

# Megatherioidea (Mammalia, Xenarthra, Tardigrada) from the Pinturas Formation (Early Miocene), Santa Cruz Province (Argentina) and their chronological implications

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**Abstract** Pyroclastic and epiclastic continental sediments bearing the “fauna Astrapothericulense” from the Pinturas Formation of Ameghino crop out mainly at several localities at the upper valley of the Pinturas River and its tributaries, northwestern Santa Cruz Province, Argentina. These continental sediments are referred to the Burdigalian Stage and constitute the basis for the recognition of the Pinturas Formation. The fauna recorded in the Pinturas Formation mainly consists of mammals, specially rodents, native ungulates, xenarthrans and primates. Here we describe the first association of Megatherioidea (Mammalia, Xenarthra, Tardigrada) from different localities of the Pinturas Formation with accurate geographic and stratigraphic provenance. The Megatherioidea from the Pinturas Formation presented herein are represented by (1) *Schismotherium* cf. *binum*; (2) *Hapalops* sp.; and (3) a Megatherioidea indet. In addition, the holotypes of *Schismotherium binum* (MACN A 11750), *Hapalops curvus* (MACN A 11140), and *Pelecycodon arcuatus* were

collected from the “fauna Astrapothericulense” of Ameghino; unfortunately, it is not easy to determine if they were collected from the Pinturas Formation since they are part of Ameghino’s Collection (MACN), but were collected a time when the Pinturas Formation had not yet been proposed. The presence of a species of *Schismotherium* and of *Hapalops* in the Pinturas Formation represent accurate early records for these genera, but not necessarily the earliest. The age of the Pinturas Formation could overlap, partially or totally, with the age of the Santa Cruz Formation at the Atlantic coast, where most Early Miocene Megatherioidea were collected.

**Keywords** Ground sloths · Burdigalian stage · Diversity · South America

**Kurzfassung** Verschiedene Fundstellen mit vulkano-klastischen und epiklastischen Sedimenten im oberen Tal des Pinturas-Flusses und dessen Nebenflüssen im Nordwesten der Provinz Santa Cruz in Argentinien enthalten die

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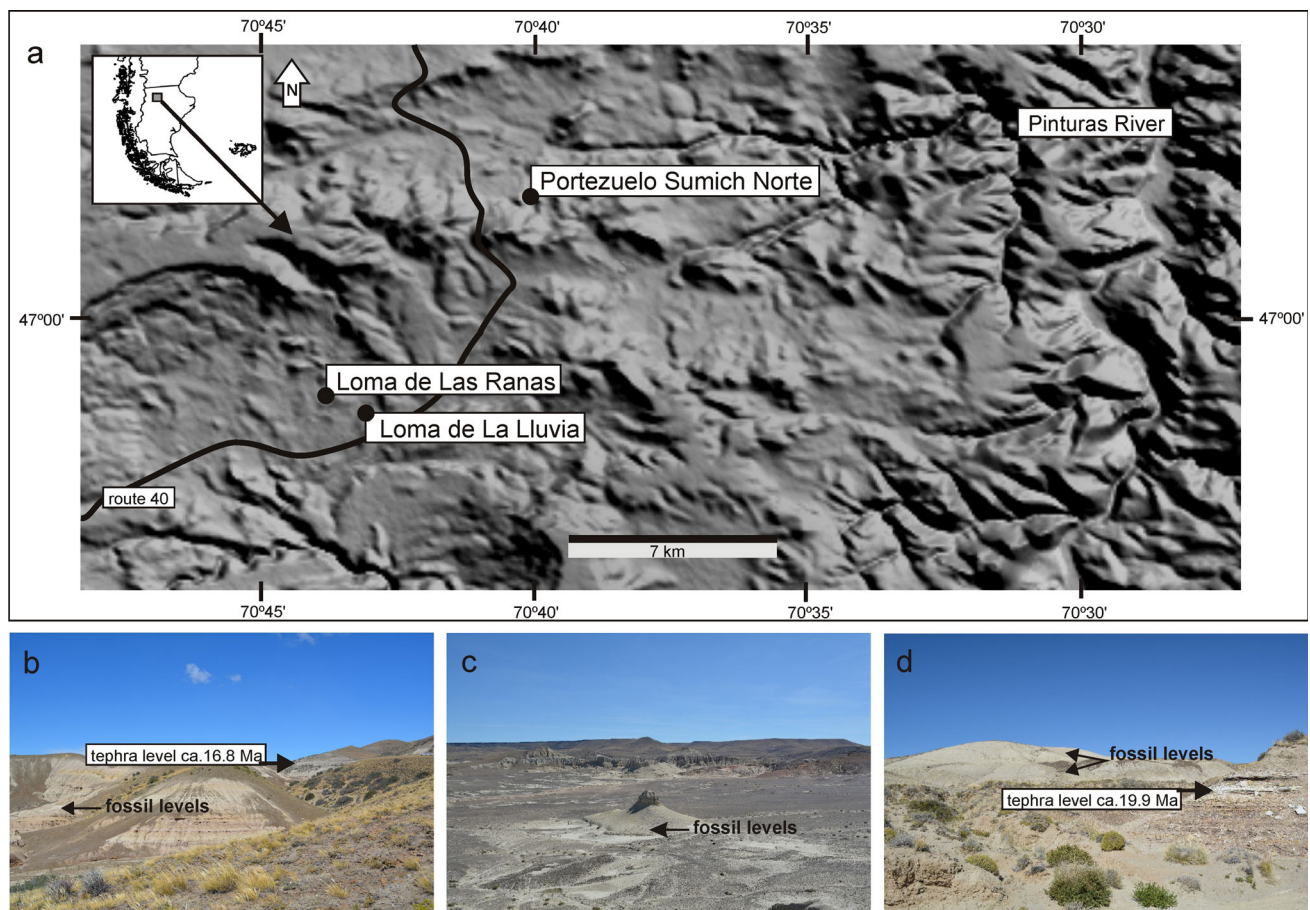
“Astrapothericulense” Fauna von Ameghino. Diese kontinentalen Sedimente repräsentieren die Burdigalia-Zone und bilden die Grundlage für die Pinturas-Formation. Die Fauna der Pinturas-Formation besteht hauptsächlich aus Mammaliern, vor allem Rodentiern, Ungulaten, Xenarthren und Primaten. Wir beschreiben hier die erste Vergesellschaftung von Megatheroiden (Mammalia, Xenarthra, Tardigrada) aus verschiedenen Fundstellen der Pinturas-Formation, für die genaue stratigraphische und geographische Daten vorliegen. Die hier beschriebenen Megatherioidea aus der Pinturas Formation sind (1) *Schismotherium* cf. *binum*, (2) *Hapalops* sp. und (3) Megatherioidea indet. Darüber hinaus wurden die Holotypen von *Schismotherium binum* (MACN A 11750), *Hapalops curvus* (MACN A 11140) und *Pelecycodon arcuatus* aus der Astrapothericulense-Fauna von Ameghino untersucht; leider lässt es sich nicht einfach, feststellen, ob sie aus der Pinturas Formation stammen, da sie Teil der Ameghino-Sammlung (MACN) sind und zu einer Zeit aufgesammelt wurden, als die Pinturas-Formation noch nicht vorgeschlagen worden war. Das Vorhandensein einer Art von *Schismotherium* und von *Hapalops* in der Pinturas

