragmentary movable osteoderm.

**Measurements.** ca.  $10.1 \times 6.2$  mm.

**Occurrence.** Level 3.



**Fig. 2.** Dasypodidae. *Macrochorobates* sp. **a.** IBIGEO-P33, **b.** IBIGEO-P37; **c.** *Vetelia* cf. *V. gandhi* IBIGEO-P40, Fixed osteoderm, **d.** Movable osteoderm, **e.** conical osteoderm from the margin of carapace; **f.** Euphractini gen et sp indet. A IBIGEO-P34; **g.** Euphractini gen et sp B. IBIGEO-P38; **h.** Euphractini gen et sp. indet C. Scale: 1 mm.

**Description.** The osteoderm has its cranial portion broken. There is a relatively narrow and straight-sided primary figure separated by deep sulci from eight peripheral figures. Two conspicuous piliferous foramina are distinguishable on the distal edge of the osteoderm, and several external surface foramina are located in the intersections of longitudinal and transverse sulci.

**Comments.** The morphology of the osteoderm resembles that of *Prozaedyus* in the distribution and number of foramina.

Gen. et sp. indet. B.

(Fig. 2g).

**Referred material.** IBIGEO-P 38, a caudal portion of a movable osteoderm.

**Measurements.**  $6.4 \times 4.1$  mm.

**Occurrence.** Level 3.

**Description.** The specimen IBIGEO-P38 has some degree of abrasion. The preserved caudal portion shows a main straight sided figure separated from at least six peripheral figures by deep sulci. There are two piliferous foramina along the posterior edge.

Gen. et sp. indet. C.

(Fig. 2h).

**Referred material.** IBIGEO-P 36, a complete movable osteoderm.

**Measurements.**  $6.1 \times 4.15$  mm.

**Occurrence.** Level 3.

**Description.** The specimen IBIGEO-P36 has a relatively smooth surface with a key-shaped cranial portion. The caudal portion has a main rectangular central figure separated from the peripheral ones by

subtle sulci. There is no transverse depression between cranial and caudal portions.

Order Notoungulata Roth, 1903.

Suborder Typotheria Zittel, 1893 (sensu Reguero and Castro, 2004).

Family Hegetotheriidae Ameghino, 1894.

Subfamily Pachyruchinae Kraglievich, 1934.

Genus *Paedotherium* Burmeister, 1888.

*Paedotherium minor* Cabrera, 1937.

(Fig. 3a–c).

**Referred material.** IBIGEO-P 19, partial left dentary with m3; IBIGEO-P20, partial right dentary with alveolar portion of p4 and complete m1-m2; IBIGEO-P21, partial left dentary with p4; IBIGEO-P22, partial left dentary with p4.

**Measurements.** IBIGEO-P 19,  $5.4 \times 2.15$  mm; IBIGEO-P20 p4,  $4.3 \times 2.36^*$  mm; m1,  $4.48 \times 2.32$  mm; m2,  $4.35 \times 2.36$  mm; IBIGEO-P21,  $4.2 \times 2.3$  mm; IBIGEO-P22,  $3.95 \times 2.109$  mm.

**Occurrence.** Level 3.

**Description.** Large pachyruchine with bilobed p4-m2 and trilobed m3. The p4 has a simple morphology with a convex lingual face, a rounded anterior lobe and a wider and triangular posterior one. The sulcus dividing the trigonid from talonid is very deep in IBIGEO-P20 in which its junction overpasses the middle of the tooth and forming an acute angle in its lingual end. In IBIGEO-P21 and IBIGEO-P22 is less pronounced reaching the middle of the tooth. Molars increase in size posteriorly. The m1-2 are similar in morphology with a sub-rounded anterior lobe separated from the posterior one by a deep sulcus. The lingual face of both molars is slightly convex. The m3 is trilobed; it has a deep labial sulcus separating the trigonid and talonid, and a shallower one dividing the talonid into two equal halves. The middle lobe of m3 is triangular in shape. The lingual face of the tooth has two flexids, one at the middle of the trigonid and the other at the middle of the talonid. Cement is visible on the labial side of molar of several specimens.

**Comments.** We assigned all specimen to *Paedotherium minor* mainly on the base of morphological similarities of teeth. However, some difference in the robustness of the dentary could be observable, being the specimens IBIGEO-P19 and IBIGEO-P22 more gracile than IBIGEO-P20 and IBIGEO-P21, but this must be corroborated with the future collection of additional and less fragmentary material.

Family Intertheriidae Ameghino, 1887.

Subfamily Intertheriinae Ameghino, 1887.

Genus *Protyotherium* Ameghino 1882.

*Protyotherium minutum* Cabrera and Kraglievich, 1931.

(Fig. 3d).

**Referred material.** IBIGEO-P39, partial left dentary with p4-m3.

**Measurements.** p4,  $4.1 \times 2.95$  mm; m1,  $6.16 \times 3.2$  mm; m2,  $6.14 \times 3.24$  mm; m3,  $7.27 \times 3.01$  mm.

**Occurrence.** Level 1.

**Description.** In overall morphology, the specimen IBIGEO-P39 resembles the remaining species of the genus. The teeth are hypsodont and imbricated. The p4-m2 are bilobed, and the m3 is trilobed. The posterior lobe of p4 is minute and located posterolingually; it is separated from the anterior lobe by a shallow sulcus. Two subtle flexi are visible on the lingual face of p4. The m1-2 are similar in shape and size. The anterior and posterior lobes are heart-shaped and separated by deep labial sulci. The lingual face of both teeth has two flexi at the middle of the trigonid and talonid. The m3 is trilobed. The trigonid is separated from the talonid by a deep labial sulcus. The talonid is divided into two halves by a notable sulcus but not deeper than the anterior sulcus. The labial face of m3 has only one flexus.

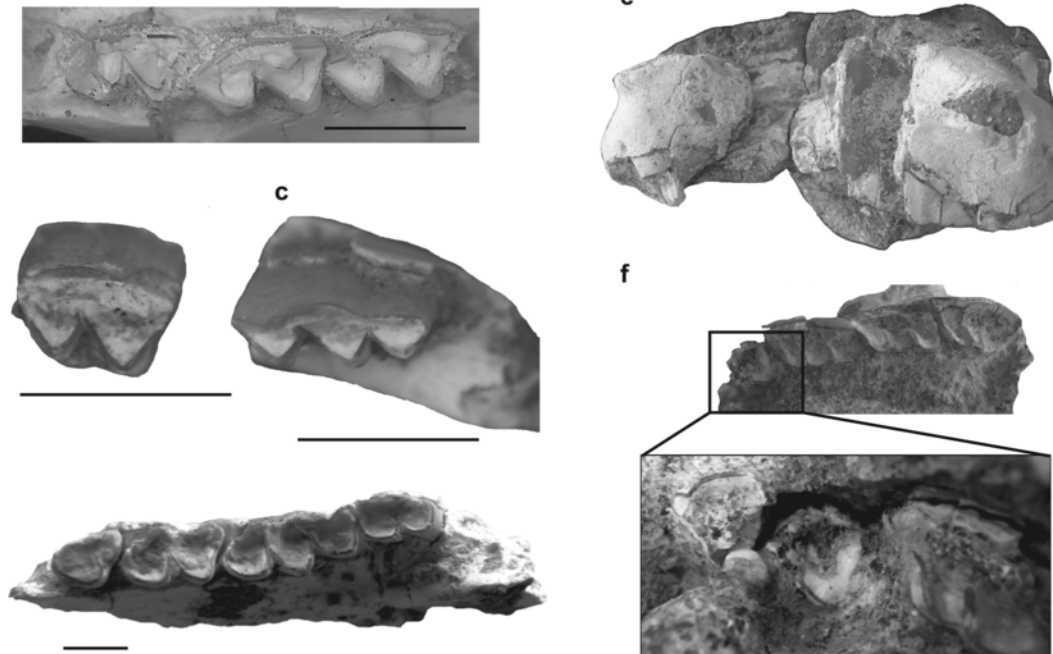
**Comments.** The specimen described here is comparable in size and shape (e.g., trilobed m3) to *P. minutum*, the tiny chasicosan species of the genus (Bond and López, 1996).

Family Mesotheriidae Alston, 1876.

Subfamily Mesotheriinae Simpson, 1945.

Genus *Typotheriopsis* Cabrera and Kraglievich 1931.

cf. *Typotheriopsis* sp.



**Fig. 3.** Notoungulata. **a.** *Paedotherium* cf. *P. minor*, IBIGEO-P20 partial right dentary with alveolar portion of p4 and complete m1-m2; **b.** IBIGEO-P22 partial left dentary with p4, **c.** IBIGEO-P19 partial left dentary with m3; **d.** *Protyotherium minutum*, IBIGEO-P39 partial left dentary with p4-m3; **e.** cf. *Typotheriopsis* sp., IBIGEO-P43 fragmentary skull in lateral view, **f.** Palatal view showing the P3-M3. Scale: 5 mm.

(Fig. 3e).

**Referred material.** IBIGEO-P43, fragmentary skull with left and right I1, left P3-4; left and right M1-3.

**Measurements.** I1,  $2.1 \times 0.8^*$  mm; P3,  $9.0 \times 9.5^*$  mm; P4,  $10.5 \times 12.0^*$  mm; M1,  $18.5 \times 9.5$  mm; M2,  $19.0 \times 10.0$  mm; M3,  $20.1 \times 10.5$  mm. Imbrication: 1,10.

**Occurrence.** Level 4.

**Description.** Large sized mesotheriinae with hypsodont teeth. Upper dental formulae: I1; P2; M3. The rodent-like rostrum is partially preserved; its short diastema seems parallel or slightly divergent posteriorly. The conserved portion of the posterior palate indicates a deep post-palatal notch reaching the level of M3. The incisors are broken, but the alveolar portion of the left I1 shows an elliptic overall shape with its main axis oriented obliquely with respect to the sagittal axis. The enamel is visible only on the labial side. Although the material is not completely prepared, there are signs of one lingual sulcus on left I1. The P3 is subtriangular and higher than P4. P4, the shortest tooth, is subtriangular in shape; judging by the preserved portion of the labial edge there is only one subtle labial flexus. Molars are trilobed, slightly imbricated and increase posteriorly in length. The M1 has its medial lobe not lingually salient with its anterior and posterior crests parallel. The anterior lobe is compressed, and the posterior one is the widest of the three lobes of M1. The M2 has its first lobe slightly compressed anteroposteriorly, and the remaining two are subequal in shape and size. The M3 has its medial lobe shorter than others and is highly enclosed by the anterior and posterior lobes.

