

A new Eocene Toxodontia (Mammalia, Notoungulata) from northwestern Argentina

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ARGENTINA

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ABSTRACT—A new species of Toxodontia (Mammalia, Notoungulata) from northwestern Argentina, *Pampahippus secundus* sp. nov., is here presented. This is based on remains recovered from outcrops of the Lumbrera Formation exposed in Salta province, Argentina. The material studied consists of mandibular, maxillary, and premaxillary fragments with complete and incomplete teeth corresponding to at least three individuals. It differs from the type species *P. arenalesi* by its smaller size and the presence of several dental features: I2 smaller than the I1 and I3, paraconule absent on the P3, upper molars wider than long and sub-quadrangular with a single crista projecting from the ectoloph, strong mesiolingual cingulum surrounding the protocone in the M1, conspicuous metacone fold on the ectoloph of M1-2, and absence of labial cingulids on lower molars. In order to define the phylogenetic position of *P. secundus* as well as different Paleogene notoungulates of northwestern Argentina we performed a cladistic analysis. This analysis supports the paraphyly of Notohippidae proposed by previous authors and validates the monophyly of the genus *Pampahippus*, which ranks as a relatively plesiomorphic taxa within Toxodontia. Moreover, a large clade of toxodontians arises from this analysis, including former ‘notohippids’, leontiniids, and toxodontids. We propose the term Toxodontoidea for this group, which represents the largest branch of an early dichotomy also leading to Homalodotheriidae. This contribution illustrates the significant and yet poorly known diversity of Paleogene toxodontians from northwestern Argentina and the importance of their study in the reconstruction of the evolutionary history of Notoungulata.

INTRODUCTION

The application of cladistic methods in the study of early-diverging notoungulates has led to significant revisions of the systematic background traditionally considered for those groups (Cifelli, 1993; Shockey, 1997; Reguero and Castro, 2004; Billet et al. 2008; Billet et al. 2009; Billet 2010; Cerdeño and Vera, 2010; Billet 2011). In this sense, groups of different taxonomic hierarchies that were treated as natural taxonomical entities for most of the 20th century and that have been object of comprehensive morphological and systematic studies are currently in a questionable position or have come to be considered as paraphyletic clusters (e.g., Notioprogonia, Archeohyracidae, Oldfieldthomasiidae, Notopithecinae). Nonetheless, it should be mentioned that, even in light of this new scope, the Order Notoungulata has maintained its character of natural group and that the two great lineages traditionally recognized are also still accepted: Typotheria and Toxodontia (Billet, 2010, 2011; García-López and Powell, 2011; Shockey et al. 2012; Billet and de Muizon, 2013).

Five families have been usually acknowledged for the Suborder Toxodontia since the redefinition made by Simpson (1945): Isotemnidae, Homalodotheriidae, Leontiniidae, Notohippidae, and Toxodontidae; this framework was accepted by several authors (McKenna, 1975; Bond, 1986; Cifelli, 1985, 1993; Mones, 1987; McKenna and Bell, 1997). Nevertheless, the monophyly for the families Isotemnidae and Notohippidae has been questioned as the result of recent and comprehensive phylogenetic surveys (Shockey, 1997; Billet, 2010, 2011). Notohippidae was defined by Ameghino on the basis of the santacrucian genus *Notohippus* Ameghino, 1891. Subsequently, this author also included taxa of Deseadan age (Ameghino, 1897; 1906). However, a few years later Loomis (1914) considered *Notohippus* as a Toxodontidae

and, in turn, proposed the family Rhynchippidae in order to include the Deseadan genera. Meanwhile, Simpson (1932) accepted the term Rhynchippidae, although he rejected the approach of Loomis regarding the position of *Notohippus* and included this genus in the Notohippidae again. Finally, Simpson (1945) divided Notohippidae into two subfamilies: Rhynchippinae and Notohippinae, although posteriorly Simpson (1967) and subsequent authors (Bond and López, 1993; Wyss et al., 1994; Shockey, 1997) questioned the validity of Rhynchippinae. The monophyletic status of the family was not disputed until the work of Shockey (1997) and, more recently, Billet (2010, 2011), who underscored the paraphyletic arrangement of the representatives of this family in different phylogenies.

The record of Notohippidae begins in the middle Eocene and is represented by the species *Pampahippus arenalesi* Bond and López, 1993 (these authors considered the bearing levels of this species as lower Eocene in age). On the other hand, the latest records are lower Miocene in age (Reig, 1981; Cifelli, 1985, 1993; Bond, 1986; Soria and Alvarenga, 1989; Shockey, 1997; Cerdeño and Vera, 2010). In northwestern Argentina, the current record of notohippids includes only one taxon, *Pampahippus arenalesi* that, as mentioned above, is considered one of its earliest representatives. This species was recovered from the Lumbrera Formation in Salta Province and it has been mentioned, with reserves, for the Geste Formation, a slightly younger unit (López, 1997).

