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Fossil mammals of the Quebrada de los Colorados Formation (late middle Eocene) at the locality of La Poma, Salta Province, Argentina

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ABSTRACT

An anatomical and taxonomic analysis of the mammalian record in the locality of La Poma in Salta Province, Argentina, is here presented. This record consists in two specimens exhumed in levels of the Quebrada de los Colorados Formation referred to the middle late Eocene. The first specimen is represented by a partial skull preserving mostly the rostrum and some dental pieces and was identified as a member of Leontiniidae, although it does not bear enough information for generic or specific determination. The second specimen is represented by more complete material, preserving much of the dentition. It was identified as a new species of the genus *Pampahippus*, traditionally included in the paraphyletic family Notohippidae. The leontiniid here studied presents several plesiomorphic features identified in other taxa of northwestern Argentina, and this material represents a new example of a pre-Deseadan basal morphotype within the family. Regarding the new species of *Pampahippus*, it shows clear signs of rising hypsodonty, representing the first case for a notoungulate lineage in the Paleogene of northwestern Argentina.

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KEYWORDS

Quebrada de los Colorados Formation; Northwestern Argentina; Leontiniidae; *Pampahippus*; Middle late Eocene

Introduction

The Quebrada de los Colorados Formation (Díaz et al. 1987) is the lowermost unit of the Payogastilla Group and was first described in the vicinity of the Angastaco locality, Calchaquí Valley, northwestern Argentina. This unit unconformably overlies the Cretaceous-Paleogene Salta Group and its upper contact is also an erosive unconformity with the Angastaco Formation (del Papa, Hongn, Payrola Bosio, et al. 2013). The thickness range between 800 and 1500 meters and is integrated by continental sediments deposited in fluvial and alluvial fan environments (del Papa, Hongn, Powell, et al. 2013). This formation preserves growth-structures and other evidences of syntectonic sedimentation suggesting deposition coeval with the first stage of Central Andes uplift (Hongn et al. 2007; Payrola Bosio et al. 2009).

The first studies in the Quebrada de los Colorados Formation assigned it to the Neogene (Díaz & Malizzia 1984); however, later research suggested that this sedimentation could have started during the Paleogene (Starck & Vergani 1996). Finally the first discovery of vertebrate fossils in the lower section at Cerro Bayo near La Poma town (see Hongn et al. 2007), together with ~38 Ma U/Pb in detrital zircon (Carrapa et al. 2012) indicate that the deposition of the Quebrada de los Colorados Formation began at least in the late middle Eocene.

The locality of La Poma is located 79 km west of Salta City, in the Calchaquí Valley, northwestern Argentina. Here, several fossil specimens were found in a sandy-fill lenticular channel, in a level identified at 38 meters from the base of the bearing unit (Figure 1). The

basal section of the Quebrada de los Colorados Formation consists of stratified red sandy siltstones and siltstones characterized by discrete simple or bifurcate traces and carbonate nodules suggesting the development of soils. These siltstones are sporadically inter-layered with silty material and 30–40 cm thick coarse-grained to pebbly sandstones beds with shallow scours bases, showing normal grading and trough-cross stratification features, indicating secondary fluvial channels. These main facies associations are laterally associated with stacked very thick conglomerates to conglomeratic sandstones strata interpreted as main fluvial channels, deposited in a sinuous fluvial system with extensive floodplains (del Papa, Hongn, Powell, et al. 2013). The osseous fragments have low preservation, possibly due to mechanical abrasion and breakage during transport accentuated by diagenetic processes.

The fossils recovered in La Poma were identified as notoungulates of the families Leontiniidae and Notohippidae. Additionally, representatives of Crocodylia and Testudinata (Hongn et al. 2007) were also found at these levels, but these specimens have not been studied in detail so far. In this contribution, we focus on the morphological and systematic study of the mammalian record for this locality and comment the main faunal implications of these findings.

Material and methods

The specimens studied were directly compared to Paleogene representatives of different families of Notoungulata. Anatomical and dental nomenclature follows the usual terms used in recent contributions dealing with notoungulates (e.g. Billet 2011; Forasiepi