Formation stellen die ältesten gesicherten Nachweise dieser Gattungen, allerdings nicht unbedingt die ältesten Nachweise überhaupt dar. Das Alter der Pinturas-Formation könnte ganz oder teilweise dem der Santa Cruz-Formation an der Atlantikküste entsprechen, von wo die meisten früh-miozänen Megatheroiden gesammelt wurden.

**Schlüsselwörter** Faultier · Burdigalian Bühne · Verschiedenheit · Südamerikas

## Introduction

Pyroclastic and epiclastic continental sediments bearing the “fauna Astrapothericulense” of Ameghino (Ameghino 1900, 1901, 1902, 1906), which the author located into a succession of faunas between the “Colpodonense” (=Colhuehuapian South American Land Mammal Age—SALMA—; Simpson 1940) and the “Notohippidense” (=basal part of the Santacrucian SALMA), crops out at several localities at the upper valley of the Pinturas River and its tributaries, northwestern Santa Cruz Province,



**Fig. 1** Study area. **a** Location map of the localities of the Pinturas Formation with Megatherioidea; **b** outcrops at Portezuelo Sumich Norte; **c** outcrops at Loma de Las Ranas; **d** outcrops at Loma de La Lluvia

Argentina (Fig. 1). In particular, the continental sediments that crop out at Estancia Ana María (Santa Cruz Province) constitute the type section of the Pinturas Formation (Bown et al. 1988; Bown and Larriestra 1990) and are referred to the Burdigalian Stage (Early Miocene, Fig. 2). However, given that sediments assigned to the Pinturas and Santa Cruz Formations crop out in the upper valley of Pinturas River (de Barrio et al. 1984), it is not clear if the entire collection of fossil mammals mentioned by Ameghino from his “fauna Astrapothericulense” were collected from the Pinturas Formation.

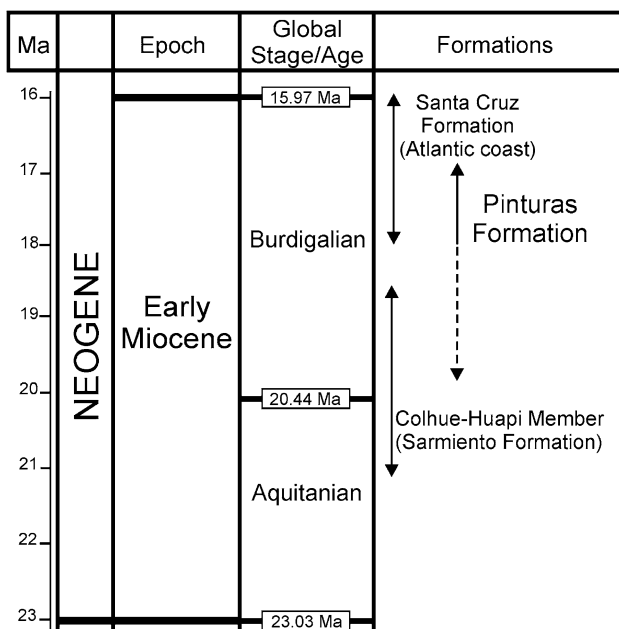
For the Pinturas Formation, Bown et al. (1988) and Bown and Larriestra (1990) recognized lower, middle and upper sequences separated by unconformities. Bown and Fleagle (1993) and Fleagle et al. (1995) suggested that lower and middle sequences of the Pinturas Formation may have been deposited prior to the basal levels of the Santa Cruz Formation at the Atlantic coast; although Perkins et al. (2012) indicated that the Pinturas Formation is coeval with the lower portion of Santa Cruz Formation (Fig. 2). The fauna recorded in the Pinturas Formation mainly consists of mammals, specially rodents, native ungulates, xenarthrans (i.e., Cingulata and Tardigrada) and primates (see Fleagle et al. 1987; Bown and Fleagle, 1993; Kramarz and Bellosi 2005; Kramarz and Bond 2005; Tejedor 2005; Goin et al. 2010; Chornogubsky and Kramarz 2012; Novo and Fleagle 2015). Among the Tardigrada, most of the remains consist of isolated teeth, fragmentary dentaries, and isolated bones of manus and pes. Studies of the fossil mammals recovered from this formation indicate a

“Pinturan faunistic association” (different from those of the older Colhuehuapian SALMA and the younger Santacrucian SALMA), in the lower and middle sequences, whereas the fauna of the upper sequence corresponds to the typical mammals recorded from the Santa Cruz Formation on the Atlantic coast (Kramarz and Bellosi 2005; Kramarz and Bond 2005; Kramarz et al. 2010).

The clade Megatherioidea (Xenarthra, Tardigrada) includes the families Megalonychidae, Nothrotheriidae and Megatheriidae, and some genera recorded from the Miocene of Patagonia, considered as basal Megatherioidea (or genera of uncertain affinities) (Gaudin 2004). The basal Megatherioidea principally include the following genera and species: *Schismotherium* with *Schismotherium fractum*, *S. splendens* and *S. binum* (see Ameghino 1887, 1899); *Peleciodon* with *P. arcuatus*, *P. cristatus*, *P. maximus*, *P. petraeus*, and *P. robustus* (see Ameghino 1891); several species of *Hapalops* (e.g., *H. longipalatus*, *H. rectangularis*, *H. curvus*) and two species of *Analcimorphus* (i.e., *A. inversus*, *A. giganteus*) (Ameghino 1887, 1899; Scott 1903, 1904; Mones 1986). Although these species were described by Ameghino, studies by Scott (1903, 1904) in which he described, compared and figured specimens recovered from the Santa Cruz Formation, allowed for a better understanding of their characteristics and relationships.