In this contribution we describe a new species of the genus *Pampahippus* for the Lumbrera Formation. This new taxon is based on cranial remains representing several individuals, allowing us to analyze traits of intraspecific variation. Additionally, we include the new species, along with several northwestern early diverging notoungulates, in a data-matrix based on a previously published work focused on notoungulates (Billet,

2010), with some modifications made on the original codification. The hypothesis resulting from the inclusion of these taxa in a phylogenetic context (in some cases for the first time) brings a new scheme of relations for the families of Toxodontia and confirms the importance of considering early diverging forms for the reconstruction of the evolutionary history in lineages of long temporal range.

Abbreviations

Institutional Abbreviations—**PVL**, Colección Paleontología Vertebrados Lillo, Tucumán, Argentina.

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

GEOLOGY

The Lumbrera Formation crops out in several localities of northwestern Argentina, mainly in Salta Province. This unit is integrated by brown and reddish, well-stratified claystones, siltstones and lenticular sandstone strata. Gomez Omil et al. (1989) and del Papa (2006) proposed that Lumbrera Formation is represented by two independent sedimentary episodes and divided the unit in ‘Lumbrera inferior’ (lower Lumbrera) and ‘Lumbrera superior’ (upper Lumbrera). Subsequent contributions have underscored the different nature of the faunal assemblages recorded for both subunits, and confirmed the existence of two sedimentary cycles (del Papa, 2006; del Papa et al., 2010). The deposits of lower Lumbrera represent sedimentation in a fluvial environment of sandy meandering style (del Papa 2006) laterally associated with a perennial fresh-water lake (del Papa et al., 2002) named as Faja Verde II (Schlagintweit,

1936). In turn, upper Lumbrera represents ephemeral fluvial and clastic ephemeral-lake systems (del Papa, 2006).

Recently, del Papa et al. (2010) dated in 39.9 Ma (U-Pb zircon) a volcanic ash layer interbedded in the upper section of the upper Lumbrera, correlating this level with the Barrancan subage of the Casamayoran SALMA (late middle Eocene). These authors also suggest that the levels of lower Lumbrera can be also correlated with the Vacan subage (middle Eocene) of the same SALMA.

MATERIALS AND METHODS

Materials

The specimens studied include mandibular, maxillary and premaxillary fragments with complete and incomplete teeth, corresponding to at least three individuals. The materials are curated in the Colección Paleontología Vertebrados Lillo (Instituto Miguel Lillo, Tucumán, Argentina). For dental features, the terminology mainly follows the nomenclature proposed by Bown and Kraus (1979), with some variations when referring to terms such as lophs and lophids (e.g., paracrist = paraloph). This is related to the lophodont nature of notoungulate cheek teeth.

They are numbered: PVL 6427, fragment of left premaxilla with I1-3; fragment of left maxilla with incomplete P2 and complete P3-4 and M1-2; fragment of right dentary with incomplete m1-3. PVL 6428, fragment of right maxilla and premaxilla with I2-3, C, incomplete P2, complete P3, and part of P4. PVL 6429, fragment of right maxilla and premaxilla with roots of I2-3, complete C, part of P1, and complete P2. PVL 6430, fragment of left maxilla with P4, part of M1, and M2. PVL 6431, fragment of left dentary with with root of i1, incomplete i2, root of i3, c, and p1, and complete

P2-4. PVL 6432, fragment of left dentary with p3-4. PVL 6433, fragment of right dentary with incomplete m3.

Cladistic methodology with TNT (Goloboff et al. 2008b) was used to explore the phylogenetic relationships. A total of 146 discrete cranial and dental characters were scored in 68 taxa. Three new dental characters and a new taxon (the Eocene toxodontia) were added to the data matrix published by Billet and de Muizon (2013). The list of characters and the data matrix are respectively available as Supplementary Data 1 and 2. A set of 12 characters were considered ordered, following Billet and de Muizon (2013). The analysis was performed considering equally weighted characters. It was conducted using traditional searches with the tree bisection reconnection algorithm (TBR) performed with 100 replications. The values of support were calculated using the Bremer support function in TNT. The following genera were added to the analysis: *Boreastylops*, *Griphotherion*, *Pampatemnus*, *Pampahippus*, *Martinmiguelia*, and *Coquenina*, were incorporated into the data matrix of Billet and de Muizon (2013).

SYSTEMATIC PALEONTOLOGY

Order NOTOUNGULATA Roth, 1903

Suborder TOXODONTIA Owen, 1853

‘Notohippidae’ Ameghino, 1895

Genus *Pampahippus* Bond and López, 1993

Type Species—*Pampahippus arenalesi* Bond and López, 1993

Revised Diagnosis—Small to medium Toxodontia with lower premolars (p3-4) showing bunoid and isolated entoconid and a distolabial crest on the trigonid. Other

features include incisor-like upper canines, brachydont cheek teeth, absence of protoloph on upper premolars, presence of distinct paraconule on posterior upper premolars, and reduced number of cristae on the central fossa of upper molars (only one in the smaller species).

Pampahippus secundus sp. nov.