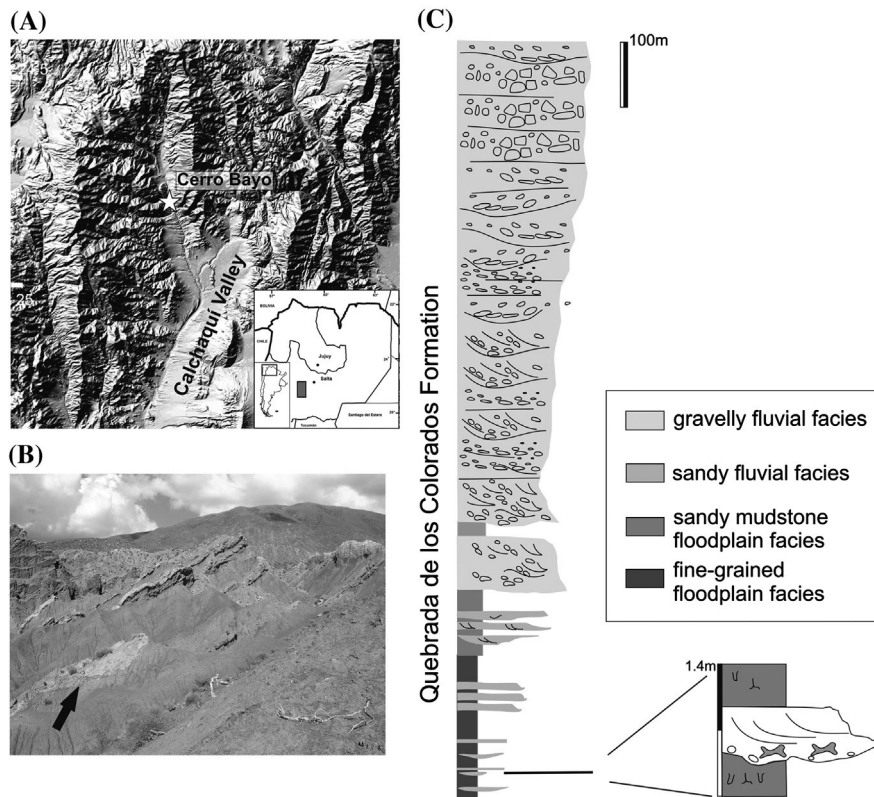


Figure 1. (A) DEM image showing the location of the study site; (B) Field aspect of the fossil-bearing level; (C) Sedimentological log of the Quebrada de los Colorados Formation at Cerro Bayo; main paleoenvironments are shown.

et al. 2014; Deraco & García-López 2015). Measurements were taken with a 0.01 resolution digital caliper.

Hypsodonty index was calculated as the ratio between crown height and mesiodistal length at the base of the tooth, following Janis (1988). However, in this case we use measurements of the second upper molar, as this tooth is preserved and fully erupted in specimens of all the species of the genus *Pampahippus*.

Institutional abbreviations

IBIGEO-P, Colección Paleontología Instituto de Bio y Geociencias del Noroeste Argentino, Rosario de Lerma, Salta, Argentina; PVL-S C.B., Colección Paleontología de Vertebrados Lillo, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina, Catálogo de Campo, Salta, Cerro Bayo.

Anatomical abbreviations

C, upper canine; I, upper incisor; i, lower incisor; M, upper molar; m, lower molar; P, upper premolar; p, lower premolar.

Systematic paleontology

Order NOTOUNGULATA Roth 1903

Suborder TOXODONTIA Owen 1853

Family LEONTINIIDAE Ameghino 1895

Leontiniidae indet.

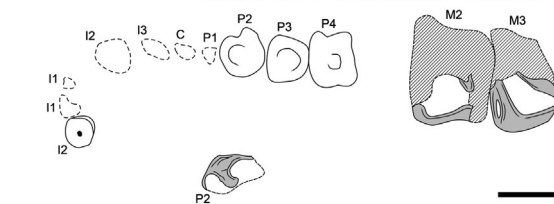


Figure 2. *Leontiniidae* indet., IBIGEO-P 80, upper dentition in occlusal view. Note: Scale bar = 20 mm.

Figures 2 and 3

Referred specimen

IBIGEO-P 80 (ex PVL-S C.B.03; see Hongn et al. 2007); partial rostral half of skull with part of the intraorbital wall and ectopterygoid crest. On the right side it preserves the alveolus of the I1, the root of the I2, and part of the lingual portion of

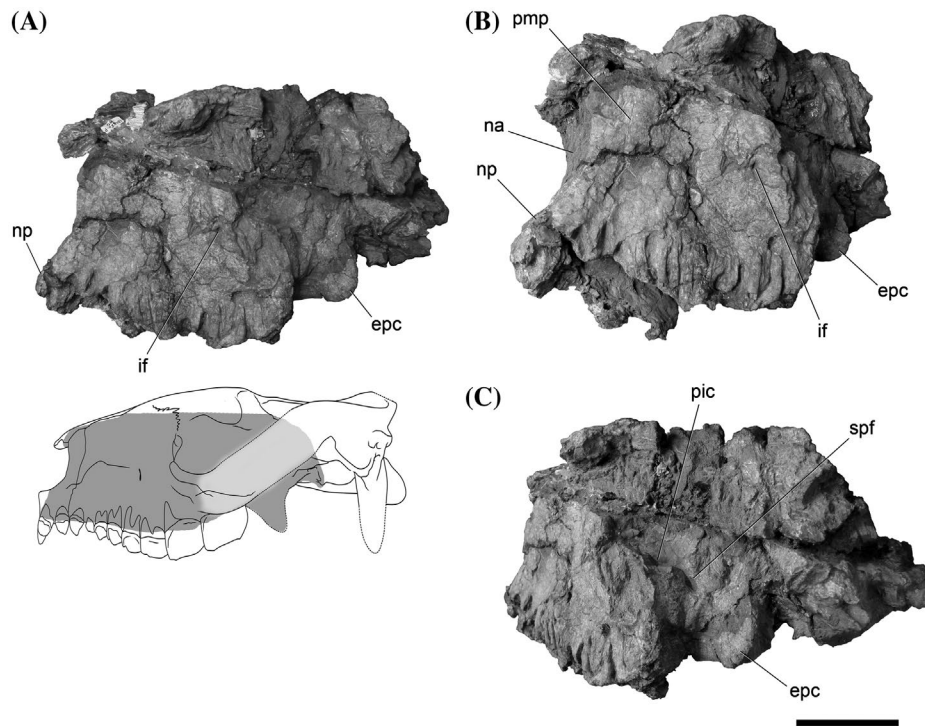


Figure 3. Leontiniidae indet., IBIGEO-P 80, partial skull. (A), lateral view and scheme of a generalized leontiniid skull showing the preserved part; (B), anterolateral view; (C), posterolateral view.