**Comments.** Two late Miocene Mesotheriinae genera are currently recognized: *Tyotheriopsis* and *Pseudotytherium*. Both are similar in size to IBIGEO-P 43. This specimen is similar to *Tyotheriopsis* in the presence of one labial sulcus on the premolar ectoloph; the low imbrication index of upper molars; the subtriangular shape of P4 without a central fossette; the parallel arrangement of the anterior and posterior edges of the middle lobe of M1; and the middle lobe of M3 short and enclosed by the others. The absence of the following derived states precludes the assignment to *Pseudotytherium*: imbrication higher than 1.5, bilobed P4 and P4 length/width ratio <1.5.

Order Rodentia Bowdich, 1821.

Suborder Hystricognathi Tullberg, 1899.

Superfamily Cavoidea Fischer, 1817.

Family Caviidae Fischer, 1817.

Gen et sp. indet A.

(Fig. 4a).

**Referred material:** IBIGEO-P41, right p4 and an isolated lobe of a lower molar.

**Measurements.** p4,  $2.96 \times 3.98$  mm.

**Occurrence.** Level 3.

**Description.** The p4 is euhyposodont and bilobed with the two lobes well-developed. The anterior lobe has a strongly developed and blunt anterior projection. The enamel is interrupted on the base of prisms, along the lingual wall.

Gen et sp. indet B.

(Fig. 4b).

**Referred material.** IBIGEO-P25 left lower molar.

**Measurements.** Length, 3.8, width, 3.8 mm; L al, 1.9 mm; W al, 3.00 mm; L pl, 1.88 mm; W pl, 3.03 mm.

**Occurrence.** Level 3.

**Description.** The molariform is euhyposodont and bilobed, with a constriction in the apex of each lobe, more pronounced in the posterior one. The fundamental external flexid is funnel-shaped, with cement on its lingual side and with its lingual apex slightly beveled. Only the buccal side of the crown is enameled. Although the crown is partially broken on its lingual side, there is not evidence of internal

flexids. The interprismatic furrow is confluent with the apex of the fundamental external flexid. The anterior and posterior lobes are connected by a narrow lingual isthmus. Both lobes are heart-shaped and similar in size.

**Comments.** Differ from *Paleocavia*, *Neocavia*, and *Cavia* in the absence of accessory fissures (hpi). This material is similar to *Orthomyctera* in the bilobed shape of the molariform; the interprismatic furrow opposed to the fundamental external flexid; the lack of internal flexids; the enamel restricted to the labial side and the constriction in the apex of the prisms but differ in the absence of the dentine crest in the middle of each lobe.

Subfamily Cardiomyinae Kraglievich, 1930 *Procardiomys* Pascual 1961.

cf. *Procardiomys* sp.

(Fig. 4c).

**Referred material.** IBIGEO-P 42 a fragment of left dentary with complete m1 or m2.

**Measurements.** L, 3.3 mm; wal, 4.1 mm; wpl, 2.00 mm.

**Occurrence.** Level 3.

**Description.** Euhyposodont bilobed molar with heart-shaped lobes. The prisms are subequal in size. The posterior prism has well-developed primary internal flexid (hpi) and the anterior one has a shallow secondary internal flexid (hsi). The enamel is interrupted along the lingual side except on hsi, hpi, and the interprismatic furrow. The fundamental external flexid (hfe) is funnel-shaped, very long, with cement.

**Comments.** We assign this material to a cardiomyine based on the presence of both hsi and hpi. The specimen IBIGEO-P 42 is similar to *Procardiomys* on the base of the shallow accessory fissures and the funnel-shaped fundamental external flexid with cement. It differs from *P. martinoi* in the smaller size (15% smaller than *P. martinoi*) and the more convex walls of the lobes. Differ from *Cardiomys*, in the deepness of the accessory fissures which are more deep in this last. Because of the affinities of cardiomyines are currently under debate (e.g. Pérez and Vucetich, 2011; Pérez et al., 2014) we assign the specimen of Palo Pintado Fm. tentatively as cf. *Procardiomys* sp.

Superfamily Octodontoidea Waterhouse 1839.

Family Abrocomidae Miller and Gidley, 1918.

*Protabrocoma* Kraglievich, 1927.

*Protabrocoma* sp.

(Fig. 4d).

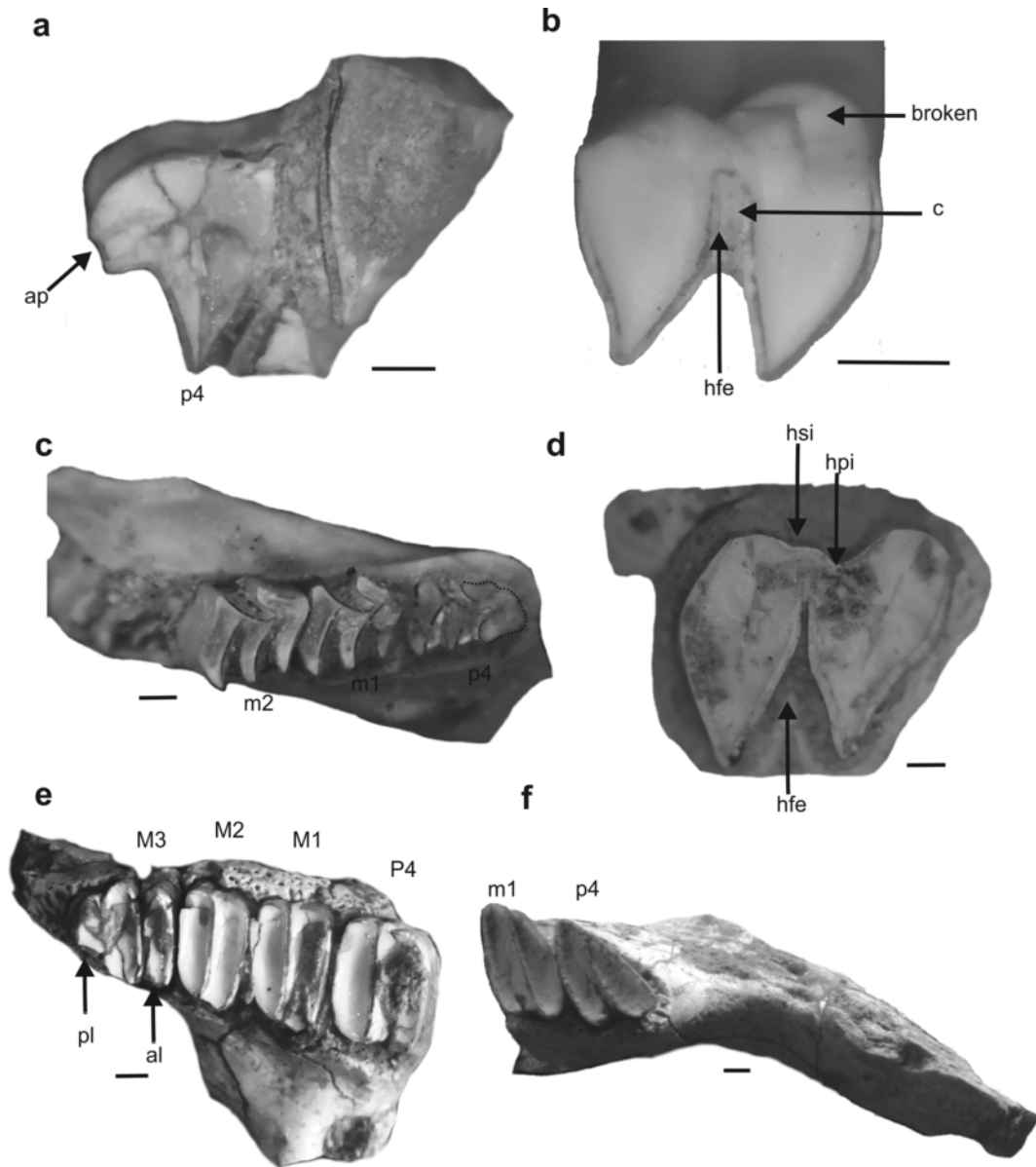
**Referred material.** IBIGEO-P 26, partial left dentary with broken p4, complete m1-2, and broken m3.

**Measurements.** Total molar row length, 8.525 mm; alveolous p4,  $2.36 \times 1.74$  mm; m1,  $2.26 \times 2.01$  mm; m2,  $2.24 \times 2.00$  mm; alveolous m3,  $2.27 \times 2.00$  mm.

**Occurrence.** Level 3.

**Description.** The specimen IBIGEO-P 26 is a partial left dentary bearing p4-m3. Mandible height is 5 mm below the first molar. The anterior margin of the coronoid apophysis is located lateral and ventral respect to the alveolar margin of molars which is a synapomorphy of Abrocomidae (Verzi and Quintana, 2005). The lateral crest of the mandible is little evident. The anterior border of the masseteric fossa is rounded, the notch for the tendon of *m. masseter medialis, pars infra-orbitalis* is subhorizontal respect to the alveolar border. Teeth are hypsodont and trilophodont. The anterolophid has rounded apex in the p4 but this corner is increasingly pointed backward in the tooth row. The enameled border of the hypolophid is markedly concave with pointed extreme. The postero-labial inflection of the posterolophid is subtle in all teeth.

**Comments.** Differs from *Abrocoma* in: 1- the inclination of the coronoid apophysis, that is less vertical in the specimen IBIGEO-P



**Fig. 4.** Rodentia. **a.** Caviidae gen et sp. indet. A IBIGEO-P41 right p4-m1; **b.** Caviidae gen et sp. indet. B IBIGEO-P25 left lower molar; **c.** cf. *Procardiomys* IBIGEO-P42 left m1; **d.** *Protabrocoma* sp. IBIGEO-P26 left dentary with p4-m2 and alveolus of m3; **e.** *Prolagostomus* sp. IBIGEO-P24 partial left maxillary with P4-M3; **f.** *Lagostomus* sp. IBIGEO-P23 partial right mandible with complete incisor and p4-m1. Scale: 1 mm. Abbreviations: al. anterior lobe; ap. Anterior projection; c. cement; hfe. fundamental external flexid; hpi. primary internal flexid; his. secondary internal flexid; pl. posterior lobe.

26; 2- the anterolophid of the p4 is less acute anteriorly than in *Abrocoma*; 3- the posterolophid is less inflected than in *Abrocoma*.

Superfamily Chinchilloidea Bennet, 1833.

Family Chinchillidae Bennet, 1833.

Subfamily Lagostominae Pocock, 1922.

Genus *Prolagostomus* Ameghino, 1887.

*Prolagostomus* sp.

(Fig. 4e).

**Referred material.** IBIGEO-P24, partial left maxillary with P4-M3, and partial right maxillary with P4-M2.

**Measurements.** P4, 2,83 × 3,98 mm (L/W 0,71); M1, 2,41 × 3,95 mm (L/W 0,61); M2, 2,05 × 3,85 mm (L/W 0,53); M3, 3,26 × 3,16 mm (L/W 1,03). Mean L/W 0,72.