(Figure 1)

Etymology—*Secundus*, latin for second or follower. In reference to the fact that this is the second species recognized for the genus.

Holotype—PVL 6426, fragment of right maxilla of a young adult individual with P2-4 and M1-3.

Locality and Stratigraphic Context—Lumbrera Formation, Lower Lumbrera member (del Papa, 2006; del Papa et al., 2010), Early-Middle Eocene (Salta Group, Santa Bárbara Subgroup). El Simbolar, Guachipas Department, Salta Province. (Fig.2)

Referred Materials—PVL 6427, fragment of left premaxilla with I1-3; fragment of left maxilla with incomplete P2 and complete P3-4 and M1-2; fragment of right dentary with incomplete m1-3. PVL 6428, fragment of right maxilla and premaxilla with I2-3, C, incomplete P2, complete P3, and part of P4. PVL 6429, fragment of right maxilla and premaxilla with roots of I2-3, complete C, part of P1, and complete P2. PVL 6430, fragment of left maxilla with P4, part of M1, and M2. PVL 6431, fragment of left dentary with with root of i1, incomplete i2, root of i3, c, and p1, and complete p2-4. PVL 6432, fragment of left dentary with p3-4. PVL 6433, fragment of right dentary with incomplete m3.

Diagnosis—The smallest species of the genus. Dentition similar to the one of *Pampahippus arenalesi* but with upper incisors showing a unique size relation

(I2<I3<I1), paracone absent on the P3, upper molars wider than long and sub-quadrangular, with a single crista projecting from the ectoloph, strong mesiolingual cingulum surrounding the protocone in the M1, conspicuous metacone fold on M1-2 ectoloph, and absence of labial cingulids on lower molars.

DESCRIPTION

Dentition

Pampahippus secundus shows a closed, complete, and brachydont dentition.

Upper Dentition—The I1 is mesiodistally enlarged and roughly square in labial view. The lingual side of this tooth is strongly concave and presents a well-developed cingulum. The internal cingulum of upper incisors forms a faint basal fossette.

The I2 and I3 are foliate, being clearly differentiated in shape from the I1 and showing a well defined crown apex. Both teeth are similar in size, although the I3 is slightly longer mesiodistally. The labial side in both teeth is convex and the lingual side is concave, with a strong cingulum present (Fig. 3A, B).

The upper canine is incisor-like and bears a vestigial cingulum on the labial side. The size of this tooth is similar to that of the I2 and I3. Dental measurements are shown in Table 1.

Only the labial half of the P1 is preserved in one of the recovered specimens (PVL 6429). The paracone is cone-shaped. The tooth is single-rooted and apparently smaller than the upper canine. A cingulum is present on the labial side (Fig. 3C).

The second upper premolar is clearly larger than the first one. It presents bunoid protocone and paracone. The protoloph is absent and the metaloph is poorly developed. On the labial wall there is deep inflection distal to paracone fold. There is no metacone fold and the metastyle is not distinct. The mesial cingulum is small; the distal

cingulum is more developed and forms a distolingual fold. The labial wall presents a small but conspicuous cingulum (Fig. 3 B, C).

The third upper premolar also presents well-developed and bunoid protocone and paracone. The protocone is larger in occlusal view, but the paracone is a higher cusp. The parastyle is small and the metacone fold is not developed. The metastyle is small but conspicuous. The protoloph is absent (i.e., there is any kind of mesial connection between paracone and protocone). The mesial, distal, and labial cingula are well-developed. The distal cingulum forms a cup or pocket like structure on its lingual end (on the distolingual wall of the protocone). The metaloph is stronger than in the P2 (Fig. 3B).

The fourth upper premolar is the largest of the series. The parastyle is mesial and prominent and is separated from the paracone by a deep labial sulcus. The paracone is relatively smaller than in the P2 and P3 and the ectoloph is more extended mesiodistally. The metacone is not developed (although there is a faint fold that indicates its position on the labial wall of the tooth) and the metastyle is differentiated on the distolabial corner. The protocone is bunoid, there is no protoloph, and the metaloph is well developed. The central fossa is developed as a narrow depression that surrounds the labial wall of the protocone. The mesial cingulum is strong and more extended than in the P3 (Fig. 1C and 4A), surrounding the lingual wall of the protocone (the cingulum ends on the distolingual wall of this cusp). The distal cingulum is clearly smaller than the anterior one and forms the same pocket-like structure of the lingual end observed in the P3. Mesially to the central fossa, there is a small, medial cuspule, which is coalescent with the mesial cingulum, although both structures are separated by a narrow valley. For its location, this small cuspule can be identified as a paraconule (Fig. 1C, 4A and B).