Abbreviations: epc, ectopterygoid crest; if, infraorbital foramen; na, nasal aperture; np, narial process; pic, posterior aperture of the infraorbital canal; pmp, premaxillary/maxillary suture; spf, sphenopalatine foramen. Note: Scale bar = 40 mm.

Table 1. Leontiniidae indet., IBIGEO-P 80, measurements (in mm) of roots and partial crowns preserved for the upper teeth and comparisons of tooth row size with other Eocene leontiniids.

	Upper teeth													
	I1		I2		I3		C							
	L	R	L	R	L	R	L	R						
Mesiodistal length	-	-	-	11.00*	-	-	-	-						
	-	-	-	9.00*	-	-	-	-						
Width	P1		P2		P3		P4		M1		M2		M3	
Mesiodistal length	-	-	12.00*	-	12.00*	-	12.00*	-	-	-	19.00*	-	-	-
Width	-	-	11.00*	-	11.00*	-	14.00*	-	-	-	23.00*	-	24.00*	-
	P1-M3 length													
			L		R									
IBIGEO-P 80			94.00*		-									
<i>Martinmiguelia fernandezii</i>			-		110.00*									
<i>Coquenina bondi</i>			123.96		125.10									

Abbreviations: L, left; R, right.

*Approximate measure.

the P2?; in turn, the left sides preserves the alveoli of I1–I3, C, and P1, the roots of P2–4, and part of the lingual portions of M2–3.

Geographic and Stratigraphic Provenance

Cerro Bayo, La Poma, Salta Province, Argentina. Quebrada de los Colorados Formation, late middle Eocene.

Description

The fossil specimen is an incomplete skull including both partial premaxilla and maxilla. On the left side, this material preserves

the broken alveoli of I1–I3, C, and P1, the roots of P2–P4, and the broken crowns of M2 and M3; on the right side, it bears the alveolus of I1, the root of I2, and the crown of the P2 partially preserved. Fragments of nasals are also present. The upper dentition is brachydont, apparently closed, and complete. The mesiodistal length of the series of postcanine teeth is very similar to that of *Martinmiguelia fernandezii* (see Table 1). The root of the I2 is hypertrophied, being this a characteristic feature in some leontiniids (Shockey et al. 2012). The mesiolabial corner of one of the premolars (probably the P2) is preserved on the right side. It bears a small mesiolingual cingulum and the mesial part of the protocone. The cingulum surrounds the protocone reaching its lingual wall, in a similar way to the condition observed

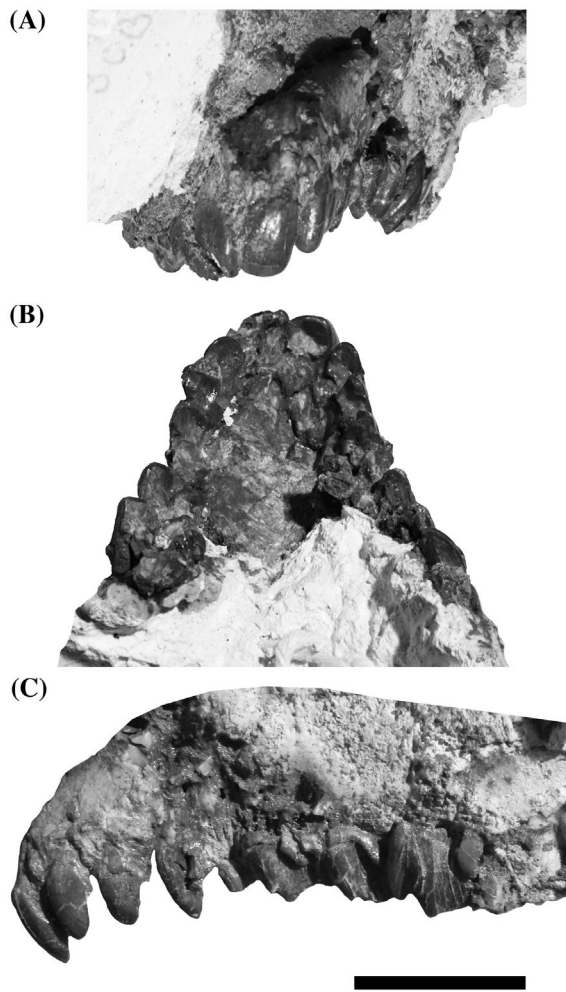


Figure 4. *Pampahippus powelli* sp. nov., IBIGEO-P81, anterior dentition. (A), anterior view; (B) occlusal view; (C), left lateral view. Note: Scale bar = 20 mm.

in specimens of *Coquenia* and *Martinmiguelia*. Regarding the molars, these teeth show a high wear degree. In both the preserved molars the protocone is clearly quadrangular, with a well-defined mesiolingual corner. Additionally, in the M2 it is evident that the central fossa is completely closed on its lingual side in this wear stage. Finally, the M3 also shows a well-developed cingulum

restricted to the mesial wall, not reaching the lingual face of the protocone.