**Occurrence:** Level 3.

**Description.** Upper dentition with bilobed P4-M2. M1-3 with the first laminae or lobe buccally protruding. The M3 is trilobed, with the third laminae drop-shaped, backwardly directed and with enamel surrounding the posterior wall of the laminae. There are two notches in the external face of M3. The first one is well-developed and divides the first and second laminae; the second one is very subtle. The third laminae is not completely separated from the second because its anterior edge is short and very lingual (Fig. 4e).

**Comments.** The specimens analyzed here are similar but slightly larger than *P. rosendoi* (Vucetich, 1984). The main similarity is the buccal projection of the first laminae in M1-3 and the drop shape of the third lobe of M3. Additionally, the specimen IBIGEO-P24 is similar in overall morphology and proportions to those figured by Croft et al. (2011) which mean L/W ratio is 0,83 from Bolivia. These speci-

mens have a drop shaped the third lobe of the M3 very wide and obliquely directed as in IBIGEO-P24.

Genus *Lagostomus* Kraglievich, 1926.

*Lagostomus* sp.

(Fig. 4f).

**Referred material.** IBIGEO-P23, partial right mandible with complete incisor and p4-m1.

**Measurements.** I1,  $4.95 \times 3.65$  mm; P4,  $4.5 \times 6.53$  mm; M1,  $3.74 \times 6.64$  mm.

**Occurrence.** Level 3.

**Description.** Lower bi-laminated cheek teeth obliquely implanted respect to the sagittal plane and anteroposteriorly compressed.

**Comments.** The specimen is comparable in the size and shape to the extinct species of *Lagostomus* (see Vucetich, 1984; Rasia and Candela, 2013).

## 5. Discussion

### 5.1. Diversity and biochronology

Three orders and seven families of eutherian mammals have been recorded from the outcrops of the Palo Pintado Fm. in the Tonco Valley. Among xenarthrans, all of them are Dasypodidae. Up to now, other families such as Pampatheriidae, Peltephilidae or Glyptodontidae have not been recorded in the Tonco Valley. In the same way, there is no record until now, referable to the order Pilosa (e.g. Megalonychidae, Megatheriidae, Mylodontidae or Nothrotheriidae). This could respond to a taphonomic bias because they are present in other Late Miocene localities of Northwestern Argentina (Brandoni et al., 2012a, b). Among native ungulates, notoungulates are the single order recorded at Tonco fauna. It is represented by the tyotherian families Hegetotheriidae, Intertheriidae, and Mesotheriidae. No toxodontids were recovered for the moment in the Tonco Valley, but this probably represents a sampling bias because they are probably present in middle levels of the Palo Pintado Fm. in other areas of the Calchaquies Valleys (Armella et al., 2016). Additionally, notoungulates are the most successful order of native ungulates and they dominate the faunas in the majority of late Miocene localities of South America (Croft, 2016). Litopterns were less abundant than notoungulates (Croft, 2016) but its absence in the Tonco fauna could respond to a sampling bias taking into account that they are present in other Late Miocene localities along the Andean Range (Brandoni et al., 2012a; Forasiepi et al., 2011). Caviomorph rodents are the most diverse group representing 50% of all species recovered from the Tonco Valley, involving the families Caviidae, Abrocomidae, and Chinchillidae. The main feature of the rodent assemblage exhumed from the Tonco Valley is the dominance of arid-adapted taxa (caviids, abrocomids and chinchillids) and the absence of typical families adapted to wet environments (e.g. neopiblemids and dynamids), which are common in the late Miocene amazonian and Mesopotamian faunas (see Kerber et al., 2016).

The absence of metatherians in the Tonco fauna is also probably due to sampling biases. Although metatherians diminished their diversity through the Neogene (Goin et al., 2016) they are common (e.g. sparassodonts, paucituberculatans, didelphimorphians, argyrolagoidean polydolopimorphians) in Late Miocene faunas of South America (Zimicz, 2014; Goin et al., 2016).

Most dasypodids found at Tonco are common genera in several late Miocene localities of South America. The genus *Macrochorobates* has been reported for the Monte Hermoso, Irene and Chapadmalal formations (Scillato Yané, 1982) in Buenos Aires province; Cerro Azul Fm. in La Pampa province and Uquía Fm. in Jujuy

province (Urrutia et al., 2008). *Vetelia gandhii* is also endemic of northwestern Argentina with a temporal distribution confined to the late Miocene (Huayquerian; Esteban and Nasif, 1996).

Among notoungulates, some genera have wide biochrons while others are more chronologically constrained. *Paedotherium* ranges from the late Miocene to the Pliocene and is a common taxon in the Chasicooan to Chapadmalalan faunas of Buenos Aires and La Pampa provinces (Cerdeño and Bond, 1998) and *P. minor* is a taxon recorded in Chasicooan and Huayquerian levels of the Pampean region (Cerdeño and Bond, 1998). *Protypotherium* has a biochron extending from the early Miocene (Cabrera and Kraglievich, 1931; Bond and López, 1996) to the Late Miocene (Huayquerian?; Tauber, 2005). *P. minutum* was previously mentioned for the Arroyo Chasicó Fm. (Chasicooan Stage/Age). Despite the fact that intertheriids are common in most early to middle Miocene faunas of South America, their record in middle latitudes remained restricted to cf. *P. attenuatum* of the Middle Miocene locality of Cerdas (Bolivia; Croft et al., 2009; Townsend and Croft, 2008). The report of *P. minutum* in this contribution constitutes the northernmost record for the species and reinforces the presence of the genus in the middle latitudes of South America. *Tyotheriopsis* was previously known from Chasicooan and Huayquerian deposits (late Miocene) of La Pampa (Rusconi, 1934; Cerdeño and Montalvo, 2001); Mendoza (Cabrera, 1937); San Juan (Rusconi, 1947) and Catamarca (Marshall and Patterson, 1981).

The rodent assemblage recovered from the Tonco Valley is composed of genera previously recorded in Chasicooan and Huayquerian localities of South America. *Protabrocoma* was previously registered in the lower and upper levels of Andalhuala Fm. in Catamarca province (Marshall and Patterson, 1981); in the “Guayquerías de San Carlos”, Huayquerías Fm. in Mendoza Province (Rovereto, 1914); in levels of Epecuén Fm (Pascual et al., 1966). in Buenos Aires province; in the “conglomerado osífero” or lower levels of Ituzaingó Fm. (Candela, 2005; Reguero and Candela, 2011; Nasif et al., 2013); in the Toro Negro Fm. (Rodríguez-Brizuela and Tauber, 2006), and in the late Miocene of Bolivia (Villarroel and Marshall, 1989). This taxon has a wide geographic distribution but a temporal one mostly restricted to the Huayquerian SALMA. *Prolagostomus* is widespread throughout middle and high latitude Miocene faunas from Argentina, Bolivia (Marshall and Sempere, 1991; Oiso, 1991; Croft, 2007; Croft et al., 2009, 2011) and Chile (Flynn et al., 2002, 2008). The first occurrence of the genus is in the early Miocene Pinturas Formation (pre-Santacrucian SALMA) of southern Argentina (Kramarz, 2002). The last occurrence is the Arroyo Chasicó Formation of east-central Argentina (Chasicooan SALMA; Bondesio et al., 1980). *Lagostomus* is a living taxon with a fossil record widely distributed geographically and temporally being recorded since the late Miocene (Chasicooan? Age) (Brandoni et al., 2012a,b; Esteban et al., 2014). *Procardiomys* is restricted to only one species, *P. martinói* from the Vivero Member of Arroyo Chasicó Fm. (Chasicooan Age, Buenos Aires province).

As mentioned before, the age of Palo Pintado Fm. is constrained between  $8.8 \pm 0.5$  Ma (Carrapa et al., 2012) and 5.27 Ma (Coutand et al., 2006), being the levels exposed in the Tonco Valley the nearest ones to the base of the unit. The age of fossil-bearing levels is approximately between 8 and 7 Ma (Payrola et al., 2017 in prep). corresponding to the late Tortonian or the Messinian/Tortonian boundary (Cohen et al., 2013).

In the current Late Cenozoic biochronological succession of South America (Fig. 5), the period mentioned above includes the Chasicooan and the lower Huayquerian ages, with the probably boundary between them around 8.7–8 Ma. (Deschamps et al., 2013; Zárate et al., 2017). Mammals recovered from the Tonco Valley are a mix of



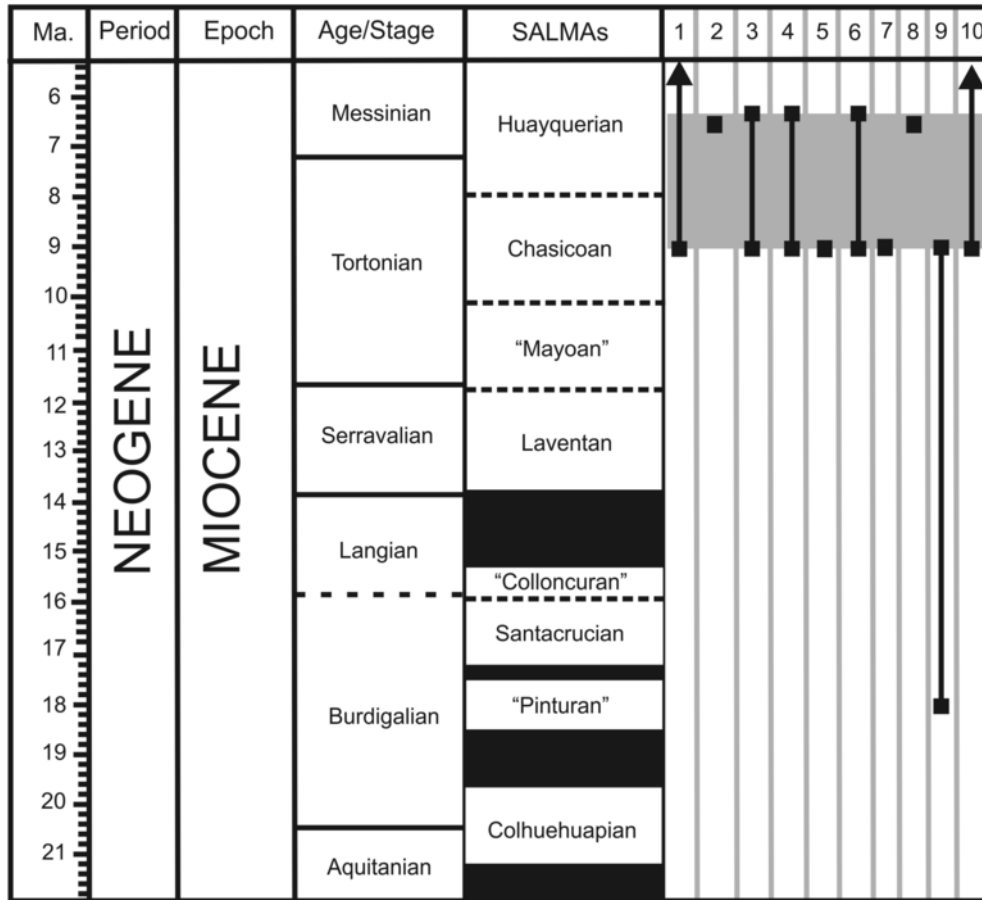


Fig. 5. South America's Cenozoic biochronological succession with the temporal distribution of genera found in the Tonco Valley. After (Cohen et al., 2013 updated; numerical ages), (Dunn et al., 2013; early Miocene), Croft et al., 2016 (middle Miocene), Zárate et al. (2017) and Tomassini et al. (2013) (late Miocene). The "Colloncuran," and "Mayoan" have not been formalized as SALMAs. Lines represent the chronologic distribution of genera previous to this work. Arrows indicate that the record continues up or down in time. 1- *Macrochorobates*, 2- *Vetelia gandhi*, 4- *Paedotherium minor*, 5- *Protypotherium minutum*, 6- *Tyotheriopsis*, 7- *Procardiomys*, 8- *Protabrocoma*, 9- *Prolagostomus*, 10- *Lagostomus*.