In the molars the ectoloph is not specially extended mesiodistally, as in other notohippids. The M1 presents a small but conspicuous parastyle. The paracone column is prominent on the labial wall of the tooth; the metacone column is vestigial. Both structures are well-separated by a shallow and wide depression, whose deeper zone is located near the paracone. The metastyle is reduced. The protocone is bunoid and clearly larger than the hypocone. There is a small sulcus between these cusps, on the lingual wall of the tooth. Protoloph and metaloph are well-developed. The protoloph is oblique (mesiolabially-distolingually) and broader than the metaloph, which is transverse. The central fossa is deep, straight, and distolingually–mesiolabially developed (it is broader on its distolingual end). There are no distinct cristae on the central fossa of this molar. There is a distolabial fossette, but this is vestigial, even in this early stage of wear. The crochet is straight, short, and it points toward the apex of the paracone. The mesial cingulum is strong and is well-extended. It surrounds the lingual wall of the protocone and reaches the hypocone, ending on the mesiolingual wall of this cusp. On the other hand, the distal cingulum is much shorter, but still well-developed. There is a small cingulum on the base of the labial wall of the tooth. It is deeper at the middle length of the ectoloph, on the base of the labial depression between paracone and metacone columns.

The second upper molar is larger and mesiodistally longer than the M1. The paracone column is more distinctive in this tooth. The metacone column is almost vestigial and is well-separated from the paracone by a labial depression, which is also wide but slightly deeper than in the M1. The parastyle is small and the metastyle stronger than in the first molar (Fig. 4A, B). The morphology and location of protocone and hypocone is similar to that observed in the M1 (i.e., protocone clearly larger, small lingual sulcus). The protoloph is slightly bended toward the ectoloph, and the metaloph

is transverse, weak, and very short. As in the M1, the crochet is short and straight, and points toward the apex of the paracone. The central fossa is very deep. There is a small, single crista (crista intermedia of Billet, 2011) that enters in the fossa from the ectoloph, mesially to the crochet. In this case, the distolabial fossette is also vestigial (as in the M1). The mesial cingulum is strong but it becomes weaker on its lingual end and surrounds the lingual wall of the protocone (Fig. 4A). There is a variable number of cuspules (1 to 3) present on the cingulum at the level of the lingual sulcus between protocone and hypocone (Fig. 4B). The distal cingulum is well-developed. There is no cingulum on the labial wall of the tooth (Fig. 1B and 4B).

The third upper molar is roughly triangular and smaller than the previous molars (Fig. 1). The paracone is the most developed cusp in the ectoloph. The parastyle is small and the metacone is not distinct. Nevertheless, the metastyle is very prominent distally. The protocone shows a normal development compared to the other molars but its shape is roughly triangular in occlusal view. The hypocone is absent. The central fossa is deep and there are no labial fossettes. The mesial cingulum is strong and surrounds the protocone showing several cuspules on its lingual extent. The distal cingulum is weak and ends on the distal wall of the protocone, on the hypocone area. There is no labial cingulum.

Lower Dentition—The only lower incisor preserved is the i2. The apical zone of the crown is missing and the only visible feature is a small cingulum on the lingual side. All incisors are small and the size of each teeth increases mesiodistally (this feature can be inferred by the size of preserved roots). The symphysis is only preserved in the specimen PVL 6431 (Fig. 5A).

The lower canine is not preserved in any specimen but (as can be observed by the diameter of its root) it is slightly bigger than the i3 and the p1. The p1 is also absent and only the root can be observed (Fig. 5A).

Lower premolars are preserved in the specimens PVL 6431 and PVL 6432. The second lower premolar is simple and there is a single crest that runs mesiodistally. The higher point of this crest probably corresponds to the protoconid. There is a well-developed sulcus on the labial side, distally to the protoconid. The labial cingulid shows a moderate development and the lingual cingulid is continuous and runs all over this surface on the tooth.

The third lower premolar is bigger and more molariform than the p2 (Fig. 5A, B). The protoconid is the highest point of the crown and presents a mesial crest (paracristid). Trigonid and talonid are separated by a strong labial sulcus. The talonid is very short showing a bunoid and isolated entoconid, without connection with the hypolophid. The labial and lingual cingulids are presents, being the lingual more developed. The labial cingulid is interrupted at the base of the protoconid.

The fourth lower premolar is similar to the anterior one but bigger and more molariform (Fig. 5B). In this case, the metaconid is the higher cusp of the crown and presents a mesial crest that runs over the protoconid zone (which is not distinct) and continues as a paracristid. Trigonid and talonid are separated by a deep labial sulcus. The talonid is proportionately more developed in this tooth than in other premolars. The entoconid is also isolated in the p4, but is slightly transversally elongated. The labial cingulid is extended on the entire labial side but the lingual cingulum is restricted to the mesiolingual sector. There is small distal cingulid on the hypoconulid zone.

No lower molar is completely preserved in the recovered specimens. There is only a fragment of m1 on the specimen PVL 6427 (Fig. 6A), in which a small

mesiolingual cingulid is observed. The trigonid is clearly shorter than the talonid in the m2. The metaconid is wide in a moderate wear stage (probably for the coalescence of the accessory cusp typically present on the mesial wall of the metaconid in basal notoungulates). There is a partially developed paralophid which runs transversely and is merged to a well-developed mesiolingual cingulid. The labial sulcus between trigonid and talonid shows a moderate development. The talonid valley is wide and shallow. The entoconid is also a wide cusp in this wear stage. There is a small sulcus between the entoconid and the mesiolingual zone of the hypoconulid.