Regarding cranial features, the premaxillae surround a very high anterior nasal aperture and form the narial process (as in other notoungulates; see Billet et al. 2008), which is conspicuous but relatively small. Posteriorly, the rostrum is high and bears the anterior aperture of the infraorbital canal (infraorbital foramen) which is located at the level of the distal side of the M2, a position slightly posterior than the usual in basal leontiniids such as *Coquenia* and *Martinmiguelia*, were it is located above the P4-M1 (VD pers. obs.). This aperture is adjacent to the anterior root of the zygomatic arch (not preserved). A small area of the anterior part of the orbitotemporal fossa is also preserved, showing the posterior aperture of the infraorbital canal and a second, most posterior aperture. The former is located very close to the anteroventral orbital rim and is relatively large. The latter structure is an irregular aperture which, given its location, probably represents the sphenopalatine foramen. This interpretation is based in the usual position observed in other Toxodontia (e.g. *Nesodon*, see Forasiepi et al. 2014). The last conspicuous feature observed is the ectopterygoid crest, preserved on the left side. This is large and is separated from the maxillar tuberosity by a large notch. The crest presents a divergent arrangement and its development is similar to the condition observed in other leontiniids, such as *Coquenia*.

'NOTOHIPPIDAE' Ameghino 1894

Genus *Pampahippus* Bond & López 1993

Type species

Pampahippus arenalesi Bond & López 1993

Type locality

Guachipas, Salta Province, Argentina. Lower Lumbrera Formation, Casamayoran (Vacan subage).

Included species

Pampahippus arenalesi Bond & López 1993; *Pampahippus secundus* Deraco & García-López 2015, *Pampahippus powelli* sp. nov.

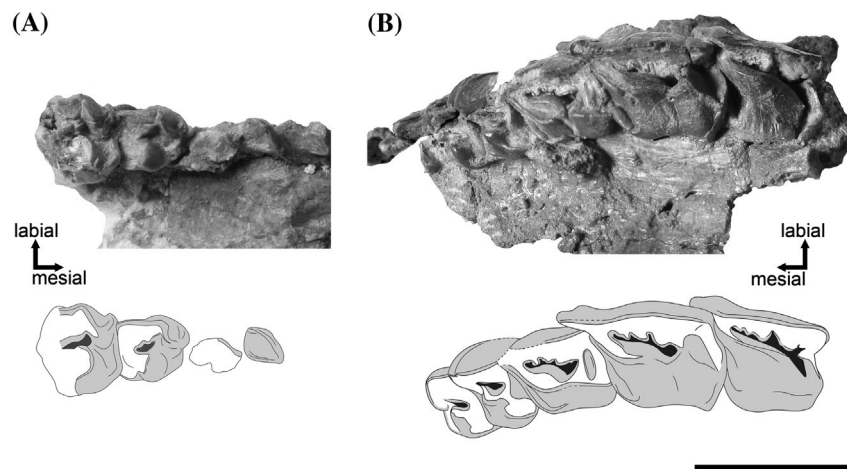


Figure 5. *Pampahippus powelli* sp. nov., IBIGEO-P 81. (A), C – P3 in occlusal view; (B), P3 – M3 in occlusal view. Note: Scale bar = 20 mm.

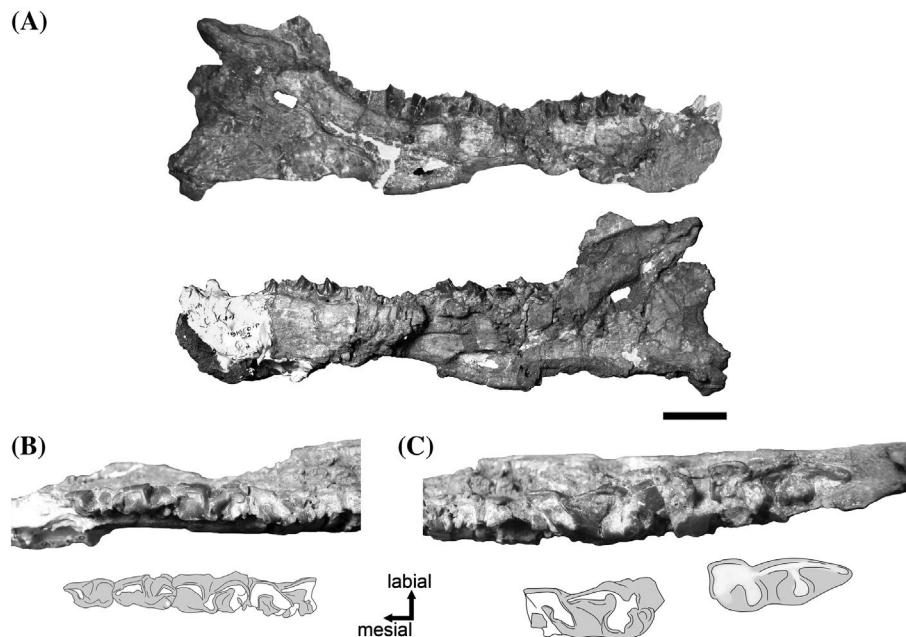


Figure 6. *Pampahippus powelli* sp. nov., IBIGEO-P 81. (A), right mandible in lateral and medial view; (B), detail of p2 – p4 and trigonid of m1 in occlusal view; (C), detail of m2 and m3 in occlusal view.

Note: Scale bars = 20 mm.