taxa common in several Chasicoan and some Huayquerian localities of South America. In order to establish a preliminary correlation with mammal ages, we consider the formally defined Late Miocene biozonation (Cione and Tonni, 2005; Cione et al., 2000) in our comparisons with the fauna exhumed in the Tonco Valley.

The Chasicoan Age refers to the faunal assemblage exhumed principally from the deposits of the Arroyo Chasicó Fm. at the locality of Laguna Chasicó (Buenos Aires province) (Pascual, 1961). This lithostratigraphic unit was divided into the lower Vivero Member and the upper Las Barrancas Member by Bondesio et al. (1980) on the base of their faunal contents and some lithological information. Posteriorly, the faunal assemblage was formally defined into two biozones: the biozone of *Chasicotherium rothi* or lower Chasicoan, corresponding to the Vivero Member (Cione and Tonni, 2005) and the biozone of *Chasicotatus ameghinoi* or upper Chasicoan exhumed from the Las Barrancas Member. Zárate et al. (2007) carried out a detailed stratigraphic study of the Arroyo Chasicó Fm. at its type locality concluding that the lithofacies identified do not support the current differentiation of the Arroyo Chasicó Formation into two members. They added a radiometric age (9.23 Ma.) based on escoria layer documented in the lower part of the exposed unit. Because of the base of the formation is not exposed they suppose a time span of at least 10 Ma- 8.7 Ma for the entire sedimentation of the Arroyo Chasicó Fm. Because of the stratigraphic provenance of the fossils of the

Arroyo Chasicó Fm. is anchored in a framework of members, the non-validity of these units states a serious problem with the above-mentioned biozonation. In this context, the biozones of the Chasicoan Age should be reexamined carefully. Taking into account this problem and for a comparative purpose, we consider the Chasicoan fauna as a whole (Fig. 5). Among the taxa recorded in the Palo Pintado Fm. in the Tonco Valley, *Paedotherium minor*, *Protypotherium minutum*, *Tyotheriopsis*, *Procardiomys*, and *Prolagostomus* are present in the Chasicoan assemblages.

Despite that the Huayquerian Age is represented by several localities along South America, mostly of them lack of radiometric ages. The sequence exposed at Puerta del Corral Quemado in Catamarca province is one of the best calibrated late Miocene sites in South America. In an attempt to establish a biozonation of the Huayquerian and Montehermosan ages, Reguero and Candela (2011) defined the *Cyonasua brevirostris* biozone in the base of Andalhualá Fm. in the Puerta de Corral Quemado site (Catamarca). These authors consider the *Cyonasua* datum as indicative of the Montehermosan Age. On this base, the underlying Chiquimil Fm. is Huayquerian in age for Reguero and Candela (2011). However, Esteban et al. (2014) questioned the validity of *Cyonasua* zone in Puerta del Corral Quemado and postulated two alternative biozones for the Chiquimil-Andalhualá sequence. The assemblage biozone of *Proeuphractus limpidus-Paleuphractus argentinus-Chasicotatus ameghinoi* (Esteban et al., 2014)

defined on the El Jarillal Member of Chiquimil Fm. The radiometric age of the El Jarillal Member (8.7–7.14 Ma) is partially equivalent to the proposed calibration of the Chasicooan Age (ca 9.5–8 Ma.) and several taxa present in this biozone (e.g. *Chasicotatus*, *Chasicomys*, *Orthomyctera*, *Cardiomys*) has been registered also in the Vivero Member of Arroyo Chasicó Fm (Cione and Tonni, 2005) suggesting Chasicooan age for the El Jarillal Member of Chiquimil Fm. (see Esteban et al., 2014). The lower section of Palo Pintado Fm. exposed in the Tonco Valley are partially equivalent in time of deposition with the El Jarillal Member of the Chiquimil Fm. In this sense, some taxa as *Vetelia*, *Macrochorobates*, *Tyotheriopsis* and *Lagostomus* registered in the Tonco Valley are also present in the El Jarillal Member (Esteban et al., 2014; Powell et al., 1998).

The assemblage biozone of *Paraeuphractus prominens-Cardiomys ameghinorum-Cardiatherium* defined in the Andalhualá Fm. probably represent the northwestern expression of the lower Huayquerian (Esteban et al., 2014). The radiometric age of this biozone is constrained between 7.14 and 5.64 Ma and correspond to the lower and middle section of the Andalhualá Fm. (Latorre et al., 1997; Esteban et al., 2014). Among taxa recorded in this biozone, *Macrochorobates* and *Protabrocoma* are present in the Tonco fauna. Another unit with probably Huayquerian fauna is that of the Desencuentro Fm. (La Rioja) which middle levels have been dated in 7.4 Ma (Georgieff et al., 2004). The mammals exhumed from this unit comes from levels below (*Pseutytherium* and *Vetelia*) and above the tuff layer (*Macrochorobates* and *Paleuphractus*). In this sense, is possible that the Desencuentro Fm. carry faunas of different ages (Chasicooan and Huayquerian?) because no dating is available for the lower levels of the unit. The Toro Negro Fm. (La Rioja province) has been considered early Pliocene in age based on dubious datation of reworked tuffs (Rodríguez Brizuela and Tauber, 2006). Posterior tuff layers dated without reworking giving an age constraint of 8.6 Ma for the middle section and 6.8 Ma for the upper one (Ciccioli et al., 2005). This dating positioning to the Toro Negro Fm. in a time span intermediate between the Chasicooan and Huayquerian stages (see Fig. 5). The mammalian contain of this unit proceed entirely from the lower member of the unit (Rodríguez Brizuela and Tauber, 2006), below the tuff layer dated in 8.6 Ma (Ciccioli et al., 2005) which states a problem with the age of fauna estimated by the authors in early Pliocene (Rodríguez Brizuela and Tauber, 2006: 269). A deep review of the unit must be made in order to clarify the taphonomic context of the mammalian remains or to revise the biochron of each registered taxa.

The remaining units carrying Huayquerian faunas, unfortunately, lack of radiometric calibration. This mark a serious problem because of the biochron of most of the typical Huayquerian taxa are relative, subtracting precision in the boundaries of biochronologic units. The best-represented fauna of “Huayquerian” age in southern South America is that of the Cerro Azul Formation (Pampean Region; Montalvo et al., 1998; Goin et al., 2000). The age of this unit has been constrained with fossils between 10 and 5.8 Ma (Visconti et al., 2010). On this base, the unit has a basal section with a potentially Chasicooan fauna and a middle one with a Huayquerian fauna (Verzi et al., 2008). However, Contreras et al. (2013) questioned the validity of the biozones postulated by Verzi et al. (2008) and suggested that the whole Cerro Azul Fm. have a fauna related with both, Chasicooan and Huayquerian stages/ages (Contreras et al., 2013:315). The “conglomerado osífero” of the lower section of Ituzaingó Fm. (Entre Ríos province) is another of the best known Huayquerian localities. Additional units with potential Huayquerian faunas are the Salicas and Toro Negro formation in La Rioja province (Rodríguez Brizuela and Tauber, 2006; Tauber, 2005) and the Morterito Fm. (Catamarca province) which has correlated with the Chiquimil Fm. (Chasicooan?)

(Anzótegui et al., 2007). The middle levels of the Aisol Fm. in Mendoza province could be Huayquerian also (Forasiepi et al., 2011). The Tonco fauna share with the above-mentioned faunas: *Macrochorobates*, *Vetelia gandhi*, *Paedotherium minor* and *Lagostomus*.

In the above context, the fauna exhumed from the lower levels of Palo Pintado Fm. in the Tonco Valley has a mix of taxa present in both Chasicooan and Huayquerian localities (Fig. 5). Taken into account that most of the typical Huayquerian faunas needed a revision, is important to reinforce the paleontological prospections in the Palo Pintado outcrops which have a fine geochronological control (Payrola et al. in prep.) to supply more information in order to clarify the relation of Chasicooan and Huayquerian ages.

## 5.2. Paleoenvironment

The Palo Pintado Fm. deposited in an anastomosing fluvial system under a climatic regime controlled by tectonism and the onset of the Low-Level Jet (LLJ) of the South American Monsoon around 7.6 Ma (Rohrmann et al., 2016). Regional wet and warm climate was inferred from paleobotany (Galli et al., 2011) and isotopic proxies (see Bywater-Reyes et al., 2010) coincident with an increase in global temperatures (Billups et al., 2008). However, a high resolution analysis of carbon and oxygen isotopes on paleosols shows that the onset of the LLJ marked three climatic phases in the deposition of Palo Pintado Fm. (Rohrmann et al., 2016). A warm seasonal climate with conspicuous wet and dry seasons previous to 7.6 Ma was followed by a pronounced wet period between 7.6 and 6.5 Ma. (see Rohrmann et al., 2016). After 6.5 Ma, orogenic uplifts transformed the basin into an inter-montane valley and the rainshadow effect dried out the environment leading to the actual configuration of the Calchaqui Valleys (see Rohrmann et al., 2016). Evidence from palynology indicate a similar scenario; a lower section of the unit characterized by seasonal climates with conspicuous dry season and an upper one more humid with a dry season less marked (Horn, 2014). The vegetation developed during the deposition of lower section was composed by forests mixed with xerophytic grasslands (Horn, 2014: 118). Our fossiliferous levels come from the lower section of the unit and correspond to times, which were previous to the establishment of the LLJ in the area.