Compared to other Early Miocene faunas (e.g., Santacrucian SALMA), the species richness of Megatherioidea from the “fauna Astrapothericulense” is low, and comprises just three species of basal Megatherioidea (*Schismotherium binum*, *Hapalops curvus*, *Peleciodon arcuatus*) and the Preprotheriinae *Propreotherium deseadense* (Ameghino 1901, 1902). In contrast, the genus *Hapalops* in the Santa Cruz Formation alone has more than 20 described species (although most are based on partial or fragmentary specimens, De Iuliis and Pujos 2006; De Iuliis et al. 2014). It is important to note that the species from the “fauna Astrapothericulense” are poorly characterized, and in some cases, the holotypes were not identified by Ameghino (the author did not provide catalog number or illustrations) or were considered lost (Mones 1986). *Schismotherium binum* and *H. curvus*, the first species of Megatherioidea from the “fauna Astrapothericulense”, were named by Ameghino (1899) before he defined this fauna. In addition, the precise geographic and stratigraphic provenance of these species are unknown; therefore, it is not clear if they were collected in the Pinturas Formation.

The aim of this contribution is to present remains of Megatherioidea recovered from different localities within the Pinturas Formation, and to compare them mainly with the Megatherioidea described by Ameghino for his “fauna Astrapothericulense”. The remains presented herein are the first ones from Pinturas Formation with accurate geographic and stratigraphic provenance (i.e., sequence into the formation), descriptions, and illustrations.



**Fig. 2** Geochronology of the Early Miocene; modified from Perkins et al. (2012), Dunn et al. (2013) and Cohen et al. (2013)

## Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA; FMNH: Field Museum of Natural History, Chicago, USA; MACN A: Colección Ameghino, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MLP: División Paleontología Vertebrados, Museo de La Plata, La Plata, Argentina; MPM-PV: Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Argentina; YPM-PU: Yale Peabody Museum (Princeton University collection), New Haven, USA.

## Anatomical abbreviations

c, caniniform; m1–3, molariform 1–3.

## Materials and methods

The following species and specimens were used for comparison: *Schismotherium binum* (MACN A 11750; “fauna Astrapothericulense”, Pinturas Formation?), *S. fractum* (MACN A 6446—as part of MACN A 6445-70, FMNH P13137, YMP PU 15361, YMP PU 15901; Santa Cruz Formation), *S. splendens* (YPM PU 15590; Santa Cruz Formation), *Pelecypodon arcuatus* (AMNH PV 9240, MACN A 4656; Santa Cruz Formation), *P. cristatus* (MACN A 4651-53; Santa Cruz Formation), *P. robustus* (MACN A 4665; Santa Cruz Formation), *Hapalops curvus* (MACN A 11140, “fauna Astrapothericulense”, Pinturas Formation?); *H. longipalatus* (MACN A 4513-16; Santa Cruz Formation), *H. crassignathus* (MACN A 4524; Santa Cruz Formation), *H. minutus* (MACN A 4527; Santa Cruz Formation), *H. cylindricus* (MACN A 4525; Santa Cruz Formation), *H. rectangularis* (MACN A 2089-90; Santa Cruz Formation), *Analcimorphus inversus* (MACN A 4626-28; Santa Cruz Formation), *A. giganteus* (MACN A 6499-6503, Santa Cruz Formation).

The dentition of the species of *Hapalops* and *Analcimorphus* is composed of five upper and four lower teeth, with a diastema between the first tooth usually identified as caniniform (C/c), and the rest of the teeth usually identified as molariforms (M/m). *Schismotherium* and *Pelecypodon*, with a dental formula of 5/4, do not have a diastema; however, the first tooth is smaller than the others and also has a different morphology (i.e., circular to subtriangular in outline), so the terms caniniform and molariforms will also be used for their dentition. For chronological purposes, we follow the International Chronostratigraphic Chart (International Commission on Stratigraphy 2015; Cohen et al. 2013) (Fig. 2).

## Geological setting

The Pinturas Formation is composed of up to 100 m of Miocene continental pyroclastic and eolian epiclastic sediments outcropping in the upper valley of the Pinturas River and its tributaries (Fig. 1a). It lies unconformably atop the Jurassic La Matilde Formation (Bahía Laura Group), and is divided by two intraformational erosional unconformities into three sequences: (a) the lower sequence, dominated by pyroclastic mudrocks upon which very mature paleosols were formed; (b) the middle sequence, composed largely by epiclastic sand occurring as barchanoid paleodunes; and (c) the upper sequence, consisting of massive, poorly bedded pyroclastic mudrocks (Bown et al. 1988; Bown and Larriestra 1990). The Pinturas Formation differs from the Santa Cruz Formation in the greater volume of pyroclastic materials, absence of marine intercalations, and the presence of mature paleosols in the lower sequence (Bown and Larriestra 1990).

The absolute ages of ca. 17.99 Ma near the base of the Pinturas Formation at Estancia el Carmen (47° 12' 44.64"S, 70° 34' 97"W), and ca. 16.8 Ma in the Santa Cruz Formation that overlies the Pinturas Formation at Portezuelo Sumich Norte (see Perkins et al. 2012 and Fleagle et al. 2012) (Fig. 1b) indicate that the lower and middle sequences from the Pinturas Formation would be similar in age to those from the coastal localities of the Santa Cruz Formation (“typical Santacrucean fauna”) with ages of ca. 18–16 Ma (Bown and Fleagle 1993; Fleagle et al. 1995; Tejedor et al. 2006; Perkins et al. 2012), and younger than those from the lower Fossil Zone of the Colhue-Huapi Member of the Sarmiento Formation (“Colhuehuapian fauna”) (Kramarz et al. 2010) with ages of ca. 20.4–20.0 Ma (Ré et al. 2010) or 21.11–18.62 Ma (Dunn et al. 2013) (Fig. 2).

In the locality of Portezuelo Sumich Norte (46° 57' 33.09"S, 70° 40' 2"W; Fig. 1a, b), numerous fossil remains (including primates) come from opposite sides of a badland ridge that probably preserves a part of the base of the middle sequence that has filled a scour cur into the top of the lower sequence (Bown and Larriestra 1990 fig. 9a; T. Bown, Pers. Com). There is an absolute age of ca. 16.8 Ma from a tuff of the Santa Cruz Formation that lies unconformably over the top of the Pinturas sequence (Bown and Larriestra 1990; Perkins et al. 2012; Fleagle et al. 2012); in Loma de Las Ranas (=Estancia Ana María) (47° 1' 29.90"S, 70° 43' 50.25"W; Fig. 1a, c), fossils came from the middle sequence which crops out at the base of a pointed hill; and in Loma de La Lluvia (47° 1' 47.03"S, 70° 43' 7.72"W; Fig. 1a, d), the fossils from the middle sequence that at this locality lies above a tephra level of ca. 19.9 Ma, which is not a confident age, and the

relationships of this level with others from Pinturas Formation are still unclear (Perkins et al. 2012; Fleagle et al. 2012).