***Pampahippus powelli* sp. nov.**

Figures 4–6

Holotype

IBIGEO-P 81 (ex PVL-S C.B.02; see Hongn et al. 2007); fragment of palate with left I1-M3 and right I1-M2 and incomplete right mandible with i1-3 (replicated by plaster casts from natural molds) and almost complete p2-m3.

Derivation of name

The name of the species honors Dr. Jaime E. Powell, former curator of the Colección Paleontología de Vertebrados Lillo, paleontology professor in the Universidad Nacional de Tucumán, and a prominent researcher of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), for his notable contributions to the knowledge of fossil mammals in northwestern Argentina.

Geographic and Stratigraphic Provenance

Cerro Bayo, La Poma, Salta Province, Argentina. Quebrada de los Colorados Formation, late middle Eocene.

Diagnosis

Middle sized species of *Pampahippus*. It shows lower third and fourth premolars with isolated and bunoid entoconid, an autapomorphic feature of the genus, and also exhibits the typical arrangement of upper premolars without protoloph seeing in the other congeneric species (*P. arenalesi* and *P. secundus*). Hypsodonty index relatively higher considering the other species

of the genus. I1 clearly larger than the I2-3 ($I1 > I2 > I3$) and with strongly concave lingual wall (spoon-like crown), differing from *P. secundus* in size proportions ($I1 > I3 > I2$) and a less concave lingual side of the I1 (I1 and I2 are unknown for *P. arenalesi*). Strong paraconule in the P4, connecting with the mesial wall of the protocone and forming a rudimentary protoloph; this condition differs from *P. arenalesi*, where the paraconule is relatively large but well separated from the protocone, and from *P. secundus*, where the paraconule is vestigial. Mesial cingulum of the P4 confined to the mesial wall; this structure surrounds the protocone lingually in other species of *Pampahippus*. Upper molars with three pre-crochet cristae as is *P. arenalesi* but differing from *P. secundus*, where there is a single pre-crochet crista. All molars are also clearly imbricated given the great development of the parastyle (larger than the other species of the genus). Upper molars lacking labial cingula as in *P. secundus* but differing from *P. arenalesi* which shows small labial cingula on these teeth. Mesial cingulum of M1 surrounding the lingual wall of the protocone as in *P. secundus* but differing from *P. arenalesi* where this structure is confined to the mesial side of the tooth. Regarding lower dentition, p2-4 with well-developed distolabial crest (differing from *P. arenalesi* and *P. secundus* where this crest is weak or vestigial), and p3 with protocristid relatively longer than in the other species of the genus.

Description

Skull

The fossil specimen only preserves a portion of the palate with a much deteriorated maxillary surface. The premaxilla is visible in palatal view and a small part of its facial exposure is also present. The incisive foramina are relatively small and elliptical apertures,

Pampahippus arenalesi and *P. secundus*. Also given the lesser wear degree, the distal cingulum does not form a distal transverse fossette (as the one described parallel to the metaloph in the M1). The metastyle is large.

The M3 is partially erupted and thus, it is unworn. As in other Paleogene notoungulates, this tooth is subtriangular in occlusal outline, lacking a well-developed hypocone. The ectoloph is very similar to that of the previous molars, although it shows a somewhat stronger paracone fold and a lower metastyle. Several cristae protrude in the central fossa, which is very deep. The tip of the protocone is very close to the ectoloph, and hence, the crown shows a 'closed' appearance. Although this feature represents a difference regarding the other species of the genus (particularly *Pampahippus secundus*), it is obviously influenced by the wear degree. The mesial cingulum is well developed and the distal cingulum is obscured by the maxilla (since the tooth is not fully erupted); nevertheless, a small enamel longitudinal fold is visible at the base of the lingual wall, between the protocone and the hypocone and this is interpreted here as the mesiolingual end of the distal cingulum.

Mandible

This specimen preserves the right mandibular body and part of the ramus (Figure 6(A)). These elements are badly broken and almost all features are obscured. The mylohyoid line is not marked on the mandibular body. Additionally, there is a limited retromolar space (probably related to the young ontogenetic stage of the specimen) and a prominent crest, developed on the medial edge of the space. This structure is common in Paleogene notoungulates (e.g. *Colbertia lumbrense*, *Griphotherion peiranoi*, *Pampatemuus infernalis*, *Simpsonotus praecursor*, *Notostylops murinus*, and *Boreastylops lumbrensis*) and even in other South American native ungulates, such as *Indalecia grandensis*. The crest has been referred as internal process by Simpson (1948), internal crest by Pascual et al. (1978), tubercle by Vucetich and Bond (1982), and posterointernal process by Bond and Vucetich (1983).

Lower dentition

Incisors were preserved only as natural molds (corresponding only to the labial wall), that were replicated by plaster casts (Figure 6(A)). The crown shape is generalized for the three incisors, and their size increases from the i1 to the i3, as in *Pampahippus arenalesi* and *P. secundus*.

The canine and the p1 are not preserved. As in the case of the upper postcanines, the morphology of the premolars strongly resembles that of the other species of the genus (Figure 6(B)). Nevertheless, some features indicate clear differences, mostly influenced by the greater mesiodistal development of these teeth. The p2 is incomplete, lacking part of the mesial end of the trigonid and the lingual side of the talonid. As in other taxa, the crown in the p2 is formed by a continuous crest, running from the paracristid, passing through the protoconid and metaconid, and reaching the distal end of the talonid. The trigonid shows a well-developed distolabial crest (see Billet 2011). This is a difference regarding the other species of the genus, where this crest is low in the p2 (although conspicuous in the p3-4). The labial

sulcus between trigonid and talonid is deep. This structure is also comparatively more developed regarding *Pampahippus arenalesi* and *P. secundus*. Finally, there is a small portion of the labial cingulid present of the talonid, which is evidenced as a small enamel fold, and the entoconid is not evident in this tooth.