Two paleo-communities form part of the floodplain setting: the savanna-like ones developed in the areas that remain dried and seasonally flooded, while the marsh depositional system developed into the low areas that were permanently flooded. The presence of well-developed grasslands is inferred from the complete dominance of hypsodont taxa among herbivorous mammals. All notoungulates and rodents have euhippsodont teeth, a feature typically related with grazer habits and open environments (Fortelius, 1985; Jacobs et al., 1999). Despite several workers documented the relation of hypsodonty with the intake of soil particles and dust deposited on the canopies of tropical rain forests (Ungar et al., 1995; Strömberg and Stidham, 2001; Barreda and Palazzesi, 2007; Strömberg et al., 2010; Damuth and Janis, 2011) the prevalence of hypsodont taxa coupled to the absence, at least for the moment, of brachyodont taxa, is suggestive of a dietary selection pressure. However, the volcanic ash layers interbedded in the Palo Pintado Formation document the volcanic input that probably contributed to increasing the ingestion of highly abrasive glass particles by herbivorous mammals.

The savanna-like community characterized by a herbaceous stratum composed of Poaceae, Amaranthaceae and Ephedraceae (Anzótegui and Cuadrado, 1996) was the habitat for the major part of the mammals recovered from Tonco Valley. The dasypodids *Macrochorobates* and *Vetelia* have been inferred as inhabitants of temperate

to warm, open habitats (Carlini and Scillato-Yané, 1996), similar to those occupied by *Zaedyus* and *Euphractus*, which actually live in the savannas and grassland of the Chaco and Cerrado lowlands (Redford and Wetzel, 1985). The species of *Paedotherium* were small terrestrial herbivorous hegetotheriids characterized by their 'rabbit-like' and ever-growing incisors and cheek teeth. Pachyrukines were traditionally considered as grazers, open habitat specialist with semi-fossorial life-style (Sinclair, 1909; Kraglievich, 1926; Cifelli, 1985; Genise, 1989; Dozo, 1997; Cerdeño and Bond, 1998; Elissamburu, 2004). *Protyotherium* has traditionally recorded as a grazer (Sinclair, 1909; Scott, 1932; Bond, 1986; Tauber, 1996) and open habitat specialist. Recently, Townsend and Croft (2008) based on enamel microwear, indicated browser habits for the Santacrucian specimens. This view was partially corroborated by Scarano et al. (2011) on the base of body mass estimations and Krapovickas (2009) by geometric morphometric analysis. Other authors consider that *Protyotherium* was most likely a generalized terrestrial herbivore tending toward cursoriality (Croft and Anderson, 2007). The families of rodents found at Tonco Valley are mostly indicative of open environments. Modern caviids are generalist in its ecological habitats (Redford and Eisenberg, 1992). *Protobrocoma* is an abrocomiid rodent whose living representatives are restricted to the Altiplano region of the Andes, occurring in rocky areas between 3700 and 5000 m (Nowak, 1991). The chinchillid rodent *Lagostomus* currently inhabits grasslands and lowland desert, feeding on grass and seeds (Nowak, 1991). They are saltatorial in its locomotion mode, and builds burrows (Nowak, 1991).

The marsh community is represented in the Tonco fauna by *Tytopheriopsis* and *Procardiomys*. *Tytopheriopsis* was a large terrestrial and semiaquatic grazer (Croft, 2016) from about 154 kg (Elissamburu, 2011), inhabitant of open environments which ecological preferences were possibly similar to that of the extant giant capybara (Bond et al., 1995). *Procardiomys* was a small hydrochoeriid rodent which living representatives are semiaquatic in its ecological habits (Canevari and Vaccaro, 2007). Vucetich et al., 2015 inferred for the extinct cardyomines a life style strongly related to permanent water bodies (Vucetich et al., 2015:332).

As mentioned before, the Palo Pintado Fm. represents three stages in the climatic evolution of environments in the Central Andes, marked by the onset of the LLJ (Rorhmann et al., 2016) and the uplift of the Andean orogen (Del Papa et al. in prep.). At least three fossiliferous levels have been identified in this unit until now; those corresponding to the lower section described in the present paper, those of the middle section and a third level corresponding to the uppermost section (e.g. Anzotegui, 2006; Reguero et al., 2014; Armella et al., 2016). This feature allows us the possibility to test the direct impact of climatic and tectonic factors in the evolution of a single mammalian fauna, by studying the change in taxonomic and or/ecological composition along the stratigraphic column. This is the main objective of our future research in the Palo Pintado Formation.

## 6. Concluding remarks

1 The mammalian assemblage up to now recovered from the Palo Pintado Fm. at Tonco Valley includes the following genera: Xenarthra, Dasypodidae: *Macrochorobates* and *Vetelia*; Notoungulata, Interatheriidae: *Protyotherium*; Hegetotheriidae: *Paedotherium*; Mesotheriidae: *Tytopheriopsis*; Rodentia, Histricognathi; Caviidae: *Procardiomys*; Abrocomidae: *Protobrocoma*; Chinchillidae: *Prolagostomus* and *Lagostomus* rodents. On a biochronologic aspect, the fauna exhumed from Palo Pintado Fm. in Tonco Valley is probably intermediate between the Chasicoan and the Huayquerian

SALMAs. The record of *Prolagostomus* constitute the first record of the genus in the northwestern Argentina.

2 The ecological composition of the Tonco fauna is indicative of grassland and marsh communities developed into the flood-plain setting under a seasonal climate with a conspicuous dry season.

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## Uncited references

Ameghino, 1889; Ameghino, 1897; Loomis, 1914; Nasif et al., 2006.

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## References

- Acevedo, T.R., Mautino, L.R., Anzotegui, M.L., Cuadrado, G., 1997. Estudio palinológico de la Formación Palo Pintado (Mioceno Superior), Provincia de Salta, Argentina. Parte II: Esporas. *Geociencias* 2, 112–120.
- Acevedo, L.T., Anzotegui, L.M., Mautino, L.R., 1998. Análisis palinológico preliminar de la Formación Palo Pintado (Mioceno superior), en Quebrada del Estanque, Salta, Argentina. In: *Comunicaciones Científicas y Técnicas de la Universidad Nacional del Nordeste*, Resistencia, Argentina, vol. 3, pp. 143–146, Resúmenes expandidos.
- Alston, E., 1876. On the classification of the order Glires. *Proc. Zoological Soc. Lond.* 61–98.
- Ameghino, F., 1882. Catálogo de las colecciones de antropología prehistórica y paleontología de Florentino Ameghino, partido de Mercedes. In: *Catálogo de la selección de la provincia de Buenos Aires (Rep. Argentina)*. pp. 35–42, Exposición Continental Sudamericana Anexo A.
- Ameghino, F., 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos Eocenos de Patagonia Austral. *Bol. del Mus. La Plata* 1, 1–26.
- Ameghino, F., 1891. Caracteres diagnósticos de cincuenta especies nuevas de mamíferos fósiles argentinos. *Rev. Argent. Hist. Nat.* 1, 129–167.
- Ameghino, F., 1894. Énumération synoptique de espèces de mammifères fossiles des formations éocènes de Patagonie. *Bol. Acad. Nac. Ciencias Córdoba* 13, 259–445.
- Antoine, P.O., Abello, M.A., Adnet, S., Altamirano, S., Ali, J., Baby, P., Billet, G., Boivin, M., Calderón, Y., Candela, A., Chabain, J., Corfu, F., Croft, D.A., Ganerød, M., Jaramillo, C., Klaus, S., Marivaux, L., Navarrete, R.E., Orliac, M.J., Parra, F., Pérez, M.E., Pujos, F., Rage, J.C., Ravel, A., Robinet, C., Roddaz, M., Tejada-Lara, J.V., Vélaz-Juarbe, J., Wesselingh, F.P., Salas-Gismondí, R., 2016. A 60-million year Cenozoic history of western Amazonian ecosystems in Contamana, eastern Peru. *Gondwana Res.* 31, 30–59.