### Systematic paleontology

XENARTHRA Cope, 1889.

TARDIGRADA Latham and Davies in Forster, 1795.

MEGATHERIOIDEA Gray, 1821.

*Schismotherium* Ameghino, 1887.

*Type species: Schismotherium fractum* Ameghino, 1887.

*Schismotherium* cf. *binum*.

Figure 3a, b.

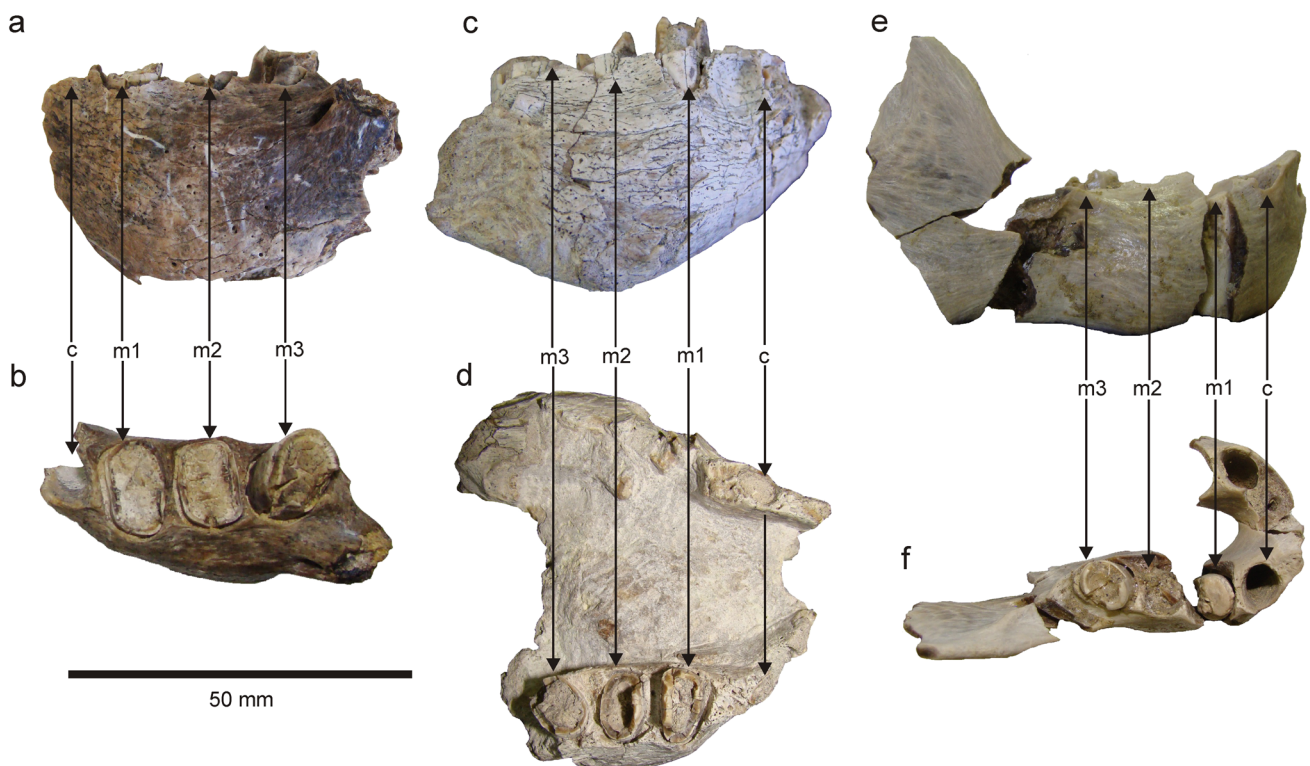
*Referred specimen:* MPM-PV 17405, fragmentary left dentary that preserves the alveolus of the first tooth (c) and three molariforms (m1-m3) (Fig. 3a, b).

*Geographic and stratigraphic provenance:* Loma de La Lluvia, Santa Cruz Province; middle sequence, Pinturas Formation (Early Miocene) (Fig. 1a, d).

*Description:* MPM-PV 17405 is represented by a fragment of a left dentary that preserves the alveolus of the first tooth

and the three molariforms (m1–m3), although not well preserved. The complete tooth row (c-m3) is 40 mm in length, whereas the molariform tooth row (m1–m3) is 32 mm in length, and the depth of the dentary is 29 mm (measured on the plane of the medial part of m2). The alveolus of the caniniform is small and it is separated from the molariforms by a thin septum. The first molariform is elliptic-trapezoidal in outline, but its occlusal surface is not preserved. The m2 is rectangular in cross-section but with rounded edges, but its occlusal surface is not preserved. The m3 is subcircular to oval in outline. The posterolateral opening of the mandibular canal lies below the alveolar plane and posterior to the posterior face of the m3.

*Comments:* Among the basal Megatherioidea (Gaudin 2004), the absence of a diastema between the first tooth and the molariform tooth row is a common feature in species of the genera *Schismotherium* and *Pelecycodon* (see Scott 1903, 1904; Gaudin 2004). Nevertheless, and although most of the species of those genera are similar in size (Table 1), *Pelecycodon* is slender and *Schismotherium* a little more robust (Scott 1903, 1904). Specimen MPM-PV 17405 is larger than most of the species of *Pelecycodon* and *Schismotherium fractum*, but it is similar in size to *Schismotherium binum* (Table 1). The absence of a diastema, the general morphology and the size of MPM-PV 17405 are



**Fig. 3** Dentaries and mandibles of Megatherioidea from the Pinturas Formation. **a, b** *Schismotherium* cf. *binum*. (MPM-PV 17405); **c, d** *Hapalops* sp. (MPM-PV 17409); **e, f** Megatherioidea indet. (MPM-PV 17407); **a, c, e** lateral view; **b, d, f** occlusal view