The p3 is more molariform than the p2. In this case, the trigonid is clearly larger than the talonid, given the great development of the paracristid and protocristid. The paracristid runs mesially from the protoconid, describing a curved trajectory, and reaching the mesial end of the trigonid. The protocristid is slightly oblique and relatively longer than in the other species of the genus. The distolabial crest of the trigonid is more conspicuous than in the p2. The metaconid is the highest cusp on the trigonid, although it is not particularly differentiated on the lingual wall of the tooth. Both the crest and the labial sulcus between trigonid and talonid show the same development and disposition than other forms of *Pampahippus* and many Paleogene notoungulates. In the talonid the hypoconid is conspicuous and presents a short cristid obliqua (this present some wear, forming a small lophid). The talonid also shows the typical trait of the genus: the conspicuous, bunodont, and isolated entoconid. The labial cingulid is evident on the entire labial side of the tooth. In turn, the cervical zone of the lingual side is not preserved, and the presence of the lingual cingulid cannot be ascertained.

The fourth premolar is very molariform. The trigonid is more quadrangular than the preceding premolars. The paracristid runs straight mesially in this case, reaching the mesiolabial end of the trigonid. At this point, the paracristid present a connection with the mesiolingual end of the lingual cingulid, which is marked all over the lingual wall of the tooth. The protocristid is similar to that of the p3, although its trajectory is more transverse. The distolabial crest of the trigonid is very prominent. Unlike the previous premolars, the metaconid shows a distinct distolingual fold, and the cristid obliqua reaches the trigonid in a more labial position on the protocristid. The talonid is more lophodont than the previous premolar. The entoconid is large and presents some wear; although it is partially broken, its isolated arrangement is still evident.

Lower molars are incompletely preserved (Figure 6(B) and (C)). The m1 shows only the trigonid, the m2 is almost complete, and the crown of the m3 is severely damaged. The trigonid in the m1 shows an oblique protolophid. The protoconid is not evident, although there is an angulated inflection that marks the limit between the protolophid and the paracristid, extended mesially. This paracristid is oriented mesiolabially and presents a strong connection with the mesial cingulid, forming a roughly transverse paralophid. This connection forms an acute angle, similar to that observed in *Pampahippus arenalesi*, although in the present material the paracristid is relatively more elongated. The mesial cingulid is strong, forming a wide valley with the protolophid. The metaconid is prominent, particularly on its distolingual wall. An accessory cusp (sometimes regarded as paraconid; see Bond & López 1993) is present on the mesiolabial wall of the metaconid. Both cusps are almost completely fused in this wear stage, although it is clear that the position of the accessory cusp was labial regarding the metaconid, as in *P. arenalesi*. There is a small labial cingulid on the base of the trigonid.

The trigonid of the m2 is very similar to that of the preceding tooth. The crown of this molar shows a general elongated

appearance (mesiodistally) as in the case of the upper molars. The trigonid shows a very oblique protolophid, extending from the metaconid (which is very sharp on its lingual wall) to the protoconid, marked in the vertex of the angle between the protolophid and the paralophid. The latter, in turn, projects mesially until it reaches the mesiolabial corner of the tooth. There is a cingulid that occupies the entire mesial wall of the trigonid and is more developed lingually. This seems to be separated from the paralophid, although it is not clear given the poor preservation in this area. The greater relative length of the paralophid represents another difference of the new species regarding *P. arenalesi*. It determines that the mesiodistal length of the trigonid and the talonid are more similar in the case of the specimen here described, contrasting with the much more shorter trigonid of *P. arenalesi*. Given a slightly lesser wear degree, the accessory cusp (or paraconid) is more independent from the metaconid in this molar than in the case of the m1. It shows a labial position regarding the metaconid, and its arrangement is comparable to that of *P. arenalesi*. The base of the labial wall of the trigonid bears a small cingulid. Although the distal surface of the cingulid is broken, it seems to reach the base of the labial sulcus, but not the talonid (as it does in *P. arenalesi*).

As in the other cogenetic species, the cristid obliqua of the m2 reaches the protolophid in a labial position, and thus, the labial sulcus is shallow. The talonid valley is wide and does not bear any accessory cusp (as it does in *Pampahippus arenalesi*) resembling the condition in *P. secundus*. The base of the entoconid is wide, and occupies a large surface of the talonid. Posteriorly, there is a deep sulcus between the entoconid and the hypoconulid, which is closed by a lingual crest.

Finally, the m3 is not fully preserved. Only the labial wall of the trigonid and, partially, the talonid can be analyzed. There is a small labial cingulid on the base of the trigonid but, since this tooth is not fully erupted, its entire development cannot be determined. Although it is broken, it seems clear that the protolophid was very oblique, as in the m2. Regarding the talonid, this is relatively larger than in previous molars given the great development of the hypoconulid, as usual for Paleogene notoungulates. The talonid valley is wide and does not present any accessory cusp. The entoconid is larger than in the other species of the genus, occupying a wide surface of the talonid. The zone of the hypoconulid is relatively larger than in *Pampahippus secundus*, resembling other Patagonian species as *Plexotemnus complicatissimus*.