- Anzótegui, L.M., 1998. Hojas de angiospermas de la Formación Palo Pintado, Mioceno Superior, Salta, Argentina. Parte Anacardiaceae, Lauraceae Moraceae *Ameghiniana* 35 (1), 25–32.
- Anzótegui, L.M., 2006. Paleofloras del Mioceno en los Valles Calchaquíes, Noroeste de Argentina: Corrientes. Universidad Nacional del Nordeste, Argentina, 266, Unpublished thesis.
- Anzótegui, L.M., Horn, M.Y., Mautino, L.R., Garralla, S.S., 2007a. Divers. Cyperaceae los Valles Calchaquíes durante el Mioceno Medio-Plioceno Bol. Asoc. Argent. Botánica 42, 117.
- Anzótegui, L.M., Garralla, S.S., Herbst, R., 2007b. Fabaceae de la Formación El Moritero (Mioceno Superior) del valle del Cajón, provincia de Catamarca, Argentina. *Ameghiniana* 44, 183–196.
- Anzótegui, L.M., Cuadrado, G.A., 1996. Palinología de la Formación Palo Pintado, Mioceno superior, Provincia de Salta, República Argentina. Parte Taxones nuevos Rev. Española Micropaleontol. 28 (3), 77–92.
- Armella, M.A., Esteban, G.I., García-López, D.A., Nasif, N.L., 2016. Vertebrados de la Formación Palo Pintado (Mioceno superior-Plioceno inferior) en la localidad de Angastaco, Provincia de Salta, Argentina. XXX Jornadas Argentinas de Paleontología de Vertebrados Actas, Buenos Aires, 156.
- Barreda, V., Palazzesi, L., 2007. Patagonian vegetation turnovers during the Paleogene–early Neogene. *Orig. arid-adapted floras Botanical Rev.* 73, 31–50.
- Bennet, E.T., 1833. On the family of Chinchillidae, and on a new genus referable to it. *Proc. Zoological Soc. Lond.* 57–60, 1833.
- Billups, K., Kelly, C., Pierce, E., 2008. The late Miocene to early Pliocene climate transition in the Southern Ocean. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 267, 31–40.
- Bonaparte, C.L.J.L., 1838. Synopsis vertebratorum systematis. *Nuovi Ann. Sci. Naturae Bologna* 2 (1), 105–133.
- Bona, P., Starck, D., Galli, C., Gasparini, Z., Reguero, M., 2014. Caiman cf. *latirostris* (Alligatoridae, Caimaninae) in the late Miocene Palo Pintado Formation, Salta province, Argentina: paleogeographic and paleoenvironmental considerations. *Ameghiniana* 51 (1), 26–36.
- Bond, M., 1986. Los ungulados fósiles de Argentina: evolución y paleoambientes. *Actas IV Congreso Argentino de Paleontología y Bioestratigrafía. Mendoza Actas* 2, 173–185.
- Bond, M., Cerdeño, E., López, G., 1995. Los ungulados nativos de América del Sur. In: Alberdi, M.T., Leone, G., Tonni, E.P. (Eds.), *Evolución Biológica y Climática de la Región Pampeana durante los últimos Cinco Millones de años*, vol 12, pp. 257–276, Monografías del Museo de Ciencias Naturales de Madrid.
- Bond, M., López, G., 1996. Las especies de *Protypotherium* (Notoungulata, Interatheriidae) de la Formación Arroyo Chasicó (Mioceno superior), provincia de Buenos Aires, Argentina. *Ameghiniana* 33, 460.
- Bondeson, P., Rabassa, J., Pascual, R., Vucetich, M. G., Scillato-Yané, G., 1980. La Formación Collón Curá de Pilcaniyeu Viejo y sus alrededores (Río Negro, República Argentina). Su antigüedad y las condiciones ambientales según su distribución de litogénesis y sus vertebrados. 2º Congreso Argentino de Paleontología y Bioestratigrafía y 1º Congreso Latinoamericano de Paleontología. pages.
- Bowdich, T.E., 1821. *An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travelers* Smith, Paris. 115.
- Brandoni, D., Schmidt, G.I., Candela, A., Noriega, J.I., Brunetto, E., Fiorelli, L.E., 2012a. Mammals from the Salicas formation (late Miocene), La Rioja province, northwestern Argentina: paleobiogeography, age, and paleoenvironment. *Ameghiniana* 49 (3), 375–387.
- Brandoni, D., Powell, J.E., González, O.E., 2012b. Anisodontherium from the late Miocene of northwestern Argentina. *Acta Palaeontol. Pol.* 57 (2), 241–249.
- Burmeister, G., 1888. Relación de un viaje a la Gobernación de Chubut. *An. del Mus. Nac. Buenos Aires* 3, 175–252.
- Butler, R., Marshall, L.G., Drake, R., Curtis, G., 1984. Magnetic polarity, stratigraphy and 40K-40Ar dating of late Miocene and early Pliocene continental deposits, Catamarca province, NW Argentina. *J. Geol.* 92, 623–636.
- Bywater-Reyes, S., Carrapa, B., Clementz, M., Schoenbohm, L., 2010. Effect of late Cenozoic aridification on sedimentation in the Eastern Cordillera of northwest Argentina (Angastaco basin). *Geology* 38 (3), 235–238. <https://doi.org/10.1130/G30532.1>.
- Cabrera, A., 1937. Notas sobre el suborden “Tyotheria”. *Notas del Mus. La Plata* 2 Paleontol. 8, 17–43.
- Cabrera, A., Kraglievich, L., 1931. Diagnoses previas de los ungulados fósiles del Arroyo Chasicó. *Notas del Mus. La Plata* 1, 107–113.
- Candela, A.M., 2005. Los roedores del “Mesopotamiense” (Mioceno tardío, Formación Ituzaingó) de la provincia de Entre Ríos (Argentina). In: Aceñolaza, F.G. (Ed.), *Temas de la Biodiversidad del Litoral Fluvial Argentino II. Miscelánea*, vol 14, pp. 37–48.
- Candela, A.M., Bonini, R., Tonni, E.P., Reguero, M., Abello, M.A., Rasia, L.L., 2013. Palaocavia (Rodentia, Caviidae) en la Formación Maimará (Mioceno tardío-Plioceno temprano), Quebrada de Humahuaca (Noroeste argentino): importancia bioestratigráfica y biogeográfica. *Ameghiniana* 50 (6).
- Canevari, M., Vaccaro, O., 2007. Guía de mamíferos del sur de América del Sur. Editorial L.O.L.A. (Literature of Latin America), Buenos Aires.
- Carlini, A.A., Scillato Yané, G.J., 1996. *Chorobates recens* (Xenarthra, Dasypodidae) y un análisis de la filogenia de los Euphractini. *Rev. del Mus. La Plata* 9, 225–238.
- Carrapa, B., Bywater-Reyes, S., DeCelles, P., Mortimer, M., Gehrels, G.E., 2012. Late Eocene–Pliocene basin evolution in the Eastern Cordillera of northwestern Argentina (25°–26°S): regional implications for Andean orogenic wedge development. *Basin Res.* 24, 249–268.
- Cerdeño, E., Bond, M., 1998. Taxonomic revision and phylogeny of *Paedotherium* and *tremacyllus* (Pachyrhinae, Hegetotheriidae, Notoungulata) from the late Miocene to pleistocene of Argentina. *J. Vertebrate Paleontology* 18, 799–811.
- Cerdeño, E., Montalvo, C.I., 2001. Los Mesotheriinae (Mesotheriidae, Notoungulata) del Mioceno superior de La Pampa, Argentina. *Rev. Española Paleontol.* 16, 63–75.
- Ciccioli, P.L., Limarino, C.O., Marensi, S.A., 2005. Nuevas edades radimétricas para la Formación Toro Negro en la Sierra de los Colorados, Sierras Pampeanas No occidentales, provincia de La Rioja. *Rev. Asoc. Geol. Argentina* 60, 251–254.
- Cifelli, R.L., 1985. South American ungulate evolution and extinction. In: Stehli, F.G., Webb, S.D. (Eds.), *The Great American Biotic Interchange*. Plenum Press, New York, pp. 249–266.
- Cione, A.L., Azpelicueta, M., Bond, M., Carlini, A.A., Casciotta, J., Cozzuol, M.A., de la Fuente, M., Gasparini, Z., Goin, F., Noriega, J., Scillato Yané, G., Soibelzon, L., Tonni, E.P., Verzi, D., Vucetich, M.G., 2000. Miocene vertebrates from Entre Ríos, eastern Argentina. In: Aceñolaza, G. (Ed.), In: Herbst, R. (Ed.), *El Neógeno en Argentina. INSUGEO Serie Correlación Geológica*, vol 14, pp. 191–237, (1–2).
- Cione, A.L., Tonni, E.P., 1995. Chronostratigraphy and ‘Land-mammal Ages’ in the Cenozoic of southern South America: principles, practices, and the ‘Uquian’ problem. *J. Paleontology* 69, 135–159.
- 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., Etcheverry, M., Cavallé, M., Llambías, E. (Eds.), *Geología y recursos minerales de la provincia de Buenos Aires*. pp. 183–200.
- Cione, L.A., Gasparini, G.M., Soibelzon, E., Soibelzon, L.E., Tonni, E.P., 2015. The Great American Biotic Interchange: a South American Perspective. *SPRINGER BRIEFS in EARTH SYSTEM SCIENCES*. Springer, New York.
- Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.X., 2013. The ICS international Chronostratigraphic Chart. *Episodes* 36, 199–204.
- Coutand, I., Carrapa, B., Deeken, A., Schmitt, A.K., Sobel, E.R., Strecker, M.R., 2006. Propagation of orographic barriers along an active range front: insights from sandstone petrography and detrital apatite fission-track thermochronology in the intramontane Angastaco basin, NW Argentina. *Basin Res.* 18, 1–26.
- Cozzuol, M., 2006. The Acre vertebrate fauna: diversity, geography and time. *J. S. Am. Earth Sci.* 21, 185–203.
- Croft, D.A., 2007. The middle Miocene (laventan) Quebrada Honda fauna, southern Bolivia, and a description of its notoungulates. *Palaeontology* 50, 277–303.
- Croft, D.A., 2016. Horned Armadillos and Rafting Monkeys: the Fascinating Fossil Mammals of South America (Life of the Past). Indiana University Press, Indiana.
- Croft, D.A., Anaya, F., 2006. A new middle Miocene hegetotheriid (Notoungulata: Tyotheria) and a phylogeny of the Hegetotheriidae. *J. Vertebrate Paleontology* 26, 387–399.
- Croft, D.A., Anaya, F., Auerbach, D., Garzzone, C., MacFadden, B., 2009. New data on Miocene Neotropical provinciality from Cerdas, Bolivia. *J. Mammalian Evol.* <https://doi.org/10.1007/s10914-009-9115-0>.
- Croft, D.A., Anderson, L.C., 2007. Locomotion in the extinct notoungulate *Protypotherium*. *Paleontol. Electrónica* 11, 1A.
- 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. *J. Vertebrate Paleontology* <https://doi.org/10.1080/02724634.2016.1163574>.
- Croft, D.A., Chick, J.M.H., Anaya, F., 2011. New middle Miocene caviomorph rodents from Quebrada Honda, Bolivia. *J. Mammalian Evol.* 18 (4), 245–268. <https://doi.org/10.1007/s10914-011-9164-z>.
- Croft, D.A., Flynn, J.J., Wyss, A.R., 2004. Notoungulata and litopterna of the early Miocene Chucal fauna, northern Chile. *Fieldiana Geol. (New Series)* 50, 1–52.
- Damuth, J., Janis, C.M., 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. *Biol. Rev.* 86 (3), 733–758.
- Deschamps, C.M., Vucetich, M.G., Montalvo, C.I., Zárate, M.A., 2013. *Capybaras* (Rodentia, Hydrochoeridae, Hydrochoerinae) and their bearing in the calibration of the late Miocene-pleistocene sequences of south America. *J. S. Am. Earth Sci.* 48, 145–158.
- Díaz, J.I., 1985. Análisis estratigráfico del Grupo Payogastilla, Terciario superior del valle Calchaquí, provincia de Salta, República Argentina. In: 4º Congreso Geológico Chileno. Actas, Antofagasta, pp. 211–234.
- Díaz, J.I., 1987. Estratigrafía y sedimentología del Terciario Superior de la región comprendida entre los valles de los ríos Calchaquí Guachipas, Provincia de Salta, República Argentina. Unpublished thesis Universidad Nacional de Tucumán.
- Díaz, J.I., Malizzia, D., 1983. Estudio Geológico y sedimentológico del Terciario Superior del Valle Calchaquí (departamento de San Carlos, Salta). *Bol. Sedimentológico* 2 (1), 8–21.
- Dozo, M.T., 1997. Paleoneurología de *Dolicavia minuscula* (Rodentia, Caviidae) y *Paedotherium insigne* (Notoungulata, Hegetotheriidae) del Plioceno de Buenos Aires, Argentina. *Ameghiniana* 34, 427–435.