**Table 1** Measurements (in mm) of the mandibles and dentaries of basal Megatherioidea

Species and specimen	TL	MTL	cL	cW	m1L	m1W	m2L	m2W	m3L	m3W	DD
<i>Schismotherium</i> cf. <i>binum</i> MPM-PV 17405	40	32	6	6.5	8	13.2	8	13	10	11.3	29
<i>Schismotherium binum</i> MACN A 11750	–	31	–	6.8	9.5	14	9	13	10.3	12	29
<i>Schismotherium fractum</i> MACN A 6446 left	34	29.5	7.9	6	6.5	9.3	6	10	8.1	8.9	28
<i>Schismotherium fractum</i> MACN A 6446 right	34.2	29.5	7.9	6.3	7	10	6.2	10	8.2	8.9	27.5
<i>Schismotherium fractum</i> YMP PU 15901	32.6	24	6.2	4.4	6	9.1	6.3	10.9	7.5	9.6	29.6 <sup>a</sup>
<i>Schismotherium fractum</i> YMP PU 15361	32	25.1	5.7	5.1	7	9.5	7.6	10	8.8	8.3	24.4
<i>Peleciodon arcuatus</i> AMNH 9240	29.2	22.7	3.8	3.2	4.7	7.6	5	8.2	6.2	7.5	22.5
<i>Peleciodon arcuatus</i> MACN A 4656	32.5	23.6	5 <sup>a</sup>	4 <sup>a</sup>	5.9	9.5	6	9.5	7.8	9	24
<i>Peleciodon cristatus</i> MACN A 4651-53 left	30	21.5	–	–	5.5	8	6	9	6.8	7.3	24.1
<i>Peleciodon cristatus</i> MACN A 4651-53 right	–	22.7	–	–	6	8.5	6	9	6.2	7.1	23
<i>Peleciodon robustus</i> MACN A 4655	30	22	7	5.5	6	8	5.8	8.2	7.2	7	–
<i>Hapalops</i> sp. MPM-PV 17409	34	25	6.5	4	5.8	10	6.2	9	9.5	8.7	23
<i>Hapalops curvus</i> MACN A 11140	35	28	–	–	–	–	–	–	–	–	21
<i>Hapalops longipalatus</i> MACN A 4515 right	37	24.8	4.5	3.7	6.2	9.2	6	9.2	7.5	8	26
<i>Hapalops longipalatus</i> MACN A 4516 left	36	23	4 <sup>a</sup>	4 <sup>a</sup>	5.5	8.8	6	8.8	7.8	8	26
<i>Hapalops rectangularis</i> MACN A 2090 left	38	27	6	4.5	6.8	9	7	9	8	8.5	24.5
<i>Hapalops rectangularis</i> MACN A 2089 right	37	27	6	–	7	9.1	7.1	10	8	8.4	24
<i>Hapalops cylindricus</i> MACN A 4525	–	–	–	–	–	–	5.8	8	7	7	–
<i>Hapalops minutus</i> MACN A 4527	–	20	–	–	5.5	7.5	5	7	7.1	6	16
<i>Hapalops crassignathus</i> MACN A 4524	–	–	–	–	–	–	6	9.2	7	6.5	20
<i>Analcimorphus inversus</i> MACN A 4627	31	20.5	3.8	3.5	5	6	5	6.2	6.5	6.5	19
<i>Analcimorphus inversus</i> MACN A 4628	–	–	4	3.8	5.5	6.5	5	6.5	–	–	19
<i>Analcimorphus giganteus</i> MACN A 6500 left	53 <sup>a</sup>	33	–	–	8	12.5	7.1	12.8	10	12	42 <sup>a</sup>
Megatherioidea indet. MPM-PV 17407	33.5	26	6	8	6.8	8.5	6.8	–	9	8.5	27

TL total length of the tooth row, MTL molariform tooth row length, c caniniform, m molariform, L length, W width, DD dentary depth

<sup>a</sup> Approximate

similar features to those present in *Schismotherium binum* (MACN A 11750); although in MACN A 11750, the m1 is a bit more trapezoidal in outline. In addition to the different size, differences between *Schismotherium binum* (MACN A 11750) and MPM-PV 17405 with *S. fractum* (MACN A 6446, FMNH P13137, YMP PU 15361, YMP PU 15901) and *S. splendens* (YMP PU 15590) are evident in the relatively oval shape and the tapered labial edges of the molariforms present in the latter species. The mentioned similarities allow for the referring of MPM-PV 17405 to *Schismotherium* cf. *binum*.

*Hapalops* Ameghino 1887.

*Type species: Hapalops rectangularis* Ameghino 1887.

*Hapalops* sp.

Figure 3c, d.

*Referred specimen:* MPM-PV 17409, mandibular fragment containing three poorly preserved right molariforms, the right caniniform (partially preserved) and the left

mandibular body with the alveolus of the caniniform (Fig. 3c, d).

*Geographic and stratigraphic provenance:* Portezuelo Sumich Norte, Santa Cruz Province; recovered from a carbonaceous mudstone, lower-middle sequences boundary, Pinturas Formation (Early Miocene) (Fig. 1a, b).

*Description:* the complete right tooth row (c-m3) is nearly 34 mm long, whereas the molariform tooth row is 25 mm in length; the depth of the dentary is 23 mm (measured on the plane of the medial part of m2). The alveolus of the caniniform is small and oval in outline and it is separated from the molariforms by a diastema of 7 mm in length. The m1 is elliptic-subtriangular in outline; its occlusal surface is broken. The m2 is nearly oval in outline. The m3 is subcircular to oval in outline; its main axis is deviated from the anteroposterior axis. The ventral margin of the dentary is convex.

*Comments:* The presence of a diastema between the caniniform and the molariform tooth row is a common

feature in species of the genera *Hapalops* and *Analcimorphus* (see Scott 1903, 1904; Gaudin 2004). The general morphology present in MPM-PV 17409 is similar to that of *Hapalops curvus* (MACN A 11140, e.g., size, length of the diastema between the caniniform and the molariform tooth row, shape of the ventral margin of the dentary). However, the described features are also present in other species of the genus; therefore, we assign MPM-PV 17409 to *Hapalops* sp.

Megatherioidea indet.

Figure 3e, f.

*Referred specimen:* MPM-PV 17407, mandibular fragment that preserves two poorly preserved right molariforms, part of the right coronoid process, the symphysis and the alveoli of both caniniforms (Fig. 3e, f).

*Geographic and stratigraphic provenance:* Loma de Las Ranas, Santa Cruz Province; middle sequence, Pinturas Formation (Early Miocene) (Fig. 1a, d).

*Description:* The complete tooth row (c-m3) is 33.5 mm long, whereas the molariform tooth row is 26 mm in length; the depth of the dentary is 27 mm (measured on the plane of the medial part of m2). The alveolus of the caniniform is small, it is oval in outline, and it is separated from the molariforms by a thin septum. The m1 is elliptic-rectangular in outline. The occlusal surface is broken. The alveolus of m2 is not well preserved. The m3 is subcircular to oval in outline; its main axis is deviated from the anteroposterior axis. The posterior margin of the mandibular symphysis is located a little forward of the medial part of the caniniform and it is markedly straight (as a vertical wall). The mental foramen is located anterior to the alveolus of the caniniform (at 6 mm). The posterolateral opening of the mandibular canal lies below the plane of the alveolar level and on the plane of the medial part of m3, at the base of the ascending ramus.