The third lower molar is partially preserved in two specimens PVL 6427 (advanced wear), and PVL 6433 (unworn). This tooth shows a short paralophid, which is not connected to the mesiolingual cingulid in the early stages of wear. The labial sulcus is conspicuous but shallow. The trigonid is proportionately shorter (mesiodistally) than in the m2. The talonid is mesiodistally expanded and shows a wide valley and a bunoid entoconid, which presents a slightly oblique entolophid (Fig. 6A, B). The hypoconulid is very developed in this case (as is usually in the m3 of paleogene notoungulates). There is a small depression between the entonocid and the hypoconulid and there is no labial cingulid (Fig. 6B). Dental measurements are detailed in Table 2.

Mandible—The mandibular body is twice as high as the p4 at the level of that tooth. At the level of the m3, the mandibular body is four to five times higher than that tooth (the same proportion in *Pampahippus arenalesi*). The mandibular symphysis is robust and slanted forward (forming a 38° angle with the alveolar line). At least four mental foramina are preserved (there is a possible fifth near the mandibular symphysis, but this cannot be corroborated due to the poor preservation of the surface). These foramina show a variable arrangement, but they are roughly at the level of canine, p1, p2/p3, and p4/m1, respectively. The labial or lateral side of the mandibular body is

smooth at its middle length. Posteriorly, below the m2-3, there are faint crests (the number varies in different individuals) that run anteriorly and ventrally from the ventral end of the coronoid crest (Fig. 6A). Probably these structures represent preservation artifacts. The ventral border of the mandibular body presents a slight notch just below the ventral end of the coronoid crest. On the medial or lingual side, the mandibular body presents a longitudinal sulcus, which ventral limit is formed by a strong osseous ridge (probably the mylohyoid line). Dorsally, near the alveolar line, the mandibular body becomes thicker. The surface at this sector presents several osseous lines or small crests, similar to that observed on the lateral side.

Just a small part of the mandibular ramus is preserved. A well-developed coronoid crest can be observed on the lateral side. This crest reaches the sector just below the distal border of the m3. On the medial side, developed on the alveolar line and just distally to the m3, there is a small but conspicuous medial process, clearly visible on the adult mandible. Apparently, this process is not well-developed in the juvenile mandible. The mandibular foramen is partially preserved (only the anterior rim) and it was located faintly below the level of the alveolar line, and slightly behind the level of the anterior border of the coronoid process.

Intraspecific Variation

The material referred as *Pampahippus secundus* is represented by 11 fragmentary specimens (including the holotype). Only some of these fragments have teeth in common, and in some cases it is difficult to determine if fragments of the same side belonged to the same individual. Nevertheless, considering the largest number of maxillae representing the same side (since there are more fragments with upper dentition) the number of individuals represented is three.

Two groups can be identified on the basis of morphological differences. The first one is integrated by the holotype, and the specimens PVL 6430 and PVL 6431. The second group includes PVL 6427, 6428, 6429, and 6432; these specimens bear slightly robust teeth. Considering upper dentition, most differences are observed in the morphology of the P3 and P4. These teeth show sub-triangular occlusal outline in the first group and sub-cuadrangular in the second. In the P4 the mesial cingulum surrounds lingually the protocone in the holotype (first group) but this condition is almost absent in the second group; moreover, the labial sulcus between parastyle and paracone folds is much stronger in the specimen PVL 6427, a representative of the second group (Fig. 4A). In the upper molars, the M2 of the first group presents a tiny accessory cuspule between the lingual walls of protocone and hypocone (Fig. 1A and 4B). This condition is different in PVL 6427 (second group) where there are several cuspules (at least four) located on a lingual extension of the mesial cingulum and (Fig. 4A).

Differences are even more subtle in lower dentition. This is only observed in premolars, since molars are poorly preserved. Lower premolars of the first group show more developed cingulids. Additionally, hypsodonty is slightly higher in the second group (and this also seems to be the case for upper teeth).

Wear differences are not significant in the sample. All specimens show a comparable wear degree, except for PVL 6433 (a mandibular fragment) which bears an unworn and incomplete m3. In this sense, it is important to note that the differences observed in the teeth cannot be attributed to ontogeny. Instead of this, these traits represent actual morphological differences, although these are subtle enough to be considered only intraspecific variation maybe due to sexual dimorphism.

Comparison with *Pampahippus arenalesi*

Morphologic similarities between *Pampahippus arenalesi* and the new species here presented are very clear. Both taxa are brachydont forms with complete and closed dentition; moreover, both species show upper molars with a well-developed ectoloph, reduced number of cristae on central fossa, and reduced distolabial fossette, and upper premolars lacking protoloph and with low metacone fold. Nevertheless, within the differences exhibited, the size is the most obvious. *P. secundus* is about 35 % smaller than *P. arenalesi* (on the basis of dental measurements) and is, in fact, the smallest toxodontian recorded so far.