- Elissamburu, A., 2004. Morphometric and morphofunctional analysis of the appendicular skeleton of Paedotherium (Mammalia, Notoungulata). *Ameghiniana* 41 (3), 363–380.
- Elissamburu, A., 2011. Estimación de la masa corporal en géneros del Orden Notoungulata. *Estud. Geol.* 68 (1), 91–111.
- 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., Nasif, N., Georgieff, S.M., 2014. Cronobioestratigrafía del Mioceno tardío-Plioceno temprano, Puerta de Corral Quemado y Villavil, provincia de Catamarca, Argentina. *Acta Geol. Lilloana* 26 (2), 165–192.
- Flynn, J.J., Charrier, R., Croft, D.A., Gans, P.B., Herriott, T.M., Wertheim, J.A., Wyss, A.R., 2008. Chronologic implications of new Miocene mammals from the Cura-Mallín and Trapa Trapa formations, Laguna del Laja area, south central Chile. *J. S. Am. Earth Sci.* 26, 412–423.
- Flynn, J.J., Croft, D.A., Charrier, R., Hérail, G., Wyss, A.R., 2002. The first Cenozoic mammal fauna from the Chilean Altiplano. *J. Vertebrate Palaeontol.* 22, 200–206.
- Fischer, G., 1817. *Adversaria zoologica. Mémoires Societé Impériale Nat. Moscou* 5, 357–428.
- Forasiepi, A.M., Martinelli, A.G., de la Fuente, M.S., Dieguez, S., Bond, M., 2011. Paleontology and stratigraphy of the Aisol formation (Neogene), san Rafael, Mendoza. In: Salfity, J.A., Marquillas, R.A. (Eds.), *Cenozoic Geology of the Central Andes of Argentina*. Instituto del Cenozoico, pp. 135–154.
- Fortelius, M., 1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. *Acta Zool. Fenn.* 180, 1–76.
- Galli, C., Anzotegui, L.M., Horn, M.Y., Morton, L.S., 2011. Paleoambiente y paleocomunidades de la Formación Palo Pintado (Mioceno-Plioceno), Provincia de Salta, Argentina. *Rev. Mex. Ciencias Geol.* 28, 161–174.
- Georgieff, S.M., Herbst, R., Esteban, G.I., Nasif, N., 2004. Análisis paleoambiental y registro paleontológico de la Formación Desencuentro (Mioceno Superior), Alto de San Nicolás, La Rioja, Argentina. *Ameghiniana* 41, 45–56.
- Genise, J.F., 1989. Las cuevas con *Actenomyx* (Rodentia, Octodontidae) de la Formación Chapadmalal (Plioceno superior) de Mar del Plata y Miramar (provincia de Buenos Aires). *Ameghiniana* 26, 33–42.
- 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). *Estud. Geol.* 56, 101–126.
- Goin, F.J., Woodburne, M.O., Zimic, A.N., Martin, G.M., Chornogubsky, L., 2016. A Brief History of South American Metatherians Evolutionary Contexts and Intercontinental Dispersals. Springer, Dordrecht.
- Herbst, R., Anzotegui, L.M., Jaln, G., 1987. Estratigrafía, paleoambientes y dos especies de *Salvinia Adanson* (Filicopsida) del Mioceno Superior de Salta, Argentina. *Rev. Fac. Ciencias Exactas Nat. Agrimens.* 7, 15–42.
- Herbst, R., Anzotegui, L.M., Esteban, G., Mautino, L.R., Morton, S., Nassif, N., 2000. Síntesis paleontológica del Mioceno de los valles Calchaquíes, noroeste argentino. In: Aceñolaza, F., Herbst, R. (Eds.), *El Neógeno de Argentina*. Instituto Superior de Correlación Geológica, Serie Correlación Geológica, vol 14, pp. 263–288.
- Horn, M.Y., 2014. Palinofloras de las formaciones Morterito y Palo Pintado (Mioceno Superior-Plioceno Inferior), Noroeste de Argentina. Unpublished Thesis Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.
- Illiger, J.K.W., 1811. *Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis*. C. Salfeld, Berlin, 301.
- Jacobs, B.F., Kingston, J.D., Jacobs, L.L., 1999. The origin of grass-dominated ecosystems. *Ann. Mo. Botanical Gard.* 86, 590–643. <https://doi.org/10.2307/2666186>.
- Kerber, L., Negri, F.R., Ribeiro, A.M., Nasif, N., Pereira Souza-Filho, J., Ferigolo, J., 2016. Tropical fossil caviomorph rodents from the Southwestern Brazilian Amazonia in the context of the South American faunas: systematics, biochronology, and paleobiogeography. *J. Mammalian Evol.* <https://doi.org/10.1007/s10914-016-9340-2>.
- Kraglievich, L., 1926. Sobre el conducto humeral en las vizcachas y paquirusos Chapadmalenses con descripción del *Paedotherium imperforatum*. *An. del Mus. Nac. Hist. Nat.* 'Bernardino Rivadavia' 34, 45–88.
- Kraglievich, L., 1927. Nota preliminar sobre nuevos géneros y especies de roedores de la fauna argentina. *Physis* 8, 591–598.
- Kraglievich, L., 1930. La formación friaseana del río Frías, río Fenix, laguna Blanca, etc. y su fauna de mamíferos. *Physis* 10, 127–161.
- Kraglievich, L., 1934. La antigüedad pliocena de las faunas de Monte Hermoso, deducidas de su comparación con las que le precedieron y sucedieron. *El Siglo Ilus.* 1–136.
- Kramarz, A.G., 2002. Roedores chinchilloideos (Hystricognathi) de la Formación Pinturas, Mioceno temprano-medio de la provincia de Santa Cruz, Argentina. *Rev. Mus. Argent. Ciencias Nat.* 4, 167–180.
- Krapovickas, J.M., 2009. Las especies del género *Protypotherium* Ameghino, 1887 (Notoungulata, Interatheriidae) del Mioceno Temprano-Medio de la provincia de Santa Cruz, República Argentina. *Mastozoología Neotropical* 16 (1).
- Krpmotic, C.M., Ciancio, M.R., Barbeito, C., Mario, R.C., Carlini, A.A., 2009. Osteoderm morphology in recent and fossil euphractine xenarthrans. *Acta Zool-Stockholm* 90 (4), 339–351.
- Latorre, C., Quade, J., McIntosh, W.C., 1997. The expansion of C4 grasses and global change in the table Mocene: stable isotope evidence from the Americas. *Earth Planet. Sci. Lett.* 146, 83–96.
- Lutz, A.I., Martínez, L.C.A., 2007. Nuevo género y especie de liana del Mioceno Superior (Formación Palo Pintado), provincia de Salta, Argentina. *Ameghiniana* 44 (1), 205–213.
- Madden, R.H., Guerrero, J., Kay, R.F., Flynn, J.J., Swisher, C.C., Walton, A.H., 1997. The laventan stage and age. In: Kay, R.F., Madden, R.H., Cifelli, R.L., Flynn, J.J. (Eds.), *Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington.
- Marshall, L.G., Hoffstetter, R., Pascual, R., 1983. Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. *Palaeovertebrata Spec.* Vol. 93, 1–93.
- Marshall, L.G., 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 Geol.* 9, 1–80.
- Marshall, L.G., Sempere, T., 1991. The Eocene to Pleistocene vertebrates of Bolivia and their stratigraphic context: a review. In: Suárez-Soruco, R. (Ed.), *Fósiles y Facies de Bolivia*, vol 1, Yacimientos Petrolíferos Fiscales Bolivianos, pp. 631–652.
- Miller, G.S., Gidley, J.W., 1918. Synopsis of the supergeneric groups of rodents. *J. Wash. Acad. Sci.* 8, 431–448.
- Montalvo, C.I., Verzi, D.H., Vucetich, M.G., Visconti, G., 1998. Nuevos Eumysopinae (Rodentia, Echimyidae) de la Formación Cerro Azul (Mioceno tardío) de La Pampa, Argentina. *5 Jornadas Geol. Geofísicas Bonaerenses Actas* 1, 57–64.
- Morton, L.S., 1992. Bivalvos de agua dulce de la Formación Palo Pintado (Mioceno Tardío) del Valle Calchaquí, provincia de Salta, Argentina. *Rev. Fac. Ciencias Exactas Nat. Agrimens.* 9, 77–91.
- Nasif, N.L., Candela, A.M., Rasia, L., Madozzo Jaén, M.C., Bonini, R., 2013. Actualización del conocimiento de los roedores del Mioceno tardío de la Mesopotamia argentina: aspectos sistemáticos, evolutivos y paleobiogeográficos. In: Noriega, J. (Ed.), *El Neógeno de la Mesopotamia Argentina*. In: Brandoni, D. (Ed.), vol 14, Asociación Paleontológica Argentina, Publicación Especial, pp. 153–169.
- Negri, F.R., Bocquentin-Villanueva, J., Ferigolo, J., Antoine, P.O., 2010. A review of tertiary mammal faunas and birds from western Amazonia. In: Hoorn, C., Wesselingh, F.P. (Eds.), *Amazonia: Landscapes and Species Evolution: a Look into the Past*. Wiley- Blackwell, Oxford, pp. 245–258.
- Nowak, R.M., 1991. *Walker's Mammals of the World*, fifth ed. Johns Hopkins University Press, Baltimore.
- Oiso, Y., 1991. New land mammal locality of middle Miocene (Colloncuran) age from Nazareno, southern Bolivia. In: Suárez-Soruco, R. (Ed.), *Fósiles y Facies de Bolivia*, Volumen I: Vertebrados. Yacimientos Petrolíferos Fiscales Bolivianos, Santa Cruz, Bolivia, pp. 653–672.
- Ortiz, P.E., García López, D.A., Babet, M.J., Pardiñas, U.F.J., Alonso Muruaga, P.J., Jayat, P.J., 2012. Exceptional Late Pliocene microvertebrate diversity in northwestern Argentina reveals a marked small mammal turnover. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 361–362.
- Pascual, R., 1961. Un nuevo *Cardiomyinae* (Rodentia, Caviidae) de la Formación Arroyo Chasicó (Plioceno inferior) de la provincia de Buenos Aires. *Ameghiniana* 2, 61–72.
- Pascual, R., Ortega Hinojosa, E.J., Gondar, D., Tonni, E., 1965. Las edades del Cenozoico mamífero de la Argentina, con especial atención a aquellas del territorio bonaerense. *An. Com. Investig. Científicas Buenos Aires* 6, 165–193.
- Pascual, R., Ortega Hinojosa, E., Gondar, D.E., Tonni, E., 1966. Paleontografía bonaerense, Fascículo IV, vertebrata. In: Borrello, A.V. (Ed.), *Comisión de Investigaciones Científicas de la Provincia de Buenos Aires*, La Plata.
- Patterson, B., Pascual, R., 1972. The fossil mammal fauna of South America. In: Keast, A., Erk, F.C., Glass, B. (Eds.), *Evolution, Mammals, and Southern Continents*. State University of New York Press, Albany, pp. 247–309.
- Pérez, M.E., Vucetich, M.G., 2011. A new extinct genus of Caviidae (Rodentia, Hystricognathi) from the Miocene of Patagonia (Argentina) and the evolution of cavioid mandibular morphology. *J. Mammalian Evol.* 1–21. <https://doi.org/10.1007/s10914-011-9154-1>.
- Pérez, M.E., Vucetich, M.G., Deschamps, C.M., 2014. Mandibular remains of *Procardiomys martinói* pascual, 1961 (Hystricognathi, Caviidae) from the Arroyo Chasicó Formation (early late Miocene) of Argentina: anatomy and the phylogenetic position of the genus within Caviidae. *Hist. Biol. Int. J. Paleobiology* 26, 16–25.
- Pocock, R.I., 1922. On the external characters of hystricomorph rodents. *Proc. Zoological Soc. Lond.* 25, 365–427.
- Pocock, R.I., 1924. The external characters of the South American edentates. *Proc. Zoological Soc. Lond.* 94, 983–1031.
- Powell, J., Mulé, P., Duarte, R., Ortiz, P., Sanagua, J., Muruaga, C., 1998. Mamíferos de la Formación Chiquimil (Mioceno Superior) de la vertiente occidental de la Sierra de Hualfín, provincia de Catamarca: *Acta Geológica Lilloana*, vol 18, 178.
- Rasia, L.L., Candela, A.M., 2013. Systematic and biostratigraphic significance of a chinchillid rodent from the Pliocene of eastern Argentina. *Acta Palaeontol. Pol.* 58 (2), 241–254.