*Comments:* Specimen MPM-PV 17407 shows some features (e.g., length of the dental series, absence of diastema) similar to those described for the species of *Schismotherium* (e.g., *S. fractum*, *S. binum*) and *Peleciodon*. In particular, it is similar in size to *S. fractum* (Table 1); whereas *S. binum* is more robust. However, the location and shape of the posterior margin of the mandibular symphysis, the location of the mental foramen, and the orientation of the main axis of m3, differ from those present in *S. fractum* and *Peleciodon arcuatus*. In specimen MPM-PV 17407, the posterior margin of the mandibular symphysis lies anterior to the medial part of the caniniform, and it is vertical, whereas in *S. fractum* and *Peleciodon arcuatus*, the margin is located more posterior and is oblique (i.e., from anterodorsal to ventroposterior). The

mental foramen in MPM-PV 17407 is anterior to the alveolus of the caniniform, whereas in *S. fractum* and *Peleciodon arcuatus* this opening is more anteriorly located. The outline of the m3 in MPM-PV 17407 is subcircular to oval, with its main axis oblique to the anteroposterior axis, whereas in *S. fractum* and *Peleciodon arcuatus*, the m3 is oval in outline with its main axis transversal to the anteroposterior axis. These differences prevented us from assigning specimen MPM-PV 17407 to a definite genus or species of basal Megatherioidea; therefore, it is herein referred to Megatherioidea indet.

## Discussion

The first records of Megatherioidea from “fauna Astrapothericulense” of Ameghino correspond to *Schismotherium binum* and *Hapalops curvus*, which were briefly mentioned by Ameghino (1899). Ameghino (1906) included the basal Megatherioidea *Schismotherium binum*, *Hapalops curvus*, *Peleciodon arcuatus*, and the Preprotheriinae *Propreprotherium deseadense* in his “fauna Astrapothericulense”. However, none of these species were diagnosed, unambiguously described, or figured. In addition, the precise geographic and stratigraphic provenance of these species are unknown, therefore making it difficult to assign their provenance to the Pinturas Formation. The original specimens used to erect the mentioned species are part of Ameghino’s Collection (MACN), from a time when the Pinturas Formation had not yet been proposed.

Regarding *Schismotherium binum*, Ameghino (1899) did not identify a holotype for this species. Although Mones (1986) considered the holotype to be lost, taking into account the few features noted by Ameghino (1899) (i.e., size, location of the posterolateral opening of the mandibular canal) of the specimen that he used to erect the species and the morphology present in MACN A 11750 (the only specimen of *Schismotherium* that comes from the “fauna Astrapothericulense” and housed at MACN as part of the Ameghino’s Collection, according to the catalogue of MACN), it is probable that MACN A 11750 corresponds to the specimen used to erect *S. binum*.

Regarding *Hapalops*, the genus is composed of more than 20 species (Mones 1986; De Iuliis and Pujos 2006), and only one (*H. curvus*) has been reported from the “fauna Astrapothericulense”. As with *S. binum*, Ameghino (1899) did not identify a holotype for *H. curvus* and Mones (1986) considered that the holotype to be lost, but judging from the brief comment given by Ameghino (1899) on the specimen that he used to erect the species, and the morphology present in MACN A 11140, it is highly probable that MACN A 11140 (the only specimen of *Hapalops* that comes from the “fauna Astrapothericulense” and housed at

MACN as part of the Ameghino's Collection) could be the holotype of *H. curvus*.

The specimens described herein are included into the basal Megatherioidea (see Gaudin 2004). The specimen MPM-PV 17405 is very similar to *Schismotherium binum* (MACN A 11750) and MPM-PV 17409 is similar to *Hapalops curvus* (MACN A 11140), although a systematic review of *Hapalops* (which includes more than 20 species, most of them erected on fragmentary remains) and the allied genera (e.g., *Xyophorus* from the Santa Cruz Formation) is needed (see Brandoni 2014). The specimen MPM-PV 17407 shares with species of *Schismotherium* and *Pelecycodon* the absence of diastema between the canine and the molariform toothrow; whereas in the species of *Hapalops* and *Analcimorphus*, the diastema is present. However, the morphological differences observed between specimen MPM-PV 17407 and species of the genera *Schismotherium* and *Pelecycodon* suggest that MPM-PV 17407 could not be placed in the known species of these genera (e.g., *S. fractum*, *S. binum*, *P. arcuatus*). Despite this, we believe it to be more convenient to refer this specimen to Megatherioidea indet. until new information allows for a more accurate analysis and placement of the specimen in a known species, or the description of a new taxon.

Ameghino (1906) considered that *Schismotherium binum*, *Hapalops curvus* and *Pelecycodon arcuatus* were present in the beds with *Astrapothericulus*, and they were not in the immediately older Colhuehuapian levels (i.e., *Colpodon* beds) or the younger fauna (Santacrucian SALMA, i.e., Santa Cruz Formation) (Fig. 2). However, Scott (Scott 1903, 1904) indicated the presence of *Pelecycodon arcuatus* in the Santa Cruz Formation. In addition, Ameghino (1897) described *Hapalops antistis* from the late Oligocene of Patagonia, although the assignment of *H. antistis* to *Hapalops* is doubtful (Carlini and Scillato-Yané 2004; Pujos and De Iuliis 2007) or incorrect (López et al. 2011). *Schismotherium*, *Pelecycodon* and *Hapalops* were mainly recorded from the Santa Cruz Formation (e.g., *S. fractum*, *S. splendens*, *P. arcuatus*, *P. cristatus*, *Hapalops elongatus*, *H. ruetimeyeri*, *H. indifferens*), and from the “fauna *Astrapothericulense*” (i.e., *S. binum*, *P. arcuatus*, *H. curvus*).

As described above, the new fossil remains presented herein come from the lower or middle sequences of the Pinturas Formation. Considering the fact that *Schismotherium binum*, *Hapalops curvus* and *Pelecycodon arcuatus* were collected from the “fauna *Astrapothericulense*”, but not necessarily from the Pinturas Formation, the records of *Schismotherium* cf. *binum*, *Hapalops* sp., and Megatherioidea indet. presented herein would be the first undoubted records of Megatherioidea for the Pinturas Formation.