Regarding dental features, incisors show a singular size combination on *P. secundus*, with I2 smaller than I1 and I3. *P. arenalesi* presents a well-differenced paraconule in P3 and P4 that is much smaller in *P. secundus*. The molars in *P. arenalesi* are longer than wide and trapezoidal in occlusal outline; the molars in *P. secundus* are more transverse (i.e., wider than long). The development of cingula constitutes another difference, since the mesial cingulum is more extended lingually in the M1 and less extended in the M2 of *P. secundus* (always regarding the expression of this feature in *P. arenalesi*).

The mentioned differences imply, to our knowledge, enough evidence to separate these two species. On the other hand, the shared features listed above are somewhat problematic, since most of them represent simplesiomorphies. Only a few characters can be considered as supporting synapomorphies for the node containing genus *Pampahippus*, and these characters are mainly referred to lower premolars (see Phylogeny).

Phylogenetic Analysis

The analyses of the data matrix (see Supplementary Data 3) yielded 90 equally parsimonious trees when analyzed of TNT (length: 419 steps). A strict consensus was calculated and the resulting tree is shown in Fig.7, along with the support values. The node Notoungulata (Node C) shows a basal polytomy including *Henricosbornia*, *Simpsonotus*, *Pampatemnus deuterus*, Notostylopidae (Node D, including *Pyrotherium*), and Typotheria and Toxodontia as main lineages of this order. As in previous analyses (Billet, 2010, 2011; García-López and Powell, 2011), these results indicate that *Pyrotherium* is closely related to *Notostylops*. With the inclusion of *Boreastylops*, Notostylopidae is recovered as a monophyletic group exclusively integrated by Paleogene forms. Typotheria is supported by several synapomorphies; these are detailed in Fig.7 and will not be discussed here.

Within Toxodontia, the result resembles previous studies (e.g., Shockey, 1997; Cerdeño and Vera, 2010; Billet, 2011) in which Isotemnidae and Notohippidae show a paraphyletic arrangement. On the other hand, Homalodotheriidae, Leontiniidae, and Toxodontidae resulted as natural groups.

The two species of the genus *Pampahippus* are located as the most basal ‘notohippids’ in a node that also includes leontiniids and toxodontids. This node is supported by four synapomorphies: incisiform canine (character 19:1), incomplete or absent protoloph (character 40:1), well-developed first lower incisor (character 50:0), and talonid well-extended distally to the entolophid in lower molars (character 65:1; autapomorphic feature). The species of *Pampahippus* are well-separated from post-Eocene ‘notohippids’ which occupy a more derived position in the cladogram, with *Argyrohippus* as sister taxon of the Toxodontidae. Only one autapomorphic feature supports the genus as a clade: presence of bunoid and isolated entoconid on P3-4, not developing entolophid (character 63:1).

DISCUSSION

The studies performed in the last decades for the Paleogene rocks of northwestern Argentina have yielded so far 15 notoungulate species. Of these, five species are included in Toxodontia and represent two 'isotemnids' (Vucetich and Bond, 1982), two leontiniids (Bond and López, 1995; Deraco et al., 2008), and one 'notohippid' (Bond and López, 1993). Usually, a generalized set of characters has been recognized for these toxodontians (Vucetich and Bond, 1982; Bond and López, 1993, 1995; Deraco et al., 2008). Additionally, as it was for other groups, these forms show a lower hypsodonty index than their southern counterparts. It should be also noted that the current record shows, in most cases, that the northwestern forms have a smaller body size than the contemporary (*sensu lato*) Patagonian forms. In other words, forms of the size of *Periphragmis* or *Thomashuxleya*, which are clearly larger than *Pampatemnus* and the northern 'isotemnid-like notohippids' (see Shockey, 1997) have not been yet recorded and, considering leontiniids, *Coquenia* and *Martinmiguelia* are very small forms when compared to *Scarrittia* and *Leontinia*, their Deseadan relatives. These faunal differences may suggest biogeographical barriers that separated northwestern Argentina from Patagonia and other regions during at least a part of the Eocene, as it was previously considered by different authors (Pascual et al. 1996; Ortiz-Jaureguizar and Cladera, 2006). Nevertheless, much work is still necessary in order to test these hypotheses.

The northwestern representatives of Eocene notoungulates have generally not been included in cladistic analysis. Nevertheless, some very recent integrative studies have included them (Shockey, 1997; Deraco et al., 2009; Billet, 2011; García-López and Powell, 2011; Shockey et al., 2012; García-López and Babot, 2014). At this point, it