- Redford, K.H., Eisenberg, J.F., 1992. *Mammals of the Neotropics. The Southern Cone*. University of Chicago, Chicago.
- Redford, K., Wetzel, 1985. *Euphractus sexcinctus*. *Mamm. Species* 252, 1–4.
- Reguero, M.A., Candela, A.M., 2008. Bioestratigrafía de las secuencias neógenas tardías de la Quebrada de Humahuaca, provincia de Jujuy. Implicancias paleoambientales y paleobiogeográficas. In: *Relatorio, 17º Congreso Geológico Argentino, 17th: San Salvador de Jujuy*. Asociación Geológica Argentina, Buenos Aires, pp. 286–296.
- 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*. Instituto del Cenozoico, pp. 411–426.
- Reguero, M.A., Candela, A.M., Galli, C.I., Bonini, R., Voglino, D., 2014. A new hypsodont notoungulate (Hegetotheriidae, Pachyrukhinae) from the late Miocene of the eastern Cordillera, Salta province, northwest of Argentina. *Andean Geol.* 42 (1), 56–70.
- Reguero, M.A., Castro, P.V., 2004. Un nuevo Trachytheriinae (Mammalia, †Notoungulata) del Deseadense (Oligoceno tardío) de Patagonia, Argentina: implicancias en la filogenia, biogeografía y bioestratigrafía de los Mesotheriidae. *Rev. Geol. Chile* 31, 45–64.
- Rodríguez-Brizuela, R., Tauber, A., 2006. Estratigrafía y mamíferos fósiles de la Formación Toro Negro (Neógeno), Departamento Vinchina, noroeste de la provincia de La Rioja, Argentina. *Ameghiniana* 43, 257–272.
- Rohrman, A., Sachse, D., Mulch, A., Pingel, H., Tofelde, S., Alonso, R.N., Strecker, M.R., 2016. Miocene orographic uplift forces rapid hydrological change in the southern central Andes. *Sci. Rep.* 6, 35678.
- Roth, S., 1903. Noticias preliminares sobre nuevos mamíferos fósiles del Cretáceo Superior y Terciario Inferior de la Patagonia [Preliminary news on the fossil mammals from the upper Cretaceous and lower tertiary of Patagonia]. *Rev. del Mus. La Plata* 11, 135–158.
- Rovereto, C., 1914. Los estratos araucanos y sus fósiles. *An. del Mus. Nac. Hist. Nat. Buenos Aires* 25.
- Rusconi, C., 1934. Algunos fósiles terciarios de la Gobernación de La Pampa argentina. *Rev. Chil. Hist. Nat.* 35, 104–106.
- Rusconi, C., 1947. Nueva especie de tipotérido de Jáchal (San Juan). *An. Soc. Científica Argent.* 143, 247–250.
- Russo, A., 1972. La estratigrafía terciaria en el noroeste argentino. 5º Congreso Geológico Argentino, Villa Carlos Paz, Resúmenes.
- Sánchez-Villagra, M.R., Aguilera, O.A., Carlini, A.A., 2010. Urumaco and Venezuelan Palaeontology. *The Fossil Record of the Northern Neotropics*. Indiana University Press.
- Scarano, A.C., Carlini, A.A., Illius, A.W., 2011. Intertheriidae (Tytopheria; Notoungulata), body size and paleoecology characterization. *Mamm. Biol.* 76, 109–114.
- Scillato-Yané, G.J., 1980. 2º Congreso Argentino de Paleontología y Bioestratigrafía y 1º Congreso Latinoamericano de Paleontología (Buenos Aires, 1978). Catálogo de los Dasyopodidae fósiles (Mammalia, Edentata) de la República Argentina, vol. 3, Actas, 7–36.
- Scillato Yané, G., 1982. *Los Dasyopodidae (Mammalia-Edentata) del Plioceno y Pleistoceno de Argentina*. Unpublished thesis. Facultad de Ciencias Naturales y Museo Universidad Nacional de La Plata.
- Scott, W.B., 1932. Mammalia of the santa Cruz beds. In: In: Scott, W.B. (Ed.), *Paleontology. Part III. Nature and Origin of the Santa Cruz Fauna with Additional Notes on the Entelonychia and Astrapotheria*, vol. vol. II, Princeton University, Stuttgart, pp. 157–192, Reports of the Princeton University Expeditions to Patagonia, 1896–1899.
- Simpson, G.G., 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* 85, 1–350.
- Simpson, G.G., 1971. The evolution of marsupials in South America. *An. Acad. Bras. Ciências* 43, 103–119.
- Sinclair, W.J., 1909. Mammalia of the santa Cruz beds. In: In: Scott, W.B. (Ed.), *Paleontology. Part I, Tytopheria*, vol. vol. I, Princeton University, Stuttgart, pp. 1–110, Reports of the Princeton University Expeditions to Patagonia, 1896–1899.
- Strömberg, C.A.E., Stidham, T.A., 2001. Dung beetle brood balls and notoungulate diet. *J. Vertebrate Paleontology* 21, 105A.
- Strömberg, C.A.E., Dunn, R., Kohn, M., Madden, R., Carlini, A., 2010. Was the evolution of hypsodonty in South America a response to the spread of grassland vegetation? New phytolith records from Gran Barranca, Argentina. *J. Vertebrate Paleontology* 171A, Society of Vertebrate Paleontology Program with Abstracts 2010.
- Tauber, A.A., 1996. Los representantes del genero *Prototytherium* (Mammalia, Notoungulata, Intertheriidae) del Mioceno temprano del sudeste de la Provincia de Santa Cruz, República Argentina. *Misc. Acad. Nac. Ciencias (Córdoba)* 95, 1–29.
- Tauber, 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.
- Townsend, B., Croft, D.A., 2008. Middle Miocene Mesotheriine Diversity at Cerdas, Bolivia and a Reconsideration of *Plesiotytherium Minus*. *Paleontología Electrónica* 13.1.1A [http://palaeo-electronica.org/2010\\_1/192/index.html](http://palaeo-electronica.org/2010_1/192/index.html).
- Tullberg, T., 1899. Über das System der Nagethiere: eine phylogenetische Studie. *Nova Acta Regiae Soc. Sci. Ups.* 3 (18), 1–514.
- Ungar, P.S., Teaford, M.F., Glander, K.E., Pastor, R.F., 1995. Dust accumulation in the canopy: a potential cause of dental microwear in primates. *Am. J. Phys. Anthropol.* 97 (2), 93–99.
- Urrutia, J., Montalvo, C., Scillato Yané, G.J., 2008. *Dasyopodidae (Xenarthra, Cingulata)* de la Formación Cerro Azul (Mioceno tardío) de la provincia de La Pampa, Argentina. *Ameghiniana* 45 (2), 289–302.
- Verzi, D.H., Quintana, C.A., 2005. The caviomorph rodents from the San Andrés Formation, east-central Argentina, and global Late Pliocene climatic change. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 219, 303–320.
- Verzi, D.H., Montalvo, C.I., Deschamps, C.M., 2008. Biostratigraphy and biochronology of the Late Miocene of central Argentina: evidence from rodents and taphonomy. *Geobios* 41, 145–155.
- Villarroel, A.C., Marshall, L.G., 1989. A new fossil land mammal locality of Late Miocene (Huayquerian) Age from Muya Huasi, southcentral Bolivia. *Bol. Serv. Geol. Boliv.* 4, 27–40, (ser. A).
- Visconti, G., Melchor, R.N., Montalvo, C.I., Umazano, A.M., de Elorriaga, E.E., 2010. Análisis litoestratigráfico de la Formación Cerro Azul (Mioceno Superior) en la Provincia de La Pampa. *Rev. Asoc. Geol. Argent.* 67 (2), 257–265.
- Vucetich, M.G., 1984. Los roedores de la Edad Friasense (Mioceno Medio) de Patagonia: *Revista del Museo de La Plata, Nueva Serie. Paleontología* 8, 47–126.
- Waterhouse, G.E., 1839. Observations on the Rodentia, with a view to point out the groups, as indicated by the structure of the crania in this order of mammals. *Mag. Nat. Hist.* 3, 90–96.
- Woodburne, M.O., 2004. *Late Cretaceous and Cenozoic Mammals of North America. Biostratigraphy and Geochronology*. Columbia University Press.
- Woodburne, M.O., 2010. The Great American biotic Interchange: dispersals, tectonics, climate, sea level and Holding pens. *J. Mammalian Evol.* 17, 245–264.
- Zárate, M.A., Schultz, P.H., Blasi, A., Heil, C., King, J., Hames, W., 2007. Geology and geochronology of type Chasicuan (late Miocene) mammal-bearing deposits of Buenos Aires (Argentina). *J. S. Am. Earth Sci.* 23, 81–90.
- Zimicz, N., 2014. Avoiding competition. The ecological history of late Cenozoic metatherian carnivores in south America. *J. Mammalian Evol.* 21, 383–393.
- Zittel, K.A. Von, 1893. *Handbuch der Palaeontologie. Abteilung I. Palaeozoologie. Band IV, Vertebrata (Mammalia)*. Munich. R. Oldenbg. 11, 799.