Considering the stratigraphic relationships, the absolute ages, the correlations with other Early Miocene units (i.e., the fauna of the lower and middle sequences of the Pinturas Formation are different to those of the Santa Cruz Formation at the Atlantic coast), it follows that the presence of a species of *Schismotherium* at the middle sequence of the locality Loma de La Lluvia, and *Hapalops* sp. in the lower-middle sequences boundary of the locality Portezuelo Sumich Norte represent accurate early records for these genera, but not necessarily the earliest.

Fleagle et al. (1995) indicated that at least the lower and middle sequences of the Pinturas Formation are older than 16.5 Ma, whereas the deposits of the Santa Cruz Formation in the Atlantic coast (i.e., Monte Leon and Cerro Observatorio) bearing Santacrucian mammals are younger than 16.5 Ma. Most biochronological studies (e.g., Bown and Fleagle 1993; Kramarz and Bellosi 2005; Kramarz and Bond 2005; Kramarz et al. 2010) agreed with these correlations. However, Perkins et al. (2012) indicated that the Santa Cruz Formation at the Atlantic coast spans the interval of 18–16 Ma. Considering the accurate ages for the Santa Cruz Formation at the Atlantic coast and the Pinturas Formation (i.e., 18–16 Ma. for the Santa Cruz Formation, and 17.99 for the base of the Pinturas Formation), and the doubtful age for the locality of Loma de La Lluvia (ca. 19.9 Ma), the age of the Pinturas Formation could overlap, partially or totally, the age of the Santa Cruz Formation at the Atlantic coast (Fig. 2), where most of Early Miocene Megatherioidea were collected. In particular, remains of *Hapalops* sp. were collected from the Estancia La Costa Member (Santa Cruz Formation) at the locality of Puesto Estancia La Costa (Vizcaíno et al. 2010), a very rich fossil locality with absolute ages of ca. 17.5 Ma (Perkins et al. 2012; Fleagle et al. 2012).

## Summary

The first records of Megatherioidea represented by *Schismotherium* cf. *binum*, *Hapalops* sp., and a Megatherioidea indet. from the Pinturas Formation are presented. Among the basal Megatherioidea, the holotypes of *Schismotherium binum*, *Hapalops curvus*, *Pelecycodon arcuatus* were collected from the “fauna *Astrapothericulense*” of Ameghino, but it is not easy to determine if they were recorded at Pinturas Formation, given that the specimens are part of the Ameghino's Collection (MACN) and were collected from a time when the Pinturas Formation had not yet been proposed. The specimens MACN A 11750 and MACN A 11140 are identified as the probable holotypes of *Schismotherium binum* and *Hapalops curvus*, respectively. The presence of a species of *Schismotherium* at the middle sequence of the locality Loma de La Lluvia, and *Hapalops*



sp. in the lower-middle sequences boundary at the locality Portezuelo Sumich Norte represent accurate and undoubted early records for these genera, but not necessarily the earliest. The age of the Pinturas Formation could overlap, partially or (less probably) totally, the age of the Santa Cruz Formation at the Atlantic coast, where most of Early Miocene Megatherioidea were collected.

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## References

- Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles colectados por Carlos Ameghino en los terrenos eocenos de Patagonia austral y depositados en el Museo de La Plata. *Boletín del Museo de La Plata* 1: 1–26.
- Ameghino, F. 1897. Mammifères crétacés de l'Argentine. Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*. *Boletín del Instituto Geográfico Argentino* 18: 1–117.
- Ameghino, F. 1891. Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el Eoceno inferior de Patagonia austral. Especies nuevas, adiciones y correcciones. *Revista Argentina de Historia Natural* 1: 289–328.
- Ameghino, F. 1899. *Sinopsis geológico-paleontológica*, Suplemento (Adiciones y correcciones). pp. 1–13, Imprenta La Libertad, La Plata.
- Ameghino, F. 1900–1902. L'âge des formations sédimentaires de Patagonie. *Anales de la Sociedad Científica Argentina* 50: 109–130, 145–165, 207–229 (1900); 51: 20–39, 65–91 (1901); 52: 189–197, 244–250 (1901); 54: 161–180, 220–240, 283–342 (1902).
- Ameghino, F. 1906. Les Formations Sédimentaires du Crétacé Supérieur et du Tertiaire de Patagonie. *Anales del Museo Nacional de Buenos Aires* 15: 1–568.
- Bown, T.M., and J.G. Fleagle. 1993. Systematics, Biostratigraphy, and Dental Evolution of the Palaeothentidae, Later Oligocene to Early-Middle Miocene (Deseadan-Santacrucian) Caenolestoid Marsupials of South America. *Journal of Paleontology* 67: 1–76.
- Bown, T.M., and C.N. Larrister. 1990. Sedimentary paleoenvironments of fossil platyrrhine localities, Miocene Pinturas Formation, Santa Cruz Province, Argentina. *Journal of Human Evolution* 19: 87–119.
- Bown, T.M., C.N. Larrister, and D.W. Powers. 1988. Análisis paleoambiental de la Fm. Pinturas (Mioceno inferior) Provincia de Santa Cruz. *Actas 2ª Reunión Argentina de Sedimentología* 1: 31–35.
- Brandoni, D. 2014. “*Xyophorus*” sp. en el Mioceno Medio de Chubut: implicancias sistemáticas, biogeográficas y biocronológicas del registro de un Nothrotheriinae en el Neógeno de la Argentina. *Ameghiniana* 51(2): 94–105.
- Carlini, A.A., and G.J. Scillato-Yané. 2004. The oldest Megalonychidae (Xenarthra: tardigrada): phylogenetic relationships and an emended diagnosis of the family. *Neues Jahrbuch für Geologie und Paläontologie Abh.* 233: 423–443.
- Chornogubsky, L., and A.G. Kramarz. 2012. Nuevos hallazgos de Microbiotheriidae (Mammalia, Marsupialia) en la Formación Pinturas (Mioceno Temprano, Argentina). *Ameghiniana* 49: 442–450.
- Cohen, K.M., S.C. Finney, P.L. Gibbard, and J.-X. Fan. 2013. updated) The ICS International Chronostratigraphic Chart. *Episodes* 36: 199–204.
- Cope, E.D. 1889. The Edentata of North America. *American Naturalist* 23: 657–664.
- de Barrio, R.E., G. Scillato Yané, and M. Bond. 1984. La Formación Santa Cruz en el borde occidental del macizo del Deseado (provincia de Santa Cruz) y su contenido paleontológico. 9º Congreso Geológico Argentino (S.C. de Bariloche). *Actas* 4: 539–556.
- De Iuliis, G. and Pujos, F. 2006. On the systematic of *Hapalops* Ameghino, 1887 (Xenarthra: Megalonychidae). *Journal of Vertebrate Paleontology* 26 (3, supplement): 55A.
- De Iuliis, G., F. Pujos, N. Toledo, M.S. Bargo, and S.F. Vizcaíno. 2014. *Eucholoeops* Ameghino, 1887 (Xenarthra, Tardigrada, Megalonychidae) from the Santa Cruz Formation, Argentine Patagonia: implications for the systematics of Santacrucian sloths. *Geodiversitas* 36: 209–255.
- Dunn, R., R. Madden, M. Kohn, M. Schmitz, C. Strömberg, A. Carlini, G. Ré, and J. Crowley. 2013. A new chronology for middle Eocene-early Miocene South American Land Mammal Ages. *Geological Society of America Bulletin* 125: 539–555.
- Fleagle, J.G., T.M. Bown, C. Swisher, and G. Buckley. 1995. Age of Pinturas and Santa Cruz Formations. *Actas 4º Congreso Argentino de Paleontología y Biostratigrafía*: 129–135.
- Fleagle, J.G., D.W. Powers, G.C. Conroy, and J.P. Watters. 1987. New fossil platyrrhines from Santa Cruz Province, Argentina. *Folia Primatologica* 48: 65–77.
- Fleagle, J.G., M.E. Perkins, M.T. Heizler, B. Nash, M.T. Bown, A.A. Tauber, M.T. Dozo, and M.F. Tejedor. 2012. Absolute and relative ages of fossil localities in the Santa Cruz and Pinturas Formations; pp. 41–58 in S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (eds), *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press.
- Gaudin, T.J. 2004. Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence. *Zoological Journal of the Linnean Society* 140: 255–305.
- Goin, F.J., M.F. Tejedor, M.A. Abello, and G.M. Martin. 2010. Un nuevo microbiotherio (Mammalia, Marsupialia, Microbiotheria) de la Fm. Pinturas (Mioceno temprano). *Provincia de Santa Cruz. Ameghiniana* 47: 117–122.
- Gray, J.E. 1821. On the natural arrangement of vertebrate animals. *London Medical Repository* 5: 296–310.
- International Commission on Stratigraphy, 2015. International Chronostratigraphic Chart. [www.stratigraphy.org](http://www.stratigraphy.org).
- Kramarz, A.G., and E.S. Bellosi. 2005. Hystricognath rodents from the Pinturas Formation, Early-Middle Miocene of Patagonia, biostratigraphic and palaeoenvironmental implications. *Journal of South American Earth Sciences* 18: 199–212.
- Kramarz, A.G., and M. Bond. 2005. Los Litopterna (Mammalia) de la Formación Pinturas, Mioceno Temprano-Medio de Patagonia. *Ameghiniana* 42: 611–625.
- Kramarz, A.G., M.G. Vucetich, A.A. Carlini, M.R. Ciancio, M.A. Abello, C. M. Deschamps, and J.N. Gelfo. 2010. A new mammal fauna at the top of the Gran Barranca sequence and its biochronological significance in Gran Barranca; Biostratigraphy and Palaeoecology; pp. 264–277 in R.H. Madden, A.A. Carlini, M.G. Vucetich, and R.F. Kay (eds), *The Paleontology of Gran*

- Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia*. Cambridge University Press.
- Latham, J., and H. Davies. 1795. Faunula Indica id est Catalogus animalium Indiae orientalis. In: Forster, J.R. (Ed.) *Zoologia Indica*. Gebauer, Halle, 38 p.
- López, G.M., M.G. Vucetich, A.A. Carlini, M. Bond, M.E. Pérez, M.R. Ciancio, M. Pérez, A.I. Arnal, and A.I. Olivares. 2011. New Miocene mammal assemblages from Neogene Manantiales basin, Cordillera Frontal, San Juan, Argentina; pp. In *Cenozoic geology of the central andes of Argentina*, ed. J.A. Salfity, and R.A. Marquillas, 211–226. Salta: SCS Publisher.
- Mones, A. 1986. Paleovertebrata Sudamericana. Catálogo Sistemático de los Vertebrados fósiles de América del Sur. Parte I. Lista Preliminar y Bibliográfica. *Courier Forschungs-Institut Senckenberg* 82: 1–625.
- Novo, N.M., and J.G. Fleagle. 2015. New specimens of Platyrrhine primates from the early Miocene Pinturas Formation, Argentina. *Ameghiniana* 52: 367–372.
- Perkins, M.E., J.G. Fleagle, M.T. Heizler, B. Nash, T.M. Bown, A.A. Tauber, and M.T. Dozo. 2012. Tephrochronology of the Miocene Santa Cruz and Pinturas Formations, Argentina, pp. 23–40 in S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (eds), *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press.
- Pujos, F., and G. De Iuliis. 2007. Late Oligocene Megatherioidea fauna (Mammalia: xenarthra) from Salla-Luribay (Bolivia): new data on basal sloth radiation and Cingulata-Tardigrada split. *Journal of Vertebrate Paleontology* 27: 132–144.
- Ré, G.H., E.S. Bellosi, M. Heizler, J.F. Vilas, R.H. Madden, A.A. Carlini, R.F. Kay, and M.G. Vucetich. 2010. A geochronology for the Sarmiento Formation at Gran Barranca, pp 46–58 in R.H. Madden, A.A. Carlini, M.G. Vucetich, and R.F. Kay (eds), *The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia*. Cambridge University Press.
- Scott, W. B. 1903–1904. Mammalia of the Santa Cruz Beds. Part 1: Edentata. *Reports of the Princeton University to Patagonia 1896-1899* 5: 1–364.
- Simpson, G.G. 1940. Review of the mammal-bearing Tertiary of South America. *Proceedings of the American Philosophy Society* 83: 649–709.
- Tejedor, M.F. 2005. New fossil platyrrhine from Argentina. *Folia Primatologica* 76: 146–150.
- Tejedor, M.F., A.A. Tauber, A.L. Rosenberger, C.C. Swisher III, and M.E. Palacios. 2006. New primate genus from the Miocene of Argentina. *PNAS* 103(14): 5437–5441.
- Vizcaíno, S.F., M.S. Bargo, R.F. Kay, R.A. Fariña, M. Di Giacomo, J.M.G. Perry, F.J. Prevosti, N. Toledo, G.H. Cassini, and J.C. Fernicola. 2010. A baseline paleoecological study for the Santa Cruz Formation (late-early Miocene) at the Atlantic coast of Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 292: 507–519.