should be noted that the generalized nature of the notoungulate representatives recorded in Eocene units of northwestern Argentina have proved to be an important impediment for the resolution of phylogenetic analyses, and, in several cases, these taxa fall far away from the post-Deseadan representatives of their (supposed) family-level groups. This lack of detailed surveys focused on the phylogenetic status of several northwestern taxa might be due among others to the limited availability of morphological studies. In most cases, original descriptions of the species recorded in northwestern units were limited to dental description and only shallower osteological analyses. In this sense, Cifelli (1993:204) stated that “a comprehensive survey of notoungulate cranial morphology is urgently needed and (...) it is likely that such a study will result in a dramatic improvement in the basis for assessing relationships within the order”. Consequently, descriptive and interpretative analyses focused on cranial osteology of northwestern forms must be developed given the singular nature of this regional fauna. Additionally, it is important to note that, in several cases, the relationships of northern taxa were discussed outside a cladistic framework. This is particularly true for ‘notohippids’; the redefinition of the family made by Bond and López (1993) and the inclusion of *Pampahippus* and other Eocene taxa without a basis of shared derived characters has led to the use of a family-level name defined on plesiomorphic features which has been used even on recent contributions (e.g., López et al., 2010).

In the phylogenetic analysis here performed, we included all northwestern Paleogene toxodontians (*Pampatemnus*, *Pampahippus*, *Martinmiguelia*, and *Coquenia*), along with other regional representatives (e.g., *Simpsonotus*, *Boreastylops*, *Colbertia*, *Griphotherion*). The inclusion of these forms brought some resolution regarding advanced toxodontians. Nevertheless, some basal nodes collapsed. One of the most significant points is the fact that both *Pampatemnus* species are separated in the

consensus cladogram. The type species of the genus, *P. infernalis*, is located as the most basal Toxodontia. Nevertheless, *P. deuterus* is excluded from this node and included in a basal polytomy along with *Henricosbornia*, *Simpsonotus*, the Notostylopidae, and tyotheres. *Pampatemnus deuterus* and *P. infernalis* were described as isotemnids belonging to the same genus but these taxa have never been analyzed in a cladistic context. The present analysis questions this assignment, as *P. deuterus* is separated in an unresolved position from the type species of the genus. In the present study, the node containing most toxodontians (Node F) is supported by two synapomorphies: presence of multiple cristae on upper molars (character 31:1) and presence of a lingual vertical ridge on lower incisors and canine (character 47:1; autapomorphy). In the recently published phylogeny of Billet (2011), the equivalent node is supported by a greater number of features and the mere presence of the vertical ridge on the anterior lower dentition is a common synapomorphy for both results. Other characters that define Toxodontia in the analysis of Billet (lingual cingulum forming a fossa on upper incisors and presence of distolabial crest on trigonid of lower premolars) are here presented as supporting features of the immediately less inclusive node, which shows *Pleurostylodon* as a sister taxon of the rest of the toxodontians. As it was pointed before, the inclusion of these generalized forms also leads to a redistribution of the characters defining the basal nodes of the lineage.

The situation of the species of *Pampahippus* is different from the one of *Pampatemnus*. These species are located in a node supported by an autapomorphic feature, bunoid and isolated entoconid on lower premolars (character 63:1), and the genus remains as a natural group. Lower premolar morphology has not received much attention. Particularly, some traits can be identified associated with the entoconid (position, development of entolophid, orientation of entolophid), although in several

cases these traits cannot be observed given the hypsodont nature of most taxa and the lack of juvenile specimens. Even so, the singular nature of the premolar entoconid in *Pampahippus* is clearly different from other Paleogene Toxodontia. *Coquenia* and *Plexotemnus* show a similar morphology but the development of a small but conspicuous entolophid represents a clear difference.

Pampahippus is located in the most basal clade of Node J, which includes a range of forms traditionally referred as ‘notohippids’ along with leontiniids and toxodontids forming respective natural groups. This node is supported by four synapomorphies (see Fig. 7) and the arrangement of monophyletic groups can be grossly compared to the node 1 of Shockey (1997) and the results of Billet (2011: fig. 10-B). Additionally, the study of ‘advanced toxodonts’ of Cifelli (1993: 206) may be considered since the clades involved are basically the same. Nevertheless, we consider that the scoring of key characters is doubtful in this last case and so that the results will not be used for comparisons. Synapomorphies supporting Node J include incisor-like canine (character 19:1), incomplete development of protoloph on premolars (character 40:1), well-developed first lower incisor (character 50:0), and talonid extending distally to the entolophid on lower molars (character 65:1). Within these characters, incisor-like canines and the incomplete protoloph on premolars are features that were also present as synapomorphies in the analyses of Shockey (1997) and Billet (2011). Additionally, characters 50 and 65 are also present in the node of the Billet’s cladogram (2011).

Notwithstanding the low support values obtained for this clade here (Fig. 7) and in equivalent arrangements for previous contributions, we interpret that this clade should be considered as a base to analyze the transitional evolutionary history of the Toxodontia through the upper Paleogene–Neogene span. Then, we propose the term Toxodontoidea for this arrangement. The proposition of suprafamiliar taxa is not

common within Notoungulata. Reguero (1999) suggested the clade Typotherioidea to include ‘archaeohyracids’, hegetotheriids, and mesotheriids and this systematic proposal was used although barely discussed in further contributions (Reguero and Castro, 2004; Reguero and Prevosti, 2010; Billet, 2011; García-López and Powell, 2011; Powell et al., 2011). Although we prefer to avoid the formal proposition of a taxon in this case, we suggest to use this term for this clade in order to establish a practical basis for comparisons and comments.