Discussion

Notoungulates of the family Leontiniidae represent a singular group of generally large-sized mammals, which older records come from Eocene deposits and that survived into the Miocene age (Villarroel & Coldwell Danis 1997; Shockey 2005; Deraco et al. 2008; Ribeiro et al. 2010; Shockey et al. 2012). Their diversity remains low for the most part of the Paleogene span of their record, rising only in the Deseadan SALMA (Croft et al. 2008). Moreover, all of the records older than the Eocene/Oligocene boundary come from northwestern Argentina. Two taxa were previously recorded in this region. *Martinmiguelia fernandesi* comes from levels of the Casa Grande Formation, and was described based on a very incomplete skull (Bond & López 1995).

Posteriorly, Deraco et al. (2008) reported the species *Coquenia bondi* for the Upper Lumbrera Formation (see del Papa 2006; del Papa et al. 2010). In this case, the morphological information is considerably higher, being this taxon represented by complete skulls and postcranial remains of several specimens. The remains of the Quebrada de los Colorados Formation add the third Paleogene unit to this record. This partial skull is too fragmentary and does not preserve diagnostic information enough to determine its precise taxonomic context. Nevertheless, incisive morphology allows its inclusion within Leontiniidae. Additionally, the brachydont nature of the postcanine teeth and the apparently closed dentition are common features among the Eocene leontiniids of northwestern Argentina (although plesiomorphic). The extended presence of leontiniids in Paleogene units of this region is remarkable when compared with the absence of pre-Deseadan representatives in Patagonia. This fact reinforces the idea of an extra-Patagonian origin for the family, noted in previous contributions (Bond & López 1995; Deraco et al. 2008).

Martinmiguelia fernandesi and *Coquenia bondi* were morphologically related and a biostratigraphic connection was proposed for their bearing units, regarded as late middle Eocene (Deraco et al. 2008). Posteriorly, Powell et al. (2011) also considered the presence of the leontiniid of Quebrada de los Colorados, as well as other mammalian records, as evidence for the correlation of this unit with Upper Lumbrera and the Casa Grande Formation. Regarding absolute ages, for the Upper Lumbrera Formation del Papa et al. (2010) provided an absolute U/Pb zircon age of 39.9 ± 0.4 Ma near the top of the sequence; as for the Quebrada de los Colorados Formation, Carrapa et al. (2012) established a maximum depositional age of 37.6 ± 1.2 (based on zircon U/Pb geochronology) in the area of Angastaco (Salta Province). These data open up the possibility of considering the basal levels of Quebrada de los Colorados as younger than the levels of Upper Lumbrera. Nevertheless, the area of La Poma, where the present specimen was collected, is located far north (more than 100 km) from Angastaco. Although previous authors referred these bearing levels to the span between the Casamayoran and Mustersan (see Hongn et al. 2007), the age cannot be precisely established or correlated. Either way, the record here described evidences the persistence of this early lineage throughout the second half of the Eocene.

Notohippids represent a traditional family of generally medium to large-sized toxodontians known from the Casamayoran (middle Eocene) to the Santacrucian SALMA (Miocene; Croft et al. 2008; Martínez et al. 2016). Most studies have recognized the paraphyletic nature of this group (Shockey 1997; Billet 2011; Deraco & García-López 2015; Martínez et al. 2016), and generally identify a basal cluster of pre-Deseadan or 'isotemnid-like notohippids' contrasting to a more advanced set of genera, directly related to the ancestral line leading to advanced Toxodontia (i.e., Toxodontidae).

The record of 'isotemnid-like notohippids' is notable in Paleogene units of northwestern Argentina. This was initiated with the species *Pampahippus arenalesi* described by Bond and López (1993) for the Lower Lumbrera Formation (see del Papa 2006; del Papa et al. 2010), more recently assigned tentatively to the Vacan stage (middle Eocene). This is considered as the most ancient notohippid, along with *Plexotemnus*, from the Barrancan stage of Patagonia (Croft et al. 2008; López et al. 2010). Posteriorly,

the genus *Pampahippus* was mentioned for the Mustersan levels of the Geste Formation in the locality of Antofagasta de la Sierra, Catamarca Province, Argentina (López 1997). Although it was referred with some reserves, this report documented the persistence of this morphotype throughout a considerable span of the second half of the Eocene. This fact was recently confirmed with the description of the second species of the genus, *P. secundus*, which also represents one of the smallest toxodontians known so far (Deraco & García-López 2015). The new species here reported brings two notable aspects in the context of the Eocene record. First, with this new species the genus is the most diverse of the northwestern representatives of Notoungulata and also of the pre-Deseadan notohippids. Second, it is the only notoungulate group of northwestern Argentina which shows some degree of specialization in terms of increasing hypsodonty before the Eocene/Oligocene boundary.

As noted above, Hongn et al. (2007) mentioned for the first time the toxodontians here analyzed, and established that these bearing levels of the Quebrada de los Colorados Formation can be referred to the span between the Casamayoran and Mustersan. With this third species of *Pampahippus*, the record of the genus spans from the Vacan to the Mustersan (also considering the record of Antofagasta de la Sierra). During this lapse, the Patagonian record indicates the development of 'relative extinctions' and a strong faunal turnover in the post-Barrancan and pre-Mustersan interval (Woodburne et al. 2014). In the case of northwestern Argentina, this pattern is barely insinuated. Along with *Pampahippus*, *Colbertia* (an oldfieldthomasiid tyotherian) also shows a continuous record from the Vacan to the Mustersan in the region (Bond 1981; López 1995, 1997; del Papa et al. 2010) and, in fact, is also known for Itaboraian levels of Brazil (Paula Couto 1952; Bond 1981; García-López & Powell 2009). On the other hand, all other records of Paleogene notoungulates in northwestern Argentina are exclusive for each stage. It is important to note at this point, that Woodburne et al. (2014) mention some clades that show continuity in the context of the above-mentioned turnovers, including the oldfieldthomasiids. Moreover, these authors observed that these turnovers affected mainly 'archaic groups that had been effectively continuous from at least the beginning of the Eocene'. In this sense, notohippids were included in the set of clades that survived or were less affected by these turnovers and continued evolving during the Paleogene and much of the Neogene. In any case, the record in northwestern Argentina is still fragmentary and not adequately calibrated and compared. Several studies are urgently needed in order to organize this record and establish it comparative context.

The higher hypsodonty degree exhibited by *Pampahippus powelli*, regarding the other species of the genus, acquires importance in the context of the faunal and climatic changes associated to the 'modernization' of the Paleogene South American mammal faunas and the regional differences extensively observed between Patagonian and extra-Patagonian localities. Toward the end of the Eocene, it was set the beginning of a series of morphological trends among mammal communities, evidenced mostly by the acquisition of progressively more hypsodont dentitions in some lineages. Additionally, several changes were also observed in the floras recorded in that interval, strikingly characterized by the advent of more open environment and the widespread of grasses (Woodburne et al. 2014). These tendencies were considered as

a prelude of the dramatic global event of the Eocene/Oligocene boundary, in which climates become much colder than in previous stages (Croft et al. 2008; Goin et al. 2012; Woodburne et al. 2014). Particularly in the case of the development of hypsodonty, the first signals of this trait in ungulate lineages were observed in the Riochican, with a rise in the Barrancan and Mustersan stages (Woodburne et al. 2014). Finally, this trend was completely established in the Tinguirirican, with the earliest South American faunas dominated by hypsodont taxa (Croft et al. 2008). Conversely, several authors have noted that these conditions were not clearly established in northwestern Argentina, indicating the possible persistence of closed, warm, and wet environments in the region (Bond 1981; Pascual et al. 1996; Ortiz-Jaureguizar & Cladera 2006; García-López & Powell 2009). Much of these differences were considered based on the lack of hypsodont taxa in fossil-bearing units of northwestern Argentina, when compared to their Patagonian counterparts. For example, the levels of Upper Lumbrera can currently be regarded as Barrancan (del Papa et al. 2010; Powell et al. 2011), and the notoungulates there reported show a generally lower hypsodonty degree than in the case of the Patagonian forms (e.g., *Dolichostylodon*; García-López & Powell 2009). Additionally, none of the protohypsodont lineages recorded in southern Barrancan localities is present in the Upper Lumbrera Formation (e.g. Archaeohyracidae and Archaeopithecidae). Regarding archaeohyracids, these are only recorded later in the Mustersan Geste Formation with the genus *Punahyrax* (Reguero et al. 2008), which also has apparently a lower hypsodonty degree than its Patagonian counterparts (e.g. *Pseudhyrax*).

In the case of *Pampahippus*, the two species reported for the Lower Lumbrera Formation, *P. arenalesi* and *P. secundus*, are brachydont and both have an hypsodonty index of 0.6 (measured on the M2). The third species here described, in turn, is clearly more hypsodont (although it cannot be regarded as protohypsodont), with a hypsodonty degree of 0.8. There is a clear temporal distance between Lower Lumbrera, regarded to the Vacan sub-age of the Casamayoran (del Papa et al. 2010) and the younger bearing levels of *P. powelli*, and then, this rise in hypsodonty documented in a single genus can be attributed to the same incipient 'modernization' observed in southern assemblages. In this way, first signs of rising hypsodonty for northwestern Argentina are recorded in the Casamayoran - Mustersan span, that is, late middle Eocene. Nevertheless, this single report is not significant enough to establish a detailed comparison or to set paleoenvironmental proxies, especially considering that other specimens of this unit, such as the leontiniid above described, do not show such specialization. Several others remains collected in the Quebrada de los Colorados Formation are currently under study in order to increase our knowledge on the evolutionary processes underwent by mammalian communities in middle latitudes of South America.

Conclusions

Here we present a detailed assessment on the mammalian record for the lower levels of the Quebrada de Los Colorados Formation in the locality of La Poma (Salta Province, Argentina).

Regarding the material IBIGEO-P 80, referred as Leontiniidae indet., comparisons made underline the plesiomorphic nature

of the specimen. This material represents a new example of a pre-Deseadan basal morphotype within the family.

The specimen IBIGEO-P 81 is here referred as a new species of the genus *Pampahippus*, *P. powelli*, based on the presence of dental synapomorphies of that clade (upper premolars without protoloph and lower third and fourth premolars with isolated and bunoid entoconid). This new taxon represents the third species of the genus, which record spans from the Vacan subage of the Casamayoran to the Mustersan SALMA. Additionally, the new species shows the first clear signs of rising hypsodonty in a notoungulate lineage endemic of northwestern Argentina.

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