Within Toxodontoidea, an interesting result is the arrangement of Leontiniidae, which forms a natural group, even with the addition of northwestern Eocene representatives. The monophyly of the Leontiniidae is supported by six synapomorphies (Node L): (I1-) I2 caniniform, circular in cross-section (character 10:1), lingual cingulum on upper incisors not form a fossa (character 15:0), strong thickening of the cingulum at mesio-lingual base of protocone on P2-4 (character 41:1), third lower incisor large and canine-like (character 51:1), continuous strong relief lambdoid crests on the dorsal edge of the posterior root of the zygomatic arch, with the medial arch deeply excavated (character 98:1) and the crista meatus and post-tympanic process squamous flattened close to or against each other (character 123:1)

In summary Toxodontoidea would then consist of ‘notohippids’ (scattered throughout the clade), leontiniids, and toxodontids. This clade should have separated from the homalodotheriids at least in the lower Eocene. Then Homalodotheriidae represents an early differentiated group that maintains its identity throughout the Neogene. Nevertheless, the oldest known homalodotheriids were recorded in Oligocene units and future records of new forms from older ages might support this scheme.

CONCLUSION

The present study describes a new species of *Pampahippus*, an early diverging toxodontian from the Lumbrera Formation (Salta, Argentina). *Pampahippus secundus* sp. nov. differs from *P. arenalesi* in several dental features: absence of multiple cristae individualized mesially to the crochet on upper cheek teeth; presence of crista intermedia running lingually from the ectoloph between the protoloph and the crochet on upper cheek teeth, and absence of lingual vertical ridge on lower incisors and canine. The genus *Pampahippus* was recovered as monophyletic in the present analysis, with an autapomorphic feature supporting the clade: presence of bunoid and isolated entoconid on P3-4, not developing entolophid.

The integrity of the genus *Pampatemnus* is not supported in the analysis. We consider that a revision of the two species included need to be performed in order to test their taxonomic status.

The inclusion of several paleogene taxa from northwestern Argentina leads to a new scheme, in which a clade containing Leontiniidae and Toxodontidae, along with several species formerly considered as ‘notohippids’, was recovered. This clade, that excludes ‘isotemnids’ and homalodotheriids, is here referred as Toxodontoidea.

Once again, these new hypothesis shows how important is to consider the early divergent forms of clades of long temporal range, even in integrative phylogenetic studies.

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FIGURE CAPTIONS

FIGURE 1. *Pampahippus secundus* sp. nov., PVL 6426, holotype. Fragment of right maxilla with P2-4 and M1-3. **A**, occlusal view; **B**, labial view; **C**, lingual view. Scale bar equals 10 mm. [planned for page width]

FIGURE 2. Geographic location of El Simbolar (Salta Province, Argentina), where the specimens presented in this contribution were found. Modified from García-López and Powell (2011). [planned for column width]

FIGURE 3. *Pampahippus secundus*. **A**, PVL 6427, fragment of left premaxilla with I1-3 in labial and lingual view; **B**, PVL 6428, fragment of right premaxilla and maxilla with I2-3, **C**, incomplete P2, complete P3, and part of P4 in occlusal, labial, and lingual view; **C**, PVL 6429, fragment of right premaxilla and maxilla with roots of I2-3, complete **C**,

part of P1, and complete P2 in occlusal, labial, and lingual view. Scale bar equals 10 mm. [planned for column width]

FIGURE 4. *Pampahippus secundus*. **A**, PVL 6427, fragment of left maxilla with incomplete P2, complete P3-4, and M1-2 in occlusal, labial, and lingual view; **B**, PVL 6430, fragment of left maxilla with P4, part of M1, and M2 in occlusal and labial view. Scale bar equals 10 mm. [planned for page width]

FIGURE 5. *Pampahippus secundus*, **A**, PVL 6431, fragment of left dentary with incomplete anterior dentition and p2-4 in occlusal, labial, and lingual view; **B**, PVL 6432, fragment of left dentary with p3 and p4 in occlusal, labial, and lingual view. Scale bar equals 10 mm. [planned for column width]

FIGURE 6. *Pampahippus secundus*. **A**, PVL 6427, fragment of right dentary with incomplete m1-3 in occlusal, labial, and lingual view; **B**, PVL 6433, fragment of right dentary with incomplete m3 in occlusal, labial, and lingual view. Scale bar equals 10 mm and is valid for all images except for the line drawing. [planned for page width]

FIGURE 7. Strict consensus tree (419 steps) showing the phylogenetic position of *Pampahippus secundus* under equally weighted characters. Circles on nodes represent synapomorphies; black circles indicate autapomorphic features and white circles homoplastic synapomorphies. Upper numbers represent character number and lower numbers character states. Letters on black circles designate nodes; numbers enclosed in boxes below the nodes indicate Bremer support values. [planned for page width]